DRAFT

The impact of hypothetical land-use scenarios on the population viability of the Endangered Carnaby's cockatoo

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Executive Summary

Background

Carnaby's cockatoo *Calyptorhynchus latirostris* is a large, long-lived, charismatic cockatoo species endemic to south-western Australia. The species is endangered as a result of the extensive past clearance and fragmentation of native vegetation for agriculture, industry and urbanization.

Carnaby's cockatoos move annually from inland breeding sites to higher rainfall areas closer to the coast during the non-breeding season, where they mass into flocks comprising adult birds, their offspring from the recently completed breeding season, and juvenile birds which have not yet become breeding adults. There are two separate populations: the western population, which migrates between the northern wheatbelt and the west coast region, and the eastern population that moves between the southern wheatbelt and south coast region. This seasonal migration brings the largest flocks into the Perth and Peel regions on the Swan Coastal Plain, where native *Banksia* woodlands and pine plantations are their principal food sources during the non-breeding period.

The future of Carnaby's cockatoo in the Perth and Peel regions will continue to be affected by the growth of the greater Perth metropolitan area. Planned clearing of *Banksia* woodlands to accommodate the growing population, coupled with the clearing of pine plantations for groundwater recharge, will place further pressure on feeding habitats of the Carnaby's cockatoo subpopulation in the regions.

The impact of proposed urban and industrial development on matters of national environmental significance listed under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) is being assessed jointly by the State and Federal governments through a Strategic Assessment of the Perth and Peel Regions. This includes consideration of impacts on the Carnaby's cockatoo subpopulation in the Perth and Peel regions.

Population viability analysis (PVA) is a tool that enables assessment of the impact of changing land-use on threatened species, such as Carnaby's cockatoo. PVAs are abstract models of complex systems and as a consequence have limitations, but all predictions of the future are based on assumptions and are error prone. The value of PVA is that assumptions and uncertainties are stated, reinforcing the rigour and transparency of environmental decision making.

The PVA has been used to evaluate the potential impact of three hypothetical land-use scenarios on both the Perth-Peel subpopulation and the whole population of the endangered Carnaby's cockatoo over the period 2001 – 2050. The three scenarios were: the 'Maximum Water' scenario (clearing 23,000 ha of existing pines on the Gnangara water mound to maximize groundwater recharge); the

'Mitigation' scenario (clearing of 23,000 ha of existing pines but with retention of pine wildings in cleared areas to mitigate the impacts on Carnaby's cockatoo); and the 'Cessation' scenario (immediate cessation of clearing of pines). The three hypothetical scenarios also included projected future clearing of ca. 10,500 ha of *Banksia* woodlands for urban and industrial development (i.e. raw materials, housing and industry) and the planting of additional *P. pinaster* plantations (5,000 ha). Each scenario was compared with projected population changes in the absence of any habitat change from 2001 values ('Reference' model).

The hypothetical land use scenarios are limited to the Swan Coastal Plain, in the western portion of the Perth-Peel Strategic Assessment Area, which supports the vast majority of the Carnaby's cockatoo subpopulation and associated foraging resources. Estimated changes in the extent of pine plantations and native *Banksia* woodland were based on the proposed development footprint available at the time and may be subject to revision.

The PVA did not consider the effects of proposed mitigation and offsets measures on the species, such as ecological restoration of *Banksia* woodlands and other revegetation initiatives, breeding enhancement programs, or any changes to habitat outside the Strategic Assessment Area. The PVA, therefore, does not provide an analysis of the overall outcome of implementing the Perth and Peel Green Growth Plan for 3.5 million.

Results

PVA has it greatest value as a heuristic tool for predicting the consequences of human actions on threatened species and for determining which parts of a species life-cycle have the greatest impact on population viability and should be the focus for designing recovery actions, monitoring programs and future research. A PVA is most robust when assessing relative model outputs rather than exact predictive outputs of abundance or extinction risk.

The initial abundance of birds used in models for the Perth-Peel subpopulation of Carnaby's cockatoo is based on estimates derived from an annual monitoring program. The initial abundance of birds used in models of the total population of the species is considerably more uncertain, because the total population size is not accurately known. Furthermore, models for the total population do not include any changes in habitat availability and carrying capacity outside the Strategic Assessment Area. As a consequence, model predictions for the total population are less reliable than those for the Perth-Peel subpopulation.

None of the hypothetical scenarios resulted in a projected extinction of either the Perth-Peel subpopulation or the total Carnaby's cockatoo population. In the absence of any habitat change after 2001, the Reference model resulted in an estimated decline of 20% by 2050. When compared with the Reference model, the Maximum Water scenario had the greatest impact, further reducing the estimated average population size of the Perth-Peel subpopulation of Carnaby's cockatoo by an additional 36%, equating to a total decline of 56% by 2050. The Mitigation and Cessation scenarios had progressively less impact reducing the estimated average population size by an additional 29% and 14%, equating to total declines of 49% and 34%, respectively. For both the Maximum Water and Mitigation scenarios the model predicts a high probability that the Perth-Peel subpopulation will fall below 50% of its 2001 value at least once during the period 2000-2050 (0.97 and 0.76, respectively).

In terms of the total population, the additional impacts of all the scenarios were <10% of both expected minimum abundance and population size compared to the Reference model. However, estimates of the risks for the total population should be treated cautiously because of uncertainty about the total population size, the proportion of the total population that relies on the Perth-Peel region for foraging and a lack of information about temporal trends in habitat and carrying capacity outside the Perth-Peel region.

The PVA also provided insights into the relative effects of breeding and survival rates on population growth. Annual adult survival rate had the greatest relative impact on population viability – even small changes in this parameter had substantial effects on population growth rate and a far greater effect than equivalent changes in either breeding rate or juvenile survival. In particular, a decrease of 5% in annual adult survival resulted in a rapid population decline. In addition to restoring breeding habitat it is therefore important to also address, where possible, threats that increase adult mortality. It is vital that current actions which reduce adult mortality, including the rescue and rehabilitation of injured birds, continue.

Conclusions

Carnaby's cockatoo has a number of traits, such as a low reproductive rate, which make it vulnerable to decline. Population monitoring shows that the Perth-Peel subpopulation is in decline, and has been for some time. The decline predicted by the Reference model is consistent with this observed decline and the Endangered status of Carnaby's cockatoo. Under the hypothetical land-use scenarios, additional declines are predicted for the subpopulation. The results of the analysis also indicate that in addition to restoring breeding habitat it is vitally important to address, where possible, threats that increase adult mortality, and to maintain and restore foraging habitat for this iconic species.

Compared to most other cockatoo species, Carnaby's cockatoo has been well-studied, and there is a substantial amount of information available for building a population model. Because adult survival has such a profound effect on population viability, however, improved resolution of demographic parameters such as the survival rates of adults and their capacity to adapt or disperse in response to habitat change are priorities for future research. Better estimates of the total population size are also needed to quantify more accurately the potential impacts of land use changes and conservation actions on the viability of the species.

Introduction

Cockatoos and parrots (Psittaciformes) are amongst the longest-lived birds, but are also amongst the most endangered, with more than half of all cockatoo species threatened (Garnett et al., 2011; Birdlife International, 2013a). The major cause of their decline has been habitat loss through clearing for agriculture and urbanization (Saunders ,1990; Garnett et al., 2011). The rapid decline of cockatoos has likely been compounded by their “slow life histories” – low reproductive rates over long lifespans (Murphy et al., 2003; Heinsohn et al., 2009).

Carnaby’s cockatoo *Calyptorhynchus latirostris* is a large, long-lived, charismatic cockatoo species endemic to south-western Australia (Saunders, 1979). The species has become endangered as a result of the extensive clearance and associated fragmentation of native vegetation during development of agriculture, industry and urbanization (Saunders & Ingram, 1995). Over the past 50 years the bird has undergone an estimated 50% decline in abundance, and its status has changed from being classified as vermin, with a bounty on its bill, to endangered (Saunders, 1990; Saunders & Ingram, 1998; Garnett et al., 2011). The species has disappeared from extensive areas of its former breeding range, particularly in the area known locally as the central Wheatbelt, and now comprises two geographically and genetically distinct ‘western’ and ‘eastern’ populations (White et al., 2014). The well-documented loss of breeding populations (Saunders, 1982, 1986, 1990), historical accounts of flock sizes (Perry et al., 1948; Johnstone et al., 2009) and declines in census numbers in recent years (Shah, 2006; Williams et al., 2015) indicate that Carnaby’s cockatoo populations have been severely affected by extensive destruction of both their breeding and foraging habitats. Currently the species is specially protected as “fauna that is rare or likely to become extinct as endangered” in Schedule 2 of the *Western Australian Wildlife Conservation Specially Protected Fauna Notice 2015* under the Wildlife Conservation Act 1950, is listed as Endangered under Australian Federal law (*Environment Protection and Biodiversity Conservation Act 1999*) and internationally by IUCN (Birdlife International 2013b).

Carnaby’s cockatoos are peripatetic, moving annually from drier inland breeding sites to higher rainfall areas closer to the coast during the non-breeding season where they mass into foraging flocks which include adult breeding birds, their offspring from the recently completed breeding season and juvenile birds which have not become breeding adults (Saunders 1980). This seasonal migration brings the largest flocks onto the northern Swan Coastal Plain along the western coast of Western Australia (Finn et al., 2014). This area includes the State capital, Perth, and from January each year Carnaby’s cockatoos are conspicuous and visible throughout much of the metropolitan area contributing to the city’s natural heritage and sense of place.

The expansion of Perth, one of Australia's fastest growing metropolitan areas (Kennewell & Shaw 2008) has had a substantial impact on the availability of food resources for Carnaby's cockatoo, affecting the number of birds that can be sustained. Widespread clearing of *Banksia* woodlands, the predominant native food source for Carnaby's cockatoo, has accelerated since 1950 and 61% of the original extent has been cleared (WAPC, 2010). Extensive pine plantations established from the 1920s have progressively replaced *Banksia* woodlands as the major food source for the cockatoos in the region, inadvertently offsetting some of the loss of native habitat (Perry, 1948; Saunders, 1974; Butcher, 2007; Stock et al., 2013). This has not been enough, however, to prevent a dramatic decline of the species in the region. Flocks of Carnaby's cockatoo on the Swan Coastal Plain once exceeded 5,000 birds (Perry, 1948; Johnstone et al., 2009; Saunders, pers. obs.), but based on an annual citizen-science survey of roost sites (the 'Great Cocky Count', Shah, 2006), flocks larger than 500 are now a rarity in the region (Shah, 2006; Berry & Owen, 2009; Finn et al., 2009,2014). Nonetheless, four of the five largest known roosting sites occur on the Swan Coastal Plain within the Perth-Peel region (Finn et al., 2014).

