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Population Dynamics of the Southern Brown Bandicoot (Isoodon Obesulus) on Ellen Brook Reserve

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POPULATION DYNAMICS OF THE

SOUTHERN BROWN BANDICOOT

(ISOODON OBESULUS)

ON ELLEN BROOK RESERVE

BY

CRAIG PENTLAND

THESIS SUBMITTED IN PARTIAL FULFILMENT
OF THE REQUIREMENTS FOR THE AWARD OF
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ABSTRACT

The small, enclosed section of Ellen Brook Reserve provided the unique opportunity to observe a population of southern-brown bandicoots (*Isoodon obesulus*) in the absence of exotic predators. The reserves small-enclosed size enabled it possible to trap the whole area (excluding the ephemeral swamps) and so emigration and immigration could be excluded. This enabled good population size estimates, and inferences on the loss of individuals due to mortality could be more strongly argued for.

An understanding of the population structure, dynamics, size and density, and body condition of *I. obesulus* in Ellen Brook Reserve, will provide important information, for the development of future management programs and for the long-term survival of this species in closed reserves of this kind.

Sampling was carried out on a monthly basis on four consecutive nights for five months and resulted in a high trap success of bandicoots (45%). The estimated population density of *I. obesulus* was high, ranging from 1.24 to 1.45 bandicoots ha^{-1} with a large degree of range overlap. The sex ratio of the adult population showed a large female bias 3:1, whereas the pouch young were close to parity. A larger proportion of the male population (50%) than the female population (20%) that were caught in the first three months were missing in August and September, suggesting a higher mortality rate of the males. A seasonal effect on body weights and intraspecific aggression (as evidence by increased scarring) was observed during this study. Sexual dimorphism was apparent with adult males being significantly heavier and larger than females. The population was dominated by sexually mature adults but with a continually increasing number of pouch young. Seventy four percent of the females were carrying pouch young by September. Although the mean ± SE litter size was slightly smaller (2.1 ± 0.1) than found in other mainland *I. obesulus* populations the fecundity still appeared to be relatively high.

Given the protection from exotic mammalian predators, this study suggests that *I. obesulus* numbers are able to build up in sufficient numbers from a small size, with a female-biased sex ratio. Although fecundity does not appear to be adversely affected by the small size of the reserve, males appear to show a higher mortality rate than females.

DECLARATION

I certify that this does not incorporate, without acknowledgment, any material previously submitted for a degree or diploma in any institution of higher education; and that to the best of my knowledge it does not contain any material previously published or written by another person except where due reference is made in the text.

Craig Pentland

16 December 1999

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CHAPTER 1. INTRODUCTION

In Australia, bandicoots and bilbies are one marsupial group that has suffered severely since European settlement, with the extinction of three species and the decline of all others (Lyne, 1990). The southern brown bandicoot (*Isoodon obesulus*) occurs over most of the southern half of Australia, including Tasmania. Although considered common in some parts of its range (A.J. Friend, 1990; Hocking, 1990), *I. obesulus* has a patchy distribution over a reduced range throughout the southern half of the continent (Aitken, 1979). Its decline is considered to be due to predation by introduced carnivores and habitat changes brought about by the interaction of several factors: introduced herbivores, changed fire regimes and land clearing (Menkhorst and Seebeck, 1990; Claridge *et al.*, 1991).

Ellen Brook Reserve is a small isolated A class reserve north of Perth. A small enclosed section of Ellen Brook Reserve that has undergone a fox-baiting program (using the compound 1080) over the last decade has seen the successful eradication of the fox (*Vulpes vulpes*), which is thought to be a major predator of *I. obesulus* (Dickman, 1988a; Claridge *et al.*, 1991). Although the main purpose of the reserve is for the protection of the western swamp tortoise (*Pseudemydura umbrina*), sightings of *I. obesulus* began to occur approximately two years after the erection of the vermin proof fence in 1990 and the commencement of the fox-baiting program (Kuchling, pers. comm.). Since then, sightings of *I. obesulus* have gradually increased. This has provided the unique opportunity for an ecological study of a possible relic population of *I. obesulus* in a small area built upon a few individuals, in the absence of migration and absence from predation from mammalian predators, such as the fox.

Although marsupial numbers have increased since the introduction of fox-baiting in Western Australia using 1080 (Kinnear *et al.*, 1988; Friend and Scanlon, 1996), remnant bushland has been substantially reduced and fragmented. So although numbers of marsupial populations have increased in fox-baited areas, a restricted gene flow between small isolated populations may have severe consequences on the long term survival of these species. The constraint of a small habitat size is exacerbated by an enclosure by a vermin proof fence, which reduces dispersal and immigration.

Determining the population structure, dynamics, size and density, and body condition of *I. obesulus* in Ellen Brook Reserve, will provide important information for the development of future management programs and for the long-term survival of this species in closed reserves of this kind. Programs such as Western Shield, that have been implemented for the resettlement of many marsupials back into mainland reserves, start with the reintroduction a small number of individuals released into a small enclosed area. An example is the western barred bandicoot (*Perameles bougainville*) which has been reintroduced into a nine hectare enclosure on Heirisson Prong (Richards and Short, 1996). Thus information collected from this study, in Ellen Brook Reserve, may also provide valuable information for the conservation of marsupial populations that are reintroduced into small, enclosed areas or isolated reserves with limited dispersal.

1.1 The bandicoot families Peramelidae and Peroryctidae

The order Peramelemorphia is represented by one superfamily, the Perameloidea, which includes all the living bandicoots and bilbies and are found only in Australia, Papua New Guinea and nearby islands. Until recently this group was divided into two families: Thylacomyidae (bilbies) and Peramelidae (bandicoots). However a recent study by Groves and Flannery (1990), placed the New Guinea genera into a separate family, Peroryctidae. The remaining species, including the bilbies, were placed into the family Peramelidae.

Although the bandicoots share the polyprotodont dentition of the family Dasyuridae, they differ from all other polyprotodonts in the development of a syndactyl hind foot, a feature characteristic also of the diprotodonts. Thus they appear to form an intermediate evolutionary group between the primitive marsupials of the polyprotodonts like the dasyuroids, and the more advanced diprotodonts like the phalangeroids (Gordon and Hulbert, 1987).

The Peroryctidae family comprises four genera *Peroryctes, Microperorycytes, Rhynchomeles*, and *Echymipera*. Except for one species (*Echimipera rufescens*), all species from the family Peroryctidae are found only in Papua New Guinea and nearby islands (Flannery, 1990). Although the single species, *E. rufescens,* is found in both Australia and New Guinea, in Australia it is confined to the Cape York Peninsula (Gordon *et al.*, 1990). More recently the Peramelidae family has been separaed into two subfamilies, the bibies into Thylacomyinae and the bandicoots into Peramelinae (Strahan, 1995). The Thylacomyinae is represented by one genus *Macrotis* (bilbies), which only contains two species, one of which is now presumed to be extinct, *Macrotis leucura* (Strahan, 1995). The Peramelinae is represented by three genera *Perameles, Isoodon,* and *Chaeropus.* However one species from *Perameles,* (*Perameles eremiana*) and the single species of *Chaeropus (C. ecaudatus),* are now presumed to be extinct (Strahan 1995). Twenty species of bandicoots have so far been described, eleven of which have been found in Australia. However, three species are now extinct. Apart from one species (*Isoodon macrourus*), the family Peramelidae is restricted to Australia.

1.1.1 General features of the bandicoots

Bandicoots are found in a diverse range of habitats, ranging from tropical rainforest to heathland and desert steppe. They are small to medium-sized marsupials ranging from 150 mm to 560 mm in length and 200 g to 4,700 g in weight (Gordon and Hulbert, 1987). They have long pointed muzzles with long jaws accommodating typical insectivorous teeth (Gordon and Hulbert, 1987). The dentition of the bandicoots consists of four or five pairs of blunt incisors in the upper jaw and three similar pairs in the lower jaw. The canines are well developed, and are accompanied by three pairs of upper and lower premolars and four pairs of sharp-crowned upper and lower molars (Strahan, 1995). Although the dentition is most suitable for an insectivorous diet, bandicoots are generally omnivorous supplementing their diet with fruit and soft tubers. The bilby on the other hand, is mostly carnivorous and hunt small mammals and lizards as well as insects (Johnson, 1987).

The hindlimbs of the bandicoot are much larger than the forelimbs and this contributes to their bounding gait. This size difference may be an evolutionary consequence of the need to retain short, powerful forelimbs for digging, while leaving the hindlimbs as the main agent of rapid locomotion (Gorden and Hulbert, 1987). The tail and ears are short in all bandicoots, whereas in the bilby, it is long, tufted tails and has long ears (Johnson, 1987).

The bandicoots are typical marsupials, in that the young are born in a rudimentary condition, and are sheltered in a pouch. However they differ from other marsupials (except for the koala) in that they possess a chorioallantoic placenta similar to that of eutherian mammals, in addition to the yolk sac (Lyne, 1990). The pouch opens downwards and backwards and contains eight teats, but generally only carries 3-4 young at a time. It is believed that the limited number of pouch young at any one time is due to the increase in teat size, which occurs with lactation. A recently vacated teat is thought to be too large for the attachment of a newborn animal (Strahan, 1995). However, Merchant (1990) has observed some newborn young to attach themselves to a recently vacated teat. The bandicoots have a very short, recorded gestation period of only 12.5 days. This is believed to be the shortest gestation period recorded for any mammal (Lyne, 1974). They also have a very short lactation period, which only lasts about 60 days. Oestrus may occur during the lactation period and a new litter of young may be born as soon as the previous young vacate the pouch (Gemmell, 1982). Bandicoots may breed all year round, but some species show a seasonal breeding pattern (Heinsohn,1966; Stoddart and Braithwaite, 1979; Craven, 1981). This combination of reproductive features strongly suggests that ancestral bandicoots underwent selection for high fecundity and rapid maturity (Lee and Cockburn, 1985), enabling the group to be opportunistic and to colonise new patches of suitable habitat quickly.

1.2 Biology/Ecology of the southern-brown bandicoot (*Isoodon obesulus*)

1.2.1 Introduction

The southern brown bandicoot (*I. obesulus*), also known locally by the Nyungah name quenda, is one of three species from the genera *Isoodon*, the short-nosed bandicoots. *I. obesulus* is a small, stout looking marsupial similar in size to that of a eutherian rabbit, and ranges from 280-360 mm in length and 400-2400 g in weight (Heinsohn, 1966; Craven, 1981; Thomas, 1984). The ears are short and rounded, with large auditory bullae. The pelage is composed of two types of hair; long, coarse, bristly guard hair and a softer under fur. The coloration of the hair on the face, dorsal and lateral areas, ranges from brownish-grey to yellowish-brown. The ventral regions are a creamy-white colour. The hind limbs like those of all bandicoots (except the Pig-footed bandicoot, *Chaeropus ecaudatus*), are longer than the forelimbs, and are similar in shape to the hind limbs of macropods. *I. obesulus* has two main gaits, a galloping motion and an ungainly quadrupedal like walking motion (Heinsohn, 1966). The tail is short and lightly furred and has no function in locomotion and is not prehensile (Strahan, 1995). *I. obesulus* is strictly terrestrial and although predominantly nocturnal it has been found active during the day (Friend. pers. comm.).

1.2.2 Distribution and habitat preference

The southern brown bandicoot is the most widely distributed species of the family Peramelidae. It is found over most of the southern half of Australia including Tasmania, and is also found as far north as Cape York. It has been divided into a number of sub-species (Fig. 1.1), which are *Isoodon obesulus affinus* (Tasmania), *Isoodon obesulus fusciventer* (WA), *Isoodon obesulus nauticus* (Nuyts Archipelago, SA), and *Isoodon obesulus obesulus* (SA, Vic, NSW) and *Isoodon obesulus peninsulae* (Cape York, Qld). However *I. o. peninsulae* is of uncertain taxonomic status, and although it is currently regarded as a subspecies of *I. obesulus*, it may eventually come to be regarded as a form of *Isoodon auratus* (Gordon *et al.*, 1990).

I. obesulus is found in a variety of habitats in its widespread distribution. Outside Western Australia it occurs primarily in scrub and heathland communities, and in open forest and woodland habitats with a dense understorey (Stoddart and Braithwaite, 1979; Menkhorst and Beardsell, 1982; Copley *et al.*, 1990; Hocking, 1990; Kemper, 1990). However, it has also been found in areas of pasture and cropland lying close to dense cover (Heinsohn, 1966; Mallick *et al.*, 1998b). In the heathlands, *I. obesulus* exhibits a clear preference for newly regenerating vegetation (Stoddart and Braithwaite, 1979). This preference may be associated with a high abundance of beetle larvae, a preferred prey type (Opie, 1980). Claridge *et al.* (1991) found that in the south-east of NSW, *I. obesulus* preferred the dense cover of the slopes and ridges rather than gullies. It has also been suggested that males and females might occupy different habitat types (Stoddart and Braithwaite, 1979;

Claridge *et al.*, 1991). In Victoria, although *I. obesulus* is generally absent from the eastern and western uplands, it does occur at altitudes of up to 1000m in the Grampians (Menkhorst and Seebeck, 1990).

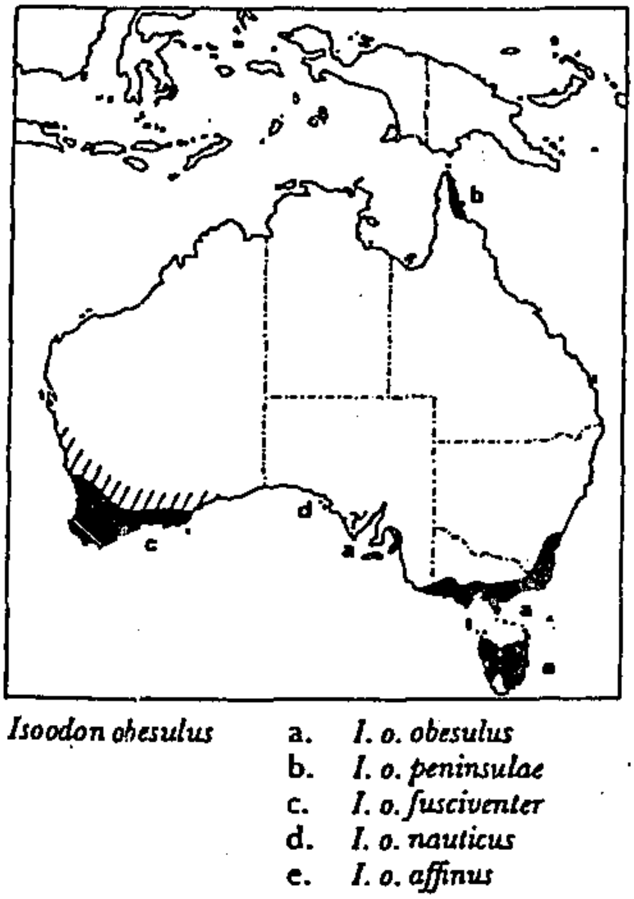


Figure 1.1 Distribution of *Isoodon Obesulus* sub-species (from Seebeck *et al.*, 1990)

In Western Australia *I. obesulus* is found on the coastal margin as far north as Yanchep and as far south as Cape Le Grand, with the furthest inland records at Wyalcatchem and Hyden (Friend, 1991). Animals show a preference for dense vegetation around wetlands and along watercourses which provide cover and abundant insect fauna (Craven, 1981; Friend, 1991). Although *I. obesulus* has declined significantly in some areas, predominantly the Southern Wheatbelt, it is still thought to be common locally (A.J. Friend, 1990). In the south-west *I. obesulus* is most widespread, where it is not strictly confined to riverine habitats, being found in coastal woodlands, heaths and flats where vegetation is dense (Christensen *et al.*, 1985). Couper (1998) found *I. obesulus* occupied two distinct types of habitat, open Jarrah (*Eucalyptus marginata*) forest and swamp habitats. She found that there were distinctive physiological differences between populations found in the two habitat types and the size of the bandicoots was significantly larger in the open Jarrah forest populations than in the swamp populations.

