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Thesis Title

Native fauna response to large scale fox control in the northern jarrah forest of south-west Western Australia: Operation Foxglove.

Thesis Abstract

In Australia, and particularly Western Australia, increases in the abundance of several species of native fauna have been attributed to reductions in population density of the introduced predator, the red fox (Vulpes vulpes). Reductions in fox density have been achieved, or inferred, through the use of 1080 baiting (dried meat baits containing the toxin sodium monofluoroacetate). In most cases, the areas baited have been relatively small and the baiting regimes have incorporated a high intensity and/or a high frequency of baiting. In 1994, a large scale 1080 baiting program, Operation Foxglove, commenced within the northern jarrah forest of south-west Western Australia. The objectives of Operation Foxglove were to: implement fox control at a landscape scale to determine efficient and cost effective baiting regimes; determine the fox abundance/density in this forest environment which would enable a sustained increase in native fauna abundance; and determine whether fox predation alone was limiting native fauna occurrence within the northern jarrah forest. The latter was deemed necessary as fox baiting programs, although not explicitly stated as such, are often seen to be the panacea for all fauna conservation issues. The research undertaken for this PhD program was the basis of Operation Foxglove.

The study area was approximately 550,000ha and was aerially baited at different frequencies: 221,400ha baited twice yearly; 130,400ha baited four times yearly; and 88,600ha baited six times yearly. Vehicle based delivery of 1080 baits was also required to ensure the margins of the forest, i.e. the forest interface with agricultural land, were also baited. There was an unbaited treatment of 103,500ha. All baits were delivered at an intensity of five baits/km2.

Some managerial and logistical constraints were imposed on the experimental design. These constraints were largely a function of conducting ecological research at a landscape scale within a production forest. Replication was limited to within-treatment replication (pseudoreplication) and the allocation of treatments was not random.

To assess the faunal response to the different baiting frequencies, the predation sensitive potoroid marsupial, the brush-tailed bettong, or woylie (Bettongia penicillata), was used as an indicator species for predation sensitive, terrestrial, mammalian fauna. Four hundred and ninety two woylies were translocated from Dryandra Woodland to 19 sites within the three baited and the unbaited treatment groups. A large subset of the translocated population and a subset of recruits to the population (n=384, translocated individuals and recruits, combined) was fitted with movement sensitive ‘mortality’ radio-collars and survivorship was monitored almost daily for 37 consecutive months.

The woylie survivorship data were analysed in an information-theoretic framework using the Known Fate model from Program MARK (White, 2001). The ΔAICc ‘best’, or preferred model, to describe the data included an effect from the baiting treatment groups (the frequency of baiting). The preferred model also included a temporal component, with survivorship reduced in winter. Model averaging of the best six models estimated woylie survivorship over the duration of the study to be 16.4% higher in the most frequently baited treatment group (six baitings per year) than in the treatment baited with the ‘standard operating procedure’ of four baitings per year. Baiting twice yearly conferred no benefit over not baiting at all. The fox and feral cat (Felis catus) were implicated as major predators of the monitored woylie population. The findings have significant implications for the department’s Western Shield Fauna Conservation and Recovery Program.

A Bayesian modelling approach was adopted when analysing count data collected from monitoring 17 sandplot networks at which fox and cat spoor were detected. The methodology incorporated development of a site specific technique to derive abundance estimates for foxes. This technique was validated through a fox removal study and was subsequently further validated as part of research with the Invasive Animals Cooperative Research Centre’s Western Australian Demonstration Site. The latter validation incorporated use of molecular techniques, specifically, species and individual identification from DNA recovered from hair and scats. Fox abundance was lowest within the six baitings per year treatment group and increased in the four and two baitings per year treatment groups and the unbaited group. Although there was considerable overlap in the 95% equal-tailed Bayesian credible intervals (95%BCI), the reduction in fox abundance achieved within the six baitings per year treatment was interpreted as biologically significant for survivorship of the woylie.

Estimating cat abundance was more problematic with little published data on cat abundance within forest areas and no reliable technique for estimating cat abundance generally. A Bayesian modelling approach was again adopted and the data from three consecutive years were analysed. In all years, the only model with any support modelled cat abundance without a treatment effect and without any explanatory variables, i.e. the estimate of cat abundance was constant across all treatment groups. The results were interpreted as reflecting the combination of the extremely sparse data and the lack of sensitivity of the sandplotting technique to detect cat presence. A revised technique is described and recommended.

Occupancy modelling was used to identify the variables which best described the presence (occurrence/occupancy), within the northern jarrah forest, for each of two in situ mammalian species, the brushtail possum (Trichosurus vulpecula hypoleucus) and the southern brown bandicoot (Isoodon obesulus). The estimated probability of occurrence for the brushtail possum revealed the importance of wandoo (Eucalyptus wandoo and E. accedens) for its tree hollow bearing ability at the 'pole' size/age class. The presence of wandoo as a pole stand was interpreted as providing a very different resource from pole stands of jarrah (E. marginata) and marri (Corymbia calophylla). Wandoo is hollow bearing in this size class whereas jarrah and marri are not. The results did not support the hypothesis that the probability of brushtail possum occupancy increased with increased frequency of baiting. The estimated probability of occurrence for the southern brown bandicoot was highest in the four baitings per year treatment group and an increase in rainfall was positively associated with occupancy and detection. The effect from baiting on the southern brown bandicoot was equivocal. The conclusion, among others, was that baiting frequencies need to be in place for a longer period of time to enable the low densities and patchy distribution of native fauna to respond through naturally occurring recruitment.

The results highlight the complexity of fauna interactions and the difficulty for conservation managers to 'get it right'. There is no single prescription which will provide the requirements of all species. A 1080 baiting frequency of six baitings per year will benefit woylies, however, presence of bandicoots was maximised in the four baitings per year treatment group, however there was a trend of decreasing occurrence over time in this treatment group.

Fox control appears beneficial for the woylie. However, it is hypothesised in some circumstances that it may lead to mesopredator release of cats. This may result in increased predation pressure on the woylie and other native fauna. This highlights the necessity of monitoring the native fauna response to baiting and, in particular, the need to monitor not only fox abundance, but the abundance of other predators (native and introduced) which may show indirect effects from any fox density reduction.

Specific research and management recommendations are made in light of these findings with particular reference to assessing whether the feral cat and native predators show a mesopredator release response to fox density reduction.

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The following book chapter, book section and grey literature are based largely on the research from my thesis

de Tores, P. J. and Marlow, N. (2012). The relative merits of predator-exclusion fencing and repeated fox baiting for protection of native fauna: five case studies from Western Australia. In: Fencing for Conservation. Restriction of Evolutionary Potential or a Riposte to Threatening Processes? (M. J. Somers and M. W. Hayward, Eds). Springer. New York, Dordrecht, Heidelberg, London.

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I declare that I have complied with the Thesis Examination Procedure.

Native fauna response to large scale fox control in the northern jarrah forest of south-west Western Australia: Operation Foxglove

Paul J. de Tores

A thesis submitted for the degree of Doctor of Philosophy
in the School of Biological, Earth and Environmental Sciences.
Faculty of Science
University of New South Wales, Sydney, Australia

2020

Acknowledgements

This thesis has taken an inordinate amount of time to reach fruition. Despite this, I hope those who read it find some of it useful and I would like to think some of the findings may eventually translate to improved conservation management practices. I originally submitted the thesis in February 2011 (even then it was a ridiculous stretch of the time allowed to complete a thesis). I received the examiners reports in early to mid-2011. The examiners' comments were largely supportive and flattering. The revisions required appeared to be minimal. However, shortly after receiving the reports my life fell apart. My employment status changed dramatically and this coincided with being diagnosed with acute lymphoblastic leukaemia, at the time considered a terminal illness.

So why is this in the acknowledgements? It is here to enable me to acknowledge the undying (no pun intended) love and support my partner, Suzanne Margaret Rosier, has provided through the trauma of an unplanned 'mid-to-late' career change and the equally unplanned medical diagnosis with the associated financial burdens. Suzanne has unselfishly given me the immense support needed to get me through the beast that is leukaemia, which just won't go away. Without Suzanne's support I would not have recovered sufficiently to return to the examiners' comments in late 2020 and get the thesis submitted. It doesn't end there. No amount of thanks can possibly compensate Suzanne for the pain inflicted upon her during field work and the gestation of this thesis. Suzanne (aka the compulsory volunteer), I hope you will forgive me and accept my thanks for the love, support and encouragement you have given in addition to the support with fieldwork, data entry and thesis and manuscript editing.

The Rosier clan contributed in many more ways. The late Bruce Rosier refreshed my understanding of fundamental mathematics, Malcolm Rosier introduced me to Stata and provided the critical training to get me over the 'frightened to use it' stage and Karl Keesman (an honorary Rosier) gave me the courage to continue with Stata. Suzanne Rajput (a 'once-was' Rosier) came to understand my requirement for fieldwork meant important adjustments were required to her life if she was to keep in contact with her mother. She quickly discovered visiting her mother at Dryandra or Dwellingup also meant participation in fieldwork.

Very special thanks go to Professor Syd Shea, former Executive Director of the Department of Conservation and Land Management (CALM) for his vision in relation to

the conservation benefits from large scale fox control and for his initial and long-term support of the project. Similarly, the late Jack Kinnear, formerly with CALM, was inspirational and encouraged my endeavours. Importantly, thanks to the grossly under-acknowledged Nicky Marlow for suggesting to Jack Kinnear that the boss (Syd Shea) may be interested in extending 1080 baiting to a landscape scale.

Thank you to Bob Seamark, Tony Peacock and Steve Lapidge from the ever morphing Vertebrate Biocontrol, Pest Animal Control and Invasive Animals Cooperative Research Centre(s) for believing the research was worthy of support. Thank you to the CRC program for existing – it gave me the opportunity to work closely with many scientists in many disciplines and also enabled me gain input from scientists and reviewers I have long revered. The CRC program set the bar very high and showed me what ‘peer review’ can really mean. The annual independent review process of the CRC also provided me with opportunity to act on the reviewers’ comments and for this I am particularly grateful to Professor Charley Krebs and Professor Tony Sinclair.

My supervisors Mike Augee and Barry Fox from the UNSW retired on me and may have given up hope in a thesis eventuating. Mike in particular was generous with his time and support. Thank you to Dave Croft and David Eldridge from UNSW and Nicky Marlow, from DEC who inherited, or were encouraged to take on, the supervisory role. Thank you also to John Triantafilis from the UNSW for putting the pressure on to get me there and supporting me to do so. Thanks again to Mike Augee in particular for the support at the initial stages of the research and again to Nicky Marlow for helping push me to the end and for realising what worked and what didn’t work on me when pressure was required to ‘get there’. Thank you to Stefan Rose, formerly of UNSW, who can never, ever be adequately repaid for the many, many ‘all-nighters’ he, Suzanne and I spent trapping and translocating woylies.

Thank you also to Mike Yung who introduced me to the true benefits of a relational database, to Rod Mell for providing assistance with database manipulation and Lisa Wright and David Brockwell for sourcing numerous references. The GIS section of CALM and DEC provided me with training in the use of GIS and also provided tremendous GIS support. Thanks in particular to John Dunn, Robyn Wilson, Shane French, Dave Robertson, Steve Jones and Geoff Banks. Similarly CALM and DEC’s Forest Management Branch provided me with a wealth of information, thanks in particular to Pat Collins, Peter Stirling, Derek Winters and the late Merv Smith.

Thank you to Frank Obens, Corey Watts, Louise Kuchel, Kaylene Parker, Cathy Lambert, Wendy Payne (nee van Luyn) and Mark Hudson for their involvement in establishing trapping grids and for their fieldwork in the northern jarrah forest trapping and monitoring woylies. Particular thanks go to Kathy Himbeck, Jim Cocking, Beth MacArthur, Marika Maxwell, Liz White and the late Mick Dillon for the mountain of fieldwork they were involved in for this project and the commitment to what seemed to be relentless tasks of sandplot monitoring, fauna trapping and radio-telemetry monitoring. Kathy, I thank you especially - you were with the project from day one and stayed to see it through to completion.

My project team invaded the Dwellingup Research Centre *en masse* and we were welcomed without question. For this I thank Joe Kinal and Kim Whitford who not only welcomed us but were forthcoming with a wealth of information on the northern jarrah forest. Neil Burrows (DEC's former Director of Science Division) and Keith Morris (former Manager of Science Division's Fauna Conservation Program) were supportive throughout.

I thank Libby Mattiske (aka E. M. Heddle) for the enormous generosity shown when carrying out the floristic and vegetation survey and Havel site-type identification at each of the 55 trapping grids used in the study. Libby, I know you lost money on this!

Funding for the project was provided by CALM (which became DEC), the Pest Animal Control Cooperative Research Centre (formerly the Vertebrate Biocontrol Cooperative Research Centre, and the Invasive Animals Cooperative Research Centre), the Australian Nature Conservation Agency and Environment Australia (now the Commonwealth Department of Sustainability, Environment, Water, Population and Communities), the CALM/Alcoa Forest Enhancement program (CAFE), the joint venture Partners of Boddington Gold Mine (Anglogold, Newcrest and Normandy) and the Western Australian Department of Commerce and Trade.

Lastly, and with an indescribable amount of appreciation, I thank David Anderson, Gary White and Richard Barker who, between them, introduced me to the information-theoretic approach, Kullback-Leibler Information, the Akaike Information Criterion, Program MARK and Bayesian modelling. This has forever changed the way I 'do science'.

Abstract

In Australia, and particularly Western Australia, increases in the abundance of several species of native fauna have been attributed to reductions in population density of the introduced predator, the red fox (*Vulpes vulpes*). Reductions in fox density have been achieved, or inferred, through the use of 1080 baiting (dried meat baits containing the toxin sodium monofluoroacetate). In most cases, the areas baited have been relatively small and the baiting regimes have incorporated a high intensity and/or a high frequency of baiting. In 1994, a large scale 1080 baiting program, Operation Foxglove, commenced within the northern jarrah forest of south-west Western Australia. The objectives of Operation Foxglove were to: implement fox control at a landscape scale to determine efficient and cost effective baiting regimes; determine the fox abundance/density in this forest environment which would enable a sustained increase in native fauna abundance; and determine whether fox predation alone was limiting native fauna occurrence within the northern jarrah forest. The latter was deemed necessary as fox baiting programs, although not explicitly stated as such, are often seen to be the panacea for all fauna conservation issues. The research undertaken for this PhD program was the basis of Operation Foxglove.

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and the lack of sensitivity of the sandplotting technique to detect cat presence. A revised technique is described and recommended.

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Fox control appears beneficial for the woylie. However, it is hypothesised in some circumstances that it may lead to mesopredator release of cats. This may result in increased predation pressure on the woylie and other native fauna. This highlights the necessity of monitoring the native fauna response to baiting and, in particular, the need to monitor not only fox abundance, but the abundance of other predators (native and introduced) which may show indirect effects from any fox density reduction.

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Abbreviation	Description
1080	Sodium monofluoroacetate
95%BCI	Bayesian 95% equal-tailed credible interval
95% CI	95% confidence interval
ΔAIC	The difference in AIC values
AIC	Akaike Information Criterion
AIC_c	A second order AIC to adjust for small samples size
Alcoa	Alcoa World Alumina, Australia
APB	The Western Australian Agriculture Protection Board
BF	Bayes Factor
BIC	Bayesian Information Criterion
CALM	The Western Australian Department of Conservation and Land Management (now Department of Biodiversity, Conservation and Attractions)
DBHOB	Diameter at breast height, over bark; where breast height is 1.3m above mineral earth on the high side of the stem being measured
DEC	The Western Australian Department of Environment and Conservation (now Department of Biodiversity, Conservation and Attractions)
DEWHA	Commonwealth Department of Environment, Water, Heritage and the Arts, subsequently DSEWPC, then the Department of Environment, now the Department of Environment and Energy
DIC	Deviance Information Criterion
DRA	Disease Risk Area, or dieback (*Phytophthora cinnamomi*) free areas
DSEWPC	Department of Sustainability, Environment, Water, Population and Communities, now the Department of Environment and Energy
EPBC Act	Environment Protection and Biodiversity Conservation Act, 1999
ESS	Effective Sample Size
FMP	Western Australian Forest Management Plan 2004-2013
GIS	Geographic Information System
GOF	Goodness of Fit test
IBRA	Interim Biogeographic Regionalisation of Australia
IACRC	Invasive Animals Cooperative Research Centre
K-L	Kullback-Leibler
MCMC	Markov chain Monte Carlo
MCSE	Monte Varlo standard error
MCP	Minimum Convex Polygon

cont. …

List of abbreviations and acronyms

(… cont)

Abbreviation	**Description**
MH	Metropolis-Hastings (algorithm)
MKTBA	Minimum number of individuals known to be alive
NSW	New South Wales, Australia
PAC CRC	Pest Animal Control Cooperative Research Centre
pwca	The number of sandplots with cat activity
QAIC	A quasi-likelihood adjustment term of AIC
QAICc	A quasi-likelihood adjustment term of AICc
RFA, WA RFA	Western Australian Regional Forest Agreement
VB CRC	Vertebrate Biocontrol Cooperative Research Centre
WA	Western Australia
Worsley	Worsley Alumina Pty Ltd

Chapter 1
Introduction

1.1 General introduction

Since the arrival of Europeans in Australia, 27 species and seven subspecies of Australian mammals have become extinct in the wild (EPBC Act, 1999). These extinctions have been variously attributed to habitat modification (primarily as a result of land clearing and introduced grazing animals), changes to fire regimes, predation by introduced predators and disease and the combined effects from these factors (Abbott, 2006; Burbidge and McKenzie, 1989; Caughley and Gunn, 1996; Johnson, 2006; Morton, 1990; Short and Smith, 1994; Smith and Quinn, 1996). These effects are further confounded when they act in concert with the unique reproductive traits of Australian mammals (eutherians and marsupials) (Johnson, 2006). The taxa showing the most dramatic decline in range and number are the non-volant terrestrial mammals (Burbidge and McKenzie, 1989). Of these, two are listed nationally[1] as Critically Endangered, 34 as Endangered and 53 as Vulnerable (EPBC Act, 1999). Thirty six of these are known to occur in Western Australia (WA) of which 24 occur only in WA (Table 1.1). The Commonwealth, state and territory government policies and management strategies adopted to attempt to arrest declines have focussed on five main areas: land acquisition to increase the total area of conservation estate (see ANZECC and MCFFA National Forest Policy Statement Implementation Sub-committee, 1997); support for management of private lands for conservation purposes; habitat restoration; habitat management through the use, or exclusion, of fire; and introduced predator control.

Notwithstanding the positive biodiversity conservation gains from the first four approaches, introduced predator control in WA and, in particular, control of the introduced red fox (*Vulpes vulpes*) in the period from 1985 to the late 1990s, demonstrated sustained fox baiting programs can result in increases in abundance of *in situ* populations of a range of native mammal species (Burbidge and Friend, 1990; Friend, 1990; Kinnear, 1990; Kinnear *et al.*, 1988; Kinnear *et al.*, 1998; Morris, 1992). Similarly, many translocations of threatened fauna carried out in the presence of fox control in WA in the 1990s were considered successful (Christensen and Leftwich, 1992; de Tores *et al.*, 1998a; Friend and Thomas, 1994; Kinnear *et al.*, 2002; Morris *et*

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[1] At the time of writing, listed as a species or subspecies in accordance with the Commonwealth of Australia's *Environment Protection and Biodiversity Conservation Act, 1999*.

al., 1995; Orell, 2004). As a consequence, the use of 1080 baits (dried meat baits containing the toxin sodium monofluoroacetate, referred to variously as sodium monofluoroacetate, sodium fluoroacetate or fluoroacetate) became a standard and integral component of conservation management in WA.

1.2 The fox in Australia

1.2.1 The introduction and spread of the fox in Australia

The fox was successfully introduced to Australia in the late 1860s to 1870s (Long, 2003; Troughton, 1957) to provide suitable hunting opportunities for the early settlers, as the native fauna was considered unsuitable (Rolls, 1969). The spread of the fox within Australia and into WA from Victoria is thought to have closely followed the path of colonisation by the rabbit (*Oryctolagus cuniculus*) (Christensen, 1980b; Jarman, 1986; Long, 1988; Long, 2003; Stodart and Parer, 1988) (Fig. 1.1). Foxes were first recorded in WA near Eucla in the period 1911-12 (Crawford 1912, cited by King and Smith, 1985). By 1916-17 foxes had reached Sandstone and Kalgoorlie; by 1925 foxes had reached Geraldton; and by the early 1930s had reached the South West Land Division, the north west coast and the south west Kimberley (Gooding, 1955; King and Smith, 1985; Long, 1988) (Fig. 1.1).

Although present in the north Kimberley, the fox has not become established there (King and Smith, 1985). Similarly, it has not become established in north Queensland nor in northern parts of the Northern Territory where there appears to be a barrier, possibly climatic, preventing its expansion into these environments (King and Smith, 1985; Wilson *et al.*, 1992). Until the late 1990s, the fox was considered absent from Tasmania, however, recent studies have confirmed its presence there (Berry *et al.*, 2007). The origin(s) of its introduction to Tasmania are unclear. Analysis of DNA recovered from fox carcasses in Tasmania suggests these introduction(s) are highly unlikely to have originated from the closest freight route (i.e. the known fox population in the Port of Melbourne) and are more likely to have multiple geographic origins (Oliver Berry[2], pers. com. and unpublished). The fox is absent from most off shore islands in WA.

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[2] Oliver Berry: IACRC post-doctoral researcher, University of Western Australia. Current address: CSIRO Marine and Atmospheric Research, Centre for Environment and Life Sciences, Wembley, Western Australia

Table 1.1: Non-volant terrestrial mammals known to occur in Western Australia and listed by the Commonwealth of Australia EPBC Act 1999 (EPBC Act, 1999) as threatened fauna in the categories of Critically Endangered, Endangered or Vulnerable.

Genus, species, subspecies (population)	Common name(s)	Where known to occur
Critically Endangered		
Potorous gilbertii	Gilbert's Potoroo	WA
Endangered		
Bettongia penicillata	brush-tailed bettong, woylie	WA (wheatbelt and southern forest, translocated to other WA sites), translocated to SA and NSW
Dasyurus hallucatus	northern quoll	WA, NT, Qld
Lagorchestes hirsutus dorreae	rufous hare-wallaby, mala (Dorre Island)	WA (Dorre Island)
Mesembriomys gouldii gouldii	Back-footed tree-rat	WA, NT
Parantechinus apicalis	dibbler	WA
Perameles bougainville bougainville	western barred bandicoot (Shark Bay)	WA
Petrogale concinna monastria	nabarlek	WA (Kimberley)
Petrogale lateralis lateralis	black-flanked rock-wallaby	WA (mainland and island)
Pseudomys shortridgei	dayang, heath rat	WA, Vic, SA
Sminthopsis psammophila	sandhill dunnart	WA, NT, SA
Vulnerable		
Bettongia lesueur lesueur	burrowing bettong, boodie (Shark Bay)	WA, SA, NT
Bettongia lesueur unnamed subsp.	burrowing bettong, boodie (Barrow and Boodie islands)	WA (Barrow and Boodie islands)
Conilurus penicillatus	brush-tailed rabbit-rat, brush-tailed tree-rat	WA, NT, Qld
Dasycercus cristicauda	mulgara	WA, NT, SA, Qld
Dasyurus geoffroii	chuditch, western quoll	WA
Isoodon auratus auratus	golden bandicoot (mainland)	WA
Isoodon auratus barrowensis	golden bandicoot (Barrow Island)	WA (Barrow Island)

(cont. …)

Table 1.1 (cont.): Non-volant terrestrial mammals known to occur in Western Australia and listed by the Commonwealth of Australia EPBC Act 1999 (EPBC Act, 1999) as threatened fauna in the categories of Critically Endangered, Endangered or Vulnerable.

Genus, species, subspecies (population)	Common name(s)	Where known to occur
Vulnerable (cont.)		
Lagorchestes conspicillatus conspicillatus	spectacled hare-wallaby (Barrow Island)	WA (Barrow Island)
Lagorchestes hirsutus bernieri	rufous hare-wallaby (Bernier Island)	WA (Bernier Island)
Lagorchestes hirsutus dorreae	rufous hare-wallaby (Dorre Island)	WA (Dorre Island)
Lagostrophus fasciatus fasciatus	banded hare-wallaby, marnine, merrnine, munning	WA (Bernier and Dorre islands)
Leporillus conditor	Wopilkara, greater stick-nest rat	WA (Shark Bay), SA, NSW
Macrotis lagotis	greater bilby	WA, NT, SA, Qld, NSW
Mesembriomys macrurus	golden-backed tree-rat	WA, NT
Myrmecobius fasciatus	numbat	WA
Osphranter robustus isabellinus	Barrow Island wallaroo, Barrow Island euro	WA (Barrow Island)
Petrogale lateralis (MacDonnell Ranges race)	warru, black-footed rock-wallaby (MacDonnell Ranges race)	WA, NT, Qld
Petrogale lateralis hacketti	Recherche rock-wallaby	WA (Mondrain Island, Wilson Island and Westall)
Petrogale lateralis (West Kimberley race)	black-footed rock-wallaby (West Kimberley race)	WA
Phascogale calura	red-tailed phascogale	WA
Phascogale tapoatafa kimberleyensis	Kimberley brush-tailed phascogale	WA
Pseudocheirus occidentalis	western ringtail possum	WA
Pseudomys fieldi	Shark Bay mouse, Djoongari, Alice Springs mouse	WA (mainland and island)
Setonix brachyurus	quokka	WA
Xeromys myoides	water mouse, false water rat	WA, Qld, NT, NSW

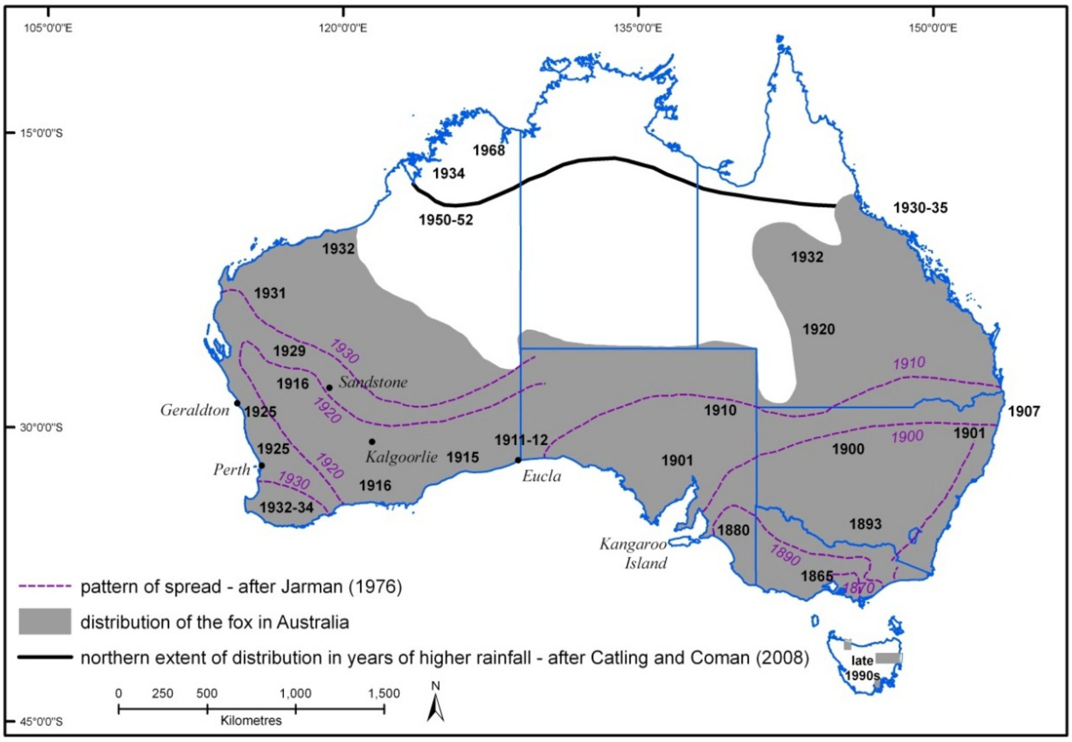

Figure 1.1: The distribution, probable dates of arrival and pattern of spread of the fox within Australia.

Dates of arrival of the fox at various localities are labelled in black, bold font, with limits of the spread shown in partial contours in decades to 1930.

Source: Redrawn from Jarman (1986) and updated from Catling and Coman (2008) and West (2008).

1.2.2 Reproduction

The reproductive cycle of the red fox in Australia corresponds seasonally to the cycle in northern hemisphere populations. The red fox is monoestrus (one annual oestrus phase, therefore one litter per year) (McIntosh, 1963). In Australian studies, oestrus has been shown to commence in June (McIlroy *et al.*, 2001; McIntosh, 1963) or July (Ryan, 1976) and peak in July to August. The gestation period is 51 to 53 days (Lloyd, 1980; McIntosh, 1963) and lactation extends from September to November (McIntosh, 1963; Ryan, 1976). Litters are born at approximately the same time each year, between July and September (McIntosh, 1963; Ryan, 1976; Saunders *et al.*, 1995). In a study of populations from two locations in central western NSW, the mean birth date was September 10th (n=67) and September 4th (n=54) for first and second year, respectively (McIlroy *et al.*, 2001). However, all studies recognise variability in this timing.

Both sexes reach maturity at approximately 9-10 months (McIntosh, 1963). Adult males experience a testicular quiescent phase from September or October to March and a peak in spermatogenic activity in July (McIntosh, 1963; Ryan, 1976), corresponding with oestrus in vixens.

Litter size is thought to be variable and, in Australia, appears to be smaller than northern hemisphere fox populations (Ryan, 1976). The most commonly used methods of determining or estimating litter size is excavating young from the den, and/or examining the number of embryos in collected females, and/or examining the number of placental scars in collected females (Allen, 1983; Lindstrom, 1986). Each method derives an estimate only. Estimates of litter size from Australian studies ranged from 3.17 to 4.60 (Table 1.2). However, estimates from these studies are non-comparable as the techniques varied; as did the method for determining mean values (see the notes for Table 1.2). None of the reported Australian studies is from forest habitat.

Several northern hemisphere studies have shown fecundity changes with age, with older vixen producing larger litters (Allen, 1984; Englund, 1970). However, Harris (1979) found this was the case for the early age cohorts only and litter size (as determined by placental scars) decreased for older vixen. Australian studies don't concur with either finding. Marlow (1992) in a study of fox ecology in the arid zone of New South Wales, found younger vixens, if producing cubs, were likely to produce the same number of cubs as older vixens. Similarly, in a study near Carnarvon, WA, placental scars did not vary with vixen age (Marlow *et al.*, 2000) and McIlroy *et al.* (2001) found vixens, over eight years old, were *"producing as many cubs as first-year breeders"*.

Although the litter size may vary, the number of cubs produced by a fox population is thought to be determined not by the litter size, but by the number of vixens breeding. Northern hemisphere studies have concluded the proportion of barren vixens in a population is determined by factors such as population density, home range size, social encounters and food availability (Lloyd, 1980) and may be influenced by social control (Macdonald, 1979; Macdonald, 1989). The percentage of barren vixens is also thought to change between age classes, with a higher percentage barren in the young

Table 1.2: Estimates of fox (*Vulpes vulpes*) litter size from Australian studies.

Study area	Estimate of litter size	Sample size	S.E.	Range	Method	Source
Carnarvon, WA	3.70	47	0.30	0-7	number of placental scars	Marlow *et al*. (2000)
Central west NSW	3.74	188	0.14	0-11	number of viable embryos (1), (2)	McIlroy *et al*. (2001)
Collected widely within NSW, the majority from ‘in and around’ regional townsites	3.70	142	0.13	1-7	number of placental scars (1), (3)	Ryan (1976)
	4.00	35	0.27	1-8	embryos *In utero* (1), (4)	
The ‘Canberra district’	3.75	8	0.56	1-8	embryos *In utero* (1), (4)	McIntosh (1963)
	3.83	6	0.60	1-5	litters collected from dens (1)	
Urban fox populations from Melbourne, Victoria	4.36	36	0.10	3-5	maximum number of cubs sighted at 17 dens during September to December, over four years (1), (5)	Marks and Bloomfield (1999b)
	4.60	9	n/a	n/a	number of placental scars (6)	

(1) Error estimates were either not presented, or presented in the cited publication as standard deviation. Standard error values presented here were derived from the data originally published.
(2) The number of viable embryos was derived from the sample of vixens which had conceived, not from the total number of vixens or adult vixens.
(3) The mean number of placental scars was derived from those vixens with placental scars only, not from the total number of vixens or adult vixens.
(4) The mean number embryos in utero were derived from those vixens with discernible embryos, not from the total number of vixens or adult vixens.
(5) The mean number of cubs per den was derived from those dens where cubs had been sighted, not from all dens.
(6) Placental scars were recorded from vixens after the final year of observational studies. Data were not presented on the range of placental scars recorded.

(yearling) age class (Lloyd, 1980). When reviewing reported studies, Marlow (1992) found barrenness was reported to range from 0.01 to 52% for northern hemisphere studies. This hasn’t been shown to be the case in Australia, but this may be a reflection the way in which litter size has been reported (see notes from Table 1.2).

1.2.3 Social Organisation

Two different types of social organisation have been reported for the fox. One is based on a mated pair system without the display of territorial behaviour. This type of social structure purports a varying degree of overlap of home ranges. The other social organisation reported is largely based on studies of populations in and around Oxford, England (Macdonald, 1979; Macdonald, 1989). Macdonald (1979) observed a social organisation based on small groups, each occupying a territory. Each group consisted of a male and a small group of closely related vixens. In this social system, a hierarchy existed with only the dominant vixen successfully raising cubs. The non-breeding vixens acted as helpers. Consistent with this, Englund (1970), from studies in Sweden, found evidence of a high percentage of non-breeding vixens.

Although the dominance hierarchy as reported by Macdonald (1979; 1989) has been widely referred to, it is unclear whether such a social structure exists in Western Australian fox populations. Similarly, there is no clear evidence in WA to support the exclusive existence of a mated pair social structure with overlapping home ranges. Phillips and Catling (1991), studying home range activity patterns of foxes in south-east New South Wales, reported paired mating with territorial behaviour. Their telemetry studies showed non-overlapping home ranges of males. Coman *et al.* (1991) studying the home range of foxes in central Victoria felt their results indicated exclusive home ranges except for a breeding pair which shared a common home range. However, unpublished results of Coman *et al.* (cited by Coman *et al.*, 1991) showed in a Victorian study, up to 30% of adult vixens may not breed in any one year. These results, when viewed with information on known cub dispersal patterns, where fewer females disperse from the natal range (see below), may support Macdonald's (1979) assertion that subordinate females act as non-breeding helpers.

Conversely, the results from research from Carnarvon, WA, as part of a study examining social organisation, supported the mated pair social organisation, as the number of cubs collected approached the number expected from a mated pair social structure (Marlow *et al.*, 2000). However, within the study area both types of social structure may exist and there may be changes to social structure over time (Marlow *et al.*, 2000).

1.2.4 Population Densities

Population density, home range and dispersal are closely related aspects of the ecology of the fox. It is generally thought that at higher population densities home ranges are smaller and dispersal distances shorter (Trewhella *et al.*, 1988). However, from a study in North Dakota, USA, Allen and Sargeant (1993) reported dispersal distance to be unaffected by population density.

Estimates of fox density have been derived from a range of methods and from various bioregions within Australia (Table 1.3). The variation in methodologies, time of year and interpretation of the data make these estimates non-comparable. Within WA, estimates have been derived from semi-arid regions only (Table 1.3). Fox densities in WA are otherwise not known and, although anecdotal accounts suggest densities are relatively low in forested areas, there has been no quantitative study of fox density in large tracts of forested land.

Table 1.3: Estimates of fox (*Vulpes vulpes*) density using varying techniques and from a range of locations and broad habitat types in Australia.
After de Tores (1994) and Saunders *et al*. (1995).

Habitat or land use and location	Estimated density (no. of foxes/km^2)	Source
Sheep and cattle grazing, Metcalfe, central Victoria.	1.2 (immediately prior to breeding) 3.0 (foxes immediately post weaning - November to December) 3.9 (in early autumn).	Coman et al. (1991)
Central Victoria	2.8	Newsome and Catling (1992)
Nadgee Nature Reserve, Coastal NSW.	0.25-0.31	Cited by Newsome and Catling (1992) as Phillips and Catling (unpublished)
Semi-arid grazing, western NSW.	2.0	Cited by Newsome and Catling (1992) as R. Burt (pers. comm.)
Arid, Fowlers Gap, central NSW.	0.93	Marlow (1992)
Agricultural grazing land, Northern Tablelands, NSW.	4.55-7.16	Thompson and Fleming (1994)
Subalpine, Kosciusko National Park, NSW.	1.8 (spring). 3.6 (summer and autumn).	Bubela *et al*. (1998)
Metropolitan Melbourne	3-16 Estimates were based on den counts and estimates of litter size	Marks and Bloomfield (1999a)
Sheep and cattle grazing and cultivated crops, central western NSW.	1.2-4.3	J Tracey (unpublished cited by Kay *et al.*, 2000)
Semi-arid, Carnarvon, WA.	0.46-0.52	Marlow *et al*. (2000)
Wool, lamb and beef production and winter cereal cropping. Cleared pasture, with remnant vegetation in the central tablelands of NSW.	0.52-0.55 (late autumn). Estimates were based on counts of natal dens, estimates of litter size and an assumption of a mated pair population structure. 0.91-1.3 (late autumn), based on the average number of dens used by vixens, otherwise with the same assumptions used above for counts based on counts of natal dens.	(Berghout, 2000)

1.2.5 Home Range and Dispersal

European and American studies have shown a variation of up 70 fold in home range size for the fox (Macdonald, 1983). The diversity of reported home range sizes is not surprising given it is largely influenced by resource availability, both in terms of the dispersion of required resources and quality of the resources.

Australian studies estimating home range size have been based on radio-telemetry techniques. Home range estimates varied from 0.6 to 1.3km^2 for an urban fringe population in Victoria, from 5.0 to 7.2km^2 for farmland and was estimated to be 4.9km^2 in ironbark (*Eucalyptus macrocarpa* and *E. sideroxylon*) forest near Bendigo, Victoria (Coman *et al.*, 1991). These figures were derived using either (i) the minimum convex polygon (MCP) method which may over-estimate home range size; or (ii) the non-parametric Fourier transform method (Anderson, 1982). When using the 90% utilisation figure (where the home range is given as the smallest area accounting for 90% of the observed animal location records), the home range size estimates were effectively halved (Coman *et al.*, 1991) and the authors acknowledged inconsistencies in the results. Marlow (1992), also using the Fourier transform method (Anderson, 1982), estimated smaller home range sizes in a study at Fowlers Gap, central NSW, where home range size varied from 0.17 to 4.21km^2, with a mean size of 1.37km^2. Marlow's (1992) home range estimates are within the range of estimates of 1.2 to 5.2km^2 for foxes in south eastern New South Wales (Phillips and Catling, 1991). However, Phillips and Catling (1991) used the MCP method, therefore, home range estimates are non-comparable to Marlow’s (1992) estimates. Estimates of home range size for an urban population of foxes in Melbourne, Victoria varied from 11.5ha (0.115km^2) to 45.8ha (0.458km^2) (n=11, with all estimates derived from a minimum of 62 location records) (Marks and Bloomfield, 1999a). Marks and Bloomfield (1999a) used the 100 % MCP estimate to enable comparison with other reported studies; however, estimates were derived for diurnal locations only. In the absence of nocturnal foraging location records, this will underestimate home range. In a study of foxes from a semi-urban environment from Dandenong Creek Valley, also in Melbourne, White *et al*. (2006) estimated the mean home range derived from the MCP method (presumably 100% MCP, as this was not stated) to be 44.6ha (0.446km^2) based on diurnal and nocturnal location records. Again, the rationale for the MCP method was to enable comparison with other studies. Home range estimates were also derived using the harmonic mean estimator (Dixon and Chapman, 1980) for 50, 95 and 75% activity isopleths and were 1.8, 6.7 and 23.9ha respectively (White *et al.*, 2006).

Phillips and Catling (1991) believed home ranges, at least for males, were non-overlapping, whereas Coman *et al*. (1991) and Marlow (1992) believed there was at least some degree of overlap of home range. Dispersal distances for male foxes are also thought to be greater than for females (Allen and Sargeant, 1993; Lloyd, 1980). The combination of collars incorporating GPS data loggers and more sophisticated home range estimators (see for example Horne, 2005; Horne and Garton, 2006; Horne *et al.*, 2008; Horne *et al.*, 2007b; Rodgers *et al.*, 2007; Seaman *et al.*, 1999) will enable greater inference from analysis of location data.

Dispersal of young from the natal range starts when cubs are approximately six months old (Lloyd, 1980) and may be influenced by population density, home range size and habitat type and quality. Consequently, dispersal distances vary. However, in a study in North Dakota, where the red fox is a native species, the dispersal distance of cubs was not related to population density (Allen and Sargeant, 1993). Mean dispersal distances recorded for Australian studies range from 3.53km for female cubs at Fowlers Gap, New South Wales (Marlow, 1992) to 11km in a study in central Victoria, with individual dispersal distances of 30km recorded (Coman *et al.*, 1991). Dispersal distances of up to 170km for males and 22km for females were recorded near Beverley, east of Perth, WA (Marlow and Thomson, unpublished). Saunders *et al.* (2002), from a study in central western NSW, reported a dispersal distance of 300km. The number of dispersing male cubs is thought to greatly outnumber dispersing female cubs (Coman *et al.*, 1991).

1.3 Fox control in Western Australia

Fauna conservation management in WA has relied heavily on the use of target specific 1080 baits for the control of foxes. Fluoroacetate is present naturally, in the form of fluoroacetic acid, in several plant species from the genus *Gastrolobium* which occurs extensively in south-west WA (King, 1990). Many species of native fauna in WA have very high levels of 1080 tolerance due to their evolutionary exposure to fluoroacetate (King *et al.*, 1978). Conversely, foxes, feral cats (*Felis catus*), dogs (*Canis familiaris*) and dingoes (*C. lupus*), all introduced to Australia, have a very low tolerance to 1080 (McIlroy, 1981). The use of 1080 delivered in a bait for fox control has been possible in WA because of this divergent level of tolerance shown by introduced and native fauna (King *et al.*, 1978; McIlroy, 1981; Twigg *et al.*, 2003).

The bait type most widely used in WA historically consisted of approximately 120g of kangaroo meat, or an alternative meat, injected with 4.5mg of 1080 in solution. Baits were then dried in racks, over approximately four days, in a forced-air drying chamber at 35^0C, which reduces the weight of the bait to 40-50g. Baits were then stored at -20^0C. The procedure was developed by research staff from the then WA Agriculture Protection Board (APB). Some variations to the drying procedures occurred where baits were required in remote locations; for example, from the mid-1980s, baits prepared in the Kalgoorlie/Goldfields, Gascoyne, Pilbara and Kimberley regions, local APB staff dried meat baits on racks left in the open (Peter Thomson[3], pers. comm.). Since the late 1990s and early 2000s, the bait has been extensively modified and a sausage or salami style bait (Probait) is now most commonly used by conservation managers in WA.

In WA, the intensity and frequency of baiting vary according to the size of the area baited, the extent of roading (de Tores, 1994) and the enthusiasm of and/or resources available to local management staff. Repeated baiting is used in recognition that foxes can disperse considerable distances and can re-colonise baited areas within relatively short periods of time (Saunders *et al.*, 1995) (see also references in Chapter 6, Section 6.4.2). This repeated baiting potentially removes foxes which have moved into a site since the previous baiting event. Baiting regimes often include a baiting event to coincide with the expected timing of cub dispersal and/or when vixens are breeding.

Small areas (up to 20,000ha) are nominally baited at a ‘standard’ frequency of four baitings per year and at an intensity of five baits/km^2. However, the baiting intensity achieved is largely dependent on the extent of the roading network used for access for vehicle based bait delivery. Programs implementing a baiting frequency of up to 13 baitings per year at baiting intensities often in excess of 20 baits/km^2 are known to be effective over small areas such as Dryandra Woodland, Boyagin Nature Reserve and at small isolated granite outcrop reserves within the WA wheatbelt.

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[3] Peter Thomson: Former Research Scientist with the Western Australian Department of Agriculture and Food (DAFAWA) and the Western Australian Agriculture Protection Board (APB).

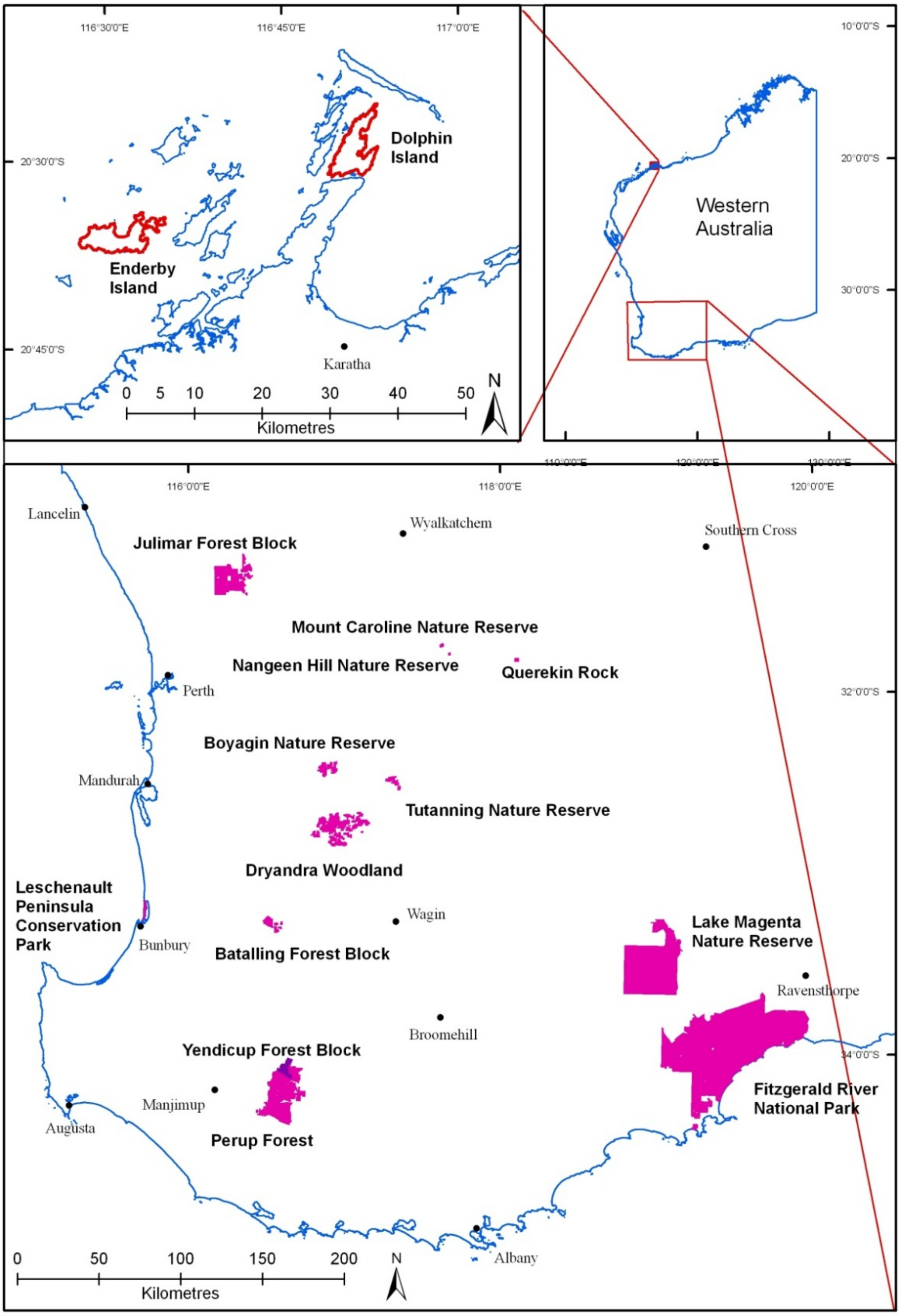

Figure 1.2: Location of landmark studies on fox (*Vulpes vulpes*) control in Western Australia in the period 1985 to the late 1990s.

1080 baiting for fox control was implemented and monitoring of prey species demonstrated or inferred: (i) increases in abundance of *in situ* populations of native mammal fauna; and/or (ii) successful translocation. See Table 1.4 for details for each site.

Table 1.4: *In situ* and translocated mammal populations known to have benefited from 1080 baiting for fox (*Vulpes vulpes*) control in the period 1985 to the late 1990s in Western Australian.

Species	Common name	Monitoring or translocation release site	Source
***In situ* populations**			
Dasyurus geoffroii	chuditch or western quoll	Batalling Forest Block	Morris (1992), Morris *et al*. (2003)
Trichosurus vulpecula hypoleucus	common brushtail possum, south-west WA	Tutanning and Boyagin nature reserves, Fitzgerald River National Park, Leschenault Peninsula Conservation Park	Kinnear (1990), Kinnear *et al*. (2002), de Tores *et al*. (1998a)
Petrogale lateralis	black-footed rock-wallaby	Mt Caroline, Nangeen Hill nature reserves (central WA wheatbelt)	Kinnear *et al*. (1988), Kinnear *et al*. (1998)
P. rothschildi	Rothschild's rock-wallaby	Dolphin and Enderby islands (Dampier Archipelago)	Kinnear *et al*. (2002)
Myrmecobius fasciatus	numbat	Dryandra Woodland	Friend (1990)
Macropus eugenii	tammar wallaby	Tutanning Nature Reserve	Kinnear (1990), Kinnear *et al*. (2002)
Bettongia penicillata	woylie or brush-tailed bettong	Dryandra Woodland, Tutanning Nature Reserve and Perup Forest	Kinnear (1990), Kinnear *et al*. al (2002), Christensen (1980b), Christensen (1980a)
Translocated populations			
Dasyurus geoffroii	chuditch	Julimar Forest Block	Morris *et al*. (1995)
Myrmecobius fasciatus	numbat	Batalling Forest	Friend and Thomas (1994)
Pseudocheirus occidentalis	western ringtail possum	Leschenault Peninsula Conservation Park	de Tores *et al*. (1998a)
P. lateralis	black-footed rock-wallaby	Querekin Rock (private property, central WA wheatbelt)	Kinnear *et al*. (2002)
Bettongia penicillata	woylie	Boyagin Nature Reserve, Batalling Forest and Yendicup Forest block (within the Perup Forest)	Kinnear *et al*. (2002), Orell (2004), Christensen and Leftwich (1992)

Populations of the numbat (*Myrmecobius fasciatus*) and brush-tailed bettong or woylie (*Bettongia penicillata*) were shown to increase at Dryandra Woodland in the presence of fox control (Friend, 1990; Kinnear *et al.*, 2002). The common, or western brushtail possum (*Trichosurus vulpecula hypoleucus*) and woylie at Boyagin Nature Reserve (Kinnear, 1990; Kinnear *et al*., 2002) and populations of black-footed rock-wallaby (*Petrogale lateralis*) at Mount Carolyn and Nangeen Hill nature reserves (Kinnear *et al*., 1988; Kinnear *et al*., 1998) were also shown to increase in size after commencement of high frequency and high intensity fox baiting programs. Similarly, translocation programs carried out in the presence of fox control in the period 1985 to the late 1990s were, in most cases, considered successful. Many of the *in situ* management and translocation successes were seen as landmark studies demonstrating the benefits from fox control (Fig. 1.2 and Table 1.4). This culminated, in 1996, in delisting the woylie from the Western Australian list of threatened species, the Commonwealth of Australia list of threatened species (EPBC Act, 1999) and IUCN Red List of Threatened Species (IUCN, 2010). In July 1998 the tammar wallaby (*Macropus eugenii*) and the southern brown bandicoot (*Isoodon obesulus*) were also delisted from the WA list of threatened species. Ironically, in 2006, the woylie was relisted as a threatened species in WA, nationally (EPBC Act) and internationally. Its listing in the latter two was in the category ‘Endangered’ – a higher level of threat than the original listing of ’Vulnerable’. It is currently listed as ‘Endangered’ (EPBC Act, 1999).

Although the circumstantial evidence implicating fox predation as a causal factor in the decline in abundance and distribution of many native species is overwhelming, it has not been possible to irrefutably demonstrate that fox predation has been largely responsible for, let alone the sole cause of, this decline. It is also unlikely such declines are the result of a single dimensional causal factor such as fox predation and most authors have attributed these declines to a suite of factors acting in concert (Burbidge and McKenzie, 1989; Johnson, 2006; Kinnear *et al.*, 2002; Lindenmayer and Recher, 1998; Morton, 1990; Short and Smith, 1994; Smith and Quinn, 1996).

1.4 The requirement for quantified analyses of native fauna response to fox control

Where fox control has been implemented in WA and where the response of native fauna has been monitored, there has been little or no corresponding monitoring of fox populations. Similarly, there has been minimal assessment of the relative importance of fox predation and other factors which have the potential to limit the size of *in situ* populations of native fauna and/or limit translocation success. Reviews of fox control programs in WA in the 1990s, and subsequently, have recommended these programs adopt more appropriate statistical analyses generally, incorporate quantitative analysis of the prey response to baiting, make better use of control (unbaited) sites, improve the level of replication and address issues such as lack of independence of sites (Caughley and Gunn, 1996; Hone, 1999; Lindenmayer and Recher, 1998; Possingham *et al.*, 2004).

In the absence of any meaningful assessment of fox abundance, fox baiting programs have therefore been unable to assess any response foxes may have shown to the imposed control measures. Additionally, the majority of WA studies on fox control are unpublished, published in the grey literature only, or in non-peer reviewed journals or magazines. Nonetheless, the circumstantial evidence, combined with the increasing body of scientific evidence led to national recognition of fox predation as a key threatening process (DEWHA, 2008a; 2008b) and there is a general recognition from conservation managers throughout Australia of the need for on-going fox control. However, this does not negate the need to quantify the relationship(s) between fox density, or any reduction achieved from baiting programs, and the effect on, and response by native fauna.

In 1994, the then Western Australian Department of Conservation and Land Management (CALM) initiated Operation Foxglove; Australia's first large scale aerial baiting program for fox control. The program was implemented to establish broad-scale fox control within the northern jarrah forest of south-west WA (de Tores, 1994). The study provided the opportunity to assess the effectiveness of different frequencies of baiting at a landscape scale and, in doing so, provided the opportunity to address many of the criticisms of fox control in WA. A second large-scale aerial baiting program, the 'Western Shield Introduced Predator Control and Fauna Recovery Program' (hereafter referred to as Western Shield) commenced in 1996 and became the umbrella program for the Department's operational fox baiting within south-west

WA. Western Shield baiting covers approximately 3.6 million ha of state forest and conservation reserves in south-west WA (de Tores and Marlow, 2012).

In WA, 1080 baiting for fox control is now seen as a necessary component of fauna conservation management (de Tores, 1994). Baiting regimes have primarily been based on vehicle delivery of baits at high baiting frequencies and intensity (see Section 1.3). However, these baiting regimes are cost prohibitive if adopted at a landscape scale.

Prior to commencement of broadscale aerial baiting for fox control in WA, field trials were carried out in the early 1990s (Thomson and Algar, 2000) to determine the effectiveness of different baiting intensities. This research was conducted at sites in four different botanical districts in WA and demonstrated a baiting intensity of five baits/km^2 resulted in bait uptake by 62-88% (average 79.5%) of the sampled fox populations (Thomson and Algar, 2000). There was no increase in bait uptake when baiting intensity increased to 10 baits/km^2 (Thomson and Algar, 2000).

There were no similar studies and no conclusive evidence of the minimum baiting frequency required to result in a sustained reduction of fox populations. However, results from Dryandra Woodland revealed populations of the numbat, woylie and common brushtail possum increased when monthly baiting was carried out (Friend, 1990; Kinnear *et al.*, 2002). Similarly, black-footed rock-wallaby populations increased in abundance and in area of occupied habitat when monthly baiting was conducted at several granite outcrop reserves in the WA wheatbelt (Kinnear *et al.*, 1988; Kinnear *et al.*, 1998).

Within forest areas at Batalling Forest Block, near Collie, baiting at three-monthly intervals resulted in an increase in capture rate of chuditch (*Dasyurus geoffroii*) (Morris *et al.*, 1995). With annual baiting, woylie capture rates also increased in the central baited core of the Perup Forest, near Manjimup. However, this increase was not observed throughout the entire reserve and woylie capture rates appeared to follow a gradient from very high in the central baiting core, to negligible at the boundary (de Tores, unpublished). This was hypothesised to be a result of baiting preventing foxes from becoming established within the central core of Perup Forest, with regular incursion of foxes at the perimeter of the baited area (de Tores, 1994).

At Perup Forest, Dryandra Woodland and Tutanning Nature Reserve, fox numbers may also be reduced as a result of secondary poisoning, i.e. by fox predation on 1080-tolerant native fauna which have eaten vegetation from the *Gastrolobium* genus, or secondary poisoning as a result of foxes consuming rabbits poisoned by 1080. The phenomenon of secondary poisoning is well documented for a range of species (see for example Algar and Kinnear, 1996; Alterio and Miller, 2000; Berny *et al.*, 1997; Brown *et al.*, 1998a; 1998b; Gillies and Pierce, 1999; Heyward and Norbury, 1999; Lloyd and McQueen, 2000; McIlroy and Gifford, 1992; Murphy *et al.*, 1999; O'Connor *et al.*, 2003).

Contrasting with the results from monthly baiting at Dryandra Woodland, Friend (unpublished) found the size of a translocated numbat population at Karroun Hill Nature Reserve failed to increase under a twice yearly baiting regime. At Karroun Hill, fox numbers were thought to have decreased as a result of twice yearly baiting, supplemented with additional baiting by staff from the WA APB. However, there was some evidence to suggest cat numbers may have increased which may have led to increased cat predation on numbats (J. A. Friend[4], pers. comm.). This phenomenon, termed mesopredator release, is discussed in Chapter 6.

1.5 Objectives

The Operation Foxglove research provided the opportunity to address some of the issues raised in previous reviews of fox control programs in WA, namely that these control programs lacked appropriate statistical analyses, lacked quantitative analysis of the fauna response to baiting, lacked control (unbaited) sites and had no or minimal assessment fox abundance (see Section 1.4 and Caughley and Gunn, 1996; Hone, 1994; Hone, 1999). As the required baiting frequency for large tracts of multiple use forest was unknown, the project also provided the opportunity to assess the effectiveness of different frequencies of 1080 baiting at a landscape scale to determine which, if any of those trialled, achieved a sufficient reduction in fox abundance to result in an increase of native fauna abundance.

Although Thomson and Algar (2000) demonstrated a baiting intensity of five baits/km^2 resulted in a bait uptake of approximately 80%, they acknowledged this rate of uptake is likely to be influenced by fox density, with a lower uptake rate at higher fox densities. Anecdotal reports indicated the northern jarrah forest study area supported fox

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[4] Tony Friend: Former Principal Research Scientist, WA Department of Environment and Conservation, Science Division

populations at low density, suggesting uptake of baits may be as high as the 80% value determined by Thomson and Algar (2000).

In recognition of the above, the specific research objectives of this PhD were to:

1. determine whether fox predation alone is limiting native fauna occurrence within the northern jarrah forest;
2. determine the fox abundance/density required in this forest environment to achieve a sustained increase in native fauna abundance; and
3. determine the most effective baiting frequency for large areas of multiple use forest.

To achieve the objectives, the northern jarrah forest project sought to undertake quantitative analysis:

(i) to estimate fox density within the treatment and control sites;

(ii) of survivorship data for woylie populations translocated to treatment (baited) and control (unbaited) sites; and

(iii) to determine the variables and model(s) which best describe the pattern(s) of presence of *in situ* populations of native fauna within treatment and control sites.

1.6 Hypotheses

The leading hypothesis is native fauna survivorship and occurrence in the northern jarrah forest is a function of fox density, with survivorship, presence and abundance reduced as fox density increases. Consistent with this is the hypothesis that the probability of the presence of native fauna will increase when the standard operational baiting regime (a baiting intensity of five baits/km^2 and a frequency of four baitings per year) is increased to a frequency of six baitings per year. A corollary is the probability of native fauna presence will be lower where 1080 baiting is at a frequency of two baitings per year and in the unbaited control. However, native fauna occurrence, distribution and abundance are unlikely to be a function of a single dimensional causal factor such as fox predation. Hence, the more explicit hypothesis is that native fauna occurrence and survivorship in the northern jarrah forest is a function of the extent of fox predation combined with complex interactions between foxes and feral cats and their predation effects, the length of time baiting has been carried out and the degree of continuity of baiting. It is also likely to be influenced by the distance from agricultural land, climatic variables, site specific variables including variations in primary productivity and the extent of structural heterogeneity of the vegetation and the extent of floristic heterogeneity. Structural and floristic heterogeneity may in turn be influenced by a suite of anthropogenic disturbance factors such as harvesting history, fire management history, mining (or proximity to mining areas) and the associated roading and presence or extent of dieback caused by the plant root pathogen *Phytophthora cinnamomi*. Confounding this, there is no *a priori* reason to expect all northern jarrah forest fauna species will respond in the same way to these habitat variables and disturbance factors. The life history traits of the suite of northern jarrah forest mammal species (specifically, relatively low fecundity and relatively long life spans, exceptions to the latter being the yellow-footed antechinus (*Antechinus flavipes*) and the brush-tailed phascogale (*Phascogale tapoatafa*)), combined with the anecdotally reported low faunal densities within the northern jarrah forest, also have the potential to further confound interpretation of monitoring results.

The project design recognised these potentially confounding effects. Additionally, the complexity of the factors affecting fauna survival, and the interactions between these factors, suggested conventional methods of monitoring and conventional null hypothesis testing would be unlikely to detect a ‘statistically significant’ increase in faunal abundance, should it occur, within the limited four to six year time frame of the project, irrespective of the biological significance of a response to the baiting program.

Consequently, hypotheses were examined in an information-theoretic framework (Anderson, 2001; Anderson and Burnham, 2002; Anderson *et al.*, 2001; Burnham and Anderson, 1998; 2001; 2002), whereby a set of *a priori* candidate models was formulated and compared to identify which model(s) best described the data. Model selection was through the use of the Akaike Information Criterion (AIC), or more specifically AICc, which incorporates an adjustment when the ratio of the sample size (n) to the number of estimable parameters (K) is less than 40 (Burnham and Anderson, 2002). An overview of the information-theoretic approach is provided in Chapter 2. Adoption of the information-theoretic approach, although not providing any additional statistical power, enabled examination of simplified, plausible hypotheses, from which inference could be drawn.

The information-theoretic approach also acknowledges that model selection is not aimed at finding a perfect model or perfect truth. It is a means by which reality can be described by simplified models, these models are then tested (or compared) and the most parsimonious model(s) can then be used to explain the complexity of interactions and responses occurring in ecological systems.

The study examined the hypothesis that survivorship of translocated populations of the brush-tailed bettong or woylie, hereafter referred to as the woylie, was a function of fox density, where the frequency of baiting was considered (and subsequently tested and confirmed) to result in differences to fox density. Specifically, woylie survivorship was hypothesised to be highest in the most frequently baited treatment group (six baitings per year) and lowest in the unbaited treatment group.

In this study, the woylie was used as an indicator species for predation sensitive, terrestrial, native mammal fauna. At commencement of the research, the woylie was absent from the northern jarrah forest. However, its former geographic range encompassed south-west WA (inclusive of the northern jarrah forest study area), much of central northern WA, south-west Northern Territory, north-west, central and eastern South Australia and most of New South Wales and Victoria (Burbidge *et al.*, 1988; de Tores and Start, 2008; Finlayson, 1958; Troughton, 1957). Its geographic range has contracted since European settlement and naturally occurring populations are now restricted to three locations in south-west WA: two small wheatbelt reserves (Dryandra Woodland and Tutanning Nature Reserve); and state forest near Manjimup (Perup Forest) (de Tores and Start, 2008) (Fig. 1.2). Use of the woylie as an indicator species required translocation of study animals from Dryandra Woodland (Fig. 2.1) to the northern jarrah forest, followed by intensive radio-telemetry monitoring of survivorship. Ideally, survivorship should be examined for each species of interest as opposed to use of a single indicator species. The decision to use the woylie as an indicator species was based on previous research which demonstrated:

- it can be successfully translocated and will respond positively to fox control (Christensen and Leftwich, 1992; Kinnear *et al.*, 2002);
- each female can produce up to three young per year (Christensen, 1980a; de Tores and Start, 2008), so reproductive success is detectable; and
- it is readily trappable and therefore suited to intensive monitoring.

1.7 Thesis structure

The location and biophysical attributes of the study area are given in Chapter 2, as is further rationale for use of the information-theoretic (Burnham and Anderson, 2002), the Bayesian model selection approach (Ellison, 2004) and a brief outline of the general methodologies adopted. A more detailed description of each methodology is described in the relevant chapters.

Assessment of fox and cat density within each treatment and validation of the technique used is reported in Chapter 3. Woylie survivorship results and the causes of mortality are reported in Chapter 4. The presence of *in situ* populations of native fauna in relation to frequency of fox baiting, climatic and site specific variables within the northern jarrah forest are reported in Chapter 5.

A synthesis of the Operation Foxglove research is provided in Chapter 6. This synthesis is placed in the context of (i) the results of the findings from more recent ‘operational’ fox control programs in WA; and (ii) the subsequent research from the northern jarrah forest and the ongoing need for fox and cat control. Chapter 6 also provides specific recommendations for future research.

1.8 Technical support, funding and administrative centre

The project was based at the Department of Conservation and Land Management (CALM) Dwellingup Research Centre. The Department changed name in 2006 to the Department of Environment and Conservation (DEC, 2006 to 2013), in 2013 to the Department of Parks and Wildlife (DPaW 2013 to 2017) and in 2017 to the Department of Biodiversity, Conservation and Attractions (DBCA from 2017). In this thesis when referring to the Department, I have primarily used the acronyms CALM and DEC, except when referring to recommendations for future management and research.

I was responsible for the project design and implementation, ensuring use of appropriate techniques, establishing the site specific research protocols, all data management and all analyses. I was also responsible for sourcing all funding, with the exception of the initial funds secured (by Jack Kinnear) from the Vertebrate Biocontrol Cooperative Research Centre (VB CRC).

I was involved to some degree in every aspect of field work and responsible for day to day supervision of all field work. Technical support was provided for data collection only and was made possible as a result of funding from CALM, the Pest Animal Control Cooperative Research Centre (PAC CRC and its predecessor, the VB CRC), the Commonwealth of Australia’s Australian Nature Conservation Agency (ANCA, subsequently the Department of Environment and Energy), Alcoa World Alumina, Australia (Alcoa) through the CALM Alcoa Forest Enhancement (CAFE) program, the

Western Australia Department of Commerce and Trade and the then joint venture partners of Boddington Gold Mine: Anglogold, Newcrest and Normandy.

Chapter 2

Operation Foxglove: the study area, experimental treatments, general methodology and statistical methods

2.1 The study area

2.1.1 Location

The northern jarrah forest of south-west WA is broadly defined as the large tract of contiguous forest, south of the upper reaches of the Swan-Avon River and north of the Preston River (Fig. 2.1). The northern jarrah forest is within the 'Northern Jarrah Forest' Subregion of the Interim Biogeographic Regionalisation of Australia (IBRA) 'Jarrah Forest' Region (Thackway and Cresswell, 1995) (Fig. 2.2). The study area covers an area of approximately 544,000ha between the latitudes 31^0 59' and 33^0 16' S and the longitudes 115^0 59' and 116^0 41' E (Fig. 2.1 & Fig. 2.2). It lies within the area more generally described as the Darling Scarp and the Darling Plateau and is bounded by cleared agricultural land to the east (the IBRA Wheatbelt Region) and by cleared agricultural and semi agricultural land to the west (the IBRA Swan Coastal Plain Region). Unless specified otherwise, the term 'northern jarrah forest' is used hereafter to refer to the 544,000ha study area only.

2.1.2 Climate

The climate of the northern jarrah forest, and south-west WA in general, is described as 'Mediterranean[5] style' (Peel *et al.*, 2007) because of the well-defined pattern of hot, dry summers and mild, wet winters (Gentilli, 1988; Wallace, 1966). This is reflected in the long-term average seasonal rainfall and average minimum and maximum summer and winter temperatures for Dwellingup, near the centre of the study area (Figure 2.1 and Table 2.1). Annual rainfall over the study area shows a gradual decline west to east (Fig. 2.3), with an orographic effect responsible for the higher rainfall immediately east of the Darling Scarp (Fig. 2.4). The number of frosts each year also shows a gradient, with few frosts annually in the north-west and over 50 annually along the eastern boundary of the study area (Havel, 1975a). However, summer drought is recognised as the major limitation to plant growth, with the effect of cold winter temperatures slowing down, but not halting plant growth (Diels 1906 as cited by Havel, 1975a).

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[5] Mediterranean refers to the category 'Csa' from the classification of climate originally formulated by Wladimir Köppen and subsequently modified.

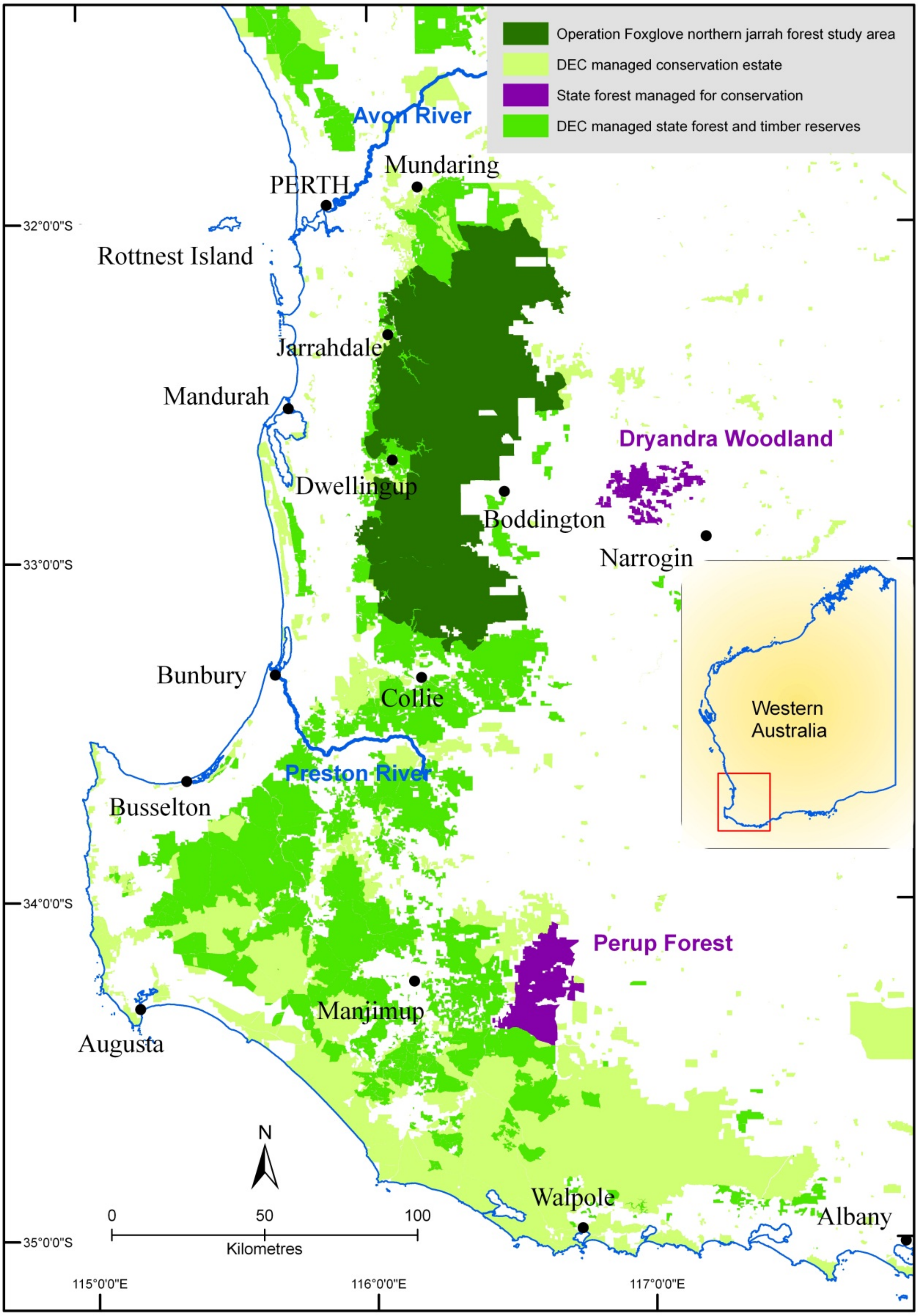

Figure 2.1: Location of the Operation Foxglove northern jarrah forest study area.

Field and laboratory work was based at CALM's Dwellingup Research Centre, located near the centre of the study area and close to the 1300mm annual rainfall isohyet (Fig. 2.3). For the period of the study (1994 to 2000) the average annual summer and winter minimum and maximum temperatures were from 0.6 to 0.9^{0}C above the long-term seasonal averages. Average summer and winter seasonal rainfall was lower than the long-term seasonal averages, however, the annual average rainfall for the study period was higher than the long-term annual average (Table 2.1).

Table 2.1: Summer and winter average minimum and maximum temperatures and average summer, winter and annual rainfall for Dwellingup, over the long term (1935 to 1993) and for the study period (1994 to 2000).

Derived from Bureau of Meteorology data.

	Average minimum and maximum summer (Dec to Feb) temps ^{0}C	Average minimum and maximum winter (June to Aug) temps ^{0}C	Average summer rainfall (mm)	Average winter rainfall (mm)	Average annual rainfall (mm)
Long term (1935-1993)					
	13.6 to 28.5	5.7 to 15.3	62.2	697	1,275
The study period (1994-2000)					
	14.5 to 29.7	6.3 to 16.0	42	674	1,394

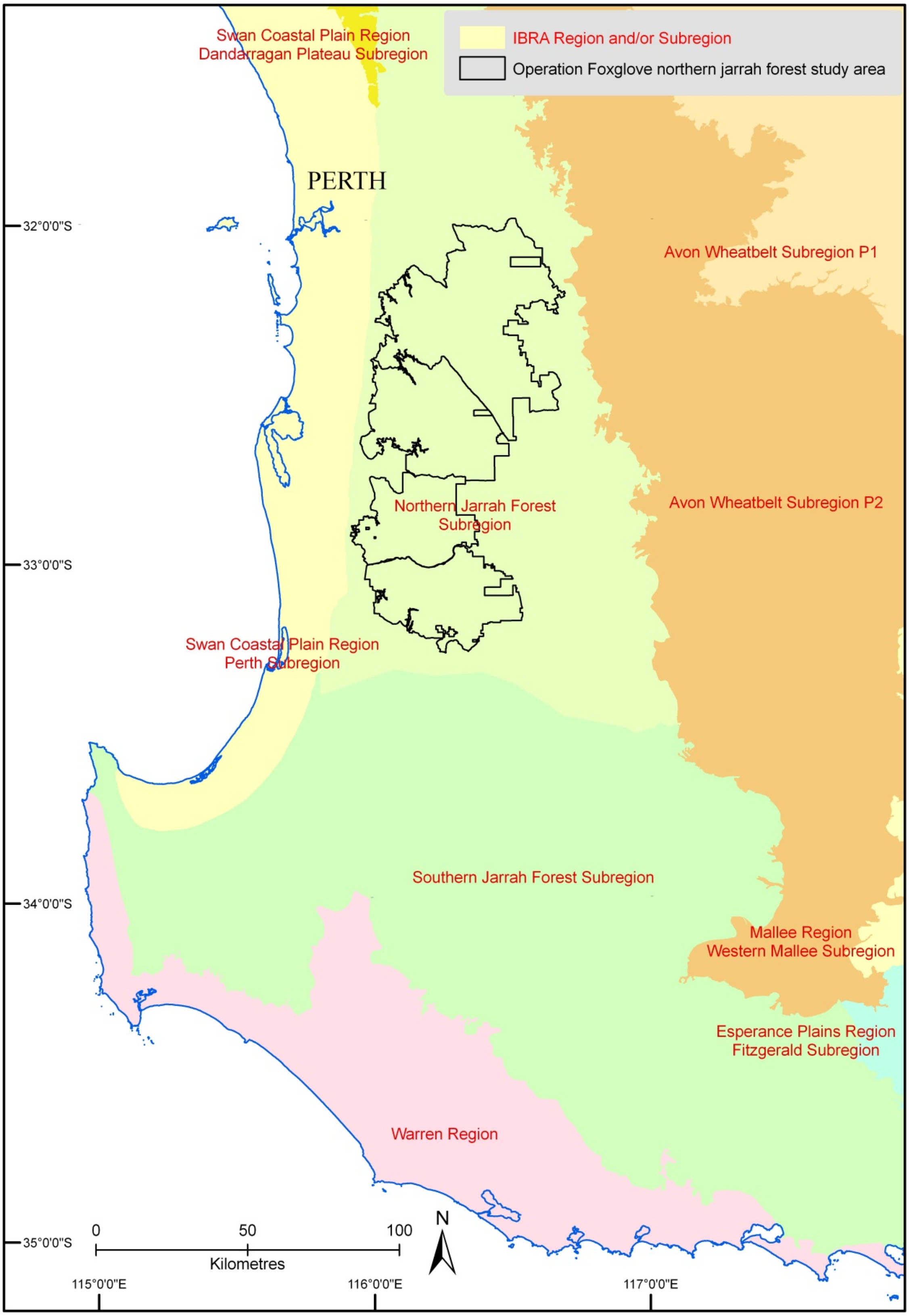

Figure 2.2: The location of the northern jarrah forest study area in relation to the Interim Biogeographic Regionalisation of Australia (IBRA) regions and subregions.

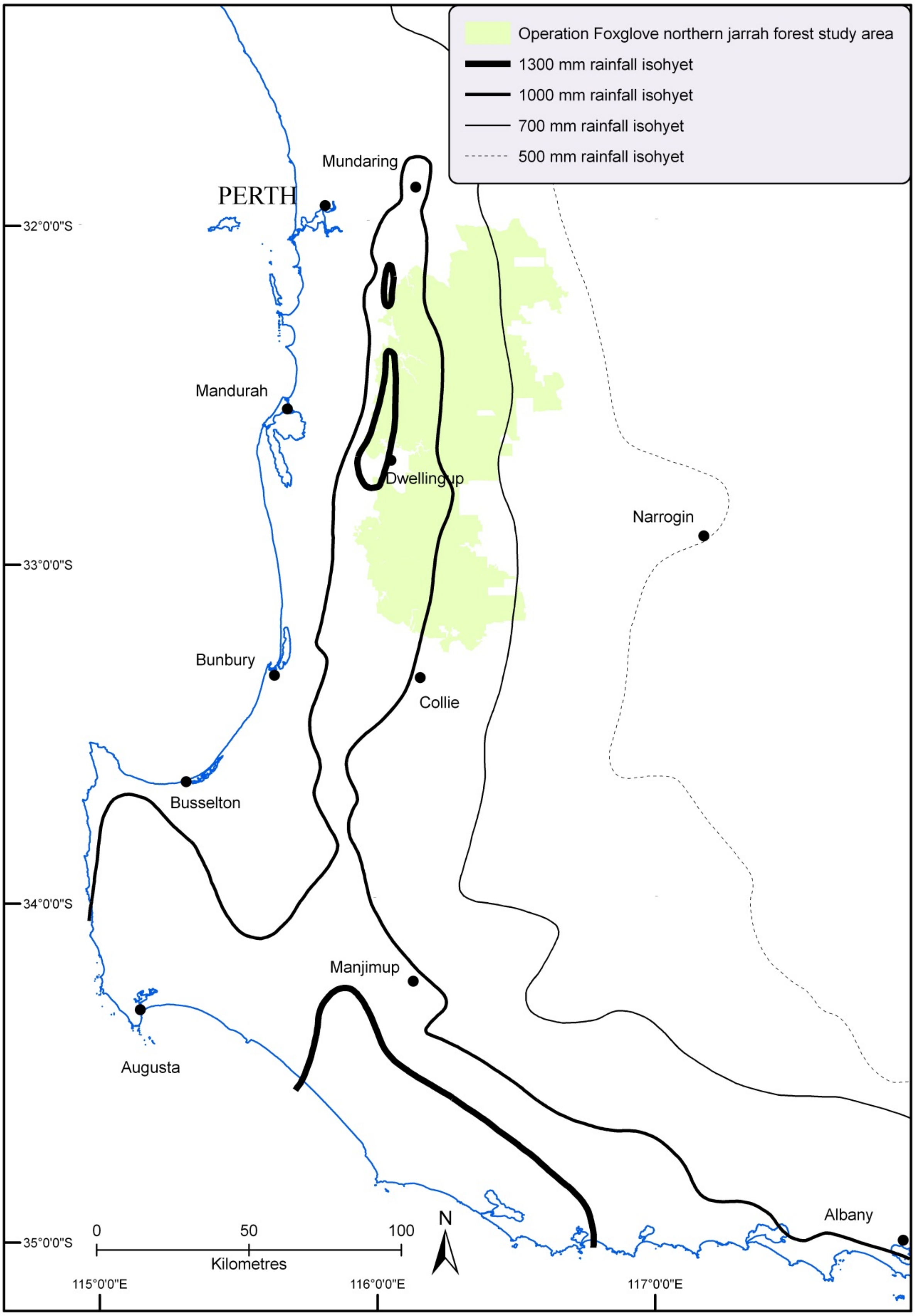

Figure 2.3: Annual rainfall isohyets for south-west Western Australia.

2.1.3 Geomorphology, landforms and soils

Hopper (2003, p14) described south-west WA as *"topographically unique among the world's five regions of Mediterranean climate, being essentially a flat stable highly-weathered low plateau, underlain by Precambrian granite bedrock occasionally emergent as domed bornhardts and inselbergs, with few mountainous areas"*. These inselbergs (or monadnocks, or isolated outcrops) are represented within the northern jarrah forest and often appear as conspicuous landmarks.

The northern jarrah forest is within the western region of the Yilgarn craton and is separated from the geologically younger Perth Basin by the visually pronounced Darling Fault (or Darling Scarp) (Fig. 2.4). The Yilgarn craton or plateau is expansive, with an area of approximately 65,000km^2. It extends from Meekatharra and Wiluna in the north, to the south coast; and from Yamarna (~130 kilometres east of Laverton) and Balladonia in the east, almost to the west coast. It has been aged at 4,404 million years *"about 130 million years older than any previously identified* [surviving crust] *on Earth"* (Wilde *et al.*, 2001). The plateau is part of the larger Yilgarn Block Province, which, in turn is part of the 'Great Plateau of Western Australia' or Western Australian Shield or Western Plateau (Havel, 1975b; Johnson, 2004).

As a result of its proximity to the scarp and the resultant higher rainfall compared to the rest of the plateau, the western region of the Yilgarn craton is highly dissected (Biggs *et al.*, 1980; Churchward and McArthur, 1980; Churchward and Dimmock, 1988; Havel, 1975b; Johnson, 2004; McArthur *et al.*, 1977). The landforms are generally undulating and comprised of lateritic uplands (Churchward and McArthur, 1980; Churchward and Dimmock, 1988; McArthur *et al.*, 1977). The altitudinal range of most of this raised, undulating Darling Plateau extends from approximately 250m to 350m above sea level, with Mount Solus (the highest peak within the study area) reaching 574m (Fig. 2.4).

The lateritic uplands are dominated by duricust (a weathered, hardened layer at or near the surface, in this case synonymous with laterite), gravel and sand. The valleys have been described as encompassing four major forms: the Goonaping, Beraking, Darkin and Helena Valley forms (Churchward and Dimmock, 1988; Mulcahy *et al.*, 1972). The deeper valleys are dominated by red and yellow duplex soils and the shallow valleys are dominated by either brown sandy gravels and gravely yellow duplex soils (known as the Pindalup unit) or by sandy gravels overlying the duricrust, or by mottled clay and

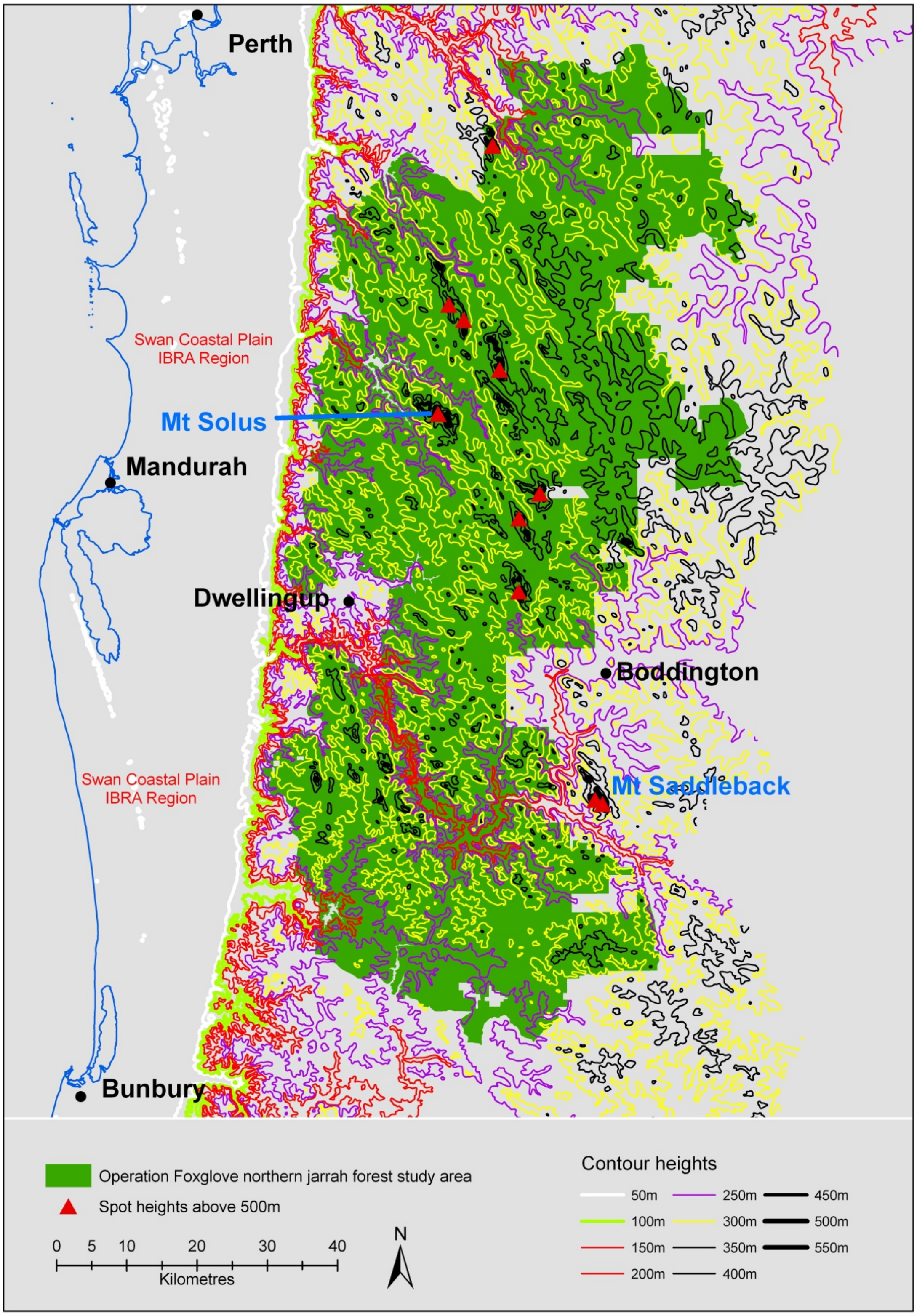

Figure 2.4: The topography of the northern jarrah forest study area.

The sharp boundary (the Darling Scarp, shown as a distinct north-south running white line) between the Swan Coastal Plain and Jarrah Forest IBRA regions is pronounced and defined by the 50 and 100m contours. Most of the Darling Plateau within the study area is between 250 and 350m altitude, with inselbergs up to 574m (Mt Solus). The peak neighbouring Mt Saddleback (outside the study area) is 577m.

yellow-brown earths (the Yarragil Unit) (Biggs *et al.*, 1980; Churchward and McArthur, 1980; Churchward and Dimmock, 1988; McArthur *et al.*, 1977). The characteristic fine-grained material and the round 'ball-bearing-like' gravels of the northern jarrah forest result from the process of laterisation, where, in the presence of humidity and/or distinct wet and dry seasons, the more readily dissolved minerals (sodium, potassium, calcium, magnesium and silicon) are progressively dissolved and others (iron and aluminium) remain as hydrated oxides (Simpson, 1966). In the extreme case of laterisation, the iron oxides are also removed leaving only the hydrated aluminium oxide ore, or bauxite (Simpson, 1966).

This laterisation has resulted in an 'inverse' drainage pattern whereby the upper reaches of streams are *"broad, open, mature valleys which become progressively steeper and more juvenile downstream"* (Havel, 1975b, p13). Historically, there has been some conjecture as to the sequence of the series of uplift events and the laterisation process. Some authors have argued the laterisation took place before uplift, others have claimed the laterisation followed uplift, or was contemporaneous with a series of minor uplifts (Biggs *et al.*, 1980; Churchward and McArthur, 1980; Churchward and Dimmock, 1988; Finkl, 1971a; 1971b; Jutson, 1934; McArthur *et al.*, 1977; Mulcahy, 1967; Mulcahy *et al.*, 1972; Woolnough, 1918). The implications and significance of these differences is discussed by Havel (1975a) who noted if laterisation was before uplift, laterites would be restricted to a narrow latitudinal band. Under the scenario of laterisation after uplift, laterites would be widespread. Anand and Paine (2002) concluded it was unwise to assign laterisation to a restricted time frame and provided evidence that laterisation had occurred prior to the Eocene Epoch (55 mya) and importantly, *"the process is* [still] *… operating in humid regions of the Darling Range"*. This view, that the laterisation process is still an active process, had previously been expressed by Smith (1952 as cited by Havel, 1975a) and appears to be the accepted belief.

As a consequence of such an ancient landscape, with a lack of recent disturbance from glaciation and volcanic eruptions, the northern jarrah forest is characterised by a nutrient impoverished soil (Lambers *et al.*, 2010). Plants dependent on soils derived from ancient landscapes in WA are characterised by low leaf phosphorous concentrations, high nitrogen to phosphorous ratios and are susceptible to phosphorous-toxicity when exposed to only slightly elevated soil phosphorous levels (Lambers *et al.*, 2010). Adaptations (plant and animal) to nutrient poor soils, combined with intense fire, which may in itself be an evolutionary consequence of low nutrients, has been hypothesised as potentially responsible for many of the anomalous features of Australia's biota (Orians and Milewski, 2007).

2.1.4 Vegetation and floristics

The northern jarrah forest is within the Darling subdistrict of the South West Botanical Province (Beard, 1980) and within one of 25 global biodiversity hotspots (Myers *et al.*, 2000). Identification of hotspots was on the basis of the concentration of endemic flora and fauna species combined with the degree of threat present (Myers *et al.*, 2000). In recognising threats to biodiversity values, identification of a 'global hotspot' indicates there is some degree of urgency for conservation measures. The need to recognise the urgency for conservation measures in south-west WA was emphasised by Hopper (2003), who noted the area is likely to support over 8,000 plant species with 75% of these being regional endemics. This number of endemic plant species is higher than the number of endemic plant and animal species combined recognised by Myers *et al.* (2000). Areas of narrow floristic endemism have been identified within the study area and at least three of Beard's (1980) vegetation associates have more than 10% of their total extent within the IBRA northern jarrah forest subregion (Williams and Mitchell, 2003).

Although referred to as the northern jarrah forest, the term 'jarrah forest' is something of a misnomer as, although jarrah (*Eucalyptus marginata*) is the dominant overstorey species, the northern jarrah forest is comprised of a diverse array of overstorey species including marri (*Corymbia calophylla*, formerly *E. calophylla*), wandoo (*E. wandoo*), powder bark wandoo (*E. accedens*), blackbutt (*E. patens*), bullich (*Eucalyptus megacarpa*) and flooded gum (*E. rudis*). These mostly occur in mixed stands but may occur in the absence of jarrah. *Eucalyptus wandoo* and *E. rudis* often occur as the single overstorey species.

Havel (2000) described the jarrah forest vegetation as forming a continuum from the wetter south west to the drier north east, with localised variations ranging from drought prone areas to waterlogged depressions. In terms of forest structure and the classification system of Specht *et al.* (1974), the jarrah forest is considered an open forest in the north and a tall forest in the south (Dell and Havel, 1988). The study area contains a wide diversity and range in vegetation structure, floristics, geomorphology and climatic variability, but falls within the 'open forest' range of this continuum.

Qualitative descriptions of the northern jarrah forest have recognised the high degree of endemism, the diversity in vegetation structure and floristics and the influences of variations in soil fertility, geomorphology and climate. Early descriptions identified the associations between jarrah and many banksias with poor soils, and the association of wandoo and marri with more fertile soils (Bell and Heddle, 1988). Bell and Heddle (1988) also cited Diels (1906) who recognised the finer detail of the association of marri with moist, relatively fertile soils; the she-oak (*Allocasuarina fraseriana*) with sandy soil; bull banksia (*Banksia grandis*) with gravelly uplands; the genera *Petrophile* and *Isopogon* with sandy loams; *Gastrolobium* with dry gravels and *Taxandria linearifolia* (formerly *Agonis linearifolia*) with swamps.

The classification system developed by Havel (1975a; 1975b) quantified overstorey and shrub structure and floristics, topographical position and soil type to derive 19 site-vegetation types (referred to hereafter as Havel site-types, or site-types). These Havel site-types are recognisable, and mappable, by identification of a limited set of canopy and understorey species (Bell and Heddle, 1988). The suite of site-types reflects the continuum of the vegetation of the jarrah forest, yet also reflects subtle changes in composition of overstorey and understorey species, soil fertility and position in the landform (Bell and Heddle, 1988; Heddle, 1979).

Havel site-types were mapped as part of this study for the purpose of modelling the variables potentially contributing to the presence of fauna species within the study area. The site-types present within the study area are described in Chapter 5.

Mattiske and Havel (1997) reviewed the plethora of vegetation classification systems previously used to describe and categorise the forests of south-west WA and proposed a mapping methodology acknowledging the inter-relatedness of the geology, geomorphology, soils, landforms and climatic factors. This formed the basis of the mapping used for the WA Regional Forest Agreement (RFA).

2.1.5 Fauna of the northern jarrah forest

Each of the three major lineages, the Dasyuromorphia, Peramelemorphia and Diprotodontia, which gave rise to all Australian marsupials, is represented to some extent within the northern jarrah forest. However, within the Diprotodontia there is a notable absence of both families from the Vombatiformes (the Phascolarctidae and Vombatidae, koala and wombats) and the Superfamily Petauridae. The non-volant native eutherian mammals are poorly represented, with the bush rat (*Rattus fuscipes*) and possibly the water rat (*Hydromys chrysogaster*) the only representatives of the Order Rodentia. The volant mammal fauna is less well known. Introduced mammals include the house mouse (*Mus musculus*), black rat (*Rattus rattus*), pig (*Sus scrofa*), ferret (*Mustela furo*), rabbit, dingo, fox and cat.

There are several studies, from the 1970s, 1980s and earlier (see Chapter 5), documenting the presence of a suite of mammals within the northern jarrah forest (see for example Christensen *et al.*, 1985; Dell, 1983; Dell and How, 1988; Serventy, 1950; Serventy *et al.*, 1954). However, most information on the occurrence and distribution of fauna in the northern jarrah forest has arisen from species specific research e.g. research on the ecology of the quokka (*Setonix brachyurus*) (Hayward, 2002), research on the quokka's response to fire (Christensen, undated; Christensen and Kimber, 1975), research on fire and western brushtail possum population demographics (How and Hillcox, 2000), or survey associated with environmental assessment of various mining proposals (see for example Alcoa of Australia Ltd and Dames and Moore, 1978; Nichols and Nichols, 1984; 2003; Nichols *et al.*, 1981; Worsley Alumina Pty Ltd, 1985; 1999; Worsley Alumina Pty Ltd and Dames and Moore, 1981).

Avifauna, herpetofauna and terrestrial invertebrate surveys have been conducted in a similar way to the mammal surveys with the majority of studies related to specific research issues (e.g. response to fire, the response to post mining rehabilitation etc.) or associated with environmental assessment of various mining proposals (see references above). Abbott (1999) compiled a comprehensive list of avifauna recorded from the forests of south-west WA in the period 1840 to 1998, however, no such reviews have been carried out for the herpetofauna of the forests of south-west WA.

In the process of assessing the native fauna response to fox baiting and the factors determining patterns of occurrence, the current project was able to partially address the lack of quantified available data on fauna occurrence from the northern jarrah forest, at least for non-volant terrestrial mammals and reptiles (see Chapter 5 and Appendix 1).

2.1.6 Land use and land tenure

The study area encompassed a range of land uses, with a large component of the study area within multiple use state forest managed for native timber production and plantation forestry. Other tenures included timber reserves, conservation estate, reserves declared under various sections of the *Conservation and Land Management Act, 1985* (CALM Act), and private property. There is also a large component of the study area within the Lane Poole Reserve or areas proposed as additions to Lane Poole Reserve. Lane Poole Reserve is comprised of various smaller reserves, with vesting either as Conservation Park or in accordance with Section 5(1)(g) of the CALM Act. Irrespective of the vesting of Lane Poole Reserve, it is managed primarily for conservation and recreation purposes.

2.1.7 Timber harvesting and associated activities

Where the purpose and/or vesting of crown estate in WA includes management for timber production purposes, such management is required to be carried out in accordance with the relevant planning instruments which include WA Forest Management Plan (FMP) (Conservation Commission of Western Australia, 2004), the WA RFA, the EPBC Act and various regulations of the CALM Act and the WA *Wildlife Conservation Act, 1950*.

Timber harvesting has historically occurred, and continues to occur, over much of the northern jarrah forest. Therefore, the study area is subject to disturbance from harvesting and from the suite of activities associated with historic and contemporary timber harvesting. Site selection for the trapping grids established for this study incorporated areas with a range of timber harvesting histories.

2.1.8 Fire

As is the case for timber harvesting practices, the northern jarrah forest study area has been subject to a range of historic and contemporary fire management regimes. The objectives of this research did not include a component to specifically examine the effect of fire management regimes or timber harvesting practices on native fauna. However, as with timber harvesting, site selection for the trapping grids established for this study incorporated areas with a range of fire histories. This aspect is discussed in Chapter 5.

2.1.9 Mining

The extreme laterisation process and resultant hydrated aluminium oxide ore, or bauxite (see section 2.1.3), has led to the granting of extensive mining leases, usually operating in accordance with a specific State Agreement Act. Mining activities are currently carried out by Alcoa World Alumina, Australia (Alcoa) and Worsley Alumina Pty Ltd (Worsley). The study sites were selected to ensure they were not within recently mined areas or within recently rehabilitated former mining areas, nor within areas proposed for mining or proposed for preparation for mining, within the study period.

2.1.10 Dieback

Dieback, or the soil borne plant root pathogen *Phytophthora cinnamomi*, poses a significant disease threat to many genera and species of plant within south-west WA. Although there are several known species of *Phytophthora*, *P. cinnamomi* is considered the most threatening to biodiversity and timber production values (Conservation Commission of Western Australia, 2004). Dieback is spread primarily as a result of movement of moist soil and plant material and its pattern of spread is closely related to the pattern of human use.

The effect of dieback is extremely varied. Detrimental effects are most pronounced on the genera and species from the plant families Proteaceae, Dilleniaceae, Epacridaceae and Xanthorrhoeaceae. Infection can result in localised loss of the entire suite of susceptible species. Infection and spread of dieback have the potential to result in loss of particular habitat types and/or vegetation communities and can significantly influence the pattern of distribution and abundance of fauna.