The future of Carnaby's cockatoo on the Swan Coastal Plain will continue to be affected by the expansion of Perth. By 2031, the city's population is projected to have increased by between 35% and 40% to between 2.2 and 2.8 million people with an estimated 3.5 million people by 2056 (ABS, 2008; WAPC, 2010). Planned clearing of *Banksia* woodlands to accommodate the growing population and associated industries, coupled with the clearing of pine plantations to manage groundwater recharge to meet the city's water needs in a drying climate, will place further pressure on feeding habitats of Carnaby's cockatoo in the region.

For the last four decades Perth's growth has been coincident with declining rainfall and this is projected to continue (Bates et al., 2008). Water management and supply agencies have had to adapt by diversifying and developing new water sources to include groundwater, desalination and water recycling, thereby reducing the city's dependence on surface water catchments. The largest source of groundwater is the Gnangara mound on the northern Swan Coastal Plain, which is important for public drinking water supply in Perth, for horticultural uses and groundwater-dependent ecosystems. This area also contains Perth's largest area of pine plantations and these have a significant impact on groundwater recharge. Measurements indicate that no recharge occurs beneath the plantations at current densities, and in some areas the trees are accessing groundwater directly. In 1996, the State Government approved the progressive harvesting of up to 23,000 ha of pines at the Gnangara, Pinjar and Yanchep pine plantations to increase water recharge to the Gnangara Mound. Following this decision, the State concluded State Agreements for the sale of the harvested timber. Since 2004, these pine plantations have been progressively harvested to meet timber supply obligations under these agreements.

The pines are also a major source of food for Carnaby's cockatoos (Stock et al., 2013) and this poses a public policy 'wicked problem' (Rittel and Webber, 1973) for planners seeking to protect water resources and a variety of threatened species.

The Western Australian Government policy "Directions 2031 and Beyond" is a high level spatial framework and strategic plan that establishes a vision for accommodating the projected population growth of the Perth and Peel Region. The impact of land-use changes proposed under Directions 2031 on matters of national environmental significance (MNES) listed under the Commonwealth EPBC Act is being assessed jointly by the State and Federal governments through a Strategic Assessment of the Perth and Peel Regions. This includes consideration of impacts on Carnaby's cockatoo.

Population viability analysis (PVA) is a modelling tool that enables robust risk assessment of the impact of changing land-use on threatened species, such as Carnaby's cockatoo. PVAs are abstract models of complex systems and as a consequence have limitations, but all predictions of the future are based on assumptions and are error prone. The value of PVA is that assumptions and uncertainties are stated reinforcing the rigour and transparency of environmental decision making (Burgman 2000).

Previously, PVAs have been developed for several cockatoos: the Glossy black-cockatoo *Calyptorhynchus lathami* (Harris et al., 2012), Palm cockatoo *Probosciger aterrimus* (Heinsohn et al., 2009), Yellow-tailed black-cockatoo *C. funereus* (Fox and Brereton, 2004), south-eastern Red-tailed black-cockatoo *C. banksia* subsp. *graptogyne* (Potts, 2015), and Carnaby's cockatoo (Cockerill et al., 2013). With the exception of Harris et al. (2012), these studies have substantial knowledge gaps in vital rates and/or carrying capacity which limit their ability to make reliable inferences. The results reported here examine the population dynamics and viability of Carnaby's cockatoo in far greater detail than the previous study of Cockerill et al. (2013) and incorporate detailed consideration of two principal food sources, and the effect of urban and industrial development. PVA works by using autecological and demographic monitoring data to parameterise a population model. This is then used to project dynamics and estimate future population size and extinction risk under alternative land-use scenarios.

In this study, PVA is used to evaluate the impact of foraging habitat loss on the Perth-Peel subpopulation and the whole population of the endangered Carnaby's cockatoo. The analysis focuses on stochastic measures of population viability for three hypothetical land-use scenarios affecting the availability of the species' primary food sources: plantation pines and *Banksia* woodlands. The most critical life history traits affecting population viability of the species are evaluated and information and recommendations for management and future monitoring are provided. This will contribute to recovery planning for Carnaby's cockatoo and planning decisions affecting the species on the Swan Coastal Plain.

Methods

Study species

Carnaby's cockatoo is restricted to the south-western corner of Australia, bounded in the north-east by the 300 mm annual rainfall isohyet (Saunders, 1990). There are two separate populations (White et al., 2014): the western population, which migrates between the central and northern agricultural region and the Swan Coastal Plain on the west coast, north to the mouth of the Murchison River, and the eastern population that moves between the southern wheatbelt and south coastal region (White, 2011; Saunders et al., 2013; White et al., 2014). The western population is genetically more diverse than the eastern population, and is estimated to be the larger of the two populations (White et al., 2014).

The species is long-lived with documented ages for wild birds still living of 28 and 29 yrs for females and 34 yrs for males (Saunders et al., 2011a; Saunders & Dawson, unpublished data). Birds do not breed until four years old, and form long-lasting pair bonds (Saunders, 1982). They nest in large hollows of eucalypts (Saunders, 1979, 1982). Juveniles (0-4 yr) accompany their parents for some time after fledging, and then find a mate and form a breeding pair. The duration and timing of these events is unknown, but birds have been recorded forming pairs and showing breeding behavior at 3 yrs old (Dawson et al., 2013). Studies at several breeding areas show that many pairs and their female offspring return to the same area to breed each year. One local breeding population, at Coomallo Creek on the western edge of the northern agricultural region, has been monitored since 1969 (Saunders, 1982; Saunders & Ingram, 1998; Saunders et al., 2013, 2014). Pairs nest in large hollows in eucalypt trees and in artificial nest boxes that have been provided to supplement natural hollows (Saunders et al., 2014). Where possible, a pair will nest in the same tree hollow used previously, provided they successfully fledged their offspring the previous year. Females lay one or two eggs (usually two), but typically only one nestling is reared. Females incubate the egg(s) for around four weeks, commencing with the laying of the first egg. The second egg is usually laid about 8 days after the first (Saunders, 1982; Saunders et al., 2013). During incubation and the first few weeks of the nestling period she is dependent on the male for food, but for the remainder of the 10-

11 week nestling period both parents forage and feed the nestling(s) (Saunders, 1980; Saunders et al., 2013). Breeding commences in the Austral winter following the commencement of seasonal rainfall and is completed by late spring or early summer (Saunders et al., 2013).

Following breeding, pairs migrate to coastal areas, accompanied by offspring from the current, and sometimes the previous, breeding cycle. Direct information on the survival rate of adults and fledglings during this migration is scant. In the breeding areas, Carnaby's cockatoo feeds mainly on the seeds of several genera of Proteaceae, including *Banksia*, *Hakea* and *Grevillea* (Saunders, 1980, 1982), and *Eucalyptus* spp. as well as invertebrates and seeds of *Erodium* sp., an agricultural weed (Saunders, 1980). At some sites, the seed of cultivated Canola (*Brassica napa* and *B. juncea*) has recently been incorporated into the diet as it has become more widely cultivated since the 1990s (Saunders et al., 2013). In the non-breeding areas the diet is similar, but also includes the seeds of several exotic species including maritime pine *Pinus pinaster*, which occurs as extensive plantations, and cultivated 'backyard' and crop trees such as liquid amber and almonds (Perry, 1948; Saunders, 1974, 1980; Butcher, 2007). In the coastal feeding areas the seeds of plantation pines are a critical component of the diet (Saunders, 1980; Stock et al., 2013). The movement from the breeding areas to the foraging areas on the Swan Coastal Plain coincides with pine seed maturation and occurs at a critical time in the life-cycle of the bird when breeding pairs are still feeding juvenile offspring (Saunders, 1974; Stock et al., 2013).

Vital rate estimates

Estimates of the relevant life history parameters and critical vital rates of Carnaby's cockatoo were determined or derived from published literature on the species and from unpublished data and expert opinions; these are summarized in Table 1 and information on the source or derivation of these values is given below.

Sex ratio. In a sample of 91 wild birds collected from the southern population during the non-breeding season (see *Adult survival rates* below) the sex ratio was approximately 1 : 1 (Saunders et al., 2011b). A sample of 130 birds collected from the northern population in 1970, also during the non-breeding season (Saunders, unpublished data) yielded 64 males and 66 females, also a sex ratio of 1 : 1.

Initial population size and age structure. The size of the Perth-Peel subpopulation in 2001 at the beginning of the model simulation period is unknown. An initial estimate of 8,000 birds was used, which is consistent with both the estimated carrying capacity in 2001-2015 (see below), and with the number of birds recorded by the Great Cocky Count monitoring program (Williams et al., 2015).

The Great Cocky Count is a citizen science program which undertakes an annual census of mixed flocks of adult and juvenile birds at nocturnal roosts in the Perth-Peel regions (Shah 2006; Finn et al., 2014; Williams et al., 2015). The Great Cocky Count is now sampling a large proportion of the birds that spend the non-breeding period in the Perth and Peel regions. In 2014, over 300 observers surveyed 180 roost sites and counted 6,671 birds at 38 occupied roosts (Finn et al., 2014).

Because of logistical difficulties, there has not been a census of Carnaby's cockatoo across its range. As a consequence there is considerable uncertainty about the size of the total population. Currently, the population is estimated to be approximately 40,000 birds, but this should be treated with caution as the confidence intervals are likely to be wide (Garnett et al., 2011).

The number of birds in each age class, i.e. the initial age/stage structure, was estimated from a deterministic population model described below.

Fecundity. The fraction of pairs nesting each year is estimated at 90%; i.e. 90% of mated females will attempt to nest each year (Saunders, pers. obs.). The number of fledglings produced by a nesting pair each year was estimated from published long-term monitoring data for fledging success rates at sites in both the western and eastern populations (Saunders et al., 2013). The number of fledglings from 610 nests at six sites over 11 years (1969 – 1976, 1996 – 1998) were analysed using a mixed effects general linear model, with sites treated as random and year as fixed effects. The annual estimates of the number of fledglings varied from 0.26 – 0.88 fledglings / nesting pair / year (mean 0.53, sd = 0.19).