From the accumulating data on the southern brown bandicoot in Australia, it appears that although this species shows a clear preference for dense cover in low shrubland, it is still found in a variety of other habitats. However, its distribution, although widespread, is relatively patchy, and its range has been significantly reduced in most states. The lack of research on the southern brown bandicoot in some states has made it difficult to make overall conclusions about its past and present distribution.

1.2.2 Diet and feeding behaviour

Although bandicoots have a polyprotodont dentition, which is ideally suited for an insectivorous and carnivorous diet, *I. obesulus* is generally considered omnivorous. It feeds on a wide range of both plant and invertebrate material including hypogeous fungi and the occasional small vertebrate (Heinsohn, 1966; Lee and Cockburn, 1985; Quin, 1985). *I. obesulus* has been found to change its diet seasonally as different food resources become available and so is considered to be a qualitatively opportunistic omnivore. Analysis of faecal samples have shown that invertebrates make up the bulk of the diet (Quin, 1985; Broughton and Dickman 1991; Mallick *et al.*, 1998a). The majority of this invertebrate proportion is derived from adult beetles and their larvae (Quin, 1985; Stoddart and Braithwaite, 1979). However, diet components vary in different habitats and depend on the analysis technique used (Quin, 1985).

It's believed that *I. obesulus* detects its prey primarily by olfaction (Quin, 1991). For subterranean food, *I. obesulus* digs in the soil with its strong fore-claws using its nose as a probe and with its eyes shut (Heinsohn, 1966). This digging action produces a characteristic conical shaped hole. The size of the hole ranges from 3-10 cm across and 6-15 cm deep, though the size and shape varies depending on the soil type (Triggs, 1997). Feeding behaviour occurs predominantly at night. *I. obesulus* emerges after sunset but before dark, with most of its activity extending for several hours after dusk, where most of this activity is directed towards feeding (Thomas, 1984; Courtenay, 1995).

1.2.4 Reproduction and growth

Like all bandicoots, the pouch of *I. obesulus* is well developed and opens backwards and downwards. It contains 8 nipples arranged in an incomplete circle. *I. obesulus* is polyoestrous and breeding may be seasonal or continuous. If it is seasonal, the length and onset time of breeding varies considerably. In Tasmania, *I. obesulus* breeds for eight months of the year from June to February (Heinsohn, 1966), whereas in Victoria, breeding season is shorter, only six months from July to December (Lobert and Lee, 1990). However, in the Grampians in central western Victoria breeding occurs all year round (Lobert and Lee, 1990). In Western Australia, breeding may occur throughout the year, but with main peaks in spring (Craven, 1981; Thomas, 1984; Thomas, 1987; Dell and How, 1988). Breeding also occurs throughout the year in the Franklin Islands in South Australia with similar spring peaks (Copley *et al.*, 1990).

Seasonal breeding may coincide with peaks in food abundance (Heinsohn, 1966; Cockburn, 1990; Lobert and Lee, 1990), or may be due to other environmental variables such as temperature, rain or day length (Stoddart and Braithwaite, 1979). Cockburn (1990) considered the trigger of cessation of breeding to be food and water availability. This was also found to cause lower litter sizes in a continuous breeding population in the Franklin Islands (Copley *et al.*, 1990). However, Stoddart and Braithwaite (1979) believe that day length is a more likely cue for the breeding season rather than rainfall, which has also been found to be the major cue for the mating period in some dasyurids (McAllen and Dickman, 1986). Barnes and Gemmell (1984) found that it was an interaction of a variety of environmental variables rather than just one, with temperature and rainfall showing the strongest association as a cue for breeding season and reproduction rate in bandicoots, with day length being less significant.

Gestation is short, ranging from 12-15 days (Stoddart and Braithwaite, 1979; Lobert and Lee, 1990). Lactation period is about 60 days, and as oestrus during lactation can occur, a new litter can be born immediately the pouch is vacated (Stoddart and Braithwaite, 1979). Tayler (1965) found that a new litter might be conceived even while the previous litter is still in the pouch. He observed that only 13 days passed between observation of a single, relatively large, but still hairless pouch young and the appearance of five small young.

Between 3 and 4 litters can be produced per year, with a mean litter size of between 3 and 4 (Heinsohn, 1966; Thomas, 1984; Lobert and Lee, 1990). Mean litter sizes vary from season to season with different age classes of females. Litter size tends to be higher in the beginning to the middle of the season (Craven, 1981; Stoddart and Braithwaite, 1979; Copley *et al.*, 1990). Stoddart and Braithwaite (1979) found that the oldest females produced the largest litters. Even within populations with continuous breeding, fertility may vary considerably if availability of food changes through out the year. If food abundance is high females appear to produce larger litters, whereas if food abundance is low then litter size and the number of litters produced decreases (Lobert and Lee, 1990).

Like all bandicoots, the period from conception to weaning for *I. obesulus* is short. Nine days after parturition sex can be determined. At 48 days the eyes open and the young are fully furred. They are weaned at around 69 days (Thomas, 1984). Thomas (1984) found that there were discrepancies between the developmental stages of *I. obesulus* in W.A. and those found by Heinsohn (1966) in Tasmania, with the bandicoots in the latter having faster growth rates. Growth rates have also been shown to vary between bandicoots in Victoria and Tasmania. In Tasmania Sexual maturity in females and males is reached at approximately four and six months respectively (Heinsohn, 1966), compared to a minimum of seven months of age in Victoria (Lobert and Lee, 1990). These differences are believed to be a consequence of the length of breeding season. In Tasmania, the eight month breeding season allows the growth to maturity of juveniles during the season of their birth, whereas the shorter six month breeding season in Victoria is too short to permit this (Lobert and Lee, 1990). Heinsohn (1966) found the strongest correlation with age to be head length whereas Thomas (1984) found that pes and forearm lengths were best correlated with age.

The high reproductive output of *I. obesulus* enables this species to quickly colonise patches of suitable habitat as they develop (Menkhorst, 1994) and to recover quickly from low population numbers when environmental conditions improve.

1.2.5 Home range

The term home range appears to be somewhat arbitrary, so Jewell (1966) has described a home range as " an arena of activity with spatial qualities that vary throughout its extent, and that is subject to great irregularity in intensity of use". Home range can vary considerably in relation to population density (Stickel, 1960; Brown, 1966), and due to changes in feeding behaviour in different seasons, because food source availability may vary (Brown, 1966).

Data on the size of home range and range overlap is conflicting between studies of *I. obesulus*. In some studies, males and to a lesser extent females, appear to be territorial, showing a minimal degree of home range overlap, both between sexes and within sexes (Heinsohn, 1966; McKenzie, 1967; Mallick *et al.*, 1988b). In other studies no evidence of territorial behaviour was found, and there was a high degree of home range overlap between individuals (Tayler, 1965; Craven, 1981; Copley *et al.*, 1990; Broughton and Dickman 1991). Generally, males showed significantly larger home ranges than females, 2.34 - 6.95 ha and 1.83 - 3.28 ha respectively (Heinsohn, 1966; Broughton and Dickman, 1991; Mallick *et al.*, 1998b) probably as a result of their larger body size (Craven, 1981).

Home range size and range overlap of *I. obesulus* is also thought to be related to both food availability and population density. At low population densities if resources are defendable and intruder pressure is low, *I. obesulus* will be territorial, but will occupy high overlapping ranges if population density is high (Broughton and Dickman, 1991). This statement clearly reflects the differences between populations in home range size and overlap. The lowest degree of overlap and largest range sizes were all found in populations with the lowest densities, 0.125 - 0.35 animals ha^{-1} (Heinsohn, 1966; McKenzie, 1967; Mallick *et al.*, 1998b). The highest degree of overlap and smallest range sizes were all found in populations with the highest densities, 0.96 - 5 animals ha^{-1} (Craven, 1981; Copley *et al.*, 1990; Lobert, 1990; Broughton and Dickman, 1991).

In *I. obesulus,* social behaviour also appears to have a significant effect on size of home range and degree of overlap. McKenzie (1967) has found that in *I. obesulus* populations both sexes can exhibit dominant hierarchies, but to a lesser extent in females, with the larger dominant individuals occupying larger home ranges. During the breeding season temporary home range extensions were detected in males, and although male ranges overlapped during this period, the interaction was only due to a dominant larger male extending its range onto that of a sub-dominant, not vice-versa.

The data show that many factors affect home range size and the degree of range overlap in *I. obesulus*. While home range size appears to be strongly correlated with body size, both the home range size and range overlap also appear to be controlled by food availability, population density and social hierarchy. The female home range generally appears to have only one function, that of suitable supply of food resources, whereas the larger home range of the male has two functions, that of food supply and to permit the males to have access to a larger number of females (Thomas, 1984).

1.2.6 Age structure and sex ratio

Sex, age, and size are three major variables that distinguish individuals in populations. The age distribution and sex ratio clearly affect the potential reproductive rate and mortality rate, and the rate of generation replacement (Yablokov, 1986).

The sex ratio of some populations may be significantly disturbed from a 1:1, favouring one sex over the other. Physiological and behavioural patterns may affect mortality of the sexes differently at different stages of their life history. Dispersal rates may differ between sexes. Juvenile males are the predominant dispersers in polygynous mammals (Greenwood, 1980; Holekamp and Sherman, 1993). In marsupials, high juvenile male dispersal has predominantly been found in macropods (Johnson, 1989) and dasyurids (Cockburn *et al.,* 1985b). This sex bias in dispersal is thought to be an important mechanism for the avoidance of inbreeding (Cockburn *et al.*, 1985b; Lee and Cockburn, 1985). Aggressive behaviour in the males may also leave them subjected to greater stress, and thus with a higher mortality rate. Sex ratios may differ under different environmental conditions (Trivers and Willard, 1973), when the condition of the female may determine her capacity to invest in offspring and the amount of investment between the sexes of the offspring (Dickman, 1988b; Cockburn, 1990). In polygynous mating systems in which the male exhibits more variation in reproductive success than females, healthy mothers will invest more per offspring and bias the degree of investment towards the males. Unhealthy mothers invest less per offspring and produce more females (Cockburn, 1990).

In *I. obesulus,* it has generally been found that the sex ratio in adults is biased towards males (Heinsohn, 1966; Mckenzie, 1967; Thomas, 1984; Dell and How, 1986; Dickman, 1988a; Copley *et al.*, 1990; Claridge *et al.*, 1991). The pouch young ratio, however, tends to be closer to parity (Heinsohn, 1966; Thomas, 1987; Dell and How, 1988). Some populations, however, have shown sex ratios bias towards females (Stoddart and Braithwaite, 1979; Craven, 1981; Thomas, 1987; Mallick *et al.*, 1998b). Trap response, dispersal, mortality and predation, are all factors that have so far been postulated to contribute to the adult sex ratio biases in *I. obesulus.*

A differential trap response between sexes is thought to be due to trap shyness, home range size and habitat preference. The observed male bias sex ratio may be partly due to the trap shyness of females (Heinsohn, 1966). If male and female *I. obesulus* occupy different habitats, then there is the potential that trapping locations will not encompass the habitat of both sexes equally, producing a possible bias in the sex ratios that may not truly represent the population as a whole. Stodddart and Braithwaite (1979) found that males and females occupy different habitats, where large adult females tend to be excluded from new regenerating heathland, which males dominated. Differences between male and female home range size may be a factor contributing to the observed male biased populations. Male *I. obesulus* have larger home ranges than females (Heinsohn, 1966; McKenzie, 1967; Craven, 1981; Mallick *et al.*, 1998b) and so the greater mobility of males may increase their chances of coming into contact with the traps than that of females (Copley *et al.*, 1990). Mortality rates may also be affected by the smaller home range size of females, where the smaller range size may make them more vulnerable to the occurrence of fire than males (Dell and How, 1988).

I. obesulus is considered a polygynous species with a high juvenile dispersal (Lobert and Lee, 1990) and it has been suggested that there may be a higher dispersal of juvenile males out of their natal areas than females (Dickman, 1988a). Male dominance hierarchy in *I. obesulus* has been observed with only a few dominant males contributing to the majority of the mating of the females in the population (McKenzie 1967; Dickman, 1988a). As density increases, space becomes limited and so in such a male dominant hierarchy, there will be a maximum number of territorial males that the population can hold. So at high density the population may self regulate with males shifting to larger home range overlaps (Broughton and Dickman, 1991), and/or a higher dispersal rate of younger males out of the population.

Preferential prey of sexes by predators has been proposed as a major factor for the male biased populations (Dickman, 1988a; Claridge *et al.*, 1991). Dickman (1988a) found that *I. obesulus* suffered relatively high predation from foxes, and although males significantly outnumbered females, females were taken more frequently than males. In areas where foxes were present, Claridge *et al.* (1991) found that a male biased sex ratio and low population density had occurred after logging, whereas prior to logging operations, sex ratios were close to parity with a slightly higher population density. The immediate effect of intensive logging is a loss of understorey necessary for bandicoot shelter and subsequently feral predators including the fox may have been responsible for losses from the bandicoot populations. The eastern barred bandicoot (*Perameles gunnii*) has also shown male biased sex ratios (Dufty, 1994a) which are thought to be caused by dominant males forcing sub-adults and adult females into sub-optimal habitat (Dufty, 1994b). Areas of sub-optimal habitat lack the necessary shelter of dense understorey and as a result, sub-adults and females may be more exposed to predators (Dufty, 1991). Female adult biased populations are generally found only in enclosed areas, where introduced predators are excluded (Craven, 1981; Thomas, 1987), and in areas where the fox is absent, such as in Tasmania (Mallick *et al.*, 1998b). However in Tasmania Heinsohn (1966) did find a male bias sex ratio in a trapping program. However results from shooting showed the sex ratio to be closer to parity, and it was these results that were thought to be the truer representation. The slight male bias in Heinsohn's (1966) studies may be due to a combination of factors including female trap shyness, lack of optimal habitat, and possible predation from cats. Although foxes are not present in Tasmania, areas that contain high numbers of cats still be influenced by predation from exotic predators. At Cranbourne in Victoria where foxes are also present, the population is female biased (Stoddart and Braithwaite, 1979). The vegetation structure at Cranbourne primarily contains dense heathland, which is virtually impenetrable to animals any larger than bandicoots and so offers greater protection from mammalian and avian predators (Lobert, 1990).