Management strategies to minimise the potential of its spread include restricting access to areas known to be free of dieback. As a consequence, there are large expanses of the northern jarrah forest designated, in accordance with Section 82 of the CALM Act, as Disease Risk Areas (DRA or dieback free). Site selection for trapping grids established for this study incorporated use of areas within and outside DRA.

2.2 The experimental treatments

The study area was comprised of four treatments or treatment groups: three baited treatments (or a single baited treatment at three different levels) and an unbaited treatment. The three baited treatment groups were aerially baited with dried meat baits. Each bait contained 4.5mg of 1080 (see Chapter 1) and each baited treatment group received baits at an intensity of 5 baits/km^2 but differed in the frequency of baiting. The baiting frequencies were two baitings per year within the northern most baited treatment of 221,400ha; four baitings per year within the central baited treatment of 130,400ha; and six baitings year within the southern baited treatment of 88,600ha. The unbaited treatment group had an area of 103,500ha (Fig. 2.5).

Aerial delivery of baits is described by Armstrong (2004). There was a 'stand-off' zone of 500m from neighbouring properties at the perimeter of the aerially baited forest. Supplementary baiting of this 'stand-off' zone or perimeter, i.e. at the interface with agricultural land, was carried out at the same intensity and at the same time as the aerial baiting. Baiting of these areas was through conventional, vehicle-based bait delivery.

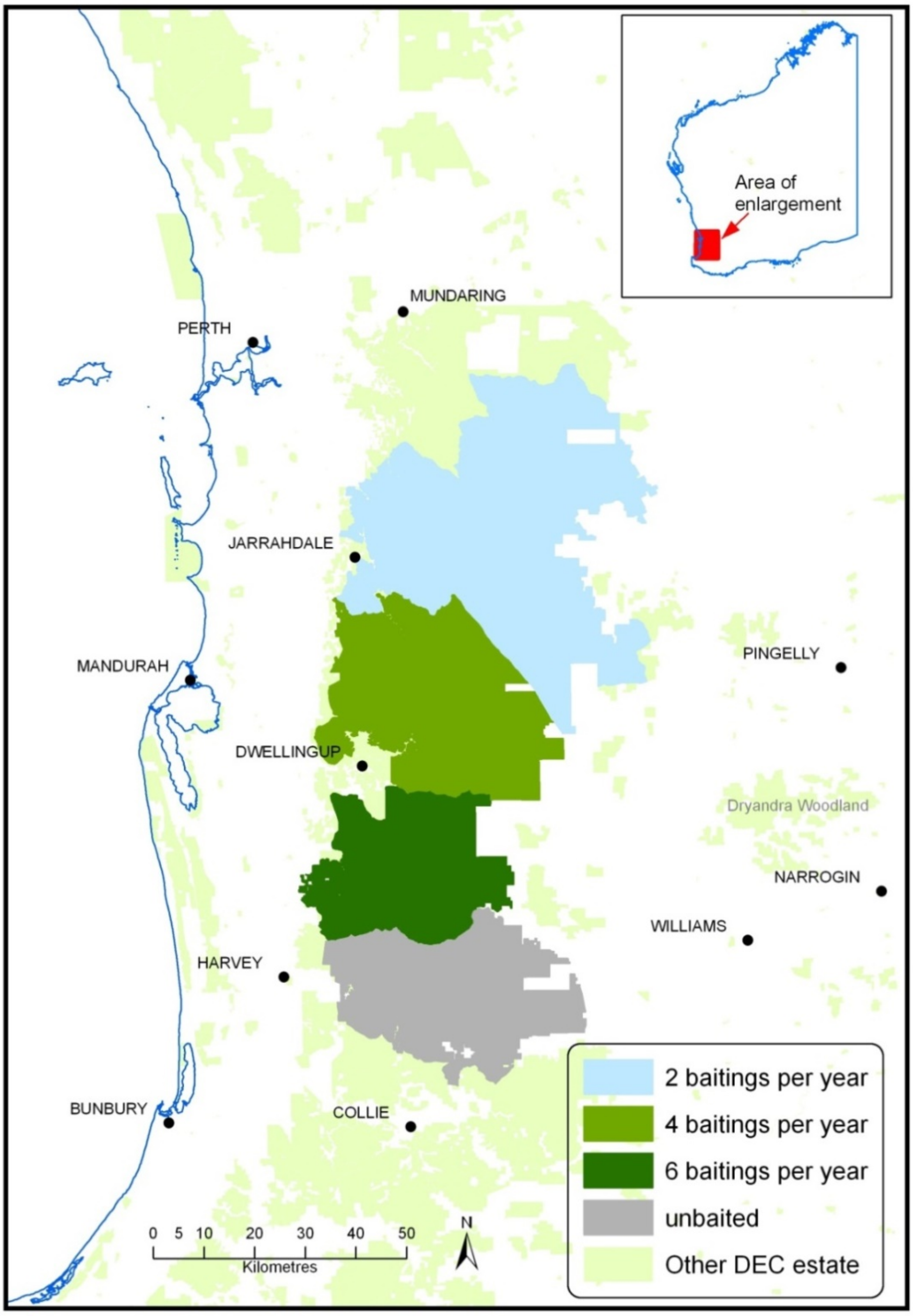

Figure 2.5 The Operation Foxglove baited treatments and unbaited control, south-west Western Australia.

1080 baiting for fox (*Vulpes vulpes*) control was implemented at a baiting intensity of five baits/km^2 within each baited treatment. Each treatment area was subject to a different baiting frequency (two, four or six baitings per year).

All aerial and supplementary baiting was carried out in March and September (for the two baitings per year treatment group), January, March, May, and September (for the four baitings per year treatment group) and January, March, May, July, September and November (for the six baitings per year treatment group). Aerial baiting commenced in July 1994 in the four baitings per year treatment group. Commencement of baiting was delayed until January 1995 in the six baitings per year treatment group (see below for description of the originally proposed unbaited treatment). Baiting continued until completion of the research program in 2000.

2.3 Constraints

2.3.1 Lack of replication

The major constraint imposed on the Operation Foxglove research was the inability to replicate at a landscape scale. Replication is often impossible, or even undesirable, when studying very large-scale systems, for example, where gross effects are anticipated and/or where only a ‘rough estimate of effect’ is required and/or when the cost of replication is prohibitive (Hurlbert, 1984). Consequently, ecological research at a landscape scale is usually carried out in the absence of true replication. Such was the case in this study where: (i) there was an anticipated, or predicted gross effect from fox baiting at a landscape scale; (ii) the cost of replication would have been prohibitive; and (iii) there were no sites suitable to plausibly replicate the northern jarrah forest.

Although there were multiple monitoring sites within each treatment and the scale of the experiment resulted in a large spatial separation between monitoring sites, the experimental design, with four treatments (three baited treatment groups and an unbaited group) constituted an un-replicated experiment. The design falls within Hurlbert’s (1984) definition of a pseudoreplicated experiment. This is further discussed below and in Chapter 6 (Section 6.1.5).

2.3.2 The rationale for pseudoreplication and a non-random allocation of treatments and monitoring sites

2.3.2.1 The treatments

Replication of the baited treatments in Operation Foxglove was not only impractical because of the prohibitive cost, but impossible (or non-sensible) because of the unique nature of the study area. Although south-west WA supports additional large tracts of contiguous forest, the biophysical attributes of these areas of contiguous forest are sufficiently different from the northern jarrah forest to be considered unsuitable as replicates. These additional areas of contiguous forest are within a different IBRA Subregion (Fig. 2.1 and Fig 2.2) and differ from the northern jarrah forest in the distribution of annual rainfall, floristic assemblage and vegetation structure. Therefore, the strategy employed was to allocate each baiting treatment over part of the northern jarrah forest.

Some compromise was required when determining the area of each treatment and when allocating the treatments spatially. Consequently, the treatments were of different size and spatial allocation was not random. Compromise was required as:

(i) replication could have been achieved by use of multiple smaller areas instead of the large treatments. However, as the purpose of the study was to assess the native fauna response to different baiting frequencies of 1080 baiting at a landscape scale, use of multiple smaller areas (although meeting the definition of replicated treatments) would not be appropriate;

(ii) although there is a consistent pattern of rainfall across all treatments, with a band of higher rainfall (700 to 1300mm annually) extending in a north-south alignment in the centre each treatment (Fig. 2.3), the northern half of the study area also encompassed large areas of lower rainfall (<700mm annually) and smaller areas of higher rainfall (>1000mm annually) (Fig. 2.3). Two mutually exclusive options were considered to accommodate this. The first was to exclude the area of lower rainfall in the northern half of the study area. The second was to increase the size of the treatment encompassing this area to ensure there were sufficient sampling locations (fauna trapping grids, woylie translocation release sites and fox monitoring sandplot networks) within that treatment to sample areas of relatively high and low rainfall. The second option was adopted as this ensured all treatments encompassed the full west-east extent of the northern jarrah forest and additionally ensured each treatment included areas which abutted agricultural land;

(iii) anecdotal accounts suggested there may be a north-south cline of increasing faunal abundance within the northern jarrah forest. Although there were no known empirical data available to support this, such a cline had the potential to confound interpretation of the results. The implications are that any north-south cline of increasing fauna abundance may be mistakenly interpreted as an effect from 1080 baiting. Therefore, a conservative approach was adopted for allocation of treatments, with the unbaited control allocated as the southern-most treatment group;

(iii) the southern boundary of the unbaited treatment group is nominal only, as the forest area to the south of the unbaited control was also unbaited. Therefore, allocation of the unbaited control as the southern-most treatment, with a common boundary with only one baited treatment, minimised the potential influence from a shadow effect from baiting. Although this could also have been achieved by allocating the unbaited control as the northern most treatment, doing so may have exacerbated any effect (or confounded interpretation) from a north-south cline in faunal abundance, if one does exist;

(iv) allocation of the two baitings per year treatment group to the northern most treatment also minimised the potential for a shadow effect from baiting. However, this did not provide any amelioration to the potential influence of a north-south cline in abundance of native fauna. Allocation of the two baitings per year treatment group as the northern treatment was also a legacy of the original design, see below;

(v) the original design for Operation Foxglove did not include a six baitings per year treatment and incorporated a larger unbaited control than was finally used. This original unbaited control encompassed what became the six baitings per year treatment group and the final unbaited treatment group. The original intent was to incorporate a split control, whereby the northern section of this larger unbaited treatment would subsequently be baited and the entire control used as part of a conventional Before and After Control and Impact (BACI) design (Stewart-Oaten *et al.*, 1986). However, CALM (political) priorities required baiting of the northern half of the proposed split control. This also had potential fauna conservation merit as the area had the largest proportion of vesting in secure conservation estate. Although this subsequently provided the opportunity to incorporate a six baitings per year treatment group, it gave no flexibility with the location of this treatment.

2.3.2.2 The monitoring sites

Monitoring sites were required within each treatment to:

(i) derive estimates of fox abundance within each treatment;
(ii) quantify the probability of woylie survivorship within each treatment group; and
(iii) determine the suite of species present within each treatment group.

The type of monitoring site required for each of the above is described in Table 2.2 and the spatial arrangement of sites is shown in Figure 2.6. Random allocation of monitoring sites within each treatment was impractical as the study area was subject to a range of operational activities including mining, timber harvesting, prescribed burning and road construction associated with these activities. The effects from these activities were unlikely to be the same or constant within and between treatment groups.

Consequently selection of sites within each treatment was subjective and excluded sites in areas subject to mining operations, timber harvesting and prescribed burning during the study period. Notwithstanding the need to maximise the distance between sites and minimise the potential for the loss of site independence, sites were selected to representatively sample areas with a harvesting history ranging from recent harvesting operations (within the past ten years) to long uncut and with a fire history ranging from recently burnt (within the past ten years) to long unburnt.

Monitoring sites were also selected to representatively sample the range of major vegetation types present. The intent was to maximise 'interspersion' as described by Hurlbert (1984). In doing so, this also minimised the influence of site specific differences within treatment groups, akin to Hurlbert's (1984) goal of minimising the differences in 'premanipulation' properties of each treatment. Stewart-Oaten *et al*. (1986) recognised this approach as appropriate as it enabled characterising the differences between locations so the effect of the imposed treatment (in this case the frequency of 1080 baiting) can be identified.

2.4 General methodology

A summary of the general monitoring methodologies and data analyses adopted is shown below (Table 2.2 and Fig. 2.6) and further detailed in the relevant chapters. Chapter 3 describes in detail the methodology to monitor fox and cat activity (sandplot networks) and the analytical technique whereby estimates of abundance were derived from count data. Chapter 4 describes in detail the methodology used to monitor woylie survivorship (radio-telemetry) and the analytical technique used to estimate woylie survivorship for each treatment group. Chapter 5 describes in detail the methodology used to determine the suite of fauna present within each monitoring site (fauna trapping grids) and the analytical technique used to estimate the probability of occurrence of two frequently trapped species (occupancy modelling).

All data were stored in relational databases (Microsoft Access 2003), conforming to principles of database normalisation (Date, 1986).

Table 2.2: The methodology and data analyses adopted for each component of the northern jarrah forest study examining native fauna response to different frequencies of 1080 baiting for control of the introduced red fox (*Vulpes vulpes*).

Component of study	**Monitoring methodology**	**Data analyses**
Fox and cat abundance estimates.	The methodology involved monitoring of spoor (prints, scats and any other visible evidence) left by foxes and cats (and other species) on a network of sandplots established on the unsealed roading around each of the trapping grids and the woylie translocation release grids. Each sandplot network consisted of 25 individual sandplots. There were five sandplot networks established in the larger, two baitings per year treatment group, and four in each of the other treatment groups.	To determine fox abundance, the count data comprised a site-specific value for the number of individual foxes detected each day, at each sandplot network. The number of individual foxes detected was based on the presence or absence of fox spoor at each sandplot within each sandplot network and on the pattern of the plots where activity was and wasn't detected. This resulted in an estimate of the minimum number of foxes known to be alive (MKTBA) and utilised the assumptions of no births or deaths and no immigration or emigration during the 10 days of monitoring at each sandplot network each year. The technique is described in detail in Chapter 3 and was validated through a removal experiment and though use of molecular techniques. To determine cat abundance, the data were count data of the number of sandplots with cat activity, within each sandplot network. For both foxes and cats, a Bayesian modelling approach was adopted to derive abundance estimates from the count data.
Survivorship of translocated populations of the woylie (*Bettongia penicillata*).	The methodology involved translocation of woylies from Dryandra Woodland to 19 release sites within the northern jarrah forest, followed by intensive radio-telemetry monitoring of survivorship. Radio-collars incorporated movement sensitive (mortality) circuitry. There were six woylie translocation release sites within the two baitings per year treatment group, five within the four baitings per year treatment group and four in each of the six baitings per year treatment group and the unbaited treatment group.	Survivorship was analysed using the staggered entry approach and the Known Fate model in Program MARK (White, 2001), with Akaike Information Criterion (AIC), adjusted for small sample size (AICc), to select the models which best describe the data. Candidate models included individual woylie covariates and site specific covariates.

(cont.)

Table 2.2 (… cont.): The methodology and data analyses adopted for each component of the northern jarrah forest study examining native fauna response to different frequencies of 1080 baiting for control of the introduced red fox (*Vulpes vulpes*).

Component of study	**Monitoring methodology**	**Data analyses**
Presence of a suite of *in situ* native species and modelling the variables influencing presence.	The methodology involved conventional trapping at 55 trapping grids established across the treatments and control, conducted seasonally for six consecutive sessions. Trapping grids were comprised of wire cage traps, Elliott Traps and pitfall traps. The wire cage trapping grid was the largest (encompassing 10.24ha) and overlaid the Elliott trapping grid (2.56ha), which in turn overlaid the pitfall trapping grid (0.64ha). There were 16, 14, 13 and 12 integrated trapping grids within each of the two, four and six baitings per year treatment groups and the unbaited treatment group, respectively.	Occupancy modelling (MacKenzie *et al.*, 2006) was used to determine the models which best described the patterns of occurrence.

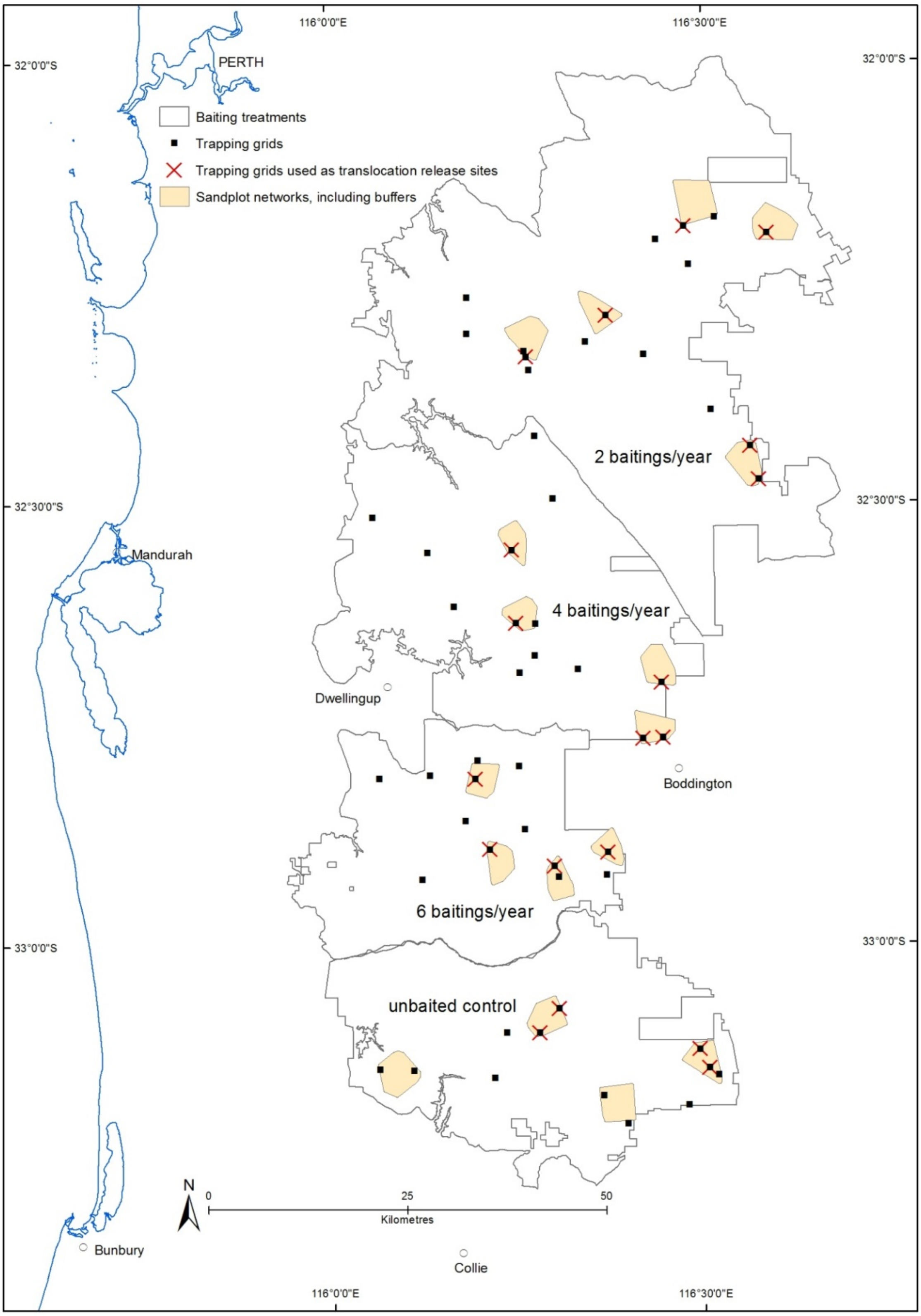

Figure 2.6 The Operation Foxglove treatments and spatial arrangement of the trapping grids, woylie translocation release sites and sandplotting networks.

Specific details are provided in Chapter 3 (sandplots), Chapter 4 (translocation release sites) and Chapter 5 (trapping grids).

2.5 Statistical methods

2.5.1 Overview

Ecological studies have historically relied on null hypothesis testing, or 'significance' testing, to determine the importance of imposed treatments and differences in population responses to site specific and other variables. The perception of 'significance' is invariably based on an arbitrarily defined level of effect, i.e. an α level or *P*-value (Anderson *et al.*, 2000; Borchers *et al.*, 2002; Burnham and Anderson, 2001; 2002; Williams *et al.*, 2002). If found to be significant, this arbitrary level of effect may, or may not, have biological meaning. A *P*-value has limited use when trying to draw inference, as it is simply the probability of obtaining a test statistic as extreme as, or more extreme than, the observed value on repeated sampling of the data, given the null hypothesis is true (Anderson *et al.*, 2000; Howson and Urbach, 1991; Wade, 2000). Importantly 'a *P*-value is not a measure of strength of evidence' (Anderson, 2007). Among statisticians, the controversy over null hypothesis testing had started by the late 1930s (Anderson, 2003a) and recent opinion expressed in the theoretical and applied ecological literature indicates there is decreasing support for an excessive or total reliance on null hypothesis testing and *P*-values (Anderson *et al.*, 2000; Borchers *et al.*, 2002; Burnham and Anderson, 2001; 2002; Johnson, 2002; Robinson and Wainer, 2002; Williams *et al.*, 2002). Of more importance to biologists is estimating the effect size, or the magnitude of any differences, and determining if the difference(s) are biologically meaningful (Anderson *et al.*, 2000).

2.5.2 The information-theoretic approach

The information-theoretic approach is a model formulation, model selection and inference approach. It is based on the premise that models are formulated from *"good data, relevant to the issue* … [and have been] *collected in an appropriate manner"* (Burnham and Anderson, 2001). It is a means by which conclusions can be drawn from modelling population parameters based on the observed data (MacKenzie *et al.*, 2006), provided those models have good support from the data. The information-theoretic approach has its basis in likelihood theory and although often described as a new paradigm for ecologists (Burnham and Anderson, 2001), its principles stem from Boltzmann's (1877 as cited by Burnham and Anderson, 2002) concept of generalised entropy, Kullback and Leibler's (1959 as cited by Burnham and Anderson, 2002) 'distance' or 'information lost' between models and on the relationship between likelihood and log-likelihood functions and Kullback-Leibler 'information' (Akaike 1973 & 1974 as cited by Burnham and Anderson, 2002).

2.5.3 The likelihood function and the Maximum Likelihood Estimate

The information-theoretic approach is based on the likelihood function, or for most purposes, the natural logarithm of the likelihood function. The convention for expressing this likelihood is that it is the likelihood of a particular numerical value (the estimate) of a parameter of interest, given the data available. This way of expressing the likelihood reverses the emphasis of the probability density function. The probability density function is a function of the unknown data (y), given the population parameters (θ, ϕ), whereas the likelihood is a function of unknown population parameters, given the data. The probability density function is expressed as:

$$\mathrm{f}\,(y;\theta,\phi)=\prod_{i=1}^{n}\mathrm{f}\,(y_i;\theta,\phi)$$

whereas, the likelihood $(\mathrm{Ł})$ function is expressed as:

$$\mathrm{Ł}(\theta,\phi;y)=\prod_{i=1}^{n}\mathrm{f}\,(\theta,\phi;y_i)$$ (Hardin and Hilbe, 2007).

The right hand side of the equations are equivalent, with both the probability density function and the likelihood function given as the product of the probabilities. However, this assumes the data (i.e. the observations) are independent and identically distributed (i.i.d.). In the absence of this assumption, the likelihood function is proportional to the joint probability density function, i.e.:

$$\mathrm{L}(\theta,\phi;\mathrm{y}_i)\propto f(y_i;\theta,\phi)$$

Importantly, the likelihood function gives the relative likelihoods for different values of the parameter θ, given the data (y) and the model (g). The generic way of expressing this is:

$$\mathrm{Ł}\ (\theta;\ y,\ \mathrm{g}) \qquad \text{or} \qquad \mathrm{Ł}\ (\theta;\ data,\ \mathrm{model}).$$

The strength of this approach is that it is possible to identify which value of θ is most likely, given the data and the model. This estimated value ($\hat{\theta}$) is found when the likelihood function achieves its maximum value and it is termed the maximum likelihood estimate (MLE). Although the value is the same in the likelihood and the log likelihood functions, it is more easily determined by maximising the log-likelihood function (often described as a model, or conditioned on a model) than by maximising the likelihood function (Borchers *et al.*, 2002). The log-likelihood function is usually expressed as:

$$\log(L(\theta_1, \theta_2, \ldots \theta_n,; \mathit{data}, \text{model}))$$

where θ_1 to θ_n are the parameters of interest and may represent years, groups, cohorts etc. and can be multinomial. As a result of this log transformation the function becomes additive, not multiplicative (Gould *et al.*, 2006).

The MLE of θ $(\hat{\theta})$ is recognised as a simple, compelling concept as it has an approximately normally distribution for large sample sizes and the expected value $\hat{\theta}$ converges with θ as the sample size increases (Williams *et al.*, 2002). Additionally, it is usually asymptotically unbiased as the sample size increases (Borchers *et al.*, 2002; Burnham and Anderson, 2002; MacKenzie *et al.*, 2006; White, 2006; Williams *et al.*, 2002).

2.5.4 Kullback-Leibler information

Kullback-Leibler (K-L) information is a measure of *'I'*, the 'information', or the information lost, or the 'distance' between true reality and an approximating model *'g'*. When formulating any approximating model, the intent is to minimise the information lost (Burnham and Anderson, 2002). To measure this requires knowledge of full reality, or truth, usually identified by the notation f.

Although there can be no model for 'truth' (f), as it would likely require an infinite number of variables, the concept of 'truth' provides a framework in which to compare f with a suite of approximating models, $g_{i\text{-}n}$. In a model selection framework, what is required, assuming full reality is not modelled (and never can be modelled) is the relative distance between models, or the relative difference in the amount of K-L information lost. Burnham and Anderson (2002) eloquently describe how this is achieved and how we can consider truth as a constant and therefore *"Truth, f, Drops Out as a Constant"* (Burnham and Anderson, 2002, p58). Therefore, there is no requirement to have full reality, or truth, as one of the candidate models.

Again, citing Burnham and Anderson (2002, p54) *"The K-L distance between models is a* fundamental quantity *in science and information theory … and is the logical basis for model selection in conjunction with likelihood inference"*.

2.5.5 Akaike and AIC, AICc and QAIC

Hirotugu Akaike (1973) determined a way to estimate the K-L information lost, based on the estimate of θ ($\hat{\theta}$). This estimate is the minimum 'expected estimate' of the relative K-L distance (Burnham and Anderson, 2002). However, Akaike found the estimate is biased when used as a model selection tool, with the bias approximately equal to the number of estimable parameters (*K*) in the approximating model (Burnham and Anderson, 2002). The criterion developed by Akaike, incorporating this correction, is known as the Akaike Information Criterion (AIC) which is given by:

$$\text{AIC}_i = -2 \log (\text{L}(\hat{\theta}_i | y_i)) + 2\text{K}_i$$

where log $(\text{L}(\hat{\theta}_i | y_i))$ is the log likelihood at its maximum point and *K* is the number of estimable parameters in the approximating model (Burnham and Anderson, 2002). This results in an increasing penalty, in terms of the AIC value, when an increased number of parameters is estimated.

Where the sample size is small, a second order bias adjustment of AIC (AICc) is used. The second order adjustment AICc is recommended when the ratio of the sample size (n) to the number of estimable parameters (K) is less than 40 (Burnham and Anderson, 2002). AICc is given as:

$$\text{AICci} = \text{AICi} + 2\text{Ki}(\text{Ki}{+}1)$$

Where used as a model selection tool, lower AIC or AICc values indicate models which better describe the data (Burnham and Anderson, 2002), i.e. they appear closer to the truth. The model considered 'best' has the lowest AIC (or AICc) value, with:

$$\Delta i \equiv \text{AIC}_{lowest} \equiv 0$$

Models with a difference in AIC (ΔAIC) of less than 2 from the 'best' model are considered to equally well describe the data and therefore have equal support. Models with a ΔAIC of 4 to 7 from the highest ranked model have considerably less support and models with a ΔAIC of 10 or more have essentially no support (Burnham and Anderson, 2002).

However, the variance derived from count data (e.g. for parameters such as $\hat{p}$ and $\hat{n}$) does not always conform with the variance assumptions of the underlying models (Burnham and Anderson, 2002). Where the sampling variance is greater than the theoretical model variance, the data are termed ‘overdispersed’ (Burnham and Anderson, 2002), i.e. there is greater variability in the collected data than expected from the statistical model. Although the estimate of the parameters of interest (e.g. $\hat{p}$ or $\hat{n}$) will often remain unaffected by this overdispersion, the precision will be overestimated (McCullagh and Nelder 1989, as cited by Burnham and Anderson, 2002). In some cases this may reflect poor model choice (i.e. a different family of models may better fit the data) and it may be addressed by using an alternative to the Poisson model, e.g. a negative binomial.

Where there is no evidence to suggest a different family of model from Poisson, the approach adopted using AIC is to estimate a dispersion parameter, or variance inflation factor. The variance inflation factor (c) can be estimated $(\hat{c})$ from the goodness of fit (GOF) χ^2 statistic and the degrees of freedom from the global model (the most parameterised model from the set of biological meaningful candidate models), where:

$\hat{c} = \chi^2/df$ (Burnham and Anderson, 2002)

This adjustment term, $\hat{c}$, is called a quasi-likelihood adjustment and is recommended only when a lack of model fit has been identified. Where a quasi-likelihood adjustment term (variance inflation factor) has been used, the number of parameters counted in the AIC must allow for the extra parameter (the $\hat{c}$ parameter). The AIC then becomes QAIC, which is given as:

$$\mathrm{QAIC} = \text{-}\ [2\ \log\ (\mathrm{L}(\hat{\theta}))/(\hat{c})] + 2\mathrm{K}$$

and QAICc is given as:

$$\mathrm{QAICc} = \mathrm{QAIC} + \frac{2K(K+1)}{n-K-1}$$ (Burnham and Anderson, 2002).

When there is no GOF test available for a particular model, as was the case for the ‘Known Fate’ model from program MARK (White, 2001) used to assess survivorship of woylies (Chapter 4), and for occupancy modelling (Chapter 5), it is possible to examine the effect of a range of values for $\hat{c}$ and assess their effect on the model outcomes (model ordering) (Gary White[6], pers. comm.). Where the ranking of models changes significantly with small increments in the value of $\hat{c}$, an adjustment of $\hat{c}$ may be required. This adjustment is considered acceptable if the adjusted value is ≤ 4. Values of $\hat{c} > 4$ indicate some structural lack of fit of the model (Burnham and Anderson, 2002). This is further described in Chapter 4.

2.5.6 Model weights and model averaging

The process of formulating a set candidate of models relies on the premise that models within the candidate set are plausible to begin with and/or are testing a particular hypothesis. However, the process of ranking models based on AIC, AICc, QAIC or QAICc alone does not necessarily address the issue of model uncertainty. Where no one model is clearly preferred, conditional inference, i.e. conditional on only one particular model, is not wise (Burnham and Anderson, 2002). Multi-model inference and model averaging incorporate the principle of using a weight of evidence (w_i) and the conditional sampling variance $(\mathrm{var}\left(\hat{\theta} \mid x, g_i\right))$ for any given model (g_i) to enable unconditional inference from the entire set of models (Burnham and Anderson, 2002).

This weighting is given by:

$$\omega_i = \frac{exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R} exp(-\frac{1}{2}\Delta_i)}$$

where Δ_i is the difference in AIC values

The relative weight of evidence of model *i* versus model *j* is the ratio $\frac{w_i}{w_j}$. However, model weights based on this ratio will change as models are added, or removed from, the confidence set. Alternatively, use of a cut-off value for Δ_i based on the relative likelihoods (i.e. $\mathrm{L}(g_i|x)/\mathrm{L}(g_{min}|x)$, usually expressed as $\mathrm{L}(g_i|x)$) will remain constant as the confidence set varies. Burnham and Anderson (2002) advocate use of a cut-off

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value, provided this value is small. Further, Burnham and Anderson (2002) imply cut-off values of 0.135, 0.082 or 0.050 are appropriate. These values correspond to a Δ_i of 4, 5 and 6, respectively.

2.5.7 Limitations of the Information-Theoretic approach

Use of the information-theoretic approach has gained considerable support since the publication of Burnham and Anderson's texts (i.e. Burnham and Anderson, 1998; 2002) (Richards, 2005). The information-theoretic approach is recognised to have many advantages over null hypothesis testing and is seen by many as the most appropriate way to analyse most ecological datasets (Johnson and Omland, 2004; Stephens *et al.*, 2005). Guthery *et al.* (2005) observed the percentage of papers published in *The Journal of Wildlife Management*, and adopting the information-theoretic approach for data analysis, rose from approximately 6% in 1999 to approximately 20% in 2003/2004.

The rationale for use of information-theoretic techniques is often based on perceived inadequacies of conventional null hypothesis testing, however, many of criticisms of null hypothesis testing also apply to the information-theoretic approach (Guthery *et al.*, 2001; Guthery *et al.*, 2005; Stephens *et al.*, 2005). For example, both approaches are subject to *"sloppy implementation, poor reporting … and incorrect implementation"* (Stephens *et al.*, 2005) and a failure to verify or validate underlying assumptions (Guthery *et al.*, 2005).

Criticisms specific to the information-theoretic approach include: (i) there are often too many models in the candidate model set; (ii) the candidate model set may include implausible models; (iii) AIC selects for models that over fit; and (iv) addition of a 'useless' variable may result in the larger model (the model with one more parameter) being within 2 AIC from the less parameterised model and therefore considered competitive (Guthery *et al.*, 2005; Link and Barker, 2006). Interestingly, each of these criticisms has been addressed and refuted in the literature, and the appropriate methodology explained to avoid these perceived weaknesses in the information-theoretic approach (see for example Anderson and Burnham, 2002; Anderson *et al.*, 2000; Burnham and Anderson, 1998; 2002).

The use of too many models may indicate a lack of understanding of the system being studied and may result in inclusion of implausible models. When formulating the set of candidate models, only those models which make biological sense should be included. This can be achieved through consideration of accepted theory, expert background knowledge and prior information (Burnham and Anderson, 2002). It is also well documented that when formulating models, care should be taken to avoid generating so many models that spurious findings become likely and to avoid including models where functional relationships between variables are uninterpretable (Johnson and Omland, 2004).

The criticism that AIC selects for models that over fit (see for example Link and Barker, 2006; Wang and Liu, 2006; Wintle *et al.*, 2003) *"has been known for decades"* (Burnham and Anderson, undated) and it is well documented that AICc does not have this tendency (Burnham and Anderson, 1998; 2002; Johnson and Omland, 2004), despite the assertions of some authors (see for example Richards, 2005). Further, AICc and AIC converge as the ratio of n (sample size) to K (number of parameters) increases.

The inclusion of a "useless" variable (Guthery *et al.*, 2005) has also been clearly addressed in the literature. Models within 2 units of the best model (i.e. ΔAICc of 2 or less) and varying from the preferred model by the inclusion of only one additional (useless) variable, have effectively no support. The larger model only appears to be competitive because it is structurally similar to the smaller model, adds only one parameter but does not improve the AICc value (Burnham and Anderson, 2002). It should not be considered competitive and should not be included in model averaging.

2.5.8 Alternative modelling methods; Bayesian modelling and use of Bayes Factors

Bayes Theorem was published through chance. It was sent to the Royal Society in London by a friend of Bayes two years after Bayes' death and published posthumously in 1763 in the Society's *Philosophical Transactions* (Bryson, 2010). It was described as having the *"unassuming"* title, '*An Essay Towards Solving a Problem in the Doctrine of Chance*' (Bryson, 2010; Howson and Urbach, 1991). Bayes Theorem, or more specifically, Bayesian statistical inference *"provides an alternative way to analyse data* … [and remedy] *many of the problems inherent in standard* [null] *hypothesis testing"* (Wade, 2000). Both Bayesian and information-theoretic approaches differ from conventional statistical analyses as they estimate a parameter's value, given the observed data, whereas null hypothesis testing (or frequentist statistics) calculates the probability of observing the data when the model and a value for the parameter(s) of interest are specified (Ellison, 1996; 2004; Howson and Urbach, 1991; Wade, 2000) (see Section 2.5.3, above).

A major difference between Bayesian methods and the information-theoretic approach is that the Bayesian approach specifies what is known before the data are analysed (known as a ‘prior’, or ‘prior distribution’) and this ‘prior’ is combined with the data to give a ‘posterior’ distribution. Therefore, the prior distribution is the probability distribution for the parameter of interest ‘prior’ to consideration of the data, i.e. a value specified from a distribution of probabilities over the range of all possible values for that parameter (Ellison, 2004; Howson and Urbach, 1991; Wade, 2000). The posterior probability is the probability distribution after consideration of the prior distribution and the data (Howson and Urbach, 1991; Wade, 2000). By adopting this approach, the posterior model gives a probability distribution of the model parameters conditional on the observed data and some prior knowledge. It therefore has two components: a likelihood component (which includes information about model parameters based on the observed data); and a prior information component (with information about model parameters before observing the data). The likelihood and prior models are combined using the Bayes rule to produce the posterior distribution:

$$\textit{Posterior} \propto \textit{Likelihood x Prior}$$

In most cases (when the integration is not easily analytically obtained) this posterior distribution needs to be estimated via simulations. Although the exact posterior distribution for any parameter of interest is usually not known, general posterior distributions can be estimated. This is most commonly achieved through use of Markov chain Monte Carlo (MCMC) sampling. Bayesian inference is based on the posterior distribution of the parameters and provides summaries of this distribution including posterior means and their Monte Carlo standard errors (MCSE) as well as credible intervals.

MCMC methods for simulating Bayesian models are often demanding in terms of computing power when specifying an efficient sampling algorithm and verifying the convergence of the algorithm to the desired posterior distribution. Although contemporary computers have made the issue of computing power largely irrelevant, verifying algorithm convergence is still necessary and should be established before proceeding to inference (StataCorp, 2017). Importantly, *“inference based on an MCMC sample is valid only if the Markov chain has converged and the sample is drawn from the desired posterior distribution”* (StataCorp, 2017). Methods for verifying convergence include, but are not limited to, examining the mixing (by visual inspection of the trace plots) and time trends within the chains of individual parameters. The trace plot of any parameter plots the simulated values for that parameter against the iteration number. A trace plot of a well-mixing parameter should traverse the posterior domain rapidly. For any parameter, when this range is traversed rapidly by the MCMC chain, the drawn lines look almost vertical and dense (examples are given in Chapter 3). Sparseness or trends in this trace plot of a parameter suggest convergence problems.

Other diagnostics which can be visually examined for each parameter include the autocorrelation plot, histogram and a kernel density estimate overlaid with densities estimated using the first and the second halves of the MCMC sample. The extent of autocorrelation and lag time can also indicate how well the algorithm has converged. Although autocorrelation is usually present in any MCMC sample, the autocorrelation plot shows the degree of autocorrelation in an MCMC sample for a range of lags, starting from lag 0 (i.e. the commencement of the chain). Autocorrelation starts from some positive value for lag 0 and decreases toward zero as the lag index increases. For a well-mixing MCMC chain, autocorrelation dies off fairly rapidly. High efficiency means good mixing (low autocorrelation) in the MCMC sample, and low efficiency means bad mixing (high autocorrelation) in the MCMC sample. Plotting the histogram depicts the general shape of the marginal posterior distribution of a model parameter and can therefore be used to compare the empirical posterior and the specified prior distributions. Additionally, if the histogram is unimodal, it also indicates a good simulation of the marginal posterior distribution.

Kernel density plots provide an alternative way to visualise the simulated marginal posterior distributions. In Stata (StataCorp, 2017), the default, when examining this graphic shows three density curves: an overall density of the entire MCMC sample; the first-half density obtained using the first half of the MCMC sample; and the second-half density obtained using the second half of the MCMC sample. If the chain has converged and mixes well, these three density curves will be close to each other. Large discrepancies between the first-half curve and the second-half curve are indicative of convergence problems.

Non-visual diagnostics include examination of the acceptance rate and summaries of the effective sample sizes (ESS), correlation times and efficiencies. Examples of these and the visual diagnostics are provided in Chapter 3, where a Bayesian modelling approach was adopted to estimate the number of foxes and cats present at various sites within the study area.

With the Bayesian approach, model selection (selection of the 'best' posterior model) is possible through AIC (or AIC_c) or through use of the Bayesian Information Criterion (BIC), where models with more support have lower AIC (or AIC_c) and BIC values. Alternative criteria used for model selection include the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002) where DIC is the posterior mean of the deviance plus the effective number of parameters in the model (Ellison, 2004; Spiegelhalter *et al.*, 2002). Each of these three criteria (AIC, BIC and DIC) incorporates a penalty term for increased model complexity. For AIC, as described above (Section 2.5.5 and Section 2.5.7) the penalty term is two times the number of parameters and AIC_c also includes an adjustment term and is recommended when the ratio of the sample size (n) to the number of estimable parameters (K) is less than 40 (Burnham and Anderson, 2002). The penalty term in BIC is the product of the number of parameters and the log of the sample size. It therefore increases with an increase in either or both. The penalty term in DIC is similar to the uncorrected AIC (i.e. not AIC_c) and is based on a term which measures the difference between the expected log likelihood and the log likelihood at the posterior mean point (StataCorp, 2017). Although DIC is designed specifically for Bayesian estimation involving Markov chain Monte Carlo methods (MCMC), Bayes Factors (or BFs) are preferred for model selection as they incorporate information about model priors (StataCorp, 2017).

The BF for two models is the ratio of their marginal likelihoods, calculated when using the same dataset (StataCorp, 2017). Various interpretations have been proposed for use of BFs in model selection (see for example Jeffreys, 1961; Kass and Raftery, 1995). Jeffreys (1961) proposed interpretation of BFs based on half units of the $\log_{10}$ scale (Table 2.3). This is further discussed in Chapter 3 where the criteria used for interpretation and model selection described by Kass and Raftery (1995) is adopted.

Table 2.3: The criteria and interpretation of Bayes Factors (BFs) proposed by Jeffreys (1961) for Bayesian model selection, pooling two of Jeffreys (1961) categories together for simplification.

BF = Bayes Factor. Typically, the worst fitting model (i.e. the model with the lowest BF) is used as the base model. In this case BFj is the Bayes Factor for Model Mj with respect to model Mb (the base model).

BF_{jb}	$\log_{10}(BF_{jb})$	Evidence against model M_b
1 to 3.2	0 to ½	Not worth more than a bare mention
3.2 to 10	½ to 1	Substantial
10 to 100	1 to 2	Strong
>100	>2	Decisive

Use of ‘prior’ knowledge, or beliefs, has been seen as both a strength and weakness of the Bayesian approach (Wintle *et al.*, 2003). Incorporating existing (prior) knowledge is intuitively attractive and allows this knowledge to be combined with new sample data in an adaptive management framework (Ellison, 1996; 2004). However, this specification of prior distributions is often arbitrary and/or subjective (Burnham and Anderson, 2002; Burnham and Anderson, undated; Ellison, 1996) and this can dominate the posterior and lead to invalid inference. However, where the evidence from the data is compelling, the prior will have little effect on the posterior (Wintle *et al.*, 2003). Nonetheless, the Bayesian approach requires specification of prior distributions even in the absence of this information. In these circumstances priors can be specified as ‘non-informative’ and reflect prior ‘ignorance’ (Ellison, 2004) of parameter values, i.e. priors are specified with the distribution centred on zero, are uniform over the range of the data, and any value for a given parameter is equally likely (Ellison, 2004; Wade, 2000; Wintle *et al.*, 2003).

Model averaging is also possible, and recommended, when adopting a Bayesian approach. Model averaging is similar to that for the information-theoretic approach described by Burnham and Anderson (2002) and may also include alternatives such as an ‘Occam’s Window’ approach to identify a reduced set of models over which model averaging can then be applied (Madigan and Raftery, 1994; Raftery *et al.*, 1997).

Bayesian methods also differ from information-theoretic through the assumption that one of the models within the candidate model set describes truth, or full reality. Link and Barker (2006) argue the Bayesian approach provides a wider framework for multi-model inference than the information-theoretic approach. They claim that *“… whether ‘truth is in the model set’ ought to be laid aside as an irrelevancy …”*. Conversely, Burnham and Anderson (2002) and Burnham and Anderson (undated) claim this is a *“buried”* assumption and, as it is an assumption for prior and posterior distributions, is theoretically *“deep”* and needs to be addressed. Nonetheless, Burnham and Anderson (undated) noted *“the fact that the information-theoretic approaches represent a simple alternative does not diminish the value of the complex and computer intensive Bayesian methods”*.

Bayesian modelling has also been shown to select for under fitting models (models with fewer parameters) when sample sizes are not large and modelling can require computer intensive methods, e.g. Markov chain Monte Carlo methods which can be slow to converge and require extremely long runs (Wintle *et al.*, 2003), although, as noted above, contemporary computers have made the argument of computer power almost irrelevant. An important distinction between information-theoretic and Bayesian approaches is that, as the name suggests, AIC values are derived from the amount of Kullback-Leibler information lost and the information-theoretic approach is based on well-founded information theory (see Section 2.5.3, above). The Bayesian approach and BIC, despite the name, are not derived from or related to information theory (Burnham and Anderson, undated).

Despite the controversy in the scientific literature over the relative merits of the information-theoretic and Bayesian approaches, there appears to be consensus as to the limitations of null hypothesis testing and the advantages of multi-model, or multi-hypothesis testing through use of information-theoretic and Bayesian approaches (Ellison, 2004; Wade, 2000). Further, if a proper experimental design and protocols are used, and only biologically plausible models compared, we might hope to select a model, whether it be through information-theoretic or Bayesian approaches, which partially represents truth (Burnham and Anderson, 2002; Burnham and Anderson, undated).

Chapter 3

Bayesian modelling to estimate fox and cat abundance

3.1 Overview

Fauna conservation managers require some mechanism to assess whether management actions are having the intended or desired outcome(s). This is usually based on some metric of population size for the species which is being 'managed'. In Australia, fox control for fauna conservation purposes is aimed at reducing fox numbers for the desired outcome of protection of the native species preyed upon by foxes. Approaches aimed at determining whether any adopted fox control program is effective have been based on a measured response of the native fauna which managers are attempting to protect. This assessment is almost invariably carried out by monitoring the abundance (or some surrogate which managers believe reflects abundance) of the native fauna protected. This approach assumes, among a suite of other assumptions:

- the technique adopted to measure native fauna is in fact a measure of abundance; and
- there is a cause and effect relationship between the implementation of fox control programs and any increase (or absence of increase) in native fauna abundance.

Equally importantly, it assumes fox control is ineffective if there is no detectable native fauna response. This may overlook the fact that fox control may have been effective (in terms of a reduction of fox numbers), but there has been an absence of a fauna response for some other reason. This absence of a fauna response may be attributable to a suite of possible causes, including predation by predators other than foxes and in particular, predation by feral cats, or because fox predation was not limiting abundance.

Much of the conservation estate within WA, and in south-west WA in particular, is baited with 1080 baits for the control of foxes. However, despite the high national and international profile of WA's Western Shield program, and despite previous recommendations to incorporate a component of monitoring to assess fox abundance (see for example Caughley and Gunn, 1996; Hone, 1999), the Western Shield program does not monitor fox abundance. Similarly, there is no monitoring of the sympatric mesopredator, the feral cat. At best, monitoring of foxes relies on the use of indices which are then used to infer abundance.

There is sufficient scepticism in the scientific literature regarding the value of indices to make reliable inference on predator abundance. Indices to predator abundance are commonly derived from track counts which reflect predator activity, not abundance (Krebs, 2018). Consequently, indices may be unreliable unless: (i) the index is validated to ensure it reflects abundance; and (ii) this validation is carried out in the environment in which the method is to be applied.

This chapter highlights why there is a need to develop and adopt quantitative measures as an alternative to indices to assess fox and cat abundance within areas managed for conservation purposes and baited for fox control. It also describes the methodology developed for, and adopted within, the northern jarrah forest study.

To justify the approach used in this study and quantify the effectiveness of fox control in terms of a reduction in fox abundance, required:

(i) *a review of the value of indices which have been widely used to infer fox and cat abundance; and*
(ii) *development of a methodology from which inference can be made about fox abundance; and*
(iii) *validation of the methodology adopted; and*
(iv) *application of this methodology at a landscape scale.*

The methodology adopted for estimating fox abundance from raw count data was based on the pattern of activity, or contagion, on sandplots at which fox spoor was detected. In doing so, the technique derived a day-10 estimate of the minimum number of foxes known to be alive (MKTBA) for each of 17 sandplot networks each year. There was no *a priori* assumption that the number of fox prints observed was correlated with the number of foxes responsible for leaving the prints, nor was there an *a priori* assumption that the number of sandplots with fox prints was related to the number of foxes present.

The MKTBA data were modelled using a Bayesian modelling approach and model averaging to determine which model(s) from a candidate set best described the data each year. Model selection for model averaging was based on the criteria proposed by Kass and Raftery (1995) (see methodology, this chapter). The data were analysed for three consecutive years. For year 1, the candidate models were run with informative priors formulated on the basis of published and unpublished research findings on fox control (see Chapter 2 and methodology this chapter). The model averaged mean posterior distributions from year 1 for the model variables of concern were then used as informative priors for year 2. Similarly, the model averaged mean posterior distributions for model variables from year 2 were then used as informative priors for year 3. For each year, the confidence model set (the models used in model averaging) was comprised of only one simple Poisson model (it had most of the model weight), with baiting treatment alone as the explanatory variable. Fox abundance was lowest within the six baitings per year treatment group and increased in the four and two baitings per year treatment groups and the unbaited treatment group. Although there was considerable overlap in the 95% equal-tailed Bayesian credible intervals (95%BCI), the reduction in fox abundance achieved within the six baitings per year treatment group was interpreted as biologically significant.

Sandplot monitoring post 1080 baiting supported the assertion that foxes quickly re-colonise baited sites close to agricultural land, with foxes shown to be present at these sites immediately after baiting. A correlation analysis of the daily MKTBA estimate against the day-10 MKTBA estimate indicated a minimum of six consecutive days of sandplot monitoring is likely required to achieve an estimate of abundance from which inference can be made. The sandplotting technique used to derive the fox MKTBA estimate was validated through a removal experiment and through use of molecular techniques. However, additional refinements are described and recommended if the technique is proposed for further use.

Estimating cat abundance was more problematic with little published data on cat abundance within forest areas and no reliable technique for estimating cat abundance generally. Consequently, cat activity was recorded as presence or no-detected-presence, whereby each event of cat presence detected at a sandplot was inferred as an individual cat. Unlike the fox data, no assumption was made regarding contagion or the pattern of cat activity on sandplots.

There was considerable uncertainty as to the most appropriate class of model for modelling the cat count data; i.e. Poisson, negative binomial (nbreg), zero inflated Poisson (zip) or a zero inflated negative binomial (zinb) model. After preliminary and exploratory modelling, a set of candidate nbreg models was formulated for each year. The data were extremely sparse and only simple models were examined. A Bayesian modelling approach was again adopted and the data from three consecutive years were analysed. Unlike the fox data, default, non-informative priors were used for modelling the year 1 data. As with the fox data, the mean of the year 1 posterior distribution for the model parameters of interest from the preferred model were used as informative priors for year 2. The year 2 mean of the posterior distribution for the model parameters from the preferred year 2 model were then used as informative priors for year 3.

In all years, the only model with any support (in terms of the criteria proposed by Kass and Raftery (1995)) modelled cat abundance without a treatment effect and without any explanatory variables, i.e. cat abundance was constant across all treatments. The results were interpreted as reflecting the combination of the extremely sparse data and the lack of sensitivity of the sandplotting technique to detect cat presence. A revised technique is described and recommended.

3.2 A review of the use of indices

3.2.1 Introduction

Although there has been no quantitative assessment of fox or cat abundance or density within forested areas managed for conservation purposes in WA, anecdotal accounts suggest densities are low in comparison with agricultural and pastoral land. Coarse estimates (guesstimates) of fox density based on the criteria for the categories of high, medium and low density as defined by Wilson *et al.* (1992), suggest the northern jarrah forest supports a low density fox population(s). Estimating abundance or density of foxes [and cats] in a forest environment is recognised as difficult (Saunders *et al.*, 1995), primarily because it is difficult to trap foxes and cats when population density is low. Reported trap success rates for foxes in forest and woodland environments elsewhere in Australia range from one fox capture every 36 trap nights at Jervis Bay, Australian Capital Territory (ACT) and Kosciusko National Park, NSW (Meek *et al.*, 1995) and one every 39.6 trap nights in Kosciusko National Park, NSW (Bubela *et al.*, 1998) to an average of one every 135 trap nights in central western NSW, which fell to one every 315 trap nights in drought conditions (Kay *et al.*, 2000).

In addition to trapping, destructive removal techniques have been used to derive estimates of fox abundance in WA. For example, a fox removal study carried out at Watheroo National Park in the Northern Sand Plain Region of WA (Algar and Kinnear, 1992) demonstrated the potential of lethal cyanide baiting and progressive removal of foxes to derive a catch per unit effort (CPUE) ‘index’ of relative fox density (Algar and Kinnear, 1992; Kinnear, 1991). However, cyanide baiting is a non-selective removal technique and its use in the northern jarrah forest would present considerable risk to non-target species. Fox removal by cyanide baiting would also impose an additional level of fox density reduction, over and above that achieved in each 1080 baited treatment, and therefore confound any analysis of the effect of baiting. Similarly, any other removal technique, such as M-44 ejectors (Busana *et al.*, 1998; van Polanen Petel *et al.*, 2004), would impose an additional level of fox density reduction and also confound interpretation of the effects from 1080 baiting. Therefore, the techniques adopted were required to be non-destructive to ensure there were no confounding effects from additional fox removal within the baited treatment sites and within the unbaited control site.

3.2.2 Indices of activity and the problems when indices are used to infer abundance of foxes and cats

Most non-destructive techniques used to infer abundance or density of canids and, to a lesser extent, felids, have relied on the use of indirect measures. These indirect measures have been widely used to record predator activity and to then infer abundance. Indirect measures result in an index, usually derived from monitoring the activity of each species as determined by the presence of spoor or other evidence of presence. In Australia, the most widely used techniques for deriving indices of activity for foxes, dingoes and dogs are based on monitoring predator activity at 'passive' sandplots (see for example Allen *et al.*, 1996; Engeman, 2005) (see also the methods section of this chapter). The data are usually in the form of track counts. The derived index of activity is often then used synonymously (and incorrectly, see for example Allen *et al.*, 1996; Cavallini, 1994; Goszczynski, 1999) as an index of abundance, or relative density, or density. Other reported indirect techniques to derive indices of activity for canids include monitoring track counts at scent stations or bait stations (Allen *et al.*, 1996; Barea-Azcón *et al.*, 2007; Griffith *et al.*, 1981; Linhart and Knowlton, 1975; Thompson and Fleming, 1994; Travaini *et al.*, 1996); monitoring activity at track plates (Gompper *et al.*, 2006; Orloff *et al.*, 1993; Taylor and Raphael, 1988); recording spotlight counts (Mahon *et al.*, 1998; Sharp *et al.*, 2001); recording tooth marks on 'chew cards' (Engeman and Witmer, 2000); recording the number of scats present (Cavallini, 1994; Webbon *et al.*, 2004); recording the number of dependent cubs at a den site (Goszczynski, 1999; Marks and Bloomfield, 1999a; Trewhella *et al.*, 1988); questionnaire surveys sent to local councils and naturalist groups (Wilkinson and Smith, 2001); and more recently camera traps (see for example Long *et al.*, 2007; Sarmento *et al.*, 2009; Vine *et al.*, 2009) and molecular methods (Foran *et al.*, 1997; Gompper *et al.*, 2006; Kohn *et al.*, 1999; Long *et al.*, 2007; Mowat and Strobeck, 2000; Piggott *et al.*, 2008; Prugh *et al.*, 2005; Ruibal *et al.*, 2009; Ruibal *et al.*, 2010; Zielinski *et al.*, 2006).

These indices of activity have been used to infer additional information, including the effectiveness of introduced predator control strategies (see for example Algar and Kinnear, 1992; Allen *et al.*, 1996; Fleming *et al.*, 1996; Molsher, 1999; Thompson and Fleming, 1994). However, there is no rationale to assume activity, or an activity index, is related to density or abundance. At best, indices of activity may have some correlation with abundance but there is no justification to assume this, nor is there justification to assume any such relationship is linear (Caughley, 1977; Diefenbach *et al.*, 1994; Williams *et al.*, 2002). Indices can only be used to make inference of abundance if detection probability is constant and if the index is proportional to abundance (Pollock *et al.*, 2002; Royle and Nichols, 2003; Williams *et al.*, 2002) or if variation in detectability can be adequately modelled in terms of covariates. These assumptions are rarely verified and, if not met, can result in biased estimates (Anderson, 2001; Nichols, 1992; White, 2005). Similarly, if detectability is recognised as being variable, corrections are rarely made to allow for this variability (Anderson, 2001; Nichols, 1992; White, 2005). To provide some level of confidence for inference, the assumptions should be validated in the environment in which the techniques are used. Nonetheless, a suite of unvalidated indirect techniques used to derive indices of activity, and subsequently infer abundance of introduced predators appears to be widely accepted in the scientific literature.

One of the earliest reported, and often cited, use of indices derived from track counts was developed to provide information on abundance of a wild canid (the coyote, *Canis latrans*) in the western United States (Linhart and Knowlton, 1975). The interest was initiated after concerns were raised over predator control programs and a realisation that there was no method available to provide reliable estimates of coyote abundance. The methodology subsequently adopted was described as *"an index of relative abundance"*, which was derived from scent stations and was calculated as:

Index = (*total animal visits / total operative station nights*) x 1,000

> where the variable *total operative station nights* was the total number of station nights, exclusive of stations which were disturbed and/or otherwise uninterpretable; and
>
> a scent station was a circular area of sifted sand, one yard in diameter, with a capsule containing a manufactured *"fermented egg"* attractant in the centre (Linhart and Knowlton, 1975).

The authors acknowledged detection heterogeneity is different for different species, including non-canids, and would be influenced by factors including the location and spacing of scent station lines. Similarly, heterogeneity in abundance was acknowledged and identified as likely to be influenced by factors including topography, vegetative cover and food. Linhart and Knowlton (1975) also noted "*we have no way to relate these indices with the actual number of coyotes present in a given area*". Substantial variation has also been shown to occur for 'between line' indices of coyote activity (Griffith *et al.*, 1981). Where this variation is a consequence of sampling design and/or detection probability, it can mask any real differences in abundance.

Trewhella *et al*. (1988) believed the most reliable method for estimating fox population density was through counts of litter size in spring. However, this method involves assumptions on sex ratio and cub mortality. Inferring density from litter counts is further confounded by the contradicting results obtained if assuming the population structure is a dominance hierarchy (with only one or very few vixens breeding within each family group) or a mated pair population structure (with each or most vixens breeding). Studies of northern hemisphere fox populations have found evidence of dominance hierarchies (Macdonald, 1979). Bubela (1995) and Berghout (2000) believed there was some evidence for the presence of dominance hierarchies in fox populations in alpine areas of NSW and the central tablelands of NSW, respectively. Whereas Marlow *et al*. (2000) found a simple mated pair structure provided the most plausible explanation for the structure of a high density fox population near Carnarvon, WA, as did McIlroy *et al*. (2001) in central-western NSW. There is otherwise a dearth of evidence from fox population studies within Australia to indicate the presence of dominance hierarchies or mated pair population structures and no information as to whether these population structures are mutually exclusive. It is likely combinations of both structures occur. It is also likely the mix of dominance hierarchies and mated pair structures show spatial and temporal variation.

Estimates of population size based on 'estimates' of litter size are reliant on an understanding of this population structure. These derived estimates will vary subject to the population structure. As the population structure is not known for fox populations in Australia, it would seem dubious at best to base population estimates on estimates of litter size. Berghout (2000) demonstrated there was still considerable variation in density estimates for a fox population from the central tablelands of NSW where a mated pair system was assumed (see Table 1.2, Chapter 1), as additional information was required on den use.

There have been several reviews, each with recommendations, on methods for estimating the size of, or deriving an index to, fox populations. Lloyd (1980) listed four techniques for population density measurements or estimates and noted no one technique is universally applicable. Wilson and Delahay (2001) reviewed a range of techniques, other than those involving capture, for estimating abundance of carnivores and highlighted the need to validate the chosen technique(s). The more thorough reviews of estimation techniques have reinforced the need to validate any use of indices and unambiguously stressed the critical requirement of incorporating an assessment of detection probability (see for example Anderson, 2001; Anderson, 2003b; Buckland *et al.*, 2004; Burnham and Anderson, 2002; Field *et al.*, 2005; Lebreton *et al.*, 1992; MacKenzie *et al.*, 2006; Royle and Nichols, 2003; White, 2005; Williams *et al.*, 2002).

Despite this, use of indirect methods to derive indices has been argued as an appropriate metric for determining abundance or relative abundances of cryptic predators such as the fox (see for example Engeman, 2005). However, if the desired outcome is to determine a population size or population density, indices will only be of value if they can be shown to be consistently proportional to abundance (Anderson, 2003b; Royle and Nichols, 2003; White, 2005; Williams *et al.*, 2002). The major limiting factor to the use of indices is usually that *"the relationship with absolute density has not been validated"* (Sadlier *et al.*, 2004). Where underlying assumptions of the technique used to derive an index are not met, the results are highly likely to be biased and/or inaccurate (Royle and Nichols, 2003; Stanley and Royle, 2005; White, 2005; Williams *et al.*, 2002) and can result in conclusions which are unfounded (Stanley and Royle, 2005). This can misinform managers of conservation estate (Field *et al.*, 2005) with the consequences that long-term land use and wildlife management decisions are based on inaccurate findings.

Justification for the use of indices is often based on the false premise that indices may be free of assumptions. In most cases there are implicit assumptions related to the derivation of indices and in some cases the assumptions required of more rigorous quantitative methodologies also apply to indices (MacKenzie and Royle, 2005; White, 2005). The requirement to meet assumptions of more robust methodologies is also regularly used as a reason for not using such methods. The irony is, many of the more robust techniques are also robust to detection and behaviour heterogeneity (White, 2005). Researchers often attempt to justify use of an index by demonstrating its correlation with another index, e.g. attempting to validate spotlight counts against track counts (Edwards *et al.*, 2000) or validating a binary track count index against an intrusion index (Blaum *et al.*, 2008). Unless one of the techniques includes a mechanism to assess the variation resulting from heterogeneity in detection, the correlations or calibrations do not equate with validation.

There are numerous examples in the scientific literature where assumptions have not been met, techniques to derive indices have not been validated, and where previous studies have been cited inappropriately to justify the use of unvalidated indices. The following example from the Gibson Desert Nature Reserve, central interior WA (Burrows *et al.*, 2003) is not an isolated occurrence and reflects current accepted practice. Burrows *et al*. (2003), in a study of broadscale baiting effectiveness reported densities for feral cats, foxes and dingoes, based on track counts. These track counts were 'standardised' to derive a count of the number of tracks per 100 km. The track counts were also reported as density and abundance estimates without any methodology provided for this conversion. Justification for the use of track counts was implied by citing Stander (1998), Servin *et al*. (1987), O'Donoghue *et al*. (1997) and Edwards *et al*. (2000). Interestingly, Stander (1998) cautioned against the approach adopted by Burrows *et al*. (2003), where use of the slope of the relationship between spoor count and abundance for one species could not be used to infer abundance from the spoor count of a second species (see example below). Stander (1998) also validated the relationship prior to making inference, whereas Burrows *et al*. (2003) did not. Servin *et al*. (1987) cautioned on the need to incorporate heterogeneity in detection as a result of roading and the type of roading (see below). Burrows *et al*. (2003) did not incorporate heterogeneity in detection. O'Donoghue *et al*. (1997) incorporated covariates for heterogeneity in abundance and detection probability and used the mean values for each covariate to derive estimates of abundance. The approach adopted by Burrows *et al*. (2003) was a major departure from each of the three examples above, yet each was cited to imply support for the methodology used. Of the other references cited by Burrows *et al*. (2003) to support use of indices derived from unvalidated track counts, Edwards *et al*. (2000) calibrated one unvalidated technique with another unvalidated technique (see above) and the remaining references cited were either from unpublished work, personal communications or un-refereed publications.

In a review of 116 'worldwide' predator manipulation studies, Salo *et al*. (2010) listed 16 studies involving removal of the red fox (Table 3.1). Eight of these studies made no assessment of fox abundance and assumed baiting had reduced fox numbers. A further seven of the 16 studies used an unvalidated index of some description to infer fox abundance. Only one study (Mahon, 1999) attempted to incorporate heterogeneity in detection probability and abundance. This was also the only study to acknowledge the lack of correlation between the two indices used to infer fox abundance (Table 3.1).

The intent of identifying weaknesses in existing techniques is not to discredit the techniques or operator(s) but to raise the awareness of the ultimate end-users (usually natural resource managers) that indices may not reflect the population parameters of interest. Such raised awareness should alert managers to the limitations of indices, provide incentive to seek the most appropriate methodology from which reliable inference can be made and result in evidence based management decisions. This should ultimately lead to improved conservation outcomes.

Table 3.1: The sixteen studies involving removal of the red fox (*Vulpes vulpes*) from the 116 predator removal studies listed by Salo *et al*. (2010).
The study reference number, primary source, location, experiment type, predator origin and predator species are as listed by Salo et al. (2010).
Experiment types are: BA = before-and-after design; NE = natural experiment; SEC = simultaneous experimental and control areas

Salo *et al*. (2010) study reference no.	**Source and/or case study**	**Location**	**Experiment type**	**Predator origin**	**Predator(s)**	**Method adopted to assess predator numbers**
4	Banks *et al*. (1998)	Australia	SEC	introduced	red fox	This study used a combination of three indices - spotlighting, scat counts and non-toxic bait uptake. All indices showed a lower count at fox removal sites, however the relationship between the counts and the estimates derived by each technique was not quantified. Therefore, there were three unvalidated indices, all or none may reflect abundance.
5	Banks (1999)	Australia	SEC	introduced	red fox	This study cited Banks *et al*. (1998) as the source for the fox removal component but referred to a fox density reduction, as opposed to the indices reported by Banks *et al*. (1998).
6	Banks *et al.* (2000)	Australia	SEC	introduced	red fox	This study also cited Banks *et al*. (1998) as the source for the fox removal component and also referred to a fox density reduction, as opposed to the indices reported by Banks *et al*. (1998).
44	Jarnemo and Liberg (2005)	Europe	BA/NE	native	red fox	Fox abundance was inferred from observer sightings divided by the number of person days in the field.
49	Kinnear *et al.* (1998)	Australia	SEC	introduced	red fox	Fox baiting was carried out at four to five weekly intervals (treatment sites) and rock wallaby populations were monitored at the treatment and unbaited sites (control sites). There was no assessment of fox abundance. Fox populations were presumed to have decreased as a result of the baiting. An index (Known To Be Alive) of rock wallaby abundance was derived based on count and capture data.

(cont. ….)

Table 3.1 (… cont.).

Salo *et al.* (2010) study reference no.	**Source and/or case study**	**Location**	**Experiment type**	**Predator origin**	**Predator(s)**	**Method adopted to assess predator numbers**
50	Kinnear *et al.*(2002), case study 1	Australia	BA	introduced	red fox	The Dampier Archipelago - fox baiting was implemented but there was no assessment of fox abundance.
50	Kinnear *et al.* (2002), case study 2a	Australia	BA	introduced	red fox	Tutanning Nature Reserve - as above.
50	Kinnear *et al.* (2002), case study 2b	Australia	BA	introduced	red fox	The Tutanning Annex - as above.
50	Kinnear *et al.* (2002), case study 3	Australia	BA	introduced	red fox	Boyagin Nature Reserve - as above.
50	Kinnear *et al.* (2002), case study 4	Australia	BA	introduced	red fox	Dryandra Woodland - as above.
50	Kinnear *et al.* (2002), case study 5	Australia	SEC	introduced	red fox	Fitzgerald River National Park - an index of fox abundance was derived through use of cyanide baiting.

(cont. ….)

Table 3.1 (… cont.).

Salo *et al.* (2010) study reference no.	**Source and/or case study**	**Location**	**Experiment type**	**Predator origin**	**Predator(s)**	**Method adopted to assess predator numbers**
62	Mahon (1999)	Australia	SEC	introduced	red fox, cat	Used a combination of off-road sandtrack counts, sandplot counts on roads and spotlighting. This study also acknowledged heterogeneity in detection and abundance attributable to roads and habitat type. Spotlighting was considered to be a poor technique for estimating abundance of foxes and cats.
83	Pech *et al.* (1992)	Australia	SEC	introduced	red fox, cat	A previous publication was cited, and summarised, to describe the methodology for fox removal and monitoring. The summary noted fox and cat numbers were assessed by spotlighting counts. The counts were described initially as an index to density. Foxes and cats were described as appearing in spotlight counts in comparable numbers and counts for each species were thereafter referred to as densities. There was no differentiation in detection probabilities for the two species and no validation of the spotlight counts and no rationale to assume spotlight counts reflected abundance.
89	Risbey *et al.* (2000)	Australia	SEC	introduced	red fox, cat	Fox and cat numbers were assessed by spotlight counts and recorded as a count per km. There was no allowance for detection probability, no validation of the count data and these values were subsequently referred to as densities.
94	Spencer *et al.* (2002)	Australia	SEC	introduced	red fox	The correct reference is Spencer (2002). Fox numbers were presumed to be reduced, or foxes were removed, but there was no estimate of fox abundance prior to, or post removal.
95	Spencer and Thompson (2005)	Australia	SEC	introduced	red fox	As above, fox numbers were presumed to be reduced and foxes were removed, but there was no estimate of fox abundance prior to, or post removal.

3.2.3 A role for indices

Despite the difficulties associated with the use of indices, it is important for researchers and natural resource managers to appreciate there are circumstances where indices may be appropriate and, when validated, can provide useful information on which management decisions can be made. However, where indices have been validated, the reported findings often include caveats on further use of that particular index. For example, Westcott (1999) found the two key assumptions required for use of an index to cassowary (*Casuarius casuarius*) abundance in forested areas of north Queensland were violated and highlighted the need to identify weaknesses of existing approaches. Drennan *et al*. (1998) compared mark-recapture derived estimates of abundance with derived indices from 'track stations' comprised of plastic rain gutters protecting a chalk covered aluminium track plate for four species of sciurid. They found the two indices (a track count and CPUE index) and estimates were strongly correlated, however, they noted the indices were less sensitive to detecting differences in abundance than the more robust mark-recapture technique. Slade and Blair (2000) found counts and use of the index of the minimum number of individuals known-to-be-alive (KTBA) gave results proportional to estimates derived from more robust mark-recapture techniques. However, they concluded the indices were restrictive and were not appropriate for comparison between species even if identical detection protocols were used and there was likely to be between-site differences in detection. From a study at sites in Kaudom Game Reserve and Tsumkwe District, Namibia, Stander (1998) found spoor frequency of leopards (*Panthera pardus*), lions (*P. leo*) and wild dogs (*Lycaon pictus*) was a function of true density. However, as reported by Slade and Blair (2000), he (Stander, 1998), found the slope of the linear relationship between spoor counts and true density to be different for each species, indicating spoor counts were non comparable between species. Stander (1998) also cautioned the slope of this relationship would likely vary as a function of habitat use and the behaviour for each species.

It is difficult to have confidence in any claimed association between indices and abundance where these indices are derived from activity on sandplots without validation and without adjustment for detection heterogeneity. This concern echoes the repeatedly raised cautions in the literature regarding use of indices to infer abundance. Williams et al. (2002) cited monitoring carnivore activity at scent stations as an example where the relationship between indices and abundance is nonlinear. Monitoring carnivore activity at scent stations was also cited (Williams *et al.*, 2002) as an example where detection probability is a function of density (see also Caughley, 1977; Diefenbach *et al.*, 1994).

3.3 Materials and methods

3.3.1 Why use sandplots to monitor predator activity?

Although there are limitations arising from the use of sandplots to derive abundance estimates from activity data, if used appropriately by skilled operators sandplots can be used to detect the presence of several species with some certainty. Results are confounded when presence or activity is interpreted as abundance. In this study sandplots were monitored for the presence of fox (and cat) spoor. However, there was no assumed association or relationship between the abundance of the species for which spoor was detected and the amount of spoor recorded at any sandplot. Similarly there was no assumed association or relationship between abundance and the number of sandplots where spoor was recorded.

3.3.2 1080 baiting and the timing of sandplot monitoring

The primary focus of this aspect of the research was to derive estimates of fox abundance within each treatment where woylies had been translocated to 19 release sites (see Chapter 4). The spatial arrangement of the sandplot networks (Fig. 3.1) was also designed to: (i) sample areas within the central core of the forest and in areas in close proximity to the forest and agricultural land interface; and (ii) maximise the distance between each network to reduce the potential for lack of independence of each sandplot network.

The timing of sandplot monitoring was planned to be carried out annually from August to September and to be completed immediately prior to an aerial and ground baiting session, i.e. monitoring avoided the period immediately post baiting and was not aimed at detecting an acute/immediate knockdown effect, but was aimed at detecting the chronic/longer-term effect of baiting. This timing was also based on the premise that (i) fox population density is reduced as a result of baiting, and (ii) a potential exists for foxes to re-colonise baited areas after a baiting event. Therefore, assessment was required prior to any potential re-colonisation. Both of these aspects were also examined as part of this study. The August to September timing (Austral late winter to early spring) was also planned to coincide with relative stability of fox home ranges (see Chapter 1). Fox home ranges are thought to become less stable in winter when breeding occurs and when males are using the landscape more widely. Monitoring in late winter to early spring also avoided any confounding issues associated with the presence of fox cubs at sandplots. Cubs become progressively more independent from late spring until mid to late summer and are unlikely to be sufficiently independent, or free ranging, and would therefore unlikely be detected at sandplots in late August to early September. Dispersal occurs from late summer to early autumn, when cubs are approximately six months old (see Chapter 1).

Within the northern jarrah forest study area, the two and four baitings per year *treatment groups* had, by March 1995, received the requisite number of baitings over the preceding 12 months. The six baitings per year treatment group had not received the requisite number of baitings until November 1995. Monitoring fox and cat activity on sandplots was conducted in August to September for five consecutive years, 1996 to 2000. Although each baited treatment received the required number of baitings in the period 1996-2000, there were logistical difficulties with aerial delivery of 1080 baits in 1996 and 1997. In 1996 and 1997, delays to aerial delivery of baits resulted in baits being delivered immediately prior to sandplot monitoring (as opposed to after completion of sandplotting), potentially confounding interpretation of these data. Therefore, data analysed are from the sandplot monitoring sessions carried out immediately prior to the September aerial delivery of 1080 baits each year for 1998, 1999 and 2000 only. An additional ten day sandplot monitoring session was carried out in October 1999, post the aerial delivery of 1080 baits. Continuous monitoring was carried out in September and October 2000 and covered the period pre, during and post 1080 baiting.

3.3.3 Use of active sandplots, configuration of each sandplot network and the spatial arrangement of the sandplot networks

Seventeen sandplot networks were established within the 1080 baited treatments and the unbaited control (Fig. 3.1). Five sandplot networks were established in the larger two baitings per year treatment group and four in each of the four and six baitings per year treatment group and the unbaited treatment group. Certified dieback (*Phytophthora cinnamomi*) free sand was imported to each sandplot network, with each network comprised of 25 individual sandplots with each sandplot approximately 1m x 1m in size and 30-40mm deep. Each sandplot was a minimum of 500m from its nearest neighbouring sandplot and was placed at the edge of an existing road or track, with the shape of the sandplot network determined by the configuration of the existing roads and tracks (all unsealed). Each sandplot network was established to ensure all sandplots were within an area no greater than 25km^2. The exact area required to capture all 25 sandplots within each network varied and was determined through use of a geographic information system (GIS) (Arc GIS, ESRI, 1999-2004) by calculating the minimum convex polygon (MCP) which encompassed all sandplots. A 250m buffer (i.e. equivalent to half the shortest distance between neighbouring sandplots) was added to the MCP. A typical configuration of a sandplot network and the area within the MCP, including the buffer, is shown in Figure 3.2.

A small cube of approximately 30g of fresh mutton was buried 10-15 mm below the surface of each sandplot. Therefore, the adopted sandplot technique falls within the ‘active’ category, as a lure and/or reward was provided. Passive plots provide no lure or reward. The sand was then raked smooth and lightly sprayed with water to assist with ‘holding’ any imprint left by a fox, cat or other species and to facilitate identification of the species responsible. Each sandplot within each network was monitored daily for ten consecutive days and the presence or absence of fox and cat spoor, or other recognisable evidence of fox or cat activity on each sandplot was recorded. Presence of fox or cat spoor was interpreted as an indication of fox or cat presence, respectively. Identifiable spoor and evidence of activity of other species were also recorded, as was presence or absence of the reward. If removed, the reward was replaced. All rewards were periodically checked and partially decomposed and ant-eaten rewards were also replaced. Sandplots showing evidence of activity and/or removal of rewards were re-raked and each sandplot, whether showing activity or not, was lightly re-sprayed with water daily. Evidence considered typical of fox activity at a sandplot is shown in Figure 3.3.

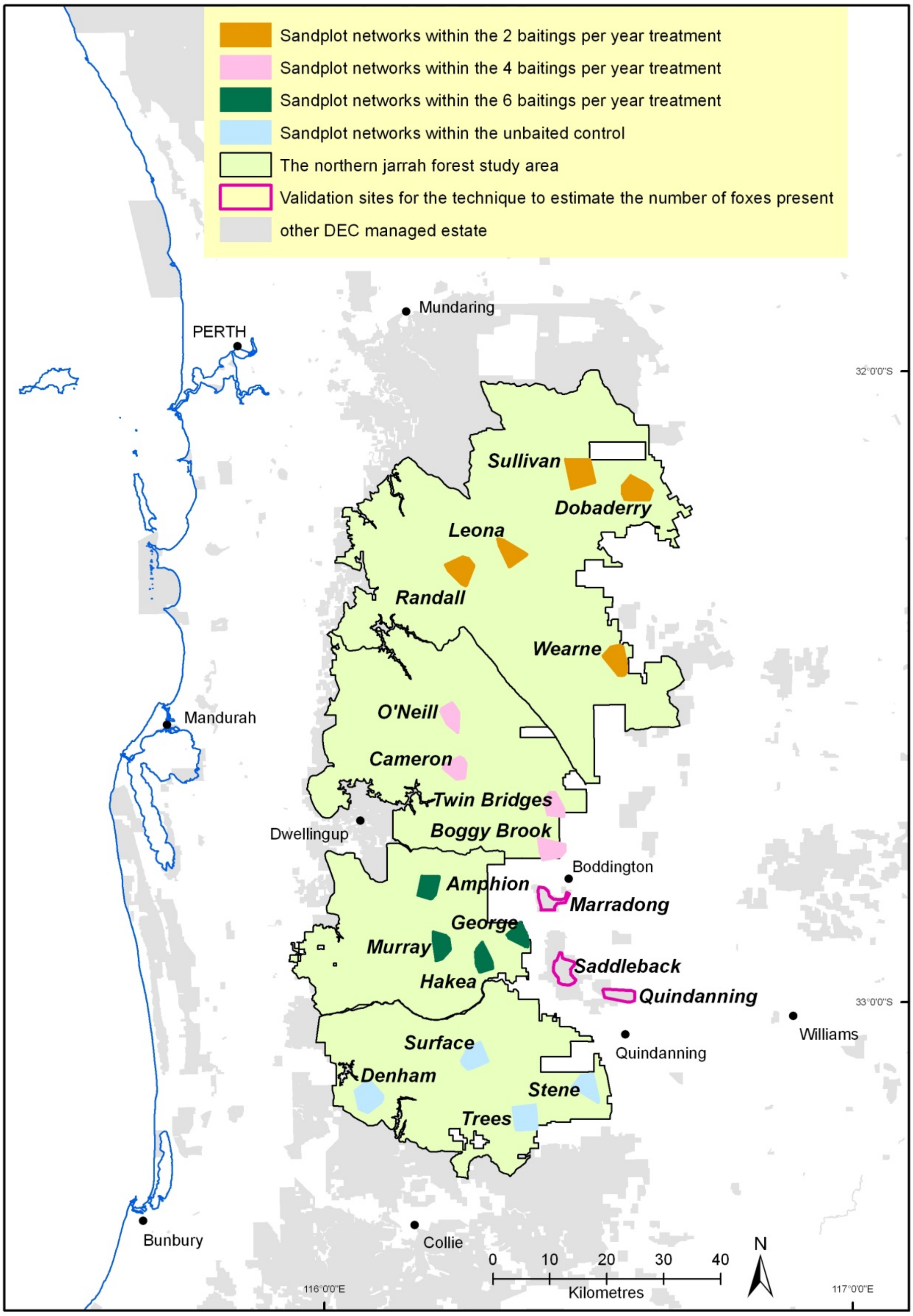


Figure 3.1: The spatial arrangement of the 17 sandplot networks where fox (*Vulpes vulpes*) activity was monitored in the northern jarrah forest, south-west Western Australia. The 'name' of each sandplot network is given in ***bold, italic*** font.

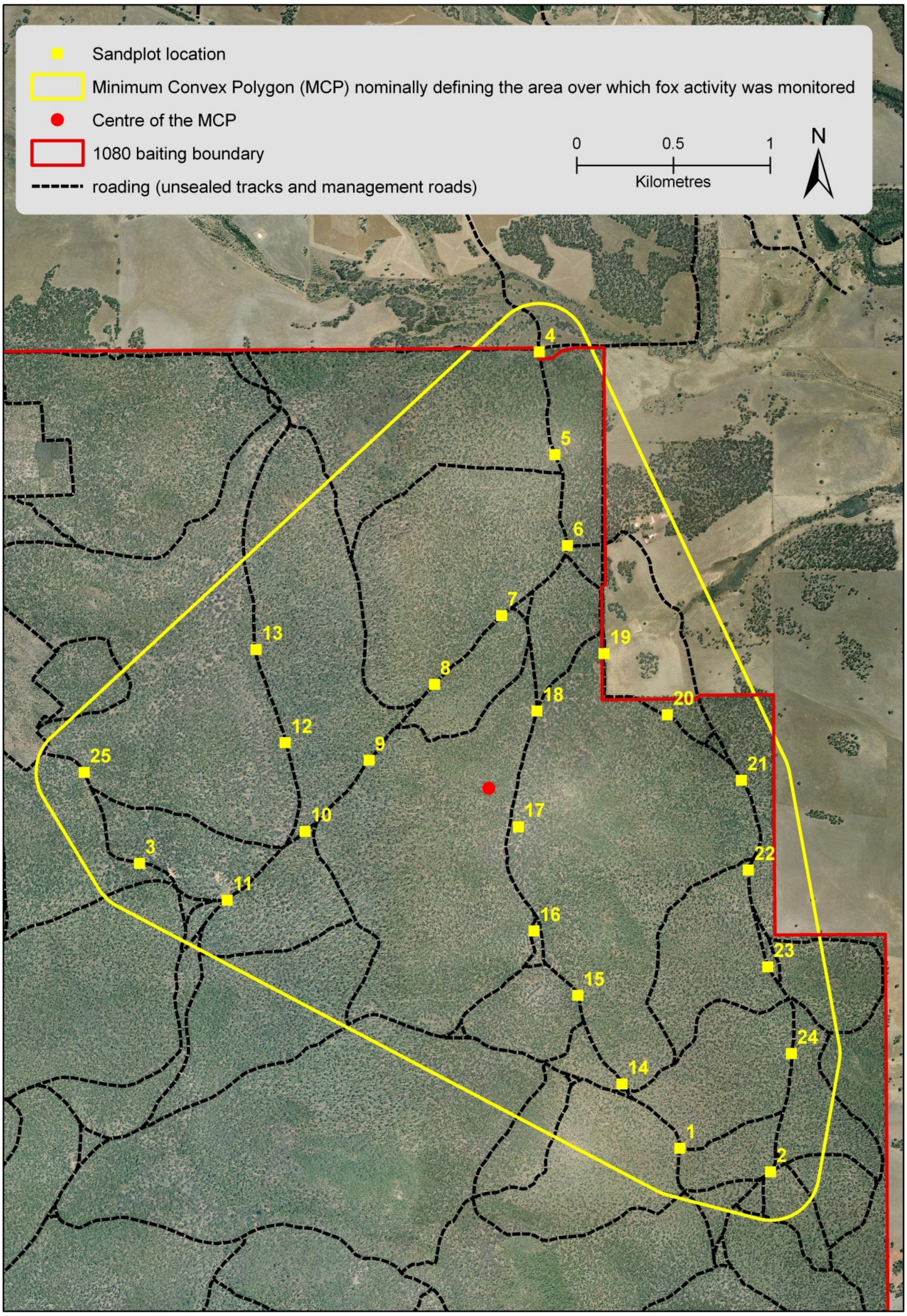


Figure 3.2 Orthophotograph showing the ‘George Block sandplot network’ at the eastern margin of the six baitings per year treatment.

The site abuts agricultural land and the area within the minimum convex polygon (which captured all sandplots within the sandplot network) includes neighbouring agricultural land.

Figure 3.3 A sandplot showing activity considered typical of fox (*Vulpes vulpes*) presence in the northern jarrah forest study.
Scratchings in the middle of plot are where the lure, or reward, was removed.

3.3.4 The northern jarrah forest estimate of the minimum number of foxes known to be alive (MKTBA) and the number of plots with cat activity (pwca)

3.3.4.1 General principles

The technique used within the northern jarrah forest was developed to enable inference of fox abundance from the pattern of fox activity detected at each sandplot network. The technique is based on identification of spoor (tracks or other evidence) left on sandplots, as is the case for most techniques which derive indices to make inference on fox abundance. However, the technique differs from the widely used techniques as there is no assumption of a relationship between fox abundance and the number of fox tracks on an individual sandplot, nor is there an assumption of a relationship between fox abundance and the number of plots showing evidence of fox activity.

There is a suite of facts, or more accurately, widely held and well documented assumptions which apply to the technique when monitoring fox activity and relevant to the northern jarrah forest study. These are:

(i) the number of foxes present at each site (abundance) is a function of a suite of site specific variables (e.g. vegetation cover, prey availability) and/or management practices (e.g. the presence and extent of 1080 baiting);

(ii) not every individual fox present will be detected, i.e. detection probability is <1 (a standard assumption for studies involving capture or counts see Buckland *et al.*, 2001; MacKenzie *et al.*, 2006);

(iii) detection probability is a function of population density (a standard assumption for studies involving animal capture or counts see Anderson, 2001; MacKenzie *et al.*, 2006; Royle, 2006; Royle and Nichols, 2003; Williams *et al.*, 2002);

(iv) detection probability is not necessarily constant between sites nor constant within each sandplotting session at any given site, with the probability of detection potentially a function of:
  - site specific variables (as for assumption (i), above for abundance); and/or
  - the number of sandplots present per unit area (the sandplot density); and/or
  - the number of plots available for interpretation; and/or
  - the number of days over which monitoring is carried out; and/or
  - the extent of roading; and/or
  - the observer.

There is an additional suite of assumptions, or reasonable assertions, also relevant to this study. These are:

(v) for the duration of monitoring, the fox populations have temporal closure, i.e. there is no immigration or emigration (a standard assumption for surveys over a short time period) and similarly, there are no births (also a standard assumption for surveys over a short time period) and no deaths (again, a standard assumption for surveys over a short time period) as each monitoring period extends for ten days only and precedes a baiting event by a minimum of the ten days of monitoring (as opposed to following a baiting event when deaths are anticipated);

(vi) for the duration of monitoring, the fox populations are geographically or spatially independent, i.e. individuals are not moving between sandplot networks;

(vii) there is no *a priori* reason to assume the number of tracks on any given sandplot reflects the number of foxes to have inspected the sandplot, i.e. multiple tracks on any given sandplot are not interpreted as multiple individuals. Multiple tracks may reflect multiple individuals, but may equally well reflect only one individual; and

(viii) a pattern of continuous activity, or contagion, or autocorrelation, if present, infers a lack of independence of each sandplot. Therefore, consecutive plots showing activity may reflect multiple individuals, but equally well may reflect one individual visiting multiple sandplots.

3.3.4.2 The count data

A positive value for detection of a fox was recorded for each sandplot when there was evidence of fox spoor on the sandplot. However, the number of foxes detected each day, at each sandplot network, was based on the 'testable' premise whereby the pattern of activity or contagion (not the number of prints or spoor per sandplot, nor the number of sandplots with observed activity) reflected the number of individual foxes detected. Where successive sandplots showed activity, this was interpreted as indicating the same individual fox had 'inspected' each sandplot. A break in continuity, with two or more sandplots showing no activity, followed by sandplots with activity, was interpreted as indicating the presence of a different individual fox. Similarly, where plots were in close proximity, but not on the same road or track, a break of 1.5 km or more between plots showing activity, followed by resumed activity, was interpreted as indicating the presence of an additional fox. The data for each day therefore constituted a non-negative integer value, or count data.

The pattern of fox activity on sandplots was mapped using the geographical information system (GIS) software ARCMap (ESRI, 1999-2004) and the number of individual foxes detected was then determined from the pattern of activity at each sandplot network. Based on the assumptions above of geographic closure and no deaths occurring during the monitoring period, the minimum number of foxes known to be alive (MKTBA) was derived daily. The daily value for the MKTBA estimate was determined by the number of foxes recorded that day and each previous day during the monitoring period. As individuals were not marked nor uniquely identified, the presence of a fox on $\text{day}_{(i)}$ could not be inferred to be either the same fox, or an additional (different) fox, if one was recorded on $\text{day}_{(i+1)}$. Hence, if one fox was recorded on $\text{day}_{(i)}$ and another on $\text{day}_{(i+1)}$, the minimum number of foxes known to be alive (MKTBA) remained as one. If two foxes were recorded on $\text{day}_{(i)}$ and only one on $\text{day}_{(i+1)}$ and every successive day, the MKTBA was two for $\text{day}_{(i)}$ and every successive day. The resultant value (or count) was the day-10 estimate of MKTBA. Figures 3.4 and 3.5 show: examples of the daily pattern of fox activity; interpretation of these patterns; the daily MKTBA estimate; and the day-10 MKTBA estimate. The methodologies used to validate the technique are described in sections 3.3.4.8 & 3.3.4.9 (below).

Subject to sufficient encounters, the technique may be applicable for inferring the number of cats present and the assumptions and assertions (above) may also apply when monitoring cat activity. However, there were no data, nor any published accounts in the peer reviewed literature, to suggest there was a similar pattern of activity (or contagion) by cats. Consequently, cat activity was recorded as a presence or absence value for each sandplot, each day, and no assumption was made regarding contagion or the pattern of cat activity on sandplots. The resultant data comprised a daily count of the number of plots with cat activity (pwca) and therefore also constituted count data. The implications from this method of detection of cats are discussed in Section 3.5 (Discussion) and Chapter 6 (summary of findings).

In addition to recording the presence of a fox and/or a cat at each plot, a subjective confidence rating (with a value of 1, 2 or 3) was applied to each recorded detection event. A rating of 1 indicated a high level of confidence of correct identification of the species responsible for the observed activity. A rating of 3 indicated a lack of confidence in identification of the species responsible. Final analysis of the data used only those recorded observations with a confidence rating of 1. Sandplots were deemed uninterpretable, or unable to be ‘read’, if they had been disturbed by heavy rain, vehicle activity or were otherwise disturbed. Therefore, the number of sandplots available for interpretation varied daily.

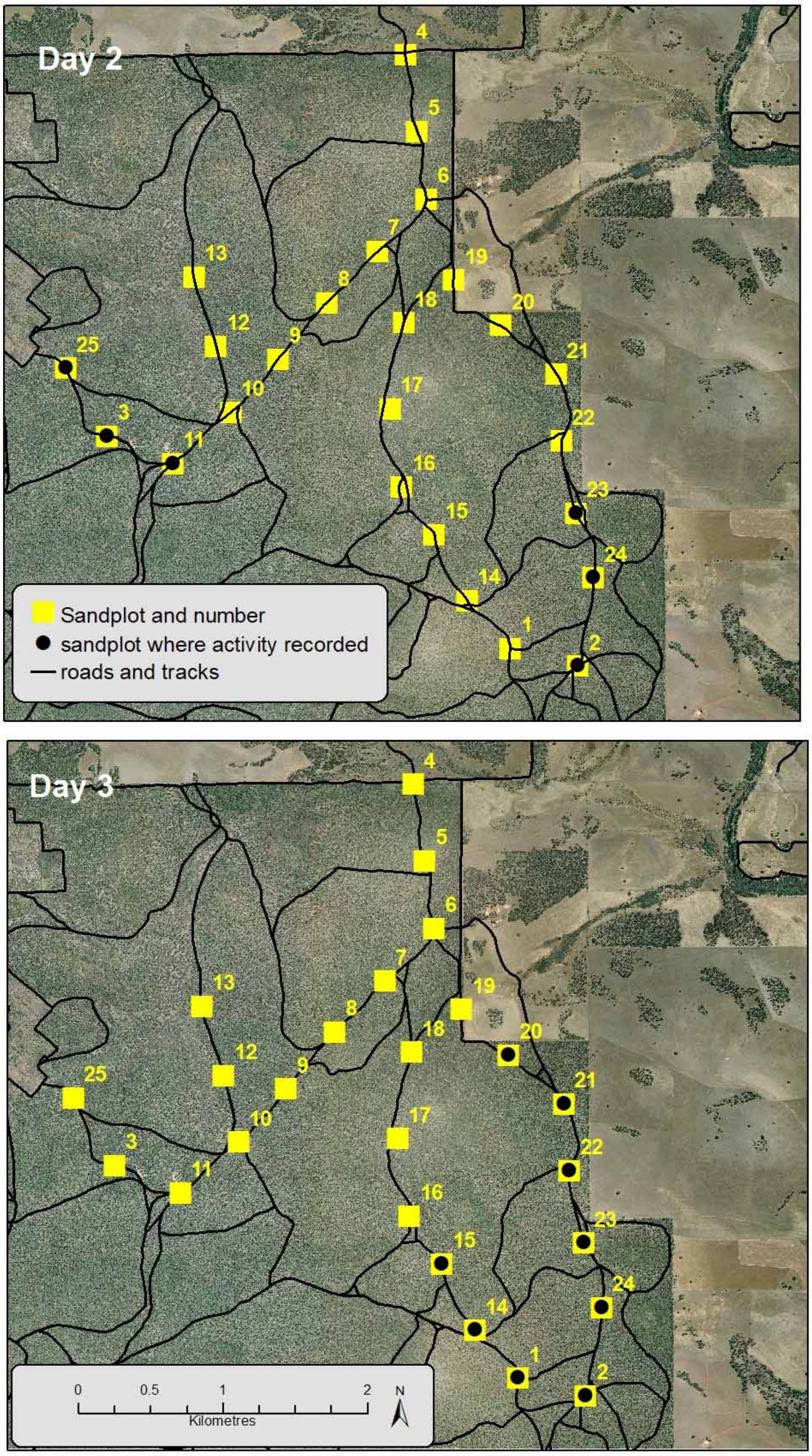
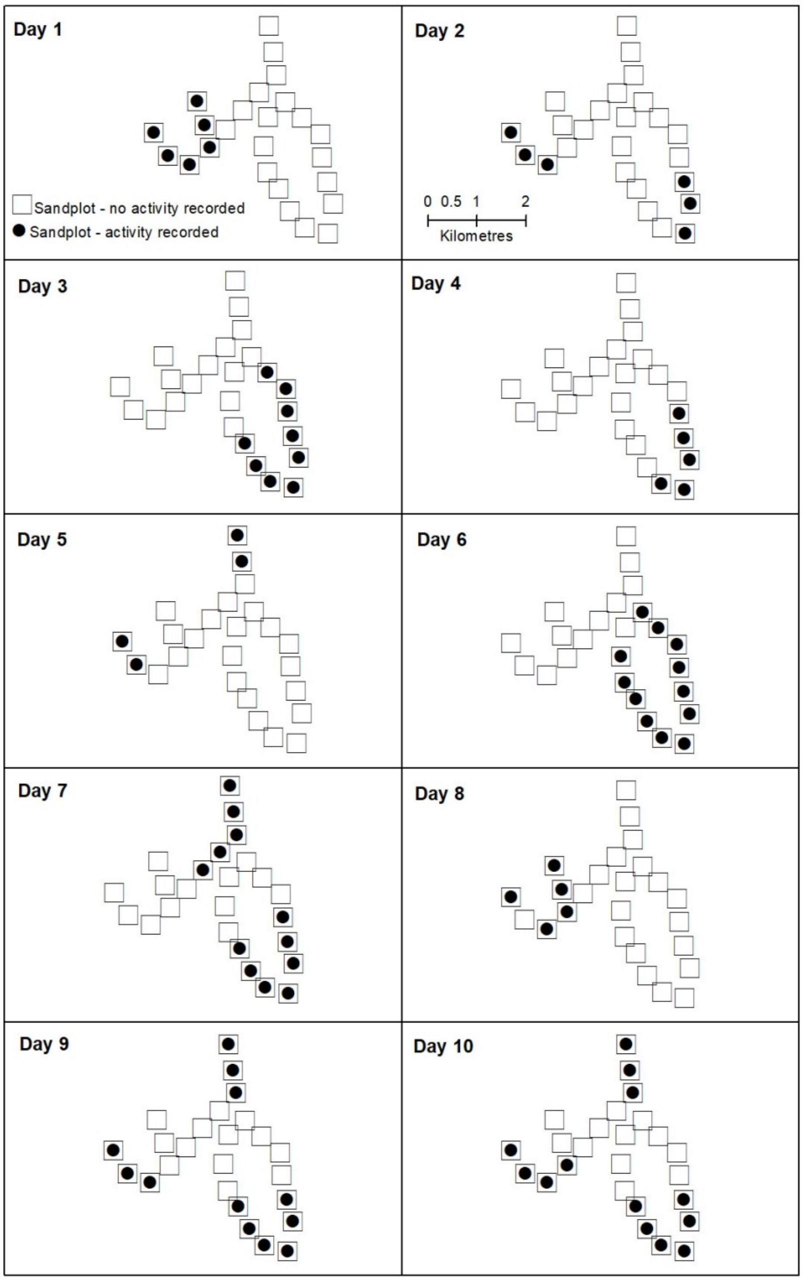


Figure 3.4 An example of an observed pattern of fox (*Vulpes vulpes*) activity at a typical sandplot network and how activity at sandplots was interpreted to estimate the number of foxes present.

Day 2: Activity was detected at six sandplots (plot numbers 2, 3, 11, 23, 24 & 25) and interpreted as two foxes, one at plots 3, 11 & 25, the second at plots 2, 23 & 24.

Day 3: Activity was detected at nine plots (three more than the example on day 2) but interpreted as only one fox.



Day	No. of plots available and interpretable	No. of plots with fox activity	No. of foxes estimated present	Minimum number of foxes known to be alive (MKTBA)
1	25	6	1	1
2	25	6	2	2
3	25	9	1	2
4	25	5	1	2
5	25	4	2	2
6	25	12	1	2
7	25	12	2	2
8	25	5	1	2
9	25	12	3	3
10	25	13	3	3

Figure 3.5 An example of fox (*Vulpes vulpes*) activity at a typical sandplot network and how the daily pattern of activity was used to derive the estimated minimum number of foxes known to be alive, for each of 10 consecutive days of monitoring, in the northern jarrah forest, south-west Western Australia.

3.3.4.3 Approaches applicable for analysis of count data

The day-10 MKTBA estimate for foxes and the number of plots with cat activity (pwca) both constitute ‘count data’, whereby the data are non-negative integers. In both cases, the count takes no account of detectability, or detection probability. In the absence of a known value for detection probability, the true population size (N) cannot be determined. The commonly used solution is to treat the estimate, or the number detected (n), as an index to N. As described in Section 3.2.2, there are major unrealistic assumptions implicit in this approach of using indices (Anderson, 2003b; MacKenzie *et al.*, 2006; Royle and Nichols, 2003; White, 2005; Williams *et al.*, 2002), including the assumption of constant detection probability (p). Where there is heterogeneity in detection (as is likely to be the case for most count and survey data), changes in the count data (n) cannot necessarily be inferred to reflect a change in the true population size (see Section 3.2.2 on the use of indices).