Adult survival rates. Although tagging or banding to enable identification of individual cockatoos has been conducted for many years, to date there has been insufficient recovery of banded birds to enable a robust estimate of annual survival rates (Saunders, 1982, 1988; Saunders et al., 2011a). Therefore, the survival rate for adult ($\geq$ 4 year old) birds was estimated from a detailed study of population age structure based on assays of pentosidine to determine the individual ages of birds from two wild flocks (Le Souëf, 2012). Pentosidine, an advanced glycation end-product found in skin collagen, accurately predicts age in many birds including Carnaby's cockatoo (Le Souëf, 2012). Using this method, a calibration curve was first determined using a sample of 50 captive birds of known age. The ages of 91 wild birds collected from the eastern population during the non-breeding season (Saunders et al., 2011b) were then determined from pentosidine assays of skin samples. Using the age structure of this sample and the method of Skalski et al. (2005), the estimated annual survival rate of the 68 adult birds was determined by Poisson regression (i.e. log-linear regression using a Poisson error distribution) of frequency against age. This gave an estimated adult survival rate of 0.927 (se = 0.017).

Juvenile survival rates. Survival rates of juveniles are believed to be less than that of adults, but precise data are scant. Based on a limited sample and using patagial tags, which were subsequently found potentially to increase mortality, Saunders (1986, 1988) found that the probability of survival for females increased with age, with the survival rate of juveniles (~ 60 %) lower than that of adults (~ 75%). However, these rates were based on detection of fledged females returning to the natal breeding area, and thus are likely to be underestimates, as some surviving individuals were probably not re-encountered. Nonetheless, they show that juvenile survival is approximately 80% of that of adults. The only information available to estimate juvenile survival is the ratio of adults to juveniles, obtained from the samples of Saunders (1974) and Le Souëf (2012). Saunders collected a random sample of 130 wild birds in the Gnangara pine plantation, 20 km north of Perth, between 6 April and 30 June 1970, which yielded 82 adults and 48 juvenile birds, a ratio of 1.7 : 1. In the Le Souëf et al. study, 30 of the 91 birds collected were juveniles (adult : juvenile ratio 2.0 : 1). To obtain estimates of juvenile survival rates, a simple deterministic model of staged-based population growth was used to determine the mortality rates of adult and juvenile birds that would be needed to produce both a stable population and age structure, with a ratio of adult to juvenile birds comparable to that observed in these studies. It was assumed that the mortality rate of fledgling birds (0-1 yr) is twice that of older juveniles (1-4 yr, m_j), which in turn is less than that of adult birds (m_a). The corresponding stage-based transition matrix for this model, applied to females only and incorporating a 90% breeding participation rate (Table 1) is:

Life stage	**Transition rate**				
Fledgling (0-1 yr)	0	0	0	0	0.2375
Juvenile (1-2 yr)	$1\text{-}2m_j$	0	0	0	0
Juvenile (2-3 yr)	0	$1\text{-}m_j$	0	0	0
Juvenile (3-4 yr)	0	0	$1\text{-}m_j$	0	0
Adult (>4 yr)	0	0	0	$1\text{-}m_j$	$1\text{-}m_a$

Matrix formulation

The stochastic simulation program RAMAS Metapop version 5 (Akçakaya, 2005) was used to simulate population trajectories. A stage-based transition matrix was constructed, with the number of individuals moving between each stage determined from the estimates of birth and survival rates described above (Table 1). There were five stages in the model: four for each year of the juvenile period, i.e. ages 0-1 through to 3-4 yrs, and one for adults, aged 4+ yrs. Because of the equal sex ratio, the long-lasting pair bond and the lack of data available for males, the model was restricted to females only. The model included demographic and environmental stochasticity. RAMAS incorporates demographic stochasticity by sampling the number of survivors from binomial distributions and fecundity from a Poisson distribution (Akçakaya, 2005). RAMAS implements environmental stochasticity at each time step by randomly selecting matrix elements within the observed variance around their mean. To reduce likely truncations due to high survival rates in some stages, samples were taken from a lognormal distribution. Constraints were imposed to ensure that all survival rates were within the bounds of 0 and 1. All simulations were run for 50 one-year steps replicated 1000 times. Survivorship, fecundity and carrying capacity were assumed to be uncorrelated as there is no evidence to indicate any correlation between these factors.

The number of stages was matched to the limited demographic data available: as more information becomes available, more life stages could be added, such as the nestling period, or by incorporating more adult stages. For example, it is thought that breeding success increases with age (Saunders unpubl. data), but there is currently insufficient data to quantify this increase accurately.

Reference model and sensitivity analysis

A Reference model was parameterized using the mean values and their standard deviations for each matrix element, and used in a sensitivity analysis to assess the relative importance of each life stage on population viability by varying each of three parameters (fecundity, juvenile survival m_j, or adult survival, m_a) by an absolute value of 5% while keeping the others unchanged and determining the resulting expected minimum abundance (EMA). It is important to note that this Reference model has no capacity for long-term population growth (i.e. $\lambda=1$). The Reference model was used as the baseline for calculating the projected impacts of the hypothetical land-use scenarios.

Because of uncertainty about the initial size of the Perth-Peel subpopulation the effect on the model of increasing the initial population sizes was also examined.

Population trend and viability under hypothetical land-use scenarios

Ongoing clearing of pine plantations and *Banksia* woodlands on the Swan Coastal Plain will affect the food resources available to Carnaby's cockatoo, and carrying capacity (K) is expected to decline (Stock et al., 2013). The impacts of potential changes in land-use on both the Perth-Peel subpopulation of Carnaby's cockatoo and the total population were modelled using three hypothetical scenarios each with a different temporal trend in K. The three scenarios were as follows: the Maximum Water scenario involves the clearing of existing pines on the Gnangara water mound to maximize groundwater recharge; the Mitigation scenario involves the clearing of existing pines, but retention of pine wildings in cleared areas to mitigate the impacts on Carnaby's cockatoo; the Cessation scenario involves the immediate cessation of clearing of pines (Table 2). All scenarios include projected future clearing of 10,489 ha of *Banksia* woodlands for raw materials, housing and industry, and the planting of 5,000 ha of *P. pinaster* plantations (Table 2). Outside the Perth-Peel region, where the rates of land clearing and habitat change are thought to be relatively minor, carrying capacity was set at a constant level 50% higher than the estimated population size.

Estimating temporal trends in K

The limiting effect of food resources on the size of the northern Perth-Peel subpopulation of Carnaby's cockatoo was investigated using a daily ration model (Appendix 1). The daily energy requirement of Carnaby's cockatoo (Cooper, 2002) was multiplied by the residence time of birds in the region each year to determine their annual energy needs. This was then compared to the annual energy production of the two principal food sources, pine plantation and banksia woodland. The estimates of the amount of food energy available from each source accounted for annual variability in seed production, the foraging thresholds ('giving-up density' at which birds cease foraging because it is energetically no longer profitable), harvesting efficiency of Carnaby's cockatoo (i.e. the fraction of seeds available that are actually consumed), and the metabolizable (as opposed to total) energy content of each food type. These values were determined from a literature review and unpublished sources, and provide more precise estimates of carrying capacity than previous studies (e.g. Valentine et al., 2014).

For the two principal food sources K (birds/hectare) was estimated for years of average seed production. For mature *P. pinaster* (>15 yrs old) in existing plantations K = 0.395 birds/hectare, for *P. pinaster* wildings and *P. pinaster* in new plantations cone bearing begins at age 7 yrs old, between 7 and 15 yrs old K = 0.1225, and between 15 and 50 yrs old K = 0.245. For mixed *Banksia* woodland K = 0.046 birds/hectare. These values were applied to the three hypothetical land-use scenarios to obtain yearly estimates of average K from 2001-2050.

Seed production varies annually in both *P. pinaster* plantations and mixed *Banksia* woodland, and this will affect the individual year-to-year values of K. Temporal variation in carrying capacity was incorporated using a ceiling model of density dependence, where the population can grow until it reaches the carrying capacity ceiling, and then remains at that level until a population decline takes it below that level. This annual variation was modelled by sampling each annual value of K from a normal distribution to give stochastic variation that matched published estimates of the annual variation in the two principal food sources (Appendix 1). This means that values above and below the average carrying capacity were sampled and included at each time-step in the model. If the population grows above the ceiling carrying capacity, however, it declined to the ceiling by the next time step. In this case the carrying capacity acts as a population ceiling above which the population cannot increase. As a consequence, the average population size or population trajectory in a model with a population ceiling may be well below the carrying capacity, because population size may be pushed below this level by annual environmental variation, but cannot increase above the ceiling.

Results

Deterministic model

The deterministic model produced a stable population size and age structure when juvenile mortality m_j = 0.20 and adult mortality m_a = 0.073, corresponding to annual survival rates for fledglings of 0.60, for juveniles of 0.80, and for adults of 0.927. Because of the higher mortality rates of juvenile birds, the adult:juvenile ratio increases from a minimum immediately after breeding, when new fledglings enter the population, to a maximum immediately before the following breeding season. The range in the ratio of adults to juveniles produced by this model was 1.71 – 2.20; at the mid-point of the breeding cycle it was 1.92:1. This ratio corresponds well with the ratios of 1.7 and 2.0:1 observed in the two samples of wild birds.

Sensitivity analysis

Adult survival rate had the greatest relative impact on population viability. Changes of 5% in this parameter had profound effects on expected minimum abundance, and a far greater effect than equivalent changes in juvenile survival or fecundity (Fig. 1). In particular, a decrease of 5% in adult survival resulted in a decline in estimated minimum abundance of 70%. Increasing the initial population size of the Perth-Peel subpopulation had no effect on the results as the ceiling-type carrying capacity method used rapidly reduced all initial population sizes to approximately equal levels.

Reference and scenario models

The three hypothetical land-use scenarios resulted in declines of K between 2001-2050 of 25% to 55% (Table. 2), whereas the Reference model assumed no decline in K. Nonetheless, the Reference model estimated a decline of ca. 20% in the Perth-Peel subpopulation and the total population of Carnaby's cockatoo over the 50 year simulation period. This decline was due to stochastic variation in K; in the absence of any limit to K (i.e. K = ∞), both the Perth-Peel subpopulation and total population remained stable (results not shown). It is unrealistic, however, to run the Reference model with unlimited carrying capacity because food resources for Carnaby's cockatoo are finite and vary from year to year (Appendix 1).