Age structure in populations of *I. obesulus* in Western Australia varies throughout the year, partly due to changing percentages of breeding females, and partly to environmental factors such as climate and food source availability affecting mortality rates (Craven, 1981; Dell and How, 1988; Thomas, 1987). Although *I. obesulus* in Western Australia has a main breeding season during spring, breeding may occur at low levels throughout the year. The highest juvenile numbers generally occur in August, September and October, and the lowest in March, April and May (Craven, 1981; Dell and How, 1988; Thomas, 1987). The sub-adults increased during autumn, due to higher breeding rates in the previous spring and decreased in November, December and January (Craven, 1981; Thomas, 1987). Lengths in breeding season vary from state to state, with Tasmania recording eight months (Heinsohn, 1966), and Victoria six months (Stoddart and Braithwaite, 1979; Lobert and Lee, 1990). These differences with Western Australia indicate the difficulty in comparing studies, since different lengths of breeding season will produce different age structures throughout the year.

The data on *I. obesulus* clearly indicates that age structure and sex ratios are a result of a complex combination of factors; however, predation from introduced predators suc as the European fox and cat has constantly re-occurred as a major factor. Further studies on the effects of predation on sex ratios and age structure are necessary for the future management of *I. obesulus* in the long term. The age structure and sex ratio are critical components in population structure as they both affect natality and mortality rates, and ultimately the growth rate. The age structure and sex ratio may reflect recent environmental conditions and so may be used to predict future outcomes of population growth. This information will, in turn, be important for future management programs for long term sustainable populations.

1.2.7 Population size and density

To understand the dynamics of a population we first need to consider the density of the population and its total population number. Immigration and birth rate, and emigration and mortality rate affect a population's size. In turn the sex ratio and age structure clearly affects the potential reproductive rate, mortality rate, rate of generation replacement, and may also affect social interactions. The carrying capacity of the ecosystem is unlikely to be fixed over any extended time. Instead, it fluctuates with environmental conditions, continually altering the size of the population the ecosystem can support. Population densities of some species may go up and down rhythmically, showing large variations below and above the carrying capacity. These cycles are seen predominantly in populations of small mammals (Krebs and Myers, 1974).

I. obesulus populations have been shown to exhibit fluctuations in population size and density and these have been attributed to changes in breeding activity (Craven, 1981; Thomas, 1987; Copley *et al.*, 1990) and /or environmental changes (Copley *et al.*, 1990; Lobert and Lee, 1990), leading to a change in the carrying capacity of the habitat, in turn leading to a change in numbers of bandicoots (Mallick *et al.*, 1998b).

Population densities can change because of variations in dispersal rates. At high densities, individuals may leave a population and seek out new habitats, since dispersal can affect the composition, size and spacing of populations, it can affect the productivity of those populations as well (Lidicker, 1962; Wynne-Edwards, 1965). High population densities in *I. obesulus* have shown a high degree of dispersal (Stoddart and Braithwaite, 1979; Lobert and Lee, 1990). Dispersal may act as a regulating mechanism, an example of which is found in an experiment on voles by Kreb *et al.* (1969). It was found that in small, enclosed areas, which permitted free movement of predators but no migration of the voles, the populations increased to a high density until food resources were virtually destroyed. The voles subsequently suffered a severe decline associated with starvation through overgrazing. A similar example has been found in populations of macropods in a small enclosed reserve (Algar, 1986). Although *I. obesulus* is omnivorous with the bulk of its diet composed of invertebrates (Quin, 1985), food resources could still be severely affected by overpopulation.

Density-limiting forces may arise from aggressive behaviour within a population, causing breakdown in parental care and a higher juvenile mortality (Calhoun, 1962). In *I. obesulus,* adult aggression towards juveniles or less-aggressive individuals may result in mortality due to stress (reducing the health and survival of an individual) or it may force the emigration of juveniles and less-aggressive individuals (Heinsohn, 1966; Thomas, 1984; Dickman, 1988a).

Aggressive behaviour in crowded populations can affect behavioural changes in individuals, which may adversely cause reproduction (Christian and Davis, 1964; Wynne-Edwards, 1965; Chitty, 1967; Myers, 1967). Although it has not been determined if high density in *I. obesulus* populations affects the number and size of litters, the survival of the young and the age at which they mature, some environmental factors have had effects. In an island population, response to drought was a reduced litter size (Copley *et al.*, 1990).

Predation from exotic predators has been attributed to the demise of many marsupial groups (Kinnear *et al.*, 1999) including bandicoots (Claridge *et al.*, 1991; Dufty, 1994a). Bandicoots have been generally found in low population densities in areas with foxes (Sampson, 1971; Claridge *et al.*, 1991) and in high densities in areas without the foxes, including enclosed reserve in Western Australia (Craven, 1981; Thomas 1987; Broughton and Dickman, 1991) and islands (Short *et al.*, 1998a). High *I. obesulus* densities have also been found in areas with a high degree of dense cover (Stoddart and Braithwaite 1979; A. J. Friend, 1990; Lobert and Lee, 1990). A combination of factors have been attributed to the demise of bandicoots which include habitat changes brought about by the interaction of several factors; introduced herbivores, changed fire regimes, and land clearing (Menkhorst and Seebeck, 1990; Claridge *et al.*, 1991).

1.2.8 Sexual size dimorphism

Sexual size dimorphism among mammals is widespread, with males usually significantly larger than females (Heske and Ostefeld, 1990), although in some species the reverse has been found (Levenson, 1990). Sexual dimorphism is associated with polygynous and promiscuous mating systems, where competition between males selects for larger body size (Selander, 1965; Lee and Cockburn, 1985). Sexual dimorphism for body size may not necessarily be associated with polygynous and promiscuous mating systems, but may favour selection for differential use of niches by the sexes, reducing intraspecific competition for resources (Heske and Ostfeld, 1990; Levenson, 1990). This has been suggested in populations of *Antechinus. stuartii*, where the two sexes appear to be behaving like two species (Braithwaite, 1973).

As *I. obesulus* is polygynous it would be expected that populations would show sexual size dimorphism with males significantly larger than females. Such has been found in all populations of *I. obesulus* so far studied throughout its distribution in all states (Heinsohn, 1966; Stoddart and Braithwaite, 1979, Craven, 1981; Copley *et al.*, 1990; Mallick *et al.*, 1998b). However, growth rates, of both sexes are similar up to an age of 234 days (Thomas, 1984), and so the sexual dimorphism may simply be due to longevity differences between males and females (Stoddart and Braithwaite, 1979). In macropods, similar growth patterns between sexes are observed up to the age of sexual maturity, but thereafter, growth rates in the male then far outstrips those of the female (Newsome, 1977). A similar pattern may also be found in *I. obesulus*, where it is not until sexual maturity is reached that growth rates differ between sexes. Cooper (1998) has found that sexual size dimorphism shows significant geographic variation in overall body size and shape, found in both male and female *I. obesulus* in the south-west of Western Australia. Although body size and shape was not correlated with climatic conditions, a strong relationship with habitat structure was found. Larger bandicoots were found in open forest habitats, while smaller bandicoots were found among swamp reeds. It is not known whether these differences in morphology found between habitat structures represent adaptive divergence, or are a result of environmental differences directly affecting the growth and development of the bandicoots. DNA testing is currently under way to determine if these differences represent adaptive divergence between local populations (Cooper, 1998).

1.3 Study aims

The major aims of the study were:

- To describe the structure and dynamics of a population of *Isoodon obesulus* in the small enclosed predator-controlled section on Ellen Brook Reserve.

- To investigate the constraints of a small enclosed reserve and a seasonal reduction of foraging area on the population structure and dynamics.

1.3.1 Specific aims

On the enclosed section of Ellen Brook Reserve, this study aimed to examine the

- Population size and density
- Age class distribution and sex ratio
- Recruitment rate
- Movement
- Reproductive condition
- Body condition
- If any sexual size dimorphism exists within the population

A survey of the literature raises a number of issues relating to ecology and management issues to remnant populations of bandicoots in Australia. From these I have identified key research questions:

1. How does a natural, seasonal reduction in foraging area in an enclosed population affect the population and dynamics?

2. How do the patterns of sex ratios relate to the issues of enclosure and predation?

3. To what extent is reproductive effort and recruitment affected by the enclosed constraints of the reserve?

Chapter 2. Methodology

2.1 Study area

Ellen Brook Reserve is located on the eastern side of the Darling Scarp on the Pinjarra Plain adjacent to the western side of the Great Northern Highway 2 km north of Upper Swan (Figure 2.1). The reserve was vested in the National Parks and Nature Conservation Authority in 1962 for the protection of the western swamp tortoise (*Pseudemydura umbrina*). The reserve is separated into two by Ellen Brook, which flows seasonally during winter rains. On the southern side of Ellen Brook in the enclosed section the reserve consists of a clayey soil, with numerous depressions forming a Gilgai complex. In the depressions drainage is poor but the surrounding higher regions are relatively well drained (Pym, 1955). It is currently managed by the Department of Conservation and Land Management (CALM). The reserve has an area of 76 ha, of which, approximately 38.8 ha, including the further extension in 1994 are enclosed within a vermin proof fence (Plate 2.1). The fence was first constructed in 1989/90 around the southern end of the reserve. This end contains the numerous depressions of the Gilgai complex, which provide the optimum habitat for the western swamp tortoise. The southern end of the enclosed section that was extended a further 10.8 ha in 1994 is slightly degraded with little understorey and a section of open pasture at its most southern point.

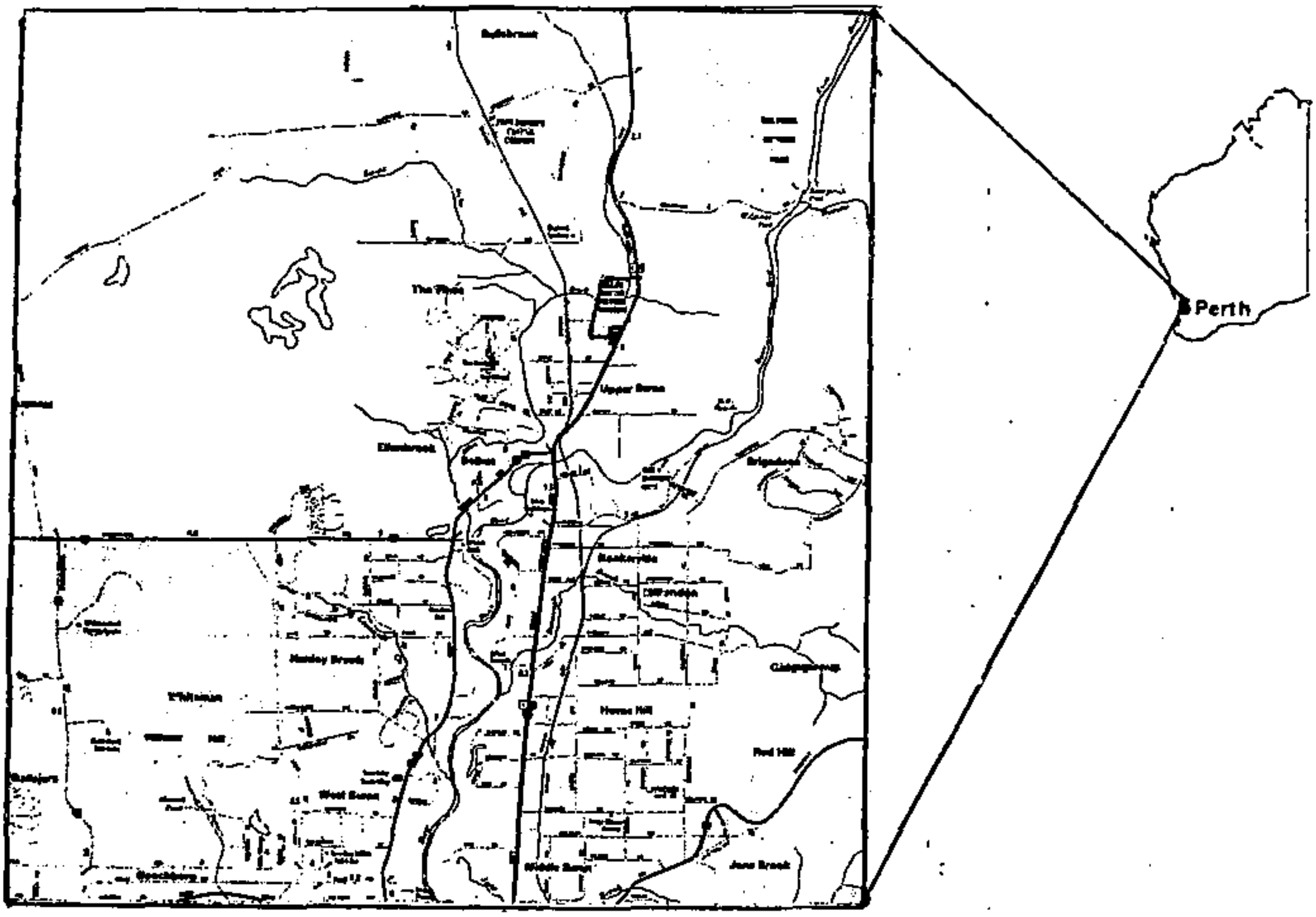


Figure 2.1 A map of Upper Swan, Western Australia, showing the location of Ellen Brook Reserve.

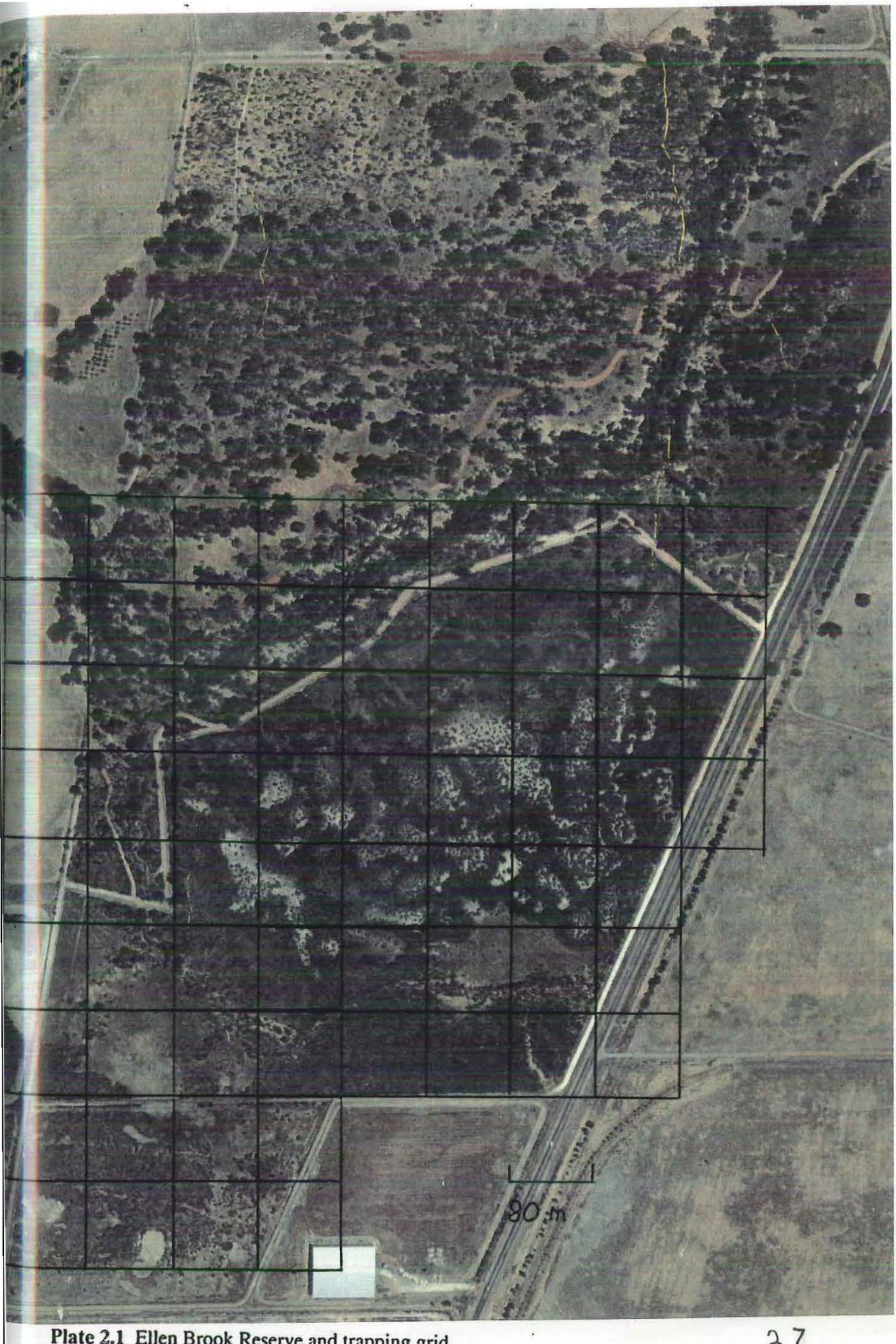


Plate 2.1 Ellen Brook Reserve and trapping grid.