Incorporating detection heterogeneity when deriving an estimate of population size is given by:

$$(E)n_i = N_i p_i$$

where:

$(E)n_i$ = the (expected) number of individuals detected, or the count data in some other form, e.g. in this study, the number of individual foxes inferred from the pattern of activity observed at sandplots;

N_i = the true population size; and

p_i = the detection probability

Heterogeneity in p_i can be a function of biophysical and management attributes (e.g. the extent of vegetation cover, or the extent of roading) and can also be a function of time (e.g. increased or decreased detection probability over time as a result of changes in behaviour, contagion etc.). However, heterogeneity in detection is also a function of population size itself (Anderson, 2001; Borchers *et al.*, 2002; MacKenzie *et al.*, 2006; Royle, 2006; Royle and Nichols, 2003; Williams *et al.*, 2002). Royle and Nichols (2003) believed this change in population size may be the most important source of detection heterogeneity. In a series of papers (Kéry, 2002; Royle, 2004a; 2004b; Royle and Nichols, 2003) the authors proposed this heterogeneity in abundance could be modelled as heterogeneity in detection (White, 2014). The technique reported by Royle and Nichols (2003) demonstrated if point counts are replicated (spatially and temporally) and the survey sites are demographically closed (no births, deaths, emigration or immigration), then using integrated likelihood methods, detection probability and abundance can be separately modelled. As Royle (2004a) noted, this concept had been described previously for an assumed binomial distribution (see Carroll and Lombard, 1985; Haldane, 1942; Oldine *et al.*, 1981). However, issues arose from these previous approaches resulting in poor stability of the maximum likelihood estimator, primarily as a result of small values for detection probability. This is the normal state of affairs for most, or at least for many, situations involving observed counts of animal populations. Carroll and Lombard's (1985) solution, using an alternative estimator (for which Royle (2004a) coined the term, the CL estimator), involved integrating the detection probability parameter from the likelihood. This approach also has issues, including a requirement to estimate the beta 'a' and 'b' (α and β) prior distribution parameters. Royle (2004a) noted for many species of birds, detection probability can be very low, and consequently choice of priors (beta a and b values) in addition to choice of *p* can be critical. This issue is not limited to avian biology and in most situations in Australia detection probabilities will be low, particularly when acquiring count data for rare or cryptic species.

Other issues with the CL estimates when values for *p* are small and beta parameters are non-informative, are that the estimates are often at the *"boundary of the parameter space"* (Royle, 2004a), i.e. are roughly equivalent to the maximum or minimum observed count from the replicated counts. Additionally, there is the potential for estimator or stability problems when there is a large proportion of zero counts, i.e. if the data are zero inflated. Further, because the CL estimator is for a total *N* (estimated for the total population, not the individual sites) from the pooled data of the replicated counts, much of the site specific information (the data structure, or co-variate information) is lost (or not used) (Royle, 2004a).

As described above, the solution proposed by Royle and Nichols (2003) was to utilise the relationship whereby heterogeneity in detection is a function of population size itself. They believed by modelling this heterogeneity in detection it was possible to estimate the underlying abundance. Theoretically, the method therefore allows estimation of abundance from repeated observations, without having to uniquely mark animals.

If a Poisson distribution is assumed, as was the case reported by Royle and Nichols (2003), the mean of the Poisson distribution (λ) can be seen to be the abundance of the species in question viewed across the metapopulation (Royle, 2004a; 2004b; 2006; Royle and Nichols, 2003). Alternatively, N_i could be assumed to have a negative binomial distribution (Kéry *et al.*, 2005; Royle, 2004a; 2004b) and therefore does not require the mean and variance to be equal. Royle and Nichols (2003) noted either assumption (a Poisson or negative binomial distribution) may be 'appealing' because it allows abundance to vary spatially, 'as would be the case in real world situations', and allows the population to be modelled.

In the approach adopted by Royle and Nichols (2003), heterogeneity in abundance, at least for that heterogeneity across the sample sites, is incorporated by viewing λ as site specific (λ_i) and this heterogeneity is incorporated as a log-linear function when deriving the MLE, and is expressed as:

$$log(\lambda_i) = \beta_0 + \sum_{k=1}^{n} \beta_k x_{ik}$$ (Kéry *et al.*, 2005; Royle, 2004a; 2004b)

$where$ x_{ik} is the k^{th} covariate contributing to the heterogeneity at site i.

Heterogeneity in detection probability can then be incorporated and modelled as a linear-logistic (logit) function of the variables influencing detection and is expressed as:

$$logit(p) = \beta_0 + \beta_1 X_i + ... + \beta_n X_k$$

where β_{1-n} are the respective coefficients for variables X_{i-k}

Royle (2004a) and Kéry *et al*. (2005) provided practical applications of the Royle/Nichols approach whereby abundance estimates were derived for five avian species from count data from the North American Breeding Bird Survey (BBS) and for eight avian species from the Swiss monitoring program for common breeding birds, respectively. These studies compared models assuming a Poisson distribution with those assuming a negative binomial distribution. Wenger and Freeman (2008) described use of the Royle/Nichols approach assuming zero-inflated distributions and found, for the same data set and using the same combinations of covariates used by Kéry *et al*. (2005), that zero-inflated negative binomial (zinb) and zero-inflated Poisson (zip) models fitted the data better (i.e. they were AIC preferred) than the models with a Poisson and negative binomial distribution used by Kéry *et al*. (2005). Wenger and Freeman (2008) further demonstrated the value of this by showing, for the mallard duck (*Anas platyrhynchos*) data from the Swiss monitoring program, a better model fit was achieved by placing some covariates on the linear-logistic component (the certain zeros) rather than the likelihood (or output) component of the model.

This choice (assumption) of distribution can be critical, for example *"if a Poisson distribution is used where there is excessive unexplained variation (overdispersion), parameter estimates may be biased"* (Wenger and Freeman, 2008). Where there is overdispersion (usually, and most easily identified by examining the mean and the variance), a negative binomial model will most likely provide a better fit to the data than a Poisson model. Selection of the appropriate model will depend not only on whether or not the data are overdispersed, but also on whether or not the data are zero-inflated. Importantly, choosing an incorrect statistical model can result in faulty inferences or predictions (Ellison, 2004).

White (2014) identified the need for caution when using the Royle/Nichols modelling approach and pointed out that although λ may be an estimate of abundance, the assumptions of geographic and demographic closure still apply. An additional critical assumption is that detection probability for individual animals is constant over time. This is unlikely to be the case. Violation of *"any or all of these assumptions will produce questionable inferences"* (White, 2014).

The technique described by Royle (2004a) and Royle and Nichols (2003) also makes the assumption that detection probability is constant for all individuals in the population. However, in mark-recapture studies when individuals within a population have a different probability of detection (or a different probability of capture), mark-recapture techniques will provide a consistently downward bias in estimates of population size (Hwang and Huggins, 2005; Pledger *et al.*, 2010). This remains the case even where a small number of individuals have a higher detection probability than the rest of the individuals in a population (Hwang and Huggins, 2005). By assuming constant detectability, the modelling method described by Royle (2004a) will likely also result in a downward bias.

The Royle and Nichols (2003) approach has been widely criticised (see for example Cooch, 2015; Hines, 2015) as having very strong assumptions and even with simple models, very small changes in detection history can result in large changes in the model output. Further, these assumptions need to be *"tested by data"* (Cooch, 2015) and if these data are available, the Royle/Nichols approach *"isn't needed"* (Cooch, 2015). Although my initial data analysis adopted the Royle/Nichols approach, in recognition of the problematic nature this approach (including the ambiguity as to whether this approach requires the population to be closed between sampling sessions), I adopted the widely accepted approach for analysis of count data through use of a Poisson regression model. More specifically, a model selection process was used at the exploratory analysis stage to compare Poisson regression models with negative binomial regression (nbreg), zero inflated Poisson (zip) and zero inflated negative binomial (zinb) models.

The importance of selecting the most appropriate class of model is demonstrated by Hu *et al*. (2011) who noted *"classically, count data follow a Poisson distribution"* but also provided examples where overdispersed and zero-inflated count data can result in zip, zinb or hurdle models providing a better fit. Hu *et al*. (2011) also highlighted *"the importance for any given data set of finding the most appropriate model for outcome data in order to arrive at the most accurate estimate of the effect of a treatment … and how an inadequately fitting model can bias in the direction of either overestimating or underestimating an effect of* [a] *treatment"*. The consequences of using a model based on assumptions of a distribution which does not fit the distribution of the data can lead to inappropriate and unfounded management recommendations.

In additional to Poisson, nbreg, zip and zinb models, modelling zero inflated data is possible through use of the Cragg hurdle regression (Cragg, 1971). In Stata (StataCorp, 2006; 2017), this is achieved through use of the 'churdle' command and enables modelling of zero-inflated data with the dependent variable as an integer or as a continuous variable. As with zip and zinb models, hurdle models are a class of models for count data which can not only accommodate excess zeros, but also has separate processes to estimate the linear-logistic component and the log likelihood (outcome) component. Therefore, in both classes of model (zero-inflated and hurdle models) the model is comprised of two components and the covariates used in each component can vary, i.e. it is not necessary to use the same covariates in the linear-logistic component and the log likelihood (output) component of the model. This enables the model selection process to compare models where any particular covariate, or combination of covariates, is placed on each component.

A major point of difference between zero-inflated and hurdle models (in addition to hurdle models accommodating a continuous dependent variable) is the way in which the linear-logistic component (i.e. the binomial or zero/non-zero component) is determined. For zero-inflated models, the source of the zero count can be from one of two origins; a structural origin or a sampling origin. The latter (the sampling zeros) assumes these zero observations occur by chance, whereas the zeros occurring from the structural origin result because of the structure of the data, with these zero observations considered to be a result of the observation being a certain zero. The relevance of this to the northern jarrah forest fox and cat data is that zero-inflated models would assume the zero counts could occur from either (i) foxes or cats simply not being detected by chance; and/or (ii) that some foxes or cats will never be detected. However, for hurdle models, the zero count is assumed to only arise from one possible origin, the structural source, or the certain zero observations. Although hurdle models are attractive by enabling detection and abundance to be modelled separately, the assumption that all zeros arise from the structure is clearly violated as a zero count for the number of foxes or cats can be attributed to either source; the sampling source (foxes or cats simply not detected when present); or to the lack of detection as a result of the model structure (the certain zeros).

The northern jarrah forest study also differs from most count data surveys as the MKTBA estimates for foxes were determined after 10 days of monitoring and the cat presence data were collected each day, for 10 days at each sandplot network. The assumptions of temporal closure and spatial independence are likely to hold over each ten day period, but would be clearly violated if the analyses derived estimates between sampling periods, i.e. between years, as was first attempted when pooling the data over all sessions and using the Royle/Nichols approach.

3.3.4.4 The Bayesian modelling approach: the fox (MKTBA) count data

The distribution of the count data (the day-10 MKTBA count) for each of the three years was plotted for visual examination. However, plotting the distribution of the count data alone is not necessarily enlightening, as it may be difficult to distinguish visually between a Poisson, negative binomial, zero-inflated Poisson and zero-inflated negative binomial distribution. As the purpose of the preliminary/exploratory analysis was to determine the most appropriate class of model to adopt for further modelling; i.e. Poisson, nbreg, zip or zinb, all models were examined more formally through a Bayesian model selection framework to determine if the data were overdispersed and/or zero-inflated. This preliminary/exploratory analysis compared the fit of a Poisson, nbreg, zip and zinb distribution for a simple model, with the variable for treatment as the only explanatory variable.

Bayesian modelling in Stata (when using the ‘bayes’ prefix prior to the regression command, be it a Poisson, nbreg, zip or zinb regression, or use of the more flexible ‘bayesmh’ command) uses the Metropolis-Hastings (MH) algorithm as the acceptance/ rejection algorithm by which the proposed distribution is ‘adapted’ to preserve ergodicity (the tendency to converge to the target distribution) as the Markov chain progresses (StataCorp, 2017). For each year, the exploratory analysis identified a Poisson distribution as the preferred, or appropriate class of model (see results) for the fox data. Model selection was based on the criteria identified by Kass and Raftery (1995) (Table 3.2). Using this approach, the worst-fitting model in terms of Bayes Factors (BFs, see Chapter 2, Section 2.5.8) is chosen as the base model and BFs are then used to compute relative probabilities of how well each model fits the data compared with the base model. Despite some authors (see for example Gelman *et al.*, 2014) believing BFs are unsuitable for assessing goodness of fit unless the base model fits the data well, Kass and Raftery (1995) demonstrated BFs can be used to compare differences between predictive scores and can therefore measure the success of different models at predicting the data. Kass and Raftery (1995) recommended use of twice the natural logarithm of the BF so as to have the same scale as the DIC and likelihood-ratio test statistic. The overarching proviso for comparison of models is that all models are fitted to the same dataset.

Table 3.2: The criteria and interpretation of Bayes Factors (BFs) proposed by Kass and Raftery (1995) for Bayesian model selection.

BF = Bayes Factor. Typically, the worst fitting model (i.e. the model with the lowest BF) is used as the base model. In this case BFj is the Bayes Factor for Model Mj with respect to model M_b (the base model).

BF_{jb}	$2\log_e(BF_{jb})$	Evidence against model M_b
1 to 3	0 to 2	Not worth more than a bare mention
3 to 20	2 to 6	Positive
20 to 150	6 to 10	Strong
>150	>10	Very strong

The preferred model for each year was also assessed through visual examination of the trace plots for each category of treatment parameter (see Chapter 2, Section 2.5.8 for explanation of the trace plots). The model was also assessed through visual examination of autocorrelation plots, and examination of the histogram and a kernel density estimates overlaid with densities estimated using the first and the second halves of the MCMC sample. Substantial overlapping of these two halves of the chain indicates the chain is not drifting. The exploratory analysis also examined the preferred

(Poisson) model acceptance rates and efficiencies of the Metropolis-Hastings algorithm (see below for descriptions). Examples are shown in the results sections.

Bayesian inference based on an MCMC sample is only valid if the Markov chain has converged and the sample is drawn from the desired posterior distribution (StataCorp, 2019). To confirm convergence of the MCMC chain requires, among other criteria, verification of convergence for all model parameters and not simply for a subset of parameters of interest. This protracted procedure was adopted as there is no single conclusive convergence criterion and assessment of multiple conditions is required to infer convergence. The more aspects of the MCMC sample examined, the more reliable are the results (StataCorp, 2019).

Gelman *et al*. (2014) also recommended comparing the results of multiple simulation sequences or multiple chains and visually comparing the results using trace and density plots for each chain as a formal test for convergence. By comparing the trace plots of different simulation sequences (different chains) for each model parameter it is possible to detect convergence irregularities and allows assessment of the overlap of the simulated marginal distributions for each parameter. When using multiple chains, Stata provides default initial values which differ for each chain, however the default values do not necessarily cover overdispersed initial values (i.e. do not necessarily cover the full range of values for all model parameters). Covering this range can be achieved by specifying initial values which differ for each chain. To infer convergence when using multiple chains requires assessment of the trace plots for each parameter for each chain. If the Markov chains have converged, there should be no substantial differences between the trace plots or between the sampled marginal distributions. When one or more of the trace plots are separated it indicates the chains have explored different domains of the posterior distribution and they have not all converged. This may be overcome by increasing the burn-in period (see below).

When using multiple simulation chains, Stata reports the simulation summaries (the log marginal-likelihood log(ML), acceptance rate and sampling efficiency, see below) averaged over all chains and also provides the Max Gelman–Rubin **Rc** convergence statistic, which is the maximum value of the statistics across chains. This Rc statistic is used for determining convergence by measuring the discrepancy between chains. A Max Gelman-Rubin Rc value of less than 1.1, averaged over all chains, is recommended as the criterion by which to infer convergence (StataCorp, 2019), however this does not negate the requirement for assessment of convergence visually through inspection of trace plots, autocorrelation plots, histogram and a kernel density estimates (first and second half). In addition to providing the averaged Max Gelman-Rubin Rc statistic, this statistic is also provided for each parameter separately for each chain, as is the mean of the posterior distribution for each parameter, the standard deviation, the Monte Carlo standard error (MCSE), the 95% equal-tailed Credible Interval and the MCMC efficiencies and correlation times (see below). Only those models deemed to have converged on the above criteria and on the additional criteria below were then used to compare the set of candidate models.

Bayesian modelling comparing the suite of candidate models for each of the three years was focused on comparing the effect on fox abundance from different levels of fox control (baiting frequencies), and deliberately compared only simple models with few parameters to provide *"an understanding of the dominant aspects of the system under study"* (Burnham and Anderson, 2002). For each year, only 12 biologically meaningful candidate models were compared. The count data (MKTBA) was the dependent variable and every model included a treatment effect (i.e. the frequency of baiting). The additional explanatory variables and the candidate models are shown in Table 3.3 and Table 3.4, respectively. Modelling the interaction effect of treatment and distance (models 05, 09, 10 and 12, Table 3.4) conformed to the principle of marginality relations (Nelder, 1992; 1994), i.e. the interaction term was modelled with inclusion of the main effect variables. None of the variables was transformed or standardised. The rationale for this was to ensure that, should the result infer an effect from a quantitative dependent variable, the result would be provided in a way to enable a meaningful interpretation. For example, if a model of interest included the variable for distance (*dist*) in addition to the effect of treatment, without standardising the *dist* variable, a result of say a 5% decrease in fox abundance with every km of distance from the forest perimeter is far more meaningful than reporting (from standardised variables) there is a 0.1 standard deviation in fox abundance with every 0.5 standard deviations in distance from the forest perimeter. Convergence issues which may result from not standardising variables (e.g. with different scales a wide variation in the range of values covered by different variables which may result in poor mixing of the MCMC chain or poor acceptance rates) can be addressed through "blocking" of parameters or increasing the MCMC chain and/or the burn-in period (see below). In addition to the variables listed in Table 3.3, there are numerous other variables which may influence fox abundance (and detection) for which no data were available. However, the data set was small and the objective was aimed at comparing the different biologically plausible models to assess the dominant effects from baiting frequency, as opposed to assessing all tapering effects from a large suite of variables.

Use of a Bayesian approach offered the opportunity to use existing knowledge of the known knockdown effect from baiting as informative priors in year 1. These informative priors in a Bayesian framework, when combined with the data, result in the posterior probability of the parameter of interest (see Chapter 2). The (model averaged) mean of the posterior distribution for all parameters from the preferred year 1 model(s) was then used as the informative priors for the year 2 models. Similarly, the (model averaged) mean of the posterior distribution for all parameters from the preferred year 2 model(s) was then used as the informative priors for the year 3 models.

Selection of the most appropriate informative priors for year 1 was also achieved through a model selection process. Initially, default (non-informative) priors (i.e. with no prior knowledge of the effect of baiting) were compared with six different informative priors. Five of the six informative priors were based on prior knowledge of the effect of baiting on fox populations (see Chapter 1, Section 1.4). Those studies reported the rate of bait uptake could be as high as 88% (Thomson and Algar, 2000). This rate of uptake reflects an acute, knockdown effect, whereas the northern jarrah forest study was aimed at assessing the chronic, long term effect from baiting. Intuitively, the longer term chronic effect from baiting would likely result in a lesser reduction in fox abundance than the acute effect, as, over a longer time frame, the resident population is subject to the effects from immigration (and emigration) of foxes to (and from) the study area between baiting events. Any resident fox population will also be subject to the effect from births and deaths occurring between baiting events (i.e. over the longer term the population is not closed). Therefore, when formulating informative priors, a conservative approach was adopted. The informative priors considered were those which modelled five different levels of reduction of the fox population, varying from 10 to 50%, modelled as constant across all baited treatments. An additional model incorporated informative priors modelling a 10%, 20% and 30% reduction in the two, four and six baitings per year treatment group respectively.

Table 3.3: The variables incorporated in the set of candidate models of fox (*Vulpes vulpes*) and cat (*Felis catus*) abundance at 17 sandplot networks within the northern jarrah forest, south-west Western Australia.

Variable	**Model *syntax***	**Description and rationale**
Treatment	*n.treat*	The baiting treatment group within which each sandplot network was located. Treatment groups differed in the annual frequency of 1080 fox baiting events and ranged from 0 (unbaited control) to two, four and six baitings per year. As there was no *a priori* rationale to assume six baitings was one and half times, three times or infinitely more effective than the four, two and unbaited treatments respectively, the covariate was treated as categorical. The *'n'* in the syntax used refers to the category of the covariate, e.g. *2.teat* refers to the two baitings per year treatment. Fox abundance was hypothesised to decrease with increased baiting frequency.
Distance	*dist*	The shortest straight line distance (km) to the edge of the forest (the interface between forest and agricultural land) from the centre of the minimum convex polygon (MCP) encompassing all sandplots within each network. Fox abundance was hypothesised to decrease with increasing distance from agricultural land as a consequence of increased dispersal distance from agricultural land. Cat abundance in relation to distance was potentially the reverse, as increased fox abundance may result in increased competition between foxes and cats and may potentially result in increased cat abundance (mesopredator release) at increased distance from agricultural land.
MCP	*mcp*	The size (ha) of the minimum convex polygon (MCP) encompassing all sandplots within each network.
Roading	*road*	The extent of roading (km) within each MCP encompassing all sandplots at each network. Fox abundance was hypothesised to increase as a result of increased access provided by an increase in the extent of roading. Cat abundance may potentially reflect a mesopredator release effect.
Plot density	*plot_dens*	The density of readable sandplots (per 100m^2) within each sandplot network (MCP) each day. This had the potential to vary daily, however this was only relevant to the cat (pwca) data where modelling was of the daily count, not the day-10 count (MKTBA) for the fox data.
Day	*day*	The day of monitoring, for day one to day 10 at each sandplot network (MCP), each year, and only relevant to the cat (pwca) data, as above.

Table 3.4: The set of 12 candidate models of fox (*Vulpes vulpes*) abundance at 17 sandplot networks within the northern jarrah forest, south-west Western Australia. X indicates the variable was included in the model. See Table 3.3 for description of each variable.

	variable				
Model number	*i.teat*dist (interaction)*	*i.treat*	*dist*	*road*	*mcp*
01		X			
02		X	X		
03		X		X	
04		X			X
05	X	X	X		
06		X	X	X	
07		X	X		X
08		X		X	X
09	X	X	X	X	
10	X	X	X		X
11		X	X	X	X
12	X	X	X	X	X

All models with informative priors were "very strongly" supported when compared to the model with default non-informative priors (see results). The model with most support (the preferred model) was the model with the "6th" *informative priors (modelling* a 10%, 20% and 30% reduction in the two, four and six baitings per year treatment respectively), albeit with only a "bare mention" of evidence against all other models with informative priors. Subject to confirmation of convergence and meeting other criteria (see below), the year 1 data were then used to compare the 12 candidate models, each with this 6th informative priors.

The 12 models in the set of candidate models for each year were also assessed with blocking where appropriate. In Stata, "blocking" is the term where model parameters are separated into two or more subsets or blocks and the Metropolis-Hastings (MH) algorithm updates are applied to each block separately. This can overcome poor mixing of the Markov chain, which may result in very low (or very high) acceptance rates. Adaptive MH algorithms are prone to this problem, especially when model parameters have very different scales. When acceptance rates are low (approaching zero) most of the proposals (i.e. the subsequent iterations in the MCMC chain) are rejected and it indicates the chain has failed to explore substantial regions of posterior domain. Conversely, when acceptance rates are high (approaching 1), the chain has again remained in a small region and has again failed to explore the whole posterior domain. Acceptance rates in the vicinity of 0.45 (or 45%) for a univariate posterior are optimal (StataCorp, 2017).

Efficiency is a measure of the degree of autocorrelation in the generated sample. Ideally the sampling efficiency (the size of the uncorrelated sample) will approximate the MCMC sample size. Sampling efficiency can be assessed by examination of the scatterplots of the simulated sample to identify the extent of correlation between variables (i.e. correlations between variables in the MCMC simulated data set). Where there is no significant correlation between variables a high sampling efficiency can be expected. Where there is significant correlation, blocking can be used to place the correlated variables in a separate block from variables not strongly correlated, and in doing so, improve the MCMC efficiency. Additionally, as the number of parameters increases, the "efficiency" of the MH algorithm decreases. Blocking can also be used in this situation to improve efficiency. As well as measuring the degree of autocorrelation in the generated sample, the efficiency is also a measure of the effective sample size (ESS) of the MCMC sample. Although the closer the ESS estimates are to the MCMC sample size, the less correlated is the MCMC sample, some correlation will occur (see below). With the MH algorithm, ESS values considerably smaller than the MCMC sample size (as low as single digit percentages) are acceptable. Values close to, or below, 1% of the MCMC sample size may indicate a requirement to improve the sampling efficiency. This can be achieved by increasing the MCMC sample size and/or by incorporating thinning.

In Stata, the default MCMC sample size is 10,000 with a burn-in period of 2,500, without thinning. This sample size and burn-in period arbitrarily determines the precision of posterior summaries, which may be different for different model parameters and will depend on the efficiency of the Markov chain (StataCorp, 2017). Although some softwares used for Bayesian modelling may highlight issues with warnings such as "there is a high autocorrelation" or report "a low level for the minimum efficiency", this doesn't resolve these issues and further highlights the importance of examining the MCMC chain. Methods to improve the MCMC convergence and the precision include extending the burn-in period, increasing the MCMC sample size and using a thinning measure.

The burn-in period is the period during which the chain is converging to its stationary distribution from its initial state. The iterations during the burn-in period are discarded from the MCMC sample used for analysis. By design, adjacent observations from the MCMC chain are likely to be positively correlated; therefore autocorrelation is typically present in MCMC samples. This is not necessarily an issue, however autocorrelation in the MCMC sample may be so high that obtaining a sample of the necessary size becomes infeasible and will require incorporating measures to reduce autocorrelation (StataCorp, 2019). One such mechanism to reduce autocorrelation is to incorporate "thinning" (or a thinning interval). When thinning is specified, a gap is created between simulated values. For example, using the command "thinning(10)" specifies that every 9 sample observations are discarded and observations 1, 11, 21, etc. are used. In addition to visual examination of the autocorrelation plots, the extent of autocorrelation can be seen by the reported "correlation times". This autocorrelation can be viewed as estimates of autocorrelation lags in the MCMC samples before the correlation drops to zero. The correlation time, ESS and efficiencies are reported in the posterior summaries. Examples are given in the results.

In addition to reporting the posterior mean, the summaries reported after simulation include posterior median estimates, estimates of the posterior standard deviation, the Monte Carlo standard errors (MCSE) and the 95%BCIs. The reported Bayesian 95% equal-tailed credible intervals differs from the frequentist interpretation of 95% confidence intervals. The frequentist interpretation of a 95% confidence interval is that by repeating an experiment multiple times and computing a 95% confidence interval each time, then 95% of those intervals will contain the true value of the parameter. However, for any given confidence interval, the probability of it containing the true value of the parameter of interest is not known, it is only possible to infer that the given confidence interval provides a plausible range for the true value of the parameter. A 95% Bayesian credible interval, on the other hand, provides a range for a parameter such that the probability that the parameter lies in that range is 95%. The equal-tailed component is defined to mean both tails of the marginal posterior distribution have the same probability. When multiple chains are used, the summary results in the estimation table are based on all chains. Consequently, the results are more precise (have smaller MCSEs) than those reported for a single chain.

For each year, BFs were used to reduce the 12 candidate models to a competitive model set which excluded those models with little support (i.e. little model weight, or posterior model probability close to zero). The competitive model set was then used for model averaging. The standard Bayesian solution for model averaging is to "model average" over all models, however Madigan and Raftery (1994) proposed a two-step process whereby some models are excluded from consideration. The first step, termed "Occam's Window" (Madigan and Raftery, 1994), eliminates models from consideration if they predict the data *"far less well"* than the model which provides the best prediction. To determine this *"far less well"* level, Madigan and Raftery (1994) proposed use of a cut-off value, which they termed *"C"*. In doing so the models excluded were those not belonging to the model set (M_{set}):

$$M_{set} : \frac{\max_l \Pr(\mathrm{M}_l \mid D)}{\Pr(\mathrm{M}_k \mid D)} \leq C$$

where $\max_l \Pr(\mathrm{M}_l \mid D)$ is the model with the highest posterior model probability; and where $\Pr(\mathrm{M}_k \mid D)$ is the posterior probability of the model of concern.

This is similar to the procedure recommended by Burnham and Anderson (2002) when using AIC or AICc (see Chapter 2). Madigan and Raftery (1994) noted the value for *"C"* is chosen by the data analyst. In practice, an equally arbitrary and subjective approach to the "Occam's Window" stage of determining the competitive model set for model averaging was adopted. Selection was based on the criteria described by Kass and Raftery (1995) (Table 3.2), whereby a model shown to have "strong" or "very strong" evidence against it when compared to the best ranked model, was not included in the competitive model set used for model averaging.

The second stage of the model selection approach described by Madigan and Raftery (1994) is again similar to the model selection approach recommended by Burnham and Anderson (2002), whereby a model is excluded from the set of competitive models if it receives less support from the data than a simpler model. This is consistent with the principles of parsimony, or the often quoted "Occam's razor", and is *"one of the most widely accepted norms of scientific investigation"* (Madigan and Raftery, 1994). Burnham and Anderson (2002) specified this in terms of AIC or $\mathrm{AIC_c}$ values and describe a model as non-competitive where such a model differs from a more competitive model by the addition of only one parameter, has an AIC or $\mathrm{AIC_c}$ value within 2 units of the more competitive model, has a similar log likelihood value to the more competitive model, but does not improve on that model.

Once the competitive model set (M_1, …, M_k) and model weights (or posterior probabilities, based on marginal likelihoods and BFs) were determined for each model within the competitive model set, the posterior distribution of the quantity/parameter of interest is given by:

$$\Pr(\Delta \mid \mathrm{D}) = \sum_{k=1}^{K} \Pr(\Delta \mid M_k, \mathrm{D}) \Pr(M_k \mid D)$$

where Δ is the parameter of interest, given the data, D; and
where $\Pr(M_k \mid D)$ is the posterior probability of model M_k.

Therefore, with model averaging, inference is not conditional on a single model. However, with the exception of year 3, only one model from the 12 candidate models was shown to have any support in terms of BFs (see the results section) and model averaging was not appropriate.

For the fox data only, a final assessment of goodness of fit was carried out by examining the posterior predictive p-values (PPPs) for functions of replicated outcomes. The replicated outcomes are outcome values simulated from the posterior predictive distribution, conditioned on the observed set of explanatory variables from the preferred model (StataCorp, 2017; 2019). The replicated data is then compared with that of the observed data. This comparison is achieved by visually examining distribution histograms. This process is different from the MCMC diagnostic checks which examine the properties of MCMC sampling (i.e. the checks of convergence). Instead, the posterior predictive checking inspects how well the specified Bayesian model describes the observed data. A more formal (quantitative) assessment compares the discrepancy in measures (PPPs) of computed statistics of interest, such as the mean, minimum and maximum statistics, of the replicated data with that of the observed data.

Although PPPs are considered a Bayesian version of classical *p*-values (Rubin, 1984), they differ substantially from frequentist *p*-values. Unlike classical prediction, which produces a single value for each observation, Bayesian prediction produces a sample of T simulated values for each observation. This is a two-step process, whereby model parameters (θ) are simulated from their posterior distribution, then, the new outcome values are simulated from the likelihood model using the simulated model parameters from the first step. The steps are then repeated for pre-specified number of MCMC iterations, T.

The replicated outcomes and PPPs were generated from the year 3 preferred model only, without model averaging (see results for the rationale). In this case the covariates were the treatment categories (*i.treat*) for the year 3 preferred Poisson model of fox abundance. A graphical model of plotted histograms was then used to compare the distributions of the observed and replicated outcomes. PPPs were then determined to quantify any discrepancy between the summaries statistics of the observed and replicated data. The PPP value reported is the proportion of cases when the statistic of interest from the simulated data is greater than or equal to the observed value. PPPs close to 0 or 1 indicate lack of model fit. For a well-fitting model, the PPP should, ideally, be close to 0.5, although values between 0.05 and 0.95 are often considered acceptable in the literature (StataCorp, 2019).

3.3.4.5 The Bayesian modelling approach: the cat (pwca) count data

As with the fox data, exploratory analysis of the cat count data (number of sandplots showing evidence of cat activity, or pwca) for each year were firstly examined visually by plotting a density histogram. The data were also examined more formally, through a Bayesian model selection framework, to determine if the data were overdispersed and/or zero-inflated. The exploratory analysis compared the fit of a Poisson, nbreg, zip and zinb distribution for a simple model, with default non-informative priors, and modelled with the variable for treatment only. Given the sparse nature of the data (see results) and the lack of any published or unpublished data to show cat abundance is affected by fox baiting, the exploratory analysis also compared the fit of a Poisson, nbreg, zip and zinb distribution for a simple model in the absence of a baiting (treatment) effect. As with the fox data, model selection for the exploratory analysis was based on the criteria identified by Kass and Raftery (1995) (Table 3.2). For each year, the exploratory analysis identified a negative binomial distribution in the absence of a baiting effect as the preferred, or appropriate class of model (see results).

Again, as for the modelled fox data, the fit of the preferred model for each year of the exploratory analysis was assessed through visual examination of the trace plots for the parameter(s) of interest, visual examination of autocorrelation plots, histogram, and the kernel density estimates overlaid with densities estimated using the first and the second halves of the MCMC sample. As with the fox data, the model deemed to have an acceptable fit on these criteria and on the criteria for ESS, correlation time, efficiency and acceptance rate was then used to compare the set of candidate models for each year.

For each year, a set of 16 candidate nbreg models was compared. The set of candidate models was restricted to simple models, with no interaction effects and, on the basis of the exploratory analysis, all without modelling a treatment effect (Table 3.5). See the exploratory analysis Sections 3.4.6.1, Section 3.4.7.1 and Section 3.4.8.1 for year 1, year 2 and year 3, respectively. Use of the daily evidence of cat activity (pwca) as the dependent variable enabled inclusion of two additional independent variables; the variable '*day'* (day one to day 10 at each sandplot network); and the variable '*plot_dens'* (the density of readable sandplots (per 100m^2 of each MCP) within each sandplot network each day) (see Table 3.3). Determining the competitive model set was not required as only one model from the 16 candidate models was shown to have any support in terms of BFs (see the results section) and model averaging was not appropriate. Examination of the posterior predictive p-values (PPPs) for functions of replicated outcomes was unable to be performed for the preferred nbreg model.

Table 3.5: The set of 16 candidate models of cat (*Felis catus*) abundance at 17 sandplot networks within the northern jarrah forest, south-west Western Australia.
x indicates the variable was included in the model. See Table 3.3 for description of each variable.

model number	variable				
	i.treat	*dist*	*day*	*road*	*plot_dens*
All models are without a treatment effect					
001					
002		x			
003			x		
004				x	
005					x
006		x	x		
007		x		x	
008		x			x
009			x	x	
010			x		x
011				x	x
012		x	x	x	
013		x	x		x
014		x		x	x
015			x	x	x
016		x	x	x	x

3.3.4.6 Determining the number of days required to monitor fox activity on sandplots

Sandplot monitoring is labour intensive and it is not known how many days are required to monitor and subsequently estimate the number of foxes (or cats) detected from which abundance estimates can then be derived and from which inference can be reliably made. However, by using the data pooled over all years and over all sandplot networks, a correlation value (*r*) was derived for each day, i.e. from the pooled data, the correlation coefficient (*r*) was determined for the correlation between the MKTBA estimate at day 1 and the day-10 MKTBA estimate, the day 2 and day-10 estimate, the day 3 and day-10 estimate, ... , the day-10 and day-10 estimate. This was then plotted to enable a visual assessment of the progressive increase in correlation for the MKTBA value over the 10 days (*r* must =1 at day 10). The intent was to determine whether sandplot monitoring could be run for fewer than 10 days, depending on what value of *r* was deemed acceptable.

3.3.4.7 Monitoring of fox activity post 1080 baiting

Once baiting occurs, the assumption of a closed population was violated as deaths are intended and are likely to occur. However, not all fox deaths from baiting will occur immediately after baiting. Thomson *et al*. (2000) demonstrated fox deaths from 1080 baiting in the semi-arid zone of WA occurred up to 43 days after a baiting event. Although the northern jarrah forest study site is in the more mesic south-west WA, and bait degradation will be more rapid than in the semi-arid zone, the longevity of toxic baits is still likely to extend for some time post-baiting, with not all fox deaths occurring immediately after baiting, i.e. there will be a time lag for some mortality events from baiting as well as an acute effect.

Assessment of fox presence at each sandplot network was carried out, post baiting, in 1999 and in 2000 (years 2 and 3). Assessment was through interpretation of the daily pattern of activity on sandplots, i.e. the estimated MKTBA was for the day of monitoring only. It was intended to determine whether foxes were present post baiting and was not intended to infer anything about fox abundance.

In 1999 post-baiting-monitoring was carried out for 10 days and commenced seven to 10 days after bait delivery. In 2000, monitoring was continuous pre, during and post baiting and continued for up to 43 days (inclusive of pre and post baiting). The daily MKTBA estimate was plotted to allow a visual assessment of the estimated number of foxes post baiting.

3.3.4.8 Validation of the technique to estimate the number of foxes present: validation through the use of trapping and removal techniques

The off-site validation of the technique to estimate the number of foxes detected at completion of 10 days of sandplot monitoring (i.e. the MKTBA estimate) required:

(i) estimating the MKTBA at a sandplot network validation site established in comparable habitat to the northern jarrah forest; followed by

(ii) lethal removal of foxes present at the validation site to assess whether the number of foxes estimated through the MKTBA concurred with the number of foxes removed. This further required the validation site to be geographically separate from the study area to prevent further reduction of fox density from that which may be achieved through 1080 baiting at the treatment sites.

Validation was proposed through lethal removal of foxes by cyanide baiting as described by Algar and Kinnear (1992) after a 10 day period of sandplot monitoring. The premise was that cyanide baiting would remove foxes detected at sandplots. The number of foxes removed would then be compared with the MKTBA estimate from the previous 10 days of monitoring.

Cyanide capsules (see Algar and Kinnear, 1992) were prepared by encasing approximately 1g of powdered sodium cyanide inclusive of 5% Tixolex (a sodium silico aluminate flowing agent) in a cylindrical wax capsule, approximately 75mm long and 7.5mm diameter. The end of the capsule was fitted with a cigarette filter to hold the cyanide in place and a hairpin was inserted through the cigarette filter into the cyanide powder. A small amount of wax was poured over the cigarette filter and hairpin to create a seal. The loop of the hairpin was left extruding from the capsule and used as a hook to secure the capsule to a swivel and fishing-line trace. In the field, the other end of the fishing-line trace (and a second swivel) was tied to a tent peg and secured firmly to the ground. Two cyanide capsules (one made from red wax, the other from white wax) were prepared for use at each baiting station. The resultant wax capsules are brittle and easily broken if interfered with by an animal. The combination of the brittle wax capsule, free-flowing cyanide powder and a tether (the fishing-line trace) is designed to result in administering a lethal dose of cyanide to an animal (in this case a fox) if the animal attempts to ingest, chew or interfere with the capsule. The tether prevents the capsule from being removed and the brittle nature of the capsule is to ensure it breaks to expose the cyanide when interfered with.

The white capsules were coated with ‘condensed milk’ to provide a sweet attractant or lure, the red capsules were coated with pureed liver. The technique has been used successfully in WA for destructive sampling of high density fox populations (see for example Marlow *et al.*, 2000; Thomson and Algar, 2000).

Activity at sandplots was continually monitored at the validation sites pre, during and post removal of any foxes. This monitoring was to assess whether removal of foxes corresponded with a cessation of detection of activity on sandplots. Validation of the technique was initially proposed to be conducted within Marradong and Saddleback forest blocks, which are isolated forest blocks within the northern jarrah forest but not within the study area (Fig. 3.1). The validation trial was scheduled to be carried out concurrently with sandplotting conducted prior to the September baiting in the northern jarrah forest study area.

Failure of the initial (September 1999) and a second attempt (October 1999) (see results and discussion) to reliably remove foxes by cyanide baiting necessitated a change of protocol for removal of foxes. A third and final site, Quindanning Forest Block (Fig. 3.1), was selected in an attempt to validate the technique for deriving the day-10 MKTBA estimate. As per the establishment of sandplots within the baited treatments and control, 25 sandplots were established on the existing roading network within Quindanning Forest Block. The MCP, inclusive of a 250m buffer, incorporating all 25 sandplots at the Quindanning sandplot network was 9.69km^2.

Removal of foxes at Quindanning Forest Block, post the 10 day monitoring period, was through trapping (Victor Softcatch 1.5 padded leg-hold traps) and euthanasia of all trapped individuals. Traps were set at each sandplot where activity had been recorded during the 10 day monitoring period. Trapping was carried out for 14 consecutive days, beyond which time re-invasion by foxes was considered likely to have occurred (see discussion).

3.3.4.9 Validation of the technique to estimate the number of foxes present: validation through the use of molecular techniques

Use of techniques such as camera traps (Long *et al.*, 2007; Sarmento *et al.*, 2009; Vine *et al.*, 2009) and recently reported molecular techniques (e.g. recovery of DNA from collected hair and scats etc.) (Foran *et al.*, 1997; Gompper *et al.*, 2006; Kohn *et al.*, 1999; Long *et al.*, 2007; Mowat and Strobeck, 2000; Piggott *et al.*, 2008; Prugh *et al.*, 2005; Ruibal *et al.*, 2009; Ruibal *et al.*, 2010; Zielinski *et al.*, 2006) provide opportunities to validate derived estimates of the number of individuals detected from sandplot counts. Molecular techniques enable identification of the species responsible for leaving hairs and scats and can also result in identification of individuals, provided sufficient DNA is recovered and appropriate markers are available for the species of interest. Capture-mark-recapture models have also been developed based on capture of samples containing DNA (see White, 2001).

A modification of the technique used to derive a MKTBA estimate was further assessed and validated in 2009 as part of the northern jarrah forest component of the DEC and Invasive Animals Cooperative Research Centre (IACRC) WA Demonstration Site. This component of the research used DNA recovered from scats and hair (Berry and Sarre, 2007) to verify the species detected and, where sufficient DNA was recovered, to identify individuals.

The research carried out through the DEC and IACRC WA Demonstration Site in the period 2006 to 2009 included monitoring of fox activity at passive and active sandplots. Sandplots consisted of a 1m wide swathe of sand raked across the width of the road. Sandplots were otherwise as described for the Operation Foxglove research (this study, i.e. with each sandplot a minimum of 500m from its nearest neighbouring sandplot and with 25 sandplots established within a maximum of 25km^2). A MCP, inclusive of a 250m buffer, was again generated to determine the area covered by each sandplot network. Each sandplot was monitored for six consecutive days only (compared with the 10 days for the Foxglove research). Two hair collection devices – the 'Sticky Wicket' (Fig. 3.6) (Algar *et al.*, unpublished) and the 'Poly Pipe' (Fig. 3.7) (Garretson *et al.*, 2008) - were provided at every second sandplot, i.e. every second sandplot had a 'Sticky Wicket' at one end and a 'Poly Pipe' at the other end. Each hair collection device also had an olfactory lure and/or reward (a small piece of rabbit secured within the Poly Pipe and a mixture of cat faeces and cat urine, 'pongo', at each Sticky Wicket). An auditory lure (a felid attracting phonic or FAP: a small plastic box containing a battery-operated electronic circuit with a speaker emitting a 'meow' sound) was also provided at every Sticky Wicket. Therefore, plots alternated between passive and active, the latter having the hair collection devices with lures and a reward. Hair collection was undertaken concurrently with sandplot monitoring. Collected hairs which were identified as fox hair through melt curve analysis (Berry and Sarre, 2007) were then genotyped to identify individual foxes. Where hair was successfully collected at sandplots and sufficient DNA extracted to enable genotyping, the pattern of activity by individual foxes could be identified and used to verify or refute the estimate derived by the MKTBA technique.

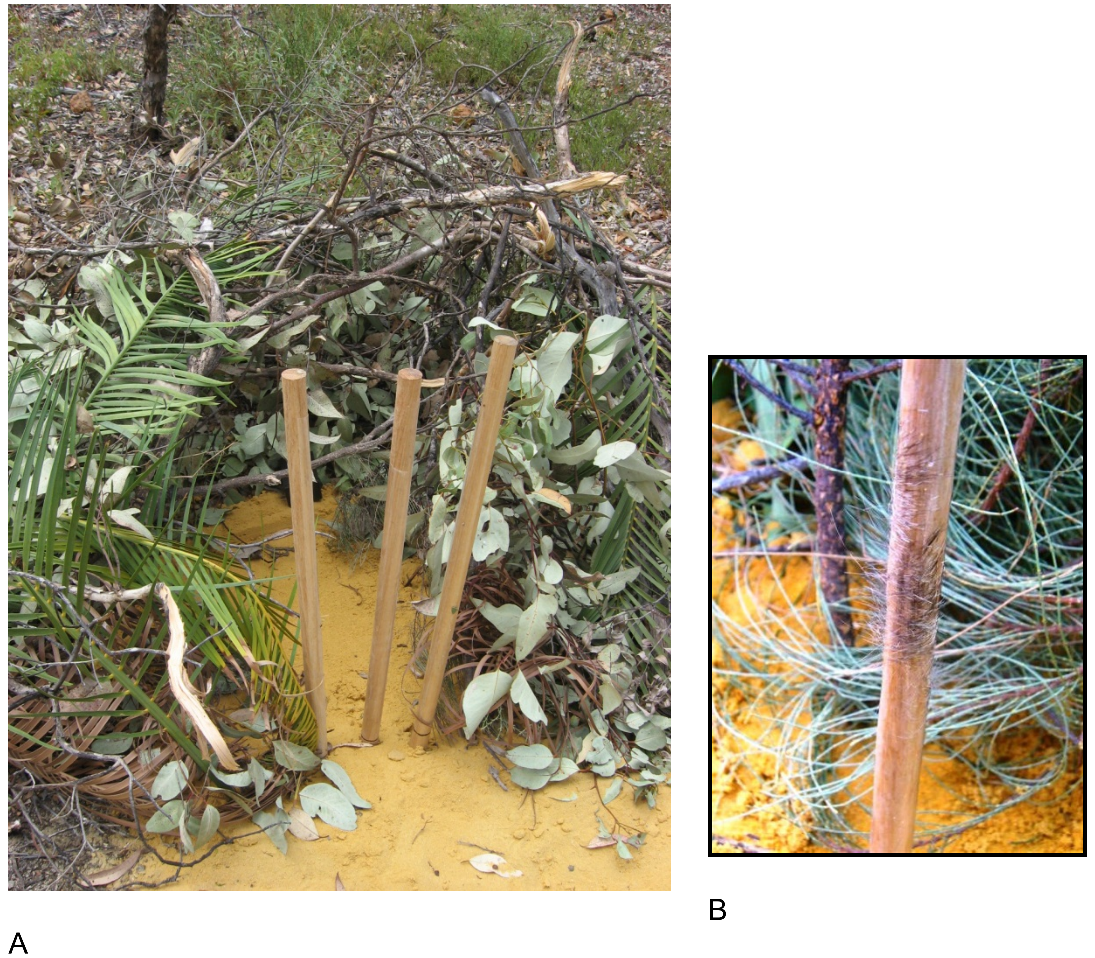


Figure 3.6: The 'Sticky Wicket' hair collection device.

A: The device shown *in situ*, designed to collect hair on double-sided tape secured to each stump of the Sticky Wicket (Algar, unpublished). The species responsible for leaving hair was determined by melt curve analysis of the DNA extracted from the collected hair. Genotyping to individual was attempted for all fox (*Vulpes vulpes*) and cat (*Felis catus*) hair when sufficient DNA was recovered.

B: Hair recovered from double sided tape (photograph for Figure 3.6B by Dave Algar).

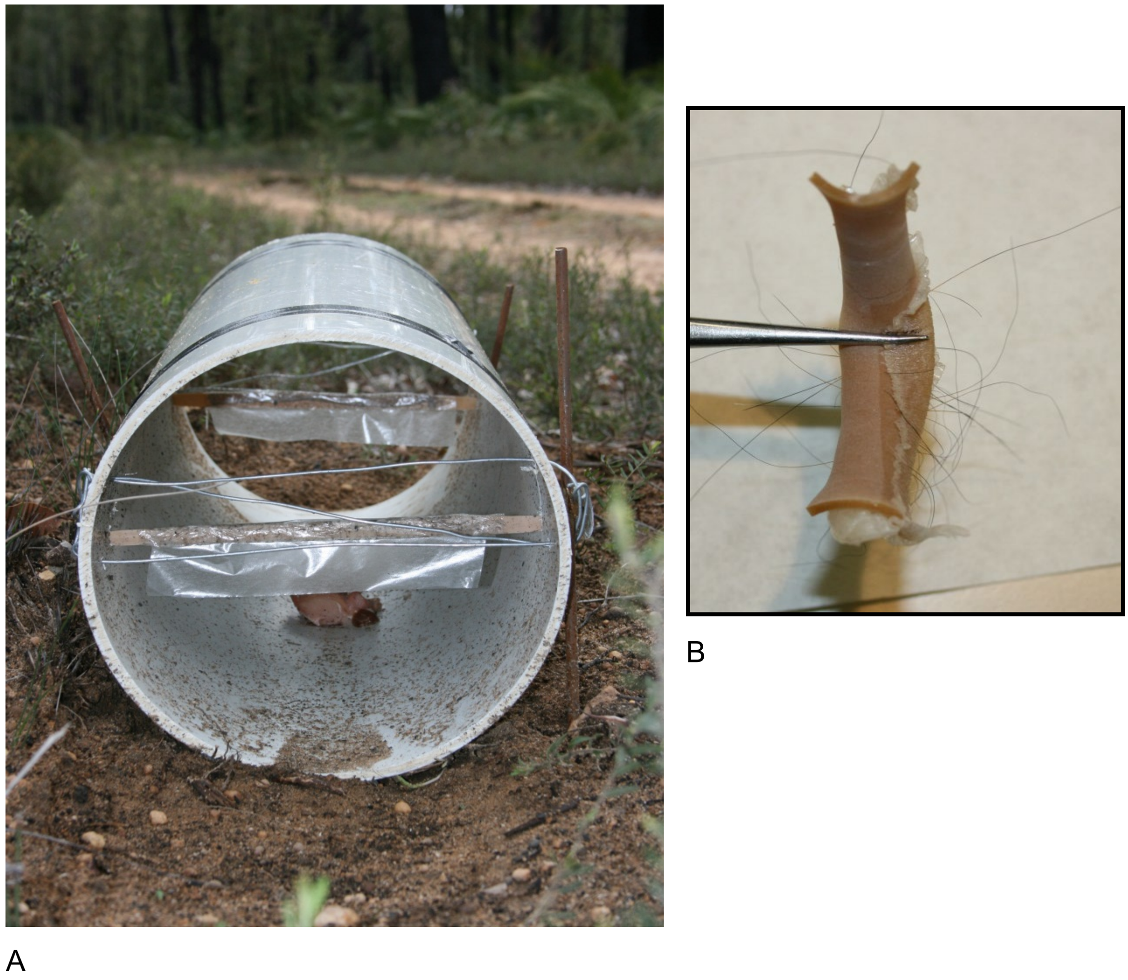


Figure 3.7: The ‘Poly Pipe’ hair collection device.

A: The device shown *in situ*, designed to collect hair on double-sided tape secured within the pipe (Garretson *et al.*, 2008). The species responsible for leaving hair was determined by melt curve analysis of the DNA extracted from the collected hair. Genotyping to individual was attempted for all fox (*Vulpes vulpes*) and cat (*Felis catus*) hair when sufficient DNA was recovered.

B: Hair collected on the double sided tape at a Poly Pipe hair collection device (photograph for Figure 3.7B by Oliver Berry).

3.4 Results

3.4.1 Detection of fox activity

Data on activity at sandplots were collected from a total of 11,778 sandplots for the 1998, 1999 and 2000 pre-baiting monitoring sessions A further 972 plots were uninterpretable. Fox activity was detected on 939 individual sand plots.

3.4.2 Fox abundance year 1

3.4.2.1 Year 1 preliminary/exploratory analysis of the fox MKTBA count data

Visual examination of the plotted count data indicated a Poisson distribution (Figure 3.8). More formal examination (model comparison and diagnostics) also identified a Poisson distribution as the most appropriate class of model for the year 1 data (Table 3.6).

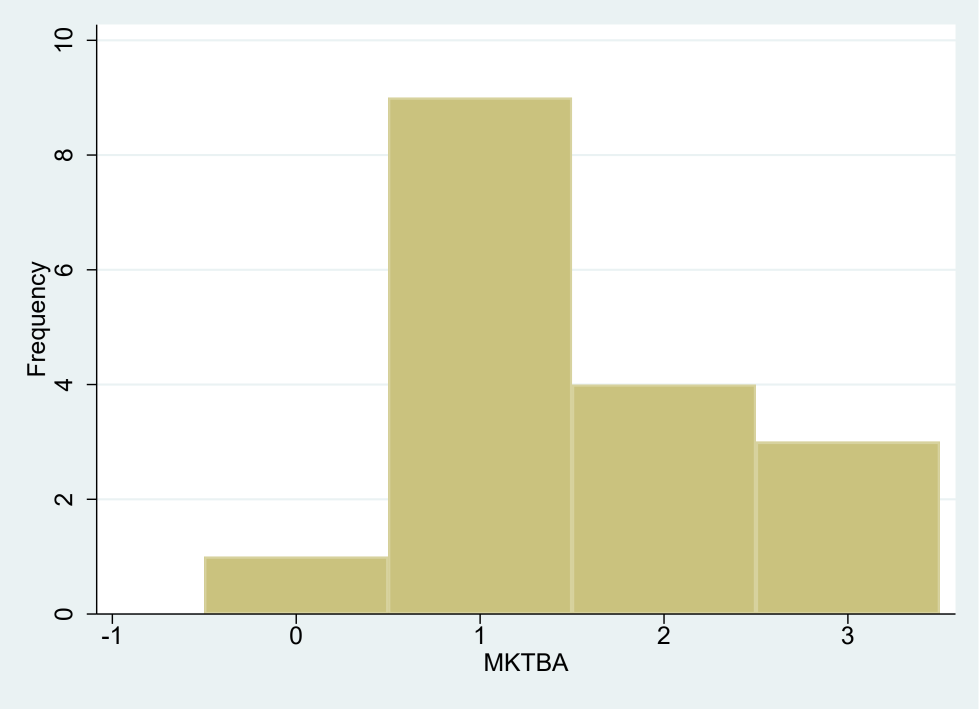


Figure 3.8: Frequency histogram for the minimum number of foxes known to be alive estimate after 10 days of monitoring (Day-10 MKTBA) from sandplots monitored for evidence of fox (*Vulpes vulpes*) activity at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 1.

Despite the relatively large difference in posterior model probabilities (pr=0.52 and pr=0.29 for the Poisson and nbreg models respectively), interpretation of the BFs and the Kass and Raftery (1995) criteria for model selection indicated there was little evidence (“bare mention”) against the nbreg model (Table 3.6). However, examination of the *ln_alpha* value (or its exponentiated value, the dispersion parameter) from the nbreg model indicated the Poisson model was more appropriate. In this case, the *ln_alpha* value was strongly negative (i.e. an exponentiated value of zero). A positive value for *alpha* indicates overdispersion, and as this value approaches zero the model (the nbreg model) reduces to the simpler Poisson model. Whereas, if the dispersion parameter is significantly greater than zero then the data are over dispersed and are better estimated using a negative binomial model than a Poisson model.

Table 3.6: Exploratory analysis of the year 1 fox (*Vulpes vulpes*) count data to identify the appropriate class of model for further modelling.

poisson = Poisson regression; nbreg = negative binomial regression; zip = zero-inflated Poisson regression; zinb = zero inflated negative binomial regression.

log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model	log(ML)	log(BF)	P(M|y)	K&R evidence
Bayes_prelim_poisson_year1	**-44.3313**	**2.0431**	**0.5211**	
Bayes_prelim_nbreg_year1	-44.9129	1.4614	0.2913	Bare mention
Bayes_prelim_zip_year1	-45.7986	0.5757	0.1201	Positive
Bayes_prelim_zinb_year1	-46.3744	.	0.0675	Positive

For the preferred (Poisson) model, visual assessment of the single chain trace plots for each category of treatment variable indicated convergence (see Chapter 2, Section 2.5.8 for explanation of the trace plots) with the trace plots for each parameter showing a good level of mixing (i.e. where the plot shows the MCMC simulated values traversing the posterior domain rapidly). Figure 3.9 shows this mixing and the trace plot for the constant term (i.e. the unbaited treatment), centred around 0.6 and it traverses the distribution quickly also explores the portions of the distribution where the density is low. Convergence was also indicated by the autocorrelation dropping-off to a low level after approximately 10 lags, the shape of the histogram was unimodal and the kernel density plots showed good overlapping of the first and second halves of the MCMC sample (Fig. 3.9). Convergence was also indicated by the range traversed by the MCMC chain for all parameters, the rapid dropping-off of autocorrelation, the unimodal histograms and the good overlapping of the first and second halves of kernel density estimate.

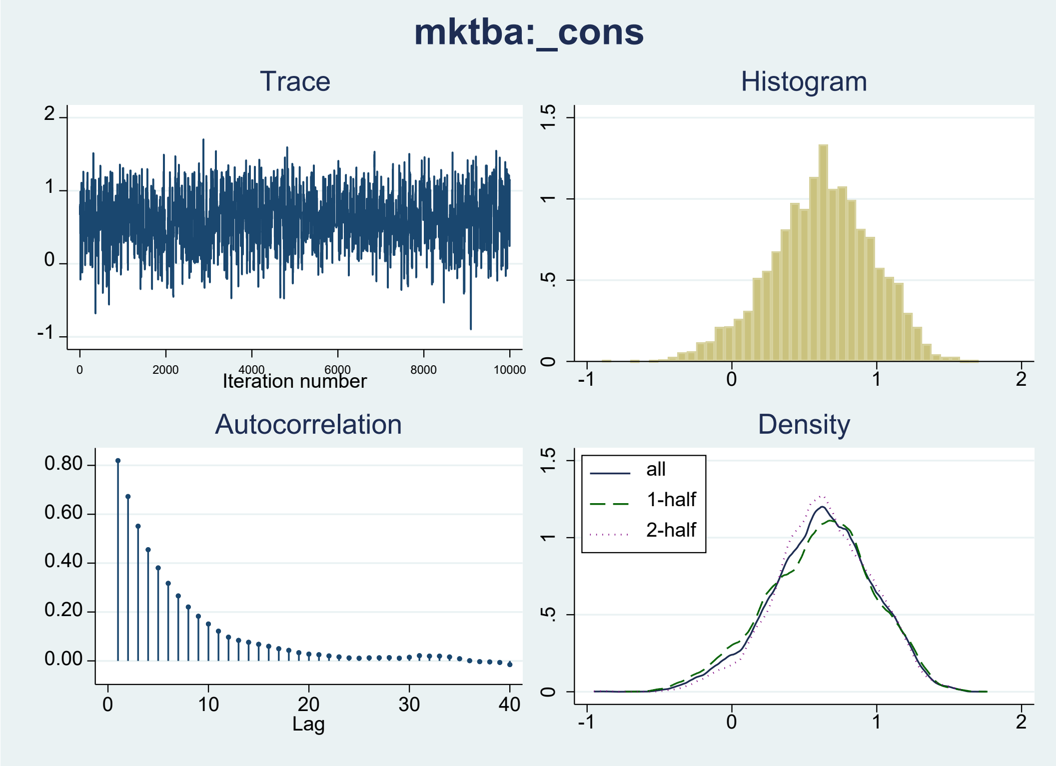


Figure 3.9: MCMC trace plot, autocorrelation plot, frequency histogram and kernel density plots to visually examine convergence of the MCMC of parameter estimate for the constant term (unbaited treatment) from the preferred bayesmh Poisson model identified in the exploratory analysis when modelling fox abundance within the northern jarrah forest, south-west Western Australia, year 1.

Examination of the diagnostic statistics when the Poisson model was run with multiple (3) chains reported a maximum Gelman–Rubin Rc statistic of 1.002, and therefore meets the convergence criteria. When examined separately, each parameter of each chain also met the convergence criterion. The average acceptance rate was 21.6% and the average efficiency was 6.7%. Therefore the Poisson model was used for year 1 model comparisons of the 12 candidate models.

3.4.2.2 Year 1 choice of informative priors

The preferred model (with the “sixth” informative priors, which modelled a 10%, 20% and 30% reduction in fox abundance in the two, four and six baitings per year treatment groups, respectively) was strongly (BF) preferred over the model with default, non-informative priors. However there was only “a bare mention” of evidence against the other models with informative priors (Table 3.7).

Table 3.7: The default non-informative priors and six informative priors compared for modelling the year 1 fox (*Vulpes vulpes*) count data to identify the preferred priors for further modelling.

log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

model	model description	log(ML)	log(BF)	P(M|y)	K&R evidence
default, non-informative priors	modelled with baiting having a constant effect on fox abundance over the unbaited and all baited treatments.	-39.6455	-	0.0000	very strong
first informative priors	modelled with baiting having a 10% reduction in fox abundance across all baited treatments when compared with the unbaited treatment.	-30.5916	9.0539	0.1640	bare mention
second informative priors	modelled with baiting having a 20% reduction in fox abundance across all baited treatments when compared with the unbaited treatment.	-30.5633	9.0823	0.1688	bare mention
third informative priors	modelled with baiting having a 30% reduction in fox abundance across all baited treatments when compared with the unbaited treatment.	-30.6900	8.9555	0.1487	bare mention
fourth informative priors	modelled with baiting having a 40% reduction in fox abundance across all baited treatments when compared with the unbaited treatment.	-30.5685	9.0771	0.1679	bare mention
fifth informative priors	modelled with baiting having a 50% reduction in fox abundance across all baited treatments when compared with the unbaited treatment.	-30.5502	9.0954	0.1710	bare mention
sixth informative priors	**modelled with baiting having a 10%, 20% and 30% reduction in fox abundance in the two, four and six baitings per year treatments, respectively when compared with the unbaited treatment**	**-30.5006**	**9.1450**	**0.1797**	

Diagnostics for the preferred model showed no evidence of the need for blocking (the matrix of the scatterplots of the simulated values indicated no significant correlations). The model acceptance rate of 18.5% was lower than the acceptance rate for four of the other five models with informative priors, however the average efficiency (4.9%) was comparable with all other models with informative priors. The correlation times were also comparable with all other models with informative priors. The trace plot for all parameters did not exhibit any trends, and traversed the distribution quickly. For all parameters the autocorrelation died off very quickly and the kernel density estimates based on the first and second halves of the sample were very similar to each other and were close to the overall density estimate.

When modelled with multiple (3) chains, the averaged acceptance rate (22.9%) and the averaged sampling efficiency (5.6%) of the preferred model improved over that reported for the single chain. The precision of the estimation results (lower MCSEs) was also improved for all model parameters. The Max Gelman-Rubin Rc value was 1.005, indicating convergence and diagnostic estimates Rc reported separately for each chain was lower than 1.1, suggesting the convergence of all chains. For all chains, visual inspection of trace plots, autocorrelation plots and kernel density estimates (first and second halves) also indicated convergence. Consequently, the preferred model (with the “sixth informative priors”) was considered to have an acceptable goodness of fit and was then used to compare the 12 candidate models for the year 1 data.

3.4.2.3 Year 1 model comparison and model selection for candidate models of fox abundance

The model ‘Poisson_01’, which modelled the treatment effect only (see Table 3.3 and Table 3.4 for description of the variables included in each model), was the only model with any support, with a posterior model probability of over 99% (Table 3.8). The Kass and Raftery (1995) criteria for model selection indicated “very strong” evidence against all other models when compared to model ‘Poisson_01’.

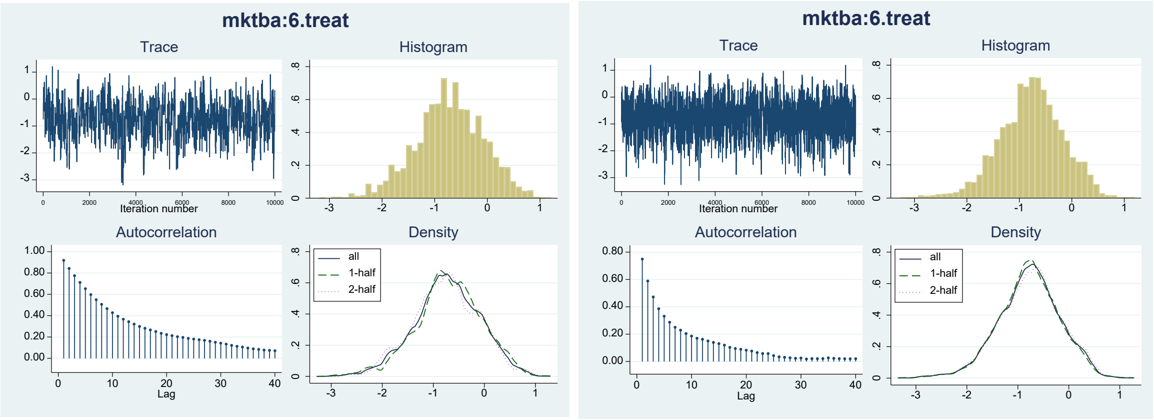
Table 3.8: Comparison of 12 candidate models of the fox (*Vulpes vulpes*) count data for year 1, with informative priors

See Table 3.3 and Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model number	log(ML)	log(BF)	P(M|y)	K&R evidence
Poisson_01	**-30.5006**	**46.1737**	**0.9929**	**-**
Poisson_02	-35.5905	41.0838	0.0061	very strong
Poisson_03	-37.4150	39.2593	0.0010	very strong
Poisson_04	-46.5105	30.1638	0.0000	very strong
Poisson_05	-50.0760	26.5983	0.0000	very strong
Poisson_06	-42.7536	33.9207	0.0000	very strong
Poisson_07	-48.3503	28.3240	0.0000	very strong
Poisson_08	-49.5942	27.0801	0.0000	very strong
Poisson_09	-57.7101	18.9642	0.0000	very strong
Poisson_10	-65.9015	10.7727	0.0000	very strong
Poisson_11	-54.9833	21.6909	0.0000	very strong
Poisson_12	-76.6743	.	0.0000	very strong

The two next ranked models were ‘Poisson_02’ and ‘Poisson _03’ which, in addition to the treatment effect, included the variable *dist* (the distance from the forest interface with agricultural land) and *road* (the extent of roading within the MCP capturing all sandplots), respectively. Each of these models differed from the ‘Poisson_01’ model (the preferred model) by adding only one variable and neither improved on the simpler model (in terms of BFs). They were therefore considered not competitive on the “Occam’s razor” principle (Madigan and Raftery, 1994). Similarly, they were considered not competitive on the “Occam’s Window” principle, subject to the arbitrarily defined value of “C”, or in this case defined by the Kass and Raftery (1995) criteria where models with “strong” or “very strong” evidence against then were not included in the competitive model set.

For the preferred model the range traversed by the MCMC chain for all parameters (shown by the trace plots) and the acceptance rate of 18.5% indicated good mixing of the MCMC chain. However, with blocking the acceptance rate was improved (increased to 43.6%) and the mean efficiency was also improved. Blocking showed similar improvements in the rate of dropping off of the autocorrelation, the unimodal shape of the histograms and the overlapping of kernel density estimates (first and second halves) (Fig. 3.10).



A B

Figure 3.10: MCMC comparison of trace plots, autocorrelation plots, frequency histograms and kernel density plots to visually examine convergence of the MCMC of parameter estimate for the six baitings per year treatment group from the preferred bayesmh Poisson model fox abundance within the northern jarrah forest, south-west Western Australia, year 1.

A: Without blocking; B: With blocking

When modelled with three chains, the precision of the estimation results was improved (lower MCSEs) for all model parameters. The Max Gelman-Rubin Rc value was 1.005, indicating convergence. When reported separately for all parameters the Rc value was lower than 1.1, suggesting the convergence of all chains. As none of the other models had any support there was no model averaging and the model parameters from the preferred model from year 1 were then used as informative priors when modelling the year 2 data.

3.4.3 Fox abundance year 2

3.4.3.1 Year 2 preliminary/exploratory analysis of the fox MKTBA count data

Visual examination of the plotted count data again indicated, but far from definitively, a Poisson distribution (Figure 3.11). More formal examination (model comparison and diagnostics) also identified a Poisson distribution as the most appropriate class of model for the year 2 data (Table 3.9). Unlike Year 1, the year 2 data showed some support for the nbreg model, however the Poisson model was preferred in terms of BFs and posterior model probability (with Pr = 46% vs Pr = 30% respectively) and by the criteria proposed by Kass and Raftery (1995), but only as a "bare mention". The output from the nbreg (the dispersion parameter) indicated the Poisson model was more appropriate with *ln-alpha* -77.73357, i.e. alpha = 0. There was no support (in terms of BFs) for the zip or zinb models.

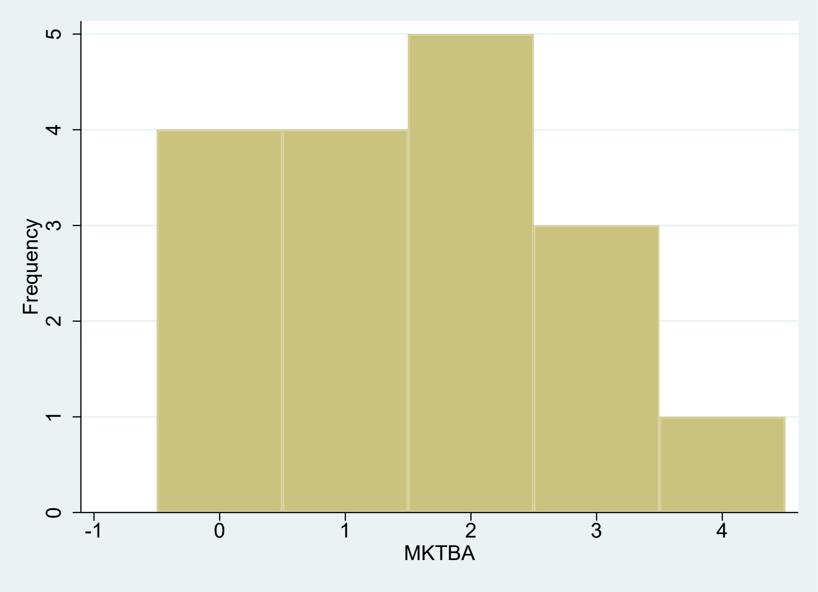


Figure 3.11: Frequency histogram for the minimum number of foxes known to be alive estimate after 10 days of monitoring (Day-10 MKTBA) from sandplots monitored for evidence of fox (*Vulpes vulpes*) activity at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 2.

Table 3.9: Exploratory analysis of the year 2 fox (*Vulpes vulpes*) count data to identify the appropriate class of model for further modelling.

poisson = Poisson regression; nbreg = negative binomial regression; zip = zero-inflated Poisson regression; zinb = zero inflated negative binomial regression.

log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model	log(ML)	log(BF)	P(M|y)	K&R evidence
Bayes_prelim_poisson_year2	**-47.1405**	**1.9821**	**0.4635**	
Bayes_prelim_nbreg_year2	-47.5754	1.5472	0.3000	Bare mention
Bayes_prelim_zip_year2	-48.1284	0.9943	0.1726	Bare mention
Bayes_prelim_zinb_year2	-49.1226	.	0.0639	Positive

As was the case for the year 1 preliminary analysis, visual assessment of the preferred (Poisson) model for the single chain trace plots for each category of treatment variable indicated convergence with the trace plots for each parameter showing a good level of mixing. The autocorrelation dropped to a low level after approximately 10 lags, the shape of the histogram was unimodal and the first and second halves of the kernel density plots showed good overlapping. The acceptance rate was 26.9%.

Examination of the diagnostic statistics when the Poisson model was run with multiple (3) chains reported a maximum Gelman–Rubin Rc statistic of 1.003, and therefore met the convergence criteria. When examined separately, each chain also met the convergence criterion. The average acceptance rate increased to 23.7%. Therefore the Poisson model was used for year 2 model comparisons of the 12 candidate models.

3.4.3.2 Year 2 model comparison and model selection from the candidate models of fox abundance

The year 2 Poisson models compared 12 candidate models with the mean of the posterior distribution of the preferred model from year 1 as informative priors. As was the case for year 1, the model Poisson_01 (Poisson_01_Y1P_Y2) was the only model with any support, with a posterior model probability of over 99% (Table 3.10). The Kass and Raftery (1995) criteria for model selection indicated “very strong” evidence against all other models.

Table 3.10: Comparison of 12 candidate models of the fox (*Vulpes vulpes*) count data for year 2, with the year 1 mean of the posterior distribution for each variable as informative priors.

See Table 3.3 and Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model	log(ML)	log(BF)	P(M|y)	K&R evidence
Poisson_01_Y1P_Y2	**-27.4114**	**52.3256**	**0.9942**	**-**
Poisson_02_Y1P_Y2	-32.7050	47.0320	0.0050	very strong
Poisson_03_Y1P_Y2	-34.5116	45.2254	0.0008	very strong
Poisson_04_Y1P_Y2	-59.6686	20.0684	0.0000	very strong
Poisson_05_Y1P_Y2	-45.3175	34.4195	0.0000	very strong
Poisson_06_Y1P_Y2	-39.9435	39.7935	0.0000	very strong
Poisson_07_Y1P_Y2	-47.2894	32.4476	0.0000	very strong
Poisson_08_Y1P_Y2	-48.2259	31.5111	0.0000	very strong
Poisson_09_Y1P_Y2	-51.5790	28.1580	0.0000	very strong
Poisson_10_Y1P_Y2	-71.8981	7.8389	0.0000	very strong
Poisson_11_Y1P_Y2	-53.5173	26.2197	0.0000	very strong
Poisson_12_Y1P_Y2	-79.7370	-	0.0000	very strong

The range traversed by the MCMC chain for all parameters of the preferred model and the acceptance rate of 27.2% indicated good mixing of the MCMC chain. Although examination of the scatterplots of the simulated samples suggested no evidence of correlation, with blocking, the acceptance rate was improved to 43.4% and the mean efficiency was also improved. Blocking also showed similar improvements in the rate of dropping-off of the autocorrelation plot. The histograms were unimodal and there was good overlapping of first and second halves of the kernel density estimates.

When the preferred model was fit with three chains, the precision of the estimation results was improved (lower MCSEs) for all model parameters. The Max Gelman-Rubin Rc value was 1.004, again indicating convergence. When reported separately for all parameters, the Rc value was lower than 1.1, suggesting the convergence of all chains. As none of the other models had any support there was no model averaging and the mean of the posterior distribution of model parameters from the preferred model from year 2 were then used as informative priors when modelling the Year 3 data.

3.4.4 Fox abundance year 3

3.4.4.1 Year 3 preliminary/exploratory analysis of the fox MKTBA count data

Visual examination of the plotted count data for year 3 again indicated a Poisson distribution, however this was again far from equivocal (Figure 3.12). Posterior model probabilities were 47.4% and 31.1% for the Poisson and nbreg model, respectively, and therefore indicated some support for the nbreg model. Similarly, the criteria defined by Kass and Raftery (1995) indicated only a "bare mention" of evidence against the nbreg model (Table 3.11). However, the dispersion parameter (with an *lnalpha* of -77.25) indicated the Poisson model was more appropriate. There was positive evidence against the zip or zinb models (Table 3.11).

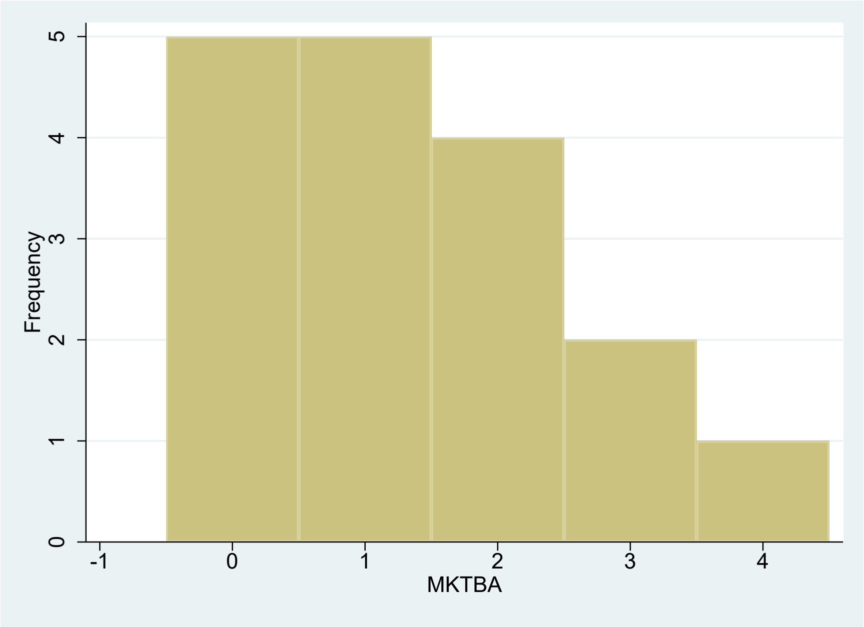


Figure 3.12: Frequency histogram for the minimum number of foxes known to be alive estimate after 10 days of monitoring (Day-10 MKTBA) from sandplots monitored for evidence of fox (*Vulpes vulpes*) activity at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 3.

As was the case for the year 1 and year 2 preliminary analysis, visual assessment of the trace plots for each category of the treatment variable the Poisson model revealed a good level of mixing. The autocorrelation dropped to a low level after approximately 10 lags, the shape of the histogram was unimodal and the first and second halves of the kernel density plots showed good overlapping. The acceptance rate was 35%.

Table 3.11: Exploratory analysis of the year 3 fox (*Vulpes vulpes*) count data to identify the appropriate class of model for further modelling.

poisson = Poisson regression; nbreg = negative binomial regression; zip = zero-inflated Poisson regression; zinb = zero inflated negative binomial regression.

log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model	log(ML)	log(BF)	P(M|y)	K&R evidence
Bayes_prelim_poisson_year3	**-41.4800**	**1.8910**	**0.4737**	**-**
Bayes_prelim_nbreg_year3	-41.9001	1.4709	0.3112	Bare mention
Bayes_prelim_zip_year3	-42.6734	0.6976	0.1436	Positive
Bayes_prelim_zinb_year3	-43.3710	.	0.0715	Positive

When the Poisson model was fit with multiple (3) MCMC chains, the average Max Gelman–Rubin Rc statistic was 1.004, and therefore met the convergence criteria. When examined separately, each chain also met the Max Gelman–Rubin Rc convergence criterion. The average acceptance rate remained high. Consequently, the Poisson model was used for year 3 model comparisons of the 12 candidate models.

3.4.4.2 Year 3 model comparison and model selection from the candidate models of fox abundance

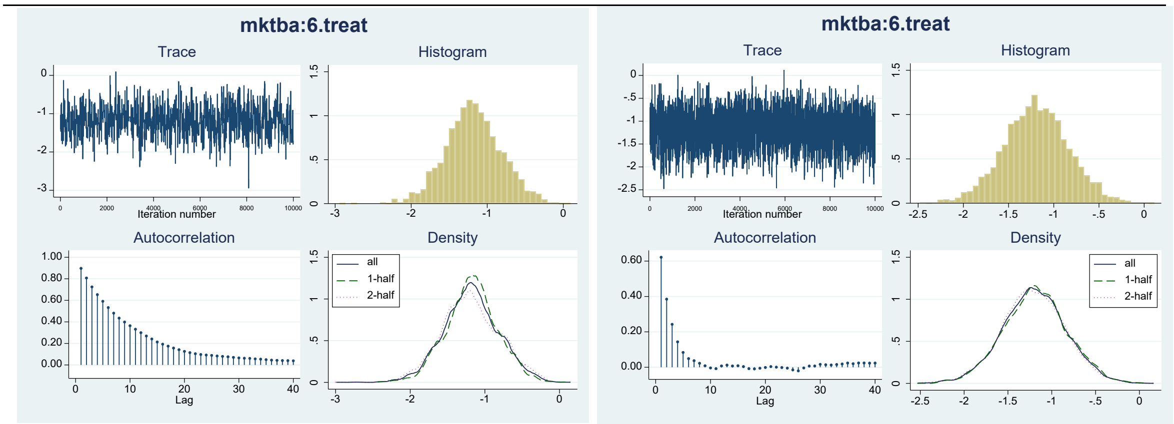
Comparison of the 12 candidate models for year 3, modelled with the mean of the posterior distribution of the preferred model from year 2 as informative priors, identified the model ‘Poisson_01_Y2P_Y3’ as having most support. Unlike years 1 and 2, there was some support for the model ‘Poisson_02_Y2P_Y3’ which include the variable *dist* (the distance from the interface with agricultural land). Nonetheless, most of the support was for the model without a distance effect (posterior model probability of 96.9% Vs 3.0%). There was “very strong” evidence against all other models (Table 3.12).

The acceptance rate for the preferred model was 17%. The scatterplot (matrix) of the simulated sample indicated no significant correlation between variables (treatment categories), however, when the model was fit with blocking, the acceptance rate increased to 43% and the sampling efficiency was improved for each category of the treatment variable. The effect of blocking was evident by the differences shown in the autocorrelation plots (Fig. 3.13). The autocorrelation became negligible after lag 6 and the trace plot revealed more rapid traversing of the marginal posterior.

Table 3.12: Comparison of 12 candidate models of the fox (*Vulpes vulpes*) count data for year 3, with the year 2 mean of the posterior distribution for each variable as informative priors.

See Table 3.3 and Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

Model	log(ML)	log(BF)	P(My)	K&R evidence
Poisson_01_Y2P_Y3	**-23.7189**	**42.3205**	**0.9689**	
Poisson_02_Y2P_Y3	-27.1930	38.8464	0.0300	Strong
Poisson_03_Y2P_Y3	-30.5617	35.4777	0.0010	Very strong
Poisson_04_Y2P_Y3	-38.1518	27.8876	0.0000	Very strong
Poisson_05_Y2P_Y3	-35.9371	30.1023	0.0000	Very strong
Poisson_06_Y2P_Y3	-34.6178	31.4216	0.0000	Very strong
Poisson_07_Y2P_Y3	-40.3406	25.6988	0.0000	Very strong
Poisson_08_Y2P_Y3	-43.2841	22.7553	0.0000	Very strong
Poisson_09_Y2P_Y3	-43.0530	22.9864	0.0000	Very strong
Poisson_10_Y2P_Y3	-67.5677	-1.5284	0.0000	Very strong
Poisson_11_Y2P_Y3	-49.8390	16.2004	0.0000	Very strong
Poisson_12_Y2P_Y3	-66.0394	.	0.0000	Very strong



A

B

Figure 3.13: MCMC comparison of trace plots, autocorrelation plots, frequency histograms and kernel density plots to visually examine convergence of the year 3 preferred ‘bayesmh’ model of fox abundance within the northern jarrah forest, south-west Western Australia.

Plots shown are for the six baitings per year treatment for the preferred model ‘Poisson_01_Y2P_Y3’. A: without blocking; B: with blocking.

When the preferred model was fit with multiple (3) chains and blocking of parameters (treatment categories), the precision of the estimation results was improved for all model treatment categories. The reported average Max Gelman–Rubin Rc statistic was 1.001, and therefore met the convergence criteria. When examined separately, each chain also met the Max Gelman–Rubin Rc convergence criterion.

The MCMC trace plot for the second ranked model ('Poisson_02_Y2P_Y3') also revealed more rapid traversing of the marginal posterior with blocking of parameters (treatment categories and the *dist* parameter). Similarly, the autocorrelation became negligible after lag 6 or 7. When fit with multiple (3) chains and with blocking of parameters, the precision of the estimation results was improved for all parameters. For both models (the preferred model and the model with a distance effect), the shape of the histogram was unimodal and the first and second halves of the kernel density plots showed good overlapping.

3.4.4.3 Year 3 model averaging, replicated outcomes and posterior predictive p-values (PPPs)

If adhering to the principles of "Occam's Window" (described in Section 3.3.4) the second ranked model ('Poisson_02_Y2P_Y3') could be exclude from the competitive model set as there was "strong" evidence against it when compared to the best (highest BF ranked) model. Similarly, on the principle of parsimony, or "Occam's razor", it could be considered a redundant or non-competitive model, as it differed from the preferred model by the addition of only one parameter (the variable *dist*) and it did not improve (in terms of BFs) on the preferred model. Nonetheless, model averaging was performed based on these two highest (BF) ranked models. Model averaging assigned a model weight of less than 3% to the model which included the variable *dist* (Table 3.13).

Table 3.13: Comparison of two topped ranked models from candidate models of the fox (*Vulpes vulpes*) count data for year 3, with the year 2 mean of the posterior distribution for each variable as informative priors.

Chains = the number of MCMC simulation chains. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font). The syntax "Y2P" refers to the informative priors.

Model	Chains	Avg log(ML)	log(BF)	P(M|y)	K&R evidence
Poisson_01B_Y2P_3Chains_Y3	**3**	**-23.6691**	**3.5206**	**0.9713**	
Poisson_02B_Y2P_3Chains_Y3	3	-27.1897	**.**	0.0287	Strong

The model averaged effect of treatment and distance is shown graphically in Fig. 3.14. Despite the classically-considered "significant effect" of distance (a pre exponentiated mean of the posterior distribution of -0.06, and an equal-tailed 95%BCI not inclusive of zero, Table 3.14), the inclusion of model 'Poisson_02_Y2P_Y3' in model averaging revealed the overall effect from distance was negligible (Fig. 3.14). There was substantial overlap of the 95%BCIs for the treatment categories (not shown in Fig. 3.14, see below and Fig. 3.15 for 95%BCI).

Similarly, graphical representation (Fig. 3.15) of the preferred model only, i.e. without model averaging (model output shown in Table 3.15), also revealed overlapping of the 95%BCIs for the treatment categories, despite the six baitings per year treatment having a classically-considered significant effect (95%BCI not including zero). Nonetheless, there was a clearly distinguishable trend of decreasing fox abundance with increasing baiting frequency.

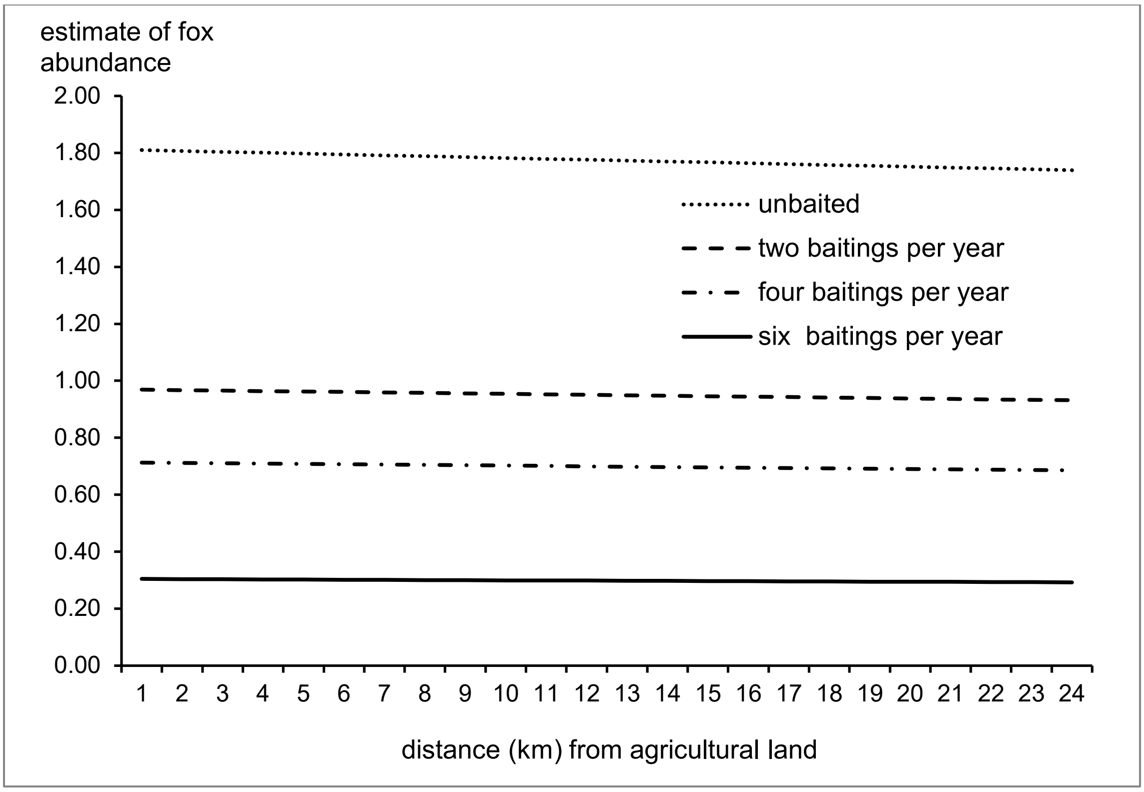


Figure 3.14: Model averaged fox abundance within the northern jarrah forest, south-west Western Australia, derived from model averaging the two topped ranked models from the year 3 'bayesmh' Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity.

Table 3.14: Output table for second ranked model ‘Poisson_02_Y2P_Y3’ fit with the blocking and three MCMC chains.

The value “Avg log marginal-likelihood” differs from value for log(ML) shown in Table 3.12 as here the model was fit with three MCMC chains and blocking.

Bayesian Poisson regression	Avg acceptance rate =	0.4397
Random-walk Metropolis-Hastings sampling	Avg efficiency: min =	0.0984
	Avg =	0.1597
	Max =	0.2151
Avg log marginal-likelihood = -27.1897	Max Gelman-Rubin Rc =	1.0010

					Equal-tailed	
mktba	Mean	Std. Dev.	MCSE	Median	[95% Cred.	Interval]
treat						
2	0.1063	0.2622	0.0037	0.1112	-0.4051	0.6228
4	-0.2235	0.2903	0.0037	-0.2198	-0.7987	0.3313
6	-1.1490	0.3796	0.0047	-1.1520	-1.8996	-0.4190
dist	-0.0598	0.0315	0.0006	-0.0582	-0.1269	-0.0027
_cons	0.7861	0.1927	0.0033	0.7891	0.4075	1.1631

Table 3.15: Output table for the preferred model ‘Poisson_01_Y2P_Y3’ fit with blocking and three MCMC chains.

The value “Avg log marginal-likelihood” differs from value for log(ML) shown in Table 3.12 as here the model was fit with three MCMC chains and blocking.

Bayesian Poisson regression	Avg acceptance rate =	0.4474
Random-walk Metropolis-Hastings sampling	Avg efficiency: min =	0.1594
	avg =	0.1875
	max =	0.2134
Avg log marginal-likelihood = -23.6691	Max Gelman-Rubin Rc =	1.0010

					Equal-tailed	
mktba	Mean	Std. Dev.	MCSE	Median	[95% Cred.	Interval]
treat						
2	-0.0340	0.2536	0.0035	-0.0298	-0.5403	0.4587
4	-0.3400	0.2787	0.0035	-0.3402	-0.8897	0.1946
6	-1.1901	0.3752	0.0047	-1.1896	-1.9476	-0.4611
_cons	0.5893	0.1652	0.0024	0.5900	0.2643	0.9052

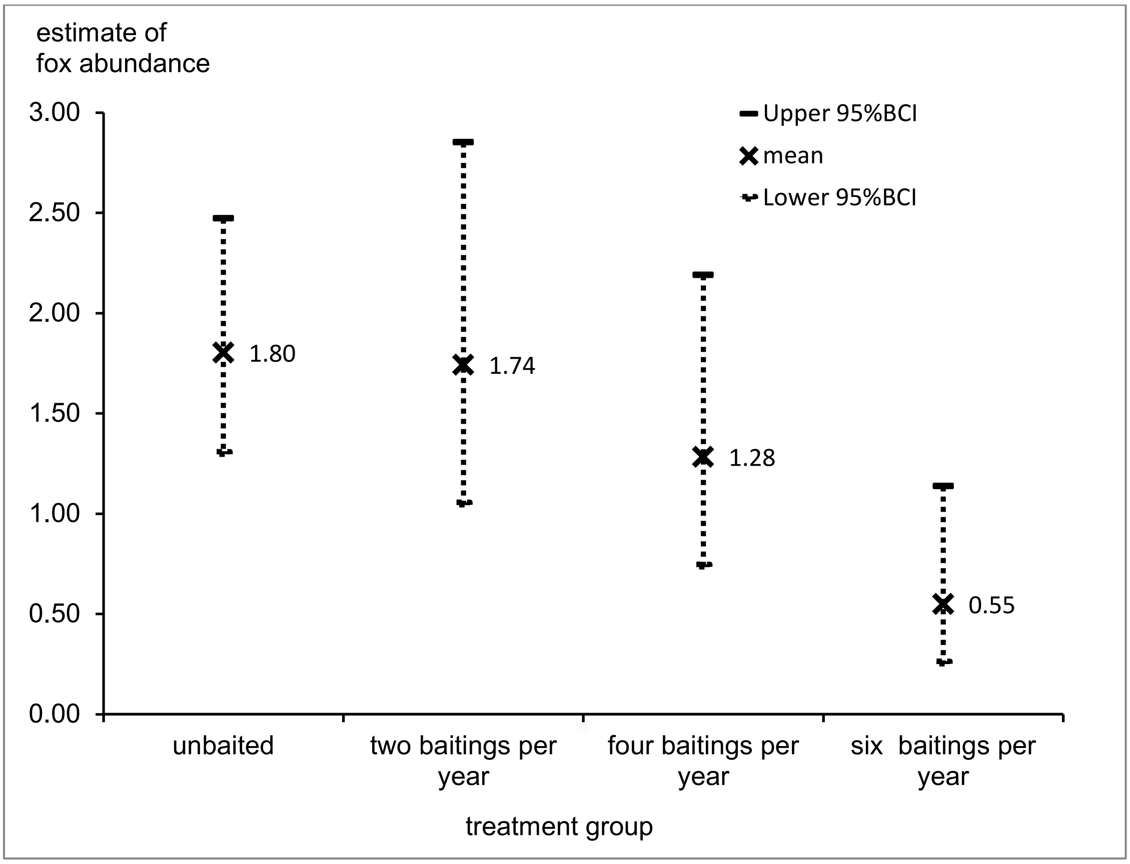


Figure 3.15: Modelled estimates fox (*Vulpes vulpes*) abundance within the northern jarrah forest, south-west Western Australia, derived from the preferred model from the year 3 ‘bayesmh’ Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity. Upper and lower 95%BCI refer to the Bayesian 95% equal-tailed credible intervals.

Visual inspection of the histograms for the observed data compared with the replicated data from the preferred model (Fig. 3.16) revealed the replicated samples covered the range of the observed distribution, i.e. the normal likelihood model captured the centre and extreme values of the distribution.

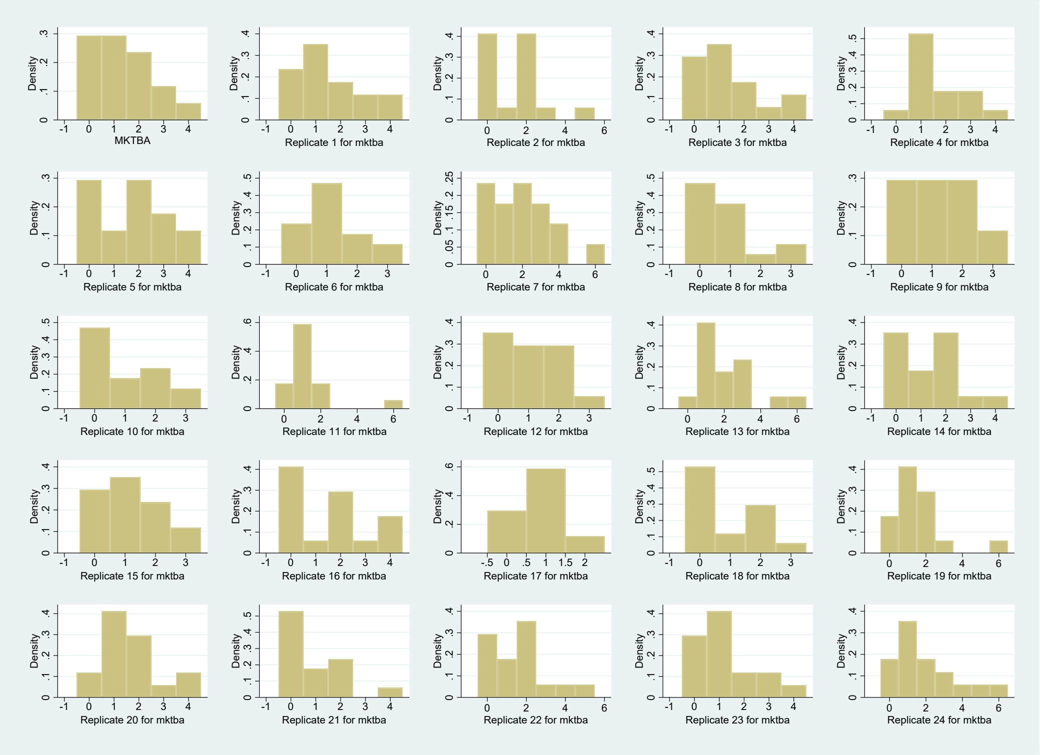


Figure 3.16: Comparison of the histograms of the observed data with histograms of the replicated data.

The histogram of the observed data is shown in top left graph. The remaining histograms are for the first 24 replicated samples drawn from the posterior predictive distribution.

The posterior predictive *p-values* were assessed for the pr_mean (posterior mean), pr_min (posterior minimum) and pr_max (posterior maximum) statistic (Table 3.16). The P(T>=T_obs) is the probability that the mean value for the replicated mean, minimum and maximum, is greater or equal to the observed value. The P(T>=T_obs) values for the mean and maximum (of 0.57 and 0.71, respectively) indicated the values are in agreement (i.e. close to 0.5) with the observed values. Although the P(T>=T_obs) value of 1 for pr_min may initially be interpreted as indicating model misfit, this discrepancy can be explained as an artefact of using a Poisson model where the minimum observed value for the MKTBA will always be 0.

Table 3.16: The posterior predictive p-values, comparing the probability that mean, maximum and minimum values for the replicated data could be as or more extreme than the observed data.

T = the test statistic computed using the replicated data; T obs = the test statistic computed using and observed data.

T	Mean	Std. Dev.	E(T_obs)	P(T>=T_obs)
pr_mean	1.4127	0.3665	1.3529	0.5725
pr_min	0.0042	0.0647	0	1.0000
pr_max	4.2207	1.2109	4	0.7097

3.4.5 Detection of cat activity

The data for cat activity was extremely sparse, with only 32 of the 11,778 sandplots showing evidence of cat activity.

3.4.6 Cat abundance year 1

3.4.6.1 Year 1 preliminary/exploratory analysis of the cat, pwca, count data

From visual examination of the plotted count data it was unclear if a nbreg or a zero inflated negative binomial (zinb) more closely fitted the distribution (Fig. 3.17). More formal examination (model comparison and diagnostics) initially identified the nbreg model as the most appropriate class of model for the year 1 data with “positive” evidence against the next ranked model, the zinb model. The posterior model probability for the nbreg and zinb was 84% and 11% respectively. However, both models were poor in terms of trace plot mixing, autocorrelation, the fit of the first and second halves of the kernel density plots, and the histograms were multimodal.