None of the hypothetical scenarios resulted in a projected extinction of either the Perth-Peel subpopulation or the total Carnaby's cockatoo population (Fig. 3). When compared with the Reference model, the Maximum Water scenario had the greatest impact, further reducing the estimated average population size of the Perth-Peel subpopulation of Carnaby's cockatoo by an additional 36%, equating to a total decline of 56% by 2050. The Mitigation and Cessation scenarios had progressively less impact reducing the estimated average subpopulation size by 29% and 14%, equating to total declines of 49% and 34%, respectively (Table 3, Fig. 3). These changes correspond with, but are slightly less than, the projected changes in average K for this region (Table 2). In terms of the total population, the additional impacts of all the scenarios were <10% of both expected minimum abundance and population size compared to the Reference model..

For the Maximum Water and Mitigation scenarios, there is a high probability (0.97 and 0.76) that the Perth-Peel subpopulation will fall below 50% of its initial value at least once in the 50 yr period (Table 4). The total population size is also projected to decline by 25% at least once during the period.

Discussion

Although, Carnaby's cockatoo is unlikely to become extinct by 2050, past (pre-2015) and hypothetical future (2015-2050) land use changes are estimated to have substantial effects on the Perth-Peel subpopulation. Even if loss of feeding habitat had ceased in 2001, the intrinsically low rate of population growth, the ceiling-type model for K, and the limiting effects on population size produced by stochastic variation in annual values of K ('lean years'), combine to predict a decline of ca.20% in the Perth-Peel subpopulation by 2050 (Reference model; Table 3). Loss of feeding habitat in the Perth and Peel regions between 2001 and 2050 is predicted to result in additional declines of 14-36%. The predicted decline is consistent with current trends in the Perth-Peel subpopulation measured by annual monitoring surveys ('Great Cocky Counts'; Shah, 2006; Finn et al., 2014; Williams et al. 2015).

Four important factors, however, need to be considered when interpreting the population trajectory results. Firstly, estimates of future population sizes are inherently imprecise (Akçakaya, 2005), and their accuracy relies upon the precision of the life history parameters used in the modelling. The model uses values based on extensive field data, and indicates that under current circumstances, the species’ fecundity and survival rates are too low to enable population growth. This is consistent with past (Garnett et al., 2011) and current (Williams et al., 2015) population trends. Secondly, the modelling of the Perth-Peel subpopulation is restricted to the two principal food sources: pine plantations in the Gnangara area and mixed *Banksia* woodlands. The carrying capacity of other, minor, food sources (see e.g. Cooper et al., 2002; Stock et al., 2011) has not been modelled, and the extent to which annual variation in these alternative food sources may interact to limit the effect of ‘lean years’ is unknown. Thirdly, it is assumed that the bird is unable to adapt its foraging behavior in response to the land-use scenarios. For example, novel food sources may exist in the Perth-Peel region which the bird is currently not utilizing. Finally, several factors relevant to Carnaby’s cockatoo populations outside the Perth and Peel regions are poorly known: the nature and extent of their food resources and hence their carrying capacity; land use changes that have affected, or will affect, this carrying capacity; and the sizes of these populations.

In common with other long-lived birds, Carnaby’s cockatoo has several life history traits that make it vulnerable to population decline. These include a low reproductive rate with low egg production (Saunders, 1982: Murphy et al. 2003; Heinsohn et al., 2009; Saunders et al., 2013) and the use of tree hollows for nesting (Saunders, 1979, 1982; Saunders et al., 1982, 2014; Garnett et al., 1999; Heinsohn et al., 2015). As a consequence, adult survival has the greatest impact on the population viability of Carnaby’s cockatoo. The population is only viable if the adult survival rate is high enough to balance this low reproductive output. To illustrate this, a simple calculation based on estimated fecundity and survival rates shows that, on average, a breeding pair will produce only one new mature adult (i.e. a recruit to the breeding population) every 6 years ($0.53 \times 0.6 \times 0.8^3$ recruits per year). Equivalently, one replacement breeding pair will be produced in 12 years, provided both parents continue to survive and reproduce over this period. This is comparable with an estimated generation time of 15 yrs (DEC, 2012). Thus, breeding pairs of Carnaby’s cockatoos need to persist long enough to support their low rate of reproduction. This demonstrates how even a small increase in adult mortality leads to population decline via recruitment failure. The sensitivity of population viability to adult survival has also been shown for other long-lived birds (Heinsohn et al., 2009; Bode & Brennan, 2011; Hernandez-Matias et al., 2013; Smith et al., 2013).

Previous work has established that the loss of foraging habitat in breeding areas and decline in availability of tree hollows in remnant eucalypt woodlands are reducing the fecundity of Carnaby’s cockatoo (Saunders and Ingram, 1995; Saunders et al., 2003) and leading to the loss of breeding groups (Saunders, 1982). Recent work investigating the benefits of renovating decrepit tree hollows and addition of artificial hollows has demonstrated that these actions allow more birds to breed

(Saunders and Dawson, unpubl. data). The results of the sensitivity analysis indicate that in addition to restoring breeding habitat it is vitally important to also address, where possible, threats that increase adult mortality.

In addition, the causes of mortality of adult birds are numerous and include extreme weather events, shooting, poisoning, and motor vehicle strikes (Saunders et al., 2011b). In the Perth region in 2013, 112 Carnaby's cockatoo were received into care following injuries (R. Dawson, pers. comm.), similar to the 100 per annum recorded for 2009-2010. These injuries are predominantly the result of motor vehicle impacts. Another 57 birds are known to have died after a severe hail storm in Perth in 2010, and at least 208 birds in the Southern population died during an extreme heat wave (Saunders et al., 2011b). In all of these instances, the reporting rates are thought to be far less than the actual numbers of deaths and injuries (Saunders et al., 2011b). It is vital that actions which reduce adult mortality continue, including rescue and rehabilitation of injured birds.

An estimate of adult survival (0.927) in the Reference and hypothetical land-use scenario models was used. This estimate is more conservative than the value (0.919) derived from the age structure measured by Le Souëf (2012) and produced a stable population with a finite rate of increase (λ) of 1 in a deterministic model. The Reference model acts as a baseline for comparing the impacts on extinction risk and projected population trends of the hypothetical land-use scenarios. The Reference model resulted in a population decline of c. 20% and this can be attributed primarily to stochastic variation in carrying capacity. As carrying capacity was implemented as a ceiling and the Reference model has no capacity for growth (λ =1), population size may fall in response to a low annual values of K, but cannot subsequently recover. Stochastic variation in the vital rates will also affect the rate of population change. The decline in the Reference model is consistent with both the known historical decline of the species and the estimated current trend based on roost counts (Garnett et al., 2011; Williams et al., 2015).

None of the modelled land-use scenarios proposed for the Perth-Peel region resulted in the extinction of Carnaby's cockatoo, and the impacts were consistent with projected changes in carrying capacity. However, caution needs to be applied in interpreting these results for several reasons. Firstly, estimates of the number of birds, the area of foraging habitat and projected future habitat losses are most accurate for the subpopulation of Carnaby's cockatoo foraging in the Perth-Peel region of the northern Swan Coastal Plain, but there is uncertainty about the total population of the species, and in particular what proportion of the total population relies on the Perth-Peel region for foraging. Secondly, there is a lack of information about temporal trends in habitat and carrying capacity outside the Perth-Peel region. Thirdly, there are several other food sources for Carnaby's cockatoos in the Perth-Peel region, including other native plant species, some remnants of past pine plantations, and non-native plants including those in suburban parks and gardens (Saunders, 1980; Shah, 2006). None of these food resources have been accounted for in the scenarios, and although it is thought that they account for a relatively minor component of the diet, they may be important in maintaining connectivity between the major foraging resources of Carnaby's cockatoos. Fourthly, the models assume that breeding success and mortality rates of Carnaby's cockatoo do not change with age. In other bird species, however, there is a tendency for middle-aged birds to have higher rates of reproduction and survival than either young or old birds (Newton, 1989). Although data are scarce for parrots, some sea-birds exhibit exceptionally slow age-related declines in survival, and some also show negligible reproductive senescence. Such slow ageing rates are limited to species with life histories characterized by delayed sexual maturation and very small clutch-sizes, such as those found in black cockatoos. Improved data on these aspects of the life history of Carnaby's cockatoo have the potential to increase the precision of the model. Finally, increased fragmentation of foraging habitat following clearing will have an unknown, but negative, effect on the on the birds' foraging efficiency. These sources of uncertainty will have some impact on the model projections. A related and potentially important issue is what role the pine plantations play in the annual breeding and recruitment cycle. This is not known. However, pine plantations provide a high density of high-energy, easily metabolized food (Stock et al., 2013) that supplies a valuable source of energy for the birds over the non-breeding season. They may also play an important role in the survival of fledgling birds that arrive in the region each year.

The three hypothetical land-use scenarios all had a negative impact on the population viability of Carnaby's cockatoo in the Perth-Peel region, due to the projected future losses of foraging habitat, but none resulted in the extirpation of the subpopulation. However, the Maximum Water scenario is projected to have a substantial impact, with a high likelihood ($p=0.97$) that the subpopulation will decline below 50% of its 2001 level at least once during the period 2001-2050. The proposed Mitigation scenario reduced the impact, but nonetheless there was still a high likelihood ($p=0.76$) that the subpopulation will fall below 50% of its 2001 level at least once during the period 2001-2050. Such declines may result in the loss of substantial genetic diversity, potentially reducing the adaptive capacity of the species (White et al., 2014).

Compared to most other cockatoo species, Carnaby's cockatoo has been well-studied over many years, and there is a substantial amount of information available for building a population model. Nevertheless, because adult mortality has such a profound effect on population viability, improved resolution of demographic parameters such as the survival rates of adults and their capacity to disperse or adapt in response to habitat change are priorities for future research. In addition, better estimates of the total population size are needed to quantify more accurately the potential impacts of land use changes and conservation actions on the viability of the species.

The projected declines in Carnaby's Black Cockatoo under the land-use scenarios are consistent with the observed decline of the subpopulation in the Perth-Peel region (Williams et al., 2015). The results of the analysis indicate that in addition to restoring breeding habitat it is vitally important to also address, where possible, threats that increase adult mortality, and to maintain foraging habitat for this iconic species.

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Table 1. Parameters used for the population viability analysis of Carnaby's cockatoo, their initial values, associated standard deviations and sources. Survival rates are annual values, except that for juveniles age 0-1, which is for the portion of the year remaining after fledging. Note that the values for initial population sizes, age structures and carrying capacities are for both sexes.