A baiting program had been carried out sporadically between 1979 and 1988 in an effort to control exotic predators (using strychnine), but proved to be inadequate for eradicating the fox (Burbidge, 1987). A new fox control technique (using the compound 1080) developed by Kinnear *et al.* (1988) was applied in the reserve in 1988, and the baiting program intensified. Since this new baiting program, bandicoots (*Isoodon obesulus*) have been observed in the enclosed area (Kuchling. pers. comm.). Foxes have been capable of finding weak links inside the fence, so regular inspection is required (Burbidge, 1987). Fox and rabbit baiting programs are ongoing. At present there is a no burn policy at Ellen Brook Reserve.

Bowman *et al.* (1989) defined the drainage pattern in the reserve by three generalised topographic zones (Fig. 2.2). Water flows in a southerly direction through the reserve until it reaches the drain. On the southern side of this drain elevation then increases in a southerly direction (Plate 2.2) and so subsequently water flows in a northerly direction until it reaches the drain.

Zone 1: This is the largest of the drainage zones containing numerous claypans. These claypans begin to fill up during early winter, after the first rains. A 17.5m contour delineates the southern boundary of this zone, which essentially represents a restrictive bund to the flow of surface water. It is this zone that represents the principal feeding and breeding areas for western swamp tortoise.

Zone 2: As the water level rises in the claypans in zone 1 and exceeds the restrictive height of the southern bunds, water overflows into zone

2. A 17.4m contour delineates the southern boundary of zone 2, again essentially represented by restrictive bund to the flow of surface water. The claypans in zone 2 are shallower than those found in zone 1.

Zone 3: As water levels continue to rise in zone 2, overflow from these Swamps then dissipates to the south and south-west, through minor depressions in zone 1 and eventually to the drainage line that flows into Ellen Brook.

Figure 2.2 Detailed topographical and drainage patterns of Ellen Brook Reserve (from Bowman Bishaw Gorham, 1989).

Plate 2.2 Southern swamps in Ellen Brook Reserve (August, 1999).

This seasonal flow of water in the reserve may have a severe impact on the habitat use by the *I. obesulus* population. As the swamps begin to fill, foraging area is substantially reduced (approximately 30-40%).

The vegetation structure inside the enclosed section of the reserve as described by Burbidge (1967) is an association of *Melaleuca lateritia* and the sedges, *Leptocarpus canus* and *L. aristatus* in the swamps (Plate 2.3-2.4). In the surrounding higher regions there is a complex association of the shrubs *Acacia cyanophylla*, *Viminaria denudata, Melaleuca viminea, Hakea varia* and *Jacksonia sternbergiana* (Plate 2.5-2.6). There are a few *Eucalyptus rudis* scattered near the western side (Plate 2.7). The extended section of the reserve is currently undergoing rehabilitation with some revegetation having already begun with the planting of *Melaleuca viminea, Melaleuca teretifolia* and *Hakea varia.*

Plate 2.3 Northern swamps in Ellen Brook Reserve (March ,1999).

Plate 2.4 Northern swamps in Ellen Brook Reserve (August, 1999).

Plate 2.5 Surrounding higher areas of *Melaleuca* spp. at the southern end of Ellen Brook Reserve (March, 1999).

Plate 2.6 Surrounding higher areas of *Melaleuca* spp. at the southern end (extended section) of Ellen Brook Reserve (March, 1999).

Plate 2.7 Clump of *Eucalyptus rudis* at the western side of Ellen Brook Reserve (August, 1999).

2.2 Trapping procedures

Bandicoots were live-trapped using small Sheffield traps 20cm x 20cm x 58cm (Plate 2.6). Traps were baited with a mixture of peanut paste, sardines and rolled oats and were placed in the center of each trap site (wherever possible) at 80m spacings on a permanent grid (Plate 2.1). Traps were only placed in the higher areas not affected by the ephemeral swamps. Trap sites were marked with either brightly painted stakes or tape. Traps were set on four consecutive nights each month from May to September. Traps remained permanently at trapping sites for the duration of the trapping program. At the end of the fourth trap night in each cycle traps were closed until the beginning of the following trapping cycle. Traps were set an hour before dusk, and cleared after sunrise. Once cleared, traps remained closed until resetting again one hour before dusk. To minimise environmental stress for animals in traps, the traps were covered with hessian and where possible placed under existing vegetation.

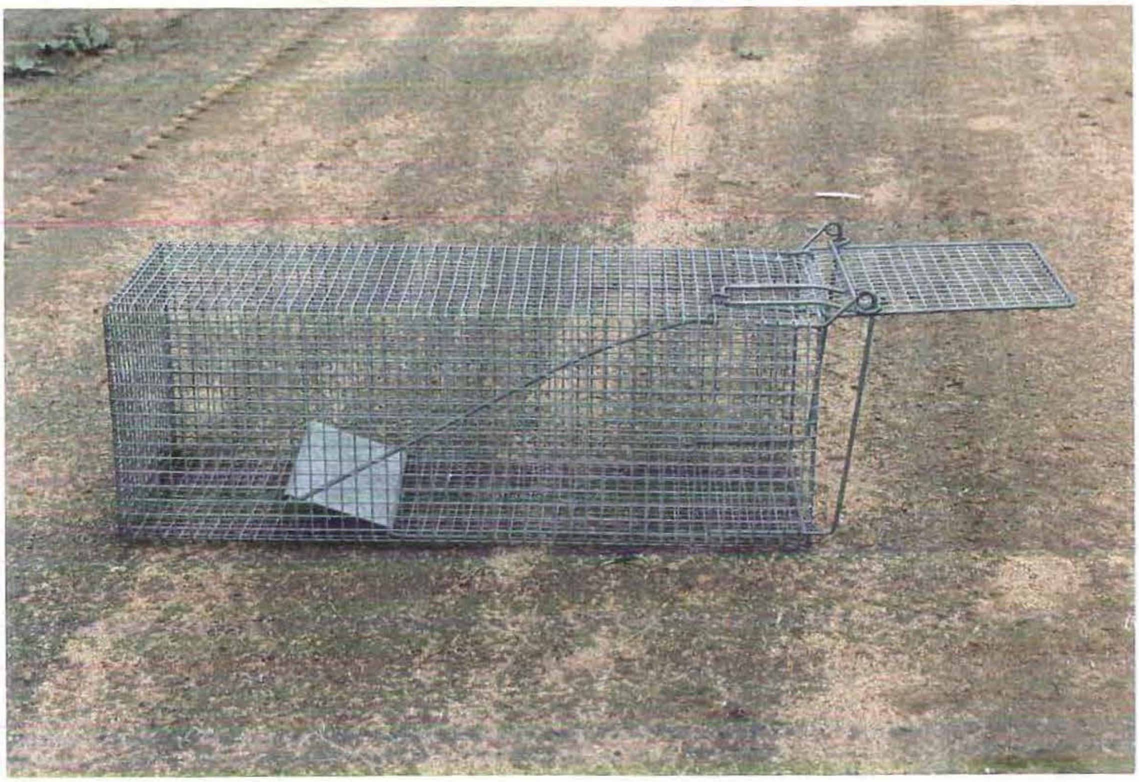


Plate 2.8 Small Sheffield trap (20 cm x 20 cm x 58 cm)

2.3 Animal measurements and observations

All bandicoots when first trapped were processed as follows:

(i) Animals were placed in a dark calico bag for handling. They were weighed to the nearest gram, using a 2 kg or 5 kg spring balance.

(ii) A number 1 trap-tag (National Band and Tag CO. Kentucky U.S.A.) was placed in each ear.

(iii) Measurements were recorded for a number of morphological characters (Figure 2.3, Plates 2.7-2.9).

- pes length (long)
- head length

- ear length, the distance from the notch at its base to the most distant tip of the auricle
- tail length, from the base of the tail to the tip
- tail width, at the widest part near the base
- forearm length, from the elbow to the most distant toe, not including the claw

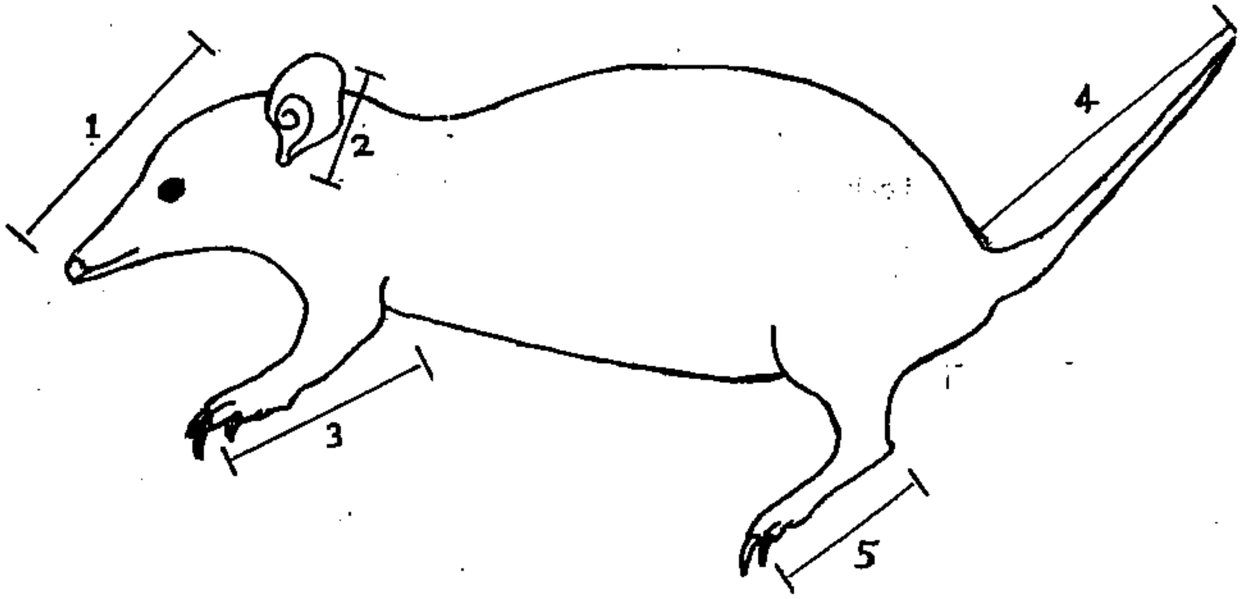
(iv) females the number of pouch young was recorded and sexed where possible. The presence of enlarged teats was used as an indicator of a previous litter. A pes length of 50mm was used to differentiate sexually mature females (Heinsohn, 1966; Mallick *et al.*, 1998b).

(v) For males, testis length was measured and for sexual maturity testes length ≥ 17mm was used as an indicator for the production of sperm cells (Heinsohn, 1966).

All measurements except tail length were measured with vernier callipers to the nearest 0.01 mm. Tail length was measured with a ruler to the nearest 1 mm. Animals were weighed at each capture. In addition to the above measurements, records of peculiar markings/injuries and general condition of the individual were made. These included scarring from fighting, condition of the tail, pouch condition and the degree of ear damage when tags were lost. When both ear tags were lost, it was still possible to determine wether the individual had been previously marked by the presence of puncture holes or tears.

To prevent the ejection of pouch young Fixomull tape was placed over the pouch. If pouch young were ejected then they were inserted back into the pouch with the subsequent application of Fixomull tape. If pouch young could not be inserted back into the pouch, then mother and pouch young were left together in a sealed bag for approximately one or two hours. After this time the bag was opened but left, so as to allow the mother leave on her own accord. All procedures were undertaken on site, and no animals were removed from the reserves.

Figure 2.3 Diagram of measurements taken from *I. obesulus*..



1: **Head length**

2: **Ear length**

3: **Forearm length**

4: **Tail length**

5: **Pes length**

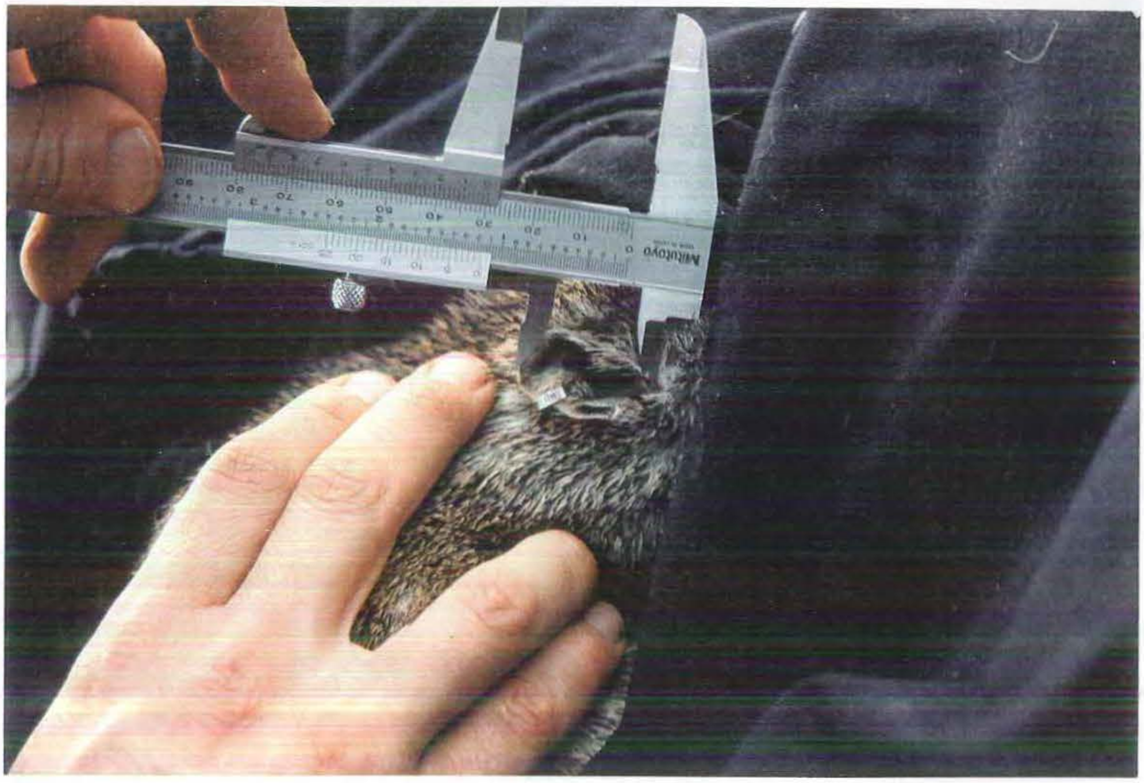


Plate 2.9 Measurement of *I. obesulus* ear length.

