Ecology and management of overabundant koala 
(*Phascolarctos cinereus*) populations.

by

Natasha McLean

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of The University of Melbourne

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2003
Koala and Natasha,
on the McLean’s property, Riddells Creek, Victoria, 1978
Declaration

This is to certify that

(i) this thesis comprises only my original work, except where indicated in the preface,

(ii) due acknowledgement has been made in the text to all other material used, and

(iii) this thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies, and appendices.

Natasha McLean

2003
Preface

I collected much of the cross-sectional data used in this thesis while I was employed by Parks Victoria and the Department of Natural Resources and Environment, DNRE (now the Department of Sustainability and Environment, DSE). Kath Handasyde and Roger Martin provided raw data on known-age koalas that were used in Chapters 3, 5, 6 and 7. Ross Williamson provided unpublished data regarding the population size at Snake Island and this data were used in Chapter 8. The Department of Natural Resources and Environment (particularly Peter Menkhorst, Alan Crouch and Merril Halley) provided unpublished data on the numbers of koalas translocated from French Island and Sandy Point between 1985 and 1999.

Michael McCarthy wrote the WinBUGS code for the parameterisation of the model in Chapter 8 and Margaret Donald (The University of Melbourne Statistical Consulting Centre) wrote a preliminary version of the WinBUGS code for the development of the growth curves in Chapter 3.

Kath Handasyde and Michael McCarthy contributed many important recommendations that improved this thesis.
Abstract

Overabundant species may have considerable impacts on their habitat, other species and their own populations, thereby threatening biodiversity. Koalas (*Phascolarctos cinereus*) are overabundant at a number of locations in southeastern Australia due to low mortality and the inability of individuals to emigrate. This has led to the over-browsing of their food resources. Active management is required in order to prevent habitat degradation and the starvation of koalas particularly in populations without *Chlamydia*-infection, a disease that can cause infertility in females. Predictive population modelling is required if we are to understand the dynamics of the overabundant populations and investigate the consequences and effectiveness of different management strategies. Accurate data for the parameters that contribute to population growth, such as age structure, sex ratio, and age-specific schedules of mortality and fecundity, are therefore needed. In this study, the values of these parameters were determined for overabundant koala populations at Snake Island, Framlingham, Mt Eccles and French Island (Victoria). Data from additional populations were used to ascertain some parameters. These data were used to build stage-structured models to predict population growth of one *Chlamydia*-free and one *Chlamydia*-infected koala population.

Parameters that are important in determining population growth often vary with age. Therefore, the age of koalas was determined by examining growth curves based on head length in juveniles and the relationship between chronological age and tooth wear in known-age koalas. Tooth wear rates (up to tooth wear class (TWC) III) did not differ significantly between three koala populations or between male and female koalas. The accuracy of predicting age using growth curves decreased with increasing head length. At head lengths of about 100 mm, the curves allowed age to be calculated within ± two months.

The age structure and sex ratio of a population have major influences on population dynamics. The koala population age structures were highly skewed towards the younger age classes with over 50% (range: females 54-80%; males 64-83%) of koalas in TWC I – III at all sites. The adult sex ratio was significantly female-biased on Snake Island and at Framlingham, male-biased at Mt Eccles in 1999 and at parity at
Mt Eccles in 2001 and on French Island. The population level juvenile sex ratio did not differ significantly from parity at any site.

The habitat condition (degree of defoliation of preferred food trees) and disease status of populations may have a large impact on the body condition of koalas. In turn, the body condition of individuals may affect their mating opportunities, and their conception and weaning rates, and thus population growth rates. Body condition was assessed using body mass, a muscle condition score and a size-body mass (morphometric) index. Koalas were in better body condition when younger, and in populations without *Chlamydia*-infection and at sites with the least defoliation. Body condition was better in reproductive females than non-reproductive females, indicating that females with better body condition have a higher likelihood of breeding.

The timing of sexual maturity, and of births within the year, and the effect of age and condition on the reproductive status of female koalas strongly influence fecundity and population dynamics. At sexual maturity, female koalas had a mean age (and 95% confidence interval) of 24.4 months (23.5 – 25.3), a mean head length of 125 mm (124 – 127) and a mean body mass of 6.6 kg (6.3 – 6.8). Therefore, females were considered sexually mature if they were greater than 6 kg within the current breeding season. Only 7.4% of independent females produced young when they weighed less than 6 kg. The breeding season was more contracted at Framlingham and Mt Eccles (85% and 91% of births, respectively, occurred between December and March) than on Snake and French Islands (where 46% and 53% of births, respectively, were recorded in the same period). Fecundity declined with age at all sites after peaking at TWC II on Snake Island and at Mt Eccles, TWC III at Framlingham and TWC IVA on French Island. Females in good body condition had a greater probability of producing a young than females in poor body condition.

Temporal and spatial variation in fecundity was also assessed. Overall fecundity was higher in the *Chlamydia*-free populations (65.6 – 81.1%) than in the *Chlamydia*-infected populations (32.3 – 38.8%). There was little inter-annual temporal variation in fecundity at all except one population, where this variation was probably due to the severe defoliation of preferred food trees. *Chlamydia*-infected koala populations, such
as those on Snake Island and at Mt Eccles, still have the potential to become overabundant despite having lower fecundity.