Parameter	**Value**	**Std. dev.**	**Source**
Sex ratio	1 : 1		Saunders et al., 2014; Saunders, unpublished data
Modeled sex	Females only		
Proportion of females nesting	90 %	0 %	Saunders, pers. comm.
Initial population size – Perth-Peel region	8,000		Williams et al., 2015
Initial carrying capacity – Perth-Peel region (pine plantations and mixed *Banksia* woodland;)	12,452	15%	Appendix 1
Initial age structure– Perth-Peel region (4 juvenile stages / adults)	1200; 720; 570; 460 / 5,050		Reference model
Initial population size – outside Perth-Peel region	32,000		Garnett et al. (2011)
Initial carrying capacity – outside Perth-Peel region	48,000	18%	Appendix 1
Initial age structure – outside Perth-Peel region (4 juvenile stages / adults)	4,800; 2,880; 2,280; 1,840 / 20,200		Reference model
Age at which breeding commences	4 yrs		Saunders, 1982; Saunders et al., 2011; Saunders & Ingram, 1998
Number of fledglings per nest (x proportion of females nesting)	0.5277 (x 0.9)	0.1892	Saunders et al., 2013
Survival - juveniles age 0-1	0.60	0.12	Reference model
Survival - juveniles age 1-2	0.80	0.16	Reference model
Survival - juveniles age 2-3	0.80	0.16	Reference model
Survival - juveniles age 3-4	0.80	0.16	Reference model
Survival – adults	0.927	0.015	Reference model

Table 2. The area (ha) of each land use retained under three hypothetical land-use scenarios for the Gnangara-Pinjar pine plantation and *Banksia* woodland in the Perth-Peel region, and the projected change (%) in carrying capacity (K) of Carnaby's cockatoo for 2001–2050.

	Scenario		
Land use	**Maximum Water**	**Mitigation**	**Cessation**
Existing pine plantation	0	0	8,050
Replanted pine plantation	5,000	5,000	5,000
Pine wildings	0	16,825	0
Grassland	16,825	0	8,775
Pine plantation cleared for urban purposes	1,175	1,175	1,175
Banksia woodland	95,629	95,629	95,629
Change in carrying capacity (K)	-55%	-48%	-25%

Table 3. Average minimum population size (Expected Minimum Abundance, EMA) and estimated mean population size at 2050 for the Perth-Peel subpopulation and total population of Carnaby's black-cockatoo, for three hypothetical land-use scenarios. Changes relative to the initial population estimates (8,000 birds for the Perth-Peel subpopulation and 40,000 for the total population) are in parentheses.

	Perth-Peel subpopulation		**Total population**	
	EMA	**Mean population size**	**EMA**	**Mean population size**
Reference model	5,136 (-36%)	6,432 (-20%)	26,100 (-35%)	31,072 (-22%)
Scenario models				
Maximum Water	3,012 (-62%)	3,550 (-56%)	23,764 (-41%)	27,944 (-30%)
Mitigation	3,466 (-57%)	4,054 (-49%)	24,340 (-39%)	28,560 (-29%)
Cessation	4,278 (-47%)	5,246 (-34%)	25,336 (-37%)	29,954 (-25%)

Table 4. Probability of 25%, 50% and 75% interval declines at least once in the period 2001-2050 for the Perth-Peel subpopulation and the total population of Carnaby's cockatoo, for the Reference model and three hypothetical land-use scenarios.

	Perth-Peel subpopulation			**Total population**		
	25%	**50%**	**75%**	**25%**	**50%**	**75%**
Reference model	0.72	0.21	0.00	0.74	0.14	0.00
Scenario models						
Cessation	0.96	0.39	0.01	0.80	0.16	0.00
Mitigation	1.00	0.76	0.03	0.84	0.21	0.00
Maximum Water	1.00	0.97	0.05	0.86	0.26	0.00

Figure 1. The relative impact on extinction risk (Expected Minimum Abundance, EMA) of Carnaby's cockatoo of changes of ± 5% in adult survival, juvenile survival and fecundity.

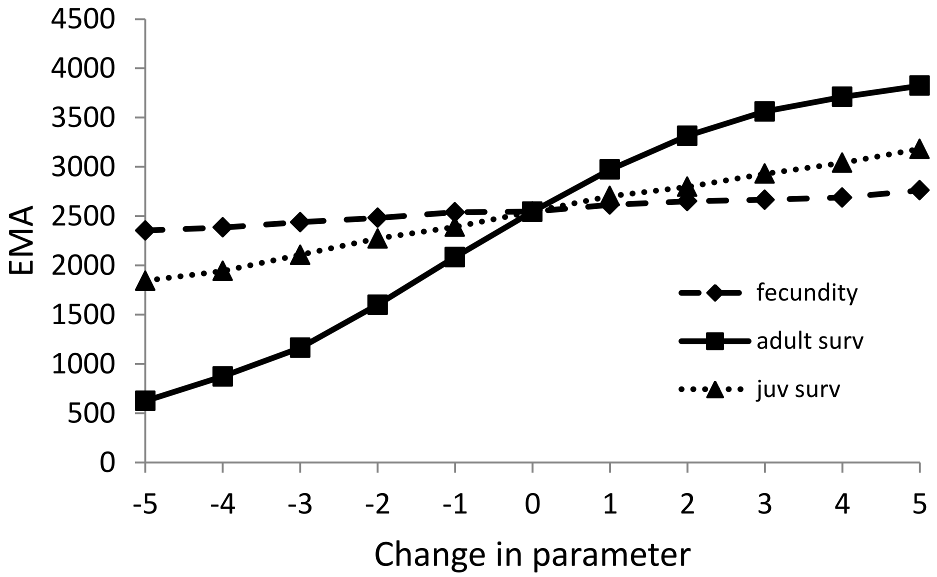
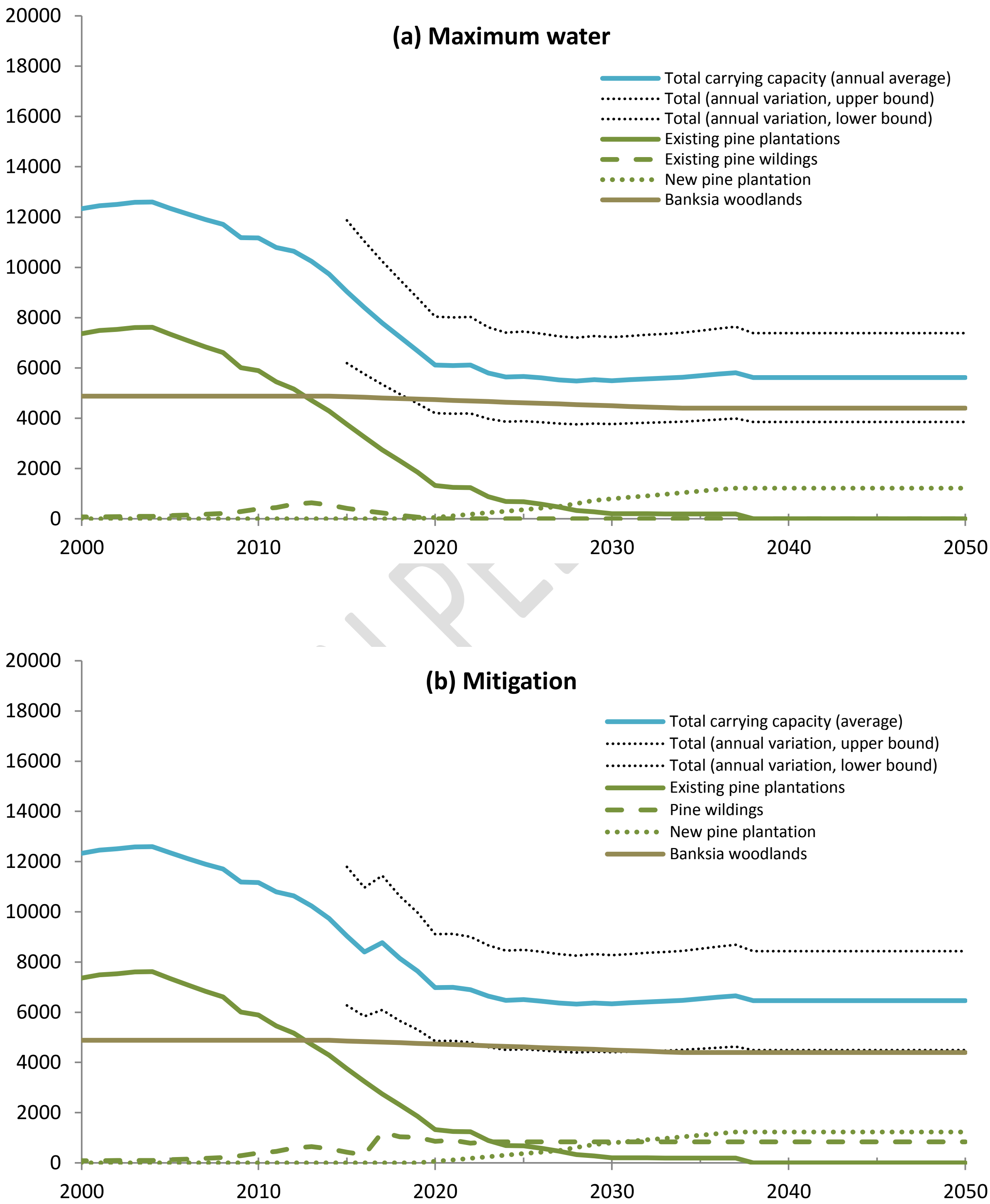
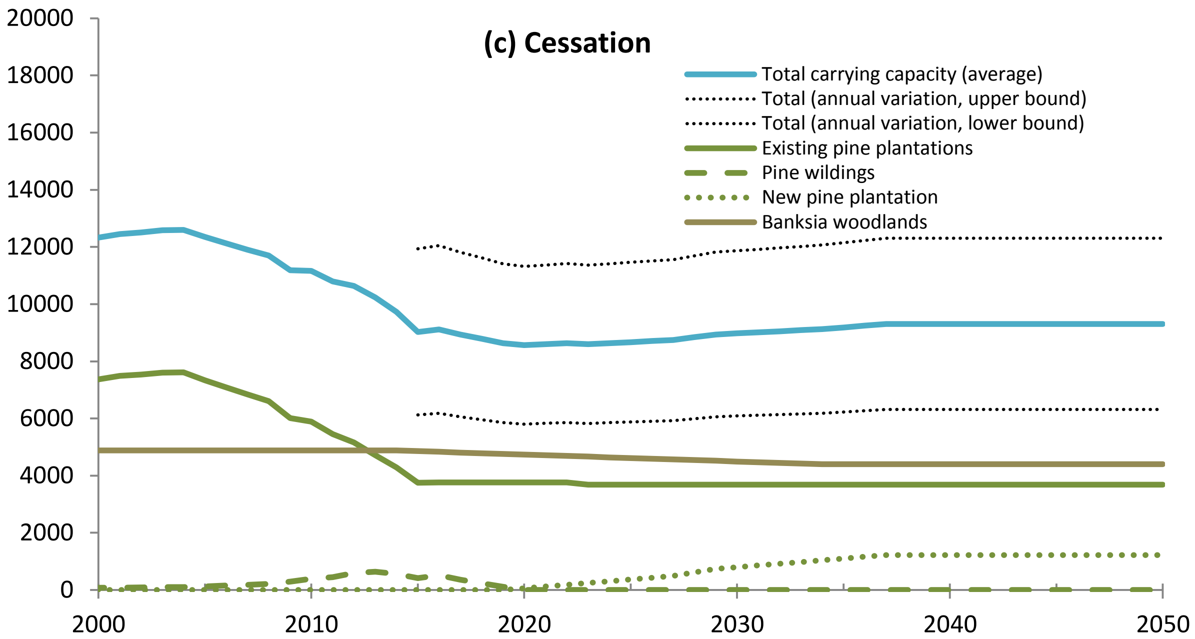