Plate 2.10 Measurement of *I. obesulus* pes length.

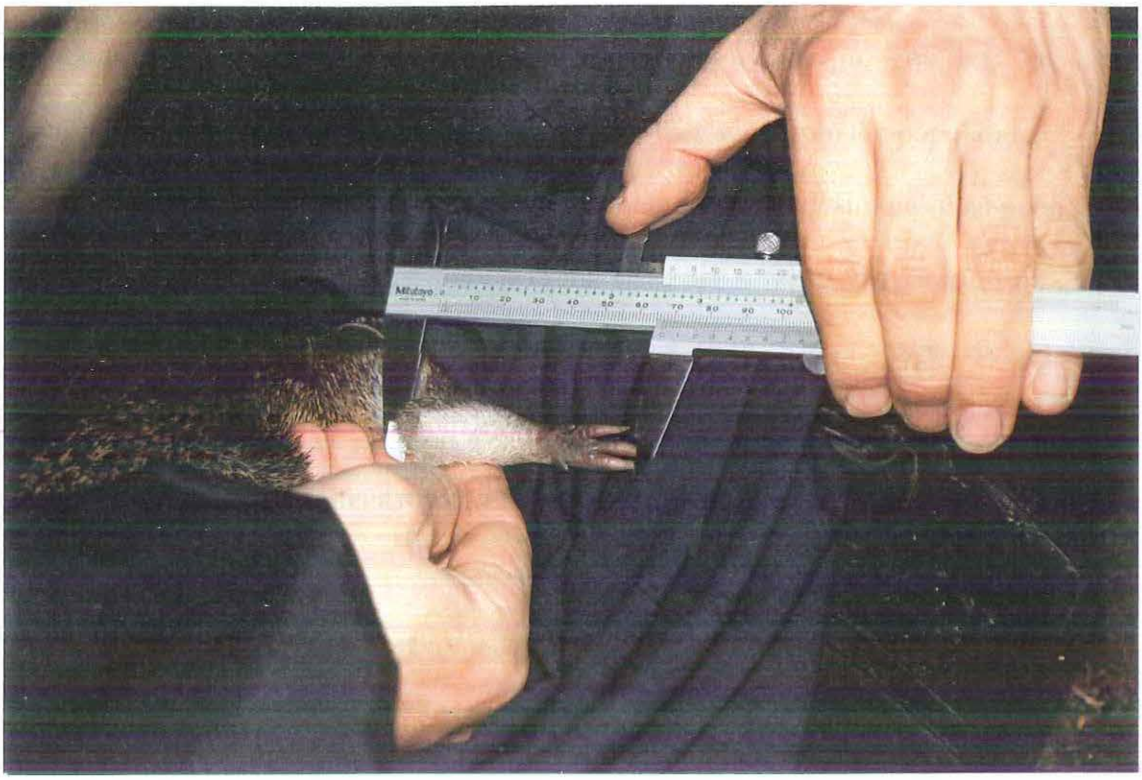


Plate 2.11 Measurement of *I. obesulus* forearm length

2.4 Data analysis.

Raw data was transferred into Excel 97 and where appropriate t-tests were applied. For analysis of variance, raw data was transferred to SPPS version 6.1. All data was tested for normality.

2.4.1 Population size

A wide variety of models have been developed for mark-recapture methods. They generally belong to one of two general categories; those appropriate for closed populations and those appropriate for open populations. A closed model assumes that the population has a constant size during the study, where there are no permanent deletions (deaths and/or emigration) or additions (births and/or immigration). An open model however does allow for additions and deletions from the population during the entire study. Although closed models are statistically simpler than open models, they have a major disadvantage in that their use is limited to short-term studies only, where births and deaths can be ignored (Pollock *et al.*, 1990). When closed models are applied to open populations estimates will be significantly biased, usually overestimated, (Greenwood, 1997).

There have been a variety of open models developed for mark-recapture studies. The parameters measured in these models include population size, survival rate, recruitment, and capture probability. These models are stochastic, so the parameters are subject to random variation during the study. The general method of choice for population size estimates using open models is the Jolly-Seber method, which allows for time variation in the population due to behavioural response or heterogeneity (Tanner, 1978; Pollock *et al.*, 1990; Greenwood, 1997). This multiple Mark -recapture procedure requires a minimum of three operations. However the calculations do not depend upon the captures being made at regular intervals. The Jolly-Seber method like all mark-recapture estimates requires a number of essential conditions. These conditions are.

- There is no heterogeneity between animals in their catchability.
- There is no trap response, that catching and marking do not affect mortality or emigration rates.
- Emigration is permanent.
- Marked animals do not lose their marks and all marks are reported on recovery.

Bandicoots have a high reproductive rate (Lee and Cockburn, 1985), and in Western Australia *I. obesulus* may breed all year round (Craven, 1981). Because of this the Jolly-Seber method was chosen for this study since multiple recaptures were taken over a period of five months, so gains and losses in the population from births and deaths could not be excluded and so made it inappropriate to use a closed model. As the area of sampling is completely enclosed, it was assumed that immigration and emigration was not applicable. The program JOLLY (Krebs, 1995) was used to estimate population size, survival probability, and dilution rates from multiple censuses on open populations by means of the Jolly-Seber method. It calculates large standard errors from the formulae given in Seber (1982) and computes 95% confidence limits as given in Manly (1984).

Variations in captures can produce huge biases in the estimates of population size. In bandicoot populations females may be trap shy (Heinsohn, 1966). Trap-shyness result in overestimates of population size and huge biases may be found in sex ratios. Other differences in catchability may be found if too few traps are used, or spacing of traps are too wide. If spacing between traps is too wide, some animal's home ranges may not include a trap. Home range size in *I. obesulus* has been shown to vary greatly between populations, ranging from 0.28 - 9.44 ha (Craven, 1981; Broughton and Dickman, 1991). The 80m spacings used in this study would adequately accommodate the *I. obesulus* home range sizes.

As heterogeneity between animals in catchability can produce severe negative bias in the estimates of population size (Greenwood, 1997), tests of equal catchability were done using the program LESLIE (Krebs, 1995). This program computes the Leslie, Chitty, and Chitty test of equal catchability appropriate to open populations subject to births and deaths and to data designed for the Jolly-Seber method of estimation (Krebs, 1989).

Heterogenous capture probabilities, however, are relatively unimportant when average capture probabilities are high (Pollock *et al.,* 1990). Using the Jolly-Seber method Carothers (1979) found that even when strong evidence of heterogeneity was found the bias was negligible (< 0.01). This illustrates the robustness of the Jolly-Seber survival rate estimator to heterogenous capture probabilities (Pollock *et al.,* 1990).

2.4.2 Body size and condition

For all morphological measurements values are given as means with SD. For statistical analysis t-tests were used to compare the morphological characteristics between sexes, for adults, to test for sexual dimorphism. Monthly weights were compared between and within sexes and used as a condition indicator. The incidence of scarring was used as an indication of aggressive behaviour and was compared monthly between and within sexes.

2.4.3 Reproduction

Monthly reproductive condition of females was characterised by actively reproducing (with pouch young or enlarged teats) or not actively reproducing (no pouch young and no enlarged teats). Ratios were expressed in percentages. A one-factor ANOVA was used to compare monthly litter sizes. A paired t-test was used to compare the number of young in a litter from first to last capture to determine if there is a significant loss of pouch young during trapping. The reproductive condition of females was separated into weight classes and a one-factor ANOVA was applied to compare litter sizes.

2.4.4 Age structure and sex ratio

The age structure was divided into three main categories; Juveniles (growing and developing), Sub-adults (full-grown but not reproductive), and Adults. Sex ratios were observed monthly and pooled to determine if they differed from parity. Where necessary Chi-square analysis was used to test sex ratios for adults and pouch young against the assumption of parity.

2.4.5 Movement

I. obesulus movement was investigated using trapping data, where it was expressed as the mean distance moved by individuals between successive captures within 24 hours and were examined in relation to sex. The maximum and minimum distances moved between any two captures, within a monthly trapping session was also calculated for both sexes. This technique is widely used as an index of relative movements (Copley *et al.*, 1990; Friend, 1997; Leung, 1999; Short *et al.*, 1998a). A one-factor ANOVA was applied to the distances moved between captures within monthly trapping sessions. A t-test was applied to determine if there was any significant difference in the distances moved between sexes.

2.5 Ethical considerations

Research on *I. obesulus* was approved by the Edith Cowan University Animal Experimentation Ethics committee. The study was conducted under the license approved by the Department of Conservation and Land Management.

CHAPTER 3. RESULTS

3.1 Trap and tag success

Estimation of population size using mark and recapture methods relies for its precision on trap success and equal catchability of sub-groups. For example, differences in trap response may produce biases, and loss of identification marks/tags will lead to population estimates being overestimated. For these reasons, total trap success and extent of ear tag loss were determined, and the success of recaptures of both sexes was compared.

In this study, 754 trap nights yielded 343 captures, a trap success of 45%. There was a marked increase in trap success from May to June (Table 3.1).

The mean ± SE total number of recaptures for males was 5.2 ± 0.90 and for females 4.5 ± 0.41, with no significant difference between the sexes ($t_{56} = 0.89$, $P > 0.05$). A large percentage of bandicoots (87.8% of males, 93.5% of females) were caught on more than one occasion. These results suggest that there was no variability in trap response between the sexes and that there was no trap shyness in these animals. Only two bandicoots, both females, were caught consecutively in the same trap within a single trapping session, suggesting any trap happiness was minimal.

Table 3.1 Monthly trap success (%) of *I. obesulus* on Ellen Brook Reserve.

	Trap	success (%)		
May	June	July	Aug.	Sept.
21.2	56.5	61.3	47.6	45.8

No animals were excluded from the analyses due to tag loss. For recaptured animals, 155 ear tags were applied. Forty of these tags were lost, resulting in a 25.8% tag loss. However only two animals were captured with both tags missing and these animals were easily identified from their descriptive features. Ear damage from tag loss was minimal. The high trap response of both sexes, with all individuals included in the analyses, provided a particularly good data-set for the estimation of population parameters.

3.2 Population size and density

Population size was estimated for June, July and August (Table 3.2) using the Jolly-Seber method and varied between 56.1 and 48.3. The three monthly size estimates equate to density estimates of 1.45, 1.43 and 1.24 bandicoots ha^{-1} respectively. The population size decreased from June to August, however the probability of survival for marked individuals remained high. The 95% confidence limits calculated for the population estimates using the method of Manly (1984) are narrow and the SE are small, suggesting that sample estimates were close to the actual population mean.

The Leslie, Chitty, and Chitty Test of Equal Catchability was applied to the marked segment of the population for the period July to August. This test estimated that 7.5 new individuals entered the marked population, compared with the observed number of 7.0. This represents, an over-estimate, of 6.7 %, which is a relatively small bias and so suggests that there is an equal catchability within the marked population.

Table 3.2 Population size (mean ± large SE) and associated parameters of *I. obesulus* in Ellen Brook Reserve, estimated using the Jolly-Seber method.

	Population size	95% confidence limits	Probability of survival	Number joining
May	—	—	0.896 ± .064	—
June	56.1 ± 3.6	52.7 - 64.9	0.881 ± .049	6.2 ± 2.6
July	55.6 ± 3.6	52 – 57.9	0.876 ± .054	0.4 ± 1.1
August	48.3 ± 6.5	45.4 –50.4	—	—

The number of new bandicoots entering the trapped population decreased from June to July (Table 3.2) and during the August and September trapping sessions no new bandicoots were captured. These results suggest a low recruitment of *I. obesulus* into the population during this period and together with the high recapture success during the months of August and September, suggest that the majority of *I. obesulus* from this population were trapped.

The Jolly-Seber method does not distinguish between losses due to mortality and losses due to emigration. The probability of survival is therefore a reflection of these two factors combined. In this study of a small-enclosed reserve, where the total dry foraging area was trapped, emigration was not a factor. Probability of survival is therefore largely a reflection of mortality rates. Although the probability of survival remained high, the Jolly-Seber method does not compute values for the last two trapping sessions (August and September). During this period 50% of all males and 20% of all females were not recaptured and this is reflected by the decrease in estimated population size in August.

3.3 Body size and condition

Sexual dimorphism was clearly apparent with adult male *I. obesulus* significantly larger and heavier than females (Table 3.3). Ear length was the only metric to exhibit no sexual dimorphism. Tail lengths have not been included because many bandicoots had lost a section of their tail.

Table 3.3 Body dimensions (mean ± SD) of male and female *I. obesulus*.
* P < 0.05.

Dimensions	Male (n)	Female (n)	t-value
Weight (g)	1030 ± 320 (15)	830 ± 180 (47)	2.30*
Pes length (mm)	62.44 ± 3.14 (15)	56.97 ± 2.65 (47)	6.64*
Head length (mm)	83.96 ± 5.53 (15)	79.59 ± 5.65 (44)	2.96*
Forearm length (mm)	76.33 ± 5.68 (15)	70.50 ± 4.57 (47)	4.01*
Ear length (mm)	27.58 ± 3.77 (15)	27.56 ± 2.65 (47)	NS
Tail width (mm)	11.76 ± 1.01 (14)	10.79 ± 0.91 (45)	3.42*

Monthly weights were used as condition indicators of the bandicoots during the study. The data presented in Figure 3.1 is from those animals caught at least once in each trapping session. Mean weights of both males and females decreased from May to August, with the trend being more marked in females (Figure 3.1). Both male and female weights increased in September. However, unlike males, the females had not yet returned to the mean weight recorded at the beginning of the study. All bandicoots excluded from the analyses in Figure 3.1, also experienced weight loss between June and August and an increase in weight when recaptured in September.

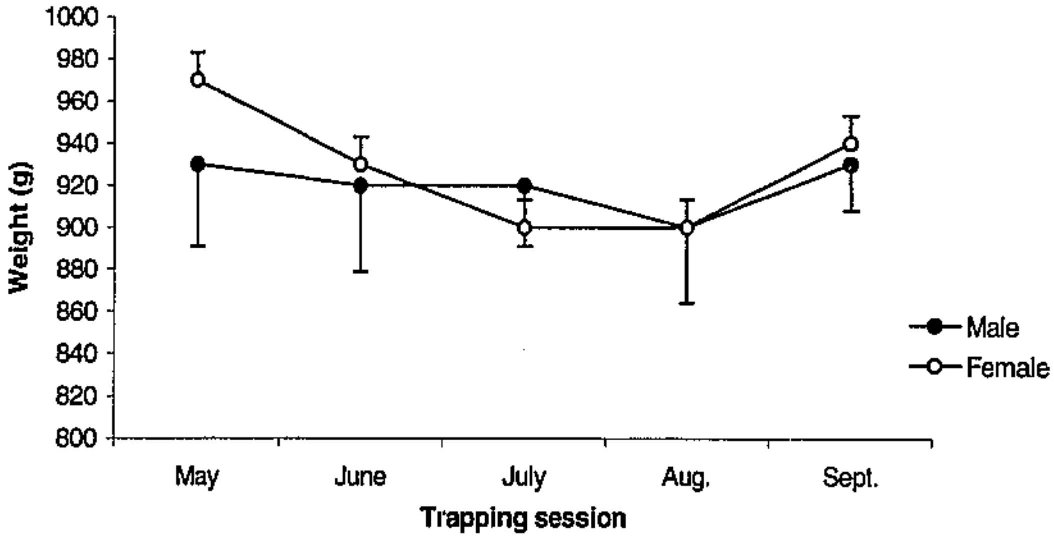


Figure 3.1 Mean monthly weights of adult *I. obesulus*. Error bars indicate one SE.