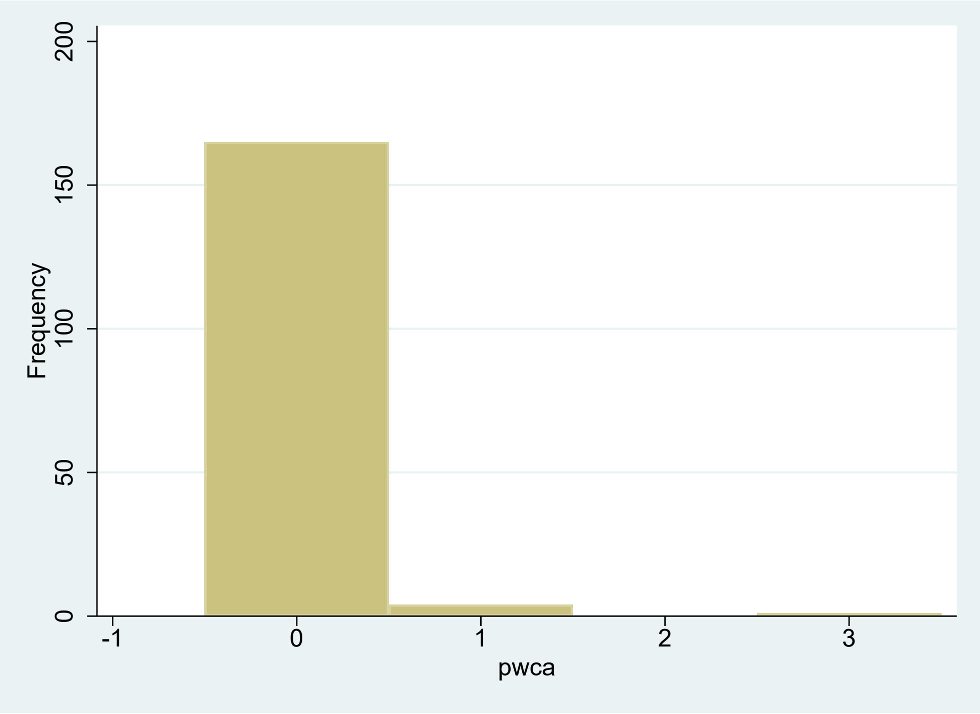
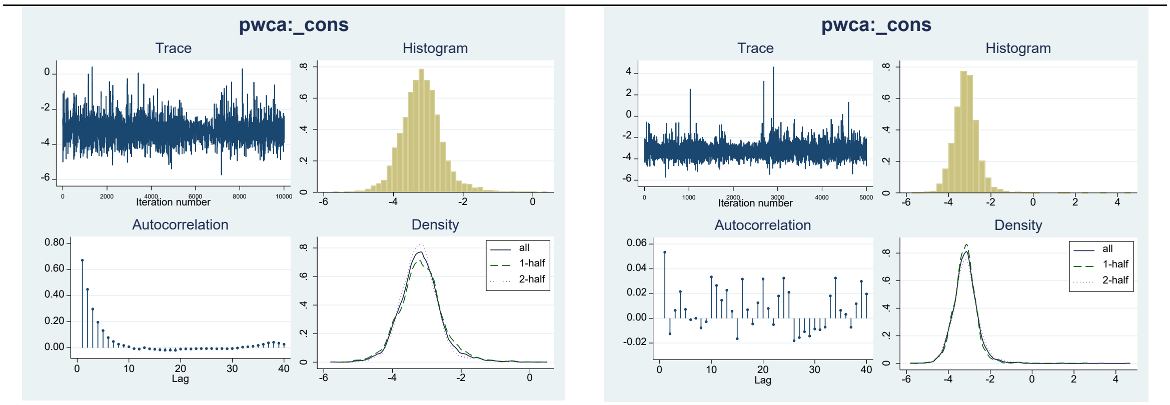


Figure 3.17: Frequency histogram for the number of sandplots with cat (*Felis catus*) activity (pwca) from sandplots monitored at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 1.

The models were then fit with blocking of parameters (the treatment categories), an increased MCMC sample size, a longer burn-in period and thinning. Although these models had comparable support in terms of BFs, most were again poor in terms of trace plot mixing, autocorrelation, the fit of the histograms (often multimodal) and the first and second halves of the kernel density plots. The exception was the nbreg model fitted without a treatment effect and the same nbreg model fitted with blocking, a larger MCMC sample size, a longer burn-in period and thinning (Fig. 3.18).

The latter nbreg model was preferred on the basis of the visual examination of trace plots, autocorrelation, histograms and the first and second half of the kernel density plots. It had a log(ML) value comparable with the zip and zinb models also modelled without a treatment effect and also fit with a larger MCMC sample size, a longer burn-in period and thinning. This nbreg model, with non-informative priors, was then the basis for comparison of the year 1 candidate model set which compared the 16 models (model 001 to 016) from Table 3.5.



A B

Figure 3.18: MCMC comparison of trace plots, autocorrelation plots, frequency histograms and kernel density plots to visually examine convergence and model fit from modelling year 1 cat (*Felis catus*) abundance within the northern jarrah forest, south-west Western Australia.

Plots shown are for the constant term for the two nbreg models identified in the preliminary analysis as having the best fit. A: modelled without a baiting treatment effect; B: without a baiting treatment effect and with blocking, a larger MCMC sample size, a longer burn-in period and thinning.

3.4.6.2 Year 1 model comparison and model selection from the candidate models of cat abundance

The only model with any support from the 16 candidate nbreg models was model ‘nbreg_001_Y1’ (Table 3.17) which modelled cat abundance as constant across the unbaited and all baited treatment groups. The posterior model probability was greater than 96%. The acceptance rate for the preferred model was 44% and the range traversed by the MCMC chain indicated good mixing. The unimodal histogram, the overlapping of kernel density estimates and rapid dropping-off of the autocorrelation, all indicated model convergence. In the absence of support for any other model, there was no model averaging.

The Max Gelman–Rubin Rc statistic when the preferred nbreg model was fit with three MCMC chains was 1.09, which met the convergence criteria. When examined separately the convergence criterion was met for all parameters in each chain. With three MCMC chains, the average acceptance rate increased to 47%.

Table 3.17: Comparison of 16 candidate models, with non-informative priors, of cat (*Felis catus*) abundance for year 1, in the northern jarrah forest, south-west Western Australia.

See Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

model	log(ML)	log(BF)	P(M|y)	K&R evidence
nbreg_001_Y1	**-32.4621**	**14.3944**	**0.9608**	
nbreg_005_Y1	-35.7305	11.1260	0.0366	strong
nbreg_002_Y1	-39.2696	7.5869	0.0011	very strong
nbreg_003_Y1	-39.5301	7.3265	0.0008	very strong
nbreg_004_Y1	-40.2730	6.5835	0.0004	very strong
nbreg_010_Y1	-41.1515	5.7050	0.0002	very strong
nbreg_008_Y1	-41.5521	5.3044	0.0001	very strong
nbreg_013_Y1	-42.2584	4.5982	0.0001	very strong
nbreg_011_Y1	-42.6395	4.2170	0.0000	very strong
nbreg_009_Y1	-44.4627	2.3938	0.0000	very strong
nbreg_014_Y1	-44.6122	2.2443	0.0000	very strong
nbreg_015_Y1	-44.9579	1.8986	0.0000	very strong
nbreg_006_Y1	-45.3203	1.5362	0.0000	very strong
nbreg_012_Y1	-45.7306	1.1260	0.0000	very strong
nbreg_016_Y1	-46.8233	0.0333	0.0000	very strong
nbreg_007_Y1	-46.8565	.	0.0000	very strong

3.4.7 Cat abundance Year 2

3.4.7.1 Year 2 preliminary/exploratory analysis of the cat, pwca, count data

As was the case for the year 1 results, it was unclear from visual examination if a nbreg or zinb distribution more closely fitted the distribution of the plotted count data for year 2 (Fig. 3.19). There was considerable model uncertainty when comparing the models more formally, with only a “bare mention” of evidence against each model when compared to the model with highest posterior model probability (the zinb model).

When fitted with blocking of parameters, an increased MCMC sample size, a longer burn-in period and thinning, all models had comparable support in terms of BFs, however most were again poor in terms of trace plot mixing, autocorrelation, the fit of the histograms, and the first and second halves of the kernel density plots. As was the case or the year 1 data, the nbreg model fit without a treatment effect and with blocking, a larger MCMC sample size, a longer burn-in period and thinning was preferred on the basis of the visual examination of trace plots, autocorrelation, histograms and the first and second half of the kernel density plots. It had a log(ML) value comparable with the zip and zinb models also modelled without a treatment effect and also fit with a larger MCMC sample size, a longer burn-in period and thinning. This nbreg model, with the mean of the posterior distribution (for the *pwca:_constant* and *lnalpha* terms) from the year 1 model as informative priors, was then the basis for comparison of the year 2 candidate model set.

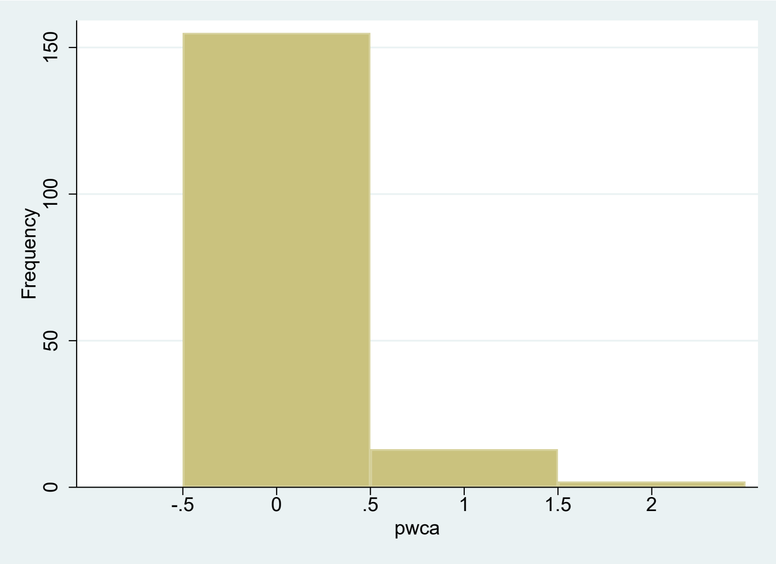


Figure 3.19: Frequency histogram for the number of sandplots with cat (*Felis catus*) activity (pwca) from sandplots monitored at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 2.

3.4.7.2 Year 2 model comparison and model selection from the candidate models of cat abundance

Again, as was the case for year 1, the preferred model from the 16 candidate models for year 2 (model nbreg_001_Y2, Table 3.18) modelled cat abundance as constant across the unbaited and all baited treatments with a posterior model probability greater than 97%. The acceptance rate for the preferred model was 42% and the range traversed by the MCMC chain indicated good mixing. The unimodal histogram, the overlapping of kernel density estimates and rapid dropping-off of the autocorrelation, all indicated model convergence (Fig 3.20). In the absence of support for any other model, there was no model averaging.

When the preferred nbreg model was fit with three MCMC chains, the Max Gelman–Rubin Rc statistic was 1.0, which met the convergence criteria. When examined separately, the convergence criterion (Rc< 1.1) was met for all parameters. With three MCMC chains, the average acceptance rate increased to 44%.

Table 3.18: Comparison of 16 candidate models, with the mean of the posterior distribution from Year 1 as informative priors, for cat (*Felis catus*) abundance for year 2, in the northern jarrah forest, south-west Western Australia.

See Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

model	log(ML)	log(BF)	P(My)	K&R evidence
nbreg_001_Y2	**-59.1457**	**26.3621**	**0.9729**	
nbreg_005_Y2	-62.7849	22.7228	0.0256	strong
nbreg_003_Y2	-66.1715	19.3363	0.0009	very strong
nbreg_002_Y2	-66.8624	18.6454	0.0004	very strong
nbreg_004_Y2	-67.8640	17.6437	0.0002	very strong
nbreg_010_Y2	-69.8311	15.6767	0.0000	very strong
nbreg_011_Y2	-70.5580	14.9498	0.0000	very strong
nbreg_008_Y2	-70.7449	14.7628	0.0000	very strong
nbreg_006_Y2	-73.9709	11.5369	0.0000	very strong
nbreg_009_Y2	-74.8805	10.6272	0.0000	very strong
nbreg_007_Y2	-75.5522	9.9556	0.0000	very strong
nbreg_015_Y2	-77.5879	7.9199	0.0000	very strong
nbreg_013_Y2	-77.8456	7.6621	0.0000	very strong
nbreg_014_Y2	-78.5541	6.9536	0.0000	very strong
nbreg_012_Y2	-82.7032	2.8045	0.0000	very strong
nbreg_016_Y2	-85.5078	.	0.0000	very strong

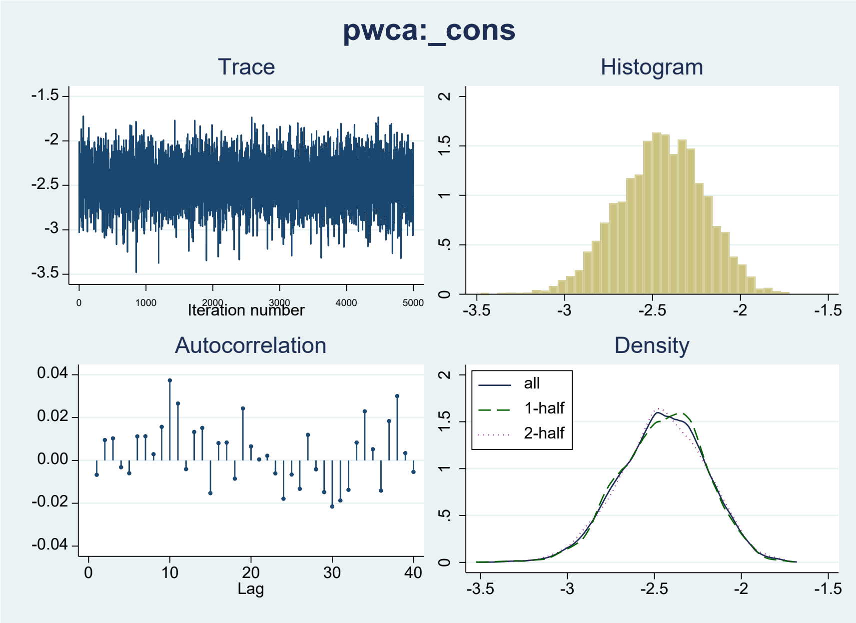


Figure 3.20: MCMC trace plot, autocorrelation plot, frequency histogram and kernel density plots to visually examine convergence of the MCMC of parameter estimate for the constant term (pwca_cons) from the preferred bayesmh nbreg model identified when modelling 16 candidate models of cat (*Felis catus*) abundance within the northern jarrah forest, south-west Western Australia, year 2.

3.4.8 Cat abundance Year 3

3.4.8.1 Year 3 preliminary/exploratory analysis of the cat, pwca, count data

As was the case for year 1 and year 2, the frequency histogram for the number of sandplots showing evidence of cat activity was strongly skewed to the right, with a high proportion of zeros (Fig. 3.21). Therefore, it was again unclear from visual examination of the plotted count data whether a nbreg, zip or zinb distribution more closely fitted the distribution. When comparing the models more formally, the nbreg model had most support with a posterior model probability of 53% compared to the next ranked model (the Poisson model) with a posterior model probability of 33%. Despite the differences in posterior model probabilities, in terms of BFs there was only a “bare mention” of evidence against each of the Poisson, zip and zinb. When fit with blocking all models were again comparable.

Although the log(ML) values were comparable, when fit without a treatment effect and with blocking, a larger MCMC sample size, a longer burn-in period and thinning, the nbreg model was again preferred on the basis of the visual examination of trace plots, autocorrelation, histograms and the first and second half of the kernel density plots. The nbreg model, with the mean of the posterior distribution from the year 2 model as informative priors (for the pwca:_*cons* and *lnalpha* terms), was then the basis for comparison of the year 3 candidate model set.

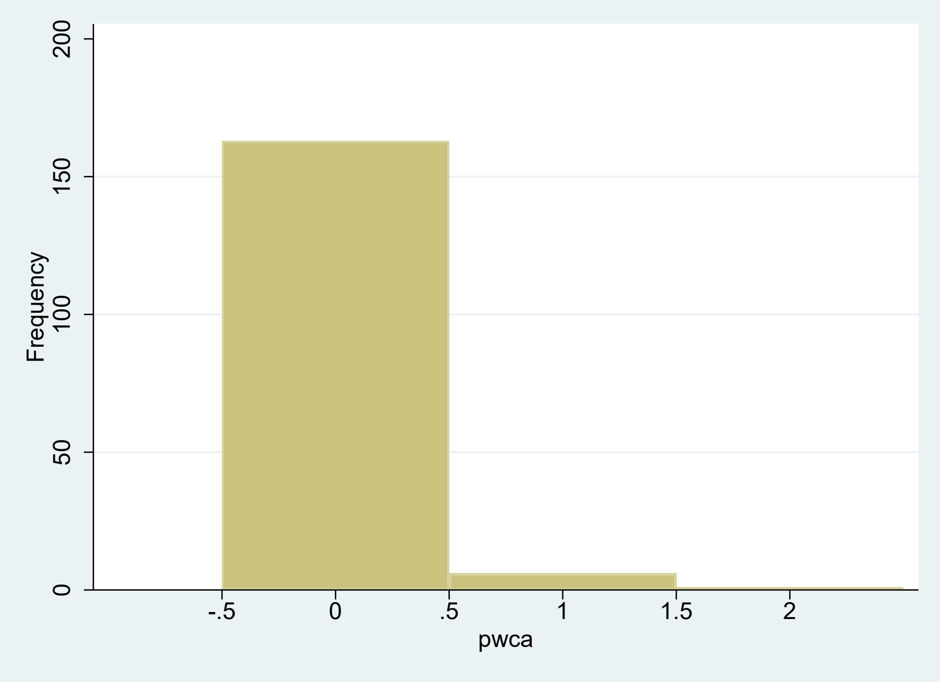


Figure 3.21: Frequency histogram for the number of sandplots with cat (*Felis catus*) activity (pwca) from sandplots monitored at 17 sandplot networks, pre delivery of 1080 baits for fox control, within the northern jarrah forest, south-west Western Australia, year 3.

3.4.8.2 Year 3 model comparison and model selection from the candidate models of cat abundance

Comparison of the year 3 candidate models, with the mean of the posterior distribution from year 2 as informative priors, revealed only two models to have any support; model 'nbreg_001_Y3'; and model 'nbreg_003_Y3' (Table 3.19). The preferred model (nbreg_001_Y3) was again the model with cat abundance modelled as constant across the unbaited and all baited treatments and with no additional explanatory variables. The posterior model probability was 89%. Although the next ranked model (nbreg_003_Y3), which included the variable '*day*', had a posterior model probability of 10%, it was considered non-competitive, or redundant, as it differed from the preferred model by the addition of only one parameter (the variable '*day*') and did not improve on the simpler model. In the absence of support for any other model, there was no model averaging.

Table 3.19: Comparison of 16 candidate models, with the mean of the posterior distribution from Year 2 as informative priors, for cat (*Felis catus*) abundance for Year 3, in the northern jarrah forest, south-west Western Australia.

See Table 3.4 for model variables. log(ML) = the natural log of the marginal likelihood; log(BF) = the natural log of the Bayes factor; P(M|y) = the posterior probability of the model; K&R evidence refers the criteria identified by Kass and Raftery (1995) (see Table 3.2) which compares the evidence against each model compared to the preferred model (in bold font).

model	log(ML)	log(BF)	P(M|y)	K&R evidence
nbreg_001_Y3	**-34.3961**	**21.0726**	**0.8911**	
nbreg_003_Y3	-36.5755	18.8932	0.1008	Positive
nbreg_005_Y3	-39.6944	15.7743	0.0045	Very strong
nbreg_010_Y3	-40.1843	15.2844	0.0027	Very strong
nbreg_002_Y3	-41.7956	13.6731	0.0005	Very strong
nbreg_004_Y3	-42.9600	12.5087	0.0002	Very strong
nbreg_009_Y3	-43.0752	12.3935	0.0002	Very strong
nbreg_006_Y3	-43.4328	12.0359	0.0001	Very strong
nbreg_008_Y3	-47.1509	8.3178	0.0000	Very strong
nbreg_013_Y3	-47.7528	7.7159	0.0000	Very strong
nbreg_011_Y3	-48.0100	7.4587	0.0000	Very strong
nbreg_015_Y3	-48.1443	7.3244	0.0000	Very strong
nbreg_007_Y3	-50.4366	5.0322	0.0000	Very strong
nbreg_012_Y3	-50.5859	4.8828	0.0000	Very strong
nbreg_014_Y3	-55.4377	0.0310	0.0000	Very strong
nbreg_016_Y3	-55.4687	.	0.0000	Very strong

The acceptance rate for the preferred model was 45.3%. The unimodal histogram, the overlapping of kernel density estimates and rapid dropping-off of the autocorrelation, all indicated model convergence (Fig 3.22). When the preferred nbreg model was fit with three MCMC chains (Fig. 3.23), the Max Gelman–Rubin Rc statistic was 1.0, and therefore met the convergence criteria. When examined separately, the convergence criterion (Rc<1.1) was met for all parameters. With three MCMC chains, the average acceptance rate was reduced minimally to 44.9%

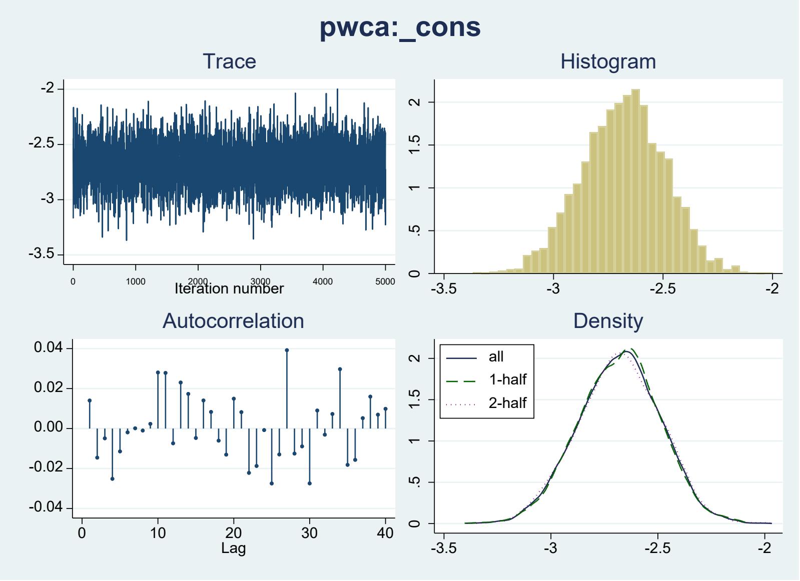


Figure 3.22: MCMC trace plot, autocorrelation plot, frequency histogram and kernel density plots to visually examine convergence of the MCMC of parameter estimate for the constant term (pwca_cons) from the preferred bayesmh nbreg model identified when modelling 16 candidate models of cat (*Felis catus*) abundance within the northern jarrah forest, south-west Western Australia, Year 3.

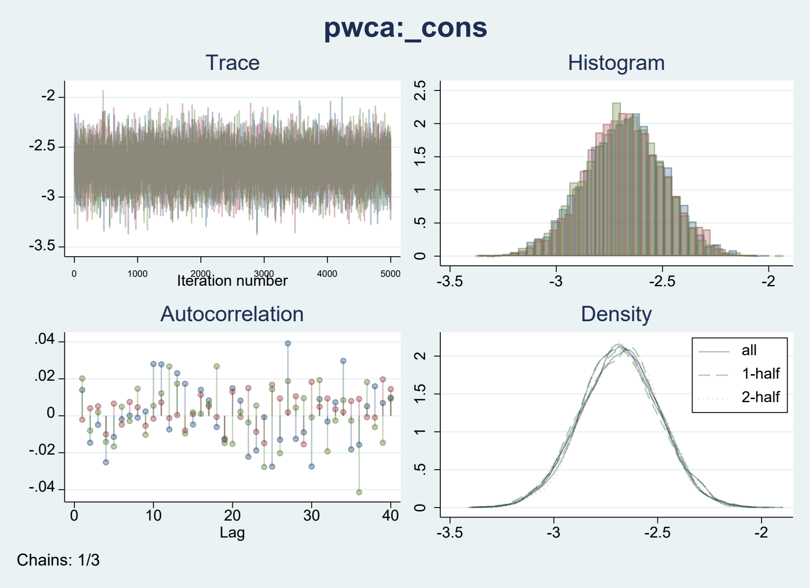


Figure 3.23: The MCMC trace plot, autocorrelation plot, frequency histogram and kernel density plots (for three chains) to visually examine convergence of the MCMC of parameter estimate for the constant term (pwca_cons) from the preferred bayesmh nbreg model identified when modelling 16 candidate models of cat (*Felis catus*) abundance within the northern jarrah forest, south-west Western Australia, year 3.

The images appear blurred as all three chains are shown overlapping, with each chain shown in a different colour.

The predicted outcome (predicted abundance of cats, i.e. exponentiated values from Table 3.20, with predicted values constant across all treatments) from the preferred model was 0.069 cats per average MCP, with a predicted median of 0.688 and a 95%BCI of 0.05 to 1.60.

Table 3.20: Output table (part only) for the preferred model 'Poisson_01_Y2P_Y3' for cat abundance, fit with blocking and three MCMC chains.
The value "Avg log marginal-likelihood" differs from value for log(ML) shown in Table 3.19 as here the model was fit with three MCMC chains and blocking.

Avg log marginal-likelihood = -34.405739 Max Gelman-Rubin Rc = 1.000

	Mean	Std. Dev.	MCSE	Median	Equal-tailed [95% Cred. Interval]	
pwca:_cons	-2.6818	0.1884	0.0015	-2.6811	-3.0588	-2.3154

3.4.9 Determining the number of days required to monitor sandplots

The correlation coefficient between the MKTBA estimate at each day (days one to 10) and the MKTBA estimate at day 10 showed an asymptote at days six and seven (r values of 0.69 for both days), then increased again through days eight to 10 (Fig. 3.24).

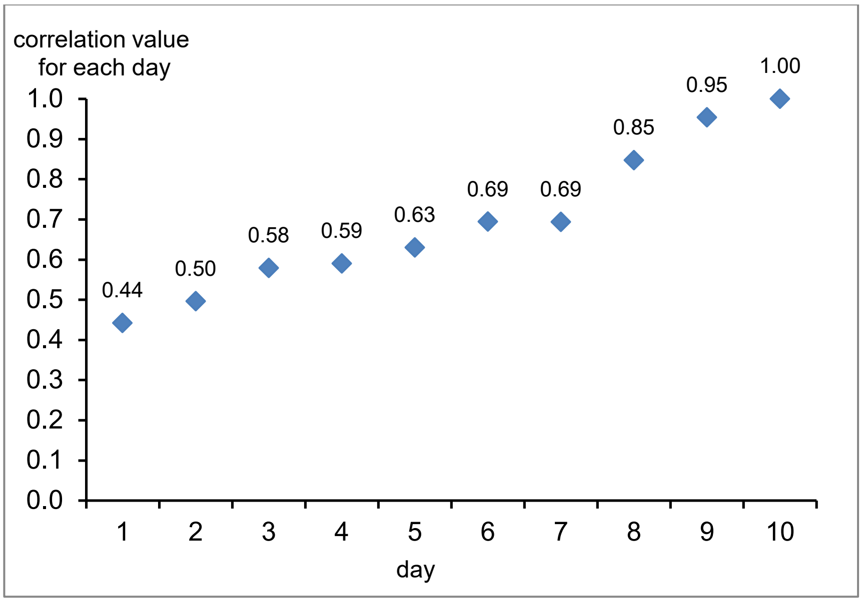


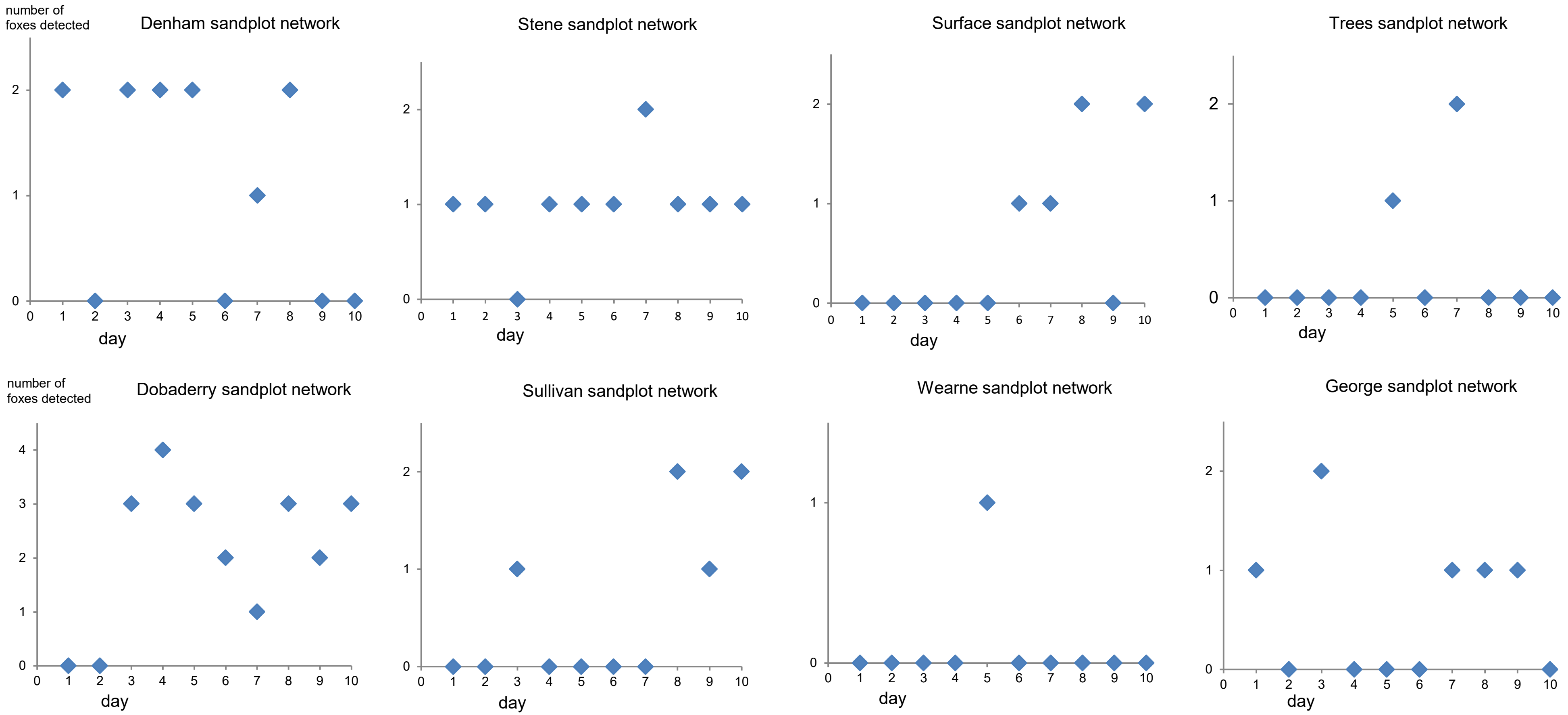
Figure 3.24: The correlation value (*r*) from the pooled data where the fox MKTBA estimate for each day was correlated with the day-10 MKTBA estimate, from monitoring sandplots within the northern jarrah forest, south-west Western Australia.

3.4.10 Monitoring of fox activity post 1080 baiting

Evidence of fox activity was observed at 170 and 424 sandplots post baiting in 1999 and 2000 respectively. In 1999, post-baiting monitoring indicated foxes were present at all sandplot networks within the unbaited treatment group (Fig. 3.25). Conversely, the data from the baited treatment groups indicated minimal fox numbers, with foxes detected at only four of the thirteen sandplot networks within the baited treatments. Three of these were within the two baitings per year treatment group and one within the six baitings per year treatment group (Fig. 3.25). Within the exception of Sullivan sandplot network (within the two baitings per year treatment group), foxes detected within the baited treatments were all at sites at the interface with agricultural land (Wearne and Dobaderry sandplot networks within the two and George sandplot network within the six baitings per year treatment group*, Fig. 3.1*).

In 2000, foxes were again (as expected) detected at all unbaited sandplot networks (Fig. 3.26) and at seven of the thirteen sandplot networks within the baited treatments (Fig. 3.27). At unbaited sandplot networks, the first 10 days monitoring (not shown in Figure 3.26) corresponded to the ten day pre-baiting monitoring at all treatments. Similarly, the monitoring day shown in Figure 3.27 for the sandplot networks within baited treatments indicates the total number of days monitored. For example, at Dobaderry sandplot network, pre-baiting was carried out for days one to 13, baiting occurred on days 14 and 15 and post-baiting monitoring was carried out for days 16 to 38. This duration of monitoring pre-1080-baiting varied as a consequence of delays to the scheduled aerial baiting program.

Four of the seven sandplot networks where foxes were detected within baited treatment groups post-baiting were at the forest interface with agricultural land. The fifth (Hakea) is only 3.7km from agricultural land (Fig. 3.27).



Denham sandplot network

Stene sandplot network

Surface sandplot network

Trees sandplot network

Dobaderry sandplot network

Sullivan sandplot network

Wearne sandplot network

George sandplot network

Figure 3.25: The daily estimated number of foxes at sandplot networks post 1080 baiting in September 1999.

Foxes were detected at all sandplot networks within the unbaited treatment (Denham, Stene, Surface and Trees sandplot networks), at three of the five sandplot networks within the two baitings per year treatment (Dobaderry, Sullivan and Wearne sandplot networks), at none within the four baitings per year treatment and at only one in the six baitings per year treatment (George sandplot network).

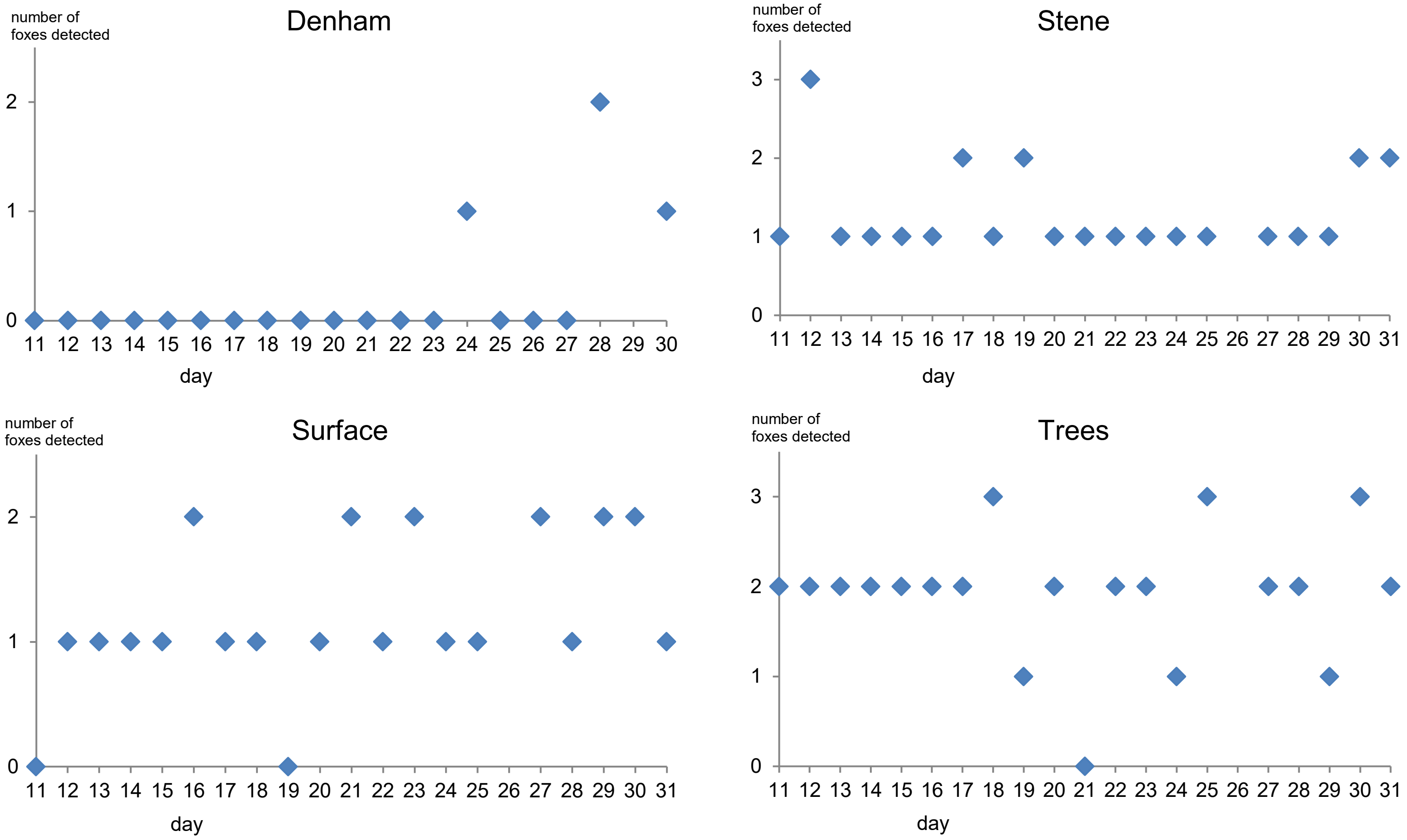


Figure 3.26: The daily estimated number of foxes at sandplot networks within the unbaited treatment, post 1080 baiting in September 2000. Foxes were detected at all sandplot networks within the unbaited treatment. The first 10 days monitoring for all unbaited sandplot networks (not shown) corresponded to the pre-baiting monitoring at the unbaited and all baited treatments.

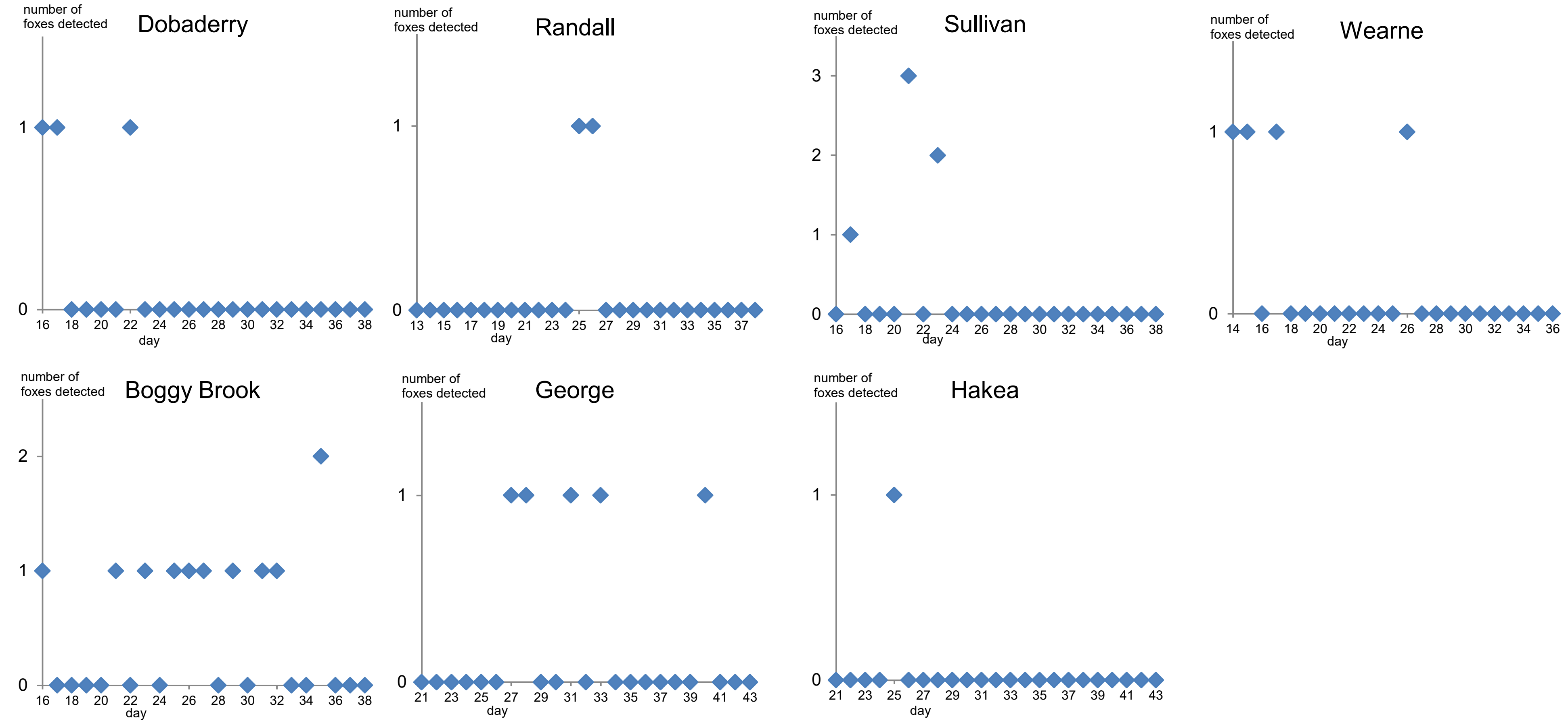


Figure 3.27: The daily estimated number of foxes at sandplot networks within the baited treatment post 1080 baiting in September 2000.

Foxes were detected at seven of the thirteen sandplot networks within the baited treatments. Four of these (Dobaderry, Randall, Sullivan and Wearne) were in the two baitings per year treatment, one (Boggy Brook) was within the four baitings per year treatment and two (George and Hakea) were within the six baitings per year treatment. The day of monitoring (x axis) excludes the period where monitoring was carried out prior to delivery of 1080 baits. The first day of monitoring post baiting is day 13 for Randall, day 14 for Wearne, day 16 for Dobaderry, Sullivan and Boggy Brook and day 21 for George and Hakea sandplot networks.

3.4.11 Validation of the MKTBA estimate of the number of foxes present

3.4.11.1 Validation through use of trapping and removal techniques

Sandplot monitoring was carried out at Marradong Forest Block (Fig. 3.1) over the 10 day period from 11 to 20 September 1999. There was a maximum of two foxes detected on any given day. Cyanide bait stations were set from day 11 at each sandplot. Monitoring of fox activity continued for 10 days and numerous capsules showed evidence of interference from foxes and/or cats, with several capsules broken. No fox deaths were recorded. An area within a radius of approximately 50 m was searched thoroughly for the presence of carcasses at each site where a capsule was broken. Several capsules also appeared to have been 'licked clean' of the lure. This phenomenon has previously been observed and attributed to foxes (Jack Kinnear[7], pers. com.). There was one non-target death of a chuditch. Cyanide baiting stopped after 10 days. The attempt to validate the MKTBA estimate was aborted as, despite foxes being recorded as present, cyanide baiting did not result in any fox kills.

The sandplotting and cyanide baiting procedure was repeated in the period from 9 to 18 October 1999 at Marradong Forest Block and concurrently at a second site, Saddleback Forest Block (Fig. 3.1). There was a maximum of two foxes detected on any given day at each site. A higher level of quality control was adopted when making the cyanide capsules to reduce the possibility of premature capsule breakage if interfered with by a fox. A range of alternatives was also trialled for presentation and securing the cyanide capsules. Cyanide baiting was carried out for 10 days and resulted in no fox kills at Marradong and two fox kills at Saddleback, with one non-target death (a chuditch) at Marradong. The number of fox kills at Saddleback concurred with the estimated number of foxes determined by sandplotting. However, prior to either of the cyanide deaths, additional fox activity was recorded at Saddleback, suggesting the presence of at least one and possibly two additional foxes. Activity on sandplots ceased at the sandplots corresponding to the second cyanide death. Activity resumed at the plots where the first cyanide death was recorded and ceased where the additional fox activity had previously been recorded. Cyanide capsules were damaged at both sites with no corresponding evidence of a death and capsules again showed evidence of being 'licked clean'. The attempt to validate the technique was again aborted as foxes were clearly present, yet cyanide baiting was again not resulting in a kill of all foxes present.

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[7] Jack Kinnear: Former Principal Research Scientist, Western Australian Department of Environment and Conservation, Science Division

The final attempt to validate the technique was at Quindanning Forest Block (Fig. 3.1), where cyanide baiting was supplemented with conventional fox trapping techniques. The pattern of roading, sandplot configuration and the MCP capturing all sandplots at the Quindanning site are shown in Figure 3.28. Activity on sandplots was monitored for 10 consecutive days, commencing 30 October 1999. The maximum number of foxes estimated on any one day was three adults (Table 3.21, Fig. 3.29). However, as the validation process had been delayed and monitoring extended into November, fox cubs were also present and were detected (Table 3.21). Cyanide bait stations were established at every sandplot, as described above, and paired Victor Softcatch size 1.5 padded leg-hold traps were also set at each sandplot where activity had been recorded. Trapping and cyanide baiting commenced on day 11 and two adult foxes and four fox cubs were trapped and euthanased. None was killed by cyanide baiting.

The day and location at which each fox was trapped and removed and the activity recorded post removal is shown in Table 3.22 and Figure 3.30. At cessation of trapping, activity was present at sandplots 5 and 6 only (Fig. 3.30). The number of foxes removed and the sole remaining area of activity post removal was consistent with the interpretation of the sandplot activity and inferred the presence of three adult foxes, one of which was not trapped. The area of inferred activity for each fox during the monitoring period is shown in Figure 3.31.

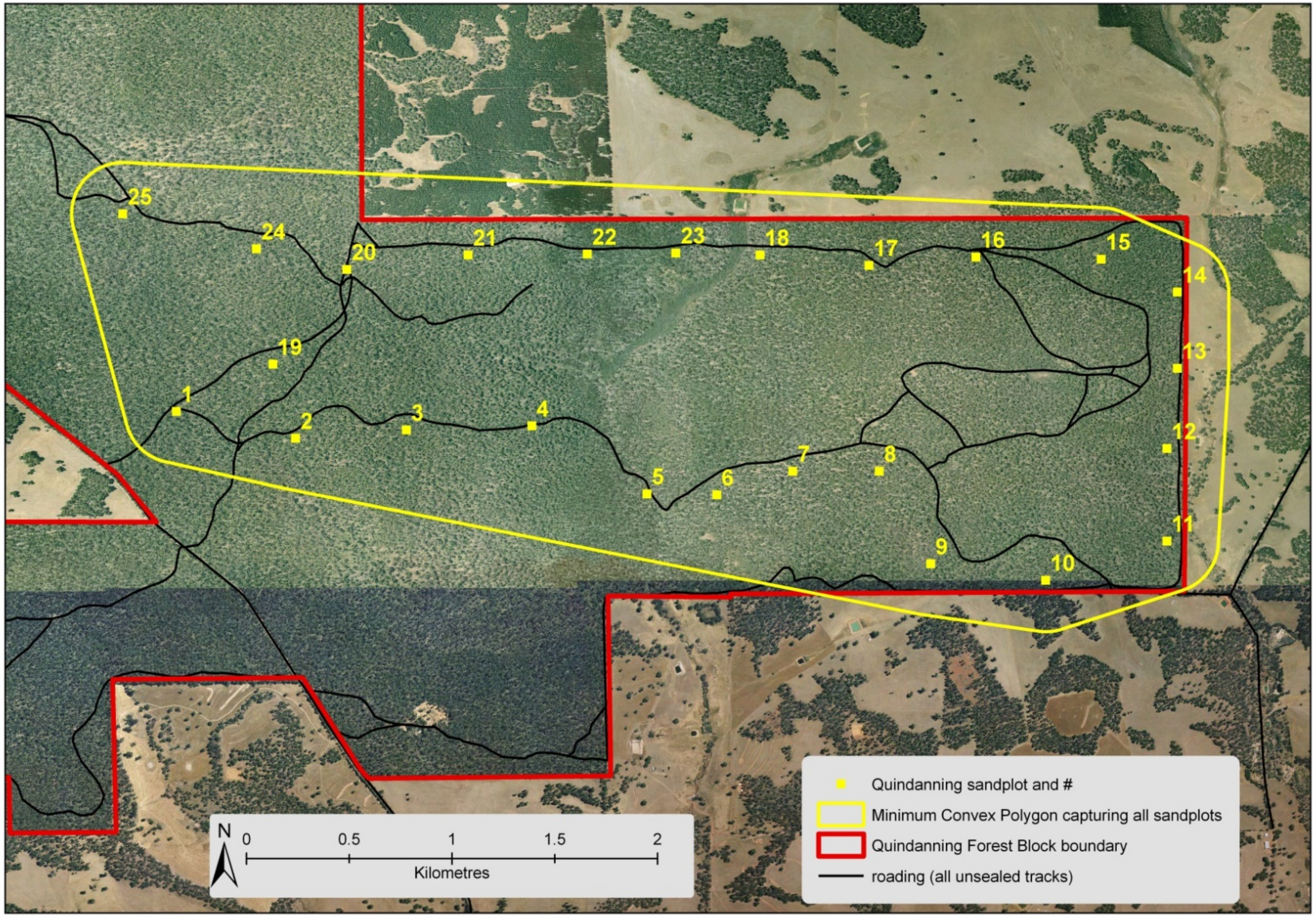

Figure 3.28 Composite orthophotograph of Quindanning Forest Block showing the location of individual sandplots monitored daily for evidence of fox (*Vulpes vulpes*) activity for 10 consecutive days.

Table 3.21: Estimated number of individual adult foxes (*Vulpes vulpes*) from sandplot monitoring for each of 10 days at Quindanning Forest Block, northern jarrah forest, south-west Western Australia.

Monitoring day	Estimated number of adult foxes	Plots at which presence detected	Comment
1	2	(1 & 24) (12)	Appeared to be adult and juvenile tracks at sandplot 12
2	3	(1), (22) (10, 11 & 12)	Appeared to be adult and juvenile tracks at sandplots 10, 11 & 12
3	2	(1, 19 & 20) (10, 11, 12 & 13)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13
4	2	(4, 6? & 8?) (10, 11, 12, 13, 15 & 16)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13. Interpretation of this pattern as indicating the presence of 2 foxes, as opposed to 1, incorporates information from the previous 3 days of monitoring, as per the MKTBA protocol
5	2	(1, 19 & 20) (10, 11, 12 & 13)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13
6	2	(1, 19 & 20) (10, 11, 12 & 13)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13
7	3	(1), (7) (10, 11, 12 & 13)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13
8	1	(10, 11, 12 & 13)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12 & 13
9	2	(6, 7) (10, 11, 12, 13 & 14)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12, 13 & 14
10	2	(1, 2, 3, 4 & 5) (10, 11, 12, 13 & 14)	Appeared to be adult and juvenile tracks at sandplots 10, 11, 12, 13 & 14

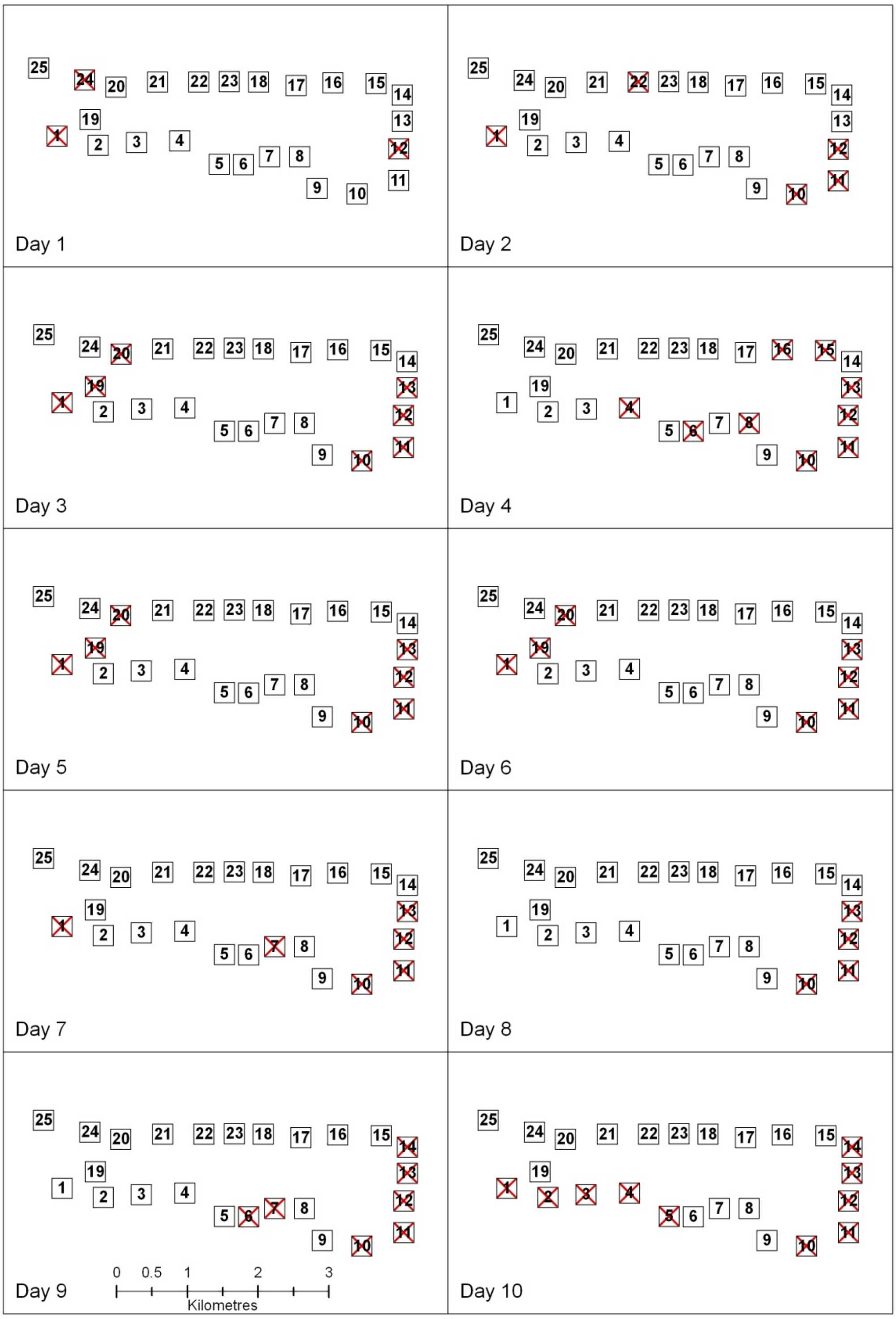

Figure 3.29 The pattern of fox activity on sandplots for 10 consecutive days of monitoring fox (*Vulpes vulpes*) activity at Quindanning Forest Block, northern jarrah forest, south-west Western Australia.

4	location of sandplot and sandplot number
X	location where fox activity was recorded

Table 3.22: Foxes (*Vulpes vulpes*) trapped post the 10 days of monitoring activity at sandplots at Quindanning Forest Block, northern jarrah forest, south-west Western Australia.

Day post commencement of fox trapping	**Sandplot number where fox trapped**	**Activity recorded at capture location post capture**	**Comment**
Day 3	12	Activity continued	Juvenile male trapped, vixen sighted, not trapped
Day 5	12	Activity continued	Juvenile female trapped, vixen sighted, not trapped
Day 7 am	11	Activity continued, activity appeared to be from juvenile	Vixen trapped
Day 7 pm	12	Activity continued, activity appeared to be from juvenile	Juvenile male trapped
Day 8	12	Activity indicative of a fifth cub continued at sandplot 11 for one additional day, then ceased	Juvenile male trapped
Day 9	1	Activity ceased	Adult male trapped

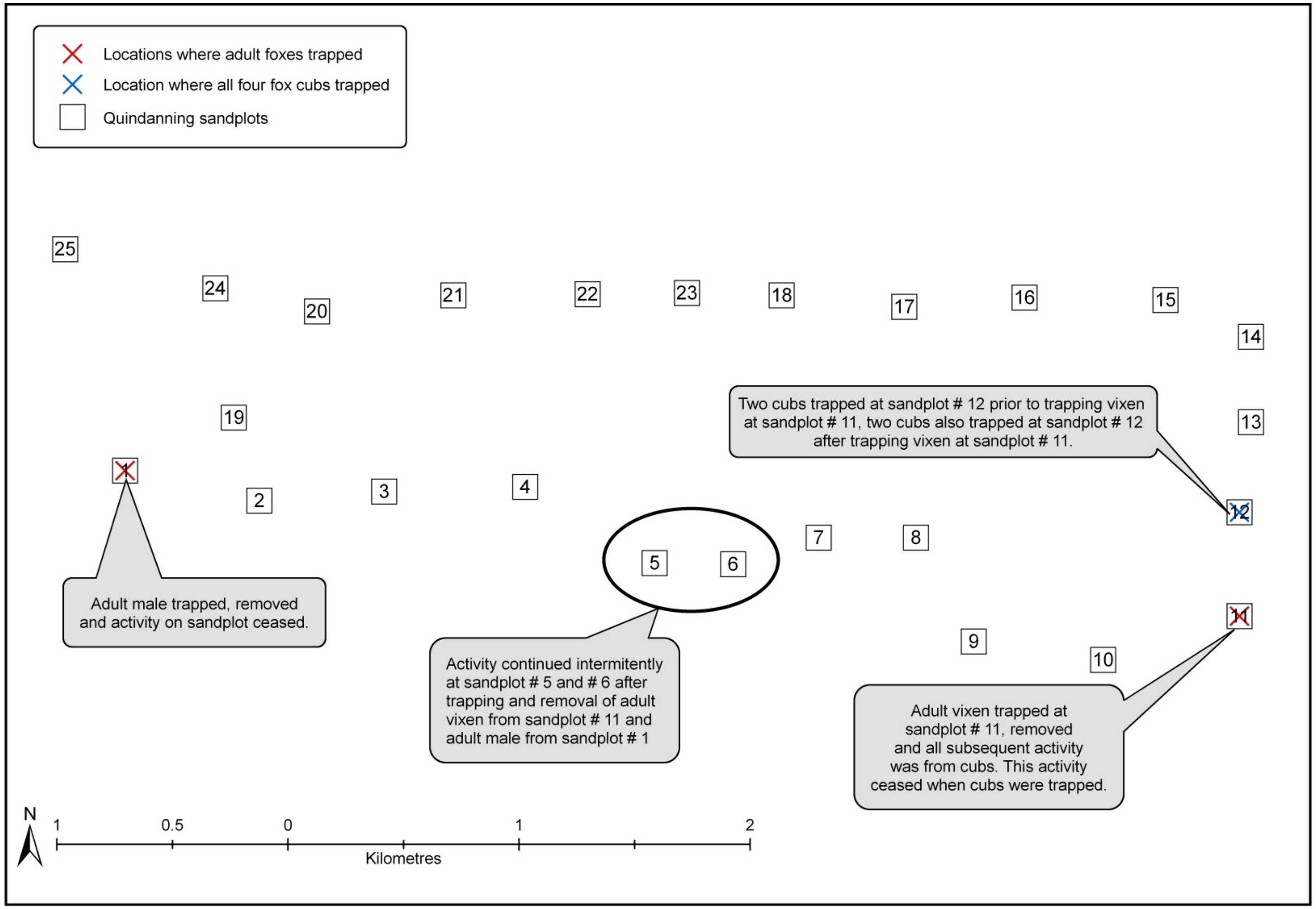

Figure 3.30: The location where adult and juvenile foxes (*Vulpes vulpes*) were trapped, post the 10 day period of monitoring fox activity at sandplots, Quindanning Forest Block, northern jarrah forest, south-west Western Australia.

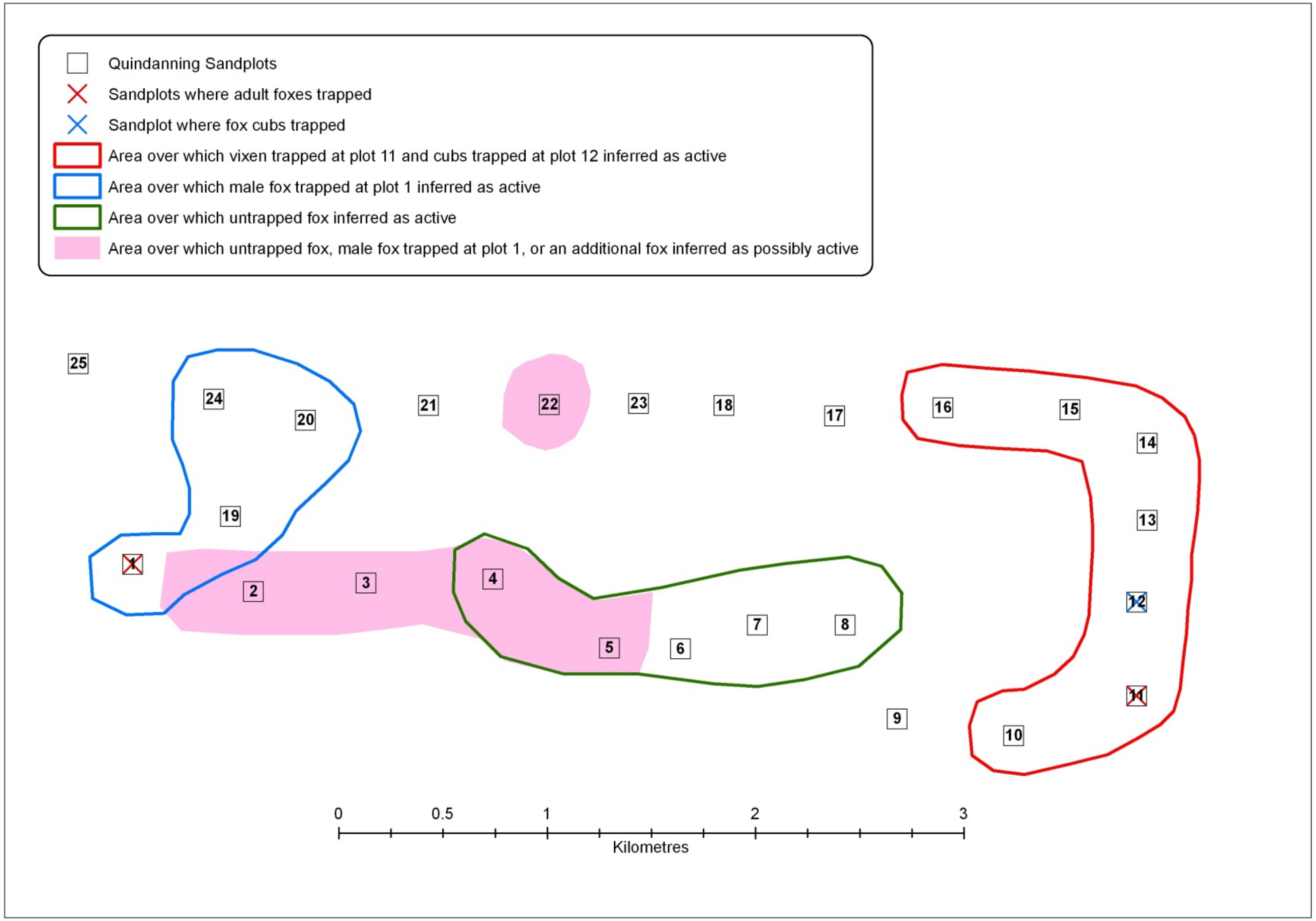

Figure 3.31: Areas of inferred activity for foxes (*Vulpes vulpes*) trapped at sandplots within Quindanning Forest Block, northern jarrah forest, south-west Western Australia.

3.4.11.2 Validation through use of molecular techniques

This aspect of the research was undertaken as part of the DEC and IACRC Western Australian Demonstration Site and provided an opportunity to further assess the validity of the methodology for estimating the number of foxes present within a sandplot network. The research examined if the number of individual foxes identified through genotyping DNA recovered from hair concurred with the number estimated to be present (the MKTBA estimate). Data from the 'Seventy Seven Road' sandplot network from the Spring 2008 sandplot monitoring session are presented as they provided the highest proportion of hair samples from which DNA was recovered and genotypes obtained. The sandplot network is within the unbaited treatment group of the Operation Foxglove study area (1994 to 2000) and within the unbaited treatment of the WA Demonstration Site (2006 to 2009). The network layout and location of each sandplot is shown in Figure 3.32.

There was only one day (day 6) on which fox activity was recorded on more than one sandplot and where the confidence rating was '1'. At day six (the final day of monitoring) the estimated number of foxes detected (the MKTBA estimate) was 1 (Table 3.23).

Hair samples were collected on five of the six days (days 2 to 6) and from multiple plots, with 16 hair samples collected in total. All collected hair samples yielded DNA and 15 of the 16 samples were identified as fox, the 16th (from plot number 26 on day 3) was identified as chuditch (Table 3.23). All samples confirmed to be fox were able to be genotyped and all were genotyped as the same individual female fox which concurred with the MKTBA estimate.

Table 3.23: Sandplots from the DEC and IACRC ‘Seventy Seven Road’ sandplot network where fox (*Vulpes vulpes*) activity was detected.

Monitoring day	Sandplot number where fox activity detected	Estimated number of foxes	MKTBA estimate	Number of hair samples collected	Plot number where hair sample collected
1	-	0	0	0	
2	-	0	0	1	26
3	8	1	1	7	3, 8, 10, 16, 18, 20, 26
4	18	1	1	3	12, 18, 20
5	20	1	1	1	20
6	11 & 18	1	1	4	3, 18, 20, 26

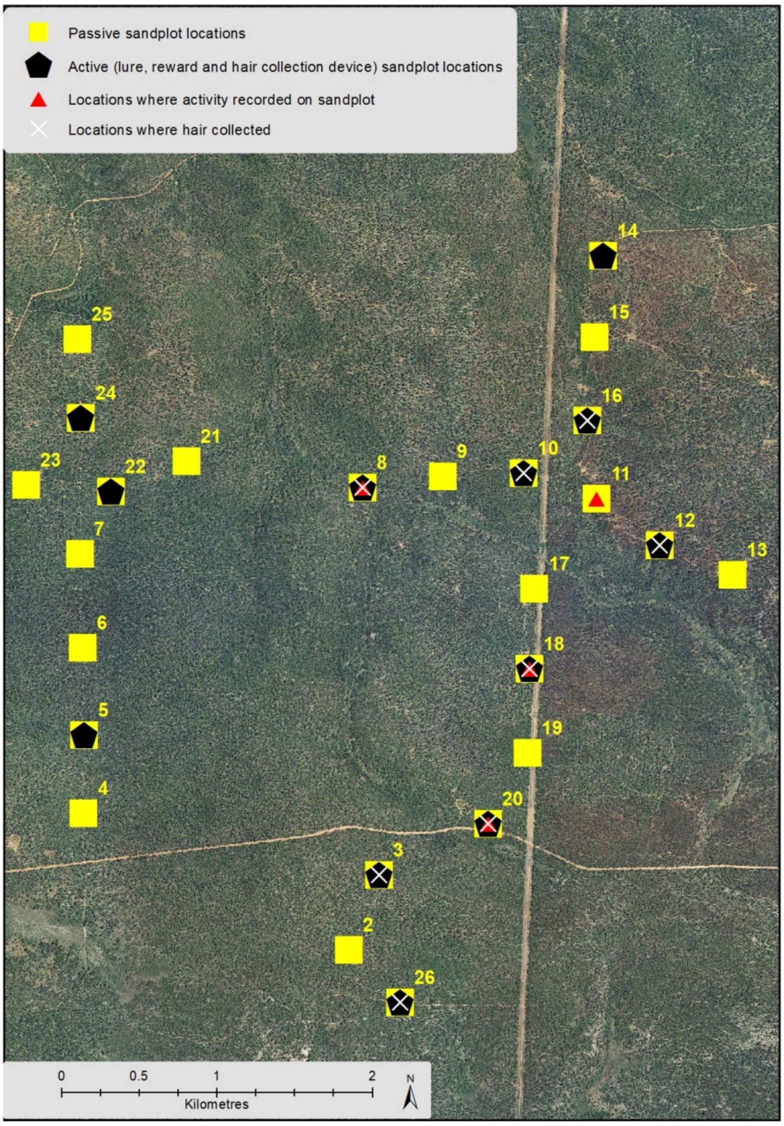

Figure 3.32: Seventy Seven Road sandplot network where molecular techniques were adopted to assess the validity of the MKTBA methodology used to estimate number of individual foxes (*Vulpes vulpes*) detected.

3.5 Discussion

3.5.1 General assessment of the effect from 1080 baiting for fox control

The inference from the final year (year 3) estimates of fox abundance (Fig. 3.15, shown again below) is that 1080 baiting for fox control resulted in a reduction in fox abundance. Although the 95%BCI were overlapping, there was a pattern of reduced fox abundance with an increase in the frequency of baiting. The biological significance of this is demonstrated in Chapter 4 (woylie survivorship). There was no support for the hypothesis that the distance from agricultural land affected fox abundance, however, recruitment or re-invasion of foxes post baiting occurred more rapidly at sites closer to the forest interface with agricultural land (Figs. 3.25, 3.26 and 3.27).

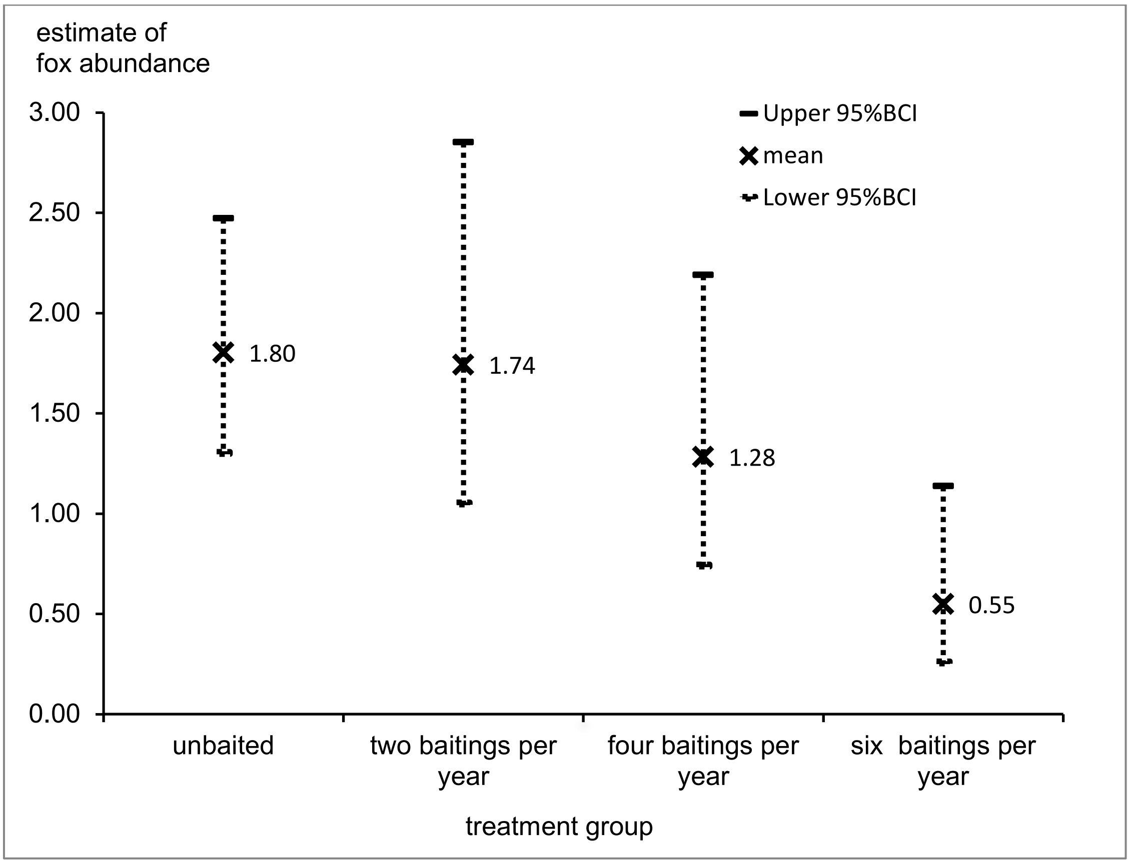

Figure 3.15: Modelled estimates fox abundance within the northern jarrah forest, south-west Western Australia, derived from the preferred model from the year 3 'bayesmh' Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity. Upper and lower 95%BCI refers to the Bayesian 95% equal-tailed credible intervals.

There was an anomalous effect for year 1 and year 2, whereby fox abundance was estimated to be higher in the four than in the two baitings per year treatment group (Fig. 3.33 and Fig. 3.34), however the was considerable overlap in 95%BCIs. Nonetheless, in all years, fox abundance modelled from the mean of the posterior distribution from the preferred model was lowest in the six baitings per year treatment group, again with considerable overlap in 95%BCIs.

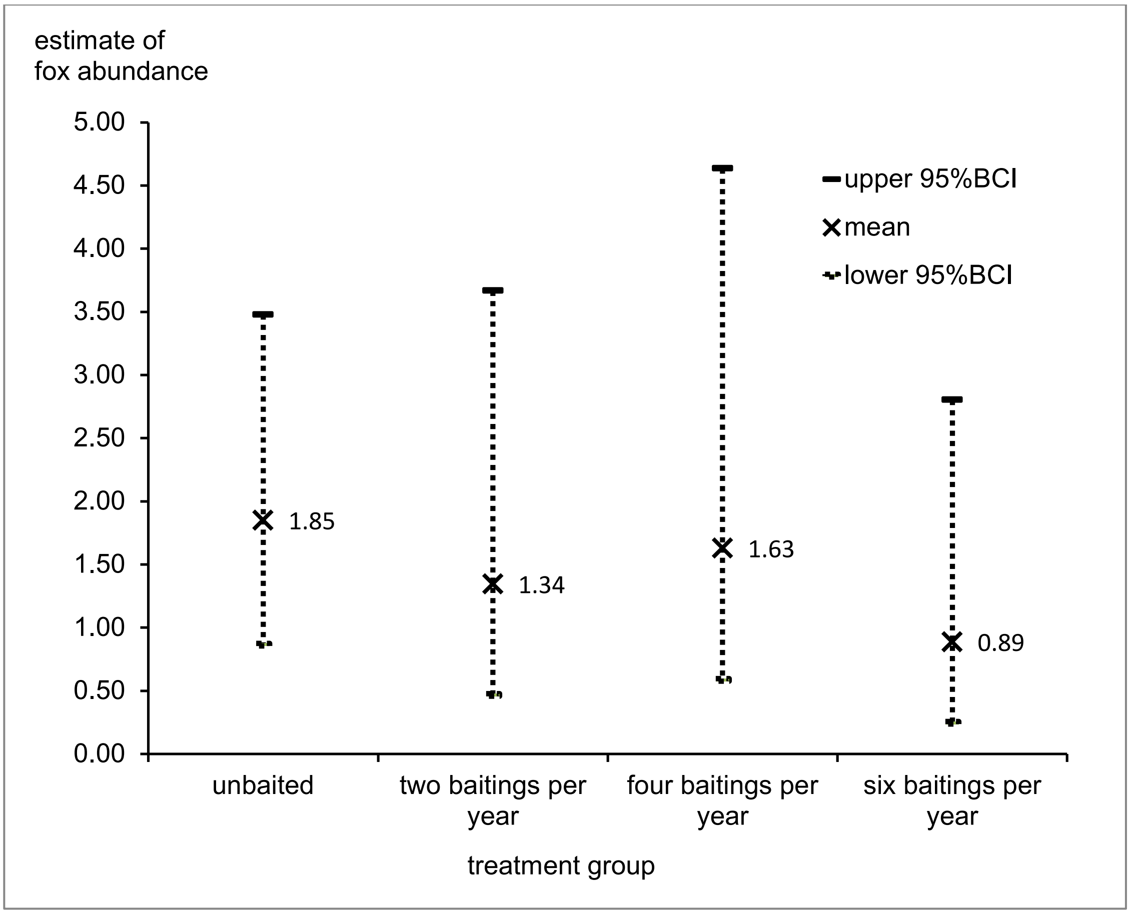

Figure 3.33: Modelled estimates fox abundance within the northern jarrah forest, south-west Western Australia, derived from the preferred model from the year 1 ‘bayesmh’ Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity. Upper and lower 95%BCI refers to the Bayesian 95% equal-tailed credible intervals.

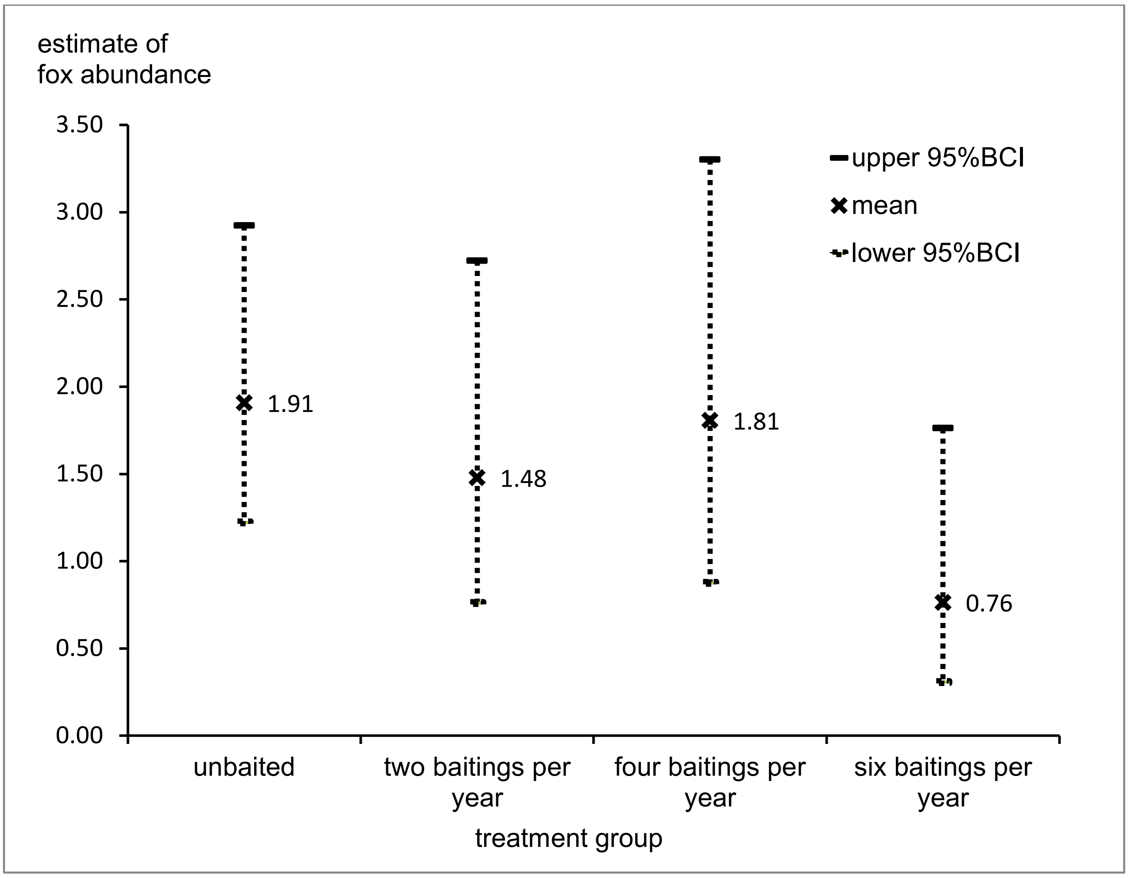

Figure 3.34: Modelled estimates fox abundance within the northern jarrah forest, south-west Western Australia, derived from the preferred model from the year 2 'bayesmh' Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity. Upper and lower 95%BCI refers to the Bayesian 95% equal-tailed credible intervals.

3.5.2 Indices and estimates

One of the most widely used indirect methods for assessing predator abundance is based on the use of sandplots as described by Engeman (2005). The analyses of data collected this way and the derived 'index' has changed little from the index proposed by Linhart and Knowlton (1975) for which the authors noted "*we have no way to relate these indices with the actual number of coyotes present in a given area"*. In the absence of validation of the indexing technique used, the same still applies.

Further issues with the use of the widely used indexing methods include use of methods which are often referred to by wording such as 'we adopted a variation of the index method describe by …' without specifying what these variations are. In the absence of specifying the methodology it is difficult to assess the validity of that methodology or if critical assumptions have been met or violated.

The method adopted in the northern jarrah forest and described in this chapter was designed for use in a forest environment with a perceived low density of introduced predators. However, the technique used to estimate the MKTBA may also be applicable in other low predator density environments. In lieu of sandplotting, use of camera stations, hair collection stations and various other molecular techniques are all amenable to the model selection and inference approach used, irrespective of the way in which the count data are collected. The critical issues then become determining the distribution of the count data collected, assessing when to assume a Poisson, negative binomial, zero-inflated or alternative distribution and therefore determining which model or models should be used and determining whether assumptions have been met.

3.5.3 The number of days required when monitoring fox activity and deriving an estimate of fox abundance

There is a considerable body of literature from mark-recapture studies recommending the minimum threshold for the number of days required for each trapping session to ensure the derived population estimates are indicative of the population present (see for example Lebreton *et al.*, 1992; Otis *et al.*, 1978; White, 2005). The same principles also apply when deriving estimate from methods other than mark-recapture. Lebreton *et al*. (1992) noted a minimum (in this case a technical absolute minimum) of three occasions was required to estimate one survival rate and "*no meaningful inference on population dynamics can be made from one survival"*. Otis *et al*. (1978) recommended five to seven (ideally more) trapping sessions were required for population estimates. Methodologies exist for determining the minimum number of required trapping days when using a trapping web design (Anderson *et al.*, 1983; Buckland *et al.*, 2004; Lukacs *et al.*, 2005; Wilson and Anderson, 1985). For trapping webs, the assumption of the probability of detection at the centre of the web = 1 is taken as met when no new captures are recorded at the centre of the web. Once identified, this period (until there are no new captures) can then be set as the minimum number of days to monitor any given trapping web.

The minimum number of days required for deriving estimates from interpretation of activity at sandplots is not known. The plot of the correlation matrix using the pooled data from days one to 10 for the three years of analysed data from the northern jarrah forest study was only partially asymptotic at days six and seven (Fig. 3.24) with an *r*-value of 0.69. This indicates the minimum number of days required to monitor sandplots for fox presence may be able to be reduced from ten to six or seven, provided this *r*-value is deemed acceptable by the analyst, manager, or operator and provided the monitoring is in habitat comparable to the habitat in which the *r*-value was obtained, in this case, the northern jarrah forest. Fewer days than this is not recommended. This result was used as the rationale to reduce the number of days (from ten to six) when monitoring sandplots as part of the IACRC and DEC WA Demonstration Site research program (2006 to 2009, see Chapter 6). The current 'norm' in WA when monitoring fox presence from sandplots is to monitor for three days only. The results from this study suggest this in inadequate to derive an estimate of fox abundance from which inference can be reliably made.

3.5.4 Recruitment of foxes post 1080 baiting

With the exception of Sullivan sandplot network, monitoring within the baited treatments post-baiting in 1999 detected fox presence at perimeter sites only (Fig. 3.25). Although Sullivan sandplot network is 10.8 km from the forest margin and is not considered a perimeter site, it borders an inholding of cleared agricultural land (Fig. 3.1) and therefore provides an opportunity for fox re-invasion from agricultural land, if foxes are present there. In 2000, with the exception of Randall sandplot network (within the two baitings per year treatment), monitoring within the baited treatments, post-baiting, again detected fox presence at perimeter sites only, inclusive of Sullivan sandplot network. Interestingly, the fox re-invasion detected at Randall sandplot network, the sandplot network furthest from the forest/agricultural land interface, was not detected until 12 days post baiting (Fig. 3.27).

A plausible interpretation is that fox baiting has less effect on fox abundance at sites close to agricultural land as these sites provide the opportunity for re-invasion from the adjoining agricultural land. However, there are no data to suggest baiting at perimeter sites didn't kill foxes. The most parsimonious explanation is that fox abundance at these sites was reduced as a result of baiting and there was a subsequent and immediate recruitment of foxes from neighbouring agricultural land. The results also suggest, in the presence of 1080 baiting, dispersal and recruitment into baited areas is not restricted to the traditionally perceived late summer to early autumn period of juvenile dispersal.

The implications for conservation management are:

(i) Fox control through 1080 baiting at a frequency of six baitings per year with a baiting intensity of five baits/km^2 achieved a greater reduction in fox abundance than the standard regime of four baitings per year, and a greater reduction than two baitings per year and the unbaited treatments, albeit with considerable overlap of 95%BCIs. Conventional interpretation of the overlapping 95%BCIs would suggest there is no “significant” difference between treatments and could therefore be used as justification for no baiting at all. However, the results from the woylie survivorship study (Chapter 4) demonstrate baiting at a frequency of six baitings per year conferred a biologically significant difference in woylie survivorship. Therefore, *a* baiting regime of six baitings per year, at a baiting intensity of five baits/km^2, is recommended to achieve the conservation objective of reduced fox density over large tracts of multiple use forest.

(ii) Baiting regimes of two and four baitings per year may be less effective than six baitings per year and at sites close to agricultural land they may be simply ‘turning over’ the fox population with replacement of individuals through immediate recruitment from dispersal or immigration.

(iii) The biodiversity effects from fox density reduction followed by rapid recruitment may be quite different from, and a greater threat to biodiversity conservation than, the continued presence of a stable, low density fox population which is not being ‘turned over’ by periodic baiting (Berger *et al.*, 2008). This is also discussed in Chapter 6.

3.5.5 Variables influencing fox abundance

When modelling fox (and cat) abundance, the northern jarrah forest study assessed models with a limited number of potential explanatory variables. These models (Table 3.4 for foxes; Table 3.5 for cats) did not include the large suite of potential habitat and biophysical variables likely to affect fox and cat abundance and focussed on assessing the effect from the frequency of 1080 baiting. The aim was to assess the dominant effects from baiting frequency and to assess the effects from a limited number of anthropogenic factors. None of the anthropogenic factors were identified as explanatory variables in relation to fox or cat abundance.

The effect of anthropogenic factors, roading in particular, was considered by Griffith *et al*. (1981) as likely to influence detectability of coyotes. The type of roading also influenced detectability of kit foxes (*Vulpes macrotis mutica*) in the San Joaquin Valley, California (Smith *et al.*, 2005) and the red fox in Spain (Servin *et al.*, 1987). In addition to the caveats Stander (1998) placed on inference from indices from spoor counts (where the regression coefficients for the relationship between spoor counts and true density were different for each species, see Section 3.2), he also found detectability to vary with habitat heterogeneity and with the extent of roading within each study site. This wasn’t shown to be the case in the northern jarrah forest.

3.5.6 Validating the methodologies used to estimate the minimum number of foxes present

The cyanide baiting technique has been described as suitable for estimating relative abundance (Algar and Kinnear, 1992), however, failure of cyanide baiting to remove foxes at the validation sites in the northern jarrah forest suggests cyanide baiting has limited potential for inference of fox abundance when that abundance is low. This no doubt reflects that the probability of detection (and in this case the probability of a cyanide death) is dependent on population size. Burrows *et al*. (2003) found use of cyanide was unreliable when attempting to estimate feral cat numbers in the Gibson Desert Nature Reserve, WA and, as was the case in the northern jarrah forest study, Burrows *et al*. (2003) also *"abandoned"* cyanide baiting as a technique to estimate predator numbers.

The number of adult foxes trapped, combined with the individual fox not trapped and known to still be present at the Quindanning validation site, concurred with the MKTBA estimate from the pattern of activity on sandplots. Similarly, genotyping from DNA recovered from collected hairs at the Seventy Seven Road sandplot network from the IACRC Demonstration Site concurred with the MKTBA estimate. The hair collection technique was also more sensitive to detection of foxes and detected fox presence on 15 occasions, compared to detection on only five occasions from spoor (Table 3.23). The results from genotyping also confirmed a single fox had visited a number of sandplots, despite multiple records of fox activity over multiple sandplots. The genotyping also confirmed there was no relationship between the number of plots visited and the number of foxes present and demonstrated a single fox had visited multiple sandplots. This is a further indictment of the use of unvalidated indices and, in particular, is a strong argument against using a measure of activity on sandplots to infer abundance.

3.5.7 Qualifications on use of the estimate for the minimum number of foxes known to be alive

Although the technique to derive an estimate for the MKTBA was validated in the northern jarrah forest, caution should be shown if applying this technique elsewhere, as it may not be appropriate. There are five aspects which require consideration before applying the technique elsewhere.

Firstly: it is unlikely the pattern of activity at sandplots and the MKTBA estimate could be used to infer the number of foxes present if the fox population was at high density as the pattern of contagion at sandplots is also likely to vary with density. Similarly, although the presence of contagion or autocorrelation (continuity of activity at successive plots) assisted with interpretation of the northern jarrah forest sandplot data, it is also known to confound interpretation of carnivore activity on sandplots (see for example Sargeant *et al.*, 1998). This reinforces the need for site specific validation. In the absence of this site specific validation, the technique is not recommended.

Secondly: the technique also assumes independence of all sandplot networks, i.e. spatial or geographical closure. The northern jarrah forest research was carried out at a landscape scale and the average distance between neighbouring sandplot networks was 11.3km, with the closest two sandplot networks (George and Hakea) separated by 7.5km. The most isolated (Wearne) was 26.5km from its nearest neighbouring sandplot network (Leona) (Fig. 3.1). The area encompassed by the MCP for each sandplot network ranged from 11.2 (George) to 23.5km^2 (Sullivan) (Fig. 3.1). The combination of carrying out the research at a landscape scale, with relatively small areas used to monitor fox activity on sandplots and relatively large distances between sandplot networks, suggests spatial closure is likely, but it is not guaranteed. Obbard *et al*. (2010) demonstrated violation of the assumption of spatial closure when deriving estimates of density for carnivores. This resulted in large overestimates of predator density (Obbard *et al.*, 2010). Violation of this assumption for the northern jarrah forest fox density estimates would also result in overestimates of fox density.

Thirdly: by design, establishing a sandplot network on an existing roading system falls within the category of sampling methodologies termed ‘convenience sampling’ (Anderson, 2001). As the name suggests, the term applies to placing traps or any indirect sampling tool (e.g. sandplots or scent stations) at positions of convenience for the researcher or manager. This includes roads, easily accessible geographic features, recreation sites and known locations of high density for the species being sampled. Therefore, the results have the potential to be of limited inference value as they provide information about the features sampled (Anderson, 2001), or the occurrence of a particular species in relation to those features. In the case of the northern jarrah forest sandplotting data, the results should be interpreted as derived estimates of fox abundance within areas of the northern jarrah forest associated with roading. Relationships between the extent of roading and frequency of spoor have been observed for other carnivores. Stander (1998) believed the frequency of detection of spoor from carnivores was random when the habitat was uniform but acknowledged this was not the case in more heterogeneous habitat. An example where roads may influence estimates of abundance was provided from a study of track counts of the mountain lion (*Felis condor californica*) in California, where tracks were reported as most likely to be found on roads along streams and at other specific geographic features (Smallwood and Fitzhugh, 1995). Hard road surfaces, including sealed roads, were avoided by mountain lions in Arizona and Utah (Van Dyke *et al.*, 1986), and Griffith *et al*. (1981) believed there was strong circumstantial evidence to indicate use of roads by coyotes was inversely proportional to the amount of human activity. Clearly, there are multiple potential explanatory variables influencing detectability of carnivore spoor on roads.

Fourthly: the technique used to estimate the MKTBA for foxes in this study is species specific. Any heterogeneity in detection and abundance of foxes is highly unlikely to apply to other predators, or any other species (see Slade and Blair, 2000; Stander, 1998). This was evidenced in the northern jarrah forest data by very few detections of cat presence, despite cats being known to be present. Cats were found to be preying on radio-collared woylies (see Chapter 4) and were also detected at low density in cage traps, yet were detected with confidence on only 32 occasions on the 1m x 1m sandplots over the three years of sandplot monitoring. The small sandplots have subsequently been shown to be less sensitive to detection of cats than a 1m wide swathe of sand across the width of a road when used in conjunction with molecular analysis of collected hair samples (unpublished data from the northern jarrah forest component of the DEC and IACRC WA Demonstration Site, see also Chapter 6).

Finally: sandplotting may not be the most appropriate method to derive estimates of abundance. The uncertainty associated with sandplotting and interpretation of spoor would suggest proven molecular techniques can now be used more efficiently and can provide information on the species and individual present. Use of molecular techniques to identify (genotype) individuals from DNA recovered from hair and scats has become a standard ecological tool. The technology is proven but can be problematic logistically, as there are still some major impediments to its practical use as a field tool and impediments to its routine use to estimate abundance of predators at low densities. Ideally, data on genotypes should be treated the same way data on capture histories of known individuals are treated from conventional mark-recapture studies, i.e. with population parameters derived through use of robust and proven mark-recapture and survivorship analyses and verification of the assumptions of such analyses. For example, Program MARK (White, 2001) can now be used to derive population parameters from capture histories of genotyped individuals and can also incorporate varying levels of misidentification of genotypes. However, when collecting hair and scat samples from introduced predators within conservation estate, data are always likely to be sparse. Use of molecular techniques may be able to provide ecologists with additional data points, but is unlikely to be the panacea for the issue of sparse data.

Use of molecular techniques appears to have been embraced by agencies responsible for conservation management. However, these agencies, nationally and internationally, do not have a good track record with appropriate planning, implementation and interpretation of fauna survey and management programs requiring quantitative analyses (see examples given by Belovsky *et al.*, 2004; Chase, 1986; Moir and Block, 2001). It is reasonably safe to speculate, in the absence of a paradigm shift in the way conservation agencies do business, lack of well-considered approaches to collection and analyses of information gleamed from use of molecular techniques will dilute the limited resources available for conservation management generally and for quantitative analyses of population parameters in particular. Nonetheless, use of molecular techniques is recommended (see recommendations below) and, if data collection is planned and implemented to meet clear objectives and appropriate quantitative analyses are carried out, use of data on genotypes has the potential to improve conservation outcomes generally and improve understanding of introduced predator ecology in particular. However, caution still stands, as appeals in the past of Nichols (1992), White (2005) and Anderson (2001) to incorporate appropriate estimators in wildlife studies appear to have fallen on deaf ears:

> *"Numbers … are not always data, and many numbers (large sample size) do not always mean good data. Instead, the word data implies an information content with respect to some objective. Often numbers can be collected, but they may not represent data because they have little meaning and cannot be interpreted without making critical, but very unrealistic, assumptions. Such numbers are not trustworthy and cannot lead to valid inferences about the population of interest"* (Anderson, 2001, p1296).

3.5.8 Cat abundance in the presence of fox control

Unlike the fox data, the data on cat abundance indicated abundance was constant across all treatments. This result is highly likely to be a function of the data being extremely sparse and the lack of sensitivity of the technique to detect cat presence. It may also reflect a predisposition of cats to avoid tracks or roads (for which there is negligible published data) and/or to avoid areas where foxes are present. The latter is consistent with cats showing a mesopredator release response (see below and Chapter 6).

Although there was no support for models incorporating the variable for the number of days involved in assessing cat abundance (models 003, 006, 009, 010, 012, 013, 015 and 016; Table 3.5), other studies have demonstrated this may occur for some predators. For example, in a trial assessing bait preferences and visitation rates of the Culpeo fox (formerly *Pseudalopex culpaeus*, now *Lycalopex culpaeus*) and the South American gray fox (formerly *P. griseus*, now *L. griseus*) in Patagonia, Travaini *et al.* (2001) found detection (visitation) increase with successive days of monitoring. An observer effect has also been recorded for detection of coyote visits to scent stations (Griffith *et al.*, 1981, and previously by Hodges 1975 as cited by Griffith et al., 1981).

Importantly, cats were detected with confidence on only 32 occasions on the 1m x 1m sandplots over the three years of sandplot monitoring and the 1m x 1m sandplots have subsequently been shown to be less effective than a large swath of sand when used to detect cat presence. Although there was no support for the presence of mesopredator release of cats in the presence of fox control, this again may be an artefact of the lack of sensitivity of the sandplotting technique. The phenomenon of mesopredator release is well documented in the literature. However, there is a dearth of empirical data providing unequivocal evidence for mesopredator release. The implications from mesopredator release of cats, whether it be release from exploitative competition and/or interference competition, are discussed in Chapter 6.

3.6 Recommendations for further use of sandplots and interpretation of data collected from fox and cat activity on sandplots

There seems little value in carrying out fox baiting programs for fauna conservation purposes if populations of the fauna species requiring protection, and the fox population(s) targeted by the control measures, are not monitored. In these circumstances, the effectiveness of the control measures cannot be assessed. The use of estimates for the MKTBA combined with application of Bayesian modelling techniques to derive estimates of fox abundance within the northern jarrah forest of south-west WA appears appropriate for continued use in this environment. However, monitoring objectives should be clearly specified to ensure the monitoring protocols are designed to meet specifications which enable the data collected to be appropriately analysed. For example, Western Shield program has a stated aim to *“reduce fox density on conservation lands … ”* (Burbidge *et al.*, 1996), but there is no monitoring program in place to determine trends in fox populations. Similarly, the Western Shield program recognised cats as a potential threat to biodiversity values (Bailey, 1996) and further recognised cat abundance may increase in the presence of reduced fox abundance. Although more recent research (post 2011) has provided additional support for the hypothesis that cats are significant predators of native fauna and that this predation may increase when fox control is implemented, there is no broadscale monitoring of either species throughout the areas covered by Western Shield.

The issue of assessing predator abundance can be addressed through modifications of the sandplotting technique to incorporate molecular analysis of DNA extracted from collected hair samples. This is recommended with some major qualifications (see below). Until operational constraints are resolved and protocols can be routinely applied to collect and analyse predator hair and scats, use of molecular techniques may be limited. Similarly, the temptation to rapidly and widely deploy use of camera stations needs to be carefully considered to ensure the data can be appropriately managed, stored and analysed (Krebs, 2018; Moll *et al.*, 2020).

Given the limitations of alternatives, if sandplot monitoring continues to be used for monitoring fox populations within forest areas of south-west WA, and forest habitat elsewhere, and its use is to assess the fauna conservation value and effectiveness of the fox baiting programs in terms of their ability to reduce fox abundance, use of MKTBA estimates is recommended. However, the following monitoring protocols apply only to habitat similar to open forest or tall-open forest, and although they are potentially applicable to large areas of conservation estate generally, the caveats below also apply:

1. Sandplot monitoring should be conducted annually and, when conducted in areas subject to fox control through baiting, monitoring should be scheduled for September and timed to maximise the period between the last bait delivery event and commencement of the six day monitoring period (see 7, below).
2. The recommended method for establishing each sandplot network is as described in Section 3.3, where each plot is a minimum of 500m from its nearest neighbouring sandplot and each network is comprised of a minimum of 25 sandplots, all within a nominal area no greater than 25km^2. Each sandplot should be approximately 1m wide. The recommended variation from the method used in this study (Section 3.3) is that sandplots should span the width of the road (unlike the 1m x 1m sandplots used in Operation Foxglove).

3. A hair collection device should be placed at each sandplot. The Poly Pipe was found preferable to the Sticky Wicket hair collection device. The latter is not recommended for use in a forest environment as it is considerably less effective in terms of the number of hairs collected. This may be, in part, because the double-sided tape when used in the 'Sticky Wicket' configuration is exposed directly to moisture and sunlight and becomes less effective in Mediterranean or mesic forest environments than the 'Poly Pipe' device. The Poly Pipe provides protection to the tape which is housed within the pipe and not exposed to environmental conditions.
4. A non-toxic lure should be provided (and secured) in the centre of the pipe.
5. Sandplots should be raked smooth and, optionally, lightly sprayed with water daily.
6. Prior to the first day of monitoring, an attempt should be made to locate and collect all predator scats within the monitored area. A sample (a thin scraping of the outer layer of the scat) and duplicate sample should be collected and stored in a salt saturated dimethyl sulphoxide and EDT solution (Seutin *et al.*, 1991) for subsequent DNA extraction and analysis.
7. Monitoring of sandplots and Poly Pipes is required for a minimum of six consecutive days.
8. The condition of each sandplot and any evidence of spoor must be recorded and each plot re-raked and sprayed. Each hair collection device should be inspected, double-sided tape removed and replaced if hairs are present and the reward refreshed as required. Hairs can be stored as described by Garretson *et al.* (2008). The presence of all 'new' predator scats should be recorded and scrapings collected and stored as described above for subsequent extraction of DNA for identification to species and individual.
9. Monitoring of fox activity on sandplots should be focused on deriving estimates of the number of individuals detected (the MKTBA), as opposed to an index of activity which may or may not have a relationship to abundance. If adopted in a forest environment, interpretation of the patterns of activity on sandplots may be as described in Section 3.4, where continuity of activity (contagion or autocorrelation) is interpreted as a single fox.
10. The results from molecular analyses to identify the species responsible for leaving hair or scats (e.g. melt curve analysis) and subsequent genotyping, can then be used to validate (or refute) the assumptions made from the pattern of activity on sandplots (9, above).