Figure 2. Estimated carrying capacity (K) for Carnaby's cockatoo under three hypothetical land-use scenarios: (a-c) Maximum water, Mitigation and Cessation; and (d) average total carrying capacity for the Reference model and hypothetical land-use scenarios. Total carrying capacity is the sum of the four food components.




(c) Cessation
Total carrying capacity (average)
Total (annual variation, upper bound)
Total (annual variation, lower bound)
Existing pine plantations
Pine wildings
New pine plantation
Banksia woodlands
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
2000
2010
2020
2030
2040
2050

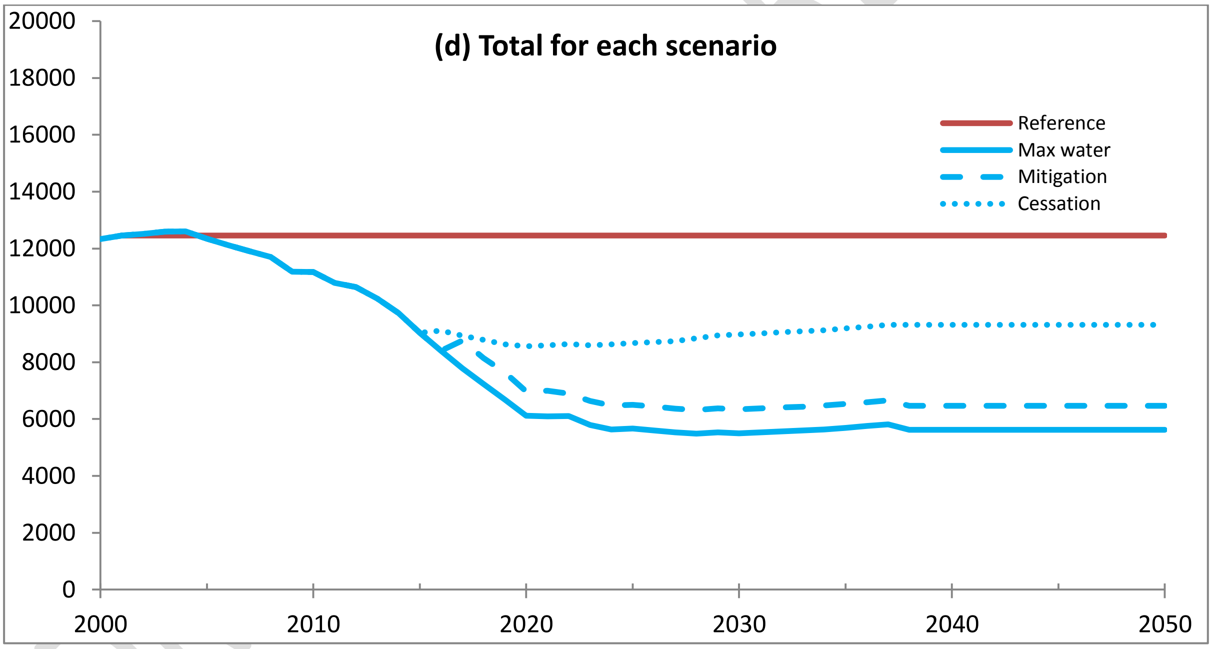
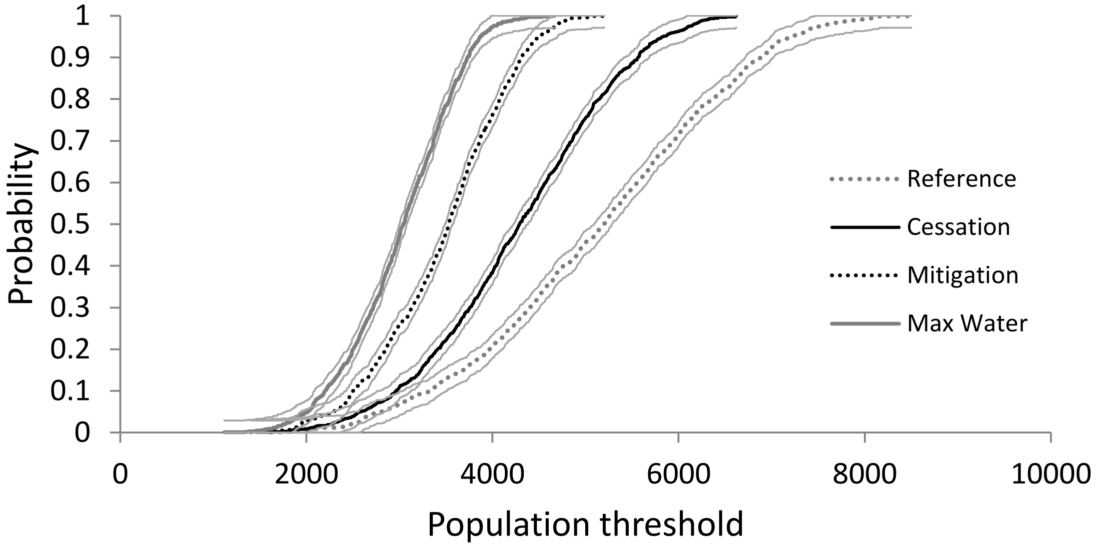

(d) Total for each scenario
Reference
Max water
Mitigation
Cessation
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
2000
2010
2020
2030
2040
2050

Figure 3. Quasi-extinction risk curves for a) the Perth-Peel subpopulation and b) the total population of Carnaby’s Black Cockatoo for the Reference model and three hypothetical land-use scenarios.

a)



b)

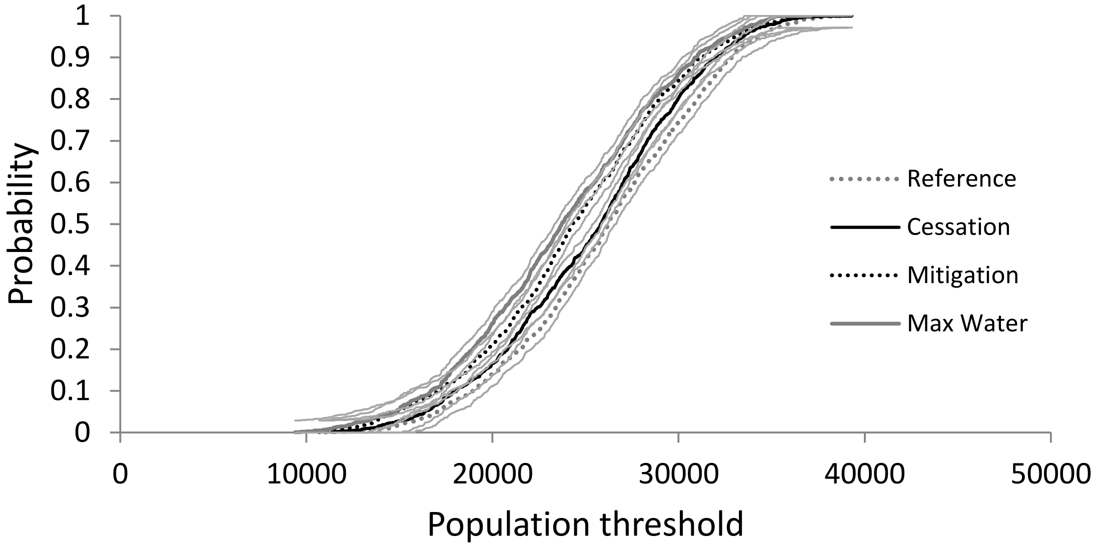
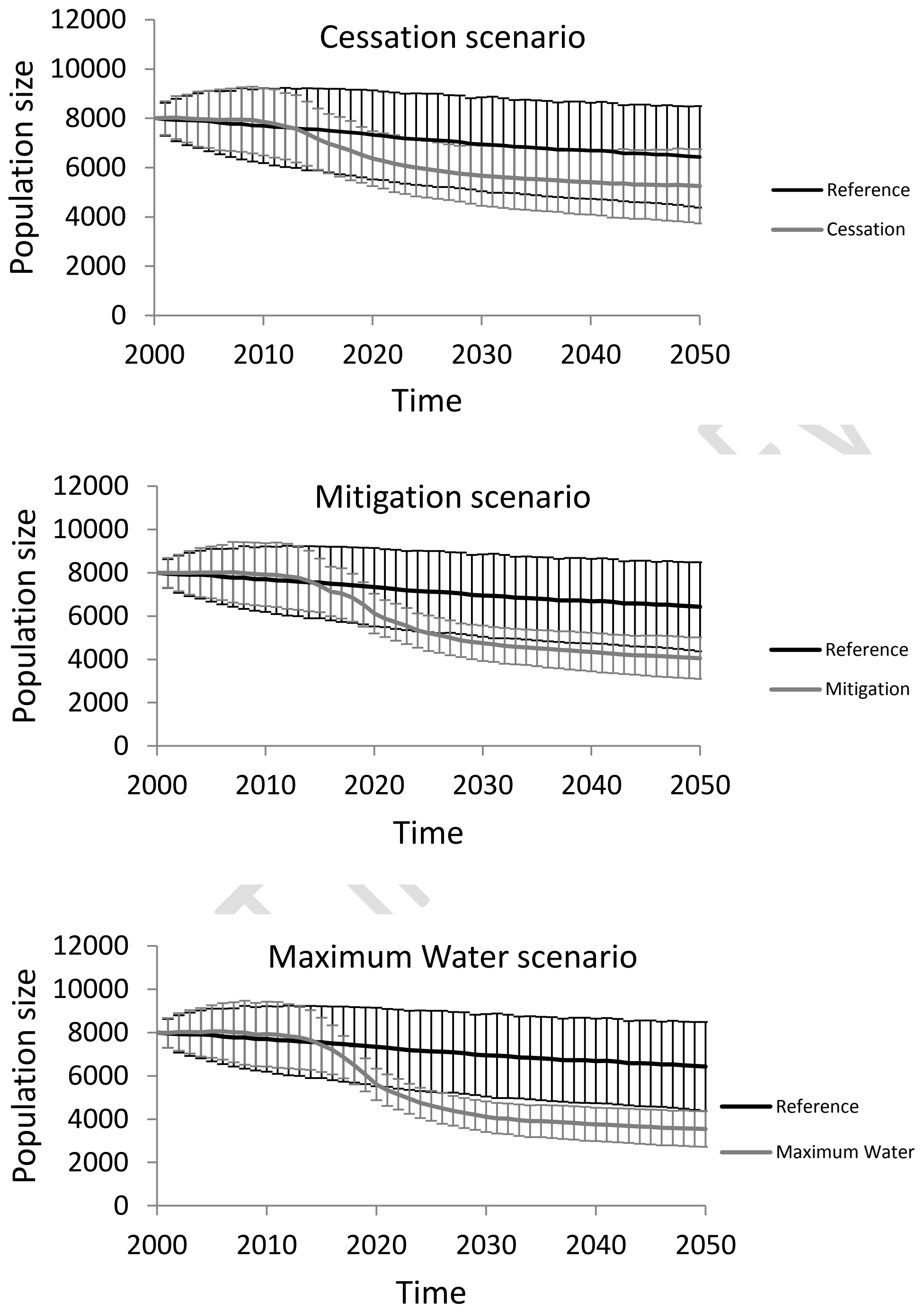