The incidence of scarring was used as an indication of aggressive behaviour. Animals of both sexes showed an increase in the incidence of scarring over the trapping period (Figure 3.2). This was particularly evident in males. Scarring was more frequently observed in males (68.8%) than females (49.9%). Individuals of both sexes had also lost sections of their tails during the study period.

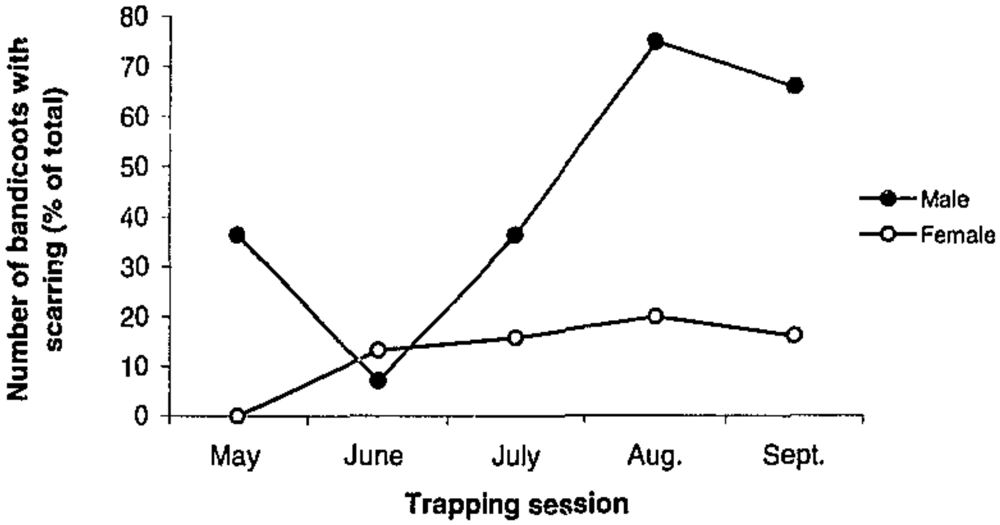


Figure 3.2 The percentage of male and female *I. obesulus* showing evidence of scarring throughout the monthly trapping sessions in Ellen Brook Reserve.

3.4 Reproduction

3.4.1 Breeding

Thirty-seven of the 49 females trapped showed signs of breeding (34 carrying pouch young and 3 with enlarged teats). Females with pouch young were trapped in all trapping sessions (Figure 3.3). The percentage of females carrying pouch young remained relatively stable during the months of May (46.7%), June (44.7%) and July (42.1%), but increased in August (62.9%) and September (74.2%).

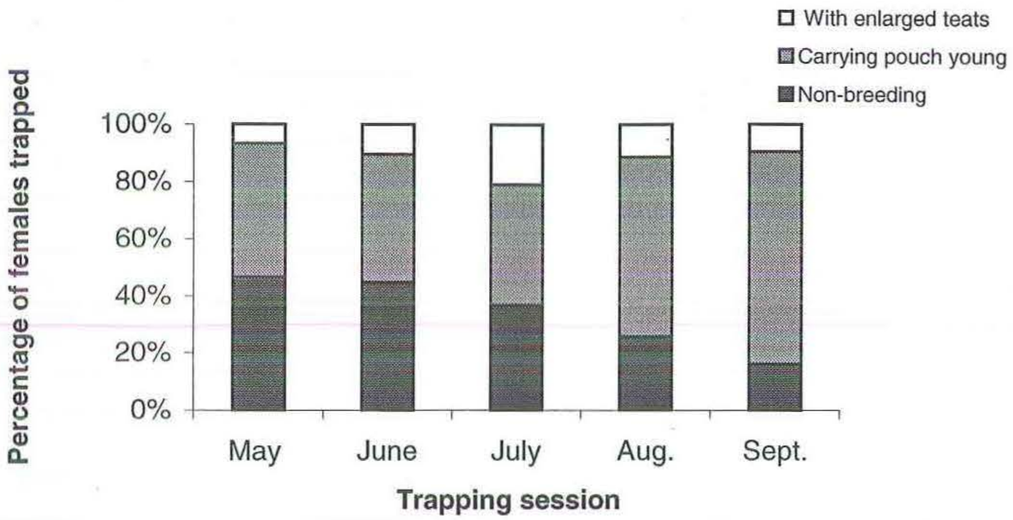


Figure 3.3 Relative proportions of breeding *I. obesulus* females at each trapping session on Ellen Brook Reserve.

3.4.2 Litter size

Excluding recaptures, sixty-four litters, totalling 132 pouch young were recorded during the entire study. The mean ± SE litter size was 2.1 ± 0.1 and sizes ranged between 1 and 5, with 2 being the most common (56.2%) of litters. There was no significant difference in the mean litter size between months ($F_{4,80} = 2.13$, $P > 0.05$), though there was a trend of increasing litter size and size of range over the study period (Table 3.4).

Ten out of 34 females lost a total of 13 pouch young (11.9% of total young) between captures, from 11 litters, during the trapping period. A paired t-test was used to compare the number of young in a litter from the first to last capture to determine if pouch young mortality during trapping was significant. There was a significant difference between the number of pouch young on the first and last capture present over this period ($t_{68} = 3.6$, $P > 0.05$). The loss of pouch may have also already occurred before the first capture, which was indicated by vacant swollen teats.

Table 3.4 Litter size and size range of litters of *I. obesulus* for each trapping session.

Litter size	May	June	July	Aug.	Sept.
Mean ± (SD)	1.7 ± 0.5	1.6 ± 0.6	1.8 ± 0.5	2.0 ± 0.9	2.3 ± 1.0
Range	1-2	1-3	1-3	1-4	1-5

The ejection of pouch young occurred only on a few occasions and only when young were well developed (fully furred and approximately 70 mm in body length). Only two pouch young were recorded as direct mortalities due to trapping. Both resulted from the mother treading on the ejected young.

3.4.3 Reproduction within weight classes

To determine if there was any weight-dependent pattern in reproductive status of females, bandicoots were clustered into weight classes as shown in Figure 3.4 and the number of reproducing females (as indicated by presence of pouch young or enlarged teats) was calculated for each weight class. No female *I. obesulus* below 500 g showed signs of reproduction. There was a marked change in the ratio of reproducing to non-reproducing females from the 601-700 g to the 701-800 g weight class. Although the highest number of actively reproducing females was found in the weight range 701-900 g, the ratio remained relatively unchanged until the 1101-1200 g weight class. While only four females exceeded 1100 g in weight, all had pouch young.

Figure 3.4 Female *I. obesulus* reproductive condition between weight classes on Ellen Brook Reserve

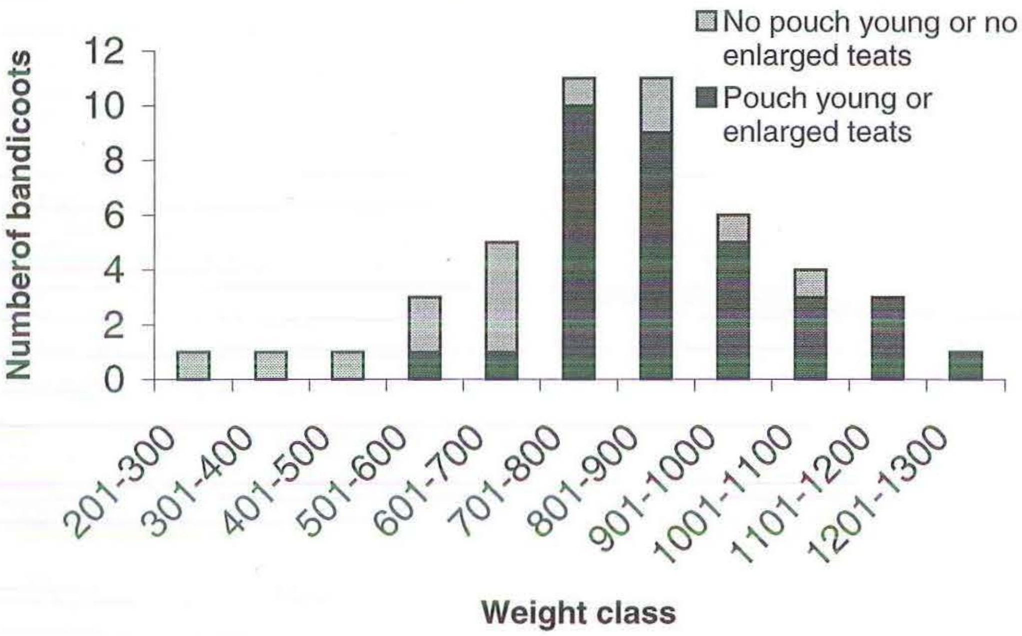


Table 3.5 presents the reproductive characteristics of *I. obesulus* clustered into weight classes. There was a significant effect of female weight class on mean litter size ($F_{7,56} = 0.946$, $P < 0.05$) though the relationship was not linear. However, there was a trend towards a wider range of litter sizes with increasing weight. As there is a large variation between numbers of females in each weight class, total pouch young numbers and number of litters cannot be compared directly.

The 700-1000 g weight range comprised 71% of all the reproductively active females found in this population and contributed to 73% of all pouch young produced during the study period. The 801-900 g weight class produced the highest number of pouch young and litters, although female numbers were smaller than those found in the 701-800 g weight class. The optimum weight class for reproductive output in this population therefore appears to be 801-900 g.

Table 3.5 Reproductive characteristics of *I. obesulus* among weight classes.

Weight Class (g)	Mean Litter size	Number of pouch young	Pouch young Range	Number of litters	Mean number of litters	Number of Females
501-600	2	2	1	1	1	1
601-700	1.5	3	1-2	2	1	2
701-800	1.93	27	1-2	14	1.4	10
801-900	2.26	43	1-3	19	2.11	9
901-1000	2	26	1-4	13	2.6	5
1001-1100	1.3	4	1-2	3	1	3
1101-1200	2.1	19	1-4	9	3	3
1201-1300	2.67	8	1-5	3	1	1

The highest number of actively reproducing females and the highest percentage of pouch young were both represented by the 701-1000 g weight range (Figure 3.4 and Table 3.5). Although some large numbers of pouch young were also found in higher weight classes they were only represented by a small number of females. Thus the bulk of the reproductive output is predominantly by females between 701-1000 g body weight.

3.4.4 Sexual maturity

The smallest female recorded with pouch young weighed 530 g, with a pes length of 52 mm. In the studies of Mallick *et al.*'s (1998b) and Heinsohn's (1966) the smallest breeding females had similar pes lengths of 50 mm and 52 mm respectively. The pes length of 50 mm was therefore used to differentiate sexually mature females in the Ellen Brook Reserve population of *I. obesulus*.. Using this criterion, only two females were deemed to be sexually immature.

For males, the smallest sperm producing testes length was found to be 17 mm (Heinsohn, 1966). This length was therefore used to differentiate sexually mature males. Using this criterion, only one male was sexually immature. The testes length (mean ± SD) of the adults was 20.8 ± 2.3 mm, with a range of 17 - 27 mm.

3.5 Age structure and sex ratio

Fifteen males and 47 females were trapped during the study, resulting in a female biased 3:1 sex ratio. In the first trapping session, the sex ratio was not significantly different from parity ($X^2 = 0.615$, $P > 0.25$). The subsequent trapping sessions yielded greater numbers of females, but not males (for the latter the trend was the reverse), resulting in consistently female-biased sex ratios (Figure 3.5).

Of the 44 litters that were sexed, the sex ratio of pouch young was not significantly different from parity ($X^2 = 1.16$, $P > 0.25$).

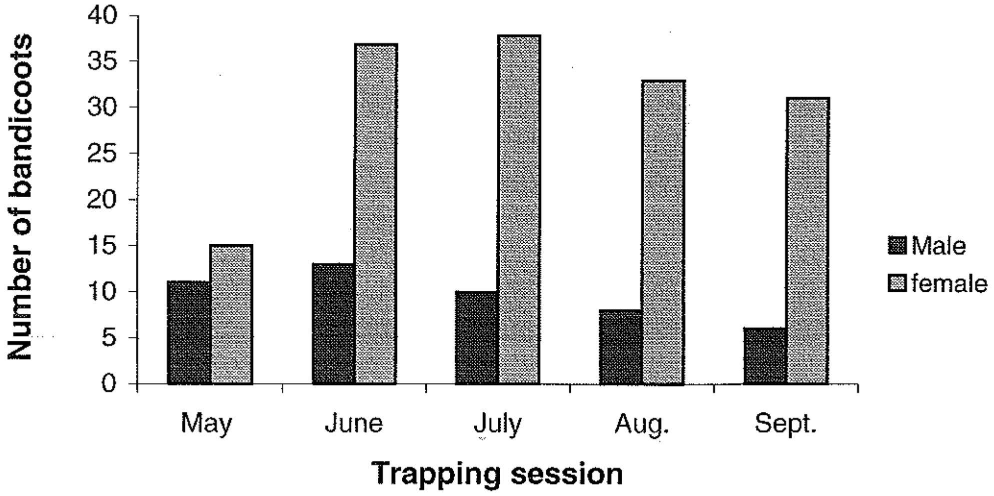


Figure 3.5 Number of male and female *I. obesulus* caught in each trapping session.

As only three sub-adults were caught during the study (1 male and 2 females), the captured population was dominated by sexually mature adults, with an increasing number of pouch young throughout the study period (Figure 3.6).

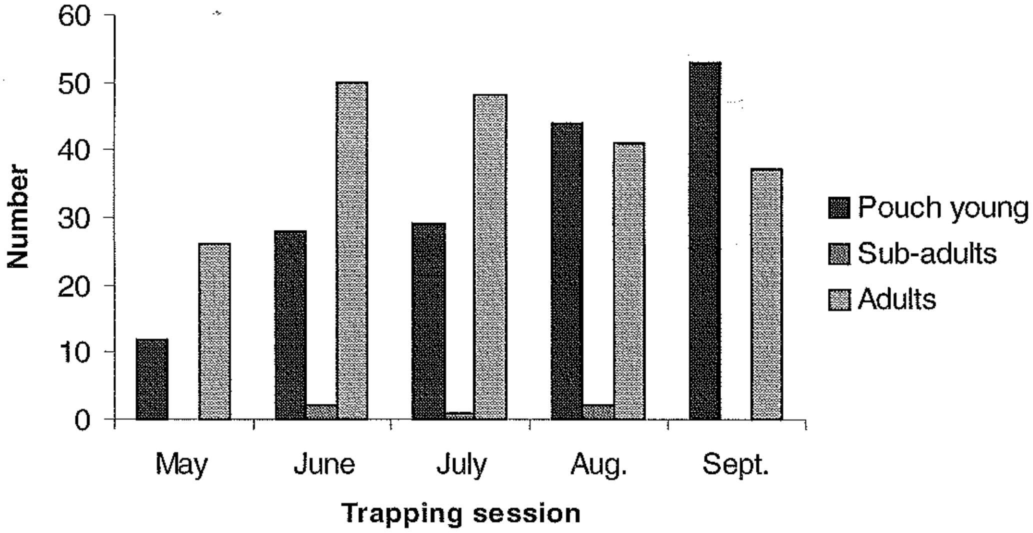


Figure 3.6 The age structure of *I. obesulus* in Ellen Brook Reserve.