11. Use of information-theoretic or Bayesian modelling techniques and adoption of a model selection and inference approach is recommended. If adopting Bayesian modelling, informative priors are now available (this research and the research cited). Exploratory analysis of count data is essential to determine the most appropriate distribution functions for modelling.
12. Selecting the variables to include in modelling is best determined by an understanding of the species biology and behaviour (in this case, the fox and cat) and by understanding the site-specific factors which are most likely to influence detection and abundance. These may include the extent of roading, weather conditions and habitat.

Chapter 4

Survivorship of translocated populations of the brush-tailed bettong, or woylie, *Bettongia penicillata ogilbyi*, a predation sensitive indicator species

4.1 Introduction

4.1.1 The rationale for translocation and use of the woylie as an indicator species

The suite of non-volant native mammalian species known to occur within the northern jarrah forest includes several species with the potential to respond to fox control (see Chapter 5, Table 5.1). However, historic records, opportunistic surveys, surveys targeting specific species or sites and preliminary trapping prior to commencing the current research, indicated all native resident mammalian populations were at low abundance. This supported the premise that, should a fauna response to 1080 baiting occur, it was unlikely to be detected at any level of significance through conventional null hypothesis testing within the time frame of the current research program. The biological significance of any such response would also be unlikely to be detected.

Given this, populations of the woylie were proposed for translocation to the study area as it is considered an indicator species for ground dwelling terrestrial mammalian fauna sensitive to fox predation. Intensive monitoring was proposed to determine the fate of each woylie within each of the different baiting and unbaited treatment groups. The decision to use the woylie as an indicator species was based on previous research which demonstrated:

- it can be successfully translocated (Christensen and Leftwich, 1992; Delroy *et al.*, 1986; Nelson *et al.*, 1992);
- it has the capability to show a response to fox control as females reach sexual maturity at six months of age, it is a continuous breeder and each female can produce up to three young per year (Smith, 1989; 1992; 1994), therefore, reproductive success is detectable;
- it readily enters wire cage traps and is amenable to monitoring through conventional trapping (personal observations); and
- adults are sufficiently large to be fitted with radio-collars (personal observations) with a battery life in excess of six months and are therefore suited to intensive survivorship monitoring.

The woylie was further considered suitable for translocation in terms of biodiversity conservation outcomes. The woylie's former geographic range included the northern jarrah forest (Christensen and Leftwich, 1992; de Tores and Start, 2008), from which it had become locally extinct. Therefore, successful translocation would result in re-established woylie populations within part of its former geographic range.

Translocation of woylies was carried out in two phases. The first phase was a pilot study, where a subset of the translocated woylies was radio-collared and survivorship intensively monitored over an eight month period. The second phase was a longer-term study, again involving intensive monitoring of a subset of translocated woylies and recruits to the population. Use of the woylie as an indicator species required translocation of study animals from Dryandra Woodland (Chapter 2, Fig. 2.1) to the northern jarrah forest.

4.1.2 Hypotheses

Hypotheses were formulated in a model selection framework. The overriding hypothesis was that woylie survivorship would likely be a function of fox density which, in turn, was hypothesised to be a function of the frequency of 1080 baiting (see Chapter 3). The relationship between woylie survivorship and the frequency of baiting was further hypothesised to be influenced by a suite of covariates. These covariates were incorporated into a set of candidate models to describe the woylie survivorship data. Model selection was through the use of AICc and QAICc (Burnham and Anderson, 2002) and, combined with model averaging, was used to determine which model, or models, best described the data.

4.2 Materials, methods and monitoring protocols

4.2.1 The 1080 baited treatments and unbaited control

The 1080 baited treatments and the unbaited control are as described in Chapter 2 (see Fig. 2.5). Aerial delivery of 1080 baits (see Armstrong, 2004) provided bait coverage over all but the margin of the forest (the interface with agricultural land). Therefore, vehicle based delivery was used to bait the forest margin. Aerial and vehicle delivery of baits was at a baiting intensity of five baits/km^2 and bait delivery was coordinated to ensure vehicle delivery coincided with aerial delivery.

The experimental design incorporated a monitoring component, whereby the suite of resident small mammalian and reptilian species was monitored through a conventional fauna trapping program. The integrated trapping grid comprised 'Sheffield' wire cage traps (Sheffield Wire Products, Welshpool, WA), Elliott traps (Elliott Scientific

Equipment, Upwey, Victoria) and pitfall traps at 55 trapping grids. The largest grid within each of the 55 integrated grids was comprised of 25 wire cage traps suitable for trapping woylies at a trap spacing of 80 x 80m and covered an area of 10.24ha. (see Chapter 5, Fig. 5.2). Twelve trapping grids were established in the unbaited treatment, 16 in the larger two baitings per year treatment group, 14 in the four baitings per year treatment group and 13 in the six baitings per year treatment group (Chapter 5, Figure 5.1). Four of these trapping grids (Twin Bridges Road and Boggy Brook Road in the four and Hakea Road and George within the six baitings per year treatment group) were used as release sites for the pilot translocation study of woylie survivorship. An additional 15 grids were included as translocation release grids for the longer-term study, with a combined total of 19 grids used for release of woylies over the pilot and longer-term study. Twin Bridges Road was not included in the longer-term study (Table 4.1, Fig. 4.1).

Table 4.1: Trapping grids used as translocation release sites for the woylie (*Bettongia penicillata ogilbyi*) within the northern jarrah forest, south-west Western Australia. The trapping grids identified as part of the pilot study and/or the longer-term survivorship study of translocated woylies were also used to monitor the suite of *in situ* fauna (see Chapter 5).

Treatment and trapping grid name	Pilot and/or longer term study
unbaited control	
Seventy Seven Road	Longer term study only
Tanglin Road	Longer term study only
Stockyard	Longer term study only
Winooka	Longer term study only
two baitings per year	
Dobaderry	Longer term study only
Korner Road	Longer term study only
Schulstaad Road	Longer term study only
Paddy	Longer term study only
Thompson Road	Longer term study only
Wearne	Longer term study only
four baitings per year	
O’Neill	Longer term study only
Gordon Road	Longer term study only
Twin Bridges Road	Pilot study only
Boggy Brook Road	Pilot study and longer term study
Housebrook Road	Longer term study only
six baitings per year	
Amphion	Longer term study only
Murray	Longer term study only
Hakea Road	Pilot study and longer term study
George	Pilot study and longer term study

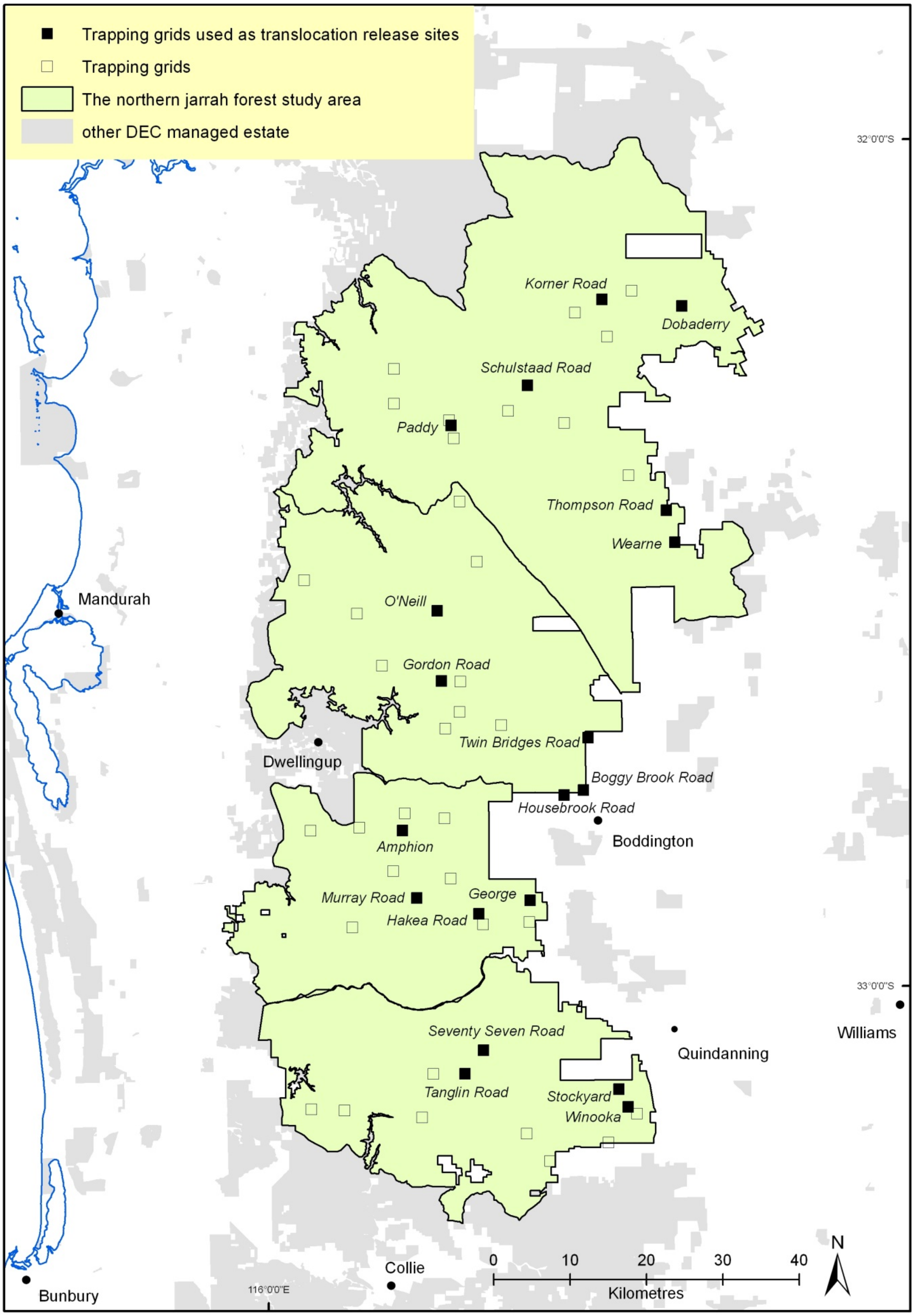

Figure 4.1: Translocation release sites for the woylie (*Bettongia penicillata ogilbyi*) within the northern jarrah forest, south-west Western Australia.

4.2.2 Woylie capture, handling, anaesthesia and morphometric data collection

All translocated woylies were sourced from Dryandra Woodland, approximately 50km east of the eastern margin of the northern jarrah forest study site (Chapter 2, Fig. 2.1). Trapping for translocation was conducted along roadsides within Dryandra Woodland. The traps used were ‘Sheffield’ wire cages, approximately 700mm deep x 300mm wide x 300mm high, constructed of 25 x 25 x 2mm galvanised weld mesh and triggered by a flat ‘trip plate’. Each trap was baited with a mixture of rolled oats, peanut butter and honey. Traps were cleared within one hour of first light and each trapped animal was transported, in a hessian bag, to a field station established at Dryandra Village (within Dryandra Woodland).

Preliminary observations indicated woylies contracted their muscles when physically restrained. Although a subjective assessment, this seemed more pronounced for the leg and neck muscles. The latter “muscling up” prevented an appropriate fit of radio-collars. If fitted when woylies were muscled-up, the radio-collars had the potential to become loose when the woylie subsequently relaxed after release. This could result in slipped collars or could allow the woylie’s forelimbs to become caught between the collar and neck. Therefore, to ensure radio-collars were appropriately fitted, ensure reliability of all morphometric measurements and avoid the requirement for physical restraint, all data recording, ear tissue sampling and radio-collaring (see below) was carried out when each woylie had been sedated. This was also considered a precautionary measure to reduce the possibility of capture myopathy. Sedation also enabled thorough examination of pouches, identification of presence of pouch young and ensured confident assessment of the sex of each pouch young.

Each woylie was weighed to obtain the gross weight (inclusive of the hessian bag and any pouch young), the net weight estimated and a combination of Ketamine (ketamine hydrochloride) and Xylazine (xylazine hydrochloride) was administered intramuscularly, at a nominal dose of 16-18mg/kg Ketamine and 5-6mg/kg Xylazine, for estimated net weights in the range 600 to 1600g. The actual dose administered was determined once each woylie had been sedated and net weight was known. Upon effect, a non-steroidal lubricant (Lacrilube) was applied to the inside of the lower eyelid of each eye to prevent desiccation of the conjunctiva. As part of the anaesthesia process (induction and the recovery), data were recorded for the time of induction, effect time, respiration rate (or more specifically, any anomalies to a ‘natural’ pattern of respiration), time to first spontaneous movement, time to attain an upright position and time to full recovery.

During recovery each woylie was held in a cool, quiet and dark room and kept within the hessian bag in which it had been originally placed when removed from the trap.

Standard morphometric data were collected (weight, head length, head-body length, pes length and tail length). The pes measurement was taken from the right pes and measured from the end of the calcaneum to the tip of the fourth phalange (i.e. a measure of the 'long pes'). The breeding status of each woylie was determined. Testes size was allocated to one of three categories: (i) undeveloped; (ii) developed and small; (iii) developed and large. Females were examined to determine if pouch young were present and, if so, the sex and size of the pouch young was also determined. Pouch condition and breeding status were described by one, or a combination, of the following:

- pouch undeveloped (for juvenile and sub-adult woylies);
- pouch unused (or appearing as unused);
- pouch empty or pouch young present;
- pouch not distended, or pouch distended, or grossly distended;
- teats elongated or not elongated;
- lactating or not lactating; and
- mammary not enlarged, enlarged, slightly enlarged or grossly enlarged.

An ear tissue sample (a 5mm diameter biopsy) was collected from each animal. Ear tissue samples were stored in a 5ml vial of dimethyl sulfoxide (DMSO) in a saturated salt solution, similar to that described by Seutin *et al*. (1991), and stored for subsequent genetic analysis (not included within the current study). Each translocated woylie and each trapped recruit to the population was identifiable by an external marker created by the ear tissue biopsy (males were biopsied in the left ear, females the right). Each woylie was also implanted subcutaneously with a uniquely numbered Trovan® microchip (Trovan, Ltd. http://www.trovan.com/index.html) to enable identification of each individual. The use of a uniquely numbered Trovan® microchip and a uniquely identifiable radio-collar met the guidelines for double tagging, which reduces the possibility of violation of the assumption of no lost tags (White and Garrott, 1990; White and Burnham, 1999).

Morphometric data collection and radio-collaring were carried out during the day and each translocated woylie was released at night, within 22 hours of capture. Trapped individuals not included in the translocation program were released at their point of capture, within Dryandra Woodland.

4.2.3 Woylie body condition

A measure of ‘body condition’ was derived for each translocated woylie at the time of translocation. Similarly, a measure of body condition was derived at the time of first capture for each recruit to the population. Body condition was derived as described by Krebs and Singleton (1993), differing only by using a model selection process (AICc) to determine the model which best described the regression between body weight (g) and head-body length (mm). Ordinary least squares (OLS) regression models compared were: (i) a linear relationship; (ii) a log-linear relationship; and (iii) a log-log relationship between body weight and head-body length. The statistical software Stata (StataCorp, 2006) (Version 10.1) was used for the OLS regression modelling. Regression models were determined separately for each sex. Females were weighed without pouch young (young were removed from the pouch and returned after weighing). Females with grossly enlarged mammary glands and those with pouch young too small to be removed from the pouch were excluded from the regression modelling. The metric used for body condition was the ratio of the observed body weight to the predicted body weight from the preferred regression model.

Body condition at the time of first collaring was included as an individual covariate in five models from the set of 82 candidate models proposed to describe survivorship (see below). A body condition value of 1 (parity in the ratio of observed and predicted weight) was assigned where the value was unable to be derived, e.g. for females with grossly enlarged mammary glands and/or where the net body weight was inclusive of small pouch young.

4.2.4 Radio-collaring

A combination of whip and loop aerial radio-collars was used and each telemetry unit was comprised of a two-stage transmitter with a brass loop collar secured with a small steel bolt and double nut. The brass loop was covered with a layer of black adhesive heatshrink over a layer of non-adhesive heatshrink. A small section of adhesive heatshrink was also used to cover the nut and bolt, once secured. All radio-collars incorporated movement sensitive (mortality) circuitry, with a period of 2.5 hours of inactivity required to trigger the non-latching mortality mode. Live mode was indicated by a pulse rate of 50-60 beats per minute (bpm) and mortality mode by 100-110 bpm. Radio-collars were initially supplied by AVM (AVM Instrument Company Ltd, Auburn, California, USA, http://www.avminstrument.com/). Subsequently a combination of AVM and Biotrack (Biotrack Ltd, Wareham, Dorset, UK. http://www.lotek.com/biotrack.htm) whip and loop aerial collars were used. The maximum collar weigh was 24g. In all cases, collars were configured to minimise weight, maximise cell life and maximise signal strength (i.e. configured to maximise pulse length without compromising cell life). Alignment of the cell and tag and positioning of whip emergence from the collar was designed to minimise the potential for injury to woylies. Collars were only fitted to adult and large sub-adult woylies with a net weight of 800g or more. Collar weight was nominally less than 3% of bodyweight.

The use of mortality collars in the northern jarrah forest study was a significant departure from the *status quo* of radio-telemetry studies at the time. With the exception of a concurrent study examining survivorship of the western ringtail possum, *Pseudocheirus occidentalis*, (de Tores, 2009; de Tores and Rosier, in prep; de Tores *et al.*, 1998a; de Tores *et al.*, 2004), mortality collars had not been used in any Australian mammal study.

4.2.5 The pilot translocation release sites and monitoring protocols

A pilot study was carried out to: (i) assess the frequency of monitoring required to enable rapid detection and assessment of mortality events; (ii) develop protocols for determining the cause of death; and (iii) develop protocols for determining the predator species responsible for each woylie predation event.

The releases of radio-collared woylies for the pilot study were at four of the 55 grids used for the trapping study of resident native fauna (Chapter 5); Boggy Brook Road, Twin Bridges Road, Hakea Road and George (Table 4.1 and Fig. 4.1). Radio-telemetry survivorship monitoring was conducted over the period from initial release (January 1995) until commencement of releases for the longer-term study (September 1995). A protocol was established whereby each radio-collar signal was ‘searched for’ daily. If a ‘live’ signal was detected the data recorded were: (i) the ‘best’ frequency for signal detection, i.e. if there had been a frequency drift, the datasheet was adjusted to record the current ‘actual’ frequency; (ii) the location where the signal was detected – if detected at more than one location, the location where the signal was strongest was noted; (iii) the signal strength (subjectively assessed to fall within the range of 1 to 5); and (iv) the compass bearing to the signal. If a ‘dead’ signal (mortality mode) was detected, the signal was tracked to its location (using a Biotel RX3 transceiver and handheld Yagi aerial) to confirm the status of the radio collared woylie, or to confirm the woylie and/or radio-collar was stationary (i.e. to confirm whether the woylie was dead, or if the collar was transmitting in mortality mode and the woylie was still alive). The details recorded for each confirmed mortality event included:

- the date, time and geographical location of detection of mortality to compare with the date and location of the last known live signal;
- a general description of the carcass, e.g. if it was entire or limbs removed or otherwise dismembered;
- if the lower jaw was removed; possibly an indication of fox predation;
- if the carcass was cached and, if so, the nature of the caching, e.g. if it was in an excavated digging site and uncovered, or covered with soil, litter or otherwise covered;
- the extent of decomposition, the presence of maggots and/or flies and if the eyes were intact or absent. This was to assist with identification of the date and time of death;
- a description of the head and neck, e.g. if there was minor or extensive crushing from chewing and if the head was severed and the brain removed;
- a description of the abdomen, e.g. if the abdomen was opened, if there was visible presence of abdominal crushing and if abdominal organs were visible or removed;
- a description of the skin, e.g. was there presence of one, several or multiple puncture marks; if there was evidence of chewing and if the skin was turned inside out;
- a description of the fur, and in particular, if there were any areas of fur loss. This was to avoid inadvertently associating fur loss to the mortality event, this information was later compared to the recorded fur condition at the time of last handling;
- a description of the collar, e.g. if it was compressed or misshapen, if it had fur and/or blood on it, if teeth marks were present and, if so, the size and number of teeth marks;
- the location of collar, e.g. if it was detached from the carcass, buried away from the carcass, etc.;
- a description and collection of any evidence of predator(s) at the site of the carcass, e.g. scats, fur, fox den, etc.;
- the estimated date of death; and
- an assessment, at the time of data collection in the field, of the cause of death and reason(s) for the decision.

All located woylie carcasses were recovered and held for further examination in the laboratory to attempt to determine the cause of death and, if death was attributed to predation, to assist in determining the predator responsible. A set of diagnostic characteristics was developed to distinguish between predators. The diagnostic checklist was progressively refined during the pilot and longer-term study.

Where a signal was unable to be detected, a considered assessment was made in each case to determine if a more protracted search for the radio signal was undertaken immediately, or if monitoring of the remaining animals continued. Where a radio signal had not been detected on two consecutive monitoring days, a protracted search was programmed into the monitoring schedule. A protracted search required two operators; a driver and a radio receiver operator, to systematically search an area within a radius of 10km from the last known location for the missing signal. This was achieved by driving the existing road and track network, progressively radiating out from the location of the last known signal, while concurrently monitoring for the missing signal (Fig. 4.2). This process also enabled the monitoring to include a search for a frequency drift of ±0.020KHz. Although this procedure was labour intensive, it enabled a large area to be efficiently searched. The procedure also ensured the driver was not distracted by attempting to operate the radio receiver and drive concurrently and thus avoided introducing a safety issue.

If a radio signal was not detected after a protracted search, an aerial search was undertaken using a Cessna 172 (Fig. 4.3). A series of parallel lines, no more than 2km apart, was flown to ensure full coverage of the search area. If detected from the air, the location of each signal (the GPS of the location as recorded from the air) was ground-truthed the same or next day. Where a signal was unable to be detected after an aerial search, the animal was censored from the monitored sample. The date of censoring was given as the first date on which the signal was unable to be detected.

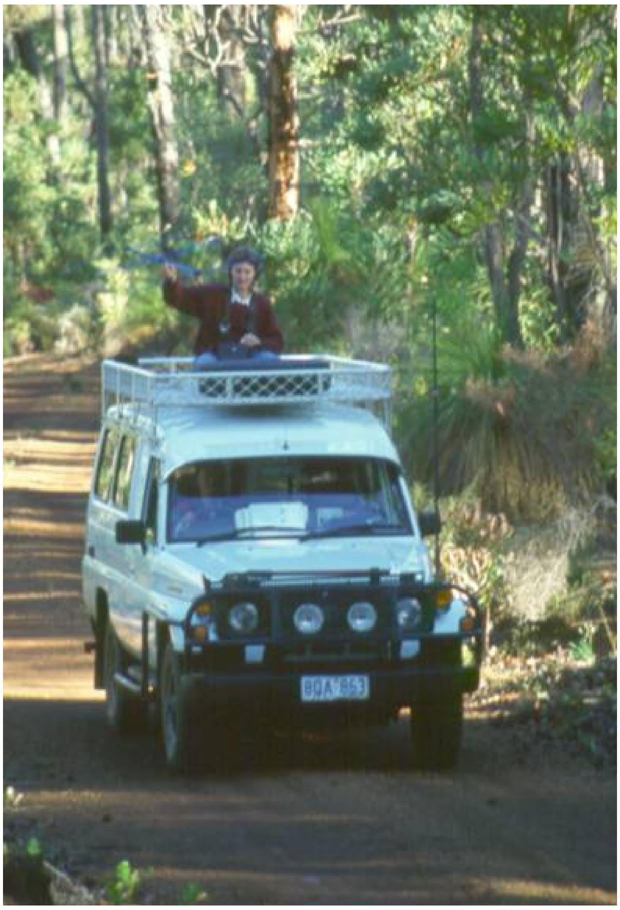

Figure 4.2: Scanning for a missing woylie (*Bettongia penicillata ogilbyi*) radio-collar signal within the northern jarrah forest, south-west Western Australia.

Figure 4.3: The Cessna 172 used for aerial searches for radio-collared woylies (*Bettongia penicillata ogilbyi*).

4.2.6 The longer-term survivorship study: translocation release sites and monitoring protocols

As part of the longer-term study, follow-up translocations were carried out at three (Boggy Brook Road, Hakea Road and George) of the four pilot study translocation release sites. Translocation releases were also carried out at 15 additional trapping grids (Table 4.1 and Fig. 4.1) used for the trapping study of resident native fauna (Chapter 5). The release grids were selected to ensure releases, within each treatment and the unbaited control, included locations within the core of the forest and at sites at, or near, the interface with agricultural land.

Releases were 'staggered' (see below and Pollock *et al.* (1989)), with the first release of the longer-term study timed to ensure that each treatment had received its requisite number of baitings over the preceding 12 months. Monitoring was carried out for 24 days of every 28 day period. Otherwise the monitoring strategy was as described for the pilot study.

4.2.7 Data analysis and the encounter history data set

Survivorship of the monitored radio-collared woylies from the longer-term study was assessed through the Known Fate model from Program MARK (White, 2001) (Version 5.1, Build 2600). The Known Fate model is derived from the Kaplan-Meier estimator (Kaplan and Meier, 1958), modified to allow for addition of data (study animals) to the data set (the monitored study animals) at different times throughout the study. This technique is usually referred to as 'staggered entry' as described by Pollock *et al.* (1989). In program MARK the Known Fate model also enables incorporation of variables (e.g. climatic, site specific habitat variables and individual animal specific variables or 'covariates') and comparison of different models to determine which model, or models, best describe the data.

The term 'Known Fate' applies as the outcome of each individual is known. Exceptions to this 'Known Fate' occur in studies, such as radio-telemetry studies, where radio-collared animals are lost from the study, e.g. as a result of collar failure or where an animal moves away from the study site. These individuals are then censored from the monitored sample. For the Known Fate model, data can be collected daily, weekly, monthly, etc. and an encounter history (radio signal detection history) is then collated for each animal for the duration of the study.

The radio-telemetry data recorded for each day of monitoring, for the pilot and the longer-term study, were coded into three categories: Alive; Dead; or No Signal. These categories indicated, respectively, if the radio signal had been detected in live mode (50-60 bpm), detected in dead mode (100-110 bpm) or had not been detected. The data were stored in a relational database (see Chapter 2). Data were then coded in 'LiveDead' format where three categories are recognised: '10' for alive at the beginning and end of the monitoring period; '00' for censored or yet to be incorporated in the data set; and '11' for alive at the beginning and dead or censored at the end of the monitoring period.

4.2.8 Modelling strategy for the long-term survivorship study

A set of *a priori* candidate models was formulated to describe the woylie survivorship data and these models were compared using AICc (see Chapter 2). Prior to establishing the set of *a priori* candidate models, a suite of potential explanatory variables was assessed for incorporation in the model formulation process. The variables (covariates) were categorised as 'real' external covariates, 'dummy' categorical individual real covariates or individual covariates. Real external variables are those where data are 'real' in the numerical data sense, e.g. a temperature value, the number of days per month above a given temperature, etc. Dummy individual variables are coded categories, e.g. coded for the season of release, whether the individual was a translocated animal or a recruit to the population (binary, categorical), etc. Real individual covariates are continuous data, e.g. the value for body condition (Table 4.2).

The statistical software Stata (StataCorp, 2006) was used to derive a correlation matrix from all individual covariates with continuous data. The suite of potential explanatory variables and potential models was reduced by excluding correlated variables within any given constrained model. Continuous individual covariates were scaled to negate the need for standardisation. The range for each scaled variable is also shown in Table 4.2. All models which included an interaction effect were modelled with the inclusion of the main effect variables (Nelder, 1992; 1994).

Models were constructed in Program MARK using the design matrix, whereby additive and interaction effects could be modelled. Data were input with four discrete groups; the three baited treatment groups; and the unbaited treatment group. Exploratory analysis was carried out to compare models where groups were modelled separately and in combination (Table 4.3). The rationale for combining groups is also given in

Table 4.3. The purpose of the exploratory analysis was to reduce the number of non-competitive models.

The exploratory analysis (see results) identified the preferred model as the model where groups were not combined (Exploratory Model 1, $S_{(g)}$). Therefore, the set of candidate models was based on Exploratory Model 1 and five different model sets were formulated in the total set of 82 candidate models (Table 4.4).

The full time-dependent model (model syntax is $S_{(\mathrm{g})*(\mathrm{t})}$), whereby survivorship is modelled as a function of time and an interaction between each group at each time interval, was considered irrelevant. However, it did serve as a useful construct: the design matrix produced by running the full time dependent model from the set of predefined models in MARK was used to validate the design structure (the design matrix) for less parameterised models which incorporated individual and external covariates. The irrelevance of the $S_{(g)*(t)}$ model is because time *per se* is not of biological relevance unless there is some imperative to compare survivorship between different time periods. In this study, the time periods which were of biological interest were dictated by weather conditions, i.e. it was of interest to compare survivorship between seasons. However, seasons themselves were not the issue of concern. The issue of concern was the relationship between survivorship and the actual temperatures, or the cumulative and/or interaction effects from temperature and rainfall. These data were included as external, real covariates (Table 4.2 and Table 4.4).

Table 4.2: The potential explanatory variables influencing survivorship of woylies (*Bettongia penicillata ogilbyi*) within the northern jarrah forest, south-west Western Australia.

External and individual covariates (modelling syntax)	Description and rationale or justification for consideration in the *a priori* set of candidate models	Type of variable (range)
External variables		
Summer temperatures (*hightemp*)	The number of days in each month where the maximum temperature was 35^0C or more. Extended periods of high daily maxima were hypothesised to reduce survivorship probability.	Real (0-11)
Winter temperatures (*lowtemp*)	The number of days in each month with an overnight minimum temperature of 5^0C or less. Extended periods of low daily maxima were hypothesised to reduce survivorship probability.	Real (0-19)
Rainfall (*rain*)	The number of days in each month with a daily rainfall of more than 10mm. Extended periods of rainfall were hypothesised to reduce survivorship probability.	Real (0-14)
Individual covariates		
Translocation release or first collaring was in summer (*summer*)	The probability of woylie survivorship was hypothesised to decrease if translocation release is in summer. This period also corresponds to the time when fox dispersal is known to occur or is considered to be highest, which may also lead to increased predation.	Categorical (binary)
Translocation release or first collaring was in winter (*winter*)	The probability of woylie survivorship may be decreased if translocation release is in winter as a result of higher physiological demands during winter. Adult male fox home range is considered to be least stable during winter, i.e. during mating when males may be dispersing more widely. Predation may increase during this period as a result of individual male foxes foraging over increased areas, or alternatively, predation may be less if foraging effort by male foxes is less during this period.	Categorical (binary)
Translocation release or first collaring was in the period when breeding vixen are lactating (*lactat*)	The physiological demand from lactating vixens was hypothesised to result in increased predation by vixens during this period, or alternatively, predation may be less if vixens spend less time foraging when nursing cubs.	Categorical (binary)
Sex of the animal (*sex*)	The sex of the animal. Survivorship may differ between sexes.	Categorical (binary)

(cont. …)

Table 4.2 (… cont.)

External and individual covariates (modelling syntax)	Description and rationale or justification for consideration in the *a priori* set of candidate models	Type of variable (range)
Origin of the animal (*origin*)	The origin of each animal, with two categories - translocated animals or recruits. Translocated animals were those translocated to the site. Recruits were new to the population, post translocation (i.e. young produced within the study site and subsequently included in the monitored sample). Survivorship may be a function of the origin of the animals. This covariate was included on the premise that recruits to the population may have a higher probability of survivorship than translocated animals as recruits have had no requirement to 'adjust' to a new environment, post translocation.	Categorical (binary)
Naivety of each animal (*naive*)	A measure of each animal's naivety to the environment, with two coded values – 'naïve' and 'not naïve'. 'Naïve' animals were those translocated to the study site where they became part of the monitored population and incorporated in the survivorship analysis from the first day they were released. Animals considered 'not naïve' were those which were recruits to the population, or animals which had been released prior to the time they were incorporated in the monitored sample. For example, an animal released prior to 12 September 1995 and later incorporated into the monitored sample, either at 12 September 1995, or some later stage, was considered 'not naïve'. The hypothesis was 'not naïve' animals would have a higher probability of survivorship as they have some familiarity with their environment.	Categorical (binary)
Woylie condition (*cond*)	This is a subjective measure of the health of the individual (see text - methodology and results). A continuous variable, with values expected to be normally distributed with a mean value of 1. The probability of survivorship was expected to be lower for animals in poor condition.	Continuous (0.843-1.198)

(cont. …)

Table 4.2 (… cont.)

External and individual covariates (modelling syntax)	Description and rationale or justification for consideration in the *a priori* set of candidate models	Type of variable (range)
Distance (*dist*)	The distance (km) from the translocation release site to the interface with agricultural land or, in the case of recruits, the distance from the first capture site to the interface with agricultural land. The hypothesis is that survivorship is a function of fox density, which in turn may be a function of the distance from agricultural land – i.e. decreasing fox density with increasing distance. Exploratory analysis was performed, using the time dependent survivorship model without an interaction effect (*g*+*t*) to assess if this relationship was best described as linear, log linear or asymptotic (with an inverse exponential transformation).	Continuous (0.351-21.474)
Conspecifics (*conspecs*)	The number of conspecifics known to be alive (through radio-telemetry records) and in the vicinity of the release site at the time of the initial release. The premise is that, as the number of conspecifics increases, the probability of survivorship for each newly released woylie increases. Exploratory analysis was performed, using the fully time dependent survivorship model (g*t) to assess if this relationship was best described by a linear, log linear, asymptotic or a normalised-quadratic relationship.	Continuous (0-13)
Conspecifics, same sex (*cons_same*)	The number of conspecifics of the same sex known to be alive in the vicinity of the release site at the time of the initial release.	Continuous (0-7)
Conspecifics, opposite sex (*cons_opp*)	The number of conspecifics of the opposite sex known to be alive in the vicinity of the release site at the time of the initial release	Continuous (0-7)
Distance to closest town site (*town*)	The distance to the closest town site (km), with woylie survivorship hypothesised as increasing, as a result of decreasing anthropogenic disturbance, with increasing distance.	Continuous (4.687-42.259)
Sealed roads (*sealed*)	The extent of sealed roads (in linear km) within a 10 km radius of the initial translocation release site for translocated animals or within a 10km radius of the first capture site for recruits to the population. The extent of roading was considered to reflect the extent of anthropogenic disturbance. The presence of roading was also considered to have the potential to facilitate fox, and possibly cat, access and mobility.	Continuous (0-58.9)

(cont. …)

Table 4.2 (… cont.)

External and individual covariates (modelling syntax)	Description and rationale or justification for consideration in the *a priori* set of candidate models	Type of variable (range)
Unsealed roads (*unsealed*)	The extent of unsealed roads (in linear km) within a 10km radius of the initial translocation release site for translocated animals or within a 10km radius of the first capture site for recruits to the population, as per above, but with unsealed roading reflecting disturbance primarily from forest management activities.	Continuous (56-224.5)
Total roads (*road*)	The total combined extent of sealed and unsealed roads (in linear km) within a 10km radius of the initial translocation release site for translocated animals or within a 10km radius of the first capture site for recruits to the population, as above.	Continuous (71.7-238.9)
Freehold title land (*parcels*)	The number of freehold title land parcels within a 10km radius of the initial translocation release site for translocated animals or within a 10km radius of the first capture site for recruits to the population. This was considered to reflect the extent of anthropogenic disturbance through habitat fragmentation. There was also a pattern of an increased number of freehold title land parcels at sites closer town sites. The premise is that these two anthropogenic disturbances (the number freehold title land parcels and proximity to town sites) may also reflect 'hotspots' of feral cat abundance through the provision of rubbish tips – there are more rubbish tips as the number of town sites increases and many rural land holders establish rubbish tips. These rubbish tips may serve as possible source points for invasion by feral cats.	Continuous (0-782)
The area of freehold land (*freehold*)	The area (in ha.) of freehold land within a 10km radius of the initial translocation release site for translocated animals or within a 10km radius of the first capture site for recruits to the population. This was also considered to be an indication of the extent of anthropogenic disturbance. The premise was that larger values for the extent of freehold land reflect an increase in the edge effect (interface between the forest and agricultural land), with a corresponding increase in the potential for foxes to invade or reinvade forest areas post 1080 baiting events.	Continuous (0-297.37)

Table 4.3: The set of candidate exploratory models to describe survivorship of translocated populations of the woylie (*Bettongia penicillata ogilbyi*). Treatment groups were modelled separately and in different combinations considered of biological and management interest.

Model syntax: $S_{(g)}$ represents a group effect, where the treatment groups are modelled with different survivorship; $S_{(g[6+4],[2],[0])}$ combines the six and four baitings per year treatment groups; $S_{(g[6+4],[2+0])}$ combines the six and four baitings per year treatment group and combines the two baitings per year treatment group with the unbaited treatment group.

Model name	Modelling syntax	Description and rationale or hypothesis
Exploratory Model 1	$S_{(g)}$	The model hypothesises survivorship probability is different in each group (each baited treatment group and the unbaited treatment group) and is based on the underlying hypothesis that survivorship would be highest in the six, followed by the four, the two baitings per year treatment group and lowest in the unbaited treatment group.
Exploratory Model 2	$S_{(g[6+4],[2],[0])}$	This model hypothesises survivorship probability is the same for the six and four baitings per year treatment group, different in the two baitings per year treatment group and different again in the unbaited treatment group. This is based on the management assertion that six baitings per year confers no additional benefit, in terms of woylie survivorship, than the four baitings per year treatment group.
Exploratory Model 3	$S_{(g[6+4],[2+0])}$	This model hypothesises survivorship probability is the same for the six and four baitings per year treatment groups and this survivorship is different from the combined two baitings per year treatment group and the unbaited treatment group. This is based on the management assertion that six baitings per year confers no additional benefit, in terms of woylie survivorship, than four baitings per year and further, the protection conferred to woylie survivorship in the four baitings per year treatment group is greater than that conferred from the two baitings per year treatment group and the unbaited treatment group, i.e. with survivorship modelled the same for the two baitings per year and the unbaited treatment group.

Following pages:

Table 4.4: The *a priori* candidate models to describe woylie (*Bettongia penicillata ogilbyi*) survivorship in the presence of different frequencies of sodium monofluoroacetate baiting for control of the red fox (*Vulpes vulpes*) in the northern jarrah forest, south-west Western Australia.

The underlying hypothesis is survivorship would be highest in the six baitings per year treatment group, followed by the four, the two and lowest in the unbaited treatment group.

Generic syntax are as per Lebreton *et al*. (1992) where: $S_{(g)*(t)}$ represents the fully time dependent model; $S_{(g)+(t)}$ represents the time dependent model without an interaction effect (neither was included, see text); $S_{(g+cov)}$ represents the linear model constrained by an individual covariate; and $S_{(g+cov*cov)}$ represents the linear model constrained by an interaction between two individual covariates. The description of each covariate is given in Table 4.2.

Less generic syntax are: $S(_{g+t\_hightemp})$ where the time variable is replaced by an external time covariate, in this example '*hightemp*', i.e. the number of days in each month where the temperature was above 35^0C.

Table 4.4: (caption on previous page).

Model Set 1: Survivorship was modelled for each group (treatment) with constraints from individual covariates and without constraint from the external (climatic) covariates used in model sets 2, 3, 4 and 5.

Model set and model number	Modelling syntax	Description and rationale
Model 1.01	$S_{(g)}$	The groups (treatments) alone are modelled to explain the differences in survivorship, with the probability of survivorship hypothesised as different between all groups
Model 1.02	$S_{(g+sex)}$	Model 1.1 constrained by the individual covariate for the sex of each woylie
Model 1.03	$S_{(g+origin)}$	Model 1.1 constrained by the individual covariate for the origin of each woylie
Model 1.04	$S_{(g+naïve)}$	Model 1.1 constrained by the individual covariate for the naivety of each woylie
Model 1.05	$S_{(g+origin+naïve)}$	Model 1.1 constrained by the individual covariate for the origin and naivety of each woylie
Model 1.05a	$S_{(g+cond)}$	Model 1.1 constrained by the individual covariate for the condition of each woylie
Model 1.06	$S_{(g+dist)}$	Model 1.1 constrained by the individual covariate for distance
Model 1.07	$S_{(g+dist+dist\_sq)}$	Model 1.1 constrained by the individual covariate for distance and a quadratic term for distance
Model 1.08	$S_{(g+ln\_dist)}$	Model 1.1 constrained by the individual covariate for the log of distance
Model 1.09	$S_{(g+asym\_dist)}$	Model 1.1 constrained by the individual covariate for the distance with an inverse exponential transformation
Model 1.14	$S_{(g+town)}$	Model 1.1 constrained by the individual covariate for the distance to the closest town site
Model 1.15	$S_{(g+sealed)}$	Model 1.1 constrained by the individual covariate for the extent of sealed roads
Model 1.16	$S_{(g+unsealed)}$	Model 1.1 constrained by the individual covariate for the extent of unsealed roads
Model 1.17	$S_{(g+winter)}$	Model 1.1 constrained by the individual covariate for release or first capture in winter
Model 1.18	$S_{(g+summer)}$	Model 1.1 constrained by the individual covariate for release or first capture in summer
Model 1.19	$S_{(g+lactat)}$	Model 1.1 constrained by the individual covariate for release or first capture when vixen are lactating
Model 1.20	$S_{(g+conspecs)}$	Model 1.1 constrained by the individual covariate for release or the number of conspecifics

(cont. …)

Table 4.4: (… cont.)

Model Set 2: Survivorship was modelled for each group (treatment) and constrained by the external real covariate ‘*hightemp*’ and the additional constraints described in Model Set 1.

Model set and model number	Modelling syntax	Description and rationale
Model 2.01	$S_{(g+hightemp)}$	Model 1.01 constrained by the additional real covariate *hightemp*
Model 2.02	$S_{(g+hightemp+sex)}$	Model 1.02 constrained by the additional real covariate *hightemp*
Model 2.03	$S_{(g+hightemp+origin)}$	Model 1.03 constrained by the additional real covariate *hightemp*
Model 2.04	$S_{(g+hightemp+naïve)}$	Model 1.04 constrained by the additional real covariate *hightemp*
Model 2.05	$S_{(g+hightemp+origin+naïve)}$	Model 1.05 constrained by the additional real covariate *hightemp*
Model 2.05a	$S_{(g+hightemp+cond)}$	Model 1.05a constrained by the additional real covariate *hightemp*
Model 2.06	$S_{(g+hightemp+dist)}$	Model 1.06 constrained by the additional real covariate *hightemp*
Model 2.07	$S_{(g+hightemp+dist+dist\_sq)}$	Model 1.07 constrained by the additional real covariate *hightemp*
Model 2.08	$S_{(g+hightemp+ln\_dist)}$	Model 1.08 constrained by the additional real covariate *hightemp*
Model 2.09	$S_{(g+hightemp+asym\_dist)}$	Model 1.09 constrained by the additional real covariate *hightemp*
Model 2.14	$S_{(g+hightemp+town)}$	Model 1.14 constrained by the additional real covariate *hightemp*
Model 2.15	$S_{(g+hightemp+sealed)}$	Model 1.15 constrained by the additional real covariate *hightemp*
Model 2.16	$S_{(g+hightemp+unsealed)}$	Model 1.16 constrained by the additional real covariate *hightemp*
Model 2.17	$S_{(g+hightemp+summer)}$	Model 1.18 constrained by the additional real covariate *hightemp*
Model 2.18	$S_{(g+hightemp+lactat)}$	Model 1.19 constrained by the additional real covariate *hightemp*
Model 2.19	$S_{(g+hightemp+conspec)}$	Model 1.20 constrained by the additional real covariate *hightemp*

(cont. …)

Table 4.4: (… cont.)

Model Set 3: Survivorship was modelled for each group (treatment) and constrained by the external real covariate '*lowtemp*' and the additional constraints described in Model Set 1.

Model set and model number	Modelling syntax	Description and rationale
Model 3.01	$S_{(g+lowtemp)}$	Model 1.01 constrained by the additional real covariate *lowtemp*
Model 3.02	$S_{(g+lowtemp+sex)}$	Model 1.02 constrained by the additional real covariate *lowtemp*
Model 3.03	$S_{(g+lowtemp+origin)}$	Model 1.03 constrained by the additional real covariate *lowtemp*
Model 3.04	$S_{(g+lowtemp+naïve)}$	Model 1.04 constrained by the additional real covariate *lowtemp*
Model 3.05	$S_{(g+lowtemp+origin+naïve)}$	Model 1.05 constrained by the additional real covariate *lowtemp*
Model 3.05a	$S_{(g+lowtemp+cond)}$	Model 1.05a constrained by the additional real covariate *lowtemp*
Model 3.06	$S_{(g+lowtemp+dist)}$	Model 1.06 constrained by the additional real covariate *lowtemp*
Model 3.07	$S_{(g+lowtemp+dist+dist\_sq)}$	Model 1.07 constrained by the additional real covariate *lowtemp*
Model 3.08	$S_{(g+lowtemp+ln\_dist)}$	Model 1.08 constrained by the additional real covariate *lowtemp*
Model 3.09	$S_{(g+lowtemp+asym\_dist)}$	Model 1.09 constrained by the additional real covariate *lowtemp*
Model 3.14	$S_{(g+lowtemp+town)}$	Model 1.14 constrained by the additional real covariate *lowtemp*
Model 3.15	$S_{(g+lowtemp+sealed)}$	Model 1.15 constrained by the additional real covariate *lowtemp*
Model 3.16	$S_{(g+owtemp+unsealed)}$	Model 1.16 constrained by the additional real covariate *lowtemp*
Model 3.17	$S_{(g+lowtemp+winter)}$	Model 1.17 constrained by the additional real covariate *lowtemp*
Model 3.18	$S_{(g+lowtemp+lactat)}$	Model 1.19 constrained by the additional real covariate *lowtemp*
Model 3.19	$S_{(g+lowtemp+conspecs)}$	Model 1.20 constrained by the additional real covariate *lowtemp*

(cont. …)

Table 4.4: (… cont.)

Model Set 4: Survivorship was modelled for each group (treatment) and constrained by the external real covariate '*rain*' and the additional constraints described in Model Set 1.

Model set and model number	Modelling syntax	Description and rationale
Model 4.01	$S_{(g+rain)}$	Model 1.01 constrained by the additional real covariate *rain*
Model 4.02	$S_{(g+rain+sex)}$	Model 1.02 constrained by the additional real covariate *rain*
Model 4.03	$S_{(g+rain+origin)}$	Model 1.03 constrained by the additional real covariate *rain*
Model 4.04	$S_{(g+rain+naïve)}$	Model 1.04 constrained by the additional real covariate *rain*
Model 4.05	$S_{(g+rain+origin+naïve)}$	Model 1.05 constrained by the additional real covariate *rain*
Model 4.05a	$S_{(g+rain+cond)}$	Model 1.05a constrained by the additional real covariate *rain*
Model 4.06	$S_{(g+rain+dist)}$	Model 1.06 constrained by the additional real covariate *rain*
Model 4.07	$S_{(g+rain+dist+dist\_sq)}$	Model 1.07 constrained by the additional real covariate *rain*
Model 4.08	$S_{(g+rain+ln\_dist)}$	Model 1.08 constrained by the additional real covariate *rain*
Model 4.09	$S_{(g+rain+asym\_dist)}$	Model 1.09 constrained by the additional real covariate *rain*
Model 4.14	$S_{(g+rain+town)}$	Model 1.14 constrained by the additional real covariate *rain*
Model 4.15	$S_{(g+rain+sealed)}$	Model 1.15 constrained by the additional real covariate *rain*
Model 4.16	$S_{(g+rain+unsealed)}$	Model 1.16 constrained by the additional real covariate *rain*
Model 4.17	$S_{(g+rain+winter)}$	Model 1.17 constrained by the additional real covariate *rain*
Model 4.18	$S_{(g+rain+lactat)}$	Model 1.19 constrained by the additional real covariate *rain*
Model 4.19	$S_{(g+rain+conspecs)}$	Model 1.20 constrained by the additional real covariate *rain*
Model 4.20	$S_{(g+rain+lowtemp)}$	Model 1.19 constrained by the additional real covariate *rain* and *lowtemp*

(cont. …)

Table 4.4: (… cont.)

Model Set 5: Survivorship was modelled for each group (treatment) and constrained by the product (the interaction) of the external real covariates ‘*lowtemp*’ and ‘*rain*’ and the additional constraints described in Model Set 1.

Model set and model number	Modelling syntax	Description and rationale
Model 5.01	$S_{(g+(lowtemp*rain))}$	Model 1.01 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.02	$S_{((g+(lowtemp*rain)+sex)}$	Model 1.02 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.03	$S_{((g+(lowtemp*rain)+origin)}$	Model 1.03 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.04	$S_{((g+(lowtemp*rain)+\text{naïve})}$	Model 1.04 constrained by the interaction two real covariates *lowtemp* and *rain* in
Model 5.05	$S_{((g+(lowtemp*rain)+origin+\text{naïve})}$	Model 1.05 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.05a	$S_{(g+(lowtemp*rain)+cond)}$	Model 1.05a constrained by the product of the two real covariates lowtemp and rain
Model 5.06	$S_{(g+(lowtemp*rain) +dist)}$	Model 1.06 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.07	$S_{(g+(lowtemp*rain)+dist+dist\_sq)}$	Model 1.07 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.08	$S_{(g+(lowtemp*rain)+ln\_dist)}$	Model 1.08 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.09	$S_{(g+(lowtemp*rain)+asym\_dist)}$	Model 1.19 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.14	$S_{(g+(lowtemp*rain)+town)}$	Model 1.14 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.15	$S_{(g+(lowtemp*rain)+sealed)}$	Model 1.15 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.16	$S_{(g+(lowtemp*rain)+unsealed)}$	Model 1.16 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.17	$S_{(g+(lowtemp*rain)+winter)}$	Model 1.17 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.18	$S_{(g+(lowtemp*rain)+lactat)}$	Model 1.19 constrained by the interaction two real covariates *lowtemp* and *rain*
Model 5.19	$S_{(g+(lowtemp*rain)+conspecs)}$	Model 1.20 constrained by the interaction two real covariates *lowtemp* and *rain*

4.2.9 Model selection and goodness of fit

Model selection from the set of candidate models (Table 4.4) was initially based on AICc. In the absence of a suitable Goodness of Fit (GOF) test for the Known Fate model (Cooch and White, 2004), there was no quantitative method to assess the preferred models for overdispersion. Therefore, manual adjustments were made to the variance inflation factor ($\hat{c}$, a measure of overdispersion – see Chapter 2). Adjustment to $\hat{c}$ was in increments of 0.25, commencing with the unadjusted $\hat{c}$ value of 1.0, to a maximum adjustment of 2.0. Where the ranking of 'better' models does not change with progressive changes in $\hat{c}$, this indicates a lack of evidence for structural problems with the model. However, where the $\hat{c}$ value is substantially above 1 (as indicated either by a χ^2 test or by incrementing the $\hat{c}$ value) there is no way to determine if this is a result of overdispersion or a failure of the model to adequately describe the data (Lebreton *et al.*, 1992). Lebreton *et al*. al (1992) recommended a maximum adjustment of $\hat{c}$ to 3 and further noted larger values, in the vicinity of 10, almost certainly indicate the model structure is inadequate.

4.2.10 Model averaging

Model averaging was then carried out on the subset of models with an AICc within 4 units of the top ranked model (see Chapter 2 and Burnham and Anderson, 2002). Non-competitive or redundant models were excluded from model averaging. The term non-competitive as describe by Burnham and Anderson (2002) refers to a model that has been specified twice. Here the term redundant or non-competitive model is also used for models which differ from a more competitive model by the addition of only one parameter, have an AIC or AICc value within 2 units of the more competitive model, have a similar log likelihood value to the more competitive model, but do not improve on that model.

4.3 Results

4.3.1 The number of woylies translocated and radio-collared sample sizes

A total of 492 woylies was translocated from Dryandra Woodland to 19 sites within the northern jarrah forest (Table 4.1 and Table 4.5). Eighty-one woylies were translocated as part of the pilot study and 34 of these were radio-collared. Survivorship was monitored daily. Eight of the 34 radio-collared woylies were known to be alive and with functional radio-collars at the end of the pilot study. These surviving woylies were then included in the monitored sample for the longer-term study.

A further 411 woylies were translocated as part of the longer-term monitoring study and 331 of these were radio-collared and intensively monitored. An additional six woylies, released as part of the pilot study and not radio-collared when first released, were subsequently re-trapped, radio-collared and included in the monitored sample for the longer-term study.

There were 183 known (trapped) recruits to the population, all trapped during the longer-term study. Thirty-nine of these were radio-collared and included in the monitored sample. Therefore, a total of 384 radio-collared woylies was monitored during the longer-term study.

4.3.2 Pilot study

All 81 woylies included in the pilot study were translocated in the period 25 to 30 January 1995 (Table 4.5). Of the 34 radio-collared woylies, eight were known to be alive at completion of the pilot study (September 1995) (Table 4.6). Foxes were considered the predator responsible for the majority of deaths attributed to predation. The fate of all radio-collared woylies is shown in Table 4.6.

In all cases where death was attributed to fox or cat predation the carcass had been recovered within 48 hours of the last recorded ‘live’ signal and there was a reduced possibility of confounding a predation event with scavenging. Where the cause of death was attributed to predation but was unable to be attributed to a predator species, the period between the last recorded live signal and confirmation of death ranged from two to 21 days. Differentiating between predation and scavenging was confounded with increased time between detection of the last live radio signal and confirmation of mortality.

The monitoring schedule had attempted to monitor every radio-collared woylie daily, however, logistics deemed this impossible. Adjustments were made to the monitoring schedule to maximise the frequency of monitoring of each radio-collared woylie. The list of essential information collected for every known mortality event was progressively refined to facilitate identification of the cause of death (see results from the longer-term study and discussion). The processing protocols were subsequently changed to ensure a tighter fit of radio-collars to reduce the possibility of woylies being able to ‘slip collars’.

Table 4.5: The number of woylies (*Bettongia penicillata ogilbyi*) translocated from Dryandra Woodland to 19 sites within the northern jarrah forest, south-west Western Australia.

* Indicates the pilot study release dates.

Treatment Translocation release grid	Translocation release dates	No. of females translocated	No. of males translocated
Two baitings per year			
Dobaderry	5 Oct 1995	5	4
	3 Dec 1995	1	
	11 Nov 1997	5	5
	3 July 1998	3	4
Korner Road	5 Oct 1995	5	4
	3 Dec 1995	1	
	11 Nov 1997	4	5
	3 July 1998	3	3
Paddy	18 Sept 1995	6	4
	8 Nov 1997	5	5
	2 July 1998	2	3
Schulstaad Road	13 - 14 Sept 1995	6	4
	26 Sept 1995	1	
	13 Nov 1997	5	5
	2 July 1998	4	4
Thompson Road	12 - 14 Sept 1995	6	4
	30 Sept 1995	1	2
	15 Nov 1997	5	4
	3 July 1998	3	1
Wearne	1 Oct 1995	6	4
	15 Nov 1997	4	4
	2 - 3 July 1998	2	2
Four baitings per year			
Boggy Brook Road	28 - 30 Jan 1995*	12	9
	18 - 19 Sept 1995	4	4
	30 Sept 1995	2	
	28 Jan 1997	1	1
	2 Nov 1997	4	1
Gordon Road	27 - 30 Sept 1995	6	4
	28 Jan 1997	1	2
	8 Nov 1997		4
	21 June 1998	1	4
Housebrook Road	19 - 26 Sept 1995	6	5
	27 Jan 1997	4	4
	2 Nov 1997	4	5
	21 June 1998	1	2

(cont. …)

Table 4.5 (… cont.)

Treatment Translocation release grid	Translocation release dates	No. of females translocated	No. of males translocated
Four baitings per year (… cont.)			
O'Neill	30 Sept - 1 Oct 1995	6	5
	6 - 8 Nov 1997	4	5
	21 June 1998		1
Twin Bridges Road	29 Jan 1995*	12	8
Six baitings per year			
Amphion	5 - 8 Dec 1995	5	5
	30 Jan - 4 Feb 1997	3	2
	4 Nov 1997	3	3
	19 June 1998	2	2
George	26 Jan 1995*	12	8
	21 Nov 1995	3	4
	8 Dec 1995	3	
	1 Nov 1997	1	2
	4 Nov 1997	1	
Hakea Road	25 to 30 Jan 1995*	12	8
	20 - 21 Nov 1995	3	4
	8 Dec 1995	3	
	19 June 1998	1	4
Murray Road	7 - 8 Dec 1995	6	4
	4 Feb 1997	4	
	4 Nov 1997	3	5
	19 June 1998	3	3
Unbaited control			
Seventy Seven Road	1 - 3 Jan 1996	6	4
	8 Feb 1997	2	1
	29 June 1998	4	2
Stockyard	3 Jan 1996	6	4
	7 Feb 1997	2	
	27 Dec 1997	2	
	29 June 1998	3	4
Tanglin Road	8 Dec 1995	4	2
	1 Jan 1996	2	2
	7 Feb 1997	4	4
	29 June 1998	4	2
Winooka	2 - 4 Jan 1996	5	4
	7 Feb 1997	2	2
	27 Dec 1997	3	
	29 June 1998		4
Total		**268**	**224**

Table 4.6: The fate of woylies (*Bettongia penicillata ogilbyi*) fitted with radio-collars, translocated to the northern jarrah forest of south-west Western Australia and intensively monitored as part of the pilot study.

Fate or outcome	Number of individuals	Comments
Survived	8	Four of these were from the Boggy Brook Road release site, two from Hakea Road and two from Twin Bridges Road. All were subsequently incorporated in the monitored sample for the longer-term study.
Predation by fox	7	Characteristics considered indicative of fox predation included caching of the carcass, thoracic bruising and/or crushing, severed head, severed limbs, visible puncture marks (tooth marks) on carcass and/or the radio-collar, minor to extensive lateral compression of the radio-collar. In most cases the woylie had been alive the previous day, so the evidence attributed to foxes was considered less likely to be result of scavenging than predation.
Predation by cat	1	Body partly covered by sticks and leaves, flanks exposed. Large tooth marks on collar. Intestine removed from body but not eaten.
Predation – unable to be attributed to a predator species but considered to be fox or cat predation	2	Large tooth marks in collar, collar slightly misshapen but not laterally compressed. Remains partially buried under leaves only.
Predation – unable to be attributed to a predator species	2	Insufficient evidence from the site where the carcass, or where the collar only was retrieved. Predation implied by large tooth marks in the collar.
Miscellaneous	2	One road kill and one drowning. The drowned animal was found with its forelimb caught in the radio-collar.
Unknown	5	In most cases there was insufficient evidence from the site where the carcass and/or collar was retrieved. It was unclear if tooth marks (if present) in the collar were from one or multiple species and/or individuals, i.e. they were not all the same size. There was usually a relatively long period between the last detected radio-collar signal and collection of the carcass or collar. This also confounded differentiating between predation and scavenging.
Censored	7	Three of the censored woylies appeared to have slipped their radio-collar and the collar only was retrieved, unmarked.

4.3.3 Longer-term study

4.3.3.1 Correlation matrix for covariates considered for inclusion in survivorship modelling

A pair-wise correlation analysis of the individual covariates with continuous data (Table 4.2) considered for inclusion in the candidate model set was performed in Stata (StataCorp, 2006). The results were comparable for the Pearson and Spearman correlation (Table 4.7). The latter is less sensitive to the effect from outliers.

Limited value was placed on p values as there is 'low utility' of p values from correlations. This is in addition to the limited value placed on p values generally (see Chapter 2), which are often not particularly meaningful as the variance of the test statistic markedly declines with increasing sample size. Consequently, weakly correlated data will have a statistically significant p value if there is a large sample size. A Bonferroni correction is often used in recognition of this, however, as this correction results in a substantial reduction of statistical power (Nakagawa, 2004), no emphasis was placed on the resultant p values from this analysis. Stata (StataCorp, 2006) provides the option to calculate the Pearson product moment correlation and also produce confidence intervals. The Spearman option can also be specified and Table 4.7 shows the confidence intervals for each Spearman correlation coefficient. Confidence intervals were small in all cases. Strongly correlated covariates were not used when modelling woylie survivorship.

The number of conspecifics known to be alive and radio-collared at the time of release was strongly correlated with the number conspecifics of the same sex and conspecifics of the opposite sex, so conspecifics only was used in the modelling. The distance from the midpoint of the translocation release site was correlated with the number of freehold title land parcels and with the area of freehold land within a 10km radius of the initial translocation release. Similarly, the number of freehold title land parcels was strongly correlated with the area of freehold land, so distance only was used in lieu of 'parcels' and 'freehold'. The total combined extent of sealed and unsealed roads (in linear km) within a 10km radius of the initial translocation release site was strongly correlated with extent of unsealed roads but, interestingly, not correlated with the extent of sealed road. Therefore, the variable for the total length of road was not used and the variables for the length of unsealed and sealed road were both retained.

Table 4.7: The correlation matrix from individual covariates with continuous data considered for inclusion in models to describe survivorship of woylies (*Bettongia penicillata ogilbyi*) in the northern jarrah forest, south-west Western Australia.

The Spearman correlation coefficient (*rho*) is shown for each pair of covariates, with 384 observations in all cases. Values in brackets are the 95% confidence intervals for the correlation coefficient. A description of each covariate and syntax is given in Table 4.2.

	conspecs	*cons_same*	*cons_opp*	*dist*	*town*	*sealed*	*unsealed*	*roads*	*parcels*	*freehold*
conspecs	1									
cons_same	0.86 (0.84 - 0.89)	1								
cons_opp	0.91 (0.89 - 0.93)	0.61 (0.55 - 0.67)	1							
dist	0.04 (-0.06 - 0.14)	0.07 (-0.03 - 0.17)	0.03 (-0.07 - 0.13)	1						
town	0.07 (-0.03 - 0.17)	0.0788 (-0.02 - 0.18)	0.0974 (0.00 - 0.20)	0.4775 (0.40 - 0.55)	1					
sealed	0.11 (0.01 - 0.22)	0.06 (-0.04 - 0.16)	0.09 (-0.01 - 0.19)	-0.15 (-0.25 - -0.05)	-0.41 (-0.49 - -0.33)	1				
unsealed	-0.10 (-0.20 - 0.00)	-0.10 (-0.20 - 0.00)	-0.13 (-0.22 - -0.03)	0.34 (0.25 - 0.42)	-0.29 (-0.38 - -0.20)	0.10 (0.00 - 0.20)	1			
roads	-0.06 (-0.16 - 0.04)	-0.09 (-0.19 - 0.01)	-0.09 (-0.18 - 0.02)	0.16 (0.06 - 0.25)	-0.44 (-0.52 - -0.35)	0.46 (0.37 - 0.53)	0.91 (0.89 - 0.92)	1		
parcels	-0.05 (-0.15 - 0.05)	-0.07 (-0.17 - 0.03)	-0.07 (-0.17 - 0.03)	-0.79 (-0.83 - -0.76)	-0.68 (-0.73 - -0.62)	0.39 (0.30 - 0.47)	0.01 (-0.09 - 0.11)	0.25 (0.15 - 0.34)	1	
freehold	-0.09 (-0.19 - 0.01)	-0.09 (-0.19 - 0.01)	-0.10 (-0.20 - 0.00)	-0.80 (-0.84 - -0.76)	-0.59 (-0.65 - -0.52)	0.28 (0.18 - 0.37)	-0.10 (-0.19 - 0.01)	0.13 (0.03 - 0.22)	0.95 (0.93 - 0.96)	1

4.3.3.2 Encounter histories

The survivorship of each radio-collared woylie was nominally monitored for 24 days of every 28 day period. The data were then concatenated to 37 monthly encounter occasions (for the months September 1995 to September 1998, inclusive). A typical encounter history is:

```
/* Bp F4035 */
10101010101010101010101010101010101010101010101010101010101010101011000000
 0 1 0 0 0 1 16.837 283.484569 2.82357884567566 0.999999951271414 1 1 4 1 3 19.191 0
126.5 126.5 1 1.36 0 0 1 ;
```

Where Bp F4035 indicates the species (Bp=*Bettongia penicillata ogilbyi*), the sex of the animal (F=female), the treatment of release (4=the four baitings per year treatment) and the individual number for, in this case, the 35th female woylie released or trapped as a recruit in this treatment group.

The first 74 values (each '1' or '0') are paired and each paired value indicates the status of the individual animal for each of the 37 months of monitoring. The first pair above, '10', indicates Bp F4035 was alive at the beginning of the first monitoring period and at the end of this period. The paired value '11' indicates Bp F4035 died in the 34th month. The final three pairs of '00' following '11' in the 34th month, indicate Bp F4035 was no longer in the monitored sample. The first four digits in line 3 ('0 1 0 0') indicate the group (four baitings per year). The remaining values reflect the individual covariate values.

A paired value of '00' not preceded by '11' indicates where an animal is censored, i.e. either temporarily or permanently lost from the monitored sample. Animals may be censored as a result of collar failure, undetected mortality, dispersal from the study area etc. The encounter history would appear as: 101010000000001010, where the paired '00's indicate the period over which the animal was temporarily lost from the monitored sample and re-entered the study where '10' re-appears.

4.3.3.3 Exploratory analysis

All three of the exploratory models had some degree of support from the data. The preferred model (Exploratory Model 1, Table 4.8) was used as the starting model for the *a priori* candidate model set and was constrained by a suite of external real covariates and individual covariates (Table 4.4). Although Exploratory Model 3 had strong support (ΔAICc within 2 units of the preferred model), further constraint of this model (and Exploratory Model 2) would have been unable to assess the effect size (implied by Exploratory Model 1) between each of the four groups.

Table 4.8: Model ranking based on AICc for the three exploratory models compared to describe survivorship of translocated populations of the woylie (*Bettongia penicillata ogilbyi*) in the northern jarrah forest, south-west Western Australia. The preferred model is indicated by a ΔAICc of 0, shown in bold font.

Model and model syntax	AICc	ΔAICc	AICc Weights	Model Likelihood	Number of parameters
Exploratory Model 1 $S_{(g)}$	**1551.581**	**0**	**0.5839**	**1**	**4**
Exploratory Model 3 $S_{(g[6+4],[2+0])}$	1552.957	1.3763	0.2934	0.5025	2
Exploratory Model 2 $S_{(g[6+4],[2],[0])}$	1554.702	3.1211	0.1226	0.21	3

4.3.3.4 Survivorship analysis: the preferred model

The preferred model (i.e. the model with most support from the data) to describe the woylie survivorship data was Model 3.17 (Table 4.9, Fig. 4.4 and Fig. 4.5), where survivorship was a function of the group (i.e. the baiting treatment group) constrained by the external covariate for '*lowtemp*' (i.e. the number of days in each month with an overnight minimum temperature of 5^0C or less) and the individual covariate for '*winter*' (a binary covariate coding '1' if the translocation release was in winter).

The parameter estimates from the preferred model (Table 4.9) showed a progressive increase in survivorship probability with increased frequency of baiting. Conversely, estimated survivorship decreased with an increase in the number of days each month with an overnight minimum temperature of 5^0C or less (Fig. 4.4). Survivorship also decreased if the translocation release was in winter, or for a recruit, if the date of capture and 'staggered entry' to the monitored sample was in winter (Table 4.9).

The preferred model estimated the probability of survivorship over the entire study to be 16.01% higher in the six than in the four baitings per year treatment group, Pr=0.2327 and Pr=0.0726, respectively. There was no appreciable difference in survivorship between the two baitings per year treatment and the unbaited treatment group (Table 4.10, Fig. 4.4 and Fig. 4.5).

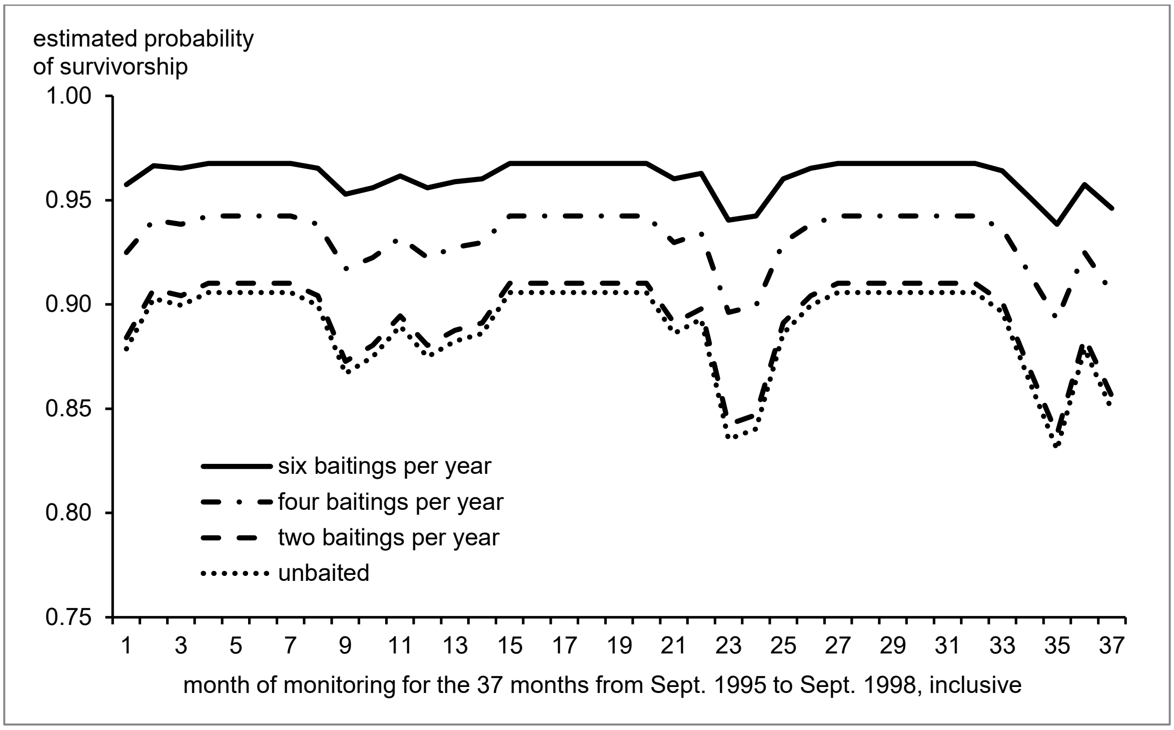

Figure 4.4: The preferred model to describe survivorship of woylies (*Bettongia penicillata ogilbyi*) translocated to baited and unbaited sites within the northern jarrah forest, south-west Western Australia.

Standard errors and 95% confidence intervals are provided in Table 4.10 and Fig. 4.5

Table 4.9: Parameter estimates (β coefficients) for the preferred model to describe woylie (*Bettongia penicillata ogilbyi*) survivorship in the northern jarrah forest, south-west Western Australia.

For the preferred model, Model 3.17, *S g1* is the β parameter estimate for survivorship for the two baitings per year treatment, *S g2* the four baitings per year and *S g3* the six baitings per year treatment. The intercept is in the absence of baiting. See text for description of the individual covariate '*winter*' and real external covariate '*lowtemp*'.

Parameter	Estimate	Std. error	Lower 95% confidence interval	Upper 95% confidence interval
S Intercept	2.3855	0.1571	2.0776	2.6933
S g1	0.0522	0.1842	-0.3089	0.4133
S g2	0.5314	0.2043	0.1309	0.9319
S g3	1.1348	0.2194	0.7048	1.5648
winter	-0.4795	0.2060	-0.8833	-0.0758
lowtemp	-0.0355	0.0115	-0.0580	-0.0130

Table 4.10: Estimates of survivorship probability derived from the preferred model for translocated populations of the woylie (*Bettongia penicillata ogilbyi*) in each of four treatments for the duration of the study in the northern jarrah forest, south-west Western Australia.

Treatment group	Estimate of survivorship probability	Std. error	Lower 95% confidence interval	Upper 95% confidence interval
Unbaited	0.0129	0.0074	0.0041	0.0394
Two baitings per year	0.0159	0.0076	0.0062	0.0401
Four baitings per year	0.0726	0.0282	0.0334	0.1509
Six baitings per year	0.2327	0.0560	0.1409	0.3592

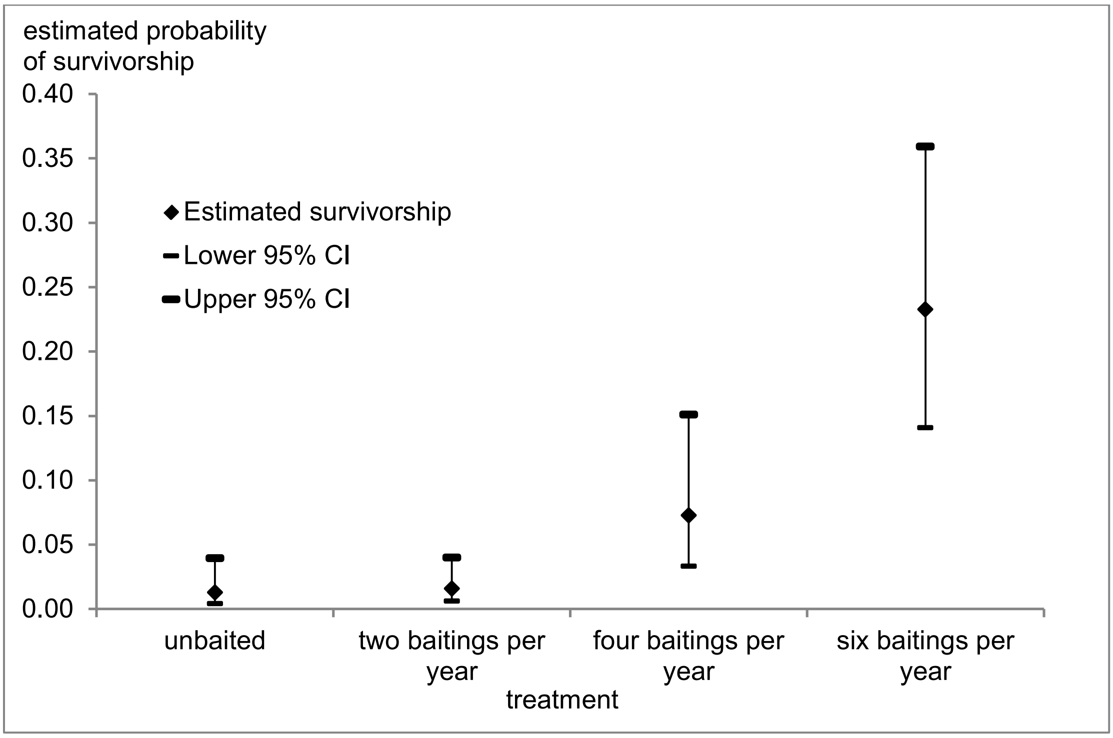

Figure 4.5: Estimated probability of survivorship from the preferred model for woylies (*Bettongia penicillata ogilbyi*) translocated to baited and unbaited sites within the northern jarrah forest, south-west Western Australia.

Sample size (n)=384. Survivorship probability estimates are for the 37 month duration of the study and are conditional on the preferred model. Error bars are the 95% confidence intervals based on the unconditional standard errors. The 95% CIs are asymmetrical as Program MARK initially calculates the 95% CI on the logit scale, then backtransforms to the probability scale. Because the logit transform is not linear, the reconstituted 95% CI is not necessarily symmetrical around the parameter estimate, especially for parameters estimated near the [0, 1] boundaries (Cooch and White, 2004).

4.3.3.5 Goodness of fit and variance inflation factor

There was no major re-ordering of the model rankings with adjustments to the estimate of the variance inflation factor $(\hat{c})$ (Table 4.11). Model 3.17 remained the top ranked model through all changes to $\hat{c}$. The more parameterised models were penalised with progressive increases in the value of $\hat{c}$. This indicates there was no evidence to suggest structural problems with the models. Therefore, model averaging was carried out without adjustment to $\hat{c}$.

Table 4.11: Model rankings for the 15 highest ranked (lowest AICc) models with adjustments to the variance inflation factor $(\hat{c})$ for $\hat{c}$ values of 1.0 to 2.0, in increments of 0.25. Includes eight non-competitive or redundant* models, two of which were also non-competitive** as they duplicated another model (see text).

	Model ranking with progressive increments in $\hat{c}$. Adjusted value of $\hat{c}$				
Model	1.00 (unadjusted)	1.25	1.50	1.75	2.0
3.17 $S_{(g+winter+lowtemp)}$	1	1	1	1	1
5.17 $S_{(g+winter+lowtemp*rain)}$	2	2	7	10	18
3.07 $S_{(g+dist+dist\_sq+lowtemp)}$	3	4	6	8	8
3.14 $S_{(g+town+lowtemp)}$	4	5	3	3	3
3.16 $S_{(g+unsealed+lowtemp)}$	5	6	4	4	4
3.01 $S_{(g+lowtemp)}$	6	3	2	2	2
4.20 $S_{(g+lowtemp+rain)}^{*}$	7	7	5	5	5
3.15 $S_{(g+sealed+lowtemp)}^{*}$	8	8	8	6	6
3.09 $S_{(g+asym\_dist+lowtemp)}^{*,**}$	9	9	9	7	7
3.18 $S_{(g+lactat+lowtemp)}^{*}$	10	10	10	9	9
5.07 $S_{(g+dist+dist\_sq+lowtemp*rain)}$	11	21	22	26	27
3.06 $S_{(g+dist+lowtemp)}^{*}$	12	11	11	11	10
3.02 $S_{(g+sex+lowtemp)}^{*}$	13	12	12	12	11
3.19 $S_{(g+conspecs+lowtemp)}^{*}$	14	13	13	13	12
3.08 $S_{(g+ln\_dist+lowtemp)}^{*,**}$	15	14	14	14	13

4.3.3.6 Survivorship analysis: model averaging

After running all model sets, redundant and non-competitive models could be identified. Review of the highest ranked models (Table 4.12) revealed some model redundancy. Models which included the variable for the distance from agricultural land were modelled with survivorship a function of a linear relationship, a linear relationship with a quadratic term, a log relationship and as an inverse exponential (i.e. asymptotic) relationship with distance. There was no *a priori* rationale to exclude any of these possibilities. Model 3.08 and Model 3.09 (Table 4.12) were considered non-competitive as they were duplicating Model 3.07. The latter indicated distance was best modelled with a linear and quadratic term.

Table 4.12: Output from Program MARK showing the 15 highest ranked (lowest AICc) models to describe woylie (*Bettongia penicillata ogilbyi*) survivorship in the northern jarrah forest, south-west Western Australia.

Includes eight non-competitive or redundant* models, two of which were also non-competitive** (see text).

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
3.17 $S_{(g+winter+lowtemp)}$	**1529.5360**	**0.0000**	**0.2344**	**1.0000**	**6**	**1517.5079**	**1517.5079**
5.17 $S_{(g+winter+lowtemp*rain)}$	1531.1364	1.6004	0.1053	0.4492	8	1515.0881	1515.0881
3.07 $S_{(g+dist+dist\_sq+lowtemp)}$	1532.0507	2.5147	0.0667	0.2844	7	1518.0132	1518.0132
3.14 $S_{(g+town+lowtemp)}$	1532.5640	3.0280	0.0516	0.2200	6	1520.5359	1520.5359
3.16 $S_{(g+unsealed+lowtemp)}$	1532.6673	3.1313	0.0490	0.2090	6	1520.6392	1520.6392
3.01 $S_{(g+lowtemp)}$	1532.7543	3.2183	0.0469	0.2000	5	1522.7342	1522.7342
4.20 $S_{(g+lowtemp+rain)}$*	1532.9614	3.4254	0.0423	0.1804	6	1520.9333	1520.9333
3.15 $S_{(g+sealed+lowtemp)}$*	1533.2085	3.6725	0.0374	0.1594	6	1521.1804	1521.1804
3.09 $S_{(g+asym\_dist+lowtemp)}$*,**	1533.3460	3.8100	0.0349	0.1488	6	1521.3179	1521.3179
3.18 $S_{(g+lactat+lowtemp)}$*	1534.0908	4.5548	0.0240	0.1026	6	1522.0627	1522.0627
5.07 $S_{(g+dist+dist\_sq+lowtemp*rain)}$	1534.1318	4.5958	0.0236	0.1005	9	1516.0715	1516.0715
3.06 $S_{(g+dist+lowtemp)}$*	1534.3818	4.8458	0.0208	0.0887	6	1522.3537	1522.3537
3.02 $S_{(g+sex+lowtemp)}$*	1534.4708	4.9348	0.0199	0.0848	6	1522.4427	1522.4427
3.19 $S_{(g+conspecs+lowtemp)}$*	1534.5479	5.0119	0.0191	0.0816	6	1522.5198	1522.5198
3.08 $S_{(g+ln\_dist+lowtemp)}$*,**	1534.5723	5.0363	0.0189	0.0806	6	1522.5442	1522.5442

Table 4.13: The preferred model (in bold font) and those models with an AICc within 4 of the preferred model and used for model averaging to describe woylie (*Bettongia penicillata ogilbyi*) survivorship in the northern jarrah forest, south-west Western Australia.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
3.17 $S_{(g+winter+lowtemp)}$	**1529.5360**	**0.0000**	**0.4233**	**1.0000**	**6**	**1517.5079**	**1517.5079**
5.17 $S_{(g+winter+lowtemp*rain)}$	1531.1364	1.6004	0.1901	0.4492	8	1515.0881	1515.0881
3.07 $S_{(g+dist+dist\_sq+lowtemp)}$	1532.0507	2.5147	0.1204	0.2844	7	1518.0132	1518.0132
3.14 $S_{(g+town+lowtemp)}$	1532.5640	3.0280	0.0931	0.2200	6	1520.5359	1520.5359
3.16 $S_{(g+unsealed+lowtemp)}$	1532.6673	3.1313	0.0884	0.2090	6	1520.6392	1520.6392
3.01 $S_{(g+lowtemp)}$	1532.7543	3.2183	0.0847	0.2000	5	1522.7342	1522.7342

Models 3.08, 3.19, 3.02, 3.06, 3.18, 3.09, 3.15 and 4.20 (Table 4.12) were considered non-competitive or redundant despite the ΔAICc values close to the preferred model. These models only differed from Model 3.01 by an AICc value from 0.21 to 1.80 units, however, the structure of these models differed from Model 3.01 by the addition of only one parameter. Where two such models differ by less than 2 AIC units and the larger model does not improve on the less parameterised model, the larger model is not supported and appears competitive simply because it is similar to the supported model (Burnham and Anderson, 2002). Consequently, model averaging did not include these models.

Model uncertainty was addressed through model averaging, with seven models used to model average (Table 4.13). Model average estimates $(\hat{\bar{\theta}})$ were derived for survivorship and for standard errors based on the individual model weights (W_i) (once recalculated for the model set used for model averaging, Table 4.13). The model average estimate is given by:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} W_i \hat{\theta}_i \qquad \text{(Burnham and Anderson, 2002)}$$

where:

$\hat{\bar{\theta}}$ is the model averaged estimate of θ;
W_i is the weight of evidence for the fitted model g_i; and
$\hat{\theta}_i$ is the estimated parameter of interest in model g_i.

Model averaging included all competitive models with relative likelihoods of 0.135 or above, i.e. models where the AICc was within 4 of the ‘best’ model (Burnham and Anderson, 2002). All models with relative likelihoods of 0.135 or larger (equates to an AICc value within 4 of the top ranked model) included the temporal covariate ‘*lowtemp*’ (Model Set 3) or the product (or interaction effect) of the temporal covariates ‘*lowtemp*’ and ‘*rain*’ (Model Set 5).

Model selection indicated strong or equal support (ΔAICc<2.0) for the second ranked model, Model 5.17 (Table 4.13), with the latter including an interaction between the external covariates ‘*lowtemp*’ and ‘*rain*’. The interaction effect from Model 5.17 is shown in Figure 4.6 and the effect from a quadratic term for distance (Model 3.07) is shown in Figure 4.7. The latter shows a decreasing estimated probability of survival with increasing distance from agricultural land for the first 7 to 8km, followed by an increase in estimated survivorship at distances further than 8km from agricultural land. The effect of distance decreased as the number of days where the minimum overnight temp was 5^0C or less increases.

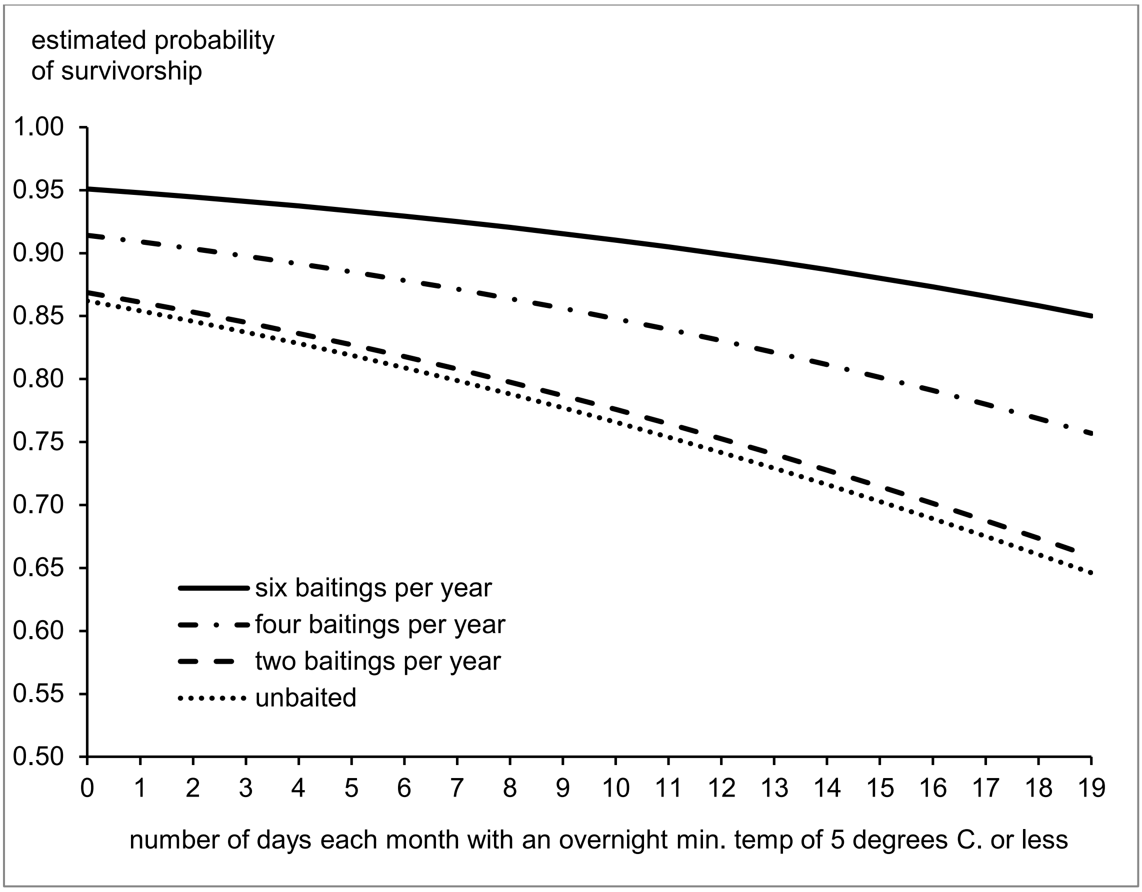

Figure 4.6: Graphical representation of Model 5.17 from the confidence model set to describe estimated woylie (*Bettongia penicillata ogilbyi*) survivorship within the northern jarrah forest, south-west Western Australia.

This model has an interaction effect between the external covariates '*lowtemp*' and '*rain*'. The figure shows the effect of an increase in the number of days per month where the overnight minimum temperature was 5^0C or less and where the external covariate '*rain*' (the number of days per month with a daily rainfall of 10mm or more) is held constant at zero. The binary covariate for '*winter*' was coded '1' (i.e. translocation release in winter).

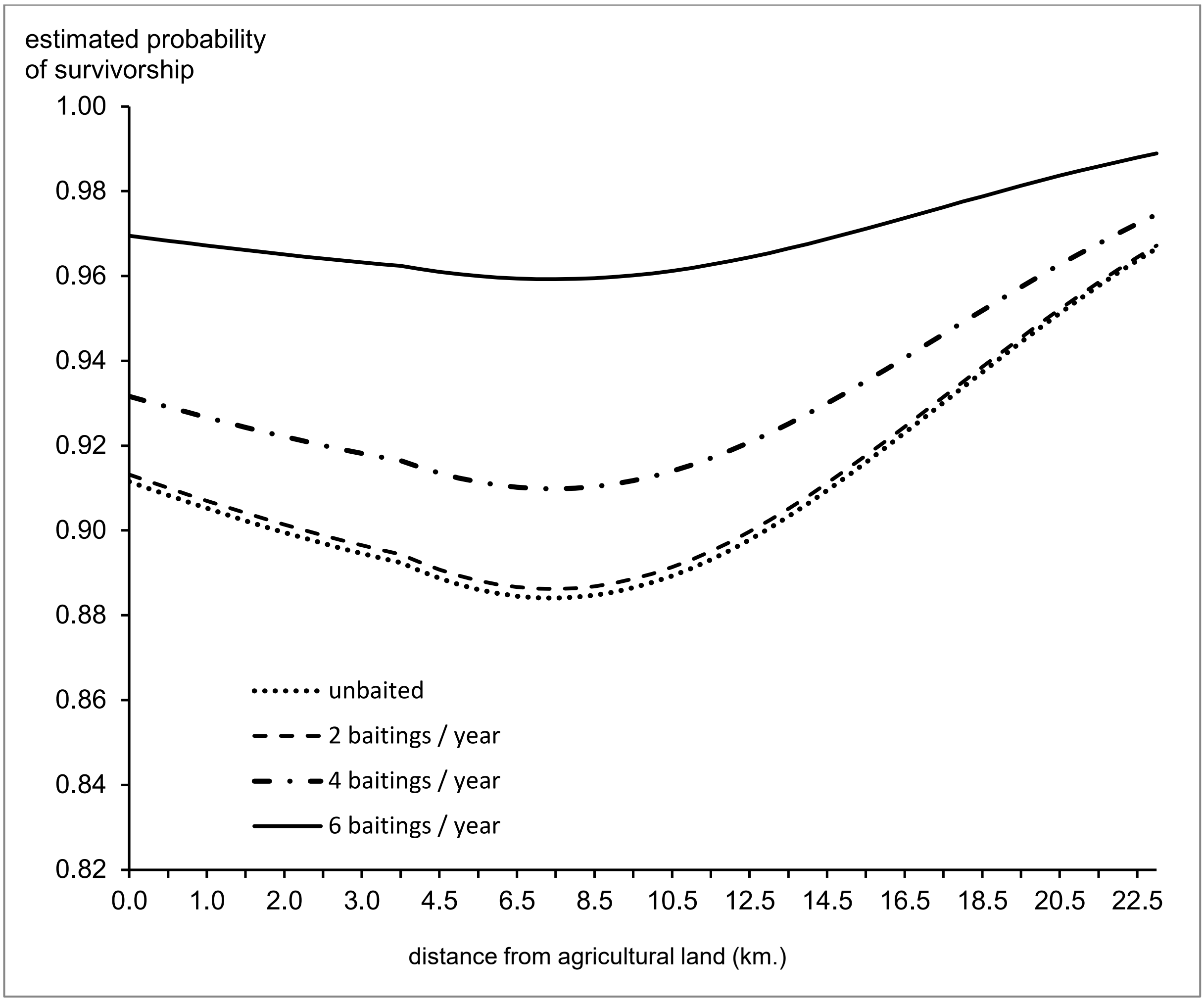

Figure 4.7: Graphical representation of Model 3.07 from the competitive model set used for model averaging to describe woylie (*Bettongia penicillata ogilbyi*) survivorship within the northern jarrah forest, south-west Western Australia.

This model includes a quadratic term for the covariate for '*dist*' (the distance from agricultural land), graphed with the number of days where the overnight minimum was 5^0C or less held constant at zero.

The unconditional estimates of survivorship, with unconditional standard errors (Table 4.14 and Fig. 4.8) strongly infer estimated survivorship probability in the six baitings per year treatment group is higher than all other treatments. The estimate of survivorship probability over the 37 month duration of the study is 23.6% in the six baitings per year treatment group, 16.4% higher than estimated survivorship in the four baitings per year treatment group (prob *S*=0.072 or 7.2%).

Table 4.14: Model averaged survivorship estimates for woylies (*Bettongia penicillata ogilbyi*) translocated to the northern jarrah forest of south-west Western Australia.

Treatment group	Estimate survivorship	Std Error	Lower 95% confidence interval	Upper 95% confidence interval
unbaited	0.0139	0.0084	0.0043	0.0446
two baitings per year	0.0188	0.0101	0.0065	0.0533
four baitings per year	0.0715	0.0299	0.0308	0.1569
six baitings per year	0.2358	0.0578	0.1413	0.3666

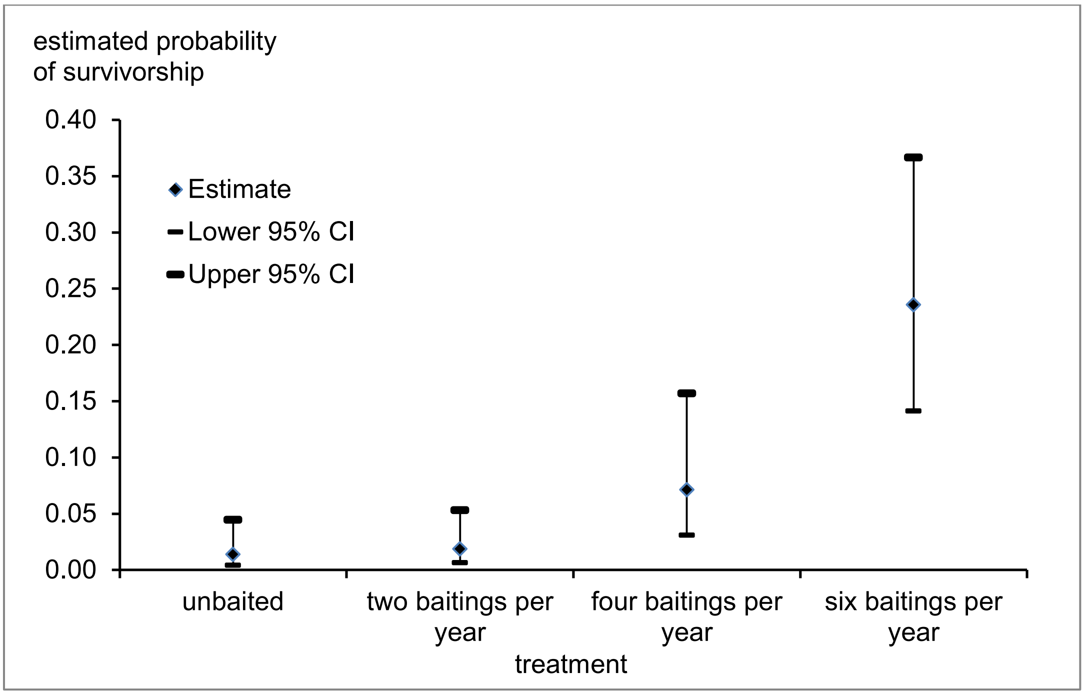

Figure 4.8: Model averaged estimate of survivorship probability for woylies (*Bettongia penicillata ogilbyi*) translocated to baited and unbaited sites within the northern jarrah forest, south-west Western Australia.

Sample size (n)=384. Survivorship probability estimates are unconditional and are for the 37 month duration of the study. Error bars are the 95% confidence intervals based on model weights.

4.3.3.7 Animal condition

Sixty three female and 154 male woylies were used to derive a value for the condition of female and male woylies respectively. For both sexes the relationship between weight and head-body length was best described by a log-log model (Fig. 4.9).

For females, the relationship is given by:

$\ln \text{weight (g)} = 2.86494 \text{ x } \ln \text{head-body length (mm)- } 9.496519$

and for males:

$\ln \text{weight (g)} = 2.60565 \text{ x } \ln \text{head-body length (mm) - } 8.009391$

Removal of the outlier for the regression model for males (see Fig. 4.9B) did not result in an improved fit (R^2 value).

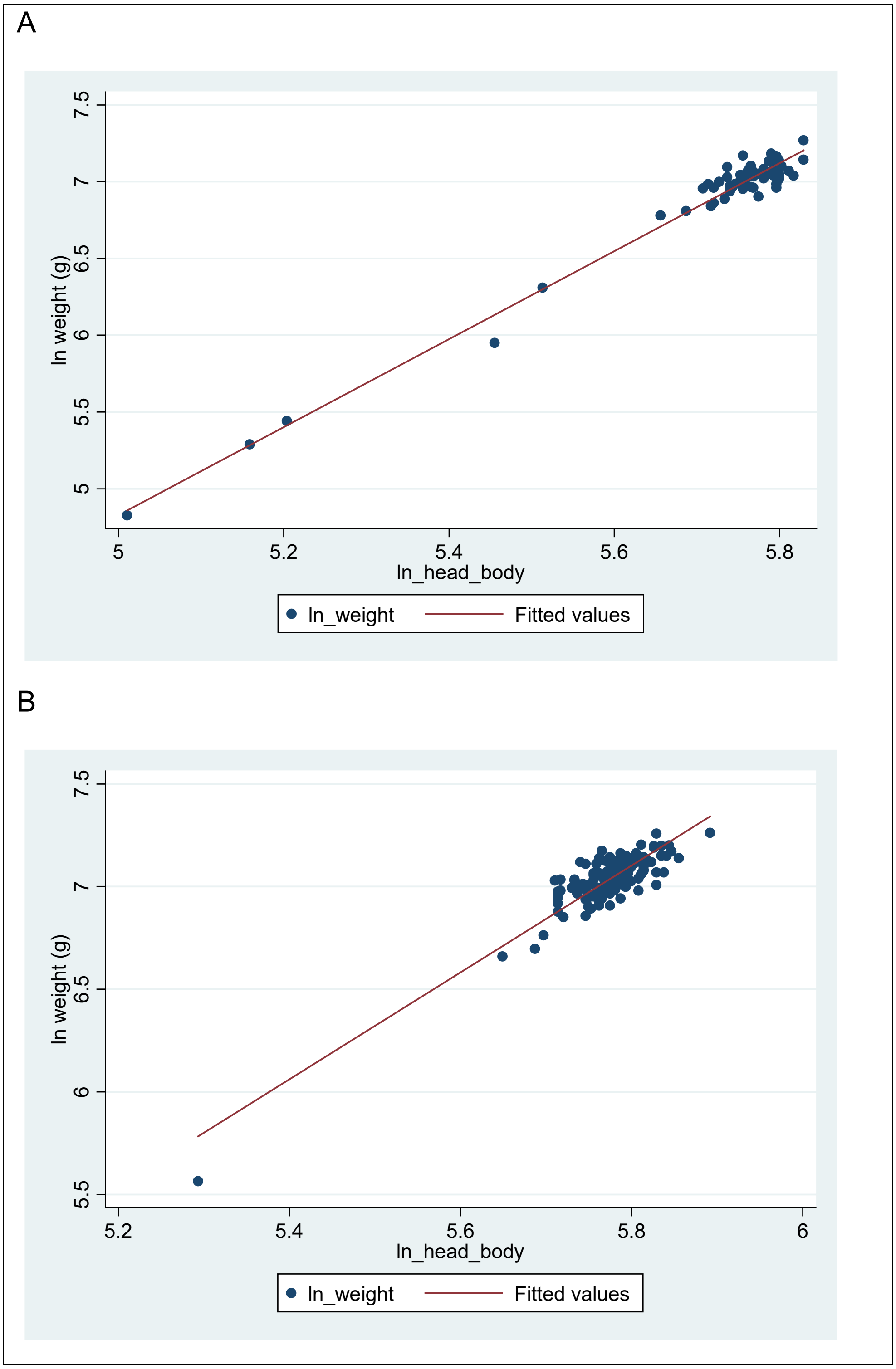

Figure 4.9: Ordinary least squares log-log regression models for weight (g) and head-body length (mm) of translocated woylies (*Bettongia penicillata ogilbyi*) and recruits to the population within the northern jarrah forest of south-west Western Australia.