Figure 4. Population trajectory summaries for three hypothetical land-use scenarios over 2001-2050 for the Perth-Peel subpopulation of Carnaby's Black Cockatoo. Values are means together with standard deviations.



Appendix 1

The carrying capacity of *Pinus pinaster* plantations and mixed *Banksia attenuata*/*B. menziesii* woodlands for Carnaby's cockatoo in the Perth-Peel region

The carrying capacity of *Pinus pinaster* plantations and mixed *Banksia attenuata*/*B. menziesii* woodlands in the Perth region were determined from the published estimates of three key values: the annual amount of seed available; the fraction of seed harvested (including the foraging threshold, or giving-up density of food, at which continued foraging is no longer profitable); and the energy content of each food. These values were used to calculate the amount of metabolizable energy available for consumption by cockatoos and equated with their daily energy requirement to determine the carrying capacity of each food source.

1. Seed production in pine plantations and *Banksia* woodlands

Pines. Plantations of *P. pinaster* in the region produce an annual crop of cones resulting from pollination 2 years previously (Hopkins and Butcher, 1994). In its native range, *P. pinaster* trees retain a fraction of unopened cones (serotiny; Tapias et al., 2001) creating a canopy seed store. However, serotiny has not been reported in the *P. pinaster* plantations in the Perth region and seed production is assumed to be annual.

Seed weight. Pine seeds mature and reach full size in March-April in most years – seeds from cones picked in January and February have a lower weight than mature seeds and a very low germination rate, even after the cone is allowed to dry out, whereas most seeds collected in April or later are of normal size and colour and have consistently high germination rates (Hopkins and Butcher, 1994). Data collected at two seed orchards over many years gave an average weight of 0.0502 g for mature seed (Hopkins and Butcher, 1994), very similar to the 0.0505 g value measured by Stock et al. (2013). As Carnaby's cockatoos begin to consume pine seeds in January, before they are full size, the average weight of harvested pine seeds was estimated as 0.050 g.

Seed production. Seed production of *P. pinaster* was tabulated for seed orchards and plantations in the Perth region and for native forests in Spain. The data collected by Stock et al. (2013) was for a single year across stands of varying age (16 – 80 years), whereas the other studies collected data over several years (Table 1). Seed orchards are small stands (~ 10 ha) managed to maximize seed production for the establishment of broad scale timber plantations; management includes weed control, thinning, pruning and the use of fertilizers (Hopkins and Butcher, 1994). Yield data include the Joondalup seed orchard during the six year period when it had reached maximum yields; data for a second seed orchard at Mullaloo were excluded because cockatoos had intermittent impacts on seed yield (Hopkins and Butcher, 1994; Butcher, 2007) but peak production was 28.0 kg/ha. The highest yields (> 25 kg/ha) were in seed orchards and in 70-year-old plantation stands and was substantially more than native stands of the species.

Annual variation in seed production. Seed production was highly variable between years, with production about half or twice the average in low- and high-yielding years, respectively, resulting in four-fold differences between the highest and lowest yields. The four-fold variation in seed production was consistent in both native stands and plantations. We therefore used half and twice the average yield as estimates of the seed production in low- and high-yielding years, respectively. The only available estimate of annual seed production in the pine plantations north of Perth is that of Stock et al. (2013). This value (8.90 kg/ha) lies well within the range of variation exhibited by seed orchards, and so was used as the average seed production of pine plantations for subsequent calculations.

Table 1. Seed production of *Pinus pinaster* in plantations and seed orchards in the Perth region and in native stands.

Location and time of study	Stand age (years)	Average number of seeds/ha	Weight of whole seeds produced (kg/ha)	Range (kg/ha)	Study
Plantation, Gnangara region, Perth 2009/10	Overall	178 000	8.90	4.9 – 26.6	Stock et al. (2013)
	<50 or >70	113 000	5.6	4.9 – 6.4	
	55	282 000	14.1		
	70	533 000	26.6		
Seed orchard, Joondalup, Perth, 1971-1976	8 – 14[1]		13	6.1 – 24.5	Hopkins and Butcher (1994); Butcher (2007)
Native forest, central Spain, 2000 and 2004-2007	Mixed	93 000	4.65	1.9 – 8.0	Juez et al. (2014)
Native forest, central Spain, 2000 and 2004-2007	Mixed	114 730	5.74	2.5 – 8.9	Juez et al. (2014)

[1] Established from cuttings

Banksias. Several studies have reported the amount of canopy-held seeds in native *Banksia* woodlands in the study region. Many *Banksia* species are serotinous and the duration of canopy seed storage varies both between species and geographically within species (Cowling and Lamont, 1985; Cowling et al., 1987). In the Perth region *B. attenuata* stores seed for four or more years, with half of the canopy-held seed crop being from the most recent flowering (Cowling and Lamont, 1985). In contrast, *B. menziesii* sheds almost all seed once mature. However, the canopy-stored seed crop is available for foraging by cockatoos each year and so seed production for these species is treated as annual.

Seed weight. Seed weights of several species were reported by Cowling et al. (1987), Stock et al. (2013) and Johnston (2013). For *B. attenuata*, the estimated seed weight varied slightly between studies and the average was 0.105 g (Table 2).

Seed production. The weight of seeds produced per unit area is greatest for *Banksia sessilis*, *B. attenuata* and *B. prionotes*, with stands of the other species holding < 0.4 kg/ha (Table 3). Both *B. sessilis* and *B. prionotes* have relatively small seeds but a high density of plants and hence a relatively large weight of seeds is produced. For species other than *B. attenuata* and *B. menziesii*, few sites have been assessed and only in a single study (Johnston, 2013).

Due to their wide distribution and relatively high seed yield the mixed stands of *B. attenuata* and *B. menziesii* are the most important native food sources for Carnaby's cockatoo and only these two species are considered further. The seed production values (2.41 and 0.30 kg/ha, respectively) from the two most extensive studies, Johnston (2013) and Valentine et al. (2014), were used in subsequent calculations. Of the other species, *B. sessilis* is produces relatively high seed yields and is likely to be the next most important native food, but the paucity of data prevents its inclusion in this study.

Table 2. Seed weights of various *Banksia* species foraged by Carnaby's cockatoo.

Species	Location and year	Weight of whole seed (g)	Weight of husked seed (g)	Source
B. attenuata	Unspecified	0.1081	0.0800	Stock et al. (2013)
	Northern swan coastal plain, 2010/11	0.101[1]	0.075	Johnston (2013)
	Mt. Adams, northern swan coastal plain, 1983	0.1052		Cowling et al. (1987)
B. menziesii	Northern swan coastal plain, 2010/11		0.053	Johnston (2013)
	Mt. Adams, northern swan coastal plain, 1983	0.0867		Cowling et al. (1987)
B. prionotes	Northern swan coastal plain, 2010/11		0.019	Johnston (2013)
	Mt. Adams, northern swan coastal plain, 1983	0.0198		Cowling et al. (1987)
B. sessilis	Unspecified	0.0068		Stock et al. (2013)
	Northern swan coastal plain, 2010/11		0.007	Johnston (2013)

[1] Calculated from husked weight, assuming a husk fraction of 26% (Table 6)

Annual variation in seed production. All the studies collected data in only a single year (Valentine et al. (2014) conducted sampling over two years, but sampled each site only once), but variation between the various studies provides an upper estimate of inter-annual variation in seed production for *B. attenuata* and *B. menziesii*, which was about 3.5 – 5 fold, respectively. Comparing cone production between the two sampling years of their study, Valentine et al. (2014) found 5-fold variation in in *B. menziesii* but no variation in *B. attenuata*. In line with the similar variation in pine seed production, we therefore used half and twice the annual seed production as estimated values for low- and high-yielding years, respectively. However, the seed bank dynamics of *B. attenuata* mean that annual seed production is only half of the canopy-stored seed (Cowling and Lamont, 1985), so that in low- and high-yielding years the amount of seed available will decrease or increase by approximately 40% and 60%, respectively.

Table 3. Stand and reproductive statistics for various *Banksia* species in the Perth region, Western Australia.