Of the 3 sub-adults captured during the study, the male was found in a very poor condition on its last capture (July), and died shortly after. One female was caught in June and the other in August and both were in good condition on their first capture. However one female had not gained any weight from June to August and was severely scarred at its last capture in August.

Thus, the population was dominated by sexually mature adults, but with an increasing number of juveniles (as pouch young) throughout the study period.

3.6 Movement

I. obesulus movement was investigated using trapping recapture data. The distance males moved (mean ± SD) over 24 hours was 213.3 ± 143.8 m (range 80 - 613 m) and for females it was 131.4 ± 94 m (range 0 - 400 m). The difference in the mean distance moved between sexes over 24 hours was significant ($t_{38} = 2.64$, $P < 0.05$) with males showing the greater movement.

To determine if the distance bandicoots moved changed during the study period a one-way ANOVA was applied to the distances moved between captures within each monthly trapping session. This was not significantly different for females ($F_{3,80} = .152$, $P > 0.05$) but was significantly different for males ($F_{3,40} = 1.192$, $P < 0.05$). Males increased their movement during the months of July and August.

As described previously the reserve was extended in 1994-95 at the southern end by an enclosed fence. Trapping data was compared between the two areas (the original and extended area), to determine if bandicoots were utilising the extended area to the same degree as the original area. Trapping data was also used to determine if there was any indication of an increase in movement into the extended area throughout the winter months, when foraging area is substantially more reduced in the original area than the extended area.

There was no significant difference in the mean captures of bandicoots per trap between the original and extended areas ($t_{11} = 1.03$, $P > 0.05$). Thus the population appears to have substantially dispersed into the extended area and there is no spatial heterogeneity in the population. However, differences were found in the trap success between monthly trapping sessions. Trap success increased steadily throughout the study period in the extended area, whereas in the original area it peaked in July with a decrease in August - September (Table 3.6).

Table 3.6 Monthly trap success (%) of *I. obesulus* on Ellen Brook Reserve.

Trapping area	Trap success (%)				
	May	June	July	Aug.	Sept.
Original area	19.1	53.3	58.6	48	48.6
Extended area	7.1	39.3	46.4	50	60.7

All bandicoots trapped in the extended area were also trapped in the main area. No new bandicoots were trapped in the extended area in August and only one new bandicoot was trapped in this area in September. It had previously been captured 8 times in the main area. These data suggest that bandicoots utilising the extended area at the beginning of the study had increased their foraging into this area over the study period. At the same time, the filling of the ephemeral swamps was substantially reducing available foraging area in the original reserve.

The number of different bandicoots caught at any one trap during the study was also used as an indication of home range overlap. The mean number of individual bandicoots caught at any one trap was 6.3, with a range from 2-11. Within sexes a maximum of 8 females or 5 males were caught at any one trap during the study. These results suggest that the bandicoot home ranges overlap considerably for both sexes throughout the reserve.

Overall, these results indicate that there is a high degree of movement and home range overlap within the population for both sexes, but with males increasing their movement during the winter months. Bandicoots also appear to be utilising the extended area to a higher degree towards the end of winter, when the foraging area in the original main section is more reduced due to the increased coverage from ephemeral swamps.

CHAPTER 4. DISCUSSION

4.1 Population size and density

The population size estimate equates to a relatively high density of *I. obesulus* on Ellen Brook Reserve. This indicates that in the absence of exotic mammalian predators a small population of *I. obesulus* can substantially increase in size over a period of 9-10 years. Conversely, fox predation has been suggested to be a principal factor for the demise of *I. obesulus* on the mainland of Australia (Clarridge *et al.*, 1991; Dell and How, 1988). In Western Australia, Dickman (1988a), also found that *I. obesulus* suffered relatively high predation from foxes, where 16 % of fox faeces collected contained *I. obesulus* fur. Most recently, fox predation is considered to be the principle factor limiting the size and distribution of a wide range of marsupial groups (Kinnear *et al.*, 1999).

In Ellen Brook Reserve no sightings of *I. obesulus* were recorded prior to the erection of the vermin proof fence and an intensified baiting program (using the compound 1080) in 1990. The first sightings of *I. obesulus* occurred inside the enclosed section approximately 2-3 years after the erection of the fence (Kuchling, pers. comm.). Over this period to the present time, sightings steadily increased and recently a few sightings occurred outside the enclosed section in the south-western corner of the reserve near dense remnant vegetation (Martyn. pers. comm). During this study no signs of bandicoots (scats or diggings) were found outside the enclosed section, however there were sightings of foxes and cats. These observations, together with the trapping results of this study, suggest that the fox had a marked effect on *I. obesulus* numbers in the Ellen Brook area.

Population densities of *I. obesulus* vary considerably across Australia between the study areas (Table 4.1). Part of this variation may reflect habitat differences between the areas. *I. obesulus* has a preference for dense understorey (Dell and How, 1988; Friend, 1991; Mallick *et al.*, 1998b), and the low densities of the Tasmanian studies (where the fox is absent) have been attributed to a lack of dense ground cover and prevalence of open pasture (Heinsohn, 1966; Mallick *et al.*, 1998b).

Table 4.1 Density estimates of *Isoodon obesulus* numbers (ha^{-1}). A summary of Australian studies.

Density (nos.ha^{-1})	Location	Source
0 - 0.35	Tasmania (south-east)	Mallick *et al.* (1998b)
0.07 - 0.2	Tasmania (north-west)	Heinsohn (1964)
1 – 5	Victoria (Cranbourne)	Lobert and Lee (1990)
1.8 – 2.7	Victoria (Cranbourne)	Stoddart and Braithwaite (1979)
0.01 - 0.09	NSW (Eden)	Claridge *et al.* (1991)
1.3 –1.4	SA (Franklin Islands)	Copley *et al.* (1990)
0.4	WA (Tuttanning Reserve)	Sampson (1971)
0.61 –1.48	WA (Harry Waring Marsupial Reserve)	Craven (1981)
1 – 2	WA (Harry Waring Marsupial Reserve)	Broughton and Dickman (1991)
1.24 – 1.44	WA (Ellen Brook Reserve)	This study (1999)

However, the variation in density in these studies can also be correlated with presence/absence of exotic predators. Considering only Western Australian studies, the density of *I. obesulus* in Ellen Brook Reserve is similar to that in the Harry Waring Marsupial Reserve (Craven, 1981; Broughton and Dickman 1991), but substantially higher than that in Tuttanning Reserve (Sampson, 1971). The history of the Harry Waring Marsupial Reserve is similar to that of Ellen Brook Reserve, where numbers of *I. obesulus,* have increased since the enclosure and exclusion of exotic mammalian predators (Monzu, 1970; Craven, 1981; Broughton and Dickman, 1991). Tuttaning Reserve, on the other hand, was an open reserve, with exotic mammalian predators present (Sampson, 1971). The Tuttaning Reserve study also included areas of open habitat and so differences may be also partly due to habitat preference. Low capture rates of *I. obesulus* in W.A have also been recorded on the Darling Scarp in areas with the presence of exotic mammalian predators, with the highest captures only found in dense heath understorey (Dell and How, 1988).

Although high densities of *I. obesulus* have been found in the presence of exotic predators in Cranbourne, Victoria (Stoddart and Braithwaite, 1979; Lobert and Lee, 1990), the substantial area of dense heath understorey present can explain it. Lobert (1990) suggests that this understorey is virtually impenetrable to large mammalian predators, such as the fox, and so offers *I. obesulus* greater protection from mammalian predators. In this way, the dense heath habitat acts as a predation refugia (Kinnear *et al.*, 1999). Exotic mammalian predators and habitat loss are both important factors contributing to the demise of *I. obesulus* and are possibly interconnected, with predation further exacerbated by loss of particular habitats.

Population size and density did not remain stable during the winter months in Ellen Brook Reserve, but instead decreased from July to August. This occurred concomitantly with a reduction in foraging area due to the filling of the swamps. In the absence of other contributing factors (eg mortality) one would expect an increased movement of bandicoots to the drier ground (where all traps were placed), with a resultant apparent increase in density (assuming that there was no trap saturation). Craven (1981) described such an increased density effect as a dry lakebed seasonally filled. Craven (1981) suggested that the increase in density resulted from bandicoots that had been forced to move out as the water level rose, rather than as a result of an influx of new recruits (no sub-adults were captured during this time). In contrast, in Ellen Brook Reserve, the *I. obesulus* population density actually decreased in August (reflected in the changes in population size estimates). The trap success was high throughout the study and it could be argued that a higher density of traps would be needed to reflect any real increase in density (eg two traps per trap site). However, trap success declined in August and September and in some locations, trap success was low throughout the study, even in areas which appeared to support ideal bandicoot habitat (eg dense heath). One possible explanation is that the population decrease is due to an increase in mortality toward the end of winter.

4.2 Body size and condition

Sexual dimorphism was clearly evident in *I. obesulus* in Ellen Brook Reserve, with adult males significantly larger and heavier than females. This finding is consistent with other studies (Table 4.2). Dickman (1988a) suggests this may be strongly associated with the polygynous mating system where competition between males is a selection pressure for larger body size (Selander, 1965; Lee and Cockburn, 1985). Growth rates of males and females are similar up to 234 days of age (Thomas, 1984). It is possible that this sexual dimorphism may be due to a difference in longevity between males and females (Stoddart and Braithwaite, 1979), or to a difference in growth rates of males at maturity (Newsome, 1977).

Table 4.2 A comparison of body weights for *I. obesulus* populations.

Mean weight (g)		Location	Source
Male	Female		
1244.8	1000.6	Tasmania	Mallick *et al.* (1998b)
614.19	476.09	Victoria	Stoddart and Braithwaite (1979)
1274	901	WA	Dell and How (1988)
1033	778	Victoria	McKenzie (1967)
1140	849	WA	Thomas (1984)
1165.9	946.6	Tasmania	Heinsohn (1966)
1030	830	WA	This study (1999)

There was a seasonal effect on body weight in both sexes of *I.obesulus*, with the lowest mean weights occurring in August. This seasonal pattern was more marked in females. Similar patterns have been found in an *I. obesulus* population on the Darling Scarp in Western Australia, where females were heaviest in spring-autumn and lightest in winter (Dell and How, 1988). Hall (1983) also found evidence of a seasonal effect on body weight in females in *I. macrourus* but not males.

An explanation for why loss of body weight is found is that the seasonal changes are accompanied by a reduction in food resources and the filling of the swamps further exacerbates this. Any subsequent increased mortality rates would then be reflected in the decrease in population size in August. Fifty percent of all males trapped in the earlier months of the study were not recaptured in August or September, compared with 20% of females Thus while females body weight decreased more sharply than males, a larger percentage of the males were missing from the trapped population. Some of these males had not shown any degree of trap shyness prior to this. Two direct mortalities were recorded. One large adult female and one small sub-adult male, both died between August and September. So although body weight showed a seasonal effect, the decrease in body weight cannot be primarily attributed to the reduction of foraging area, as seasonal effects on body condition in bandicoots have also been found without a direct reduction in foraging area (Hall, 1983; Dell and How, 1988).

The decline in body weight could reflect poor conditions during the winter months, which may be exacerbated by an increase in intraspecific aggression. Signs of intraspecific aggression (scarring) increased in both sexes, with the trend being more marked in males, over the study period. With a high density of animals in an enclosed reserve, the seasonal decline in foraging area could increase the probability of individuals coming into contact, resulting in an increased intraspecific aggression between individuals (shown from signs of scarring).

I. obesulus is a solitary animal and when conspecifics come into contact there is often highly aggressive male – male behaviour and to a lesser degree female-male and female-female interactions (Heinsohn, 1966; Thomas, 1984). When aggressive behaviour has been observed, a submissive animal crouches with its back to the dominant animal, which may then attack the submissive animal's back and rump region with its hind foot, removing hair (scarring) and sometimes scratching the skin (Heinsohn, 1966; Thomas, 1984). In an enclosed reserve in Western Australia Thomas (1987) found that there was a greater effect of intraspecific aggression (scarring) in male than female *I. obesulus*. It has been suggested that young females are more acceptable as recruits by mature bandicoots, than young males. (Thomas, 1987). This is supported by findings that have shown up to 72 % of the attacks from large male *I. obesulus* > 1250 g are on smaller males (Dickman, 1988a) and more young males than females are evicted from their natal areas by dominant males (Stoddart and Braithwaite, 1979). It has also been shown that although *I. obesulus* are solitary animals a population can exhibit a male dominant hierarchy, this can also be seen in females to a lesser degree (McKenzie, 1967).

An increase in evidence of intraspecific aggression in both sexes may not be only due to competition for resources from the decreased foraging area. During the trapping period, the percentage of breeding females increased and competition between males for mating rights may also have been another trigger for intraspecific aggression (Thomas, 1987).

4.3 Reproduction

Breeding occurred during the May-July period but showed a marked increase in August and September. These results are similar to those found in other *I. obesulus* populations in Western Australia (Craven, 1981; Thomas, 1987; Dell and How, 1988). During this study the July to August period appeared to be the optimal time for breeding for *I. obesulus* in Ellen Brook Reserve, when 74.3 % of all females showed signs of breeding in August and 83.9 % in September.

Although litter size increased over the study period, the mean size of 2.1 is lower than that found in other studies both of *I. obesulus* and other bandicoot species (Table 4.3). It may be that litter size is adversely affected by the constraints of a relatively dense population in a small enclosure. *I. obesulus* show a high level of juvenile dispersal (Stoddart and Braithwaite, 1979) and when population densities are high, dispersal may act as an important safety valve (Lidicker, 1962). When dispersal is limited, as in Ellen Brook Reserve, density-dependent behaviour may adversely affect the population condition (Christian and Davis, 1964; Wynne-Edwards, 1965; Chitty, 1967; Myers, 1967). Small mean litter sizes have been found in island bandicoot populations (Table 4.3), where dispersal is also limited and population densities are high. (Copley *et al.*, 1990; Short *et al.*, 1998a). The enclosure of Ellen Brook Reserve, creates, a similar island effect with similar impacts on reproduction. Environmental factors such as drought (Copley *et al.*, 1990) and food abundance (Lobert and Lee, 1990) have also been suggested to affect litter size. When food abundance is low females produce both fewer and smaller litters (Lobert and Lee, 1990). At Ellen Brook Reserve, largest litter sizes were recorded in September, which was found in all other Western Australian studies (Craven, 1981; Thomas, 1987).

The majority of actively reproducing female *I. obesulus* (71%) in Ellen Brook Reserve fell within the weight range of 701-1000 g and contributed to 73% of all pouch young produced during the study. There were very few breeding females found in the weight classes below 701-800 g and no breeding females were found below 530 g. So although young females have been shown to reach sexual maturity at a

Table 4.3 A comparison of litter size for bandicoot populations.