A: females. B: males

4.3.3.8 The fate of each radio-collared woylie

Of the 384 radio-collared woylies, 96 were known to be alive at completion of the study (Table 4.15). Two of these (Bp M6004 and Bp F6012) were from the pilot translocation. Both were released at the Hakea Road grid in January 1995. Bp M6004 was collared at the time of release. Bp F6012 was initially released un-collared and entered the monitored sample when re-trapped and collared on 3 March 1998.

The fate of all radio-collared woylies is shown in Table 4.15. Foxes were considered the predator responsible 61 of the 201 deaths attributed to predation. The diagnostic features used to differentiate between predator species (Table 4.16) are not exhaustive and not every feature indicative of each predator species was present on each occasion when a carcass and/or radio-collar was recovered. Any single characteristic alone does not enable differentiation between predation and scavenging. Similarly, there is no ability to determine whether two (or more) predator species have interfered with the carcass and/or radio-collar.

Figure 4.10 shows images of woylies where mortality was attributed to fox predation. Figure 4.11 shows an image of a radio-collar where there was evidence to suggest cat and fox predation but predation was unable to be attributed to either species. Figure 4.12 shows images of woylie predation where there was evidence for predation and/or scavenging by a cat and/or a raptor.

Figure 4.13 shows images of radio-collars (recovered from dead western ringtail possums as part of a concurrent research project) where there is evidence of chuditch tooth marks on the collars (see discussion for prey size and chuditch predation). The unambiguous case of predation by a python is shown in Figure 4.14. In this case the woylie was known to be alive when monitored the previous day.

Table 4.15: The fate of 384 radio-collared woylies (*Bettongia penicillata ogilbyi*) monitored intensively for survivorship for 37 months, within the northern jarrah forest, south-west Western Australia.

Fate or outcome	**Number of individuals**	**Comments**
Survived.	96	Two of these were from the pilot translocation.
Predation by fox.	61	Carcasses recovered showed characteristics considered indicative of predation by fox, see Table 4.16.
Predation by fox?	6	Carcasses recovered were indicative of predation, however these were only partly indicative of predation by fox.
Predation by fox or cat?	21	Carcasses recovered were indicative of predation, and the characteristics were consistent with those indicative of predation by fox and predation by cat.
Predation by cat.	46	Carcasses recovered had characteristics considered indicative of predation by cat, see Table 4.16.
Predation by cat?	14	Although carcasses recovered were indicative of predation, they were only partly indicative of predation by cat.
Predation by cat or chuditch?	1	Carcasses recovered were indicative of predation, and the characteristics were consistent with those indicative of predation by cat and predation by chuditch.
Predation by chuditch?	1	Carcasses recovered were only partly indicative of predation by chuditch.
Predation by python.	3	Carcasses were recovered when the mortality signal was tracked to a python.
Predation by raptor or possibly raptor.	2	Carcasses recovered had characteristics considered indicative of predation by raptor, see Table 4.16.
Predation – unable to be attributed to a predator species.	46	There was Insufficient evidence at the site from where the carcass, or the collar only, was retrieved to infer the predator species. However, predation was implied - e.g. by tooth marks in the collar and where the animal was recorded alive the previous day.
Miscellaneous.	6	Three road kills and one drowning. One of the remaining deaths was considered to have been a result of the woylie's forelimb being caught in the collar, the other by injuries from the collar.

(cont. …)

Table 4.15 (… cont.)

Fate or outcome	**Number of individuals**	**Comments**
Cause of death unknown.	17	In most cases there was insufficient evidence from the site where the carcass and/or collar was retrieved. It was unclear if tooth marks (if present) in the collar were from one or multiple species and/or individuals, i.e. they were not all the same size. There was usually a relatively long period between the last detected radio-collar signal and collection of the carcass or collar. This also confounded differentiating between predation and scavenging.
Censored.	64	Four of the censored woylies had their collar removed as a forelimb was caught in the collar and there was evidence of injury from the collar. A fifth was censored as it showed injury from the collar (without a forelimb being caught). Two of the censored animals were detected from an aerial search. The signal was weak in both cases and the animals were unable to be located on the ground. One of these was transmitting in mortality mode, the other in live mode.

Table 4.16 Diagnostic features used to differentiate between woylie (*Bettongia penicillata ogilbyi*) mortality events attributed to cat (*Felis catus*), fox (*Vulpes vulpes*), chuditch (*Dasyurus geoffroii*) and raptor predation and/or scavenging events in the northern jarrah forest, south-west Western Australia.

Predator species	Characteristics considered indicative of each predator and observable on recovered carcasses and/or on recovered collars or observed at the site where the carcass and/or collar was recovered	Additional comments
Fox	Carcass can be entire or only partially recovered or the head only recovered (Fig. 4.10). Carcass often cached and, if so, will be buried under soil or other debris with evidence of digging or excavation under and/or beside the cached carcass. If the carcass is dismembered, limbs may be present at the site, often with evidence of puncture wounds (Fig. 4.10), chewing and crushing. If the abdominal cavity is opened, stomach and intestines have usually been removed and presumably eaten or cached elsewhere. Abdomen may be crushed and abdominal or thoracic organs may be absent or present. Head can be entire and/or crushed. The carcass (and/or collar only) may be recovered from an obvious fox den where there is other evidence of fox predation, e.g. recovered from a den where sheep and or western grey kangaroo remains are present. Condition of radio-collar can range from undamaged (can still be in place on carcass or undamaged and removed from carcass), to grossly compressed and misshapen (laterally compressed) with numerous teeth marks. If teeth marks are present they are almost invariably large (see additional comments) and indicative of canid teeth. Ears are often chewed or absent. Lower jaw may be absent. Noticeable odour of fox or fox urine.	Not all features are present at every site where a carcass is recovered, particularly if the cached carcass is in an excavated (dug out) hole and buried. Mounds of leaves, litter and soil were thought to more likely be indicative of caching by cats. There are anecdotal accounts to suggest when cubs are present (September to February), smaller teeth marks may also be evident on the collar. If the collar only is recovered there was usually no attempt to attribute the death to predation or to a specific predator. Death is usually only attributed to predation if there has been a very short time between detecting the last live signal and retrieving the radio-collar. Teeth marks alone are not used to attribute death to a predator unless there is other strong evidence to do so, for example, if the retrieved collar was cached, if it was at a fox den site and the woylie was known to be alive within the previous 24 hours.

(cont. …)

Table 4.16 (… cont.)

Predator species	**Characteristics considered indicative of each predator and observable on recovered carcasses and/or on recovered collars or observed at the site where the carcass and/or collar was recovered**	**Additional comments**
Cat	Carcass can be entire or only partially recovered. If cached, the carcass will be buried, or only partially buried, usually under leaf litter with no evidence of digging or excavation under and/or beside the cached carcass. Puncture wounds may be present.	
	If abdominal cavity is open, stomach and intestines are usually remaining (either *in situ* or beside the carcass). Abdominal and thoracic organs may be removed. Skin often peeled back from limbs and body, flesh removed (presumably eaten). Head may be attached to body or detached, often with the brain removed. The condition of the radio-collar may be similar to radio-collars damaged by foxes. There may be large tooth marks and some degree of lateral compression of the collar and it may therefore be difficult to distinguish between cat and fox teeth marks (Fig. 4.11). Skin often peeled back from limbs and body, flesh removed (presumably eaten).	Carcasses with skin peeled back and flesh removed may also be characteristic of raptor predation. Similarly, removal of the brain may be indicative of predation by a raptor. Additional evidence is required to differentiate between cat and raptor predation. The position of the retrieved carcass may be in the open, below a branch, straddled across a log or have sections on either side of a log (all implicating raptor) as opposed to concealed or partially concealed under shrubs, or under or in a log (implicating cat more than raptor).
	Noticeable cat urine odour.	
		As for foxes. If only the collar is recovered, death cannot be attributed to predation without supporting evidence.

(cont. …)

Table 4.16 (… cont.)

Predator species	Characteristics considered indicative of each predator and observable on recovered carcasses and/or on recovered collars or observed at the site where the carcass and/or collar was recovered	Additional comments
Raptor	Carcasses are rarely entire. The skin may be peeled back and may appear similar to carcasses where mortality is attributed to cat predation (Fig 4.12). See additional comments for attributes of cat predation events. The brain may be removed. The carcass may be draped across a log or fallen branch, directly below a branch or eyrie or straddled above ground across a branch. There may be evidence of excreted uric acid. Regurgitated pellets may be present.	See additional comments, above, for similarities with the attributes of cat predation events
Chuditch	Characteristics are similar to those for foxes and cats, however, there is less likely to be thoracic crushing. Chuditch tooth marks in radio-collars are noticeably smaller than those left by cats and foxes (Fig. 4.13). Carcasses may be within hollow logs, however this may also be the case for cat predation events (see additional comments).	During a concurrent component of this study, a radio-collared possum was detected in mortality mode and the mortality event was being investigated. The signal was tracked to a hollow log and an adult chuditch was flushed from the hollow and the possum carcass was recovered from within the log (Cocking and MacArthur, unpublished). Presumably the chuditch had preyed upon the possum.
Python	Characteristics are unambiguous if the prey species has been consumed by a python and is still within the python's digestive system (Fig. 4.14). If the radio-collar only is recovered and has been excreted by a python, this may be evidenced by lateral compression of the collar and/or the presence of a python scat. See additional comments.	Pythons are ambush predators and therefore unlikely to be scavenging on a dead woylie. Pythons, in this case the south-west carpet python (*Morelia spilota imbricata*), have a scat or faecal pellet easily distinguished from other predators because of the scat's shape, a uric acid deposit at one end and the presence of python teeth within the scat (Pearson, 2002).

Figure 4.10: Photographs of woylie (*Bettongia penicillata ogilbyi*) carcasses where mortality was attributed to predation by a fox (*Vulpes vulpes*).

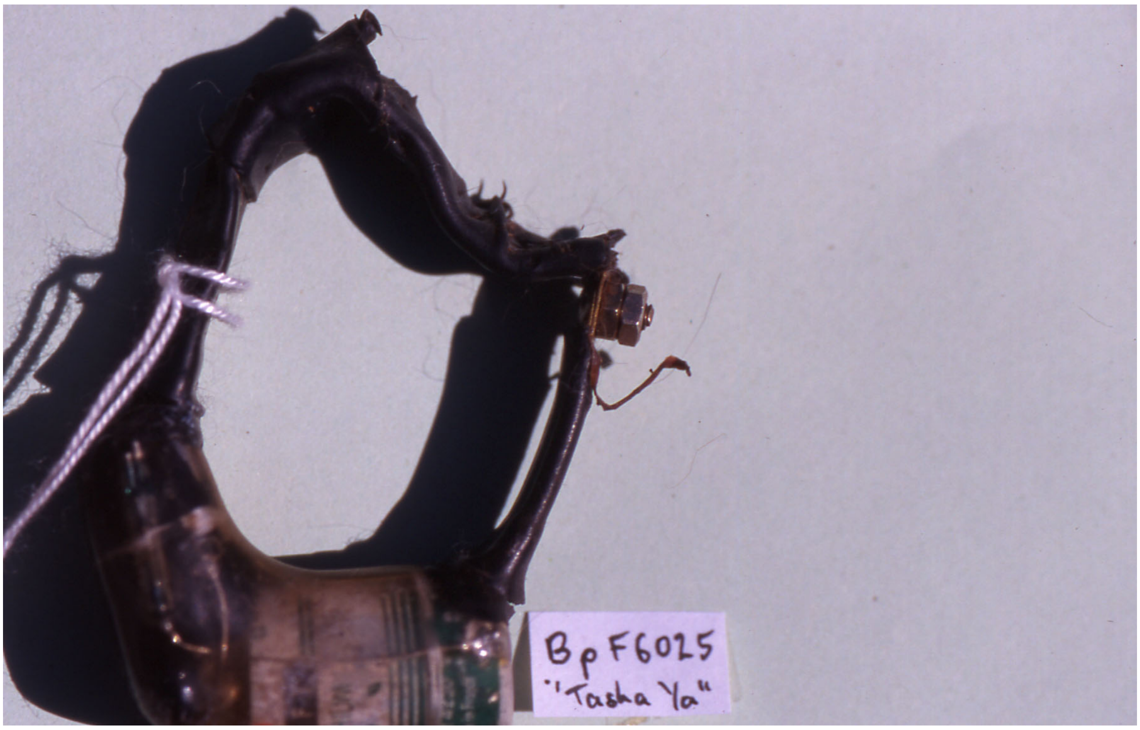

Figure 4.11: Photograph of a radio-collar recovered from the remains of a woylie (*Bettongia penicillata ogilbyi*) (Bp F6025) where mortality was attributed to predation but was unable to be attributed to either a fox (*Vulpes vulpes*) or a cat (*Felis catus*).

The collar and two small patches of fur only were recovered. The collar was strongly compressed and misshapen (both are indicative of a fox and less so of a cat), there were numerous large teeth marks (indicative of fox and cat) and the collar was recovered from the top of leaf litter (indicative of a cat). There was more than one week between the last recorded 'live' signal and location of the collar and remains.

Figure 4.12: Photographs of woylie (*Bettongia penicillata ogilbyi*) mortalities where evidence is insufficient to differentiate between predation by a raptor or cat (*Felis catus*).

In both cases the there was more than one week between the last recorded 'live' signal and location of the carcass.

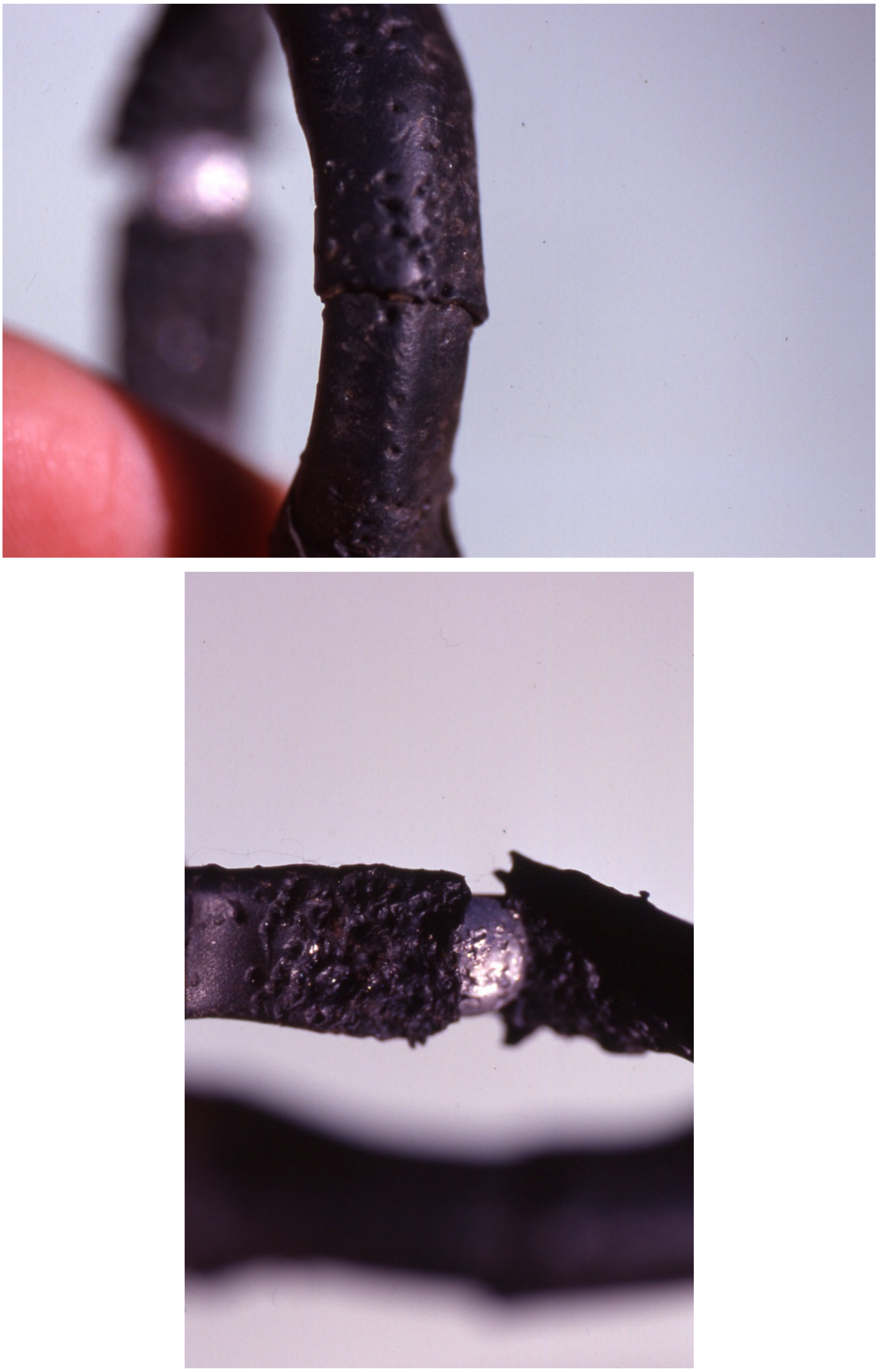

Figure 4.13: Photographs of radio-collars removed from western ringtail possum (*Pseudocheirus occidentalis*) carcasses where mortality was attributed to predation by a chuditch (*Dasyurus geoffroii*).

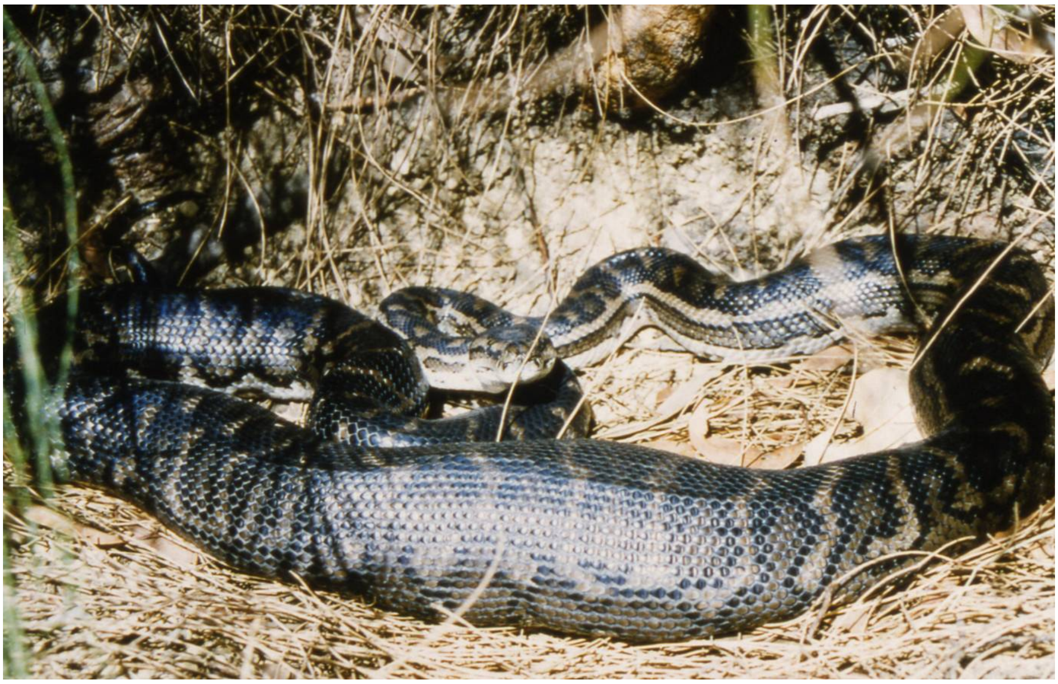

Figure 4.14: Photograph of a south-west carpet python (*Morelia spilota imbricata*) after preying upon a radio-collared woylie (*Bettongia penicillata ogilbyi*).
Photograph by Kathy Himbeck

4.4 Discussion

4.4.1 Woylie survivorship

Previous analysis of the woylie survivorship data (de Tores, 1999; de Tores *et al.*, 1998b) used the Kaplan-Meier staggered entry design as described by Pollock *et al.* (1989) and found woylie survivorship was highest in the six baitings per year treatment group. There was also evidence to suggest the four and six baitings per year treatment groups had comparable levels of survivorship at distances of 5km or more from agricultural land. However, the previous analysis was unable to assess competing models or hypotheses. The current analysis, using the Known Fate model in Program MARK, was able to assess alternative models in a model selection framework and, through use of AICc, identify which of these models had most support from the data. In recognition of model uncertainty, the current analysis also incorporated model averaging over the 'AICc best' models. Unconditional estimates of survivorship probability and the associated standard errors were derived for each treatment (Fig. 4.8 and Table 4.14).

The results revealed the estimated probability survivorship of woylies was higher in the six baitings per year treatment group than the four baitings per year treatment group, with a survivorship probability of 23.6% and 7.2%, respectively. The results further suggest baiting twice yearly may confer no conservation benefit, in terms of woylie survivorship, over not baiting at all (Fig. 4.8 and Table 4.14). These findings have considerable management implications for continued broad-scale baiting for fox control in south-west WA (see below and Chapter 6). The covariates within the preferred model identified a temporal component when estimating survivorship probability (the variable '*lowtemp*') and also identified survivorship probability was lower if the translocation release was in winter (Fig. 4.4, Fig. 4.5 and Table 4.13). Estimated survivorship was also lower where there was an increase in the number of days with the overnight minimum temperature of 5^0C or less (hereafter abbreviated as 'temp $\leq 5^0$C'). Figure 4.6 provides a graphical representation of Model 5.17 showing the relationship between estimated woylie survivorship and temp $\leq 5^0$C, with survivorship decreasing across all treatments as the number of days with temp $\leq 5^0$C increases. Figure 4.15 gives a graphical representation of the relationship between the time of year of known woylie mortalities and the number of days with temp $\leq 5^0$C.

The combined associations of a lower estimated survivorship probability and (i) the number of days with temp $\leq 5^0$C; and (ii) translocation release in winter, is not surprising. The woylie's former distribution suggests it is an arid adapted species. This would also confer adaptation to low overnight temperatures, but not necessarily to cold winter diurnal temperatures generally. Although a lower probability of survivorship with a winter translocation release in consistent with a lower probability of survivorship in winter generally, neither the number of days with temp $\leq 5\ ^0$C nor winter translocation release identifies the cause of this lower survivorship. Plausible hypotheses to explain this lower survivorship include:

(1) the woylie is poorly adapted to winter conditions in the more mesic south-west and has an intrinsically lower level of survivorship there than in the semi-arid areas of its former distribution. This would also infer there is a lower level of survivorship in the Perup Forest (near Manjimup) than at Dryandra Woodland and Tutanning Nature Reserve (see Fig. 1.2, Chapter 1). These three locations are the only known locations of naturally occurring woylie populations; or

(2) an alternative to hypothesis (1) above is that populations are equally well adapted to the local environment and there is no *a priori* rationale for a difference in survivorship between the three extant locations. The inference is individuals sourced from the Perup Forest may be better suited for translocation to other forest areas, including the northern jarrah forest, than those from the wheatbelt locations (Dryandra Woodland and Tutanning Nature Reserve), despite Dryandra

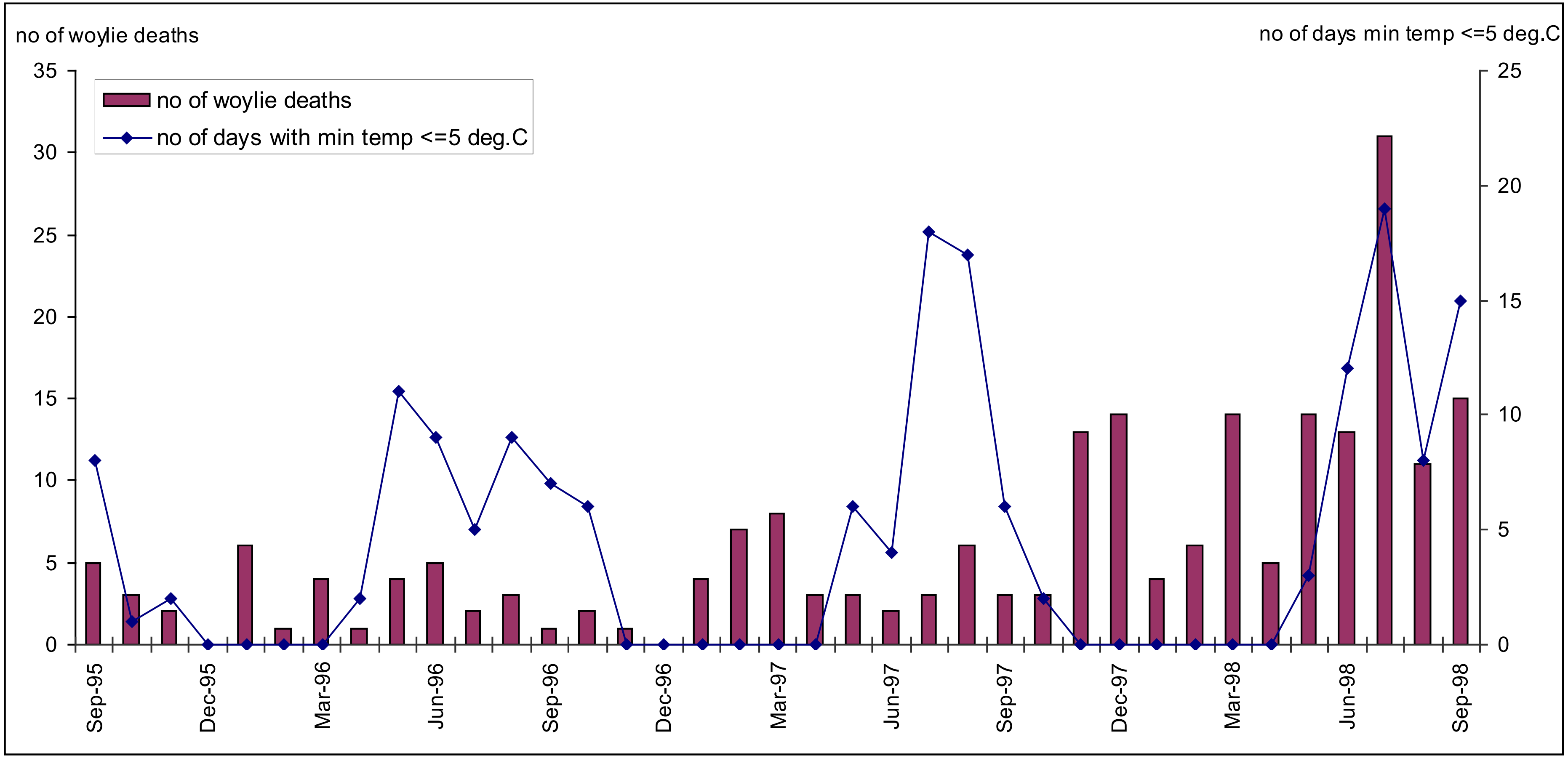

Figure 4.15: Graphical representation of the relationship between the number of woylie (*Bettongia penicillata ogilbyi*) deaths each month and the number of days each month with a minimum overnight temperature of 5 ^{0}C or less.

Woylie deaths are inclusive of all causes: predation where the predator species is known; predation where the predator species is unknown; deaths as a result of unknown causes; and miscellaneous deaths (see Table 4.15) (n = 224).

being only 50km from the eastern margin of the northern jarrah forest; or

(3) the level of predation by introduced predators is higher in winter. This may be a function of increased foraging activity by foxes during winter, consistent with the period when male home range breaks down and foxes are mating (see Chapter 1, Section 1.2.5); or

(4) there is a reduced effectiveness of 1080 baiting programs in winter. This may be a function of bait exposure to rainfall and leaching of 1080. This hypothesis and hypothesis (3), above, are not mutually exclusive.

Lower winter survival has been reported for other species. When examining survivorship of racoons (*Procyon lotor*), Pitt *et al.* (2008) found the seven best ranked models (ΔAICc<2 and accounting for 96% of the model weights) all included a component for winter severity. They believed winter climatic constraints influenced the northern limit of range extension for racoons. They were able to correlate lower winter survival with winter severity but unable to correlate lower winter survival with winter body condition, or with body condition for the preceding autumn.

Interestingly, Pitt *et al.* (2008) did not rely on the widely used (and often criticised) index of body condition based on the regression of body mass on size (or based on the mass–size residuals). They used a plethysmograph to measure electrical resistance, or bioelectrical impedance, to derive an estimate for body condition. Pitt *et al.* (2008) defined body condition as the percentage total body fat as determined by calibrating the plethysmograph data. Electrical conductivity has been used to derive a measure of body condition for at least two marsupial species: the southern hairy-nosed wombat (*Lasiorhinus latifrons*) (Woolnough *et al.*, 1997); and the northern brown bandicoot (*Isoodon macrourus*) (Parker and Krockenberger, 2002). Parker and Krockenberger (2002) found no advantage from using electrical conductivity and concluded use of the conventional mass-size residual method was more appropriate, at least for deriving a body condition index for the northern brown bandicoot. However, they derived a value for total body water only. Woolnough *et al.* (1997) found estimates from bioelectrical impedance analysis accurately measured body fat and total body water. Developments in bioelectrical impedance analysis enable accurate measures of total body fat, density of fat-free body mass, total body water, mass of skeletal muscle and total body potassium. The technology has been widely used in the meat and livestock industry for over 15 years (see for example Berg and Marchello, 1994; Berg *et al.*, 1996).

In contrast, use of the mass-size residual approach has been shown to result in measurement error, and observer differences can result in biases in the collected data (Blackwell *et al.*, 2006). The use of the mass-size residual approach has been widely used, misused and debated in the scientific literature (see for example Bamford, 1970; Blackwell *et al.*, 2006; Boos *et al.*, 2005; Humphreys *et al.*, 1984; Johnstone *et al.*, 2010; Krebs and Singleton, 1993; Schulte-Hostedde *et al.*, 2005; Stirling *et al.*, 2008; Viggers *et al.*, 1998; Wayne *et al.*, 2005).

The absence of the covariate for body condition in any of the competitive models for woylie survivorship in the northern jarrah forest (Table 4.13) should be interpreted cautiously as it is unlikely body condition is not related to survivorship. The absence of the variable for body condition in the competitive models could potentially be because: (i) the data were poorly recorded; or (ii) the index does not reflect condition; or (iii) only 'healthy' woylies were translocated. These options are not mutually exclusive, however, given the very strong correlation in the regressions (Fig. 4.9A and Fig. 4.9B) the first explanation is unlikely.

The confidence model set (Table 4.13) included one model (Model 3.07) with a covariate for the distance from agricultural land, with distance modelled as a linear and quadratic term (see Fig. 4.7). Unlike the original analyses which estimated survivorship to be higher at sites greater than 5km from agricultural land (de Tores, 1999; de Tores *et al.*, 1998b), the current analysis indicated a decreasing estimate of survivorship probability for the first 7 to 8km, but qualified by the quadratic term which indicated an increase in estimated survivorship at distances further than 7 or 8km from agricultural land. Although survivorship increased at distances greater than 7km, the effect of baiting diminished (the differences between treatments diminished) with increasing distance and also diminished with increasing number of days where temp $\leq 5^0$C. However, over the range of distances in this study, estimated survivorship remained highest in the six baitings per year treatment group, irrespective of the distance from the interface with agricultural land.

4.4.2 The woylie as an indicator species

Use of indicator species and the validity and extent of inference which can be made from findings based on indicator species is debateable (see for example Calver and Dell, 1998; Cushman *et al.*, 2010; Landres *et al.*, 1988; Lindenmayer, 1999). Tulloch *et al.* (2011) demonstrated how the perceived cost of a monitoring program can influence the choice of indicator species. The study sought the response from ten ‘experts’, five of whom responded. They were asked to score 12 competing medium size mammalian species on the basis of 17 criteria. The data were analysed using a ‘qualitative’ and a ‘quantitative’ approach and the species were ranked to identify one indicator species to monitor to assess the response to fox control in south-west WA. The woylie was selected when costs were not taken into consideration in the qualitative approach. The brushtail possum was selected when costs were incorporated ‘sensibly’ in the qualitative approach and was selected again in the quantitative approach.

Although the woylie may be a good indicator species, inference will always be limited if the data are collected from only one species. The concept of relying on only one species for inference is also illogical, as most monitoring programs assessing the response of one medium size mammalian species can, with minimal additional cost, also collect data on other medium size mammals. The northern jarrah forest trapping program and results from occupancy modelling (Chapter 5) showed the estimated probability occurrence (occupancy) of brushtail possums and southern brown bandicoots was determined by very different site specific variables. All data were collected concurrently. Relying on one species to reflect the response of many seems to be burdened by the same issues applying to use of indices generally. Further, selecting an indicator species to monitor on the basis of costs has no ecological foundation.

4.4.3 Animal handling and radio-telemetry

Operation Foxglove protocols for handling and ‘processing’ woylies incorporated use of anaesthesia as an alternative to physical restraint. Ketamine and Xylazine were used in combination and allowed thorough examination of the reproductive status of each woylie, appropriate fitting of radio-collars and accurate collection of morphometric data in the absence of (perceived) stress to the woylies and real stress to the animal handlers. Ketamine is now listed as a Schedule 8 Controlled Drug through the Poisons Standard (2010) which has legal effect through state legislation. In WA, this is through the WA Poisons Act 1964. Ketamine is also known to have hallucinogenic effects and a relatively long recovery time. However, unlike other reported woylie translocations (see for example Bellchambers, 2001; Priddel and Wheeler, 2004), there was no loss of pouch young during translocation to the northern jarrah forest. This may be attributable to the use of anaesthesia. Alternatives to Ketamine include the injectable anaesthetic, Zoletil. However Zoletil has a relatively long recovery time (similar to Ketamine, personal observations and unpublished data). Isoflurane gas inhalation anaesthesia has a considerably shorter effect time than Ketamine, a negligible recovery time and no hallucinogenic effects. Isoflurane gas inhalation anaesthesia has been successfully used for anaesthesia of woylies, western ringtail possums, western brushtail possums, foxes and cats (personal observations and unpublished data from research on the western ringtail possum and Clarke, 2011). Use of anaesthesia and Isoflurane gas inhalation anaesthesia in particular has the potential to reduce any trauma experienced by an animal while being fitted with a radio-collar.

The role of radio-telemetry in wildlife monitoring programs has been questioned and trapping has been proposed as an equivalent alternative (Priddel and Wheeler, 2004). However, reliance on trapping alone also poses risks to wildlife and substantially reduces the information obtained from monitoring programs. In the case of the woylie, there is a known capture myopathy effect (personal observations and unpublished records). White and Garrott (1990) cautioned researchers to investigate the potential effects from fitting radio-collars and there is substantial evidence to implicate radio-collars as contributing to reduced survivorship probability and poor translocation outcomes which can bias interpretation of spatial use patterns (see for example Brooks *et al.*, 2008; Gursky, 1998; Lariviere and Messier, 1998; Swenson *et al.*, 1999; Tuyttens *et al.*, 2002). Anecdotal accounts recommend a collar weight of no more than 5% of the study animal's body weight, however there are no published accounts to support use of this value. In a western ringtail possum translocation study (de Tores, 2009; de Tores *et al.*, 2004), satellite radio-collars fitted to feral cats, with all collars weighing less than 5% of the animal's body weight, were considered responsible for changes in the dietary intake and hunting capabilities of feral cats (personal observations and unpublished data from research on the western ringtail possum, see Chapter 6, Section 6.4.2.3). The implication from this was that radio-collared cats become less efficient at predation of live prey and more susceptible to conventional 1080 fox baiting programs.

Conversely, Berteaux *et al*. (1996) and Cypher (1997) found no effect from collars fitted to meadow voles (*Microtus pennsylvanicus*) and San Joaquin kit foxes, respectively. The use of radio-telemetry enables early detection of mortality events which is critical if information is required on the cause of death. Confidence in determining the cause of death and/or the predator responsible for a predation event decreases with increasing time between detecting the last live signal and when the carcass or collar is retrieved. Use of movement sensitive mortality transmitters fitted to woylies released in the northern jarrah forest enabled collection of such data and quantitative assessment of the differences in survival probability between each of the baited treatments and the unbaited control.

4.4.4 Who killed the bettong?

There has been much debate in the recent scientific literature regarding interactions between predators and the potential for mesopredator release (see Chapter 6 for discussion and references). The issues associated with mesopredator release in the Australian environment are complex and quite different from most of the international published examples. The international literature is largely focussed on interactions between native predators. The major mammalian predators of Australian fauna are introduced species, specifically the dingo, fox and cat.

Discriminating between the predator species potentially responsible for each woylie predation event in the northern jarrah forest was largely subjective. The characteristics observed on a woylie carcass and attributable to a fox and cat overlapped considerably (Table 4.16). Nonetheless, there is evidence to implicate the cat as a significant predator of woylies (see Table 4.15 and Fig. 4.16). The long term biodiversity conservation implications and management implications of this are discussed in Chapter 6, as is the use of existing molecular techniques to differentiate between predator species and genotyping individual predators.

4.5 Recommendations

4.5.1 1080 baiting frequency

The northern jarrah forest research estimated woylie survivorship to be higher in the six baitings per year treatment group than when baited in accordance with the operational standard baiting frequency of four baitings per year. The difference in survivorship (23.6% Vs 7.2%) over the 37 month period of the study, albeit with overlapping confidence intervals, is interpreted as biologically significant. At distances more than ~7km from agricultural land the effect of baiting is diminished, nonetheless, at a distance of 23km the increased baiting frequency still resulted in an increase in woylie survivorship (Fig. 4.7). As most conservation reserves in south-west WA have irregular boundaries and rarely have a 23km radius, a regime of six baitings per year is recommended.

4.5.2 Future translocations of the woylie

The estimated probability of woylie survivorship was lower for translocations carried out in winter and survivorship decreased with an increase in the number of days with an overnight minimum temperature of 5^0C or less. Although there is no unequivocal ‘cause-and-effect’ relationship and the lower winter survivorship may be a result of reduced 1080 efficacy in winter, it is recommended that woylie translocations are not carried out in winter, and further, it is recommended any *in situ* woylie monitoring programs using radio-telemetry are not commenced in winter.

4.5.3 Animal handling, use of anaesthesia and radio-collars

There were no woylie mortality events attributed to animal handling nor to the use of anaesthesia. The use of anaesthesia is recommended for all non-trivial monitoring and research programs where the alternative is physical restraint. However, as Ketamine is now a Schedule 8 Controlled Drug and as Zoletil has a comparably long recovery time, Isoflurane gas inhalation anaesthesia is recommended for all woylie translocations and all non-trivial monitoring programs where physical restraint is otherwise required, e.g. when fitting radio-collars, when accurate morphometric data are required, when the reproductive status of females is required, when the size and sex of pouch young are required, etc. Personal observations suggest that resistance to this recommendation may be based on the perception of reduced machismo if an animal can't be physically restrained when fitting a radio-collar.

Woylies appeared to show no ill effects from fitting radio-collars, once appropriately fitted and facilitated by use of anaesthesia. However, all collars used in the northern jarrah forest weighed less than 3% of body weight. With increasing capability to miniaturise radio-collars, this 3% of body weight should be seen as a maximum when selecting collars for use on woylies.

4.5.4 Predation by cats

There were 110 predation events confidently attributed to a predator species (Table 4.15), with 46 (42%) of these attributed to predation by feral cats. However, only 6 (13%) were from the unbaited control. A lower level of cat predation in the unbaited control, or more precisely, a higher level of cat predation in the fox baited treatments, is consistent with the hypothesis of mesopredator release of cats in the baited treatments. The implication is that a long-term effect of broad-scale fox baiting may result in increased cat abundance and a net loss in biodiversity values. Therefore, it is recommended that fox and cat monitoring is conducted where fox control is carried out, with monitoring targeted to quantitatively test the mesopredator release hypothesis (see Chapter 6).

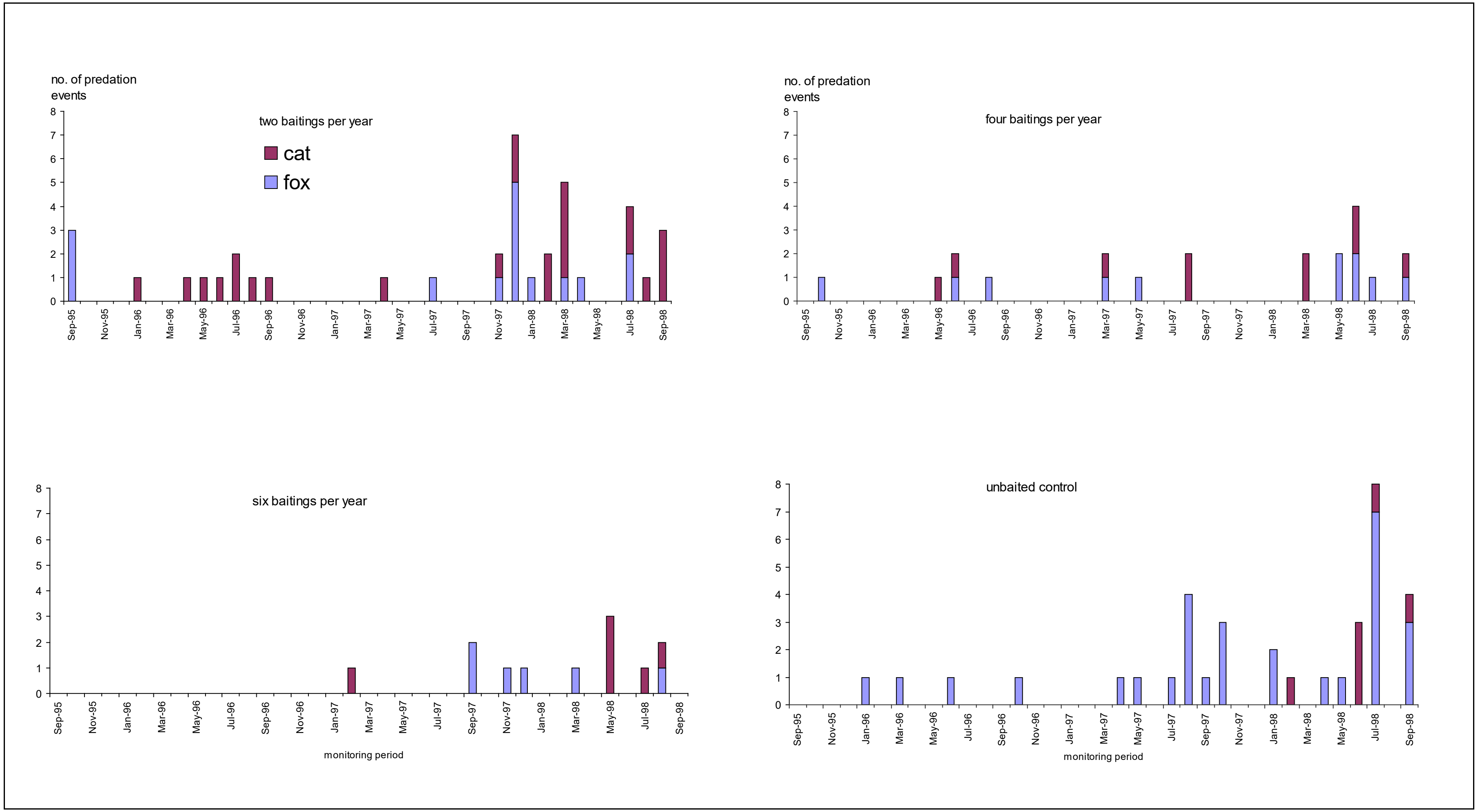

Figure 4.16: The proportion of woylie (*Bettongia penicillata ogilbyi*) mortality events attributed to predation by foxes (*Vulpes vulpes*) and cats (*Felis catus*), each month, within each of the northern jarrah forest fox control treatments.

Chapter 5

Occupancy modelling: the variables influencing presence of resident mammal fauna within the northern jarrah forest

5.1 Introduction, objectives and hypotheses

The suite of non-volant native mammalian fauna within the northern jarrah forest has been anecdotally reported to be at low abundance, with little or no quantified data available on population density for any *in situ* species. Although several species of threatened mammals are known to occur within the northern jarrah forest, it is considered to be a region of low productivity (Andrew Burbidge[8], pers. comm.) and has less mammalian species richness than forest areas from eastern Australia (Nichols and Muir, 1988). Published and grey literature reports of the species recorded from the northern jarrah forest are consistent with these anecdotal accounts. Those species known, or thought to occur within the northern jarrah forest and with the potential to respond to fox control are listed in Table 5.1. Introduced mammalian fauna known to occur with the northern jarrah forest are the fox, feral cat, black rat, house mouse, rabbit and feral pig. The ferret has been reported although its presence is unconfirmed. Personal observations indicate the dingo is extremely rare in the northern jarrah forest, and south-west WA generally, and individuals present are likely to have hybridised with wild dogs (Peter Thomson[9], pers. comm.).

Four mammalian species; the numbat, western ringtail possum, woylie and tammar wallaby were considered absent from the northern jarrah forest, however each was known, or was thought to have previously occurred there. There are also unconfirmed reports from the 1970s of the burrowing bettong (or boodie, *Bettongia lesueur*) from the eastern margin of the jarrah forest, near Boddington (personal discussions with neighbouring landholders). Small populations of the numbat, western ringtail possum and tammar wallaby were translocated to the northern jarrah forest in the 1990s. The woylie was translocated to the study area as part of the current study (Chapter 4).

In recognition of the anticipated low abundance of resident mammalian fauna in the northern jarrah forest, and the limited potential for this suite of fauna to respond to fox control within the timeframe of the project, the major objective of determining if there was a fauna response to fox baiting was addressed through the woylie translocation

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[8] Andrew Burbidge: Former Director, Western Australian Threatened Species and Communities Unit, WA Department of Environment and Conservation.

[9] Peter Thomson: Former Research Scientist with the Western Australian Department of Agriculture and Food (DAFAWA) and the Western Australian Agriculture Protection Board (APB).

research. However, it is unlikely the distribution of native fauna in any forest area is a function of a single dimensional causal factor such as the abundance of an introduced predator. It was therefore hypothesised the occurrence, distribution and abundance of the suite of *in situ* native fauna is likely to be a function of various factors and complex interactions between these factors (see Section 1.6 Hypotheses).

This chapter reports on the occurrence (presence or occupancy) of the brushtail possum (*Trichosurus vulpecula hypoleucus*) and the southern brown bandicoot (*Isoodon obesulus*) at each of 55 integrated trapping grids established within the study area. The trapping data from these grids were sparse in terms of the requirements for mark-recapture techniques. Consequently the trapping data were analysed using occupancy modelling procedures (MacKenzie *et al.*, 2002; MacKenzie *et al.*, 2006) in Program MARK (White, 2001; 2020). The analysis was carried out to assess the relative importance of fox control and site specific habitat variables in relation to the distribution and occurrence of the brushtail possum and southern brown bandicoot. Hypotheses were set in an information-theoretic framework (Burnham and Anderson, 2002) and a set of candidate models was formulated to explain the data on presence for the two medium size mammal species most frequently trapped during routine trapping sessions as part of the Western Shield program (Orell, 2004) (see Chapter 1). These two species, the brushtail possum (or western brushtail possum or brushtail or possum – the terms are used interchangeably) and the southern brown bandicoot represent an arboreal and terrestrial species, respectively. The Western Shield trapping data for these species plus the trapping data for the chuditch and woylie is the primary means of assessment of the effectiveness of the Western Shield program. However, to date, analysis of DEC's Western Shield trapping data has relied on capture success rates only. Therefore, analysis of trapping data for the brushtail possum and southern brown bandicoot (this chapter) and analysis of radio-telemetry data for the woylie (Chapter 4) provide the opportunity to quantitatively assess the effectiveness of DEC's operational four baitings per year regime.

The entire suite of mammalian, reptilian and amphibian species trapped at each grid as part of this research is reported in Appendix 1.

Table 5.1: Native, non-volant mammalian species known, or thought to occur within the northern jarrah forest study area and with the potential to respond to fox (*Vulpes vulpes*) control.

Common names and ordering of species is as per the ordering and nomenclature used by Van Dyck and Strahan (2008).

Species	Common name	Source and comments
Tachyglossus aculaetus	echidna	Uncommon in the northern jarrah forest (personal observations) and on the Darling Scarp (Dell, 1983; Dell and How, 1988).
Dasyurus geoffroii	chuditch	Sparsely (Soderquist and Serena, 1993) and patchily (personal observations) distributed within the northern jarrah forest. Reported as present on the Darling Scarp outside the current study area (Dell, 1983; Dell and How, 1988) and was thought to have previously (prior to the early 1980s) been common in wandoo and jarrah woodland (Dell, 1983; Dell and How, 1988). It has been extensively studied within the northern jarrah forest at sites in the Murray River area, near Dwellingup (Serena and Soderquist, 1989; Soderquist and Serena, 1994; 2000), where, even in 'high-quality' habitat, it occurs at low density (Serena and Soderquist, 2008).
Antechinus flavipes	yellow-footed antechinus	A high density population was known from one site only, Amphion Forest Block (Mick Dillon[10] pers. comm., various *ad hoc* local trapping programs and this study), however, it occurs throughout the northern jarrah forest study area (personal observations and this study). It is considered uncommon on the Darling Scarp (Dell, 1983; Dell and How, 1988) outside the current study area.
Phascogale tapoatafa	brush-tailed phascogale	*Phascogale tapoatafa* from south-west WA is now recognised as the subspecies *Phascogale tapoatafa wambenger* (Aplin *et al.*, 2015) and recorded infrequently within the northern jarrah forest study area (personal observations and this study). Studies have been carried out in the southern jarrah forest (Rhind, 2002; Rhind and Bradley, 2002; Rhind *et al.*, 2001), however, there are no studies from the northern jarrah forest. The brush-tailed phascogale has been reported from the Darling Scarp but is considered uncommon there (Dell, 1983; Dell and How, 1988).
Sminthopsis dolichura	little long-tailed dunnart	Studies of *Sminthopsis* spp have been specifically in relation to fire and have been reported from remnant vegetation within the WA wheatbelt (Friend *et al.*, 1997), however, there are no studies from the northern jarrah forest. The *Sminthopsis* spp complex was considered uncommon on the Darling Scarp (Dell, 1983; Dell and How, 1988).
S. gilbertii	Gilbert's dunnart	
S. griseoventer	grey-bellied dunnart	

(cont …)

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[10] Mick Dillon: Former Senior Technical Officer, WA Department of Conservation and Land Management, Science Division, Dwellingup Research Centre.

Table 5.1 (… cont.)

Species	Common name	Source and comments
Isoodon obesulus	southern brown bandicoot	Studies have been conducted in the southern jarrah forest in relation to fox control (Burrows and Christensen, 2002), in the Perth metropolitan area in relation to general demographics (Sanderson and Kraehenbuehl, 2006) and in relation to habitat fragmentation and mitigation measures (Harris *et al.*, 2010). The southern brown bandicoot has been previously reported from the Darling Scarp (Dell, 1971; 1983; Dell and How, 1988), outside the current study area. It was considered 'moderately common' (Dell, 1983) in riparian thickets and adjacent jarrah and wandoo woodland, although not specifically stated as occurring within the northern jarrah forest. Personal observations and the current study (see Appendix 1) indicate it is widespread and moderately common within the northern jarrah forest study area.
Cercartetus concinnus	western pigmy-possum	Recorded from the Darling Plateau (Loaring, 1954) outside the current study area. It was described as 'moderately common' in jarrah and wandoo woodlands in the mid-1980s (Dell, 1983). Personal observations and the current study indicate it is widespread and moderately common within the northern jarrah forest study area.
Tarsipes rostratus	honey possum	Known to be present in the northern jarrah forest (personal observations) but infrequently recorded, despite being reported as *"moderately common"* on the Darling Scarp (Dell, 1983). Its presence is strongly associated with heath (Dell, 1983; Renfree, 2008) and it was described by Renfree (2008) as *"common only on the coastal sandplain heaths of south-western Western Australia"*. It was described by Nichols and Muir (1988) as *"almost non-existent in normal jarrah forest"*, which presumably is a reference to jarrah forest without the presence of heath, where nectar may be less abundant. It was recorded infrequently in the current study, at low numbers and at only three of the 55 trapping grids (Appendix 1).
Trichosurus vulpecula hypoleucus	brushtail possum or western brushtail possum	Anecdotally considered to be widespread within the northern jarrah forest and known to be present on the Darling Scarp (Dell, 1983; Dell and How, 1988). Studies have examined the availability of tree hollows in the jarrah forest generally, inclusive of the northern jarrah forest (Abbott and Whitford, 2001), however, there are no published accounts on brushtail possum demographics from the northern jarrah forest. Population studies (Wayne, 2005; Wayne *et al.*, 2005) have been carried out in the southern jarrah forests. Personal observations and the current study indicate it is has a patchy distribution within the northern jarrah forest study area and abundance varies considerably.

(cont. …)

Table 5.1 (… cont.)

Species	Common name	Source and comments
Macropus irma	western brush wallaby	Regularly and frequently recorded in the northern jarrah forest (personal observations).
Setonix brachyurus	quokka	Historically occurred widely throughout south-west WA (de Tores *et al.*, 2007). Populations within the northern jarrah forest are now restricted to densely vegetated creek lines with a mosaic of recently burnt and long unburnt *Taxandria linearifolia* (Hayward *et al.*, 2008; Hayward *et al.*, 2007). These populations are thought to be the terminal remnants of a collapsing metapopulation (Hayward *et al.*, 2003).
Hydromys chysogaster	water rat	Reported as occurring on the Darling Plateau (Dell and How, 1988) outside the current study area. The geographic range includes the northern jarrah forest (Olsen, 2008) and it was reported as inhabiting freshwater steams in the western zone of the forest (Nichols and Muir, 1988), however its presence in the northern jarrah forest was not specifically stated and the authors noted no detailed studies [of water rat habitat] have been carried out in the jarrah forest. It was not recorded by Hayward (2002) when he trapped quokka habitat (freshwater swamps) within the northern jarrah forest. It was not detected in the current study (Appendix 1), however this may reflect the absence of trapping in the immediate vicinity of freshwater streams.
Rattus fuscipes	bush rat	Despite being described as *"widespread along the forested coast and ranges"* (Lunney, 2008), this does not appear to be the case in WA. It was not included in the list of mammalian fauna from the Darling Scarp (Dell, 1983; Dell and How, 1988), was not recorded in the current study and may be absent from the northern jarrah forest.

5.2 Materials and methods

5.2.1 Trapping grids, site selection, trapping regime and trapping protocols

The allocation of treatments is described in Section 2.2 (The experimental treatments) and Section 2.3 (Constraints). Selection of the trapping grids (Fig. 5.1), or sites, within each treatment was not random and was largely determined by the requirement to ensure all trapping grids were outside areas scheduled for bauxite and gold mining for the anticipated duration of the study. Similarly, extensive negotiation with CALM/DEC planning and operational staff was required to ensure each trapping grid was quarantined, within a buffer zone, from timber harvesting and from any planned burn for the duration of the study (see Fig. 5.2). Notwithstanding the requirement to maximise the distance between grids to reduce the potential for loss of independence, trapping grid selection was also designed to ensure grids representatively captured the diversity of dominant overstorey eucalypt species, the diversity of vegetation structure and the diversity of management history (timber harvesting and fire management histories). Site selection used CALM/DEC records on fire history and harvesting, followed by aerial photograph interpretation and extensive ground-truthing to ensure adequate coverage of habitat heterogeneity.

Fifty five 'integrated' trapping grids were established within the study area, with 16, 14, 13 and 12 grids established in each of the two, four and six baitings per year treatment groups and the unbaited treatment group, respectively (Fig. 5.1). Grids were termed 'integrated' as each was comprised of:

- 25 wire cage traps (59 x 21 x 20cm) (Sheffield Wire Products, Welshpool, WA) placed at 80 x 80m spacing, forming a grid of 102,400m^2 (10.24ha);
- 15 medium size Elliott traps (33 x 10 x 9cm) (Elliott Scientific Equipment, Upwey, Victoria), placed at 80 x 40m spacing, forming a grid of 25,600m^2 (2.56ha); and
- 15 pitfall traps (see description below), placed at 40 x 20m spacing, forming a grid of 6,400m^2 (0.64ha).

All grids (Wire cage, Elliott and pitfall) were centred at the same point (trap locations (C 03, G 03 and Y 03, Fig. 5.2), with the smallest grid (pitfall traps) overlaid by the larger grid (Elliott traps), which was overlaid by the largest grid (wire cage traps). Trap locations were numbered A 01 to E 05 for wire cage traps, F 01 to H 05 for Elliott traps and X 01 to Z 05 for pitfall traps (Fig. 5.2).

Trapping was carried out for four consecutive nights on each of six trapping sessions in Winter 1998, Spring 1998, Summer 1998/99, Autumn 1999, Winter 1999 and Spring 1999. Wire cage traps and Elliott traps were positioned to minimise exposure to direct sunlight. Each wire cage trap was partially covered with a heavy gauge hessian bag to provide protection from sunlight and rain. Each Elliott trap was fitted two small clips, one at each end, which acted as a locking mechanism (Johnson, 1996), to prevent trapped animals from opening the trap from inside. Each Elliott trap was covered with light weight hessian during summer, autumn and spring. In winter, and when trapping during periods of rain, each Elliott trap was placed in a plastic bag which covered most of the trap and left the trap entrance uncovered. In winter trap alignment was with the trap opening facing down-slope to prevent rainwater accumulating in the plastic bag and flooding the trap. A small piece of cotton wool was placed inside each Elliott trap to provide warmth and/or insulation for each trapped animal. Elliott and wire cage traps were baited with a mixture rolled oats, peanut butter, honey and sardines (cat food). The bait was replaced after day two of each trapping session and as otherwise required.

Each pitfall trap consisted of a 20 litre bucket and a seven metre long, 33cm high fibreglass drift fence (fly screen). A hole was dug at each pitfall trap location and was sufficiently deep to enable the bucket to be placed upright in the hole, with the open end of the bucket level with the surrounding mineral earth. Each bucket was secured by replacing and compacting the excavated soil around the outside of the bucket. The drift fence was then held vertically, lightly strained and placed to ensure it passed over the centre of the bucket. A small section of the drift fence was cut where it traversed the centre of the open pit (bucket). This facilitated pitfall trap lid removal and replacement. The lower 2-5cm section of the fence was buried and the fence was held upright with wire stakes. Pitfall traps were opened (lids removed) at each trapping session when wire cage and Elliott traps were set. A polystyrene tray (approximately 12 x 15cm) was placed within each pit when opened, as was a section of corrugated cardboard (part of a cardboard egg carton) to provide protection from the weather for any trapped animal. The polystyrene tray also acted as a float if the bucket accumulated rainwater. Pitfall traps were closed between trapping sessions.

Traps were cleared within two hours of first light each day. The morphometric data collected and recorded for each species or group of species is listed in Table 5.2. Each individual was marked (Table 5.2) and released at its capture location, immediately after collection of morphometric data and marking. Exceptions to this were when woylies and brushtail possums were held for radio-collaring. In these cases each radio-collared animal was released on the evening of its capture.

Figure 5.1 The location of the 55 trapping grids, trapped to determine presence of the suite of small and medium size mammals and the suite of reptilian species in the northern jarrah forest, south-west Western Australia.

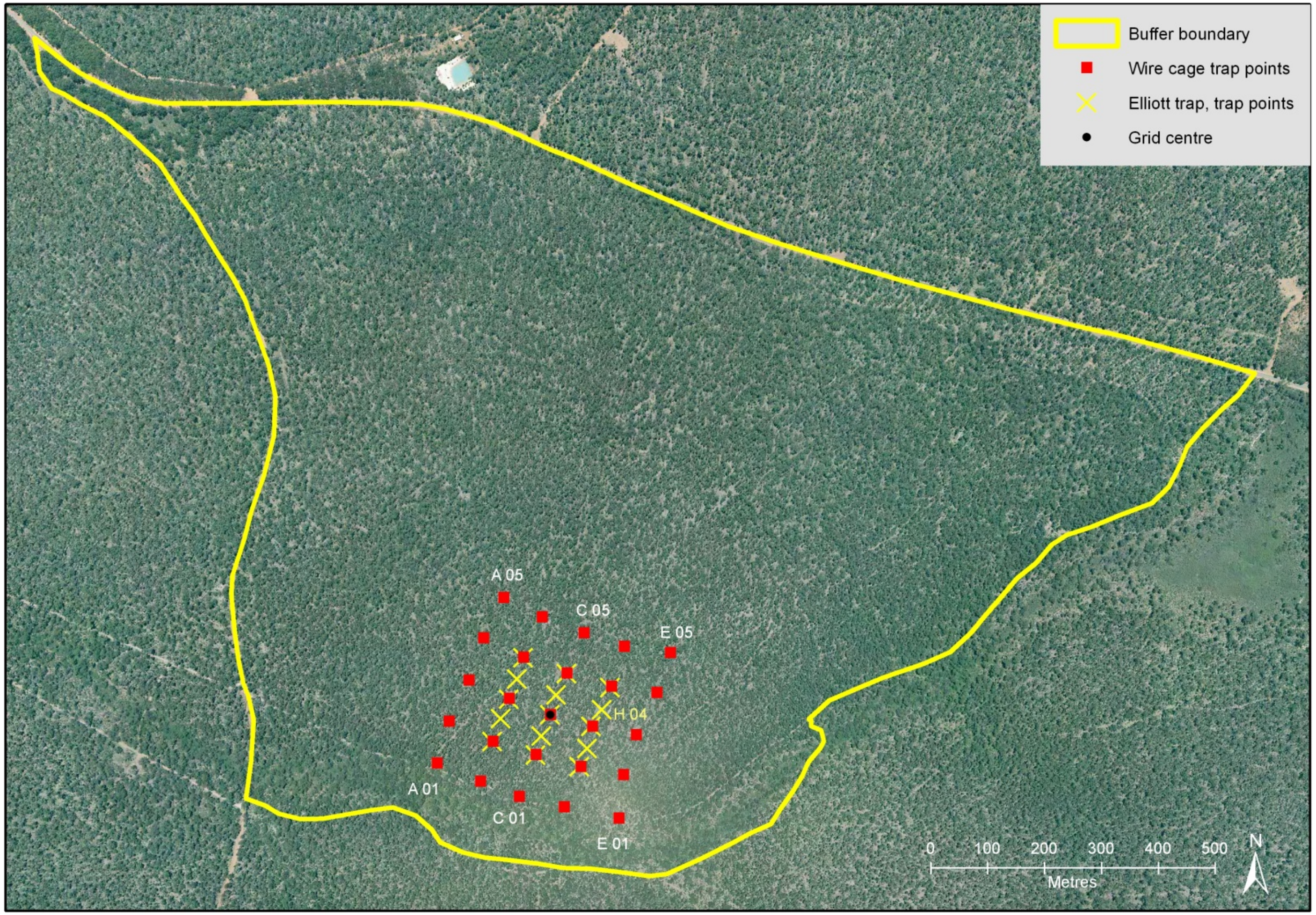

Figure 5.2 Orthophotograph showing the Twenty Six Mile Road trapping grid, the grid design and the relative positions of wire cage and Elliott traps used at each of the 55 fauna trapping grids trapped as part of Operation Foxglove in the northern jarrah forest, south-west Western Australia.

The buffer zone at each grid was quarantined from timber harvesting and planned burns for the duration of the study. Wire cage trap points were numbered A 01 to E 05, Elliott trap points were numbered F 01 to H 05 and pitfall trap points (not shown) were numbered X 01 to Z 05. All trap types were present at the grid centre (C 03, G 03 and Y 03).

Table 5.2: The marking system used to identify individual animals and the morphometric data recorded for each new and recaptured mammal, reptile and amphibian within the northern jarrah forest, south-west Western Australia.

Species or group of species	Marking system and unique identifier	Morphometric data collected
Mammals with a unique identifier allocated by treatment, e.g. Bp M6024, for the 24th (024) male (M) *Bettongia penicillata* (Bp) within the six (6) baitings per year treatment group: *Bettongia penicillata*; *Dasyurus geoffroii*; *Isoodon obesulus*; *Phascogale tapoatafa*; and *Trichosurus vulpecula hypoleucus*.	A Trovan® microchip was implanted subcutaneously, dorsally between the shoulder blades; and A 5mm diameter ear tissue biopsy was taken and served as an external marker indicating a microchip had been implanted. Males were punched in the right ear at position number 2, females, in the left ear, position number 20 (Fig. 5.3A).	Females: ○ pouch examined for presence of young and, for *Isoodon*, *Dasyurus* and *Phascogale* the number of young was also recorded. The sex of the pouch young was determined only if it was considered non-invasive and the approximate size (mm) and status (e.g. naked, furred etc.) of the young recorded; and ○ number of teats, if teats were elongated and if the animal was lactating. Males: ○ status of testes (undeveloped, developed small, developed). Males and females: ○ general condition, fur loss, scars etc.; ○ weight (g); and ○ pes (long pes), (mm).
Mammals with a unique identifier allocated by trapping grid, e.g. Af M Geo 003 for the 3rd (003) male (M) *Antechinus flavipes* (Af) from the George (G) trapping grid: *Antechinus flavipes*; *Cercartetus concinnus*; *Mus musculus*; *Sminthopsis dolichura*; *S. gilberti*; *S. griseoventer*; *Rattus fuscipes*; *R. rattus*; and *Tarsipes rostratus*.	A 1mm diameter ear tissue biopsy was taken to indicate the animal number at each trapping grid. For example Af M Geo 003 was ear punched at the number 3 position (Fig. 5.3A). The ID allocated to *Sminthopsis gilberti* and *S. griseoventer* were differentiated by the additional letter "i" or "r" respectively, e.g. Sgi F Geo 089 or Sgr F Geo 089	Female dasyurids, *Cercartetus* and *Tarsipes*: ○ pouches were examined for the presence of young and the number and sex of young. The latter only if it was non-invasive. The approximate size (mm) and status (e.g. naked, furred etc.) was recorded; and ○ number of teats, if teats were elongated and if the animal was lactating. Males: ○ status of testes (undeveloped, developed small, developed). Males and females: ○ general condition, fur loss, scars etc.; ○ weight (g); and ○ head-body length and tail length (mm) for all *Sminthopsis* spp and *Rattus* spp

(cont. …)

Table 5.2 (… cont.)

Species or group of species	Marking system and unique identifier	Morphometric data collected
Amphibians and reptiles	A toe clip (Fig. 5.3B).was taken to indicate the animal number at each trapping grid for skinks, geckoes, agamids and amphibians, or within each treatment for varanids. For example, Mo Wea 099 for the 99th (099) *Morethia obscura* (Mo) from the Wearne (Wea) trapping grid; Vg 6013 for the 13th (013) *Varanus gouldii* (Vg) form the six (6) baitings per year treatment group. Blind snakes, legless lizards and elapids were released unmarked. Pythons were held for a concurrent research project (Pearson, 2002) if required, otherwise were released unmarked.	Each amphibian and reptile was: ○ weighed; ○ general condition assessed, e.g. scale damage, tail damage, scars etc. noted; ○ snout-vent length (reptiles and amphibians) measured (mm); and ○ head-tail length (reptiles) measured (mm).

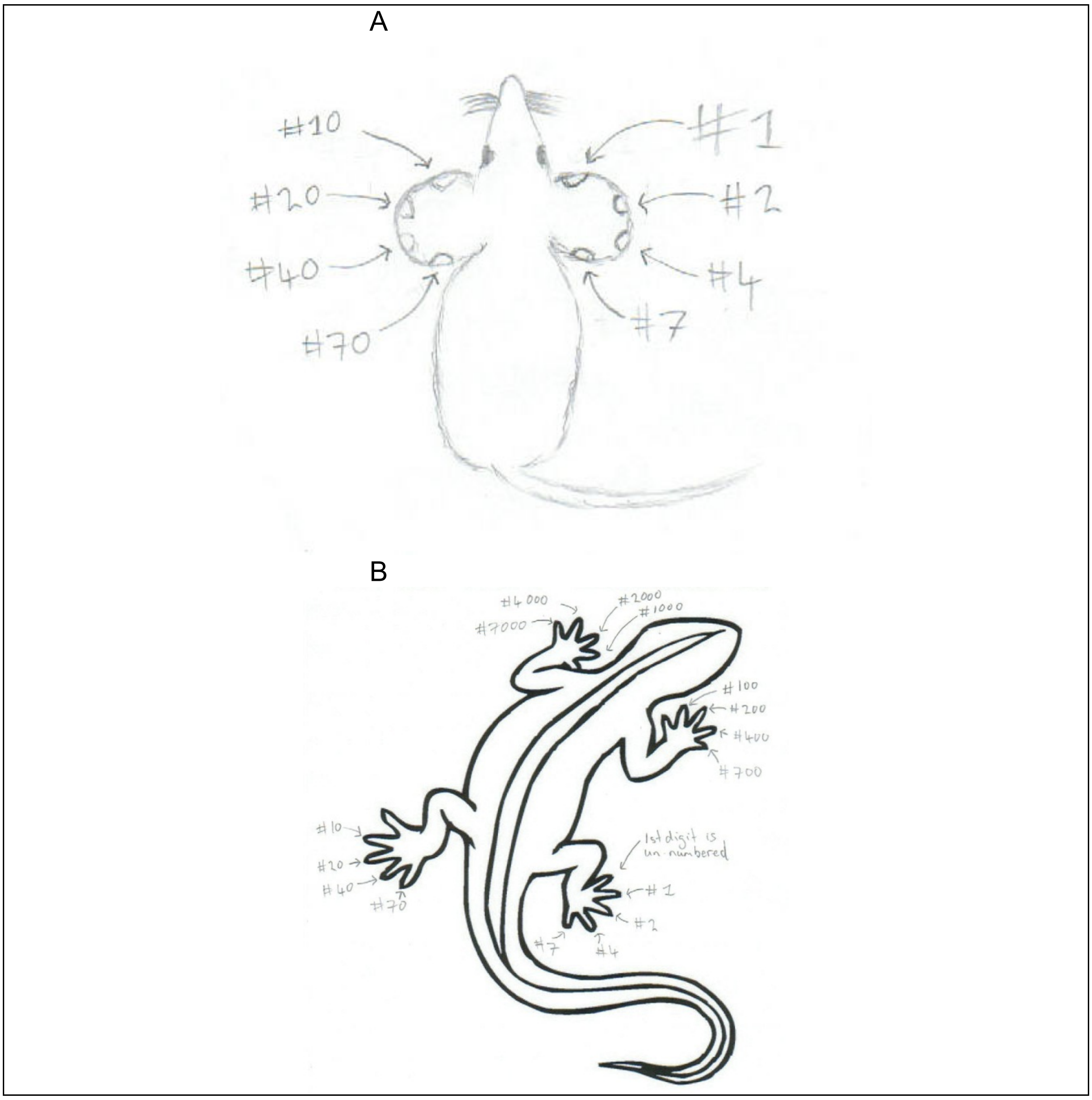

Figure 5.3 The system used to mark and allocate a unique identifier to fauna trapped as part of Operation Foxglove research in the northern jarrah forest of south-west Western Australia.

A: Ear punch (biopsy) locations for mammals.

B: Toe clip positions for reptiles and amphibians.

A maximum of two ear biopsies are taken or two toes clipped from each ear or foot, respectively.

To identify as individual number:

001	position # 1 is biopsied, or toe # 1 clipped
002	position # 2 is biopsied or clipped
003	positions # 1 & 2 are biopsied or clipped
004	position # 4 is biopsied or clipped
005	positions # 4 & 1 are biopsied or clipped
006	positions # 4 & 2 are biopsied or clipped
007	position # 7 is biopsied or clipped
008	positions # 7 & 1 are biopsied or clipped
009	positions # 7 & 2 are biopsied or clipped
010	position # 10 is biopsied or clipped
011	positions # 10 & 1 are biopsied or clipped, etc.

5.2.2 Habitat assessment at trapping grids

Each integrated trapping grid covered an area of approximately 10.2ha and, although the vegetation structure within each grid appeared superficially homogenous, there was a varying degree of structural heterogeneity and/or habitat heterogeneity, within and between grids (sites). The 'between-site' habitat heterogeneity and, to a lesser extent, the 'within-site' heterogeneity, is likely attributable to a suite of factors including climate and geomorphology. Forest management practices, particularly silvicultural practices, timber harvesting, prescribed burning and the roading activities associated with these activities, have imposed several additional layers of complexity to this heterogeneity.

Historical and contemporary CALM/DEC records enabled broadscale delineation of strata based on dominant overstorey vegetation, fire history and timber harvesting history. Similarly, Alcoa and Worsley mining records were used to identify areas previously mined and subject to post-mining rehabilitation. Rehabilitation areas, areas proposed for mining, or proposed for pre mining vegetation clearing during the life of the study, were excluded from those sites potentially available to establish trapping grids.

Although the fire history and timber harvesting records were used to identify burn and harvesting boundaries at the logging coupe and forest block scale, the mosaic resulting from any given burn and harvesting operation resulted in considerable heterogeneity within each burn and harvesting operation boundary. Consequently, there was insufficient detail at the scale of the trapping grids to confidently categorise trapping grids by their documented logging and fire history alone. Therefore, each trapping grid was individually assessed to quantify the extent of habitat heterogeneity.

The floristics and vegetation of the northern jarrah forest have been well studied in relation to climate and geomorphology, largely as a result of the history of use of the jarrah forest for commercial timber harvesting, bauxite mining and gold mining. Consequently, there is a wealth of information on the forest structure, at least at the macro scale (see for example Havel, 1975a; 1975b; Havel, 2000; Heddle, 1979; Heddle *et al.*, 1980; Mattiske and Havel, 1997; 1998). Havel (1975a; 1975b) developed the concept of site-types, now referred to as Havel site-types (see Section 2.1.4), to describe the continuum of vegetation of the jarrah forest and to reflect the subtle changes in plant species, soil nutrients and position in the landform (Bell and Heddle, 1988; Heddle, 1979). The Havel site-type classification system uses a subset of the canopy and understorey species to identify and map 19 unique site-types. Full descriptions of each are given in Havel (1975a; 1975b). Combinations of these site-types are also recognised.

Havel site-types were identified (Mattiske Consulting, unpublished) and mapped at each of the 55 trapping grids. An example of site-types present within a trapping grid is shown in Figure 5.4. Each site-type was representatively sampled to assess habitat characteristics. Sample points were established at the location of wire cage trap points (A 01 to E 05, Fig. 5.2), or more specifically, as close to each trap point as possible but avoiding areas of trampled vegetation associated with repeat visits to each trap point. The number of sample points within each site type was determined by the number of trap points within each mapped site-type (Table 5.3). For example, at Jarrick Road trapping grid (Fig 5.4), two trap points were in site-type D (lower slope jarrah), 13 in site-type P (jarrah and sheoak) and 10 in site-type S (jarrah and bull banksia, *Banksia grandis*). Therefore, one sample point was assessed within site-type D, and three within each of site-type P and S. The data collection protocols for each variable with the potential to influence fauna presence (and abundance) are given in Table 5.4.

The variable '*fuel age*' (Table 5.4) was obtained from CALM/DEC records for the number of years since the last known burn. This is generally considered to reflect the extent of accumulated fuel (combustible ground cover), however, this single figure value is recorded for the total extent of the last know burn and does not reflect the complex post-fire mosaic of vegetation at the scale required to assess habitat used by most small to medium sized fauna species. The habitat attributes (Table 5.4 and Table 5.5) which were considered to better reflect fire history, or at least the effects from the most recent fire, were: the depth of leaf litter; the extent of ground cover; the understorey cover; and the number of fallen logs within the small and large fallen log category (Table 5.4). Data on the number of stems ≥2.5cm diameter for each of the dominant or co-dominant overstorey species, combined with the number of stems within each of the four categories veteran, pile, pole and sapling (Table 5.5), were considered to reflect the timber harvesting history. To some extent, harvesting history was also expected to be reflected in the understorey attributes of percentage shrub cover (above and below 0.5m), the number of standing stumps and the number of fallen logs in the category 'circumference >127cm'. If present, evidence of coppicing was also recorded for *Corymbia* and each of the eucalypt species. Similarly as part of a concurrent study assessing den tree use by brushtail possums (de Tores *et al.*, unpublished-b), a modified version of the eight categories of 'tree form' described by Whitford (2002) was used to classify each stem into one of 10 categories (Appendix 2).

Table 5.3: The criteria to determine the number of vegetation sample points assessed within each identified Havel site-type at each trapping grid within the northern jarrah forest, south-west Western Australia.

Points A01 to E05 refer to the 25 wire cage trap points (Fig. 5.2)

Number of trapping points (A 01 to E 05) within each site-type	Number of sample points established within the mapped site-type
1-4	1
5-8	2
9-15	3
16-24	4
25	5

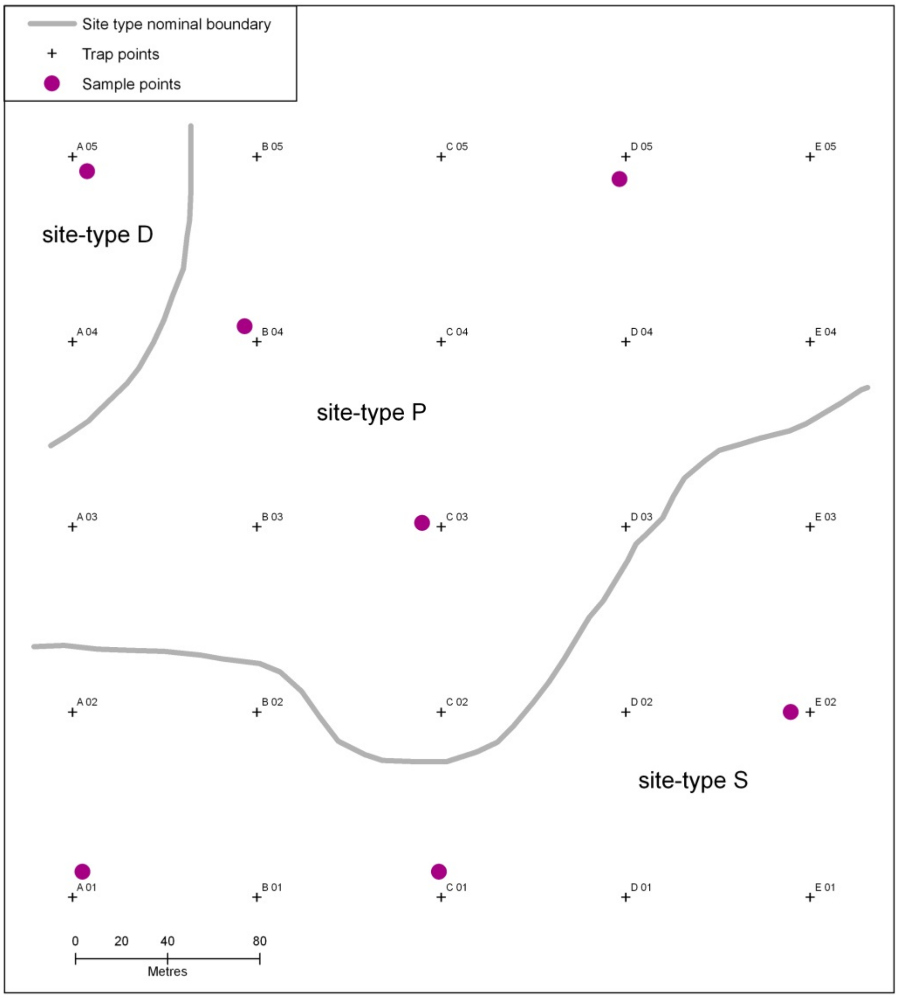

Figure 5.4: An example of Havel site-type mapping and vegetation sample site locations at the Jarrick Road grid, within the northern jarrah forest, south-west Western Australia.

Site-type D: lower slope jarrah (*Eucalyptus marginata*)
Site-type P: jarrah and sheoak (*Allocasuarina fraseriana*)
Site-type S: jarrah and bull banksia (*Banksia grandis*).

Table 5.4: The site specific habitat variables, protocols for data collection and how the data were used in occupancy modelling for 55 fauna trapping grids within the northern jarrah forest, south-west Western Australia.

See text, Table 5.3 and Fig. 5.4 for the explanation of ‘sample point’ and ‘trap point’.

Habitat attribute	Data collection protocol	Occupancy modelling covariate and syntax
Leaf litter depth	At each sample point, litter depth (mm) was recorded at four points, once in each of the four quadrants of a 1 x 1m quadrat placed approximately 5m (to avoid trampled areas) from the trap point.	The mean of the sample point values for each grid was used as the covariate value for: ‘*litter*’.
Ground cover	Recorded at each sample point as the percentage ground cover falling within one of six ordinal categories (1-6) of 0, <10, 10-30, 31-50, 51-70 and >70% for each of:	The mean of the sample point values for each grid was used as the covariate value for:
	bare earth;	‘*earth*’;
	rocks;	‘*rock*’;
	leaf litter, fallen sticks or woody debris;	‘*debris*’; and
	herbs or forbs.	‘*forbs*’.
Understorey or shrub cover	Recorded at the sample point as the percentage shrub cover, for all shrubs combined, falling within one of six ordinal categories (1-6) of 0, <10, 10-30, 31-50, 51-70 and >70%, for shrubs:	The mean of the sample point values for each grid was used as the covariate value for:
	up to 0.5m; and	‘*shrubs_b’*
	above 0.5m.	‘*shrubs_a’*
Fallen logs	Recorded at each sample point as the number of fallen logs with a circumference:	The total count for each trapping grid was used as the covariate value for:
	≥ 60cm and up to 127cm; and	‘*small_logs*’
	>127cm.	‘*large_logs*’
Tree stems in jarrah, marri and wandoo	The number of stems (trees), tree height and DBHOB of the dominant overstorey species; jarrah (jar), marri (mar), wandoo (wan), blackbutt (bla) (*E. patens*) and flooded gum (rud) (*E. rudis*), within 10m of each sample point and with a diameter ≥2.5cm and classed as a veteran (vet), pile (pil), pole (pol), or sapling (sap). See Table 5.5 for definition categories.	The total count for each trapping grid was used as the covariate value for: ‘*jar_vet’*; ‘*jar_pil*’; ‘*jar_pol*’; ‘*jar_sap*’ ‘*mar_vet*’ ‘*mar_pil*’; ‘*mar_pol*’; ‘*mar_sap*’; ‘*wan_vet*’; ‘*wan_pil*’; ‘*wan_pol*’; ‘*wan_sap*’ ‘*pat_vet;*’ ‘*pat_pil;*’ ‘*pat_pol;*’ ‘*pat_sap;*’ ‘*rud_vet*’; ‘*rud_pil*; ‘*rud_pol*’; ‘*rud_sap*’; ‘*bul_vet*’ ‘*bul_pil’* ‘*bul_pol*’ ‘*bul_sap*’

(cont. …)

Table 5.4 (… cont.)

Habitat attribute	Data collection protocol	Occupancy modelling covariate and syntax	
Overstorey and mid canopy species exclusive of jarrah, marri and wandoo	The total number of stems for overstorey species, exclusive of the dominant jarrah forest overstorey species jarrah, marri and wandoo, with a diameter ≥2.5cm and within 10m of each sample point. In addition to the eucalypts blackbutt, flooded gum, bullich, this included *Allocasuarina fraseriana* (western she oak) *A. huegeliana* (rock sheoak) *Banksia littoralis* (western swamp banksia) *B. grandis* (bull banksia) and *Melaleuca* spp (paperbarks). Several of these species included smaller forms which were classed as shrubs, below.	The total count for each trapping grid was used as the covariate value for:	
		Description:	Variable name:
		The number of *B. grandis* tree stems	*‘tree_B_gra’*
		The number of *Allocasuarina* tree stems	‘*tree_both_allo*’
		The total number of tree stems (incl. all *Banksia* & *Allocasuarina*)	‘*tree_tot*’
Shrub species	The total number of shrub stems within 10m of each sample point and with a diameter ≥2.5cm. This is in addition to the ordinal values assigned to the shrub cover for the variables *shrubs_a* and *shrubs_b*, described above. The dominant shrub species included *Persoonia longifolia* (long-leaf persoonia or snottygobble), *Mirbelia dilatata* (holly-leaved mirbelia), *Hakea undulata* (wavy-leaved hakea), *Hovea trisperma* (common hovea), *Banksia sessilis* (parrot bush) and *Acacia saligna* (golden wattle). The latter two species also occur as a small tree. *Xanthorrhoea preissii* (Balga grass tree) and *X. gracilis* (graceful grass tree), monocotyledons and probably technically not a shrub, were included in the total shrub count.	The total count for each trapping grid was used as the covariate value for:	
		Description:	Variable name:
		The number of *Banksia* shrub stems	‘*shrubs_ban*’
		The number of *Allocasuarina* shrub stems	‘*shrubs_alloc*’
		The number of *Hakea* shrub stems	‘*shrubs_hak*’
		The total number of shrub stems (incl. all *Banksia* , *Hakea* and *Allocasuarina* and *Xanthorrhoea*)	‘*shrubs_tot*’
Stumps	The number of standing cut or senescing or dead stumps within 10m of each sample point was recorded, irrespective of species.	The total count for each trapping grid was used as the covariate value for: ‘*stumps*’	
Presence of *Phytophthora cinnamomi*, dieback	Dieback presence was identified from the mapped areas termed disease risk area (DRA) in CALM/DEC's GIS corporate data. Dieback was assumed absent in DRA and assumed present in all areas outside DRA.	Dieback was coded as a binary individual covariate, 1 for presence (outside DRA), 0 for presumed absence (within DRA): ‘*Pc*’	
Annual rainfall	The annual rainfall for each grid was obtained from the rainfall isohyet layer from CALM/DEC's GIS corporate data.	Each grid was given the value of the closest (distance) rainfall isohyet when isohyets were plotted at 100 mm intervals: ‘*rain*’	
Fuel age	The years since the last known wildfire or hazard reduction burn. Data obtained from CALM/DEC's fuel age records.	‘*age*’	

Table 5.5: Description of each size category used to describe overstorey and mid-storey species during vegetation sampling at sample-points in each identified Havel site-type within each of 55 fauna trapping grids within the northern jarrah forest, south-west Western Australia.

Category	Description
Sapling	Stem with circumference >2.5cm and up to 50cm (16cm diameter).
Pole	Stem >50cm circumference (16cm diameter) and up to 140cm in (up to 44.5cm diameter).
Pile	Stem >140cm in circumference (>44.5cm diameter), with a healthy crown, some senescence usually present.
Veteran	Stem >140cm in circumference (>44.5cm diameter), with stagnating crown.

5.2.3 Data analysis: the modelling strategy

Analysis of trapping data used the '*Robust Design Occupancy with psi(1), gamma, epsilon*' option in Program MARK (Cooch and White, 2019; White, 2001; 2020) which models the probability of occupancy (ψ) and detection (p) and has the option to parameterise for the probability of an occupied site becoming unoccupied or locally extinct (ϵ) and conversely, the probability of an unoccupied site becoming occupied (γ). The robust design assumes population closure within trapping sessions with no assumption of population closure between trapping sessions. The Robust Design Occupancy model also estimates the derived parameter for the ratio of consecutive occupancy rates (λ).

The exploratory analysis constrained occupancy by treatment group, $\psi(\mathrm{g})$. Detection probability (p) was modelled with and without a seasonal effect, ($season_t$) and (*season.*), respectively; and with and without a daily effect (i.e. within each trapping session), ($session_t$) and (*session.*) respectively. Seven combinations were modelled, namely where *p* was:

(i) allowed to vary for each treatment group and between and within seasons (the latter means allowed to vary each day within each trapping season), $\psi(\mathrm{g})$ $p(g, season_t, session_t)$; or

(ii) allowed to vary for each treatment group and between each season and constant within each trapping session, $\psi(\mathrm{g})$ $p(g, season_t, session.)$; or

(iii) allowed to vary for each group between each season but with the same probability of detection for Winter 1998 and Winter 1999, and for Spring 1998 and Spring 1999, and constant within each trapping session $\psi(\mathrm{g})$ *p*(*g, season$_{t\ winter,spring}$, session.*); or

(iv) allowed to vary for each group but constant for all seasons and constant within each trapping session; $\psi(\mathrm{g})$ *p*(*g, season., session.*); or

(v) allowed to vary for each group and between and within seasons but the same probability of detection for Winter 1998 and Winter 1999, and for Spring 1998 and Spring 1999, and allowed to vary each day within each trapping session $\psi(\mathrm{g})$ *p*(*g, season$_{t\ winter,spring}$, session$_t$*); or

(vi) constant for each group and varying between seasons but again with the same probability of detection for Winter 1998 and Winter 1999, and for Spring 1998 and Spring 1999, and constant within each trapping session $\psi(\mathrm{g})$ *p*(*g.*, *season$_{t\ winter,spring}$, session.*), or

(vii) constant for each group between and within trapping seasons, $\psi(\mathrm{g})$ *p*(*g.*, *season., session.*).

The exploratory analysis also included modelling of the parameters for the probability of an occupied site becoming unoccupied or locally extinct (ε) and the probability of an unoccupied site becoming occupied (γ). Therefore, each of the above models was fitted with both parameters, ε and γ, which either:

(a) varied between groups and varied within each season (ε (*g*)*season$_t$*), (γ (*g*) *season$_t$*); or

(b) varied between groups and were constant within each season (ε (*g*) *season.*) (γ (*g*) *season.*); or

(c) were constant between groups and constant within each season $\varepsilon(.)$, $\gamma(.)$.

The preferred model from the exploratory analysis was then parameterised for comparison of the set of candidate models by placing additional constraints on occupancy $\psi(g + covariate)$ and with further constraints on detection $p(g + covariate)$. The number of candidate models for each species varied in accordance with the species biology, or more specifically, with the information known, available on, and/or inferred from the biology and ecology of each species. Not all combinations of variables were modelled and only biologically plausible models were included in each candidate set. A confidence model set, comprised of models with a ΔAICc with 4 units of the preferred (AICc best) model, was then used for model averaging. The confidence model set excluded models considered non-competitive, as described in Chapter 3 and Chapter 4, i.e. where the 2-unit penalty of adding an additional parameter was not compensated with an increase in model fit.

A Spearman correlation analysis (StataCorp, 2006) was used to identify correlated variables, as the Spearman correlation can also assess correlations between ordinal, categorical variables and is less sensitive to outliers. In the absence of outliers, a Spearman correlation is similar to a Pearson correlation. The only non-ordinal categorical variable was the variable for the presence of dieback (*Pc*) and was therefore not included in the correlation analysis. The variables for all size classes for flooded gum (*E. rudis*), i.e. *rud_vet*, *rud_pil*, *rud_pol* and *rud_sap*, were excluded from all models and from the correlation analysis as there was only one, zero, one and one record for each variable, respectively. Similarly, the variables *wan_pil*, *bla_vet* and *bla_pil* were excluded from the correlation analysis and all models as there was only one, ten and four records respectively. The variables *wan_vet* (39 records) and *wan_pol* (183 records) were highly correlated, with a Spearman (*rho*) value of 0.822. Both variables were *a priori* considered potentially important to the brushtail possum because of the hollow bearing potential of wandoo in both size classes (see below). Although both variables (*wan_vet* and *wan_pol*) were used in the candidate model set, only one was used in any given model. The variables *tree_tot* and *tree_B_grandis* for the total number of stems and the number of *Banksia grandis* stems, respectively, were correlated with Spearman (rho) value of 0.823. As for the variables *wan_vet* and *wan_pol*, only one of these was used in any given model.

5.2.4 The candidate models to describe occupancy for the brushtail possum

The brushtail possum is a facultative user of tree hollows and, within the northern jarrah forest, has been recorded using tree hollows in overstorey vegetation of jarrah, marri, wandoo, blackbutt (*E. patens*) and rudis within the height/ size category of ‘veteran’ and ‘pile’ (de Tores *et al.*, unpublished-b). Both categories include eucalypt species with a circumference at breast height >140cm (diameter >44.5 cm) and differ only in the condition of the crown. Unlike jarrah, marri, blackbutt and flooded gum which are not hollow bearing in the size category ‘pole’, wandoo commonly is (both species, *E. wandoo* and *E. accedens*), with stems as small as 21.9 cm in diameter recorded as hollow bearing and known to be used by brushtail possums (de Tores *et* *al.*, unpublished-b). Although size class (Table 5.5) alone was considered likely to influence occupancy, size class, crown condition and tree form (see Appendix 2) were also considered likely to work in concert and increase the probability of occupancy, i.e. larger tress with a senescing crown and a senescing tree form were considered likely to provide suitable denning habitat.

In recognition of the brushtail possum's known use of tree hollows, and its known diet and foraging habits (see How and Hillcox, 2000; Kerle, 1983; Kerle and Howe, 2008), the candidate models incorporated different combinations of variables potentially reflecting denning use and foraging habits (Table 5.6). The candidate models were based on the exploratory analysis which identified the preferred model as that which constrained detection (*p*) as different for each group, constant between seasons and constant within each trapping session; i.e. model (iv) above: $\psi(\mathrm{g})$ *p*(*g, season., session.*); and which further allowed both ε and γ to vary between groups but remain constant between seasons; option (b) above: (ε (*g*) *season.*) (γ (*g*) *season.*). However, the parameter estimate of ψ for the six baitings per year treatment (group 3) was unrealistic and indicated a lack of convergence. Similarly, the estimate was also unrealistic for the ε parameter for the same treatment group for all 'between-season' periods and for the ε parameter for treatment group 1 (the two baitings per year treatment group) for all 'between-season' periods (Table 5.7). The unrealistic parameter estimate for the six baitings per year treatment group, group 3, (approaching the zero boundary, $\psi g3 = 0.345 \times 10^{-7}$) is not surprising, as brushtail possums were detected infrequently and in fewer trapping grids than in the other treatment groups.

The pattern of an unrealistic parameter estimate for group 3, describe above, was repeated in all candidate models of the exploratory analysis. The analysis also often produced models with unrealistic estimates for other parameters. The model with the least issues in terms of unrealistic parameter estimates was also based on model (iv) above, but with the parameters ε and γ held constant between groups and constant between seasons $\varepsilon(.)$, $\gamma(.)$ (i.e. option (c), above). However, the parameter estimate for ψ for group 3 (and its standard error and therefore upper and lower confidence intervals) was still unrealistic. The most pragmatic solution was to use the model with the parameters ε and γ held constant between groups and constant between seasons (i.e. model $\psi(\mathrm{g})$ $\varepsilon(.)$ $\gamma(.)$*p*(*g, season., session.*), and address the issue of the unrealistic estimate for parameter ψ for group 3 by either:

(i) setting the value (fixing the parameter value); or

(ii) using the Profile Likelihood option to compute the ‘profile likelihood confidence interval’; or

(iii) using a set value as the starting value for the MLE.

All options were compared (see discussion), with option (i) producing the only realistic estimate (albeit a pre-determined and set option) of ψ for group 3. The fixed or set value for ψ_{group3} was 0.001 in recognition of the lower 95% CI value (zero) when the value was not set and that there were no brushtail possum captures at all in this group (the six baitings per year treatment group) in the first season.

Table 5.6: The variables used singly and in combination and the rationale for inclusion of each in the candidate models to describe occurrence of the brushtail possum (*Trichosurus vulpecula hypoleucus*) from 55 fauna trapping grids within the northern jarrah forest, south-west Western Australia.

Variables were used separately and in combination to constrain the model ψ (*g*, *g*3=0.045,+*covariate*) ε (.) γ (.) p (*g*+*covariate*) (see text).

Variables, as described in Table 5.4 and Table 5.5, used independently or in combination.	Rationale
jar_vet, mar_vet, jar_pil, mar_pil	Stems (trees) in the categories of veteran and pile for overstorey species of jarrah, marri, wandoo and blackbutt have the potential to be hollow bearing.
wan_pol	This size class for wandoo has the potential to be hollow bearing. It may also enable access to larger den trees and/or may provide a food resource.
jar_pol, mar_pol, wan_pol	Stems in the category ‘pole’ for the overstorey species of jarrah, marri and blackbutt have the potential to enable access to larger den trees and/or may provide a food resource.
jar_sap, mar_sap, wan_sap, bla_sap	The presence of saplings for all eucalypts and marri may enable access to larger den trees and/or may provide a food resource and/or may facilitate predator avoidance and therefore have the potential to influence ψ and p.
stumps	The presence of stumps may reflect a history of timber harvesting and the potential for a reduced availability of den trees and therefore has the potential to negatively influence ψ. Conversely, and subject to tree form, the presence of stumps may also positively influence ψ by provision of a denning opportunity.
large_logs	The presence of large logs may provide a denning opportunity and facilitate predator avoidance and has the potential to influence ψ and p.

(cont. …)

Table 5.6 (… cont.)

Variables, as described in Table 5.4 and Table 5.5, used independently or in combination.	Rationale
shrubs_a, shrubs_b, shrubs_ban, shrubs_alloc, shrubs_hak, shrubs_tot	The presence of shrubs provide a potential food resource and may provide vegetative cover and therefore has the potential to provide a predation refuge and/or provide access to taller vegetation and facilitate predator avoidance, and therefore has the potential to influence ψ and p.
tree_B_gra, tree_both_allo	*Banksia grandis* and both commonly occurring large *Allocasuarina* have the potential to be a food source and provide access to larger den trees.
tree_tot	The total number of trees comprised largely of *Banksia grandis*, other banksias and *Allocasuarina* represents a potential food source and may provide access to larger den trees. Correlated with *tree_B_grandis*, see text.
litter	The diet of the brushtail possum is known to include carrion (personal observations) and invertebrates (personal observations and Inions, 1985). Litter, or the invertebrate fauna within the litter layer, provides a potential food resource.
earth, *rock*, *forbs*	Each of these variables represent areas of minimal or reduced vegetation cover and may be associated with increased foraging (foraging over a wider area) and each has the potential to increase predation risk and therefore influence p and/or ψ.
rain	Increased rainfall may be associated with increased food availability.
Pc	The effects of dieback are varied and can result in localised and larger scale loss of structural and floristic complexity. Presence of dieback may be associated with a decreased food resource. It may also be associated with less vegetative cover which may increase foraging areas and/or increase predation risk. It has the potential to influence both ψ and p.

Table 5.7: Parameter estimates for the probability of occupancy (ψ), detection (p), extirpation (ε) and colonisation (γ) from the exploratory analysis model (iv)(b) to describe occurrence of the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest of south-west Western Australia.

Extirpation (ε_t) is the probability that an occupied site in season/session *t* becomes unoccupied or locally extinct in season/session *t*+1.
Colonisation (γ_t) is the probability that an unoccupied site in season/session *t* becomes occupied or in season/session *t*+1.

This model, model (iv)(b), was not used for further analysis (see text).

Treatment group	Parameter	Parameter estimate	Std. Error	Lower 95% confidence interval	Upper 95% confidence interval
two baitings per year	ε	5.75E-11	5.07E-07	9.94E-07	9.94E-07
	γ	0.0323	0.0452	0.0211	0.2256
	ψ	0.1896	0.0986	0.0623	0.4516
	p	0.7384	0.0452	0.6407	0.8171
four baitings per year	ε	0.1493	0.0697	0.0565	0.3396
	γ	0.1744	0.0613	0.0839	0.3274
	ψ	0.2956	0.1249	0.1147	0.5763
	p	0.5817	0.0442	0.4934	0.6651
six baitings per year	ε	2.70E-19	1.40E-14	-2.73E-14	2.73E-14
	γ	0.2824	0.1134	0.1161	0.5410
	ψ	1.37E-11	1.26E-07	-2.46E-07	2.46E-07
	p	0.1079	0.0358	0.0551	0.2005
unbaited	ε	0.0735	0.0452	0.0211	0.2256
	γ	0.1647	0.0801	0.0593	0.3816
	ψ	0.5037	0.1454	0.2450	0.7605
	p	0.7502	0.0340	0.6780	0.8107

5.2.5 The candidate models to describe occupancy for the southern brown bandicoot

As with the brushtail possum, the preferred model from the exploratory analysis identified the model which constrained detection (*p*) as different for each group, and constant between and within seasons for each treatment group (model (iv) described in Section 5.2.3 above, i.e.: $\psi(\mathrm{g})$ *p*(*g, season., session.*) and which further allowed both ε and γ to vary between groups and remain constant between seasons; option (b) above (ε (*g*) *season.*) (γ (*g*) *season.*). Also as per the brushtail possum exploratory analysis, the ψ parameter estimate for one of the treatment groups (this time the unbaited treatment group) was unrealistic (with estimates for ψ = 0.5370, Std. Dev = 58.1818 and 95% CI of 0.74×10^{-200} to 1.0.) and again indicated a lack of convergence as misspecification as the MLE approached the boundary. However, the lower limit of the 95% CI (effectively zero) reflected the very few occurrences of bandicoot captures in the unbaited control with no captures in the first season. The parameter estimates for ε and γ for the unbaited treatment group were also unrealistic (95% CI for each was effectively from zero to one) as was the estimate for detection (p) in every trapping session for the unbaited treatment (again with 95% CIs for each session effectively from zero to one).