Species	Location and time of study	Number of sites occupied/ sampled	Average number of trees/ha	Average number of cones/tree	Average number of follicles/cone	Average number of intact seeds/follicle	Average number of seeds/ Ha	Average weight of whole seeds kg/ha[1]	Study
B. attenuata	Gnangara region, Perth, 2008 and 2010	44/44	248	6.6	15.10[2]	-	31389[3]	3.30	Valentine et al. (2014)
	Northern swan coastal plain, 2010/11	21/21	338	2.93	11.56[4]	1.27	14539	1.53	Johnston (2013)
	Jandakot region, Perth	4/4	-	4.31	14.67	0.60	11381[5]	1.20	Brundrett, unpub.
	Gnangara region, Perth	3/3	200	11.03	-	-	32387[6]	3.40	Brundrett, unpub.
	Jandakot, Perth		333	6.7					Bamford and Bamford (2004)
	Yardanogo, northern swan coastal plain, 1983	2/2	410	25.4[7]	3.6[4]	0.95	35616	3.74	Cowling et al. (1987)
B. menziesii	Gnangara region, Perth, 2008 and 2010	43/44	187	2.8	6.65[4]	-	3795[8]	0.33	Valentine et al. (2014)
	Northern swan coastal plain, 2010/11	20/21	200	2.32	6.20	1.09	3136	0.27	Johnston (2013)
	Gnangara region, Perth	3/3	-	2.70	-	-	3649[8,9]	0.32	Brundrett, unpub.
	Jandakot, Perth		167	6.5					Bamford and Bamford (2004)
	Yardanogo, northern swan coastal plain, 1983	2/2	100	15.4[7]	2.9[4]	0.67	2992	0.26	Cowling et al. (1987)
B. grandis	Northern swan coastal plain, 2010/11	4/21	10	1.09	56.3	0.57	350	0.03	Johnston (2013)
B ilicifolia	Northern swan coastal plain, 2010/11	8/21	12	44.46	1.3	1.08	749	0.04	Johnston (2013)
B. prionotes	Northern swan coastal plain, 2010/11	3/21	2078	1.23	26.6	0.47	31954	0.63	Johnston (2013)
	Yardanogo, northern swan coastal plain, 1983	2/2	510	7.9	32.2		103494	2.05	Cowling et al. (1987)
B. sessilis	Northern swan coastal plain, 2010/11	8/21	4054	86.74	1.2	1.17	493708	3.36	Johnston (2013)

[1] Whole seed weights from table 2
[2] Values calculated from 27 sites
[3] Assuming 1.27 seed/follicle, based on Johnston (2013)
[4] Includes open follicles
[5] Assuming 300 trees/ha
[6] Assuming 11.56 follicles/cone and 1.27 seed/follicle, based on Johnston (2013)
[7] Includes barren cones.
[8] Assuming 1.09 seed/follicle, based on Johnston (2013).
[9] Assuming 200 trees/ha and 6.20 cones/tree, based on Johnston (2013).

2. Seed harvesting rates

The number of seeds consumed by Carnaby's cockatoo depends upon its ability to effectively access and consume ('harvest') the available seed. Birds will continue to forage until the density of the food source falls to a level where any additional effort in locating the food exceeds the energy reward in finding it – this is the 'giving-up' energy density or foraging threshold at which foraging is no longer profitable. As the seed sources considered here are clustered in cones, two foraging rates are relevant – the fraction of cones foraged, and the fraction of seeds harvested from each foraged cone. We used the former to determine the foraging threshold and the latter to determine the harvest rate.

Foraging thresholds. Stock et al. (2013) recorded the density of cones that remained after Carnaby's cockatoo fed in pine plantations over a 12 month period. This indicated a giving-up density or foraging threshold of approximately 50 cones/ha. Cones contain an average 129 seeds (Stock et al., 2013), giving a threshold of 0.32 kg/ha. In *Banksia* woodlands, Johnston (2013) recorded foraging data for Carnaby's cockatoo feeding over a 12 month period and recorded the average number of cones remaining after foraging (Table 4). The lower estimate of foraging threshold (97 cones/ha for *B. menziesii*) was used for both species.

Harvesting rates. For pines, the entire seed contents of many cones are consumed, but some have only a portion of seeds removed and are then dropped. Saunders (1974) found that 9% of cones were dropped completely uneaten, and a fraction was only partially eaten. Similarly, Perry (1948) reported that 20% of cones were dropped. However, birds may return to consume seeds from previously dropped cones (Perry, 1948; Saunders, 1974; Stock et al., 2013). Thus, the fraction of seeds actually consumed has not been accurately quantified, but assuming that all of the seeds from initially foraged cones and half from dropped cones were consumed gives an estimate of 90%. For *Banksia* species, the fraction of seeds harvested from each cone was determined by Valentine et al. (2014) and Johnston (2013) (Table 4). For *B. attenuata* and *B. menziesii*, the rates of seed harvesting varied between 22 and 40%, respectively, and the average value (32.5%) was used as the harvesting rate. It is worth noting, however, that many cones had open follicles that had released seed prior to foraging by cockatoos. Only 27% and 10%, respectively, of closed follicles were left unforaged (Johnston, 2013) so the harvest rate of seeds from closed follicles may be as high as 73–90%. These foraging threshold and harvest rate figures applied to the available weight of each food determine the total weight of seeds that can be consumed from each food resource (Table 5).

Table 4. Estimated foraging thresholds and harvest rates of *Pinus pinaster* and *Banksia* seeds by Carnaby's cockatoo.

Species	Foraging threshold (cones/ha)	Fraction of follicles foraged/cone (%)	Estimated seed harvest rate/ foraged cone (%)	Source
P. pinaster	50		90	Stock et al. (2013)
B. attenuata	345	22	32.5	Johnston (2013)
		30		Valentine et al. (2014)
B. menziesii	97	40		Johnston (2013)
		38		Valentine et al. (2014)

Table 5. Total weight of seeds available for consumption by Carnaby's cockatoo in *Pinus pinaster* plantations and mixed *Banksia* woodlands.

Source	Average weight of whole seeds produced (kg/ha)	Foraging threshold (kg/ha)	Harvest rate of foraged cones (%)	Total seed consumption (kg/ha)
P. pinaster plantations	8.90	0.32	90	7.72
Mixed *B. attenuata*/ *B. menziesii* woodlands	2.71	0.23	33	0.81

3. Total and metabolizable energy content

Total energy content. The ratio of husk to cotyledon weights and the energy content of seed kernels were determined by Stock et al. (2013) and are reproduced in Table 6.

Table 6. Weights of whole and dehusked seeds of *Pinus pinaster* and *Banksia* spp. and their energy content.

Species	Average weight of whole seed (g)	Husk fraction (%)	Average weight of dehusked seed (g)	Energy content of dehusked seed (kJ/g)
P. pinaster	0.050	60	0.020	24.922
B. attenuata	0.105	26	0.078	17.267
B. menziesii	0.0867	39[1]	0.053	

[1] Calculated by combining data in Cowling et al. (1987) and Johnston (2013)
[2] Assuming energy content equal to that of *B. attenuata*

Metabolizable energy content. There is a metabolic cost of digesting food and each animal species varies in its ability to convert the energy content of a given food item to metabolizable energy (Janzen, 1971). Fibre content is an important determinant of digestibility, as foods with high fibre contents are less digestible resulting in a lower metabolized energy yield. The metabolizable energy content of *P. pinaster* and *Banksia* spp. seeds when fed to Carnaby's cockatoo is unknown, but estimates can be made from comparable data in the literature. For budgerigars fed various commercially-available seeds the metabolized energy was high (88 - 93%; Earle & Clarke, 1991), with consistently high metabolization of fat (87 – 91%) and lower but variable metabolization of protein (72 – 91%, average 81%). As it has high fat and low (4%) fibre content (Stock et al., 2013), similar to commercial parrot food, an estimate of 90% was used for the metabolization rate of *P. pinaster* seed consumed by Carnaby's cockatoo. The higher fibre (26% for *B. attenuata*) and protein content of *Banksia* seeds and relatively low fat content (Stock et al., 2013) indicates that they are less digestible than pine seeds and an estimate of 80% for the metabolization rate was used. Applying these metabolization rates to the total weight of seeds consumed gives the metabolized energy (Table 7).

Table 7. Total energy available to be harvested by Carnaby's cockatoo for *Pinus pinaster* plantations and mixed *Banksia* woodlands.

Source	Weight of seeds available (kg/ha)	Total energy available (MJ/ha)	Metabolizable energy available (MJ/ha)
P. pinaster plantations	7.72	77.0	69.3
Mixed *B. attenuata*/ *B. menziesii* woodlands	0.81	10.1	8.1

4. Total annual energy needs and carrying capacity

Annual energy requirement. The field metabolic rate of Carnaby's cockatoo is estimated to be 0.726 MJ/day (Cooper et al., 2002). To determine the total energy requirements of each bird during the period it forages in the Perth-Peel region, an estimate of the number of days the birds spend in the region is needed. Stock et al. (2013) recorded feeding evidence for 8 months (Jan – Aug) over a 12 month sampling period, giving a residence time of 228 days/yr. However, Finn et al. (2009) state that "[A fraction] of the population might remain in the [Gnangara region] during the non-breeding period, suggesting that between 600-1500 birds might be present from August-December". Similarly, Hopkins and Butcher (1994) found that "Bird feeding on the ripening cones was greatest from May to December continuing throughout the summer on the ripe crop". Johnston (2013) found feeding evidence throughout the year in *Banksia* woodland sites, but this was lowest between October and December. To allow for this, 10% of the Carnaby's cockatoo population was assumed to be resident, giving an average residence time of 242 days per bird. Thus, the total annual energy requirement is 175.5 MJ/bird.

Carrying capacity. The area of each food resource needed to meet this energy need can be determined for from this energy need and the annual seed production from each food resource (Table 8). In a year of average seed yield, plantations of *P. pinaster* have the capacity to support about 8 times the number of birds as mixed *B. attenuata* and *B. menziesii* woodlands.

Table 8. Estimated average carrying capacity of P*inus pinaster* plantations and mixed *Banksia attenuata*/*B. menziesii* woodlands birds supported per hectare in the Perth-Peel region.

Source	Metabolizable energy available (MJ/ha)	Annual energy need (MJ/bird)	Carrying capacity (birds/ha)	Area needed to support 1 bird (ha)
P. pinaster plantations	69.3	175.5	0.395	2.5
Mixed *B. attenuata*/ *B. menziesii* woodlands	8.1	175.5	0.046	21.7

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