Mean litter size	Range	Location	Source
Isodon obesulus			
3.05	1-5	Tasmania (south-east)	Mallick *et al.* (1998b)
3.17	1-6	Victoria (Cranbourne)	Stoddart & Braithwaite (1979)
2.53	1-5	WA (Darling Scarp)	Dell & How(1988)
2.58	1-6	Victoria (Cranbourne)	Lobert & Lee (1990)
2.8	1-4	Tasmania	Heinsohn (1966)
2.9	1-5	WA	Thomas (1984)
2.06	1-4	SA (Franklin Islands)	Copley *et al.* (1990)
2.06	1-5	WA	This study (1999)
P. bougainville			
1.8	1-3	Dorre & Bernier Islands	Short *et al.* (1998a)
I. macrourus			
2.7	1-5	Northern Territory	G.R. Friend (1990)
2.9	1-5	Queensland	Hall (1983)
P. nasuta			
2.44	___	NSW	Lyne (1964)
P. gunnii			
2.2	___	Victoria	Dufty (1994b)

weight of only 530 g in this study, optimum, breeding condition, is not reached until the 701-800 g weight class. There is some evidence that body weight affects breeding condition in female bandicoots in Ellen Brook Reserve, with a trend of increasing ranges of litter size with increasing weight. Positive linear relationships between litter size and weight or age of females have been found in some bandicoot populations (Stoddart and Braithwaite, 1979; Hall, 1983; Short *et al.*, 1998a) but not in others (Lobert and Lee, 1990; Dufty, 1994b). Although body weights of females decreased from May to August, it does not appear to have affected the ability of females to breed throughout the winter months, since the percentage of females carrying pouch young continued to increase during this period.

4.4 Age structure and sex ratio

The adult sex ratio was female biased (3:1), which is an unusual outcome. Sex ratio of pouch young remained close to parity, suggesting that either mortality rates of post-pouch stages differ between sexes, or that there is sex-dependent variation in trapping response. Sex ratios of bandicoot populations vary across studies (Table 4.4). Where substantial bias occurs, it usually favours males. The pouch young sex ratios in bandicoots are predominantly close to parity. Thus biased adult sex ratios are reflective of other influences such as differential sex dispersal ratios out of the population (Stoddart and Braithwaite, 1979), predation (Dickman, 1988a; Claridge *et al.*, 1991; Dufty, 1994b) and variability in trap response between sexes. Variability in trap response between sexes is thought to be due to differences in trap shyness, trap happiness, home range size and habitat preference.

Table 4.4 A comparison of sex ratios in bandicoot populations.

Adult ♂ : ♀	Pouch Young ♂ : ♀	Location	Source
I. obesulus			
1 : 1.2	1 : 1.4	Tasmania	Mallick *et al.* (1998b)
1 : 1.2	___	Victoria	Stoddart and Braithwaite (1979)
10 : 1	___	NSW	Claridge *et al.* (1991)
1 : 1	1.4 : 1	SA	Copley *et al.* (1990)
1 : 1.6	___	WA	Craven (1981)
1 : 2	1 : 1	WA	Thomas (1987)
1 : 0.5	1 : 1	WA	Dell and How (1988)
2 : 1	___	WA	Dickman (1988a)
1.4 : 1	1 : 1.2	Tasmania	Heinsohn (1966)
1 : 0.6	___	WA	Thomas (1984)
P. Bougainville			
1.7 : 1	1.2 : 1	WA	Short *et al.* (1998a)
I. macrourus			
1.5 : 1	___	QLD	G.R. Friend (1990)
1 :1	1 : 0.8	QLD	Hall (1983)
P. gunnii			
2 : 1	___	Victoria	Clark *et al.* (1995)
1.1 : 1	___	Victoria	Brown (1985)
1.7 : 1	1 :1	Victoria	Dufty (1994b)
2.1 : 1	1.2 : 1	Victoria	Dufty (1991)
1 : 1	1.2 : 1	Tasmania	Heinsohn (1966)

Male biased populations have been attributed to female trap shyness (Heinsohn, 1966) and the larger home range of males (Heinsohn, 1966; Craven, 1981; Copley *et al.*, 1990; Mallick *et al.*, 1998b). Variability in trap response did not play any role in the Ellen Brook Reserve *I. obesulus* population. A large percentage of bandicoots of both sexes were caught on more than one occasion, only two bandicoots were caught consecutively in the same trap within a single monthly trapping session and there was no significant difference in recaptures between the sexes ($t_{56} = 0.89$, $P > 0.05$). Sex-dependent habitat preferences could also result in sex ratio biases if trap locations are not representative of all habitat types (Stoddart and Braithwaite, 1979). In this study trap locations included all the habitat types found in the enclosed reserve and there was no variability in trap response which could be correlated with habitat type.

Fox predation has been proposed as a major factor leading to male biased bandicoot populations (Dickman, 1988a; Claridge *et al*, 1991). Dominant males are thought to occupy dense understorey, forcing sub-adults and adult females into sub-optimal habitat (Dufty, 1994b), which is more exposed to predators (Dufty, 1991). Like this study in Ellen Brook Reserve, studies which found female biased populations were in a enclosed reserve, where exotic predators are excluded (Craven, 1981; Thomas, 1987) or in open areas without the presence of the fox, such as Tasmania (Mallick *et al.*, 1998b). However in the latter study the adult female bias could be reflective of a female bias in pouch young (Table 4.4). One study has shown a female biased ratio in an *I. obesulus* population in Victoria (Stoddart and Braithwaite, 1979). The trapping area contained primarily very dense heathland, which is virtually impenetrable to animals any larger than bandicoots and so offers greater protection from large mammalian predators, such as the fox (Lobert, 1990). This would provide sufficient optimum habitat for both sexes and as there would be little sub-optimum habitat that dominant males could force sub-adults and adult females into, so differential fox predation between sexes may not occur. This suggests that where there is a high degree of open pasture or understorey, fox predation will skew the population sex ratios towards males.

There is a predominance of males in all studied populations of bandicoots in Australia where the fox is present (Table 4.4). In addition the decline of some island populations (where the fox is absent) has been attributed to cat predation (Short *et al.*, 1998b) and this may account for a small adult male bias found in Tasmania (Heinsohn, 1966). These results suggest that in the absence of fox predation, a female biased population can occur. However, some bandicoot populations on islands are male biased in the absence of exotic mammalian predators (Short *et al.*, 1998a). Although this appears to be due to trapping response (Short *et al.*, 1998a) and so may not be a true reflection of the actual population. Short *et al.* (1998a) did find that there were periods when sex ratio was skewed towards females on both Bernier and Dorre Islands and a previous study on Dorre Island had shown a predominantly male biased population (Richards and Short, 1996). The predominance of males was highest during the breeding season, when there is greater mobility of males and when females carrying large pouch young may be less likely to leave or forage far from their nest and therefore less likely to encounter traps (Short *et al.*, 1998a).

What are the possible reasons for female biased ratios in the absence of the fox? In non-enclosed areas it could be due to a higher dispersal rate of males, a common feature of both eutherian (Greenwood, 1980; Holekamp and Sherman, 1993), and marsupial (Johnson, 1989; Cockburn *et al.*, 1985) populations. In enclosed areas where dispersal is limited there may be a higher male mortality rate. There is a higher rate of dispersal of independent juvenile bandicoots (Stoddart and Braithwite, 1979; Brown, 1985) and this predominantly applies to males which are thought to be aggressively evicted from their natal areas by dominant males (Stoddart and Braithwaite, 1979; Dickman, 1988a).

In the enclosed Ellen Brook Reserve, the sex ratio became increasingly female biased over the study period. From July onwards, this was due to fewer adult males being trapped together than an increase in females. As the breeding pattern in *I. obesulus* in Western Australia would show a very low natality rate in the previous autumn months and with a limited dispersal area, one inference which can be made, is that there was a higher mortality of adult males. As dispersal is limited, aggressive behaviour may increase between males (Thomas 1987). This may result in increased mortality, either directly or indirectly from an increase in stress. Such potential mortality would be exacerbated by the seasonal decline in forging area due to the filling of the ephemeral swamps. Animals forced into the surrounding drier areas may not find a suitable home range size, unless a new vacant home range becomes available from a loss of a previous bandicoot (McKenzie, 1967). This in turn will increase intraspecific competition, which may result in an increased mortality. An increased in mortality in adults is reflected in the decreasing population size from July to August and the suggestion of a higher level of male mortality is supported by a larger percentage of missing males in August and September. An increase in aggressive behaviour is suggested by the higher ratio of the incidence of scarring which is more markedly apparent in males. Thus limited dispersal opportunities may change behaviour patterns, which increases the mortality rate of males rather than females. More research is needed on the dispersal patterns of bandicoots with a focus on limited space.

Adults dominated the *I. obesulus* age structure in Ellen Brook Reserve. The low number of sub-adults in this population may have been a consequence of a lower reproductive rate during the previous late summer and autumn months (Craven, 1981; Thomas, 1984; Thomas, 1987; Dell and How, 1988), rather than a low trapability of sub-adults. Age structures in bandicoot populations are not static but change seasonally as a result of changes in the reproduction rate and environmental factors such as climate and food availability (Craven, 1981; Copley *et al.*, 1990, Dufty, 1994a).

Some bandicoot populations, which are in a declining phase, often exhibit a population structure dominated by older individuals (due to a decreasing number of young). This pattern is more marked in females due to predominant loss of young adult females (Claridge *et al.*, 1991; Dufty, 1994a). In Ellen Brook Reserve adult males are predominantly in a larger weight class (≥ 750g), whereas the adult females show a relatively normal distribution. The male population could be said to be in a declining phase. The increasing sex ratio bias towards females reflects this. The low recruitment of sub-adults into the population during the study, with a decrease in population size, suggests that the population was declining towards the end of winter. This decline is shown predominantly in the males and suggests a higher mortality rate of males. However this effect may be seasonal and the limited time period of this study limits inferences, which can be made.

4.5 Movement

The mean distances moved by bandicoots, at Ellen Brook Reserve between captures, with males recording greater distances than females, is similar to that found by Dell and How (1988) in the Darling Scarp (WA). The greater distances moved in *I. obesulus* males is a common finding in a number of studies (McKenzie, 1967; Lobert, 1990; Broughton and Dickman, 1991, Mallick *et al*,. 1998b). The larger home range of male bandicoots is `attributed to a larger body size (Craven, 1981) and provides the potential for access to a greater number of females (Thomas, 1984; Courtenay, 1995). The increase in movement of males over the study period may reflect their increased home ranges to better access to receptive females (Copley *et al.*, 1990; Short *et al.*, 1998a). Increases in the number of actively breeding females in Ellen Brook Reserve also occurred at this time.

The large number of individuals caught at any one trap suggests that home ranges overlap considerably. Broughton and Dickman (1991) suggest that at low population densities, if resources are defendable and intruder pressure low, *I. obesulus* will be territorial but when population densities are high it will occupy high overlapping ranges. There is considerable support for this inference in the literature (Heinsohn, 1966; McKenzie, 1967; Craven, 1981; Copley *et al.*, 1990; Lobert, 1990; Mallick *et al.*, 1998b). The data in this study support this, as there appears to be a large degree of home range overlap when population density is high.

Particular consideration of the extended section added in 1994 to Ellen Brook Reserve provides additional interesting insights into the movement of these bandicoots. The habitat in the extended area is substantially more open and degraded than that of the original area but is less affected by the ephemeral swamps, with approximately 10 % of its area under water during the winter months compared to 50 % in the original area. Bandicoots appeared to be utilising the extended area to the same degree as the main area, however bandicoots increased their movement into the extended area. This suggests that the bandicoots, which included the extended area in their home range at the beginning of the study, were utilising this area to a higher degree as the adjacent original area became inundated with water.

4.5 General discussion

Fox predation has been suggested as a primary factor for the demise of bandicoot populations and male biased sex ratios (Dickman, 1988a; Clarridge *et al.*, 1991; Dufty, 1994b). As bandicoots have a high fecundity (Thomas, 1984; Lobert and Lee, 1990) and are able to recolonise new habitats quickly (Stoddart and Braithwait, 1979), given the protection from exotic mammalian predators, this study suggests that *I. obesulus* numbers are able to increase to a relatively high density from a small number of individuals, though with a sex ratio that is female biased, while the sex ratio was close to parity at the beginning of the study, this may have been due to an initial lower trap response of females and not a true representation of the whole population. The female biased sex ratio increased throughout the study and this was not due to a continued change in trap response in the females but mainly to a decrease in the number of males trapped. During the study there was a reduction in foraging area due to the seasonal filling of the ephemeral swamps. The decrease in the foraging area and other severe environmental changes such as the climate coincided with a reduction in mean body weights for both sexes and an increase in signs of intraspecific aggression (scarring), with a subsequent decrease in the population size estimate from July to August. These observations suggest that there was a higher mortality rate due to changes in the environmental conditions. However this may be partly due to lower recruitment of sub-adults into the population during this period. The higher percentage of all the males compared to the females not recaptured during August and September reflects the decrease in the population size estimate and suggests a higher mortality rate in the male population, increasing female bias of the sex ratio. The constraints of a small-enclosed reserve exacerbated by a seasonal reduction in foraging area may result in a higher male mortality rate. This may be due to the limited dispersal of males, which are the predominant dispersers rather than females (Stoddart and Braithwaite, 1979) and the males lower tolerance towards other males rather than females (Thomas, 1984; Dickman, 1988a). This would be exacerbated during the peak breeding season and so results in an increase in mortality either directly or indirectly from stress due to intraspecific aggression. The reduction in foraging area does appear to have some effect on the pattern of bandicoot movement where bandicoots are forced to utilise the higher drier areas in the extended area even though the extended area is somewhat degraded.

Although the reserve is small and enclosed, it does not appear to adversely effect the fecundity, except for a slightly smaller mean litter size, an observation which has also been found in island bandicoot populations (Copley *et al.*, 1990; Short *et al.*, 1998a). Although there was a decrease in the body weights found in both sexes from May to

August, with a reduction in the foraging area, these factors also did not appear to have any adverse effect on the fecundity of this *I. obesulus* population. The numbers of actively reproducing females, mean litter size and mean litter range all continually increased, over this period (May-August).

The small time scale limited the study. Trapping was carried out during a time of low recruitment of sub-adults into the population and so the low numbers (3) of this cohort meant that sex ratios could not be calculated. As 4 of the 5 trapping months were done during the period when that the ephemeral swamps filled, traps could not be placed in these areas to determine if bandicoots were in fact using them when dry.

The results of this study have raised a number of questions. There has been no detailed research on the dispersal patterns on bandicoots, on whether dispersal varies with sex, density and environmental changes. Are female biased sex ratios the norm in the absence of the fox, or are they a result of the constraints of a small enclosure? The observations of bandicoots since in and around Ellen Brook Reserve suggest that this population grew from a small number of individuals. The population therefore provides a unique opportunity to study the genetics of a small population arising from a bottle-neck situation. More long-term studies in areas with and without foxes in open and dense habitats in unenclosed and enclosed areas would provide important information for the long-term management and survival of this species. Although this study and others suggest that fox predation is a primary factor in the demise of bandicoots, effecting changes in sex ratio and age structure, other factors such as a lack adequate optimum habitat and dispersal opportunities may play important roles.

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