The pragmatic and most conservative option was to again set or 'fix' the value for ψ (this time for group 4, the unbaited treatment group) and parameterise as per the second ranked model from the exploratory analysis, with p varying between groups and constant for each group between and within each trapping season (option (iv) from Section 5.2.3, 'The Modelling Strategy') and to also hold ε and γ constant ($\varepsilon(.)$, $\gamma(.)$), i.e. constant between groups and constant within each season (i.e. option (c) above). The fixed or set value for ψ_{group4} was 0.001 in recognition of the lower 95%CI value (zero) when the value was not set and (as was the case for the brushtail possum in the six baitings per year treatment group) where there was no bandicoot captures at all in the unbaited treatment group in the first season. This model was then parameterised to constrain ψ and p with six covariates (Table 5.8) used singly and in combination.

Table 5.8: Variables used in the candidate models to describe the data for occupancy (ψ) by the southern brown bandicoot (*Isoodon obesulus*) at 55 trapping grids within the northern jarrah forest of south-west Western Australia.

Variables (covariates) were used separately and in combination to constrain the model: ψ (g, g4=0.001, $+_{covariate}$) ε (.) γ (.) p ($g+_{covariate}$).

Variables, as described in Table 5.4 and Table 5.5, used independently or in combination.	Rationale in relation to inclusion in models to describe the data for southern brown bandicoot occupancy
rain	Increased rainfall may be associated with increased food availability and has the potential to increase ψ.
Pc	The effects of dieback are varied and can result in localised and larger scale loss of structural and floristic complexity. As for the brushtail possum, presence of dieback may be associated with a decreased food resource. It may also be associated with less vegetative cover and may increase predation risk. It has the potential to influence ψ and p.
litter	The presence of a deep litter layer may increase availability of dietary items and increased nesting opportunities.
small_logs	An increase in the number of fallen logs with a circumference ≥60cm and up to 127cm has the potential to provide refuge from predation and provide nesting opportunities and may influence both ψ and p.
large_logs	An increase in the number of fallen logs with a circumference >127cm has the potential to provide refuge from predators or provide nesting sites, or both.
shrubs_tot	Potentially provides a food resource and an increase in the density of the shrub layer may also provide increased protection from predation. It has the potential to influence ψ and p.

5.3 Results

5.3.1 The fauna species trapped

The species detected (trapped at least once) at each trapping grid are shown in Appendix 1. As anticipated, not all species were trapped at every grid and the patterns of presence did not appear to be determined by the presence of 1080 baiting alone. Data analysis for occupancy modelling was restricted to the two medium size mammal species most frequently trapped during routine trapping sessions as part of the Western Shield program, the brushtail possum (*Trichosurus vulpecula hypoleucus*) and the southern brown bandicoot (*Isoodon obesulus*).

5.3.2 The brushtail possum

5.3.2.1 The brushtail possum: the preferred model

The variables (covariates) listed in Table 5.6 were used singly and in combination to constrain the model ψ (*g*, *g*3=0.045,+*covariate*) ε (.) γ (.) p (*g*+*covariate*). For all models, ε and γ were held constant with estimated values from the preferred model of 0.02 and 0.12, respectively (Table 5.9). Similarly, for all models, the probability of detection (*p*) was held constant between and within all seasons but varied between treatment groups. However *p* was constrained by different combinations of variables in each model. For the preferred model (Model 425, Table 5.9 and Table 5.10), and all models within the confidence model set, *p* was constrained by the variables *large_logs* (the number of fallen logs with a circumference >127cm), *mar_sap* (the number of marri saplings) and *shrubs_hak* (the number of *Hakea* spp. stems with a shrub form, within 10m of each sample point and with a diameter ≥2.5cm). The β coefficient was positive and significant in the classical sense (i.e. the estimated 95% CIs did not encompass zero) for the number of large logs and for the number of marri saplings (i.e. there was an increased probability of detection with an increase in the number of large logs and marri stems). The β coefficient was negative and significant for the number of *Hakea* stems with a shrub form. The estimated probability of detection from the preferred model was highest for the unbaited treatment group (*p*=0.81), then the two *baitings per year* treatment group (*p*=0.78), the four baitings per year treatment group (*p*=0.40), and with the lowest estimate for the six baitings per year treatment group (*p*=0.11) (Table 5.9).

The preferred model differed from all other models in the confidence set (Table 5.10) only in the covariate constraints on occupancy (ψ), with ψ constrained by the variables *jar_pil*, *mar_pil* (the number of stems in the size/age category ‘pile’ for jarrah and marri, respectively), *wan_pol* (the number of wandoo stems in the size/age category ‘pole’), *mar_sap* (the number of marri stems in the size/age category ‘sapling’) and *Pc* (the presence of jarrah dieback, *Phytophthora cinnamomi*). The estimated values for occupancy (Table 5.9) ordered differently from the estimates for detection, with the estimate for ψ highest for the unbaited treatment group (ψ=0.33), then the four baitings per year treatment group (ψ=0.20), then the two baitings per year treatment group (ψ=0.03). The estimated value for ψ for the six baitings per year treatment group was the fixed value of 0.001 (see methods and discussion). All values appeared to be realistic and reflected the raw data and observations. The β coefficients were positive and significant for *wan_pol* and *mar_sap*, negative and significant for *mar_pil*, and positive, but not significant for *jar_pil* and *Pc*. The effect on occupancy from the significant variables *wan_pol*, *mar_sap* and *mar_pil* are shown in Fig 5.5, 5.6 and 5.7, respectively. The only counter intuitive result was the negative β value for *mar_pil* (Fig. 5.7).

Program MARK also reported the 'derived' parameter estimates for occupancy $(\hat{\psi})$ for each season for each treatment group, which is derived through the recursive equation: $\psi_{t+1} = \psi_t(1-\varepsilon_t) + (1-\psi_t)\gamma_t$ (Cooch and White, 2019). So, although ψ was modelled with a fixed value for the six baitings per year treatment group and with ε and γ constant, the estimate $\hat{\psi}$ was updated seasonally by the encounter history which enabled identification of any seasonal trend. For the preferred model, each treatment group showed estimated occupancy $(\hat{\psi})$ to be increasing seasonally (Table 5.11).

Table 5.9: Estimates for the probability of occupancy (ψ), detection (p), extirpation (ε) and colonisation (γ) from the preferred model to describe occurrence of the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest, south-west Western Australia.

Extirpation (ε_t) is the probability that an occupied site in season/session *t* becomes unoccupied or locally extinct in season/session *t*+1.
Colonisation (γ_t) is the probability that an unoccupied site in season/session *t* becomes occupied or in season/session *t*+1.
* See text and discussion.

Treatment group	Parameter	Parameter estimate	Std. Error	Lower 95% confidence interval	Upper 95% confidence interval
two baitings per year	ε	0.0214	0.0208	0.0031	0.1329
	γ	0.1213	0.0271	0.0774	0.1850
	ψ	0.0294	0.0500	0.0010	0.4839
	p	0.7826	0.0446	0.6830	0.8575
four baitings per year	ε	0.0214	0.0208	0.0031	0.1329
	γ	0.1213	0.0271	0.0774	0.1850
	ψ	0.2044	0.1866	0.0264	0.7089
	p	0.3950	0.0454	0.3102	0.4866
six baitings per year	ε	0.0214	0.0208	0.0031	0.1329
	γ	0.1213	0.0271	0.0774	0.1850
	ψ	0.0010*	0.0000*	0.0010*	0.0010*
	p	0.1118	0.0346	0.0598	0.1995
unbaited	ε	0.0214	0.0208	0.0031	0.1329
	γ	0.1213	0.0271	0.0774	0.1850
	ψ	0.3296	0.2683	0.0435	0.8415
	p	0.8141	0.0312	0.7450	0.8678

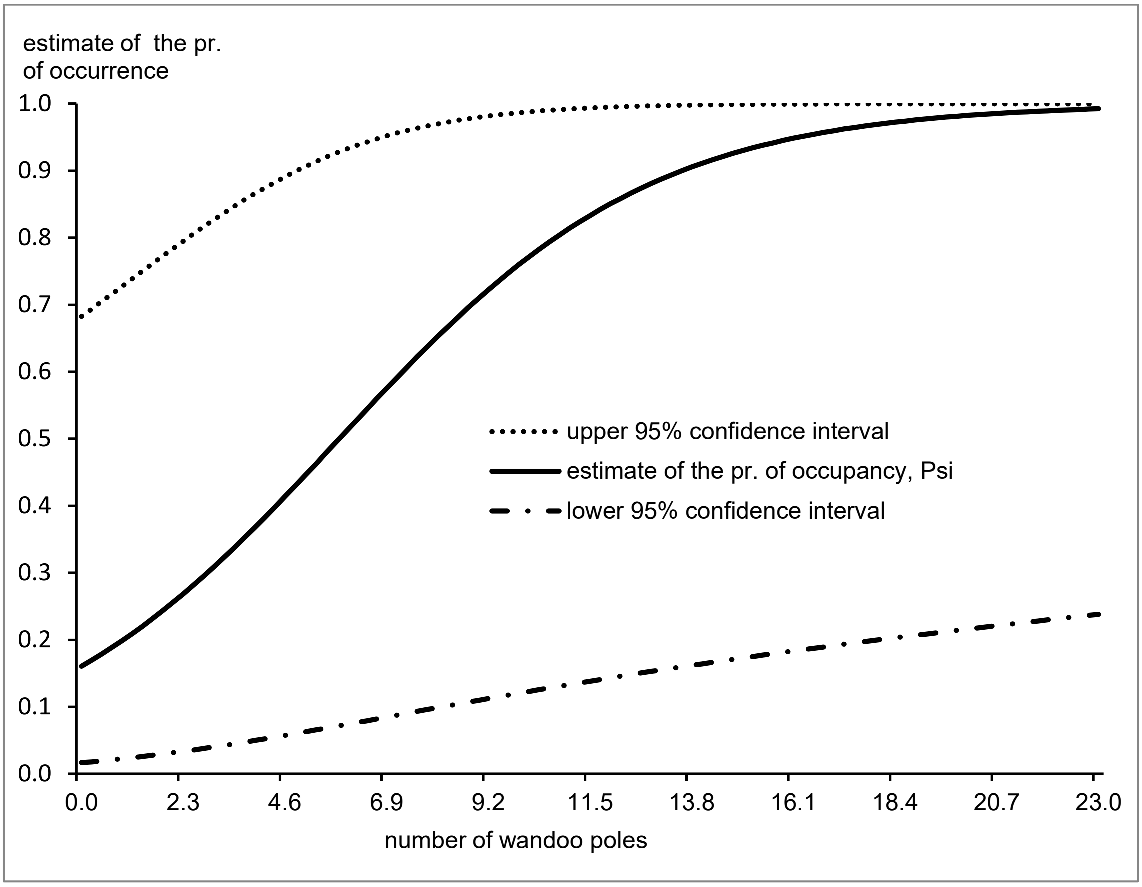

Figure 5.5: Fitted curve for the estimated probability of occupancy (ψ) for the brushtail possum (*Trichosurus vulpecula hypoleucus*) over the range of values recorded for the variable for the number of wandoo (*Eucalyptus wandoo* and *E. accedens*) poles at trapping grids within the northern jarrah forest, south-west Western Australia.

Values are fitted for the unbaited treatment group from the preferred model with the mean value for other covariates constraining ψ (see text).

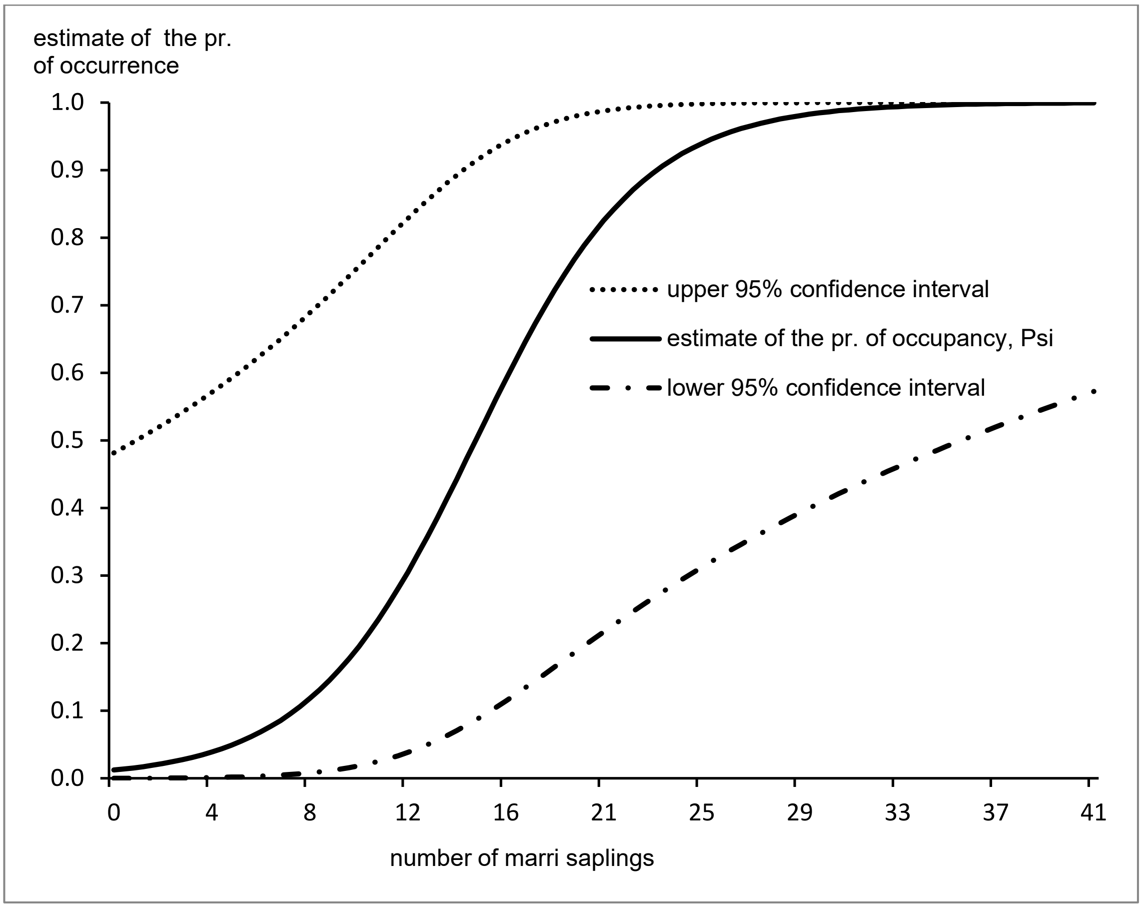

Figure 5.6: Fitted curve for the estimated probability of occupancy (ψ) for the brushtail possum (*Trichosurus vulpecula hypoleucus*) over the range of values recorded for the variable for the number of marri (*Corymbia calophylla*) saplings within the northern jarrah forest, south-west Western Australia.

Values are fitted for the unbaited treatment group from the preferred model with the mean value for other covariates constraining ψ (see text).

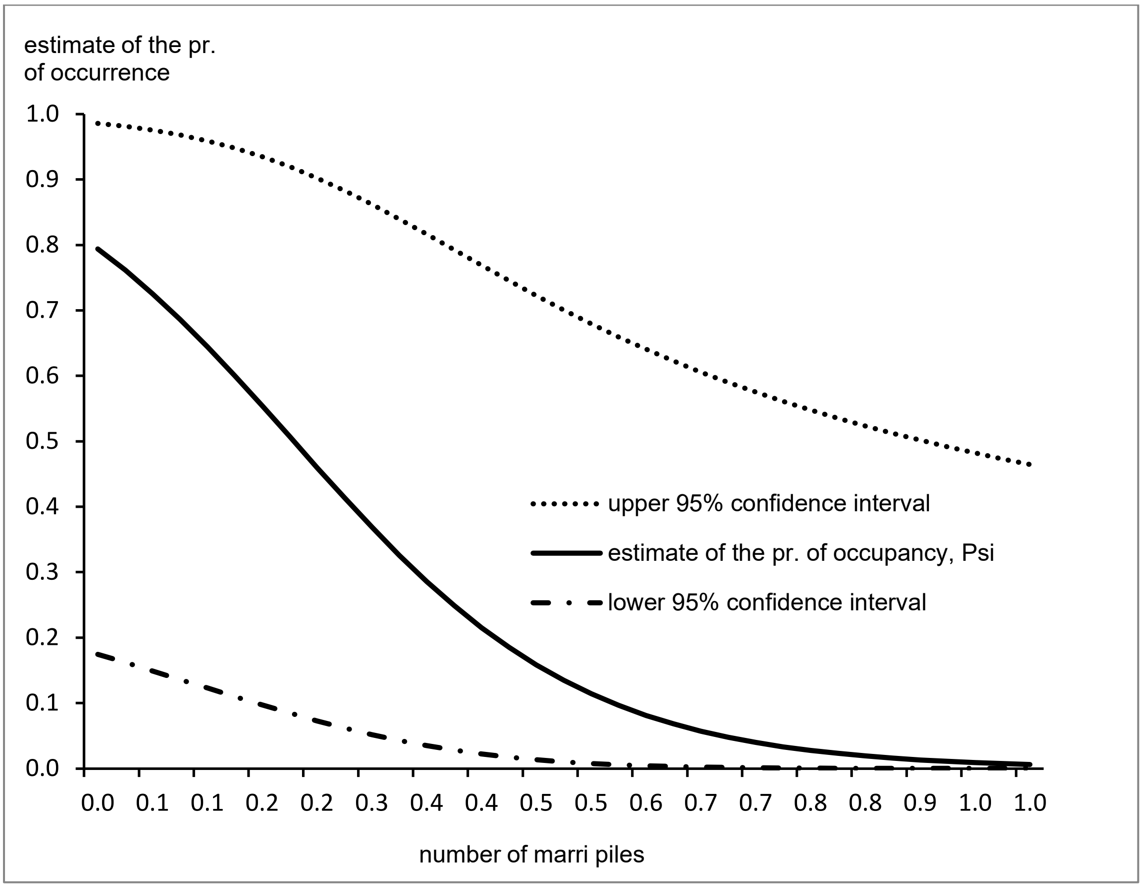

Figure 5.7: Fitted curve for the estimated probability of occupancy (ψ) for the brushtail possum (*Trichosurus vulpecula hypoleucus*) over the range of values from zero to one, for the variable for the number of marri (*Corymbia calophylla*) piles within the northern jarrah forest, south-west Western Australia.

Values are fitted for the unbaited treatment group from the preferred model with the mean value for other covariates constraining ψ (see text).

Table 5.10: The preferred model and models with support, ranked in order of AICc, to determine which model(s) are best supported by the data to describe presence or occupancy (ψ) and detection (p) of the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest of south-west Western Australia.

The preferred model is indicated by a ΔAICc of 0.00 and is shown in bold. Models shown are those with a ΔAICc weight of 1% or more. Individual covariates are described in Table 5.4 and Table 5.5 and the rationale for their inclusion in a model is given in Table 5.6. See text for the rationale for 'fixing' ψ for treatment group 3. Model 000 is the model with no constraints on ψ or p.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num Par	-2log(L)
Model 425 ψ (*g*, *g3*=0.001 + *jar_pil* + *mar_pil* + *wan_pol* + *mar_sap* + *Pc*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	**766.6858**	**0.0000**	**0.2120**	**1.0000**	**17**	**730.7243**
Model 267A ψ (*g*, *g3*=0.001 + *mar_pil* + *wan_pol* + *mar_sap* + *Pc* + *tree_tot*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	767.2487	0.5629	0.1600	0.7547	17	731.2872
Model 267B ψ (*g*, *g3*=0.001 + *mar_pil* + *wan_pol* + *mar_sap* + *Pc*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	767.2494	0.5636	0.1599	0.7544	16	733.5114
Model 267C ψ (*g*, *g3*=0.001 + *mar_pil* + *wan_pol* + *mar_sap* + *stumps*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	767.3839	0.6981	0.1495	0.7054	16	733.6459
Model 267D ψ (g, g3=0.001 + *mar_pil* + *wan_pol* + *mar_sap* + *tree_tot)* $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	768.7432	2.0574	0.0758	0.3575	16	735.0052
Model 460 ψ (g, g3=0.001 + *jar_vet* + *jar_pil* + *mar_pil* + *wan_pol* + mar_sap + Pc) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	768.8665	2.1807	0.0712	0.3361	18	730.6671
Model 373 ψ (g, g3=0.001 + *jar_vet* + *mar_pil* + *wan_pol* + *mar_sap* + *Pc*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	769.2201	2.5343	0.0597	0.2816	17	733.2585
Model 531 ψ (g, g3=0.001 + *jar_vet* + *mar_vet* + *mar_pil* + *wan_pol* + mar_sap) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	769.8547	3.1689	0.0435	0.2050	18	731.6553
Model 274 ψ (g, g3=0.001 + *mar_pil* + *wan_pol* + *shrubs_tot* + Pc) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	770.7045	4.0187	0.0284	0.1341	16	736.9665
Model 408 ψ (g, g3=0.001 + *mar_vet* + *mar_pil* + *wan_pol* + *mar_sap*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	770.9366	4.2508	0.0253	0.1194	16	737.1986
Model 438 ψ (g, g3=0.001 + *jar_pil* + *mar_pil* + *wan_pol* + *Pc* + *forbs*+ *wan_sap*) $\varepsilon(.)$ $\gamma(.)$ p (*g* + *large_logs* + *mar_sap* + *shrubs_hak*)	772.0123	5.3265	0.0148	0.0697	18	733.8129
Model 000 ψ (*g*, *g3*=0.001 + covariates) $\varepsilon(.)$ $\gamma(.)$ p (g + covariates)	817.6704	50.9846	0.0000	0.0000	9	799.1079

Table 5.11: Derived estimates for the probability of occupancy $(\hat{\psi})$ for each of six consecutive seasons for each treatment group from the preferred model to describe occurrence of the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest, south-west Western Australia.

For * and ** see text (discussion)

treatment group and season	$\hat{\psi}$	Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval
two baitings per year				
Winter	0.0294	0.0500	-0.0685**	0.1273
Spring	0.1465	0.0491	0.0502	0.2428
Summer	0.2469	0.0570	0.1351	0.3587
Autumn	0.3329	0.0659	0.2039	0.4620
Winter	0.4067	0.0732	0.2633	0.5501
Spring	0.4700	0.0787	0.3158	0.6242
four baitings per year				
Winter	0.2044	0.1866	-0.1613**	0.5700
Spring	0.2965	0.1600	-0.0171**	0.6101
Summer	0.3755	0.1400	0.1011	0.6498
Autumn	0.4432	0.1250	0.1981	0.6883
Winter	0.5012	0.1142	0.2775	0.7250
Spring	0.5510	0.1064	0.3425	0.7596
six baitings per year				
Winter	0.0010*	0.0000*	0.0010*	0.0010*
Spring	0.1221	0.0270	0.0692	0.1751
Summer	0.2260	0.0468	0.1343	0.3177
Autumn	0.3150	0.0609	0.1956	0.4345
Winter	0.3914	0.0710	0.2523	0.5305
Spring	0.4568	0.0779	0.3041	0.6096
unbaited				
Winter	0.3296	0.2683	-0.1962**	0.8554
Spring	0.4039	0.2302	-0.0473**	0.8550
Summer	0.4675	0.1990	0.0774	0.8576
Autumn	0.5221	0.1738	0.1815	0.8627
Winter	0.5689	0.1536	0.2679	0.8699
Spring	0.6090	0.1377	0.3391	0.8789

5.3.2.2 The brushtail possum: model averaging

There was considerable model uncertainty, with the confidence model set used for model averaging comprised of eleven models (Table 5.10), with each model placing different constraints on the general model: ψ (*g*, *g*3=0.001+*covariates*) ε (.) γ (.) p (*g*+*covariates*). The preferred model had 21.2% of the model weight. Each model in the confidence model set had considerable support when compared to the model with no constraints (Model 000, Table 5.10) which had a ΔAICc of 50.98 when compared to the AICc best model.

Consistent with the preferred model, the variable for the number of wandoo poles and the variable for the number of marri piles were present in each of the eleven models as a constraint on ψ. Also consistent with the preferred model, the β coefficient for wandoo poles was positive for all models and significant in eight. The variable for the number of marri piles was negative in each model and significant in nine of the eleven models. Again as per the preferred model, the β coefficient for marri saplings was positive and significant in each of the nine models in which it occurred. The variable *Pc* (presence of jarrah dieback) was present (with a positive but not significant β coefficient) in each of the seven models in which it occurred.

Not present in the preferred model, but present in the confidence model set and influencing the probability of occupancy (ψ), were the variables *tree_tot* (the total number of non-eucalypt and non *Corymbia* trees), *stumps* (the number of standing cut or senescing or dead stumps), *jar_vet* (the number of jarrah stems in the age/size class veteran), *mar_vet* (the number of marri stems in the age/size class veteran), *forbs* (an ordinal variable for the percentage of ground cover with herbs or forbs) and *wan_sap* (the number of wandoo stems in the age/size class sapling) (Table 5.10). The variable *tree_tot* occurred in two models (Model 267A and Model 267D) and in both cases the β coefficient was negative and not significant. The variable *stumps* occurred in only one model, the β coefficient was positive and not significant. The variables for jarrah and marri veterans occurred in three and one model, respectively, and in all cases the β coefficient was negative and not significant. The variable for forbs and wandoo sapling occurred once each, and in the same model (Model 438, Table 5.10, with a model weight of <1.5%), with a negative and not significant β coefficient. The variable *shrubs_tot* was also present in only one model, with a positive and significant β coefficient.

The model averaged estimate for the probability of occupancy was lowest (ψ = 0.001, Table 5.12) in the six baitings per year treatment group. However, this value was set as a fixed parameter as a consequence of the exploratory analysis which consistently generated models with unrealistic values (see methodology and discussion). The estimated probability of occupancy and the 95% CIs for each of the other treatment groups appeared ordered as anticipated from the raw data, although lower than anticipated, with ψ estimated highest in the unbaited treatment group (ψ=0.37), followed by the four (ψ=0.15) and two (ψ=0.04) baitings per year treatment groups respectively (Table 5.12). The model averaged estimates for the probability of localised extinction/extirpation (ε) and colonisation (γ) were 0.02 and 0.12, respectively (Table 5.13).

The model averaged derived parameter estimates for occupancy $(\hat{\psi})$ for each treatment group, for each trapping session within each season (Table 5.14) appeared more in keeping with expectations from the raw data. As was the case for the preferred model, there was a season pattern of increasing occupancy for each treatment group.

For all models within the confidence model set (Table 5.10), the detection parameter (*p*) was constrained by the treatment group plus the variables *large_logs*, *mar_sap* and *shrubs_hak*, as described for the preferred model. Again consistent with the preferred model, the β co-efficient for the variables for large logs and marri saplings were positive and significant in each model and the β co-efficient for the variable for *Hakea* shrubs was negative and significant in each model.

Table 5.12: Model-averaged estimates for the probability of occupancy (ψ) for the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest, south-west Western Australia.

ψ for the six baitings per year treatment group was 'set', see text.

Treatment group	ψ model weighted average	Std Error unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Variation of parameter estimate attributable to model variation (%)
two baitings per year	0.0432	0.0690	0.0017	0.5439	36.12
four baitings per year	0.1543	0.1667	0.0147	0.6907	15.41
six baitings per year	0.0010	0.0000	0.0010	0.0010	0.00
unbaited	0.3670	0.2802	0.0517	0.8604	26.42

Table 5.13: Model averaged estimates for the probability of extirpation (ε) and colonisation (γ) from models to describe occurrence of the brushtail possum (*Trichosurus vulpecula hypoleucus*) in the northern jarrah forest, south-west Western Australia.

ε and γ were modelled as constant across all treatment groups and across all seasons (see text).

Extirpation (ε_t) is the probability that an occupied site in season/session *t* becomes unoccupied or locally extinct in season/session *t*+1.

Colonisation (γ_t) is the probability that an unoccupied site in season/session *t* becomes occupied or in season/session *t*+1.

Parameter	Model weighted average	Std Error unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Variation of parameter estimate attributable to model variation (%)
ε	0.0212	0.0206	0.0031	0.1321	0.13
γ	0.1206	0.0271	0.0767	0.1846	0.58

Table 5.14: Model averaged derived estimates for the probability of occupancy $(\hat{\psi})$ of the brushtail possum (*Trichosurus vulpecula hypoleucus*) for each of six consecutive seasons for each treatment group in the northern jarrah forest, south-west Western Australia.

For * see text (discussion)

Treatment group Season	$\hat{\psi}$	Std Err unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Two baitings per year				
Winter	0.0432	0.0690	0.0017	0.5439
Spring	0.1577	0.0638	0.0681	0.3243
Summer	0.2560	0.0667	0.1476	0.4059
Autumn	0.3403	0.0720	0.2157	0.4917
Winter	0.4126	0.0771	0.2735	0.5673
Spring	0.4747	0.0813	0.3229	0.6314
Four baitings per year				
Winter	0.1543	0.1667	0.0147	0.6907
Spring	0.2530	0.1437	0.0709	0.6005
Summer	0.3377	0.1271	0.1434	0.6084
Autumn	0.4104	0.1155	0.2146	0.6395
Winter	0.4728	0.1074	0.2782	0.6760
Spring	0.5263	0.1019	0.3329	0.7122
Six baitings per year				
Winter	0.0010*	0.0000*	0.0010*	0.0010*
Spring	0.1214	0.0271	0.0775	0.1852
Summer	0.2248	0.0469	0.1461	0.3295
Autumn	0.3135	0.0612	0.2073	0.4436
Winter	0.3896	0.0713	0.2618	0.5346
Spring	0.4549	0.0783	0.3101	0.6079
Unbaited				
Winter	0.3670	0.2802	0.0517	0.8604
Spring	0.4358	0.2408	0.1018	0.8404
Summer	0.4948	0.2084	0.1605	0.8338
Autumn	0.5454	0.1820	0.2216	0.8349
Winter	0.5888	0.1607	0.2805	0.8402
Spring	0.6260	0.1438	0.3343	0.8480

5.3.3 The southern brown bandicoot

5.3.3.1 The southern brown bandicoot: the preferred model

In recognition of the southern brown bandicoot's habitat and dietary requirements, six covariates were used singly and in combination to constrain the model ψ (*g*, *g*4=0.001 + *covariates*) $\varepsilon(.)$ $\gamma(.)$ p (g + *covariates*), as described in Section 5.2.5. For all models, ε and γ were held constant with estimated values from the preferred model (Model 017, Table 5.17) of ε = 0.06 and γ = 0.19, respectively (Table 5.15).

Similarly, for all models, p was held constant between and within all seasons but varied between treatment groups. The preferred model constrained *p* by the covariates *rain*, *litter* and *shrubs_to*t, with the estimated value for *p* highest for the two baitings per year treatment group (*p*=0.77), then the four baitings per year treatment group (*p*=0.752), the unbaited treatment group (*p*=0.746), with the lowest estimate for the six baitings per year treatment group (*p*=0.41) (Table 5.15).

The preferred model constrained ψ by the covariates *rain* and *small_logs* (Table 5.17). The estimates for ψ were ordered differently from *p*, with the estimate of ψ highest for the four baitings per year treatment group (ψ=0.79), then the two baitings per year treatment group (ψ=0.68), then the six baitings per year treatment group (ψ=0.13). The estimated value for ψ for the unbaited treatment group was the fixed value of 0.001 (see methods and discussion). All values appeared to be realistic and again reflected the raw data and observations. The 'derived' parameter estimates for occupancy $(\hat{\psi})$ (Table 5.16) indicated occupancy was increasing seasonally in the two and six baitings per year and the unbaited treatment groups and decreasing in the four baitings per year treatment group.

For the preferred model, and for all seven models in the confidence model set used for model averaging (Table 5.17), the variable *rain* (with values determined by the annual rainfall isohyet from CALM/DEC's GIS corporate data) was present as a constraint on ψ. For the preferred model ψ was also constrained by the variable *small_logs*. The β coefficients for both covariates were significant. Increased rainfall was positively associated with ψ and an increase in the number of small logs negatively associated with ψ. The effect from the variable *small_logs* is shown for the two and four baitings per year treatment groups in Fig. 5.8. Increased rainfall was also positively associated with detection and the β coefficient was again significant. The β coefficient for the variable *shrubs_tot* was significant and negatively associated with detection.

Table 5.15: Estimates for the probability of occupancy (ψ), detection (p), extirpation (ε) and colonisation (γ) for the preferred model to describe occurrence of the southern brown bandicoot (*Isoodon obesulus*) in the northern jarrah forest, south-west Western Australia.

Extirpation (ε_t) is the probability that an occupied site in season/session *t* becomes unoccupied or locally extinct in season/ session *t*+1.
Colonisation (γ_t) is the probability that an unoccupied site in season/session *t* becomes occupied or in season/ session *t*+1.

For * see text (discussion)

Treatment group	Parameter	Parameter estimate	Std. Error	Lower 95% confidence interval	Upper 95% confidence interval
two baitings per year	ε	0.0641	0.0228	0.0314	0.1262
	γ	0.1854	0.0468	0.1102	0.2948
	ψ	0.6775	0.2004	0.2582	0.9269
	p	0.7692	0.0313	0.7024	0.8248
four baitings per year	ε	0.0641	0.0228	0.0314	0.1262
	γ	0.1854	0.0468	0.1102	0.2948
	ψ	0.7903	0.1362	0.4295	0.9497
	p	0.7515	0.0301	0.6880	0.8057
six baitings per year	ε	0.0641	0.0228	0.0314	0.1262
	γ	0.1854	0.0468	0.1102	0.2948
	ψ	0.1308	0.1231	0.0177	0.5566
	p	0.4113	0.0514	0.3155	0.5143
unbaited	ε	0.0641	0.0228	0.0314	0.1262
	γ	0.1854	0.0468	0.1102	0.2948
	ψ	0.0010*	0.0000*	0.0010*	0.0010*
	p	0.7458	41.6984	0.0000	1.0000

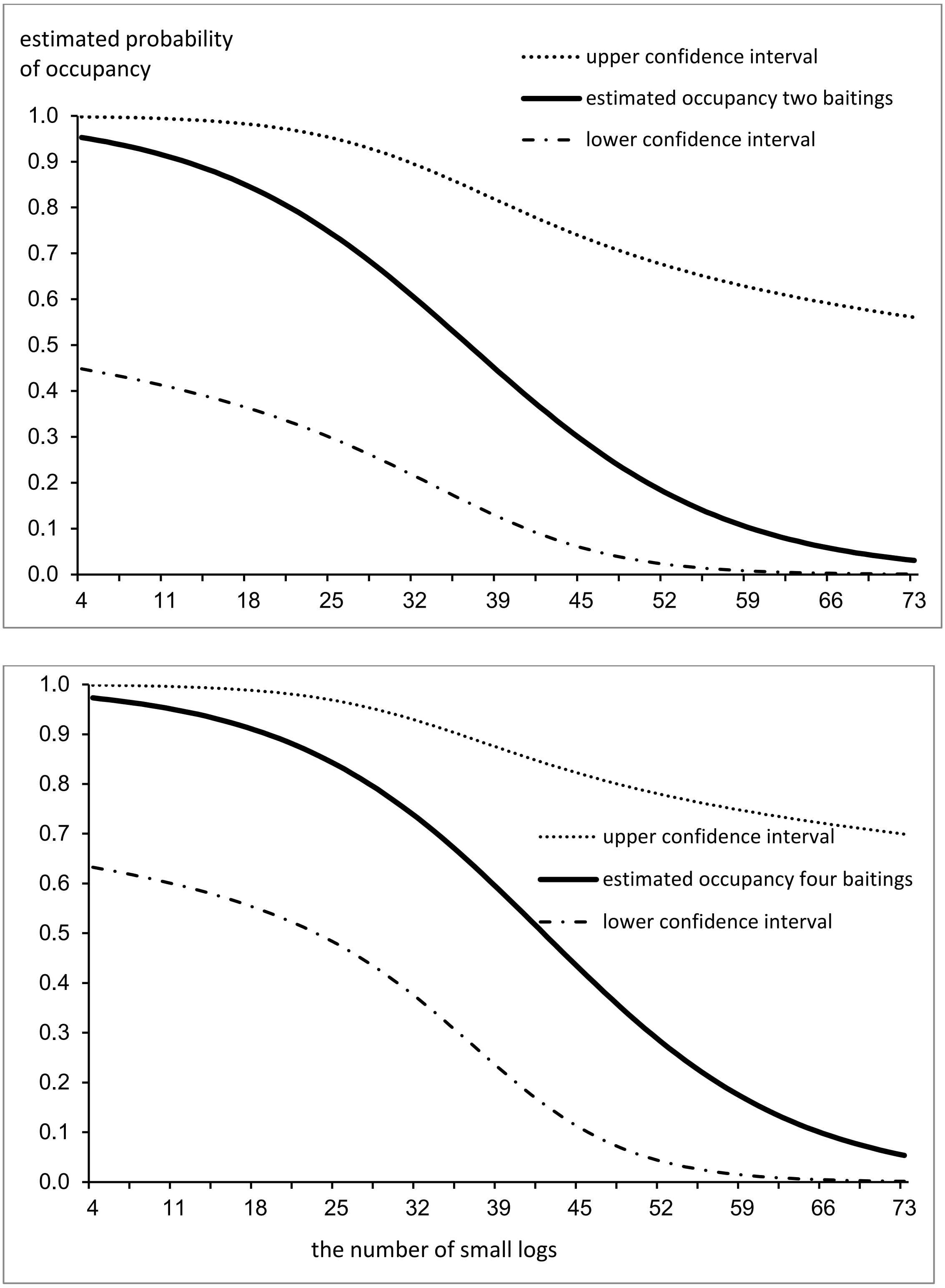

Figure 5.8: Fitted curves for the estimated probability of occupancy (ψ) of the southern brown bandicoot (*Isoodon obesulus*) over the range of values recorded for the variable *small_logs*, within the northern jarrah forest, south-west Western Australia.

Values are fitted for the preferred model for the two (upper figure) and four (lower figure) baitings per year treatment groups with the mean value for other covariates constraining ψ .

Table 5.16: Derived estimates for the probability of occupancy $(\hat{\psi})$ for each of six consecutive seasons for each treatment group from the preferred model to describe occurrence of the southern brown bandicoot (*Isoodon obesulus*) in the northern jarrah forest, south-west Western Australia.

For *, ** and *** see text (discussion)

Treatment group season	$\hat{\psi}$	Std Err	Lower 95% confidence interval	Upper 95% confidence interval
Two baitings per year				
Winter	0.6775	0.2004	0.2848	1.0702***
Spring	0.6938	0.1516	0.3966	0.9910
Summer	0.7061	0.1182	0.4745	0.9377
Autumn	0.7153	0.0966	0.5259	0.9047
Winter	0.7223	0.0841	0.5574	0.8871
Spring	0.7274	0.0777	0.5751	0.8798
Four baitings per year				
Winter	0.7903	0.1362	0.5234	1.0572***
Spring	0.7785	0.1039	0.5749	0.9821
Summer	0.7697	0.0837	0.6056	0.9338
Autumn	0.7630	0.0730	0.6200	0.9061
Winter	0.7581	0.0687	0.6234	0.8927
Spring	0.7543	0.0681	0.6209	0.8878
Six baitings per year				
Winter	0.1308	0.1231	-0.1104**	0.3720
Spring	0.2835	0.0997	0.0882	0.4789
Summer	0.3982	0.0928	0.2163	0.5800
Autumn	0.4842	0.0912	0.3056	0.6629
Winter	0.5488	0.0902	0.3720	0.7256
Spring	0.5973	0.0889	0.4229	0.7716
Unbaited				
Winter	0.0010*	0.0000*	0.0010*	0.0010*
Spring	0.1861	0.0468	0.0944	0.2778
Summer	0.3251	0.0730	0.1820	0.4681
Autumn	0.4293	0.0863	0.2602	0.5984
Winter	0.5076	0.0918	0.3276	0.6876
Spring	0.5663	0.0930	0.3841	0.7486

Table 5.17: The preferred model and models with support, ranked in order of AICc, to determine which model(s) are best supported by the data to describe presence or occupancy (ψ) and detection (p) of the southern brown bandicoot (*Isoodon obesulus*) in the northern jarrah forest, south-west Western Australia.

The preferred model is indicated by a ΔAICc of 0. Models shown are those with a ΔAICc of less than 4 units from the preferred model (shown in bold). Individual covariates are described in Table 5.4 and the rationale for their inclusion in any given model is provided in Table 5.8. See text for the rationale for 'fixing' ψ for treatment group 4, the unbaited treatment group. Model 000 is the model identified from the exploratory analysis and used as a base model parameterised to constrain ψ and p with the six covariates listed in Table 5.8.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	-2log(L)
Model 017 **ψ (g, *g* 4=0.001 + *rain* + *small_logs*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)**	**936.4987**	**0.0000**	**0.4750**	**1.0000**	**13**	**909.0069**
Model 016 ψ (g, *g* 4=0.001 + *rain* + *shrubs_tot*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	939.0152	2.5165	0.1350	0.2842	13	911.5234
Model 018 ψ (g, *g* 4=0.001 + *rain* + *large_logs*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	939.9179	3.4192	0.0859	0.1809	13	912.4261
Model 090 ψ (g, *g* 4=0.001 + *rain* + *litter* + *shrubs_tot* + *small_logs*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	940.0421	3.5434	0.0808	0.1700	15	908.0586
Model 002 ψ (g, *g* 4=0.001 + *rain*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	940.0809	3.5822	0.0792	0.1668	12	914.8074
Model 093 ψ (g, *g* 4=0.001 + *rain* + *shrubs_tot* + *small_logs* + *large_logs*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	940.2149	3.7162	0.0741	0.1560	15	908.2314
Model 087 ψ (g, *g* 4=0.001 + *rain* + *Pc* + *shrubs_tot* + *small_logs*) $\varepsilon(.)$ $\gamma(.)$ p (g + *rain* + *litter* + *shrubs_tot*)	940.3278	3.8291	0.0700	0.1474	15	908.3443
Model 000 ψ (g + *covariate*) $\varepsilon(.)$ $\gamma(.)$ p (g + *covariate*)	985.9465	49.4478	0.0000	0.0000	8	969.3682

5.3.3.2 The southern brown bandicoot: model averaging

As was the case for the brushtail possum, there was considerable model uncertainty with the confidence model set used for model averaging comprised of seven models (Table 5.17). Each model placed different constraints on ψ for the general model: ψ (*g*, *g*4=0.001,+*covariates*) ε (.) γ (.) p (*g*+*covariates*). The preferred model (Model 017) had 47.5% of the model weight and each model in the confidence model set had considerable support when compared to the model with no constraints which had a ΔAICc of 49.45 when compared to the AICc best model (Table 5.17).

The variable *rain* was present as a constraint (with a positive and significant β coefficient) on both ψ and p in all models. The variable *small_logs*, present as a 'significant' variable in the preferred model, was also present as a constraint (again with a negative β coefficient) on ψ in three additional models, albeit with CIs encompassing zero in each of these additional models. Similarly, the variable *shrubs_tot* was present (with a negative β coefficient) as a constraint on ψ in four of the seven models used for model averaging, and in all cases the CIs encompassed zero, however, it was present as a 'significant' constraint on p in all models.

As anticipated from the trapping data, the model averaged estimate for the probability of occupancy was lowest in the unbaited treatment group. However, this value was set as a fixed parameter as a consequence of the exploratory analysis which consistently generated models with unrealistic values (see methodology and discussion). The estimated probability of occupancy and the 95% Confidence Intervals for each of the other treatment groups appeared credible and concurred with the raw data, with estimate for ψ greatest (ψ=0.80) in the four baitings per year treatment (Table 5.18). The model averaged estimates for the probability of localised extinction/extirpation (ε) and colonisation (γ) were modelled as constant, with estimates of 0.06 and 0.19, respectively (Table 5.19). The derived model averaged estimates for occupancy $(\hat{\psi})$ concur with those for the preferred model with the estimates showing occupancy increasing seasonally in the two baitings per year*,* six baitings year and the unbaited treatment groups and decreasing seasonally in the four baitings per year treatment group (Table 5.20).

Table 5.18: Model-averaged estimates for the probability of occupancy (ψ) of the southern brown bandicoot (*Isoodon obesulus*) in the northern jarrah forest, south-west Western Australia.

ψ for the unbaited treatment group was 'set', see text and discussion.

Treatment group	ψ model weighted average	Std. Error unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Variation of parameter estimate attributable to model variation (%)
two baitings per year	0.6618	0.1991	0.2549	0.9180	5.37
four baitings per year	0.8024	0.1377	0.4253	0.9570	3.67
six baitings per year	0.1420	0.1328	0.0192	0.5835	10.07
unbaited	0.0010	0.0	0.001	0.001	0

Table 5.19: Model averaged estimates for the probability of extirpation (ε) and colonisation (γ) from models to describe occurrence of the southern brown bandicoot (*Isoodon obesulus*) in the northern jarrah forest, south-west Western Australia.

ε and γ were modelled as constant across all treatment groups and across all seasons (see text).

Extirpation (ε_t) is the probability that an occupied site in season/session *t* becomes unoccupied or locally extinct in season/session *t*+1.

Colonisation (γ_t) is the probability that an unoccupied site in season/session *t* becomes occupied or in season/session *t*+1.

Parameter	model weighted average	Std. Error unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval	Variation of parameter estimate attributable to model variation (%)
ε	0.0641	0.0228	0.0314	0.1262	0.0
γ	0.1851	0.0469	0.1099	0.2947	0.03

Table 5.20: Model averaged derived estimates for the probability of occupancy $(\hat{\psi})$ of the southern brown bandicoot (*Isoodon obesulus*) for each of six consecutive seasons for each treatment group in the northern jarrah forest, south-west Western Australia.

For * see text (discussion)

Treatment group	Trapping session	$\hat{\psi}$	Std Err unconditional	Lower 95% Confidence Interval	Upper 95% Confidence Interval
Two baitings per year					
	Winter	0.6618	0.1991	0.2549	0.9180
	Spring	0.6819	0.1509	0.3542	0.8934
	Summer	0.6971	0.1179	0.4352	0.8730
	Autumn	0.7085	0.0967	0.4926	0.8588
	Winter	0.7170	0.0844	0.5287	0.8513
	Spring	0.7235	0.0781	0.5490	0.8490
Four baitings per year					
	Winter	0.8024	0.1377	0.4253	0.9570
	Spring	0.7876	0.1051	0.5198	0.9270
	Summer	0.7764	0.0846	0.5718	0.9003
	Autumn	0.7681	0.0736	0.5956	0.8816
	Winter	0.7618	0.0691	0.6026	0.8709
	Spring	0.7571	0.0683	0.6008	0.8658
Six baitings per year					
	Winter	0.1420	0.1328	0.0192	0.5835
	Spring	0.2918	0.1065	0.1304	0.5309
	Summer	0.4042	0.0970	0.2355	0.5991
	Autumn	0.4886	0.0935	0.3146	0.6654
	Winter	0.5520	0.0914	0.3739	0.7176
	Spring	0.5996	0.0894	0.4191	0.7565
Unbaited					
	Winter	0.0010*	0.0000*	0.0010*	0.0010*
	Spring	0.1859	0.0469	0.1106	0.2952
	Summer	0.3247	0.0731	0.2000	0.4803
	Autumn	0.4289	0.0864	0.2733	0.5999
	Winter	0.5071	0.0920	0.3333	0.6792
	Spring	0.5659	0.0932	0.3826	0.7327

5.4 Discussion

5.4.1 The species trapped

The suite of mammalian, reptilian and amphibian species trapped (Appendix 1) and the low abundance and the patchy distribution of most species, was as anticipated from anecdotal accounts, the published and grey literature. The premise for the current study was that 1080 baiting for fox control was advantageous for effective conservation management of this suite of native terrestrial fauna. Combined with this was the expectation that, even if baiting for fox control was advantageous in a conservation sense (i.e. if abundances and/or the probability of occupancy increased), there was unlikely to be a detectable difference over the duration of the study. Alternatively, if there was a detectable difference it was unlikely to be statistically significant (see Section 1.6, pp: 20-22).

The research was also based on the premise that the pattern of fauna occurrence would not be adequately described by the single dimensional causal factor of 1080 baiting. The corollary was that there is a suite habitat and managerial (disturbance) factors which could be identified to describe the pattern(s) of presence of *in situ* populations of native fauna within treatment groups and the relative importance of these factors, including 1080 baiting, could be identified. Occupancy modelling was adopted as the preferred method to identify these factors for two of the most frequently trapped species with the northern jarrah forest, the brushtail possum and the southern brown bandicoot. The data for these species were chosen to be analysed to represent an arboreal and ground dwelling species, respectively.

5.4.2 Occupancy modelling: the brushtail possum

Brushtail possum occupancy in the northern jarrah forest was best described by the presence of wandoo poles (*E. wandoo* and *E. acedens* in the size/age category 'pole') and the presence of marri saplings, with the variable for each positively and significantly associated with brushtail possum occurrence (Figures 5.5 and 5.6). Counterintuitively, the presence of marri piles (stem circumference >140cm) was negatively, and significantly, associated with brushtail possum occurrence (Fig. 5.7). Also appearing counterintuitive was the presence of the variable for jarrah and marri veterans in three models (Model 460, Model 373 and Model 531, Table 5.10), wherein each was negatively associated, albeit not significantly, with brushtail possum occurrence. This negative association (a negative β coefficient) appears to contradict the findings from the concurrent radio-telemetry study from the six baitings per year and unbaited treatment groups, where brushtail possums were recorded in 563 different den trees, of which 162 (28.8%) were jarrah and 108 (19.2%) were marri. All but two stems, both marri, had a circumference >140cm (de Tores *et al.*, unpublished-b). This den tree count was inclusive of 14 jarrah and nine marri in the tree form category 9 (extreme senescence or stump form, see Appendix 2). Although the den tree data also included multiple records of jarrah and marri in other stages of extensive senescence, either with or without regrowth (tree form categories 6, 7, 8 and 10, Appendix 2), category 9 is the only category which would have been excluded from the veteran or pile category of occupancy modelling. A plausible explanation for occupancy modelling failing to identify jarrah and veterans as positively influencing brushtail possum occupancy is that veterans of both species were present at most trapping grids, regardless of brushtail possum occurrence.

Conversely, the strong association between wandoo poles and brushtail possum occupancy was consistent with the den tree study of de Tores *et al*. (unpublished-b), wherein 223 of the 563 (39.6%) of den trees were wandoo, 209 of which had a diameter >140cm (i.e. in the size/age category ‘pile’ or ‘veteran’). This would suggest occupancy modelling should identify wandoo veterans and/or wandoo piles as positively associated with brushtail possum occupancy. However, as the variables for wandoo poles and wandoo veterans were highly correlated (Spearman rho =0.822, see Section 5.2.3, p243), and only one variable was used in any given model, the positive and significant relationship identified was for brushtail possum occupancy and wandoo poles (Fig. 5.5). This was the case for the preferred model and all models within the confidence model set (Table 5.10) and is supportive of the hypothesis that wandoo veterans and poles (and presumably piles) are important to the brushtail possum as a hollow bearing tree. This use of wandoo, and the absence of hollow bearing jarrah and marri in the same size/age class, may warrant inclusion of wandoo poles in the forest management protocols for retention as potential den trees.

Although a facultative user of tree hollows, the radio-telemetry study of brushtail possum habitat use in the northern jarrah forest (de Tores *et al.*, unpublished-b) also recorded den sites in hollows in dead trees, in standing stumps and fallen logs. In the southern jarrah forest of south-west WA (near Manjimup), diurnal location records also reported brushtail possum use of hollow logs, hollow stumps and burrows (Wayne, 2005). At coastal sites in WA, diurnal location records have included standing stumps, fallen logs and disused rabbit warrens (Clarke, 2011; de Tores and Rosier, unpublished; Nowicki, 2007). The presence of large logs (with a positive and significant β coefficient in all models) as a constraint on detection is consistent with this known denning and foraging behaviour. The known use of senescing stumps was not reflected in the occupancy modelling results, with the exception of one model which identified stumps as a constraint on occupancy (Model 267C, Table 5.10), albeit as a not significant relationship.

The dietary preferences of the brushtail possum reflect its lack of a specialised digestive tract (Kerle and Howe, 2008). It is a generalist and, despite being an arboreal marsupial, it includes invertebrates in its diet (Inions, 1985), is known to forage on the ground and has been recorded scavenging carrion (personal observations) and consuming 1080 meat baits (personal observations; and Marlow, unpublished camera trap data). The brushtail possum is also known to include marri leaves in its diet (Davis, 2005) and the presence of marri saplings as a constraint (significant and positive) on occupancy in nine of the eleven models in the confidence model set, and as a constraint on detection (again positive and significant) in all eleven models, may reflect these dietary habits. The association of occupancy and detection with marri saplings may also reflect the brushtail possums' use of marri saplings to gain access to the overstorey marri and eucalypts. The presence of *Hakea* shrubs as a constraint on detection in all models (negative and significant) may reflect a dietary avoidance, although the lack of published literature identifying *Hakea* spp in its diet does not necessarily infer avoidance. If there is an avoidance of *Hakea* species, it may be a result of an avoidance of plant secondary metabolites. Brushtail possums have been shown to demonstrate a decrease in food intake in response to the presence of plant secondary metabolites, and although the relationship between brushtail possums and plant secondary metabolites in eucalypts is well studied (see for example DeGabriel *et al.*, 2010; DeGabriel *et al.*, 2009; Marsh *et al.*, 2003; McLean *et al.*, 2001; Scrivener *et al.*, 2004), this relationship is unreported for *Hakea*. However, Rafferty *et al*. (2005) reported consumption of *Hakea* shoot material by the western grey kangaroo was inversely, and significantly related to the phenolic content. They also reported plant physical defences, including pungent leaves, were ineffective as a deterrent. It seems unlikely an avoidance of *Hakea* reflects an avoidance of commonly occurring form of many hakeas with sharp pungent leaves. *Hakea undulata*, common as an understorey shrub species in the northern jarrah forest, flowers prolifically. As brushtail possums are also known to consume flowers, including those of *Banksia grandis* (personal observations and Inions, 1985) which is also common in the northern jarrah forest and is equally well protected by sharp pungent leaves, it seems anomalous for there to be a dietary avoidance of the common hakeas with sharp pungent leaves.

The results from occupancy modelling did not support the hypothesis that the probability of brushtail possum occupancy increased with increased baiting frequency. The results from the preferred model (Table 5.9) identified the unbaited treatment group had the highest estimated probability of occupancy (ψ=0.33), and the six baitings per year treatment group had the lowest (ψ=0.001). This ordering of estimated probability of occupancy was the same when model averaging (Table 5.12), with the highest estimate for occupancy for the unbaited treatment group (ψ=0.37), then the four baitings per year (ψ =0.15), the two baitings per year (ψ =0.04) and the six baitings per year treatment group lowest (ψ =0.001). However, the estimate for the six baitings per year treatment group was set as a consequence of the inability of the models to converge for this treatment group, or misspecification at the parameter estimate boundary. Lack of model convergence, particularly when data are sparse (which is the norm for most ecological studies in Australia) is a common issue for occupancy modelling and particularly so when parameter estimates are at the boundary (i.e. at zero or one) (Welsh *et al.*, 2013a; Welsh *et al.*, 2013b). Section 5.4.4 (below) expands on this issue.

Although the occupancy parameter was set (at 0.001) for the six baitings per year treatment group, the derived parameter estimates ($\hat{\psi}$) and the recursive equation: $\psi_{t+1} = \psi_t(1-\varepsilon_t) + (1-\psi_t)\gamma_t$ (Cooch and White, 2019), allowed each successive seasonal estimate to be updated by that season's encounter history. As a consequence, despite the initial value for ψ being set for the six baitings per year treatment group, estimates were able to be derived for each season after which the parameter had been set. Interestingly, but not surprisingly, the derived parameter estimates for the preferred model (Table 5.11) were ordered the same way as the 'real' parameter estimates, with the unbaited treatment group highest ($\hat{\psi}$ =0.61) and the six baitings per year treatment group lowest ($\hat{\psi}$ =0.46). The same pattern was shown for the model averaged derived parameter estimates (Table 5.14), with the highest estimate for the unbaited treatment group ($\hat{\psi}$ =0.63) and the lowest for the six baitings per year treatment group ($\hat{\psi}$ =0.45). Of more significance were the 95% confidence intervals (Table 5.11) which showed all treatment groups overlapping for the preferred and model averaged derived estimates, which indicates factors other than the frequency of 1080 baiting for fox control are influencing brushtail possum occurrence.

The derived parameter estimates also identified a trend of increasing occupancy for all treatment groups. This apparent trend is not necessarily a reflection of an increased probability of occupancy and may be indicative of heterogeneity in detection. This heterogeneity in detection would not necessarily be identified when comparing the candidate models (by model differences in AICc), as detection probability, although modelled as different for each treatment group, was modelled as constant between/across all seasons. Any un-modelled variation in detection (in this case an implied increase) would therefore appear as a variation (increase) in occupancy.

Occupancy modelling does provide a means to identify this in two ways. The first is in the exploratory analysis (see Section 5.2.3), where models were initially fitted (without covariate constraints) to compare models with a seasonal variation in detection (*p*) (model groups (i), (ii) and (iii) in the exploratory analysis) with models where detection was held constant for each season (model group (iv) in the exploratory analysis). However, all models where *p* varied between season were less competitive (in terms of AICc, with ΔAICc values >4 when compared to the model group (iv)), and/or were unable to converge. When models did appear to converge, the estimates were at the boundary and the 95% CIs ranged from zero to one, or CIs were estimated at zero for the upper and lower limit. Adjusting through use of profile likelihood estimates, where confidence intervals are based on the log-likelihood function as opposed to standard error and the logit transformation, did not resolve the issue. When using profile likelihood to derive the CIs there was no model improvement (by definition, AICc remains the same) and although CI estimates were marginally better for some parameters (i.e. by reducing the boundary estimates by an order of magnitude), these estimates were still unrealistic, with values as small as n^{-17} and 95% CIs at zero for the lower and upper limit. Other aspects of profile likelihood estimates are discussed in below (Section 5.4.4).

The second way occupancy modelling can accommodate variation in detection is through the use of covariates. However, this requires the data to be sufficiently robust to enable models to incorporate estimation of the additional parameters to accommodate this heterogeneity. If the data are sufficiently robust, this is the preferred and logical option, despite the misconception (see McGill, 2013) that the probability of detection (*p*) must be constant across all occupied sites.

An alternative explanation for the apparent increase in the probability of occupancy is that it is reflecting a behavioural response by brushtail possums, with possums becoming less trap-shy with repeated exposure to traps. The issue to resolve then is how to differentiate behaviour induced detection heterogeneity from site specific (habitat variables) induced detection heterogeneity. The former is consistent with the abundance estimates for the brushtail possum (not reported), where modelling of abundance and model selection supported the hypothesis of behaviour induced detection heterogeneity. Where heterogeneity in capture probability is not included in models to estimate abundance, there will be a negative bias in those abundance estimates (Pledger *et al.*, 2010). Ironically, it is often because of the perceived complexities required to obtain meaningful results from abundance estimates that analysts (and manuscript reviewers) advocate occupancy modelling (for a scathing review of this recent phenomena see McGill, 2013).

Occupancy modelling, when incorporating detection heterogeneity through the use of covariates, is also often advocated as more precise than ignoring this heterogeneity (see MacKenzie *et al.*, 2002; MacKenzie *et al.*, 2006). Welsh *et al.* (2013b) questioned this and claimed it may be impossible to determine which model fit is better; a model adjusting for non-detection (or detection heterogeneity) or a model which simply ignores imperfect detection. They (Welsh *et al.*, 2013b) further demonstrated the bias in fitted probabilities *"can be of a similar magnitude to the bias when the detection process is ignored".* Further issues associated with occupancy modelling are discussed in Section 5.4.4, below).

5.4.3 Occupancy: the southern brown bandicoot

The preferred model to describe the occurrence of the southern brown bandicoot constrained the probability of occupancy with covariates for annual average rainfall and the number of small logs (fallen logs with a circumference >60cm and up to 127cm, Table 5.17). All models in the competitive model set included rainfall as a constraint on occurrence and detection, with the β coefficient positive and significant in every model. With the exception of the preferred model, where it was present with a negative and significant β coefficient, the β coefficient for the variable for small logs (three additional models, Table 5.17) was negative but not significant.

For each model in the confidence model set (Table 5.17), the estimated probability of detection was constrained (in addition to rainfall) by the variables for *litter* (i.e. the depth of the litter layer) and *shrubs_tot* (the total number of stems in shrub form, most commonly *Persoonia longifolia*, *Mirbelia dilatata*, *Hakea undulata*, *Hovea trisperma*, *Banksia sessilis*, *Xanthorrhoea preissii*, *X. gracilis* and shrub forms of the larger *Acacia saligna, Banksia grandis* and less frequently small or shrub forms of *Allocasuarina fraseriana*). The β coefficient for litter where it appeared as a constraint on detection was positive and not significant in every model. The variable for litter was also present in one model (Model 090) as a constraint on occurrence where the β coefficient was positive, but again not significant. Conversely, the β coefficient for the total number of shrubs was negative and significant as a constraint on detection in every model and negative but not significant where it occurred as a constraint on occurrence (four models, Table 5.17).

The presence of rainfall with a positive and significant constraint on occurrence reflects the bandicoot's preference for a more mesic environment. However, the negative and significant (preferred model) and not significant (all other models in which it occurred) constraint on occurrence from small logs combined with the negative and significant β coefficient for the total number of shrubs are at odds with the known habitat requirements for the southern brown bandicoot. The bandicoot's reported habitat preference for dense understorey (Dell, 1971; Dell and How, 1988; Paull, 1995; Paull, 2008) and its foraging strategies of digging for invertebrates, roots and fungi (Paull, 2008) are not reflected in the modelling.

The results from occupancy modelling give some support to the hypothesis that the probability of occupancy for the southern brown bandicoot increased with increased baiting frequency. Occupancy estimates from the preferred model and from model averaging are lowest in the unbaited treatment group, with the 95% CIs for the unbaited treatment group not overlapping with the other treatment groups (Table 5.15 and Table 5.18). However, all baited treatment groups had overlapping 95% CIs, suggesting there is no improvement in occupancy with increased baiting frequency. This is a qualified assessment, as the occupancy estimate for the unbaited treatment group was set, as per the rationale for setting the value for occupancy in six baitings per year treatment group for the brushtail possum, i.e. because of the inability of the models to converge for this treatment group, unrealistic parameter estimates and CIs ranging from zero to one.

The results for the derived parameter estimates ($\hat{\psi}$) suggest a different conclusion. Although the $\hat{\psi}$ estimates are lowest for the unbaited treatment group (Table 5.16 and Table 5.20), the 95% CIs for all treatment groups overlap, suggesting occurrence is not a function of the frequency of 1080 baiting and is driven by other factors. The derived estimates for occupancy from the preferred model (Table 5.16) and from model averaging (Table 5.20) for the southern brown bandicoot show a different trend from those from that shown for the brushtail possum, where, for the southern brown bandicoot there is a pattern of increasing probability of occupancy for the two and six baitings per year and the unbaited treatment groups, but with a reversed pattern (a pattern of decreasing occupancy) for the four baitings per year treatment group. As was the case for the brushtail possum, this may be un-modelled variation in detection probability. Any un-modelled variation in detection (again an implied increase, at least for the two baitings per year, six baitings per year and unbaited treatment groups) could therefore appear as a variation (increase) in occupancy. Where heterogeneity in capture probability is not included in models to estimate abundance, there will be a negative bias in those abundance estimates (see Pledger *et al*. (2010) and references within). This negative bias may also apply for un-modelled heterogeneity in detection when modelling occupancy.

As suggested for the brushtail possum, the identified pattern of a decreasing probability of occupancy for the southern brown bandicoot in the four baitings per year treatment group warrants further investigation. The link between increased occupancy and higher rainfall is also of concern as the long term climatic effects from reduced rainfall and increased drying as a result of increasing temperatures may see the bandicoot's distribution contract to the central core of the northern jarrah forest (see Chapter 2, Table 2.1 and Fig. 2.3).

5.4.4 Issues with occupancy modelling

The concept of occupancy modelling appeared in the literature in 2002 with the publication by MacKenzie *et al*. (2002). Since that publication, occupancy modelling has been widely mooted to be a survey and analytical technique which allows for collection and analysis of data in a way that is less intensive (or requiring of less data) than with the techniques and analytical tools aimed at estimating abundance. Often this is incorrectly interpreted as meaning there are few assumptions associated occupancy modelling or the assumptions associated with abundance estimates can be relaxed for occupancy modelling. The assumptions of abundance estimation can appear daunting and, as outlined by Cooch and White (2019), are:

(i) The population is assumed to be closed to births, deaths, immigration and emigration within a primary sampling session (i.e. over the short period when sampling may be repeated, e.g. on consecutive days, nights etc.). There are circumstances where this major assumption can be relaxed (see Kendall, 1999); and

(ii) Temporary emigration is assumed to be either completely random, Markovian, or based on a temporary response to first capture. The distinctions between these emigration models is described in Cooch and White (2019); and

(iii) Survival probability is assumed to be the same for all animals in the population, regardless of availability for capture. This is considered the strongest assumption.

The assumptions associated with occupancy modelling, again citing Cooch and White (2019), are equally daunting and are:

1) During each primary sampling session the occupancy status at each site does not change. This is effectively assumption (i) above for abundance estimation and translates to meaning that, during the survey period, sites are closed to changes in occupancy and therefore cannot become locally extinct if initially occupied, nor become occupied if initially unoccupied; and
2) The probability of occupancy remains constant across all sites, or if this is not the case, then any heterogeneity in occupancy can (or in effect must) be modelled by incorporating site specific covariates; and
3) The probability of detection also remains constant across all occupied sites, or again, if this is not the case, then any heterogeneity in detection can be modelled by incorporating site specific covariates; and
4) Detection of the species of interest, and the detection/encounter histories of each site are independent; and
5) The species of concern is not misidentified, specifically no false positives, and detection cannot occur at an unoccupied site.

The reason for adopting occupancy modelling in the northern jarrah forest study, instead of deriving abundance estimates through Pollock's (1982) original robust design method, now known as the Robust Design method (Cooch and White, 2019), was not because of any greater ease in meeting modelling assumptions. Assumption 1), above, for occupancy modelling, is effectively the same as assumption (i) required for the Robust Design. Despite some misinterpretation in the literature as to what this assumption means (see for example McGill, 2013 where this seems to have been interpreted as meaning closure between primary sessions, whereas the intent is closure within each primary session), this is an achievable and reasonable assumption, provided each primary session is short. In the northern jarrah forest study each primary session was limited to four days.

The fourth assumption for occupancy modelling is also reasonable and achievable. Site selection within the northern jarrah forest addressed this assumption as described in Section 5.2.1 and there was no evidence of a lack of independence. Assumption 5) for occupancy modelling was not an issue and was clearly met as, unlike many occupancy modelling programs, the northern jarrah forest deployed trapping techniques and each trapped animal was readily identified. It would have difficult to misidentify another species as a brushtail possum or southern brown bandicoot.

Assumptions 2) and 3) were more problematic, albeit only identified as problematic post data collection and during data analysis. There was no expectation of constant probability for occupancy nor of constant probability for detection across the sites. Heterogeneity in both was assumed and the intent was to model this heterogeneity through site specific covariates. However, for the brushtail possum data, the presence of jarrah and marri veterans was identified as negatively associated with occupancy and the presence of marri piles was negatively and significantly associated with occupancy. All three associations are not only counterintuitive, but conflict with the widely held knowledge of brushtail possum use of, and semi dependence on, tree hollows provided by this age/size class of jarrah and marri. The results also conflict with concurrently collected data on den tree use by the brushtail possum in the northern jarrah forest (de Tores *et al.*, unpublished-b). However, occupancy modelling did confirm the importance of wandoo poles which were positively and significantly associated with brushtail possum occupancy. Similarly, occupancy modelling identified the importance of marri saplings which were also positively and significantly associated with brushtail possum occupancy.

Assumptions 2) and 3) were also problematic when analysing the southern brown bandicoot data, and again only identified as problematic during and post analysis. The southern brown bandicoot's known habitat requirements for nesting and foraging are well documented (Dell, 1971; Dell and How, 1988; Paull, 1995; Paull, 2008) and the species is known to require early successional (post fire) communities when foraging for invertebrates and fungi and dense understorey vegetation as nest sites and protection from predators (Paull, 2008). Given this, the expectation was occupancy modelling would identify variables such as small logs, litter depth and a dense shrub understorey as positively affecting occupancy. Surprisingly, small logs were identified as a negative constraint on occupancy and the variable for the total number of shrubs was identified as a negative constraint on occupancy in the models in which it occurred, and as a significant and negative constraint on detection in every model. The latter result of may reflect reduced foraging in dense understorey, however the negative association with occupancy seems anomalous. The absence of the variable for litter in all but one model (where it was positively but not significantly associated with occurrence) also seems anomalous. Importantly however, occupancy modelling identified the importance of increased rainfall as a significant constraint on occupancy and detection.

A major finding from the occupancy modelling was identifying an increase in the frequency of 1080 baiting did not increase the probability of occupancy for the brushtail possum. The effect on the southern brown bandicoot was more equivocal and the results suggest continued monitoring is required (see below). The results were not unexpected, as the original premise for using the woylie as an indicator species to assess the effectiveness of different baiting frequencies (Chapter 4) was that the *in situ* populations of native fauna were unlikely to reflect any changes in abundance in response to baiting, should it occur, within the duration of the study (see also Chapter 1, pp: 20-22). To accurately assess whether there has been a response to baiting, the baiting frequencies examined would need to be in place for a sufficient period of time to enable the low densities and patchy distribution of native fauna to respond (or not respond) through naturally occurring recruitment. If it has achieved nothing else, occupancy modelling has confirmed the patchy distribution of the brushtail possum and the southern brown bandicoot within the northern jarrah forest. The data should serve as base line information for future surveys and enable comparison with each species' presence after extended periods of baiting. However, occupancy modelling is not the quick fix to use as an argument against data collection to derive abundance estimates.

Occupancy modelling has known, but often overlooked, issues, all of which seemed to be apparent in the northern jarrah forest study. The problems encountered all are of sufficient importance\annoyance to raise questions on future use of occupancy modelling. The first was that fitted probabilities were often zero and equally often, one. Neither was considered a realistic estimate for the data from the northern jarrah forest. Welsh *et al*. (2013a; Welsh *et al.*, 2013b) identified this problem when applying occupancy modelling to survey data for Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*) and Brown Thornbill (*A. pusilla*) in pine (*Pinus radiata*) plantations in south-east NSW. They described how the problem arises as a result of the possibility of maximum likelihood equations having multiple solutions, some of which will produce the probabilities of zero or one. They reported where there were cohorts (sampling years) of no detections (sparse data) of the Yellow-rumped Thornbill the fitted probabilities *"oscillated wildly, showing occupancies of both zero and one"*. The solution they proposed was to use different starting values in the numerical algorithm. Doing this they found the estimates were often similar, but this was not always the case. They also found it difficult to replicate the original default solution (from the default starting value). With the northern jarrah forest data (for the brushtail possum and southern brown bandicoot) changing the starting value did not change the estimate from when it had previously converged (or not converged) and had reported that estimate as zero or one. Changing the starting value(s) was an easy option to trial in MARK, but didn't result in a solution. Unlike the experience reported by Welsh *et al.* (2013b), Program MARK was also able to replicate the estimate provided from the default starting value, but again, this didn't resolve the issue of unrealistic estimates.

In a simulation study Welsh *et al.* (2013b) found even in this *"ideal setting"* (i.e. when the generating model is known) a small percentage (4.6%) of samples resulted in boundary estimates (zeros or ones) and they also found an anomalous result (in 2.4% of samples) which produced a ψ=0 estimate with a non-zero estimate for p. This is impossible for any real world situation, as, if there is no occupancy (i.e. when ψ=0), there is nothing to detect and therefore p must also equal zero. They concluded a ψ =0 estimate should be interpreted as a very low probability of occupancy, and not zero. A similar pragmatic interpretation was used in the northern jarrah forest study for the below zero estimates (flagged ******) for the Lower 95% CI estimates in Table 5.11 (brushtail possum preferred model, derived estimates) and for the below zero estimates in Table 5.16 (southern brown bandicoot preferred model, derived estimates) i.e. where estimates were less than zero for the lower 95% CI estimates for $\hat{\psi}$, a non-zero, but very low value was assumed. The same rationale was applied to the upper 95% CIs for derived estimate for $\hat{\psi}$ from the preferred model for the southern brown bandicoot (Table 5.16) (flagged as *******). In this case, an upper 95% CI >1 was assumed to be 1.

When reporting the results from a simulation of sparse data (i.e. simulating a real world situation) Welsh *et al.* (2013b) found 48% of the samples produced boundary estimates for ψ and p. They also found a tendency for extreme estimates for both ψ and p and for an increase in the variability of the fitted detection estimates. Ironically, the issue of sparse data is often presented as the reason why occupancy modelling is used instead of more robust mark recapture techniques.

One of the recommendations from Welsh *et al.* (2013b), in relation occupancy modelling, addresses the relationship between abundance and occupancy. By introducing abundance to the generating model, they found increasing abundance results in an increase in the probability of occupancy, and vice versa, implying abundance and occupancy are linked. This is not the case. Occupancy may well reflect distribution, but is different from abundance and, as Welsh *et al.* (2013b) point out, occupancy and abundance are very different concepts. It is possible (and probable) to have changes in abundance without a change in occupancy; i.e. there may be a constant number of sites occupied, but each site may experience a quantum change in abundance, while occupancy remains unchanged. Conversely, it is intuitive (in fact a widely cited assumption, see Chapter 3) to expect the probability of detection to increase as abundance increases. Given a key part of ecology is the examination of distribution and abundance, Welsh *et al*. (2013b) suggest "*a focus on detection/occupancy modelling has the potential to detract from rather than add to the discipline of ecology"*. This criticism seems a little harsh, as occupancy modelling appears to have a place, but not as an alternative to abundance estimates.

Occupancy modelling of the brushtail possum and southern brown bandicoot data did clearly identify that the frequency of 1080 baiting was not the determining factor driving the occurrence/distribution of these species within the northern jarrah forest. Fixing the estimates of ψ for each species for the first season, i.e. moving the estimate from zero to 0.001, (flagged *, where occupancy was set as ψ =0.001 and reported in Table 5.9, Table 5.11 and Table 5.14 for the brushtail possum and Table 5.15, Table 5.16 and Table 5.20 for the southern brown bandicoot) enabled credible derived estimates for occupancy ($\hat{\psi}$) for both species and also provided support for some management recommendations (Chapter 6).

Despite the weaknesses experienced with attempting to use occupancy modelling, I can't concur with Welsh et al. (2013b) or McGill (2013) who seem to be suggesting incorporating detection heterogeneity in occupancy modelling studies is too problematic and is perhaps best ignored. However, I do agree incorporating detection in occupancy modelling has issues, so perhaps a more reasonable option is to encourage further development in occupancy modelling and to recognise its limitations. I concur with the recommendation of Welsh et al. (2013b) that occupancy modelling, and the use of binary presence/non-presence data, results in a loss of information which can, and should be utilised when derive abundance estimates. The corollary is that deriving abundance estimates should be the standard when the data are amenable to deriving those estimates. Further, it seems that monitoring or data collection should, as the nominal standard, aim to collect the data required to derive abundance estimates.

The option referred to in Section 5.2.4, of using the Profile Likelihood option in Program MARK to compute the 'profile likelihood confidence interval' and in doing so address the issues of lack of convergence at the boundary, or unrealistic estimates (including estimates for ψ of zero and one), was trialled for both the brushtail possum and southern brown bandicoot data. As discussed in Section 5.4.2 in relation to the brushtail possum, profile likelihood estimates of confidence intervals are based on the log-likelihood function as opposed to standard error and the logit transformation. The manual from Program MARK notes *"for any given parameter, likelihood theory shows that the 2 points 1.92 units down from the maximum of the log-likelihood function provide a 95% confidence interval when there is no extrabinomial variation. The value 1.92 is half of the chi-square value of 3.84 with 1 degree of freedom. Therefore the confidence interval can be computed with the deviance by adding 3.84 to the minimum of the deviance function, where the deviance is the log-likelihood multiplied by -2 minus the -2 log likelihood value of the saturated model"* (Cooch and White, 2019). Although Program MARK provides this option, it assumes extra binomial variation, i.e. a $\hat{c}$ value greater than 1. Given there is no goodness of fit test suitable for occupancy modelling, it seemed imprudent to assume extra binomial variation and pre-emptively adjust the value of $\hat{c}$, although this is an option (changing the value of $\hat{c}$) available in Program MARK. Nonetheless, this was attempted, with $\hat{c}$ trialled over a range of values for 1 to 4 (see Section 4.2.9, p187, as to why $\hat{c}$ values beyond 4 were not trialled, and see also Section 2.5.5, pp:49-51) (see also Lebreton *et al.*, 1992). In most trials, the resulting estimate was slightly improved, but estimates were still unrealistic. A small number of trials resulted in even more extreme estimates for ψ. The use of profile likelihood CIs had an additional limitation, as at least in Program MARK, as it could not be used when ψ or *p* was constrained by individual covariates. This limited its use to the exploratory analysis. The following quote from Gary White[11] seems prudent:

> *"the approach … does not always work correctly because of numerical problems, notably for parameters estimated on the boundary. I have found that often the optimization routine is not always able to move the parameter estimate away from the boundary*
> *"… care should be taken in using the profile likelihood capability because of the numerical problems caused with parameters at the boundary.*

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> *Unfortunately, parameters estimated at the boundary is the primary reason that the profile likelihood interval is desirable”*.

For any real world biological survey data it is reasonable to expect large variations in expected counts. Incorporating heterogeneity in detection in the analysis of data may complicate the analysis, but should not be ignored. I concur with Pacifici *et al*. (2008) who described the relevance of estimating detection probabilities with the comment:

> *“large differences in detection probabilities among species suggest that tailoring monitoring protocols to specific species of interest may produce better estimates than a single protocol applied to a wide range of species”*.

Chapter 6

Summary of findings, the implications from the findings, recommendations for management and future research

6.1 Summary

6.1.1 Woylie survivorship

The findings from Operation Foxglove have significant implications for CALM/DEC's (now the Department of Biodiversity, Conservation and Attractions) Western Shield program. The most immediate issue of concern is the finding in relation to baiting frequency and woylie survivorship. Survivorship of the woylie was found to vary with baiting treatment, with the model averaged estimate for the probability of survivorship over the life of the study 16.4 % higher in the six than in the four baitings per year treatment (Fig. 4.8, reproduced below). The 'best' model (in terms of ΔAICc) to describe the data on survivorship also included a temporal component, where survivorship was reduced when overnight minimum temperatures were 5^0C or lower (Chapter 4, Figs 4.4 & 4.5). Survivorship was also lower for woylies translocated in winter, and for recruits which were radio-collared and added to the monitored sample in winter (i.e. when radio-collared, for the first time, in winter). Possible explanations for the temporal and seasonal covariates were discussed in Chapter 4.

The woylie survivorship data had been previously modelled (de Tores, 1999; de Tores *et al.*, 1998b) and the reported results indicated estimated survivorship was a function of the baiting treatment and the distance from agricultural land. The former (the baiting effect) is consistent with the current findings, the latter (the effect of distance from agricultural land) is not, or the effect is not as linear as previously suggested. The results from current modelling indicated the treatment effect, constrained by a temporal weather covariate and constrained by the individual covariate for release in winter, is a better descriptor of woylie survivorship.

The original analysis (de Tores, 1999; de Tores *et al.*, 1998b) did not consider alternative models and was carried out for a subset of the survivorship data (from the pilot translocations only), which may explain the differences. Relative model support suggests, if distance does influence woylie survivorship, the effect is a reduced estimate of survivorship as the distance from agricultural land increases for the first ~7km, followed by an increase in the estimate of survivorship at distances further than 8km from agricultural land (Fig. 4.7). Irrespective of an effect of distance, the findings infer the increase in estimated survivorship from six baitings per year is of biological significance to the woylie and is required for the protection this iconic species.

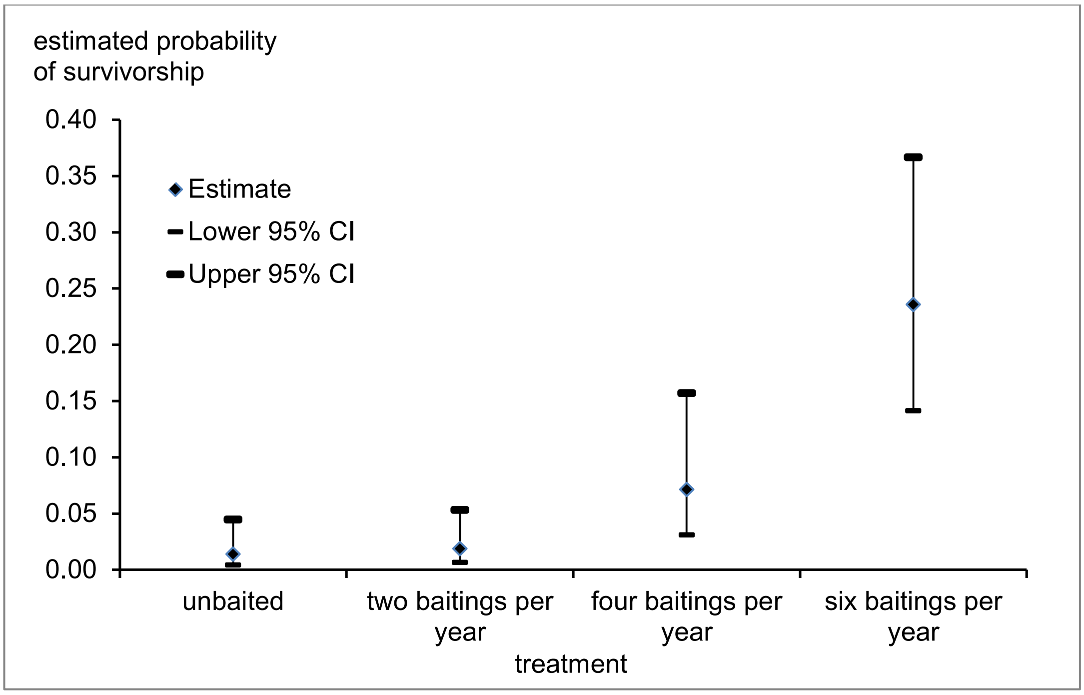

Figure 4.8: Model averaged estimate of survivorship probability for woylies (*Bettongia penicillata ogilbyi*) translocated to baited and unbaited sites within the northern jarrah forest, south-west Western Australia.

Sample size (n)=384. Survivorship probability estimates are unconditional and are for the 37 month duration of the study. Error bars are the 95% confidence intervals based on model weights.

6.1.2 Identification of the species responsible for woylie predation events

There was strong evidence from the operation Foxglove research to show woylie survivorship was limited by fox and cat predation. However, identifying the predator species responsible was subjective and based on the presence, or absence, of a combination of characteristics considered indicative of each predator. There was considerable overlap in these characteristics and many woylie deaths attributed to predation were unable to be specifically attributed to foxes, cats, chuditch or raptors. Consequently, misidentification of the predator responsible may have occurred.

Use of molecular techniques, specifically, collection of predator DNA from woylie carcasses and damaged radio-collars, has been used more recently to successfully identify the predator responsible for woylie mortalities in the post-foxglove northern jarrah forest IACRC study (de Tores *et al.*, unpublished-a). Similarly, the technique was used to identify predators responsible for woylie mortalities at Dryandra Woodland and Tutanning Nature Reserve (Marlow, Williams, Macmahon and Lawson, unpublished data from the IACRC WA Demonstration Site) and for western ringtail possum mortalities at Leschenault Peninsula Conservation Park, Yalgorup National Park, Locke Nature Reserve, Tuart Forest National Park and Gelorup (all coastal sites in south-west WA) (Clarke, 2011; de Tores, 2009). The predator responsible was identified through melt curve analysis (Berry and Sarre, 2007) and in all cases the number of predation events attributable to cats was indicative of a mesopredator release response by cats (see Section 6.4.1, below).

The extent of this phenomenon in the northern jarrah forest Operation Foxglove study may have been masked by misidentification of the predator responsible for woylie mortalities. Irrespective of the possibility of a mesopredator release of cats, this result suggests cat predation, as well as fox predation, may be limiting the survival of native fauna.

6.1.3 The baiting regime and monitoring of foxes and cats

The MKTBA estimates of fox abundance demonstrated it is possible to monitor and derive meaningful estimates of fox abundance. The results concur with conclusion that fox abundance influences the pattern of woylie survivorship, with fox abundance estimated (albeit with overlapping 95%BCIs) to be lowest in the six baitings per year treatment (Fig 3.15, reproduced below), where estimates of woylie survivorship were highest (Fig. 4.8, above).

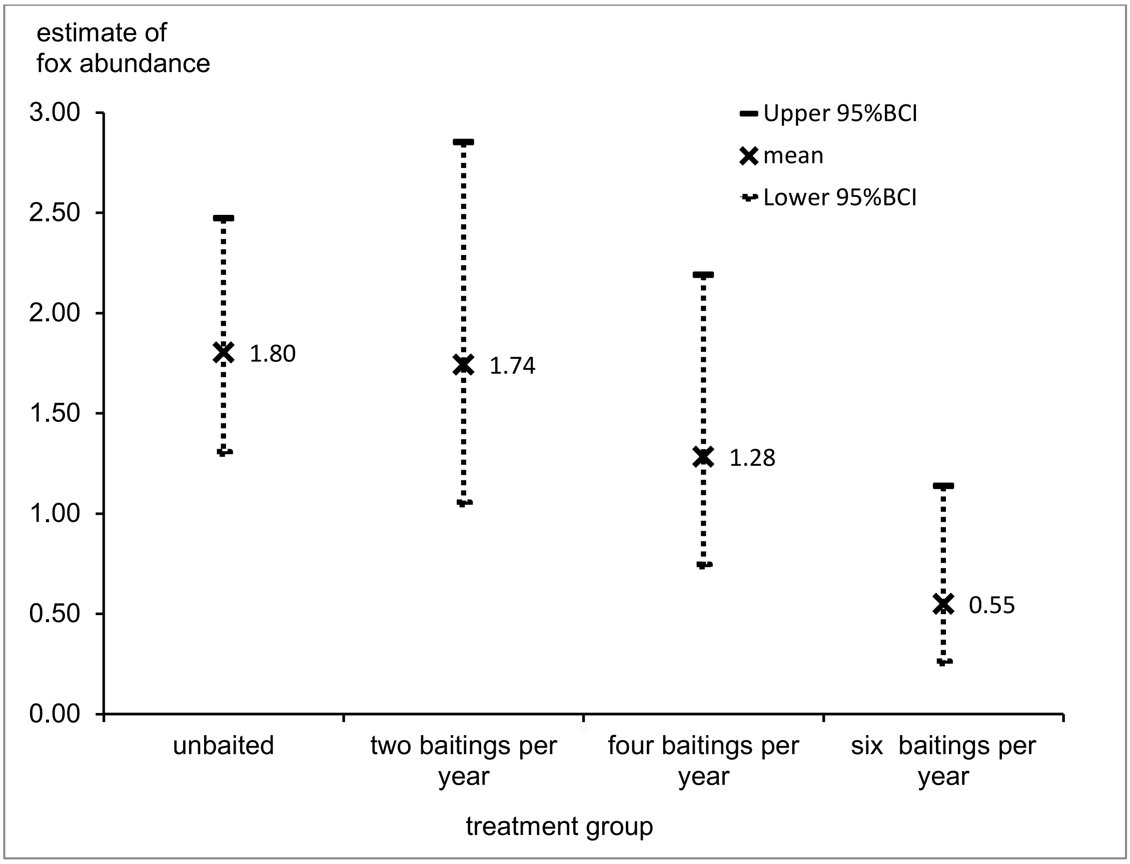

Figure 3.15: Modelled estimates fox (*Vulpes vulpes*) abundance within the northern jarrah forest, south-west Western Australia, derived from the preferred model from the year 3 'bayesmh' Poisson regression models with informative priors.

Fox abundance refers to the modelled estimate of the minimum number of foxes known to be alive (MKTBA) within the area encompassed by the MCP which captures the 25 sandplots monitored for evidence of fox activity. Upper and lower 95%BCI refer to the Bayesian 95% equal-tailed credible intervals.

Specific recommendations in relation to baiting over large areas of forest are:

1. When 1080 baiting over large areas of forest (broadly defined as areas greater than 20,000ha.) managed for the protection of predation-sensitive terrestrial native fauna, the baiting regime should be at a frequency of six baitings per year and at an intensity of five baits/km^2.
2. Aerial delivery of baits is recommended and, if neighbouring land uses preclude aerial deliver to forest boundaries (e.g. when there are neighbour sensitivities due to the presence working cattle/sheep-dogs, or domestic pets, dogs in particular), the aerial delivery should incorporate a no-delivery buffer zone of the perimeter areas. This buffer zone should also be baited, using vehicle based delivery of baits, at the same frequency and intensity as the aerial delivery. The timing should coincide with the aerial delivery.

3. The recommended schedule for bait delivery is January, March, May-June, July, September and November, but should be flexible enough to accommodate logistical constraints and unseasonal weather conditions and take advantage of favourable weather conditions, whilst attempting to ensure:
    (i) an early to mid-summer (January) and late summer (March) delivery (to coincide with any fox cub dispersal which may be occurring from natal home range territories or areas of occupancy);
    (ii) a May-June and July delivery (to coincide with vixen gestation and mating peaks, when male fox home range may break down); and
    (iii) a September delivery (when vixens are most likely to be under lactation stress and cubs are present).

Monitoring of fox and cat populations is not a trivial undertaking and requires a considerable investment of resources. However, in the absence of meaningful monitoring programs, the effectiveness of baiting (in terms of resource allocation for the baiting program and the conservation outcomes) cannot be assessed.

The methodology adopted in the northern jarrah forest research was extremely labour intensive and had site-specific design and data interpretation idiosyncrasies (i.e. it relied on a recognisable pattern of fox interactions with sandplots and also relied on the presence of contagion). The technique was ineffective at monitoring cat presence, let alone cat abundance. Consequently, the method used in the northern jarrah forest research to monitor foxes and cats is not recommended for use elsewhere. The alternative methodology, as describe in Chapter 3 (Section 3.6), is recommended for forest areas and for large areas of conservation estate generally.

6.1.4 Monitoring of native fauna

Despite ongoing baiting of large tracts of conservation estate, many of the initial fauna recoveries and translocation successes in Western Australia from the 1980s and 1990s have not been sustained. The reasons for these declines, or lack of recovery, or lack of translocation success are still largely unknown. This is in part due to the absence of appropriate monitoring and/or quantitative analysis of the monitoring data which has been collected and in part due to the short-term time frame of the monitoring program.

Although only partially informative, occupancy modelling (Chapter 5) indicated factors other than baiting frequency as explanatory variables to describe the probability of occupancy for the brushtail possum. Similarly, the effect of baiting frequency on the probability of occupancy for southern brown bandicoot was equivocal. In both cases the results were anticipated, as the original premise for using the woylie as an indicator species to assess the effectiveness of different baiting frequencies (Chapter 4) was that the *in situ* populations of native fauna (including the brushtail possum and southern brown bandicoot) were unlikely to reflect a change in abundance, should it occur, in response to baiting over the limited duration of the study (see also Chapter 1, pp: 20-22). To accurately assess whether the suite of native species within the northern jarrah forest shows a response to baiting, the baiting frequencies examined would need to be in place for a sufficient period of time to enable the low densities and patchy distribution of native fauna to respond (or not respond) through naturally occurring recruitment (reproduction and colonisation). Occupancy modelling is not the recommended tool to assess this response.

As with monitoring of fox and cat populations, monitoring of native predator and prey species is not a trivial undertaking and requires a considerable investment of resources. This may also require a commitment to longer-term monitoring. In the absence of meaningful monitoring programs, the effectiveness of baiting cannot be assessed. The requirement for studies to be relatively long-term (i.e. over more than one generation of the species of concern) has been widely recognised if the intent of the study is to elucidate a greater understanding of ecological processes (see for example Briggs and Borer, 2005; Dickman *et al.*, 1999; Fox, 1996; Gutierrez *et al.*, 2010). However, long-term studies should only be undertaken when the study is addressing questions about the long-term dynamics of a population or species or ecosystem, or involving systems subject to long-term time trends or high environmental variability (Krebs, 1991) and should not be undertaken simply to *"glorify long-term studies per se"* (Krebs, 1995).

The findings from short and long-term manipulation experiments on seed-eating rodents and ants in studies in the Chihuahuan Desert, Portal, Arizona, USA (Brown *et al.*, 2001; Resetarits Jnr and Bernardo, 1998), highlighted the importance of long term studies. From the Chihuahuan Desert short-term studies it was shown rodent populations and plant production increased after seasons of exceptionally heavy precipitation, and decreased in the intervening periods (Beatley, 1969; French *et al.*, 1974; Whitford, 1976). However, the findings of longer-term studies (from twenty-five years of data) revealed rodent populations sometimes increased during droughts (the reverse of the short-term findings) and failed to increase after exceptionally rainy periods with at least three factors contributing to a more complex dynamic: *"(i) plant* *growth and seed production were affected as much by the temporal pattern as by the overall quantity of precipitation within a season; (ii) predation, seed storage from previous seasons, and other factors mediated the response of rodent populations to fluctuations in food supply; and (iii) extreme rainfall events caused extensive rodent mortality, introducing a nonlinear component into the relation between precipitation and rodent populations"* (Brown, 2001). The long-term study also identified the dynamics of rodent populations were complex. Where three dominant species of *Dipodomys* were removed, other seed-eating rodents increased in abundance, which in turn led to increased competition for resources between these species. However this response was variable, and increases in abundance were also attributed to colonisation (Ernest and Brown, 2001; Heske *et al.*, 1994; Resetarits Jnr and Bernardo, 1998; Valone and Brown, 1995). None of these responses had been detected in short-term observational or experimental studies (Brown *et al.*, 2001). The benefits from monitoring over the long-term are eloquently summed up by Holt (2000) as: *"effects that emerge from reshuffling of the species pool will play out only over long timescales in terrestrial ecosystems".*

As identified in Chapter 3, there seems limited value in carrying out fox baiting programs for fauna conservation purposes if foxes (and cats and native predators) are not effectively monitored. The same applies to monitoring populations of the native prey species requiring protection. Monitoring is required in a way to enable inference and informed management decisions to be made as to the effectiveness of the control measures adopted. Such monitoring should adopt and an experimental and mechanistic approach, or the "deterministic paradigm" (Krebs, 1991; Krebs, 1995; 2002; 2003).

For the *Western Shield* program to achieve this, it will require a quantum shift in the approach to native fauna monitoring and a strategic move away from reporting capture success rates from three day roadside transect trapping (convenience trapping) to the use of more quantitative techniques which focus on deriving estimates of abundance. This could be achieved by a shift to the use of trapping grids (or webs) established to representatively sample habitat types and with each trapping session extended over a slightly longer period (four or five days) (see White, 2020). Of course exceptions to the use of trapping grids will occur, as may be the case when monitoring species known to be restricted to microhabitats or linear habitat patches, for example the quokka (Gibson *et al.*, 2010; Hayward, 2008; Hayward *et al.*, 2005; Hayward *et al.*, 2004) and the bush rat (Banks, 1999). Nonetheless, a quantitative approach is still recommended to enable estimates of abundance to be derived. This quantum shift will also require monitoring of control sites and monitoring to assess the abundance of foxes, cats and native mesopredators.

> *"Monitoring of populations is politically attractive but ecologically banal unless it is coupled with experimental work to understand the mechanisms behind system changes"* (Krebs, 1991).

Specific recommendations in relation to monitoring the native fauna response to repeated 1080 baiting are:

1. Monitoring of native fauna to assess the effectiveness of 1080 baiting, in terms of a native fauna response, should be undertaken in conjunction with the monitoring protocols recommended for foxes and cats, described above (Chapter 3).
2. This monitoring should aim to establish long-term monitoring sites to representatively sample the habitat (structure and floristics) within the baited and unbaited areas.
3. Monitoring protocols should be specifically formulated and designed to ensure the field methodologies are appropriate for the target species (plural) and resources are available (including human resources) to enable continuity of monitoring. Implicit in this is the requirement to move away from convenience monitoring (see Anderson, 2001). As the name suggests, convenience monitoring includes sampling at positions of convenience for the researcher or manager. This may be along roads, easily accessible geographic features, recreation sites and known locations of high density for the species being sampled. The results of convenience trapping have the potential to be of limited inference value as they provide information about the features, or the occurrence of a particular species in relation to those features.
4. Resources also need to be secured for data management, data analysis and reporting.
5. It is strongly recommended that monitoring data are analysed in an information-theoretic and/or Bayesian framework.

6.1.5 Ecological research at a landscape scale - pseudoreplication

Section 2.3.1 and Section 2.3.2 detailed the scope of the research as proposed at a landscape scale and identified:

(i) there was an anticipated, or expected gross effect from fox baiting at a landscape scale;

(ii) the cost of replication would have been prohibitive; and
(iii) there were no sites suitable to plausibly replicate the northern jarrah forest.

Therefore, by necessity, the northern jarrah forest incorporated pseudoreplication in the manner described by Hurlbert (1984). The necessity was because the intent was to identify whether the effect of predation was evident at a landscape scale. The results have shown, at this scale and across a landscape with sites showing heterogeneity in position in the landform, soil type, rainfall, vegetation structure, floristics, and disturbance patterns, there was a recognisable pattern of increased woylie survivorship in the treatment baited most frequently, i.e. the six baitings per year treatment. An alternative approach, with the traditional random allocation of treatments over multiple (replicated) sites, would, by necessity, have required a number of smaller (replicated) sites. These sites would also have shown heterogeneity in the attributes above. The data could have then been analysed in the conventional manner to assess the effect of the treatment, however, this would have provided no information on the treatment effect of baiting at a landscape scale.

Most terrestrial studies which have examined the role of apex or top order predators through the use of predator density manipulation have been conducted at relatively small scales. Similarly, prior to the northern jarrah forest research and with the exception of studies carried out within fenced exclosures/enclosures, Australian studies where there was experimental manipulation of fox density, and concurrent assessment of fox abundance and assessment of native prey response had only been conducted at a small scale. This is no doubt a reflection of the difficulties associated with large scale fox density manipulation. In a fox removal study in Namadgi National Park, south-east New South Wales (Banks, 1999), fox removal sites were replicated (two sites), however the area over which fox density was manipulated appeared to be small and were only vaguely described as 10-18km^2. There were also issues associated with the fox density manipulation (see Section 6.3). Similarly, in a fox density reduction study at Lake Burrendong, central New South Wales (Molsher *et al.*, 2017), the two removal sites were relatively small and again only vaguely described as 10-19km^2, presumably with the largest site (a non-removal site) being the 19km^2 site. Fox abundance was determined through a derived index from spotlight data, and as well as being subject to the vagaries of indices (see Section 3.2.2 and Section 3.2.3), appears to have also not conformed with the assumptions required for deriving abundance estimates from spotlighting (see Buckland *et al.*, 2001; 2004). Nonetheless, the study highlighted the difficulties in replicating a fox abundance manipulation study at a scale above that which would be considered trivial.

In ecological research, true replication is traditionally applied to small field trials where there are different expectations from the research and where multiple replicates can be easily accommodated logistically and at little additional cost. This is not the case for landscape scale research. Criticism of pseudoreplication in ecological studies seems fixated in statistical methods developed for agricultural trials developed more than 70 years ago. Such criticisms may be appropriate for experiments suited to small randomised block designs and null hypothesis testing, however "*no statistical test can show the existence of any biological phenomenon. Such a test can only tell us whether or not there is something in the data that is not easily explained away as being the result of pure chance"* (Reddingius and den Boer, 1989). Contrasting with this, contemporary statistical approaches (in particular, model selection and inference) are particularly appropriate to large-scale ecological experiments. Despite this, Hawkins (1986) noted *"some … reviewers may too zealously embrace an emerging war against pseudoreplication"*.

In Hurlbert's paper he clearly identified that pseudoreplication does not equate with such studies having a lack of scientific value (Heffner *et al.*, 1996). Critiques which identify pseudoreplication as a study's weakness invariably cite Hurlbert, yet they tend to omit that Hurlbert (1984) noted *"Replication is often impossible or undesirable when very large-scale systems (whole lakes, watersheds, rivers, etc.) are studied. When gross effects of a treatment are anticipated, or when only a rough estimate of effect is required, or when the cost of replication is very great, experiments involving unreplicated treatments may also be the only or best option"*.

As replication at a landscape scale is often nearly impossible, especially where there are large-scale environmental gradients, it may be that the spatial and temporal scales of experiments are more important than replication (Oksanen, 2001). Further, *"the concept* 'pseudoreplication' *amounts to entirely unwarranted stigmatization of a reasonable way to test predictions referring to large-scale systems"* (Oksanen, 2001).

6.2 Woylies in the northern jarrah forest post the current study

Despite previous recommendations to increase the frequency of baiting over large expanses of forest to six baitings per year, the Western Shield program has retained an 'operational' baiting regime with a bating frequency of four baitings per year. The consequences of this lower baiting frequency became evident at the commencement of the research undertaken as part of the IACRC Western Australian Demonstration Site. In the IACRC study, a remnant population of woylies was found to have persisted at George Forest Block (i.e. at the location of the George trapping grid which is within 5km of agricultural land and within the six baitings per year treatment of Operation Foxglove, Chapter 4, Fig. 4.1). In the period between Operation Foxglove finishing (2000) and the commencement of the IACRC Demonstration Site in the northern jarrah forest (2006), the Operation Foxglove baiting regimes were not maintained and baiting reverted to four baitings per year. Perimeter baiting (i.e. baiting in the stand-off zones at the forest and agricultural land interface, where aerial delivery is not carried out and baits are delivered from vehicles) was also not maintained during this period. Woylie radio-collars had been removed at completion of Operation Foxglove monitoring and there was no further monitoring of the surviving woylies. During the period post Operation Foxglove there was a documented decline in the status of the woylie (Groom, 2010) and the species was relisted as 'Threatened' in accordance with the Australian EPBC Act and as 'Endangered' in accordance with the IUCN The IUCN Red List.

At commencement the IACRC study, baiting at George Forest Block, and within much of the former Operation Foxglove study area, was reinstated at a frequency of six baitings per year. The remnant population of woylies within George Forest Block was identified and monitored. During the IACRC study the woylie population showed a progressive increase in abundance (Fig. 6.1) and, with the exception of populations within predator exclusion enclosures, was the only population known to have increased in abundance in the decade spanning 2001-2010, i.e. within the period when the woylie declined elsewhere throughout its range and was re-listed as a threatened species.

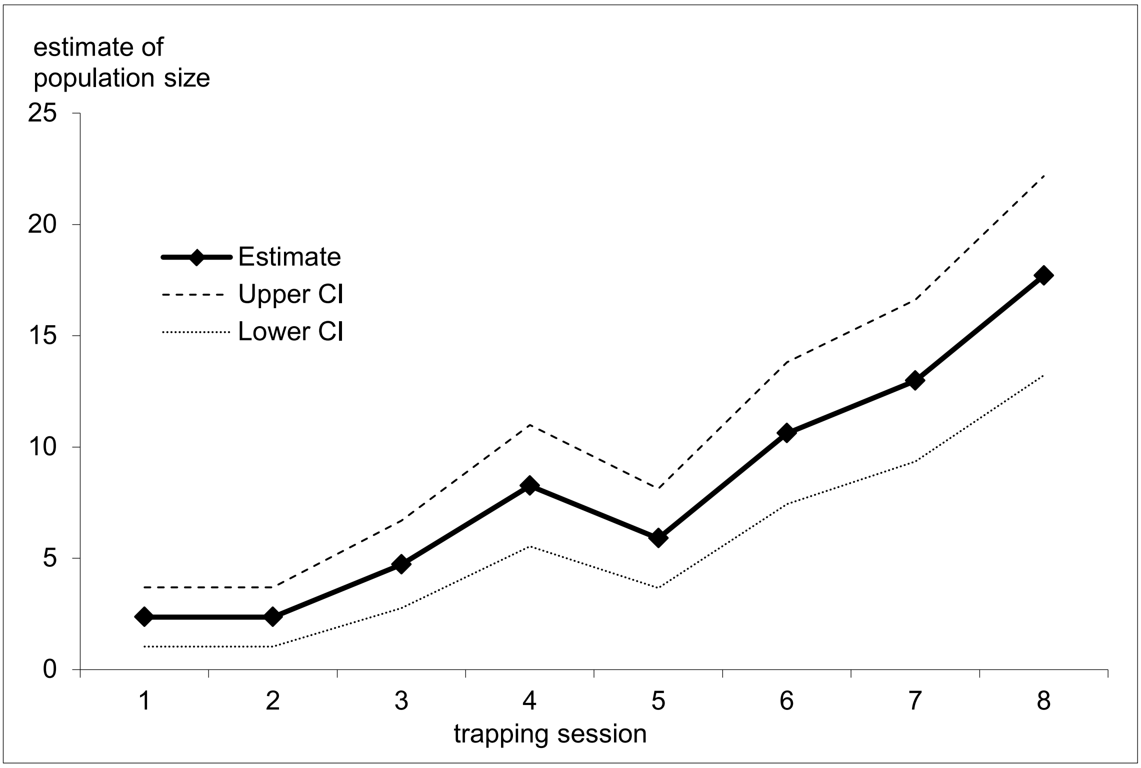

Figure 6.1: Population estimates for the woylie (*Bettongia penicillata ogilbyi*) within George Forest Block, northern jarrah forest south-west Western Australia.

Estimates were derived from analysis of mark recapture data from eight trapping sessions from Spring 2007 to Spring 2009 using the Robust Design, Huggins Full Heterogeneity Model from Program MARK (White, 2001).

The results from trapping and the woylie population estimates are consistent with northern jarrah forest Operation Foxglove results and supportive of the recommendation to increase the Western Shield baiting frequency to six baitings per year, at least where large areas of forest are baited.

6.3 The biodiversity conservation implications from the northern jarrah forest research in the context of the historical ecological literature

Irrespective of the baiting regime, repeated 1080 baiting for fox control is not a panacea for the conservation issues arising from fox predation. However, it does provide the opportunity for *in situ* and translocated populations of predation sensitive species to increase in number and potentially establish self-sustaining populations, as demonstrated by the woylie population from George Forest Block. However, for these populations to continue to be self-sustaining, by definition, they must be able to withstand some degree of predation, whether it be predation by native predators, introduced predators, or both. Unlike predator-proof fencing, which provides a barrier not only to introduced predators but also to native prey and native predators, repeated

1080 baiting allows for the potential for unrestricted emigration and immigration of native predator and prey species. The long-term biodiversity conservation implications of unrestricted immigration and emigration of native species, combined with effective control of introduced predators (specifically foxes) through repeated baiting are profound in two ways (de Tores and Marlow, 2012). Firstly; although native prey species are thought to have some inherent genetic ability to recognise a generalised mammalian predator (McLean *et al.*, 1996), introduced predators are considered to have a significantly greater predation effect than native predators (McLean *et al.*, 1996; Salo *et al.*, 2007) and this effect can be mitigated by effective fox. Secondly; with increased diversity of native predators, the diversity of prey may increase (Paine, 1966), food web stability is enhanced (Gross *et al.*, 2009; MacArthur, 1955; McCann and Hastings, 1997; McCann *et al.*, 1998; Paine, 1966; Polis, 1998; Polis *et al.*, 2000), animal populations fluctuate less violently and reduce the numerical variability of the ecosystem (Solomon, 1949) and intra-guild predator interactions increase (Finke and Denno, 2004). This in turn can dampen the negative effects from trophic cascades (Finke and Denno, 2004; McCann *et al.*, 1998). However, the arguments for and against the belief that ecosystem complexity contributes to food web stability are confounded by the inconsistency in the terminology. Over time, ecologists' have changed their understanding and interpretation of what exactly is meant by terms such as food-chains, trophic levels, trophic cascades, guilds, population regulation, population limiting factors and population regulating factors.

The trophic dynamic viewpoint introduced by Hairston *et al*. (1960) (see below) did not fit well with the earlier beliefs which had dominated the ecological literature and which had advocated complexity in food webs was destabilising. The guild concept was introduced by Root (1967) who defined a guild as *"a group of species that exploit the same class of environmental resources in a similar way"*. The concept provided a means by which to group together species *"without regard to taxonomic position, that overlap significantly in their niche requirements"*. The term arose from a study on the exploitative behaviour of the blue-gray gnatcatcher (*Polioptila caerulea*), a small passerine which feeds exclusively upon arthropods (Root, 1967). The concept drew on the Elton-Hutchinson-Macfadyen niche ideas (Elton, 1927; Hutchinson, 1953; 1957; Macfadyen, 1957). Root (1967) acknowledged membership of any guild was *"somewhat arbitrary"* and although the *"foliage-gleaning"* guild he described included only five species, there were nine other passerines which, at some stage in their feeding behaviour were leaf-gleaners and presumably could have been included in the foliage-gleaning guild.

Although the guild definition of Root (1967) allows for a *"resource-centred classification of community components rather than one based on taxonomic affinities"* (Hawkins and MacMahon, 1989), the term 'guild' has been widely used for different purposes and for community groups based largely on taxonomic criteria (see examples cited by Hawkins and MacMahon, 1989). Hawkins and MacMahon (1989) also pointed out the weakness in Root's (1967) definition which grouped guild members on the basis of them using a resource in the same manner. Hawkins and MacMahon (1989) proposed the guild concept to be most useful when a guild includes a variety of interacting taxa, whose members overlap in space and time and do not necessarily use a resource in the same manner. Hence the terms 'guild' and 'trophic level' are sometimes, used interchangeably, and not necessarily consistently.

The trophic dynamic viewpoint of Hairston *et al.* (1960) described a concept based on a three-tiered/three-trophic level system of carnivores, producers (herbivores) and plant. Hairston *et al.* (1960) believed: (1) each trophic level was limited by its respective resources in the classical density-dependent fashion; (2) Interspecific competition exists among the members of each of these three trophic levels; and (3) herbivores were seldom food-limited, and are most often predator-limited. The three-tiered/three-tropic level food chain, or the trophic dynamic view, is often referred to as the Green World Hypothesis (GWH) as a simplification to explain "why the world is green": carnivores suppress herbivores, which in turn release grazing/browsing pressure which therefore allows plants to grow unimpeded (Hairston *et al.*, 1960). At the time, the GWH was seen as heretical (see the criticisms by Ehrlich and Birch, 1967; Murdoch, 1966) as it contradicted the widely held views of respected ecologists (in particular the views of Andrewartha and Birch, 1954; Birch, 1957; Lack, 1954) whereby populations were considered to be primarily regulated by food availability and environmental conditions only, and in particular by climate (i.e. bottom-up regulation) with almost all populations considered to be resource limited and trophic exploitation (i.e. the model proposed by Hairston *et al.*, 1960) considered negligible with 'top-down' interactions (i.e., predation, herbivory) relatively unimportant (Meserve *et al.*, 1999).

The trophic dynamic viewpoint was subsequently supported by modelling (Rosenzweig, 1973; Rosenzweig and MacArthur, 1963) and laboratory studies (Slobodkin, 1961). The Hairston *et al.* (1960) linear three link model (three trophic levels) was also expanded to allow for non-integer food chains (Fretwell, 1977; 1987; Oksanen *et al.*, 1981). These non-integer food chain model(s) acknowledged the concept that prey species (such as grazing herbivores) displayed different levels of grazing efficiency and competition existed between grazing herbivore species (i.e. competing for the browsing/grazing resource). The concepts were not new and were based on well-founded food-web concepts (dating back to Elton, 1927). The tropic dynamic viewpoint (Hairston *et al.*, 1960) also acknowledged the existence of different levels of prey susceptibility to predation, differences in predators' efficiency, differences in predator efficiency as a consequence of predator size (see also the review by Diehl, 1993). However, it did not discuss trophic levels above the third level (Oksanen, 1991), whereas aquatic systems had long recognised the existence of primary and secondary predation, or a fourth trophic level (see for example Paine, 1966; Paine, 1980).

In an impressive review, Oksanen (1991) summarised what he felt was the underlying logic of Hairston *et al.* (1960). He described this in a framework of the energy capturing adaptations required of each trophic level, with different kinds of adaptations required to photosynthesize; to consume fibre-rich vegetative plant organs; and to capture mobile prey. He further argued no organism can efficiently combine any two of these ways of energy intake. Omnivores appeared to be the exception, and Oksanen (1991) recognised that omnivores can both utilise plant nutrients and prey on other animals, they are inefficient grazers and are functionally members of the carnivore trophic level, as had been stated by Hairston *et al.* (1960).

The GWH led to the 'exploitative ecosystem hypothesis' or EEH (Fretwell, 1987; Oksanen and Oksanen, 2000; Oksanen *et al.*, 1981), where plant biomass reflects the primary productivity, and below some productivity threshold herbivore biomass is insufficient to support predators (Meserve *et al.*, 1999). In this situation herbivores have weak effects on plants. In more productive environments, where herbivores are able to reach higher densities, predators can exert strong effects on herbivores and herbivores can then become regulated by predation (Meserve *et al.*, 1999). Further, gradients of decreasing primary productivity predict the number of trophic links, e.g. a three link trophic dynamic (inorganic resources – plants – folivores – predators) with decreasing primary productivity reduces to a two-link dynamic (inorganic resources – plants – folivores) (Oksanen and Oksanen, 2000).

Although the EEH is considered by some to reconcile the conflicting views of 'bottom-up' and 'top-down' limitation/regulation (see for example Choquenot and Forsyth, 2013), the dynamics of each system will be different. Trophic guilds will rarely act as homogenous blocks (Oksanen and Oksanen, 2000) and although general "*theories can organize our thinking and give directions for more specific ideas, … they will never* *suffice as comprehensive explanations of dynamics in any system"* (Oksanen and Oksanen, 2000).

With further reference to the seminal paper by Hairston *et al*. (1960), Polis *et al*. (2000) believed, somewhat unjustly, that the authors were unrealistic to simplify communities into linear food chains. This seems to overlook the importance of the second of the three conclusions of Hairston *et al*. (1960), namely, *"interspecific competition must necessarily exist among the members of each of these three trophic levels."* By inference, not only are there complex interactions within a trophic level, these trophic levels are inextricably linked through interactions between trophic levels. It would therefore appear the conclusions of Hairston *et al*. (1960) are not ignoring that more complex and non-linear relationships exist across the food-web, but provide a conceptual framework to progress the understanding of a much greater complexity.

The Hairston *et al*. (1960) trophic dynamic viewpoint also incorporated the concept of a "donor-controlled predator" (or the doomed surplus hypothesis) as had been demonstrated to exist in the famous studies of mink (*Mustela vison*) predation on muskrats (*Ondatra zibethica*) (Errington, 1946a; Errington, 1946b; Errington, 1963). The doomed surplus hypothesis advocates that predation is not limiting prey population growth and predators consume only those prey which are excluded from territories, or are sick or starving. As a consequence, only those individual prey which were "doomed" to not survive are consumed by predators. Banks (1999) believed the doomed surplus theory was supported in a study of fox predation on the native bush rat (*Rattus fuscipes*) at Namadgi National Park, in the Australian Capital Territory, where fox density reduction did not result in an increase in bush rat abundance. Interestingly Banks (1999) made his conclusion with several caveats, including the possibility of compensatory predation (mesopredator release) to explain the lack of a detectable response in the bush rat populations. Banks (1999) conclusion regarding the bush rat population size was also of concern as it was reported as an index based on minimum known to be alive (MKTA) estimates from only three consecutive nights trapping (see Section 6.1.4). Similarly, the paper which describes how estimates of fox 'density' were derived (Banks *et al.*, 1998) noted these estimates were based on three disparate indices which did not concur with each other. These analyses are subject to all of the weaknesses associated with using unvalidated indices (see Chapter 3, Section 3.2.2 and Section 3.2.3). Additionally, where spotlighting was used as an index to fox abundance, it relied on a count of animals/km over three to four consecutive nights each month. This method is highly questionable and violates many of the assumptions for deriving an estimate of abundance (and an index) from spotlight transects (see Buckland *et al.*, 2001; 2004). In addition to these concerns, the results noted *"despite a clear decline in local fox activity, baits were continually taken by reinvading foxes"* which clearly suggest foxes were still present at the fox abundance reduction sites. Further, Banks *et al*. (1998) noted fox "densities" (with no explanation how indices were converted to density) were initially lower at the sites were no fox control had been undertaken, with 12 to 18 months required before indices derived from nontoxic bait uptake indicated more baits were taken at the non-removal sites. Again the latter is an index of activity which may, or may not, correlate with abundance (see Chapter 3). Collectively, these concerns suggest a more cautious interpretation should have been taken before concluding the data support the doomed surplus theory.

The doomed surplus theory has been dismissed by some authors (see for example Sinclair and Pech, 1996). Krebs (1991) noted the prevalence of the doomed surplus view as a possible reason why the importance of predation was consistently underestimated as relevant to species which show short-term and long-term population cycling (Krebs, 1991). Sinclair and Pech (1996) believed these "doomed" animals still contribute to the population size as their death is not instantaneous, i.e. when alive they contribute to the population size. Therefore, predation of these "doomed" individuals does contribute to lowering the population size in the same way as predation of other individuals in the population reduces the population size.

Sinclair and Pech (1996) also advocated the concept of density dependence, where a population's birth rate, death rate, or both, change in response to the population density. Some authors (see for example Dempster, 1983) extended the concept of density dependence to include where a population's immigration and emigration rates also change in response to the population density. As such, immigration rates decrease and emigration rates increase as the population increases. Caughley and Sinclair (1994) defined density-dependence as occurring where *"either the proportion of the population dying increases or the proportion entering as births decreases as population density increases"*. Factors (environmental and otherwise) which cause these changes in birth and death rates are termed density-dependent factors. Again, the concepts were not new for ecologists and have been used historically to explain the generally sigmoid shape of the curve to describe the change in a population size over time. Contrasting with this is density-independence, where these rates, for example the reproductive rate, are unrelated to population density. Further, the two (density-dependence and density-independence) need not be mutually exclusive (Horn, 1968) and may both occur over all age classes. Inverse density-dependent is different again, and describes where, for example, predation can be destabilising and the rate of predation decreases as the prey population increases. This allows the prey population to rapidly increase, or conversely where the rate of predation increases as the prey population decreases and the population is driven down (Caughley and Sinclair, 1994).

The density-dependence theory advocates that although populations may fluctuate as a result of stochastic events, they remain ‘stable’, or within certain bounds or thresholds, with populations persisting indefinitely. When disturbed from a stable point (e.g. as a result of extreme environmental conditions, or other limiting factors), populations return to these stable points through density-dependent factors (such as predation) (Caughley and Sinclair, 1994; Dempster, 1983; Varley *et al.*, 1973). Staying between these is called ‘stabilisation’ (Reddingius and den Boer, 1989). Murray (Murray Jr, 1982) believed the concept of density-dependence could not be appreciated without (or separated from) the concept of density-dependent factors.

Where, for example, predation acts in a density-dependent way to return a population to a ‘stable’ point, the population is said to be ‘regulated’ by predation. The reverse is not necessarily true, i.e. not all density-dependent factors will act to regulate a population around a stable equilibrium (Hanski, 1990; Wolda, 1989). Where populations stay within narrow bounds or limits and are considered ‘stabilised’ without the presence of density-dependent factors, the term ‘regulation’ does not apply (Caughley and Sinclair, 1994; Reddingius and den Boer, 1989). It is only considered to be ‘regulation’ when this stabilisation results from density-dependent processes. Conversely, population regulation ‘requires’ the presence of density-dependent factors (Caughley and Sinclair, 1994; Reddingius and den Boer, 1989)

Although multiple density-dependent factors have the potential to regulate a population through density-dependence, as noted above, predation (and other factors) can also act in de-stabilising or inverse density dependent ways. Confusion exists in the literature where the terms are used incorrectly and interchangeably or when not clearly defined. Similarly, there is inconsistency in the literature when the terms population ‘regulating factors’ and population ‘limiting factors’ are used interchangeably.

The density-dependence theory/paradigm/approach was *“pioneered by L. 0. Howard and W. F. Fiske”* (Krebs, 1995), championed by Nicholson (1933) and Nicholson and Bailey (1935) and has been advocated by multiple authors (see for example Caughley and Sinclair, 1994; Charlesworth, 1981; Dennis and Otten, 2000; Gleeson, 1994; Hanski, 1990; Hassell, 1981; Hassell, 1986; Lima *et al.*, 1999; Lindstrom, 1991; Ricklefs, 1990; Sinclair, 1989). Importantly, the theory doesn't assume some constant stability point, but assumes a state of oscillation around an equilibrium density which may change with environmental conditions (Nicholson, 1954; Nicholson and Bailey, 1935), or assumes that *"some processes tend to stabilise population size"* (Krebs, 2002). Nicholson and Bailey (1935) concluded these oscillations *"may decrease, remain constant, or increase with time"* and in the latter situation the oscillating population may ultimately split into numerous smaller populations which in turn show oscillating densities. Strong (1986) introduced the concept of 'density-vagueness' in recognition that ecological systems in reality show a great deal of variance in their functions for birth rates and death rates and consequently make concept of an equilibrium stability impossible to measure. Similarly, spatial heterogeneity and the effects of immigration and emigration also contribute to density-vagueness (Strong, 1986).

Confusing the issue further are the concepts of a "functional response" and a "numerical response". The numerical response is simply the change (increase) in predator density in response of a change (increase) in prey density. The concept was introduced by Solomon (1949) and is closely related to the functional response where individual predators increase their predation/consumption rate as prey density increases (Holling, 1959a; 1959b). Holling (Holling, 1959a; 1959b) identified three types of functional response. Unlike the Lotka-Voltera models of the 1920s, which were inherently unstable, Holling was able to demonstrate one of these, the Type III functional response, resulted in stable regulation of prey populations at low density (Holling, 1959a; 1959b; Ricklefs, 1990).

The ability of predators to regulate prey within these "stable" bounds is itself constrained. In situations where the prey density exceeds the upper limit of the bounds within which density-dependence operates, mortality due to predation will decline. Consequently, prey density will increase (demonstrated regularly in pest species outbreaks) until some other factor(s) act to limit population growth. This phenomenon was described as an *"escape from natural enemies"* (Takahashi, 1964). Takahashi (1964) also identified situations where two alternative stable states may occur (see also the review by May, 1977b). The state to which the system returns may depend on the initial conditions and/or the size of a perturbation (May, 1977b).

Further complexities exist when the concept of prey switching is introduced. MacArthur and Levins (1967) proposed that predation pressure can result in increased niche overlap among prey species and can lead to more coexisting prey species than would occur in the absence of predation pressure. Subsequent modelling (Roughgarden and Feldman, 1975) showed support for this concept/hypothesis and further predicted that strong predation pressure can lead to complete niche overlap for competing prey species (see also May, 1977a).

Different, yet again, is the keystone predator hypothesis, or keystone predator effect, first described by Paine (1966; 1969) for marine species in intertidal zones. The keystone predator effect is a means by which predation on a more competitive prey species enables a less competitive prey species to exist, or more specifically, allows both prey species to co-exist. It is a means by which competitive exclusion is prevented. The phenomenon has also been described as ‘apparent competition’. Consistent with this hypothesis, removal of a ‘keystone predator’ can result in decreased species diversity as a result of competitive exclusion. However, the term ‘keystone’ has been used loosely and often not in accordance with the definition of Paine (1969). Keystone has been used to describe ‘keystone prey’, ‘keystone hosts’, ‘keystone modifiers’ and there is a ‘keystone-herbivore hypothesis’ (see the review by Mills *et al.*, 1993). Mills *et al.* (1993) cautioned against continued use of the term ‘keystone species’ or ‘keystone predators’ and considered doing so *“came with both technical and philosophical liabilities”*. They advocated studies on species’ interactions should focus, not on ‘keystone species’, but on the strengths and consequences of species’ interactions and cited the study by Paine (1992) as an example of this approach. This approach is consistent with the Krebs’ ‘mechanistic paradigm’ which examines, or searches for *“relationships between birth, death and movement rates, and the mechanisms controlling populations, such as disease, predation, food shortage and territoriality”* (Krebs, 1995).

The term ‘keystone species’ was adopted in a study (Estes and Palmisano, 1974) involving sea otters (*Enhydra lutris*), sea urchins (*Strongylocentrotus* sp.) and intertidal kelp beds. Estes and Palmisano (1974) were able to demonstrate that sea otter predation pressure on sea urchins prevented the kelp beds from being overgrazed. Conversely, reducing the sea otter population enabled the sea urchin population to increase which in turn resulted in a significant reduction (overgrazing) of the kelp beds. They concluded the *“sea otter is an important species in determining structures and dynamic relations within nearshore communities”* and fits Paine's (Paine, 1969) concept of a keystone species. This relationship would likely now be described as a trophic cascade, without reference to a keystone species.

The term ‘trophic cascade’ was introduced by Pace *et al*. (1999) with the concept based on the trophic dynamic viewpoint described by Hairston *et al*. (1960). Pace *et al*. (1999) defined ‘trophic cascade’ as where there are *“reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web* … and … *often originate from top predators”*. Hawkins and MacMahon (1989) added to this definition and defined a trophic cascade to include *“the propagation of indirect mutualisms between nonadjacent levels in a food chain*”.

Mesopredator release appears to have first been identified, without being given a name, by Latham (1952) when describing the relationships between the red fox, grey fox (*Urocyon cinereoargenteus*) and three species of weasels (*Mustela*). The term appears to have been coined by Soulé *et al*. (1988) and describes where removal, or reduction in the abundance, of a top order (or apex) predator results in an increase in abundance of smaller, mesopredators. In such cases, the mesopredators may be released from interference competition (including release from intra-guild predation), exploitative competition, or both.

There is mounting evidence to suggest mesopredator release has profound effects on biodiversity (see for example Crooks and Soulé, 1999; Henke and Bryant, 1999). Changes in the abundance of any one predator species, whether it be an apex predator or mesopredator, can be expected to influence not only prey species, but the abundance of other predators. If mesopredator release does occur, it may result in cascading effects on biodiversity (trophic cascades).

Although sometimes reported as only resulting in detrimental effects (see for example Courchamp *et al.*, 1999b), mesopredator release can result in both beneficial (see for example Berger *et al.*, 2008) and detrimental (see for example Bergstrom *et al.*, 2009; Rayner *et al.*, 2007) effects. Management actions can therefore become problematic when these effects become difficult to predict (Polis and Strong, 1996) and when outcomes can be counterintuitive and can vary from being of conservation benefit to being of conservation concern (Rayner *et al.*, 2007; Tompkins and Veltman, 2006).

Beneficial effects from mesopredator release also include increased food-web stability which is thought to occur when species at a high trophic level feed on multiple prey species and when species at an intermediate trophic level are fed upon by multiple predator species (Gross *et al.*, 2009). In addition to this, the top-down effects of mesopredator release are likely to act in concert with, and/or be mediated by, bottom-up effects including ecosystem productivity and by anthropogenic effects including habitat changes (see Elmhagen and Rushton, 2007).

Questions related to:

- if, why and how populations fluctuate;
- the existence of effects from density-dependence and density-dependent factors;
- contrasting viewpoints regarding the importance of bottom-up "regulation" (which it seems should be called limitation, not regulation) and top-down regulation (i.e. density-dependent factors);
- arguments over the term "niche" and over Gause's *"competitive exclusion principle"*;
- disputes as to the existence and/or extent of trophic cascades;
- the contrasting viewpoints on the doomed-surplus theory and the importance of mutualism, parasitism and disease;
- arguments as to the importance of 'keystone' predators and omnivores;
- arguments over the importance of the functional and numerical response; and
- issues relating to mesopredator release

have been debated in the literature since the emergence of the Lotka-Volterra models of the 1920s. Few of the issues have been unambiguously resolved. Given this, I question the claim of Sinclair and Pech (1996) that *"there is now over-whelming evidence for density dependence"*. In support of their argument, Sinclair and Pech (1996) cite, among others, Wolda (1989) who notes quite the opposite, namely:

> *"in spite of impressions to the contrary one may obtain from the literature, the old controversy between 'regulationists'* [which, by definition, requires density-dependence] *… and those who are not convinced that populations in nature are regulated … has never been satisfactorily solved."*

Wolda (1989) further pointed out it was impossible to differentiate "a fluctuating population size from a fluctuating equilibrium value" and noted *"such an equilibrium is a purely theoretical construct whose existence in the field is debatable and whose value cannot be measured"*.

Solomon (1949) had previously noted:

> *"Although population variation is restricted, the view that density generally fluctuates about a mean value, and the related idea that deviations from this mean set up a tendency to return to it, are over-simplifications"*.

It was recognised early in the ecological literature that these issues would not be resolved by debate. In a footnote to the paper by Murdoch (1966) which refuted the conclusions of the landmark paper of Hairston *et al*. (1960), Nelson Hairston and Frederick Smith noted:

> *"We could, of course, present counter arguments, but we feel that little purpose would be served by our doing so. Readers who found the original paper convincing* (the paper by Hairston *et al.*, 1960) *will find it easy to refute Dr. Murdoch's assertions for themselves; those who disagreed with us initially will doubtless continue to disagree, regardless of any arguments that we might present. It is clear that observation and experimentation, rather than argument, will eventually resolve the question."*

The ecological literature has placed a great deal of focus on modelling and tests to validate the equilibrium concept and the concept of density-dependence. This is despite widespread criticism that this focus is misplaced. Such a focus has been described as *"somewhat less than useful in practice"* (Wolda, 1989) and it has been claimed that *"the regulation vs. non-regulation controversy should be quietly buried and quickly be forgotten"* (Wolda, 1995), or the *"density-dependent paradigm is bankrupt because it is descriptive and* a posteriori*. It does not lead to understanding because no mechanisms are specified"* (Krebs, 1991). Krebs (1995) advocated abandoning the density-dependence paradigm *"not but because it is wrong but because it is not useful in achieving an understanding of population dynamics in the field"*.

The situation is further confounded when concepts such as the population limiting hypotheses are proposed as alternatives to density-dependence and population regulation (see for example Murray Jr, 1999). The population limiting hypotheses are considered to be *"a collection of hypotheses"* and describe situations where *"density-independent processes have a density-dependent effect"* (Murray Jr, 1999). The arguments are focused on the existence of the range of densities between a lower critical density (LCD) and an upper critical density (UCD), within which birth and death rates are constant. Below the LCD the birth rate may decrease or the death rate may increase, or both may occur. By way of example, Murray (Murray Jr, 1999) cited the situation analogous to the Allee effect, where individual fitness is positively related to population density (Stephens *et al.*, 1999). Below the LCD, disruption such as reduced encounter rates between potential mates, or reduced effectiveness of anti-predator strategies may result in a reduced birth rate (Courchamp *et al.*, 1999a). Murray (Murray Jr, 1999) considered the UCD as the essential component of the hypotheses, above which resources may decline and result in a decrease in the birth rate, or an increase in the death rate, or both. The amusing aspect to this concept is, as was pointed out by Murray (Murray Jr, 1999), that several reviewers of his population dynamics model could not see how it differed from the density-dependence population regulation model.

The northern jarrah forest research examined the hypothesis that woylie survivorship was a function of fox density, where this fox density itself was a function of baiting frequency. Specifically, woylie survivorship was hypothesised to be highest in the most frequently baited treatment group (six baitings per year) and lowest in the unbaited treatment group. By framing the hypothesis this way, the research questions were not place in a framework designed to support or refute any particular school of thought, nor was it defined by density-dependence, density-independence, or inverse density dependence paradigm. Further, by adopting an information-theoretic approach, hypotheses and alternate hypotheses were placed in a model selection framework. I see this approach as consistent with the exploitative ecosystem hypothesis (Oksanen and Oksanen, 2000) and consistent with the experimental/mechanistic paradigm which *"recognises the complexity of the factors that interact to set birth and death rates in natural populations. It does not seek to* 'explain' *the birth or death rate but rather asks how these rates* [or in the northern jarrah forest, seeks to explain how survivorship] *change as we manipulate a factor of interest"* (Krebs, 1991; Krebs, 1995). In this case, the factor of interest was the density of foxes and how this density affected woylie survivorship.

6.4 Future research: where to now?

6.4.1 Mesopredator release

Notwithstanding the comments above and what may be considered semantics regarding population limitation and regulation, there is sufficient information from the northern jarrah forest study to warrant pursuing the investigation of mesopredator release, and in particular, mesopredator release of cats in the presence of fox density reduction. Figure 4.16 and Table 4.15 (Chapter 4) revealed 46 woylie mortality events were attributed to predation by cats, despite the low detection rate of cats (Chapter 3). Although this is sufficient to implicate the cat as a significant predator of woylies, it is not sufficient evidence to demonstrate there had been a mesopredator release of cats.

Fox predation is historically recognised as a contributing factor to native fauna declines (see Section 1.2 and Section 1.3). It is now seen as a significant threat to biodiversity values and is listed as a ‘key threatening process’ in accordance with the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) (DEWHA, 2008a; 2008b). More recent declines of native fauna, combined with the lack of sustained populations after initial increases post fox control, and the lack of success of several translocation programs, have been largely attributed to predation by cats (see for example de Tores, 2008; 2009; Short, 2016). Consistent with this, a plausible hypothesis to explain recent fauna declines is that a reduction in the abundance of foxes has, in some circumstances, led to mesopredator release of the feral cat. This, in turn, may have led to increased predation by cats and declines in prey species.

Some caution must be exercised when attempting to determine whether cats have shown a mesopredator release response to fox density reduction. Our suggestion (i.e. Glen *et al.*, 2009) of adopting a ‘whole-of-community approach’ may be imprudent, or at the very least requires the community of concern to be specified. In the northern jarrah forest, complex networks of interactions are likely to exist within and between community members which includes:

- native predators (the chuditch, the two large species of varanid lizards, Gould’s goanna (*Varanus gouldii*) and Rosenberg's monitor (*Varanus rosenbergi*), the south-west carpet python (*Morelia spilota imbricata*) and possibly several species of raptor, several small reptile and mammal predators including *Phascogale tapoatafa*, *Antechinus flavipes* and *Sminthopsis* spp, and geckoes, pygopods, agamids, skinks, typhlopods and elapids, see Appendix 1); and
- introduced predators (foxes, feral cats and the omnivorous black rat); and

- large, medium-size and small herbivores (*Macropus fuliginosus*, *M. Irma*, possibly *M. eugenii*, *Setonix brachyurus* and of course *Bettongia penicillata* and the introduced *Mus musculus*, see Appendix 1); and
- the suite of native herbivores/omnivores (the brushtail possum, *Tarsipes rostratus*, *Cercartetus concinnus*, the western ringtail possum and the southern brown bandicoot [the latter possibly more appropriately placed in with predators given Oksanen's (Oksanen, 1991) description of where omnivores sit in the trophic complex and the southern brown bandicoot's dietary preference for invertebrates]).

This list is exclusive of predatory owls, the spotted nightjar and the Australian owlet-nightjar, corvids, kingfishers etc. and is also exclusive of all small passerines (as potential prey species), and exclusive of the effects from parasites and disease. Further, adopting a 'whole-of-community approach' (see below) would also require assessing the effects of anthropogenic factors, such as disturbances from timber harvesting and fire (see for example Hradsky, 2020; Hradsky *et al.*, 2017; McGregor *et al.*, 2016). Hence the quote:

> *"single factors operate jointly in nature, and the number of possible indirect and interactive effects on each species is astronomical"* (Polis, 1998).

In Western Australian terrestrial ecosystems outside the northern jarrah forest, these interactions may also be influenced by the higher order terrestrial predator, the dingo. However, within the northern jarrah forest and in the absence of the dingo, it is reasonable to hypothesise that should cats show a mesopredator release response to fox control, the nature of the response will not be a simple linear response to the level of fox density reduction, but will also be affected by the diversity of introduced and native predators and by the availability of the prey resource, which may in turn be influenced by the environmental productivity of the site (the bottom-up effect, or more specifically, the exploitative ecosystem hypothesis). Equally confounding, cats may respond to fox density reduction as a result of a release from interference competition (including intraguild predation, as defined by Polis and Holt, 1992; Polis *et al.*, 1989), or release from exploitative competition, or both. Alternatively, cats may fail to show a mesopredator release response, with cat abundance and distribution determined largely by habitat structure. This was found to be the case in the central Flinders Ranges, South Australia (Stobo-Wilson *et al.*, 2020), where feral cat abundance was influenced by habitat structure as well as fox abundance. Similarly, from a study in Tjoritja–West MacDonnell National Park in the Northern Territory (McDonald *et al.*, 2020), cat abundance was found to be mediated by habitat complexity. In a fox density manipulation study in central New South Wales (Molsher *et al.*, 2017), where fox abundance was reduced (or at least an index to abundance indicated this; see Section 6.1.5 above), cats were concluded to have shown no increase in abundance, decreased their home range size and foraged more in open habitats, however there was an increase in their consumption of invertebrates and carrion. This contrasts with the findings from a study in the wheatbelt region of Western Australia (Marlow *et al.*, 2015), where indices of cat abundance (again indices) were higher at sites where fox baiting occurred, and cat predation on woylies was inferred to have increased at fox baited sites.

Polis (1999) recommended a 'pluralistic' approach to acknowledge that no single factor (biological or abiotic) should be seen as the sole explanatory variable to describe how an ecosystem, or part of an ecosystem, behaves. In recognition of this Glen *et al.* (2009) recommended adopting a *"whole-of-community approach"* to examine environmental and abiotic interactions and effects. To adopt a pluralistic or 'whole-of-community approach' and to elicit which factors are important to long-term fauna conservation in the presence/absence of mesopredator release, also requires an evidenced based approach and the formulation of testable hypotheses. Table 6.1 lists a suite of predictions for cat survivorship, abundance, diet, habitat use, and temporal activity under the different potential outcomes from fox control. The predictions are shown for the scenario of (i) release from interference competition; and (ii) release from exploitative competition. An hypothesis has been formulated for each scenario (Table 6.2). The hypotheses are generic and idealistic, and are formulated to demonstrate the magnitude of the task required to assess the response by one mesopredator (the feral cat), to fox density reduction. To apply this at a whole of community scale would necessitate comparable measures for each mesopredator and each prey species of concern or interest.

Table 6.1: Predicted outcomes for cat (*Felis catus*) survivorship, density, diet, use of the landscape and temporal activity under the scenario whereby (i) cats are released from interference competition; and (ii) cats are released from exploitative competition.

↑ = increase. ↓ = decrease. ↔ = no change

Scenario	**Parameter**	**Predicted outcome for cat density and/or behaviour for each given outcome for fox density**		
		fox density ↓	**fox density ↑**	**fox density ↔**
1. Cats released from interference competition	Cat survivorship	↑	↔ or ↓	↔
	Cat density	↑	↔ or ↓	↔
	Cat change in diet	↔ or ↑	↔ or ↓	↔
	Cat change in use of the landscape	↑	↓ or ↔	↔
	Cat change in temporal activity	↑	↓ or ↔	↔
2. Cats released from exploitative competition	Cat survivorship	↑	↔ or ↓	↔
	Cat density	↑	↔ or ↓	↔
	Cat change in diet	↑	↔ or ↓	↔
	Cat change in use of the landscape	↔ or ↑ or ↓	↔ or ↓ or ↑	↔
	Cat change in temporal activity	↔ or ↑ or ↓	↔ or ↓ or ↑	↔

Table 6.2: Hypotheses, the parameters measured to test each hypothesis, how these parameters are measured and the type of mesopredator release response (release from interference competition or release from exploitative competition) which predicts these outcomes.

Hypothesis	**Parameters measured (predicted outcome)**	**Methodology for measuring this parameter and the necessary caveats**	**Type of mesopredator release response consistent with the predicted outcome**
Hypothesis H01: With reduced fox abundance, cat survivorship will increase.	Abundance of foxes (fox abundance will be lower in treatment sites baited for fox control than in the unbaited control site)	Use of sandplotting and molecular techniques (e.g. genotyping from routinely collected scats and hair) to determine the number of individual foxes and cats present and to derive abundance estimates.	Interference competition and/or exploitative competition
	Survivorship of cats (survivorship will be higher in treatment sites baited for fox control)	Radio-telemetry, ideally incorporating satellite and/or GPS telemetry to enable cat survivorship to be monitored. Even with this commitment to monitoring, radio-telemetry alone would not address the issue of behavioural changes which may occur when individual foxes and cats are fitted with radio-collars (see Section 6.4.2.3, Hypothesis H08 and the cautionary note regarding interpretation of data from monitoring radio-collared foxes and cats).	
Hypothesis H02: With reduced fox abundance, cat abundance will increase.	Abundance of foxes (fox abundance will be lower in treatment sites baited for fox control than in the unbaited control site)	Use of sandplotting and molecular techniques (e.g. genotyping from routinely collected scats and hair) to determine the number of individual foxes and cats present and to derive abundance estimates.	Interference competition and/or exploitative competition
	Abundance of cats (cat abundance will be higher in treatment sites baited for fox control)	The caveats above also apply.	

(cont. …)

Table 6.2 (… cont.)

Hypothesis	Parameters measured (predicted outcome)	Methodology for measuring this parameter and the necessary caveats	Type of mesopredator release response consistent with the predicted outcome
Hypothesis H03: With reduced fox abundance, the dietary intake of cats will change to include dietary items from which cats were previously excluded.	Abundance of foxes (fox abundance will be lower in treatment sites baited for fox control than in the unbaited control site)	Use of sandplotting and molecular techniques (e.g. genotyping from routinely collected scats and hair) to determine the number of individual foxes present and to derive fox abundance estimates.	Primarily exploitative competition. However, release from interference competition may also result in cats foraging more widely and/or over a greater and/or different period of time daily.
	Prey availability (determine the suite and abundance of prey present)	Surveys to determine the suite of potential prey items available and estimates of abundance for each prey species. Quantitative analyses are essential. This does not take into consideration dietary items other than prey species, e.g. fruits, berries, etc. for which availability would also need to be quantified, and will also change seasonally	
	Dietary intake of foxes (dietary items consumed by foxes will be proportionally represented relative to availability at unbaited and baited treatment sites). This assumes dietary intake is a function of food availability.	Dietary analyses of collected fox scats This also assumes dietary intake can be effectively detected from scat analysis, i.e. that all food consumed is detectable in scat analysis	
	Dietary intake of cats (dietary items consumed by foxes will be less well represented in the diet of cats at sites unbaited for fox control, and proportionally represented relative to availability at fox baited treatment sites). This also assumes dietary intake is a function of food availability.	Dietary analyses of collected cat scats The caveat above also applies.	

(cont. …)

Table 6.2 (… cont.)

Hypothesis	Parameters measured (predicted outcome)	Methodology for measuring this parameter and the necessary caveats	Type of mesopredator release response consistent with the predicted outcome
Hypothesis H04: With reduced fox abundance, spatial use of the landscape by cats will change. A greater range of major vegetation structural types and/or a greater proportion of open vegetation structural types will be used.	Abundance of foxes (fox abundance will be lower in treatment sites baited for fox control than in the unbaited control)	Use of sandplotting and molecular techniques (e.g. genotyping from routinely collected scats and hair) to determine the number of individual foxes present and to derive fox abundance estimates.	Primarily exploitative competition which may result in cats changing their pattern of spatial use of the landscape to forage more widely. Conversely, by releasing cats from exploitative competition and by reducing competition for the prey resource, cats may forage less widely as the food resource becomes more readily available.
	Habitat use and/or use of the landscape by foxes (the structural vegetation types used by foxes will need to be identified and compared, in terms of proportion of home range and availability, between the unbaited controls site and baited treatment sites)	Radio-telemetry, ideally incorporating satellite and/or GPS telemetry to enable use of the landscape by cats to be monitored. The caveats applying to radio-collaring cats described above (H01) also apply. GIS and/or aerial photograph interpretation to delineate major vegetation structural units and home range analysis, ideally this would adopt use recently developed techniques (e.g. Horne *et al.*, 2007a; Horne, 2005; Horne and Garton, 2006)	
	Habitat use and use of the landscape by cats (structural vegetation types which cats are not using, or appear to show avoidance of in the unbaited control site, will be used more, in terms of proportion of home range and availability, by cats in the treatment sites baited for fox control)	Satellite telemetry, aerial photograph interpretation to delineate major vegetation structural units and home range analysis using techniques as above.	

(cont. …)

Table 6.2 (… cont.)

Hypothesis	Parameters measured (predicted outcome)	Methodology for measuring this parameter and the necessary caveats	Type of mesopredator release response consistent with the predicted outcome.
Hypothesis H05: With reduced fox abundance, temporal use of the landscape by cats will change.	Abundance of foxes (fox abundance will be lower in treatment sites baited for fox control than in the unbaited control)	Use of sandplotting and molecular techniques (e.g. genotyping from routinely collected scats and hair) to determine the number of individual foxes present and to derive fox abundance estimates.	Primarily interference competition. However release from exploitative competition may also result in cats changing their temporal pattern of use of the landscape to forage over a greater period of time. Conversely, by releasing cats from exploitative competition by reducing competition for the prey resource, cats may need to spend less time foraging as the food resource becomes more readily available.
	Temporal use of the landscape by foxes (the temporal use of the landscape by foxes will need to be identified and will be comparable between the unbaited control site and baited treatment sites)	Radio-telemetry and temporal use of home range, using techniques as above.	
	Temporal use of the landscape by cats (temporal use of the landscape by cats will change, e.g. time periods where foxes are most active within the unbaited control will correspond to periods of less activity by cats. This pattern will not be evident, or will be less evident, in treatment sites baited for fox control)		

The enormity of the food-web complexity; the equally complex nature of the testable hypotheses; the extensive overlap in potential outcomes; the difficulty in adequately addressing the issues identified and the necessary caveats (Table 6.2), suggest examining the above hypotheses is unlikely to unequivocally result in determining if, in the presence of a demonstrated reduction in fox abundance, cats show a release from interference competition, exploitative competition, or both. From a management perspective it may not matter, as it is the biodiversity conservation outcomes which matter and, despite the issues (and caveats) identified, there is a need to determine whether cats are responding to reductions in fox abundance and if so, the magnitude of, and implications from such a response. If cats do show a mesopredator release response, this response may mask and/or prevent a response by native species. This in turn has the very real potential to send incorrect messages to conservation managers.

As altruistic as it may be to develop extensive hypothesis testing to determine all responses to fox control and to develop a whole-of-community approach, attempting to do so lacks practicality and would be cost prohibitive. In acknowledgement of this, a priority is recommended on determining, in a more pragmatic way, whether long-term repeated fox baiting results in mesopredator release of cats. However, any predator (fox) manipulation study should not only assess the population size, or at least the abundance of the predator manipulated, but should also assess the abundance of all the ‘main predators’ (Korpimäki and Krebs, 1996). In doing so, this enables assessment of the flow-on effects on other predators (mesopredators), should they occur. *“If only part of the predator assemblage is included in the manipulation, the remaining predators may have the potential to increase their predation rate, resulting in only minimal treatment effects on prey dynamics”* (Korpimäki and Krebs, 1996).

An initial focus on assessing the nature of the relationship(s) between foxes, cats, other selected mesopredators and selected prey species has the potential to overlook many of the complex interactions between native and introduced predators and entire suite of prey species, and may also limit the opportunity to fully assess the role foxes have in structuring the ecosystem. However, focusing initially on clarifying the relationship(s) between foxes, cats, other mesopredators and selected prey species will enable simplified hypotheses to be formulated and tested. Such a focus is not ignoring that more complex and non-linear relationships can (and no doubt do) exist across the northern jarrah forest food-webs, but enables simple models to be tested (see Sinclair *et al.*, 2000). These easily understandable models can then be used as an approximation of reality to provide a means by which the complexity of natural systems can be simplified and interpreted. These simple models can then be progressively refined. This experimental approach still requires the formulation of testable hypotheses (Krebs, 2002) *"all the while realizing that they are oversimplified"* (Charley Krebs[12], pers. comm.).

The northern jarrah forest component of the IACRC WA Demonstration Site examined some aspects of mesopredator release. The implications have not been fully addressed and, although there was evidence to suggest mesopredator release of cats did occur within the northern jarrah forest (de Tores *et al.*, unpublished-a), further examination and verification is required. Further, there is no *a priori* reason to expect if a mesopredator release response by cats occurred in the northern jarrah forest that it will occur in all cases where fox abundance is reduced.

Given this, the recommended priority for future research in the northern jarrah forest is to follow-up on the mesopredator release research commenced by the IACRC program. This research should focus on quantitatively determining if feral cats increase in abundance in response to fox density reduction. To accompany this, it is also recommended, in addition to monitoring fox and cat abundance, the abundance of the 'main predators' (mesopredators) is also monitored and quantified, with these main predators being the chuditch, both large varanids (*Varanus gouldii* and *V. rosenbergi*) and the south-west carpet python, all of which have been implicated as predators of the woylie (Table 4.15). It is further recommended that the prey species monitored should include the woylie, the common brushtail possum and the southern brown bandicoot. The monitoring protocols recommended are as described in Section 3.6, Section 6.1.3 and Section 6.1.4.

6.4.2 Priority for future research: issues and formulating testable hypotheses

6.4.2.1 The issues

In addition to the potential for mesopredator release of cats to occur when fox abundance is reduced, research in areas repeatedly baited for fox control also needs to also acknowledge issues arising from:

- the size of the area over which fox control is implemented;
- the perimeter to area ratio of the estate over which fox control is implemented;
- the potential for some individual foxes to persist within the baited area despite repeated baiting; and

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[12] Charles Krebs: Emeritus Professor of Population Ecology, University of British Columbia, Department of Zoology.

- the potential for monitoring procedures to confound interpretation of results.

These issues are described below. Given the potential biodiversity implications from mesopredator release of cats, should it occur, hypotheses H06 to H09, as described below, are recommended as warranting investigation as a priority for future research in the northern jarrah forest. None of the hypotheses H06 to H09 was explicitly examined by the northern jarrah forest Operation Foxglove research.

6.4.2.2 The size of the area baited and implications for mesopredator release

In Western Australia, repeated baiting over relatively small areas of conservation estate (i.e. areas of contiguous conservation estate from <1,000ha up to several thousand ha.) is usually at a frequency of twelve (monthly intervals) to thirteen (four-weekly intervals) baitings per year (de Tores, 1994). The premise for the high baiting frequency is that foxes are likely to rapidly reinvade after resident and transient populations are removed at each baiting event. The results and interpretation from Chapter 3 support this belief (see Section 3.5.4) and also indicate dispersal/re-invasion of foxes post-baiting does not necessarily conform to the conventionally held belief whereby fox dispersal is limited to juveniles dispersing from the natal range in Autumn (Newsome and Coman, 1989; Trewhella *et al.*, 1988) or limited to the period from *"late summer until the start of the breeding season"* (DEWHA, 2008a). Bacon and Macdonald (1980) also identified the possibility of this immediate re-invasion post fox removal and noted when fox abundance is reduced by a culling program (or baiting) *"social disruption is magnified"* and the opportunity arises for other foxes to move in. Similarly, this was implied by Trewhella et al. (1988) who hypothesised increased adult mortality would result in a quicker turnover of resident foxes, thereby increasing the probability of a dispersing animal finding a vacant territory. Saunders et al. (2010) also believed fox baiting programs in eastern Australia were compromised by the ability of foxes to rapidly recolonise areas after a baiting event. Newsome et al. (2014) also believed rapid re-invasion of foxes after a control program was the key reason why one-off control programs failed.

Irrespective of the baiting frequency, when baiting is carried out in relatively small areas, baits are either delivered from vehicles (thrown from vehicles) (de Tores, 1994), buried, or are tethered at fixed bait stations (de Tores, 1994; de Tores and Marlow, 2012). In all situations, the intensity of baiting can vary, and this baiting intensity is usually determined by the extent of the roading network. This often results in an uneven distribution of baits and with baiting intensities greater than the nominal five baits/km^2 (de Tores, 1994). Despite this high baiting frequency and intensity, there is still no impediment to constant and immediate reinvasion of foxes post baiting.

Contrasting with this, when repeated baiting is implemented over larger areas (usually by aerial delivery), post-baiting re-invasion of forest areas further from the interface with agricultural land requires dispersing/re-invading foxes to traverse greater distances to re-establish resident populations. This is the premise behind the reduced frequency of baiting over large areas, and in Western Australia, repeated baiting over areas >20,000ha is usually carried out at a frequency of four baitings per year (de Tores, 1994), notwithstanding previous recommendations and the current research recommending this frequency should be increased to six baitings per year (see Chapter 4, especially Fig 4.8, Table 4.14 and Section 4.4.1). Irrespective of a frequency of two, four or six baitings per year, the greater distances from the forest interface with agricultural land to the core of the northern jarrah forest will result in a longer period of time for foxes to disperse from the forest interface to the core of the forest.

The inference is that, even in the unlikely outcome of a 100% knockdown of the fox population, there is likely to be an immediate reinvasion of foxes to areas at the perimeter of larger areas of baited forest, or within the entire baited area of relatively small baited areas. It therefore follows that, at the forest interface with agricultural land, there is unlikely to be a sufficient length of ‘fox-free’ time between baiting events for cats to establish and show a release from interference or exploitative competition (see Table 6.2). This is a possible explanation for the response shown by woylies at George Forest Block when baiting recommenced as part of the IACRC WA Demonstration Site. Under such a scenario, the immediate knock-down effect and reduction in fox predation which resulted from baiting was sufficient to enable the remnant population of woylies to persist. Additionally, the presence of foxes, either through constant re-invasion from agricultural land or through the presence of foxes which had not taken a bait, was sufficient to prevent a mesopredator release of cats. With repetition of this cycle of six baitings per year and repeated removal of foxes, despite re-invasion, and without a mesopredator release of cats, woylies were able to increase in abundance (Fig. 6.1). Conversely, with increasing distance from agricultural land, with extended periods where fox abundance remains low, or where foxes are completely removed, there is the potential for cats to show a mesopredator release response.

At George Block, additional data from the IACRC research (de Tores *et al.*, unpublished-a) indicated a pattern of progressive increase in abundance of varanid lizards, chuditch, brushtail possums and the southern brown bandicoot, i.e. similar to the pattern shown by the woylie (Fig. 6.1). The implication is that these species have shown an increase in abundance as a result of fox baiting at a frequency of six baitings per year and have not been exposed to an increase in predation by cats. This is consistent with ecological theory where increased diversity of native predators is associated with an increased diversity of native prey (Paine, 1966) and enhanced food web stability (Gross *et al.*, 2009; MacArthur, 1955; McCann and Hastings, 1997; McCann *et al.*, 1998; Paine, 1966; Polis, 1998; Polis *et al.*, 2000).

The hypotheses proposed for future research are:

> **Hypothesis H06**:
>
> For large areas of forest baited at a frequency of four baitings per year, there will be a reduction in fox abundance at the forest interface with agricultural land which is sufficient to enable remnant populations of the woylie (and other predation sensitive species) to persist, but not sufficient to allow an increase in abundance. At both four and six baitings per year the re-invasion/dispersal of foxes into the forest margin will be sufficient to prevent cats from showing a mesopredator release response. However, at a frequency of six baitings per year, the reduction in fox abundance will be sufficient to enable remnant populations of the woylie (and other predation sensitive species) to persist and increase in abundance, the diversity of native predators will increase, as will the diversity of native prey species and food web stability will be enhanced.

A corollary of this is the hypothesis:

> **Hypothesis H07**:
>
> Within central parts of large expanses of forest baited to reduce fox abundance, irrespective of being baited at a frequency of two, four or six baitings per year, the reduction in fox abundance and the time required for re-invasion/dispersal by foxes from the forest perimeter will be sufficient to enable cats to show a mesopredator release response. As a consequence, predation sensitive native species will not show an increase in abundance.

These scenarios (H06 and H07) present a conundrum for wildlife managers, as they suggest:

Firstly: fox density reduction at perimeter areas of large expanses of forest can result in biodiversity gains through decreased fox abundance (and decreased fox predation) with no increase in cat predation and increases in abundance of the suite of native mesopredators and native prey species. As described above, this is consistent with ecological theory where increased diversity of native predators is associated with an increased diversity of native prey (Paine, 1966) and enhanced food web stability (Gross *et al.*, 2009; MacArthur, 1955; McCann and Hastings, 1997; McCann *et al.*, 1998; Paine, 1966; Polis, 1998; Polis *et al.*, 2000).

Secondly: fox density reduction at the central core of large expanses of forest (and other biomes) can reduce fox abundance, however, in the absence of a concurrent reduction in cat abundance, cats have the potential to show a mesopredator release response, and in doing so, become the apex predator and prevent mesopredator release of native predators and also prevent any associated increase in the diversity of native prey. In such a situation, in the absence of effective cat control, and where the fox abundance is low, stable and with no transients, allowing the resident fox population to persist may be of greater conservation value than reducing the population and facilitating a mesopredator release of cats.

6.4.2.3 Do foxes show bait aversion?

Where management of conservation estate includes fox control through baiting large areas of forest, the opportunity exists to test hypotheses which arise from previous research on fox control. Thomson and Algar (2000) reported up to 88% of a sampled fox population had consumed biomarked baits when delivered at a baiting intensity of five baits/km2. This level of bait uptake was not improved at higher baiting intensities and has been used as the rationale for the baiting intensity adopted for the northern jarrah forest Operation Foxglove research and subsequently for Western Shield. However, the question still remains as to whether the individual foxes which did not consume a bait at the initial baiting event will also not consume a bait at subsequent baiting events and, in doing so, remain bait averse. The term ‘bait averse’ in this sense is used to indicate an individual’s preference (or more accurately, its lack of preference) to consume a bait. This is different from ‘bait shyness’, which is a response to a sub-lethal dose of toxin (in this case 1080), where a fox experiences a non-lethal ‘ill’ effect from consuming a bait, and in doing so, becomes ‘shy’ of consuming another bait. There are potential adverse and beneficial biological conservation implications from bait aversion and bait-shyness.

An adverse outcome is that if the same individuals continue to not take a bait at repeated baiting events, it is feasible this could result in selection pressure for this trait and facilitate population growth of a 'bait averse' fox population. A beneficial implication of bait aversion is that a resident population of 'bait averse' foxes may have a lesser effect on prey species than a constantly changing transient population. Such an effect was shown to occur in a North American study (Berger *et al.*, 2008) involving wolves (*Canis lupus*), coyotes and pronghorn (*Antilocapra americana*), where there was a four-fold increase in pronghorn fawn survival rates at sites where wolves were present. Although the abundance of resident coyotes was similar across sites with and without wolves, the abundance of transient coyotes (in this case the mesopredator) was lower at sites used by wolves. The analogy is, in the presence of a resident population of 'bait averse' foxes, the abundance of a transient foxes would be less and the predation effect on native prey species would also be less, than in the situation where there was a high proportion of transient foxes.

A feasible hypothesis to examine is:

> **Hypothesis H08**:
>
> In the presence of repeated baiting for fox control, a percentage of the resident fox population will be 'bait averse' and will remain 'bait averse' at repeated baiting events.

By way of caution, testing this hypothesis through use of 'catch, radio-collar and release' techniques is problematic as individuals caught at a trap site and subsequently radio-collared have, by the very fact they have been lured to a trap site, shown a susceptibility or propensity to be drawn to a bait. As a consequence, individuals wary of a trap point are not only excluded from the radio-collared sample, but may also be wary of consuming a bait. In such situations, baiting-mortality of radio-collared foxes may not be indicative of the susceptibility of the entire population to baiting. This behavioural response was implied by Thomson et al. (2000) in the Gascoyne region of Western Australia, where 45 individual foxes were trapped and radio-collared. Twenty seven of these radio-collared foxes were killed within three days and all 45 were killed within 44 days of baits being laid, indicating a 100% mortality rate. Signs of 1080 poisoning were evident in all cases. However, the authors acknowledged there was unlikely to have been 100% mortality of the fox population and the overall reduction of the population was estimated at 95% (Thomson *et al.*, 2000). This suggests that 5% of the fox population may have avoided capture and radio-collaring and may also be bait averse.

Similarly, changes in the behaviour of cats when fitted with a radio-collar may confound interpretation of the effect of baiting programs. Unpublished research from radio-collared cats at a coastal site in south-west Western Australia (Leschenault Peninsula Conservation Park, see below) suggested the diet of cats may change when fitted with a radio-collar. From a small sample (n=3) of radio-collared cats, within two months of being fitted with a radio-collar, each collared cat appeared to have consumed a fox bait, with all recovered carcasses showing signs of 1080 poisoning. Each radio-collared cat was an adult and, given the limited opportunity for immigration to Leschenault Peninsula (see Section 6.4.2.4, below), can reasonably be expected to have been present at the site when it was un-collared and also exposed to 1080 baits. The inference is that once collared, a cat's hunting skill is compromised and it is more susceptible to (more likely to ingest) a toxic bait, which it would otherwise not consume. This behavioural response draws into question the interpretation of findings from research trials designed to assess the efficacy of toxic baits when bait uptake is determined by 'capture-collar-release' techniques. In a trial Fortescue Marsh in the Pilbara region of Western Australia (Comer *et al.*, 2018), the mortality of radio-collared cats after delivery of a toxic bait was interpreted as meaning the bait will also be ingested by un-collared cats. The potential for a predator species to alter its diet once fitted with a radio-collar has implications for the way research is designed and implemented and for interpretation of results. Although the monitoring procedure was supplemented through the use of predator activity indices derived from sandplots and from occupancy modelling, the use of indices of activity to infer abundance is highly questionable (see Chapter 3, Section 3.2.2 and Section 3.2.3). The use of occupancy modelling also seems inappropriate, as any assessment of bait efficacy will depend on its ability to reduce abundance. Occupancy modelling is likely to be of little value when assessing abundance (see Chapter 5). The authors also acknowledged violation of at least one of the assumptions of occupancy modelling. The same methodologies were reported by Comer *et al.* (2020) in a study from the south coast of Western Australia.

The same concerns apply to the interpretation of the efficacy of wild dog baits in a study from north-east New South Wales (Ballard *et al.*, 2020). The efficacy of the bait was assesses as the percentage mortality of radio-collared wild dogs. As in the examples above, this does not take into consideration that an individual wild dog, once lured to a trap site, has shown a susceptibility or propensity to be drawn to a bait. Interestingly, Ballard et al. (2020) acknowledged not all wild dogs within the area were lured to trap locations, as 10% of the known individual wild dogs identified from camera trapping were not trapped (in leg hold traps) and therefore were not available for radio-collaring. The fate of these individual was unknown, as was their potential to consume a bait.

Alternative techniques were used in a study from Kangaroo Island, South Australia, to assess the extent of uptake of the cat bait 'Eradicat' (Hohnen *et al.*, 2020). Again there was potential bias in the methodology, as to consume a bait, each individual animal was required to come to a bait station (where a camera was also deployed) with trapping then used to assess (by the detection of a biomarker in whiskers of trapped individuals) whether a bait had been ingested. This technique appears preferable to conventional 'capture-collar-release' techniques as the initial bait ingestion does not require capture and handling of animals, whereas 'capture-collar-release' techniques require handling animals and therefore, only those individuals which have been lured to a trap location, trapped, collared and released in the first instance, able to be assessed to determine if they have subsequently been lured to a bait. Interestingly, the results from the Kangaroo Island study contrast significantly with bait uptake trials based on 'capture-collar-release' techniques reported by Comer et al. (2018) .

6.4.2.4 How important is the perimeter to area ratio of estate over which fox control is implemented?

If the potential for cats to show a mesopredator release response is subject to the size of the area over which fox control is undertaken (see above), it therefore follows that such a response can also be influenced by the perimeter to area ratio of the baited site. A mesopredator release response (by cats and/or the south-west carpet python) was hypothesised as one of the possible causes for the collapse of what had previously been considered a successful translocation program of the western ringtail possum at Leschenault Peninsula Conservation Park, south-west Western Australia (de Tores, 2008; de Tores and Marlow, 2012; de Tores and Rosier, in prep; de Tores *et al.*, 2004; de Tores *et al.*, 2010). The translocation release site covers an area of approximately 1,070ha, and is therefore relatively small in terms of the area baited for fox control. However, the site offers negligible opportunity for recruitment (i.e. re-invasion by foxes post each baiting event) as it is connected to the mainland by a narrow isthmus of approximately 600m. The perimeter to area ratio (metres:ha) is approximately 0.56. For the same area (1,070ha) of conservation estate configured in a circular shape, the perimeter would equate to approximately 11.6km with a perimeter to area ratio of approximately 10.84. For the same 1,070ha configured in a square shape, the perimeter would equate to approximately 13.1km with a perimeter to area ratio of 12.2. In both latter situations, where the perimeter is large (i.e. the length of the reserve boundary from which re-invasion can occur) there will be a significantly greater opportunity for re-invasion by foxes than is the case at Leschenault, where reinvasion is limited to the narrow isthmus.

A feasible hypothesis to examine is:

> **Hypothesis H09**:
>
> In the presence of repeated baiting for fox control, re-invasion by foxes after each baiting event is facilitated where the perimeter to area ratio of the baited estate is large. Further, in circumstances where this ratio is small, these areas of fox baited estate may facilitate a mesopredator response more typical of the centre of large areas, where fox populations fail to re-establish post baiting, or are maintained at low abundances.

6.5 The resources required for the northern jarrah forest research

The financial and staffing requirements to conduct the northern jarrah forest Operation Foxglove research were far from trivial. Significant resources were required for the seasonal trapping at each of the 55 trapping grids and for the translocation (capture, processing, transport and release, and monitoring) of woylies. In addition to this, the resources of specialist CALM/DEC staff were required in the planning and establishment stage of the project and in particular for site selection, which involved input from CALM's Forest Management Branch (timber harvest planning and GIS sections) and Environmental Protection Branch (fire management planning and 1080 baiting).

The resources and tasks required for research component of the project for the period 1996 to 2000 were:

- one full time research scientist;
- four full time technical officers (employed as casuals because of the insecure nature of the funding);
- establishment and maintenance of the 55 trapping grids;
- seasonal monitoring (trapping) of fauna at trapping grids (including daily processing to mark individual animals and collection morphometric data);
- data collation and data entry;
- training in animal ID, animal handling, animal marking, data collation and data management;
- maintenance of equipment (including vehicle management and maintenance);
- recruitment, co-ordination, supervision and acknowledgement of volunteers;

- safety training;
- development and implementation of translocation protocols; and
- training in analytical techniques and data analysis.

The above was exclusive of the costs for research staff colleagues, specialist branch input and exclusive of all 1080 bait purchase and aerial baiting costs.

Section 1.8 identifies the funding sources. A major source of this funding was the then Commonwealth of Australia's Australian Nature Conservation Agency (ANCA), which became Environment Australia (EA) and funding was secured through the Commonwealth's Natural Heritage Trust (NHT) program. However, despite securing funding, the NHT program had a history of retrospective confirmation of this funding. This led to insecurity of the research program and jeopardised support from co-funding agencies and corporate sponsorship. The delays in funding advice also necessitated a stop-start approach to the research. This compromised the research and jeopardised the project meeting identified outcomes and milestones.

NHT funding for the project for the 1996-97 financial year was retrospectively approved in November 1997. Funding for the 1997-98 financial year was approved in March 1998. Formal advice of funding for 1998-99 was delayed until the end of the financial year, after completion of that year's field work, and funding was not approved, despite all milestones and reporting requirements being met.

Consequently, a major recommendation for future research is that funding sources should be secured through binding contractual agreements, prior to commencement of all field work.

6.6 Conclusion

The major finding from the research was that estimated woylie survivorship was 16.4% higher in the six than in the four baitings per year treatment. This was consistent with the finding that the reduction in fox abundance was greatest in the six baitings per year treatment. The effect on survivorship of increasing distance from the interface of the forest and agricultural land was less definitive, however, the results suggest there is a biological imperative for woylie survivorship, and therefore for other predation sensitive terrestrial species, to increase the standard baiting regime from four to six baitings per year. Baiting at frequency of two baitings per year conferred no increase in survivorship over not baiting at all.

Woylie mortality was highest in winter months and several explanations were considered to explain this, including increased fox predation in winter months, reduced bait efficacy in winter months and that the woylie may be poorly adapted to winter conditions in the more mesic south-west, and as a consequence, has an intrinsically lower level of survivorship in winter. All possibilities have implications for future translocations of the woylie. Although fox predation accounted for most of the mortality events attributed to predation, numerous mortality events were also attributed to cat predation.

The technique used to monitor for the presence of cats and to derived estimates of cat abundance performed poorly. Modifications are proposed and include a variation of the sandplot technique. Future monitoring of cat and fox abundance recommends use of hair collection techniques and molecular analysis of collected hair and scats with the poly-pipe hair collection device recommended for use in the more mesic south-west of Western Australia. It is strongly recommendation the Western Shield program immediately include fox and cat monitoring as part of its standard monitoring procedures. Protocols are described for this, as are protocols for monitoring native fauna. The latter recommends a quantum shift in methodologies from the convenience monitoring currently used in the Western Shield program to more quantitative techniques, carried out over longer monitoring sessions and in a manner which representatively samples habitat types.

A high priority is also recommended to determine whether, in the presence of effective fox control, feral cats show a mesopredator release response. Testable hypotheses (H06 and H07) are described and the biodiversity conservation implications are detailed. A management conundrum is identified in the scenario whereby cats show a mesopredator release from competition with foxes at the central core of large areas baited for fox control. In such situations, in the absence of effective cat control and where the fox abundance is low, stable and with no transients, allowing the resident fox population to persist may be of greater conservation value than reducing the population and facilitating a mesopredator release of cats.

Despite verbal assurances of funding, much of the difficulties encountered during the northern jarrah forest (Operation Foxglove) research stemmed from the insecurity of funding and the attendant need to curtail the planned research until the funding advice was officially received. This led to untenable staffing situations and resulted in insecurity of employment for critical technical support. By its very nature, the environmental research now proposed to assess the long term effects of repeated fox baiting, and specifically the issues related to mesopredator release, will require the research to be conducted over several generations of natural populations to acquire *"knowledge about the mechanisms of population change"* (Strong, 1986). Consequently, funding will also be required to span this period.

Monitoring is essential to long-term studies, however agencies often appear to fall into the trap of believing monitoring will provide answers as to why or how populations change. This is not the case, as monitoring alone does not identify the *"mechanisms that may limit or regulate density"* (Krebs, 2002). To find such answers, monitoring "must be coupled with experimental testing to provide useful scientific understanding" (Krebs, 1991).

Although the northern jarrah forest research has strongly indicated that predation limited woylie survivorship, it did not examine the effect of alternative limiting factors such as disease, food resource availability, limited refuge sites or many other possible factors. Nonetheless, the results suggest there is a biological imperative to increase the standard baiting regime from four to six baitings per year and to further investigate the proposed and testable hypotheses relating to mesopredator release.

Figure 6.2: the woylie (*Bettongia penicillata ogilbyi*) foraging at Dryandra Woodland, south-west Western Australia.

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Appendix 1

Mammals, reptiles and amphibians trapped at each of 55 trapping grids in the northern jarrah forest

Mammals

The nomenclature and the order of listing mammals is as per Van Dyck and Strahan (2008). The list is not exhaustive, as the species of interest in the Operation Foxglove study were those with the potential to respond to fox (*Vulpes vulpes*) control. Survey techniques for the larger macropods, specifically, the western grey kangaroo (*Macropus fuliginosus*) and the western brush wallaby (*M. irma*) were not included. Both species should be considered present at all sites.

In the northern jarrah forest, the quokka (*Setonix brachyurus*) is restricted to densely vegetated creek lines. This habitat was not sampled as part of Operation Foxglove. However a concurrent program (Hayward, 2002) examined the ecology of the quokka in the northern jarrah forest and the quokka's distribution and habitat requirements are reported elsewhere (see Alacs *et al.*, 2003; Alacs, 2001; de Tores *et al.*, 2007; Hayward, 2005; Hayward, 2008; Hayward *et al.*, 2005a; Hayward *et al.*, 2008; Hayward *et al.*, 2003; Hayward *et al.*, 2005b; Hayward *et al.*, 2007; Hayward *et al.*, 2004; Hayward *et al.*, 2005c).

The western ringtail possum (*Pseudocheirus occidentalis*) was translocated to locations near the Murray River (within the six baitings year $^{-1}$ treatment) and the population persisted until the end of Operation Foxglove in 2000 (see Millen, 1997), its status post 2000 is unknown. The tammar wallaby (*Macropus eugenii*) was translocated to rehabilitated bauxite mining areas. The fate of these animals is unknown. Similarly, the numbat (*Myrmecobius fasciatus*) was translocated to locations near Mount Dale (towards the northern end of the two baitings year $^{-1}$ treatment) and the fate of these animals is also unknown.

The list of mammalian species trapped at each grid is shown in Table A1.1. Fifteen species from eight families were recorded (see summary by family, below). The fox and feral cat (*Felis catus*), although not listed in Table A1.1, should be considered present at each trapping grid.

The summary, by family, of species trapped, is:

Tachyglossidae:
- *Tachyglossus aculeatus*

Dasyuridae:
- *Dasyurus geoffroii*
- *Antechinus flavipes*
- *Phascogale tapoatafa*
- *Sminthopsis dolichura*
- *S. gilberti*
- *S. griseoventer*
- *S.* spp

Peramelidae:
- *Isoodon obesulus*

Burramyidae:
- *Cercartetus concinnus*

Tarsipedidae:
- *Tarsipes rostratus*

Phalangeridae:
- *Trichosurus vulpecula hypoleucus*

Potoroidae:
- *Bettongia penicillata ogilbyi*

Muridae:
- *Mus musculus* *
- *Rattus rattus* *

* denotes introduced species

Table A1.1: List of mammals recorded at each trapping grid within the northern jarrah forest, south-west Western Australia as part of Operation Foxglove

	species														
Treatment and trapping grid	*Tachyglossus aculeatus*	*Dasyurus geoffroii*	*Antechinus flavipes*	*Phascogale tapoatafa*	*Sminthopsis dolichura*	*Sminthopsis gilberti*	*Sminthopsis griseoventer*	*Sminthopsis sp.*	*Isoodon obesulus*	*Cercartetus concinnus*	*Tarsipes rostratus*	*Trichosurus vulpecula*	*Bettongia penicillata*	*Mus musculus*	*Rattus rattus*
Two baitings year^{-1}															
Chandler		x	x						x			x			
Cuthbert		x	x						x	x					
Division Track		x	x					x		x				x	
Dobaderry		x				x		x		x			x	x	
East of Yarra Road			x				x			x					
Jarrahdale Road			x						x			x			
Jarrick Road		x	x						x			x			
Korner Road			x			x	x	x	x	x		x	x		
Paddy		x	x						x	x			x		
Randall		x	x						x	x	x		x		
Russell		x				x	x			x				x	
Schulstaad Road		x	x						x				x		
Sullivan		x	x			x		x	x	x				x	
Thompson Road		x	x	x				x				x	x	x	
Watershed Road			x						x						
Wearne		x	x	x		x		x		x		x	x	x	
Four baitings year^{-1}															
Boggy Brook Road		x	x	x			x		x	x		x	x	x	x
Cameron		x	x						x			x			
Duncans	x	x	x	x					x	x		x			x
Gordon Road		x	x						x	x		x	x		
Housebrook Road		x	x					x	x	x			x	x	
McCoy Road		x	x						x						x
Old Bibbulmun Track			x						x	x					
O'Neill		x	x						x	x		x	x		
Patens		x	x						x						
Pindalup		x	x						x	x		x			
Scott		x	x		x				x	x					x
Twin Bridges Road	x	x	x					x	x	x	x	x	x	x	
Wells	x	x	x	x					x			x			
Wilson		x	x				x		x	x		x			x

(cont. …)

Table A1.1 (… cont.)

	species														
Treatment and trapping grid	*Tachyglossus aculeatus*	*Dasyurus geoffroii*	*Antechinus flavipes*	*Phascogale tapoatafa*	*Sminthopsis dolichura*	*Sminthopsis gilberti*	*Sminthopsis griseoventer*	*Sminthopsis sp.*	*Isoodon obesulus*	*Cercartetus concinnus*	*Tarsipes rostratus*	*Trichosurus vulpecula*	*Bettongia penicillata*	*Mus musculus*	*Rattus rattus*
Six baitings year^{-1}															
Allan Road		x	x				x	x	x	x		x			
Amphion		x	x	x	x		x		x	x		x	x		x
Bombala		x	x				x		x	x	x				
Driver Road		x	x						x	x		x			
Four Mile Road		x	x	x					x	x		x			
George		x	x	x			x	x		x		x	x	x	
Hakea Road	x	x	x	x			x	x	x	x			x		
Hotham Creek		x	x		x		x					x	x		
Littles Road		x	x	x				x		x			x		x
Murray Road	x	x	x	x	x			x	x	x		x	x	x	
Nanga		x	x		x				x			x			
Twenty Six Mile		x	x						x						x
Yarragil Form		x	x				x	x	x	x					x
Unbaited control															
12 Mile Road		x	x		x			x		x		x			x
Chalk Road	x	x	x		x	x	x			x		x		x	x
Miner		x	x	x					x			x			
Mistley		x	x						x			x			
Myles Avenue		x	x				x			x		x			
Nalyerin		x	x		x							x			
Seventy Seven Road		x	x						x			x	x		
Stene	x	x	x	x		x						x		x	
Stockyard		x	x	x			x	x				x	x		
Surface		x	x		x	x	x		x					x	x
Tanglin Road		x	x										x	x	
Winooka	x	x	x	x					x			x	x	x	

Reptiles and amphibians

The nomenclature and order of listing for all reptiles and amphibians is as per Cogger (1992), with four exceptions. *Bassiana trilineata* is used *in lieu* of *Pseudemoia trilineata*. The latter is listed by Cogger (1992), who noted recognition of *Bassiana* as a separate genus was warranted (Cogger, 1992 appendix, p735). *Tiliqua rugosa* (Storr *et al.*, 1999) is used *in lieu* of *Trachydosaurus rugosus*. Inclusion of *Rhinoplocephalus gouldii* (which is not listed in Cogger, 1992) is as per Storr *et al*. (1986). The genus *Vermicella* as described by Storr *et al*. (1986) is used *in lieu* of *Simoselaps*.

Storr *et al*. (1981; 1999), Storr et al (1983), Storr *et al*. (1990) Storr *et al*. (1986) and Cogger (1992) were used for identification of skinks; agamids and varanids; geckos and pygopods; snakes; and amphibians, respectively. Thirty-eight reptilian species (Table A1.2 & Table A1.3) from eight families and 12 amphibian species (Table A1.4) from one family (Myobatrachidae) were recorded. The summary, by family, of reptilian species trapped is:

Gekkonidae:
- *Christinus marmoratus*
- *Crenadactylus ocellatus ocellatus*
- *Diplodactylus granariensis*
- *D. polyophthalmus*
- *Underwoodisaurus milii*

Pygopodidae:
- *Aprasia pulchella*
- *A. repens*
- *Delma fraseri*
- *Lialis burtonis*

Agamidae:
- *Pogona minor*

Varanidae:
- *Varanus gouldii*
- *V. rosenbergi*

Scincidae:
- Bassiana trilineata
- *Cryptoblepharus plagiocephalus*
- *Ctenophorus ornatus*
- *Ctenotus catenifer*
- *C. delli*
- *C. impar*
- *C. labillardieri*
- *Egernia napoleonis*

Scincidae (… cont.):
- *E. multisculata*
- *E. pulchra*
- *Hemiergis initialis*
- *H. peronii peronii*
- *Lerista distinguenda*
- *L. microtis*
- *Menetia greyii*
- *Morethia obscura*
- *Tiliqua rugosa*

Typhlopidae
- *Ramphotyphlops australis*
- *R. pinguis*

Boidae:
- *Morelia spilota imbricata*
  (not recorded at any grid, but observed numerous times within the six baitings year $^{-1}$ treatment)

Elapidae:
- *Notechis ater occidentalis*
- *Pseudonaja affinis*
- *Rhinoplocephalus gouldii*
- *Vermicella bertholdi*
- *V. bimaculata*
- *V. semifasciata*

Table A1.2: List of geckos, pygopods, agamids and varanids recorded at each trapping grid within the northern jarrah forest, south-west Western Australia as part of Operation Foxglove

Treatment and trapping grid	species												
	Christinus marmoratus	*Crenadactylus ocellatus ocellatus*	*Diplodactylus granariensis*	*Diplodactylus polyophthalmus*	*Underwoodisaurus milii*	*Aprasia pulchella*	*Aprasia repens*	*Delma fraseri*	*Lialis burtonis*	*Pygopus lepidopodus*	*Pogona minor*	*Varanus gouldii*	*Varanus rosenbergi*
Two baitings year^{-1}													
Chandler		x		x									
Cuthbert	x					x			x		x	x	
Division Track								x	x		x	x	
Dobaderry	x		x	x	x		x					x	
East of Yarra Road						x					x		
Jarrahdale Road													
Jarrick Road						x					x		
Korner Road					x			x		x	x	x	
Paddy											x		x
Randall	x								x				
Russell										x	x		
Schulstaad Road				x		x					x		
Sullivan	x			x	x			x			x	x	
Thompson Road		x						x	x		x	x	
Watershed Road	x			x		x			x				
Wearne		x	x	x							x	x	
Four baitings year^{-1}													
Boggy Brook Road		x		x							x		x
Cameron		x		x	x								
Duncans	x												x
Gordon Road	x	x											x
Housebrook Road			x	x	x	x					x	x	x
McCoy Road												x	x
Old Bibbulmun Track		x				x							
O'Neill	x					x							
Patens						x							
Pindalup	x					x							x
Scott	x			x		x					x		x
Twin Bridges Road			x	x	x	x						x	
Wells	x			x								x	x
Wilson													

(cont. …)

Table A1.2 (… cont.)

Treatment and trapping grid	species												
	Christinus marmoratus	*Crenadactylus ocellatus ocellatus*	*Diplodactylus granariensis*	*Diplodactylus polyophthalmus*	*Underwoodisaurus milii*	*Aprasia pulchella*	*Aprasia repens*	*Delma fraseri*	*Lialis burtonis*	*Pygopus lepidopodus*	*Pogona minor*	*Varanus gouldii*	*Varanus rosenbergi*
Six baitings year^{-1}													
Allan Road	x			x		x							
Amphion	x					x						x	x
Bombala				x		x						x	x
Driver Road				x									
Four Mile Road				x		x							x
George	x			x	x	x						x	x
Hakea Road	x			x		x						x	x
Hotham Creek											x		
Littles Road						x							x
Murray Road	x												
Nanga	x					x						x	
Twenty Six Mile													
Yarragil Form	x			x	x	x							
Unbaited control													
12 Mile Road	x	x		x		x		x					
Chalk Road	x			x									x
Miner	x												x
Mistley													
Myles Avenue													
Nalyerin	x												x
Seventy Seven Road	x							x					
Stene											x	x	x
Stockyard				x								x	x
Surface											x		x
Tanglin Road												x	x
Winooka												x	x

Table A1.3: List of skinks, typhlopidae, boidae and elapids recorded at each trapping grid within the northern jarrah forest, south-west Western Australia as part of Operation Foxglove

Treatment and trapping grid	species																								
	Bassiana trilineata	*Cryptoblepharus plagiocephalus*	*Ctenophorus ornatus*	*Ctenotus catenifer*	*Ctenotus delli*	*Ctenotus impar*	*Ctenotus labillardieri*	*Egernia napoleonis*	*Egernia multisculata*	*Egernia pulchra*	*Hemiergis initialis*	*Hemiergis peronii peronii*	*Lerista distinguenda*	*Lerista microtis*	*Menetia greyii*	*Morethia obscura*	*Tiliqua rugosa*	*Ramphotyphlops australis*	*Ramphotyphlops pinguis*	*Notechis ater occidentalis*	*Pseudonaja affinis*	*Rhinoplocephalus gouldii*	*Vermicella bertholdi*	*Vermicella bimaculata*	*Vermicella semifasciata*
Two baitings year^{-1}																									
Chandler		x			x						x		x		x	x	x		x						
Cuthbert	x	x			x		x	x			x		x		x	x	x								
Division Track	x	x				x		x					x			x	x	x				x			x
Dobaderry		x						x	x				x		x	x	x	x			x				x
East of Yarra Road								x					x		x		x								x
Jarrahdale Road	x	x					x	x								x									
Jarrick Road	x	x			x		x	x					x		x	x									
Korner Road		x						x					x		x		x					x			x
Paddy	x	x			x			x			x		x		x	x	x				x				
Randall		x			x		x	x			x		x		x	x	x				x	x			
Russell		x											x		x	x	x	x							
Schulstaad Road		x			x	x	x	x					x		x	x	x				x				
Sullivan		x											x		x		x	x							x
Thompson Road		x						x					x		x		x	x					x	x	
Watershed Road	x	x			x		x	x			x		x		x	x								x	
Wearne		x						x					x		x	x	x	x							x

(cont. …)

Table A1.3 (… cont.)

Treatment and trapping grid	species																								
	Bassiana trilineata	*Cryptoblepharus plagiocephalus*	*Ctenophorus ornatus*	*Ctenotus catenifer*	*Ctenotus delli*	*Ctenotus impar*	*Ctenotus labillardieri*	*Egernia napoleonis*	*Egernia multisculata*	*Egernia pulchra*	*Hemiergis initialis*	*Hemiergis peronii peronii*	*Lerista distinguenda*	*Lerista microtis*	*Menetia greyii*	*Morethia obscura*	*Tiliqua rugosa*	*Ramphotyphlops australis*	*Ramphotyphlops pinguis*	*Notechis ater occidentalis*	*Pseudonaja affinis*	*Rhinoplocephalus gouldii*	*Vermicella bertholdi*	*Vermicella bimaculata*	*Vermicella semifasciata*
Four baitings year^{-1}																									
Boggy Brook Road		x						x			x		x		x	x	x	x				x		x	x
Cameron	x	x			x		x	x			x		x		x	x									
Duncans	x	x					x	x			x		x	x	x	x		x			x				
Gordon Road		x					x	x			x		x		x	x		x							
Housebrook Road		x						x			x		x		x	x	x					x			
McCoy Road	x						x	x			x			x		x	x				x				
Old Bibbulmun Track	x	x			x		x	x			x		x		x	x	x				x				
O'Neill	x	x				x	x	x			x		x		x	x	x								
Patens	x	x						x			x		x		x	x					x				
Pindalup	x	x			x			x			x		x		x	x	x	x		x					
Scott	x	x			x		x	x			x		x		x	x	x	x			x	x			
Twin Bridges Road		x	x								x		x		x	x	x	x							
Wells	x	x						x			x		x		x	x	x					x			
Wilson	x						x	x			x		x		x	x	x								

(cont. …)

Table A1.3 (… cont.)

	species																								
Treatment and trapping grid	*Bassiana trilineata*	*Cryptoblepharus plagiocephalus*	*Ctenophorus ornatus*	*Ctenotus catenifer*	*Ctenotus delli*	*Ctenotus impar*	*Ctenotus labillardieri*	*Egernia napoleonis*	*Egernia multisculata*	*Egernia pulchra*	*Hemiergis initialis*	*Hemiergis peronii peronii*	*Lerista distinguenda*	*Lerista microtis*	*Menetia greyii*	*Morethia obscura*	*Tiliqua rugosa*	*Ramphotyphlops australis*	*Ramphotyphlops pinguis*	*Notechis ater occidentalis*	*Pseudonaja affinis*	*Rhinoplocephalus gouldii*	*Vermicella bertholdi*	*Vermicella bimaculata*	*Vermicella semifasciata*
Six baitings year^{-1}																									
Allan Road		x			x		x	x			x	x	x			x	x	x							
Amphion	x	x					x	x			x		x	x		x	x				x				
Bombala	x				x						x		x		x	x	x				x				
Driver Road	x	x					x	x			x			x	x	x	x	x			x				
Four Mile Road	x							x			x		x		x	x					x				
George	x	x			x		x	x					x		x	x	x	x				x			
Hakea Road	x	x						x			x		x		x	x	x								
Hotham Creek	x	x			x		x	x			x		x		x	x	x								
Littles Road		x					x	x			x		x		x	x	x	x							
Murray Road	x						x	x			x		x	x	x	x	x								
Nanga	x	x						x			x		x		x	x	x	x							
Twenty Six Mile	x							x			x						x								
Yarragil Form	x	x			x			x		x	x	x	x		x	x	x	x							

(cont. …)

Table A1.3 (… cont.)

	species																								
Treatment and trapping grid	*Bassiana trilineata*	*Cryptoblepharus plagiocephalus*	*Ctenophorus ornatus*	*Ctenotus catenifer*	*Ctenotus delli*	*Ctenotus impar*	*Ctenotus labillardieri*	*Egernia napoleonis*	*Egernia multisculata*	*Egernia pulchra*	*Hemiergis initialis*	*Hemiergis peronii peronii*	*Lerista distinguenda*	*Lerista microtis*	*Menetia greyii*	*Morethia obscura*	*Tiliqua rugosa*	*Ramphotyphlops australis*	*Ramphotyphlops pinguis*	*Notechis ater occidentalis*	*Pseudonaja affinis*	*Rhinoplocephalus gouldii*	*Vermicella bertholdi*	*Vermicella bimaculata*	*Vermicella semifasciata*
Unbaited control																									
12 Mile Road	x			x			x	x			x	x	x	x	x	x	x	x							
Chalk Road	x	x						x			x		x	x	x	x	x	x			x				
Miner		x						x			x		x		x	x	x								
Mistley	x	x				x		x					x		x	x	x	x							
Myles Avenue							x	x				x	x	x		x	x	x							
Nalyerin	x							x			x		x		x	x	x	x						x	
Seventy Seven Road	x	x						x			x				x	x		x				x			
Stene		x						x			x		x		x	x	x	x							
Stockyard		x						x			x		x		x	x	x	x							
Surface								x			x			x	x	x	x				x				
Tanglin Road	x						x	x			x		x	x	x	x	x	x	x						
Winooka		x			x	x		x			x		x		x	x	x	x							

Table A1.4: List of amphibians recorded at each trapping grid within the northern jarrah forest, south-west Western Australia as part of Operation Foxglove

	species											
Treatment and trapping grid	*Crinia georgiana*	*Crinia glauerti*	*Crinia pseudinsignifera*	*Crinia insignifera*	*Heleioporus albopunctatus*	*Heleioporus barycragus*	*Heleioporus eyrei*	*Heleioporus inornatus*	*Heleioporus psammophilus*	*Limnodynastes dorsalis*	*Neobatrachus pelobatoides*	*Pseudophryne guentheri*
Two baitings year^{-1}												
Chandler	x											
Cuthbert							x					
Division Track												
Dobaderry										x	x	
East of Yarra Road					x		x		x			
Jarrahdale Road	x											
Jarrick Road												
Korner Road					x						x	x
Paddy												
Randall												
Russell						x						
Schulstaad Road	x							x	x			
Sullivan										x		
Thompson Road					x	x				x	x	x
Watershed Road			x					x				
Wearne					x	x						
Four baitings year^{-1}												
Boggy Brook Road		x	x							x	x	x
Cameron	x											
Duncans	x		x					x	x			
Gordon Road												
Housebrook Road		x					x			x		x
McCoy Road	x	x	x									
Old Bibbulmun Track												
O'Neill												
Patens									x			
Pindalup							x		x			
Scott	x											
Twin Bridges Road		x				x						x
Wells	x			x								
Wilson												

(cont. …)

Table A1.4 (… cont.)

	species											
Treatment and trapping grid	*Crinia georgiana*	*Crinia glauerti*	*Crinia pseudinsignifera*	*Crinia insignifera*	*Heleioporus albopunctatus*	*Heleioporus barycragus*	*Heleioporus eyrei*	*Heleioporus inornatus*	*Heleioporus psammophilus*	*Limnodynastes dorsalis*	*Neobatrachus pelobatoides*	*Pseudophryne guentheri*
Six baitings year^{-1}												
Allan Road	x							x				
Amphion												
Bombala								x				x
Driver Road	x							x				x
Four Mile Road							x					
George						x						
Hakea Road	x											
Hotham Creek						x						x
Littles Road									x			
Murray Road								x				
Nanga	x											
Twenty Six Mile	x											
Yarragil Form	x											
Unbaited control												
12 Mile Road	x							x	x			
Chalk Road	x					x	x	x	x			x
Miner												
Mistley			x					x	x			
Myles Avenue	x							x				
Nalyerin			x			x	x	x		x		x
Seventy Seven Road						x	x				x	x
Stene												x
Stockyard									x		x	
Surface	x	x				x	x	x				x
Tanglin Road	x		x			x	x		x			x
Winooka											x	

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Appendix 2

Categories of structural 'tree form' identified as den trees used by the brushtail possum (*Trichosurus vulpecula hypoleucus)* in the northern jarrah forest, south-west Western Australia.

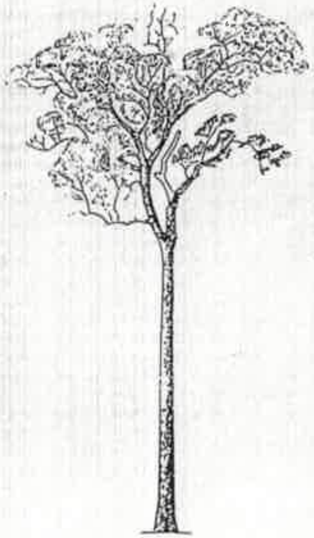
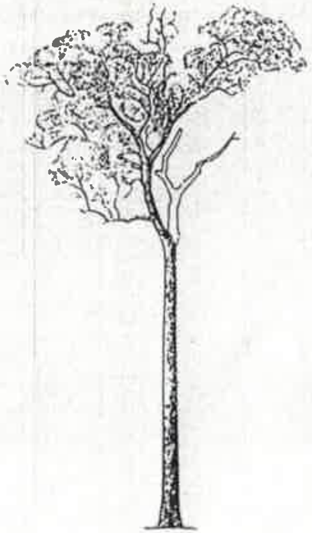
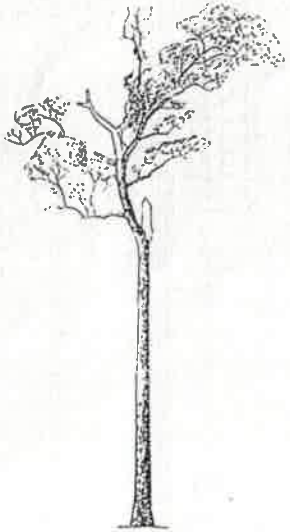
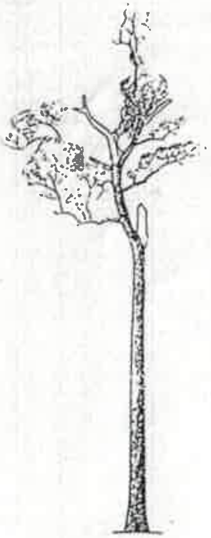
Radio telemetry studies of the brushtail possum (de Tores *et al.*, unpublished) identified ten categories (plus sub categories) of structural tree form (described and shown on the following pages) used as den trees by the brushtail possum (*Trichosurus vulpecula hypoleucus)* in the northern jarrah forest of south-west Western Australia. Drawings used to categorise each den are reproductions of, and additions to, the eight categories identified by Whitford (2002) which were used as part of an 11 stage process of classifying crown senescence for jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) from the northern and southern jarrah forests of south-west Western Australia.

de Tores, P. J., Himbeck, K., MacArthur, B., Maxwell, M., White, E. P. and Rosier, S. M. (unpublished). Use of den trees by the western brushtail possum, *Trichosurus vulpecula hypoleucus*, in the northern jarrah forest, south-west Western Australia.

Whitford, K. R. (2002). Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees 1. Hollow sizes, tree attributes and ages. *Forest Ecology and Management* 160: 201-214.

Structural tree forms

Category	Description
1	Healthy, well-structured crown, with up to 10% crown decline.
2	Crown with up to 25% decline.
3	Crown with 40-55% decline.
4	Crown with 60-75% decline.
5	Tree with dead primary crown and all foliage as secondary growth (lignotuberous or epicormics growth). Secondary growth branch diameter <25mm.
6	Tree with dead primary crown and advanced secondary growth (lignotuberous and epicormic growth). Secondary growth branch diameter >25mm, or secondary growth that replaces existing living over-mature primary crown.
7	Over-mature with up to 90% crown decline.
8	Up to 99% crown decline.
9	Stump or stag with all foliage as secondary growth, branch diameter <25mm.
10	Stump or stag with advanced secondary growth, branch diameter >25mm, includes multiple coppicing stems or single dominant stem.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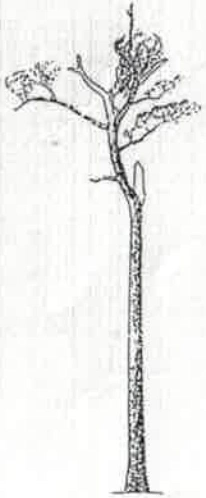	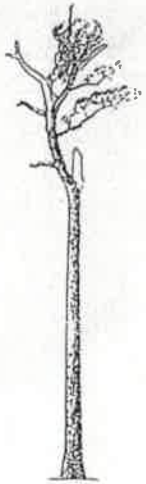		
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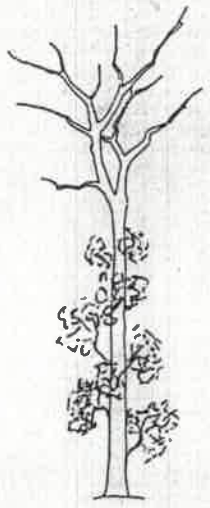

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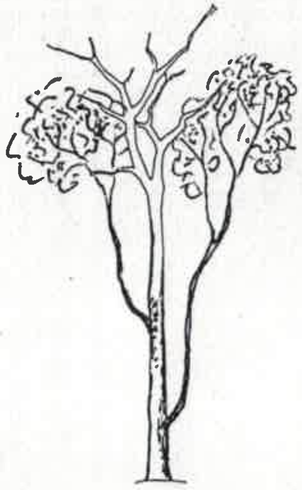

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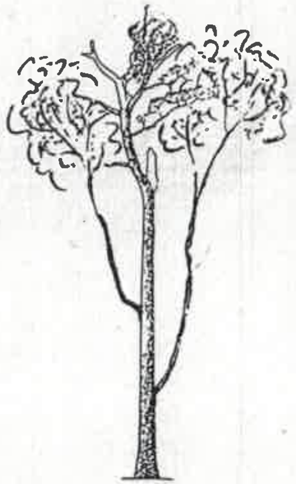

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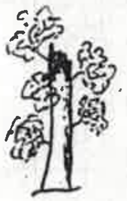

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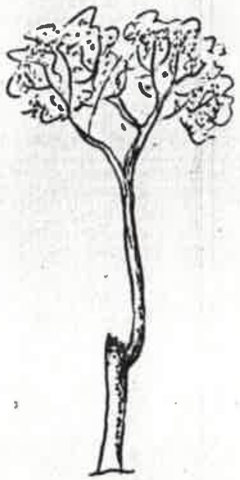

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