Juvenile and adult koala mortality rates were examined by analysing available data from the literature. Patterns of sex and age-specific mortality (or longevity) were examined using a collection of koala skulls. Annual juvenile mortality rates were variable (mean ± one standard error: pouch-young = 18% ± 6.1; back-young = 12% ± 7.6) and estimates of adult mortality rates varied with the method of data collection (from zero deaths in some studies to an annual mortality rate of 39.6%). Koalas exhibited male-biased mortality, a pattern found in other sexually dimorphic mammal species. Longevity appeared to be shorter in koalas from Snake Island compared with koalas from other Victoria localities. Ninety-five percent of the skulls from Snake Island (both males and females) were in TWC I – IVC, while 95% of the skulls from all other populations combined were in TWC I – VI (males) and TWC I – VII (females). The low adult and juvenile mortality rates of koalas probably contribute to the rapid population growth of some populations.

Population growth of female koalas in one *Chlamydia*-infected (Snake Island) and one *Chlamydia*-free (French Island) population was modelled with the population parameters described above. Bayesian techniques were used to fit the parameters to the model, and the population size was predicted in “RAMAS Metapop”. The predicted finite growth rate (λ) was 1.04 on Snake Island and between 1.17 and 1.25 on French Island giving an estimated doubling time of 20 years and 3.2-4.5 years, respectively. Currently, translocation and sterilisation are the two techniques used to manage koala populations. On Snake Island, the implementation of an annual program of sterilisation of about 200 females and translocation of 200 previously sterilised females was predicted to be required in order to reduce the population size to below 100 individuals in eight years. Annual translocation of approximately 140 – 250 females on French Island was predicted to be sufficient to maintain a stable mean population size over ten years. Delay of management actions for three years on French Island was predicted to substantially increase the translocation effort required to return the population to its current size. It is hoped that these models, which predict the outcome of koala population growth given a particular set of parameters and
assumptions, will provide a guide to the future management of overabundant koala populations in Victoria.
Acknowledgements

I would like to thank both of my supervisors, Dr Kath Handasyde and Dr Michael McCarthy. Kath, thank you for your passion, energy, encouragement and support. Kath’s thorough understanding of koala biology and the history of previous research have contributed greatly to my work. Kath’s diligence in wading through earlier drafts of this thesis was invaluable. Mick, thanks for your calm, intelligent, thoughtful and considered approach. Mick’s inspired ideas regarding analysis of data were terrific. His patient explanations of WinBUGS and development of the code for the population growth models greatly improved this thesis. Thank-you.

Koala catching

Much of the data presented in this thesis was collected while working for Parks Victoria and the Department of Natural Resources and Environment (now the Department of Sustainability and Environment). This has resulted in both limitations to the questions asked and the methods used, but also major benefits. Handling over 5500 koalas didn’t just happen by myself. There are many people to thank.

Snake Island (Parks Victoria): Ross Williamson, Steve Voros, Brian Martin, Swampy Thomas, Les Leunig, Johno Stevenson, Keith Couper, Griffo, Wal, and Nick Walton. Ross, thank-you for your support, encouragement and wisdom. Thanks to Peter Menkhorst (DNRE) who started me with koalas on Snake Island in 1997 and again at Framlingham in 1998. Framlingham (DNRE): I would like to thank the Aboriginal people of Framlingham who made me feel very welcome. It was a gift to meet Banjo Clark and spend time with him on his land. Peter Goldstraw and Ray Gilby of the Department of Natural Resources and Environment managed the program. Koala Search, Green Corps, David Middleton and Angela Broeders were integral in the program. Thanks to Steve Knox and his many Green Corps koala catching crews over the years, especially James Adams, Nicole Webb, and Andrew Smith at Framlingham. Mt Eccles National Park (Parks Victoria): Thanks to Geoff Sharrock, ranger-extraordinaire. Thanks Geoff for your patience, care, humour, gossip and most of all, friendship. Thanks to the crew at Mt Eccles including Ian Walker, Kym Schramm, Simone Cordell and all the vets, especially Tracey Bradley, Ann Miller, Phillipa
Mason, Steve Tate, Mike Jeffers and Simon Dean. French Island (Parks Victoria): Thanks to Wayne Hill, Fiona Smith, Scott Coutts, Mick Douglas, Terry Easy and Aaron Leddon who introduced me to the wonders (and mosquitos) of French Island. All the Rangers who volunteered their time to help out on Snake Island, Mt Eccles and French Island provided colour, spirit and fascinating tales. Thanks especially to the Prom for allowing their staff to spend so much time on Snake Island. Koala Conservation Centre on Phillip Island: Ashley Reed, Jon Fallow, Pete Cleary, Dave Rogerson, Neville Johnson, Stuart Murphy and Lisa caught koalas in return for being taught to read teeth and palpitate muscle condition. Thanks Ash for collecting skulls and measuring the head lengths of dead koalas. Thanks to the Phillip Island Nature Park for giving permission for this part of the work to go ahead.

**Skull collecting, measuring and rotting**

Joan Dixon and Lena Frigo of the Museum of Victoria gave me access to measure koala skulls to my hearts content, for which I am most grateful. Morwell Animal Clinic, Warrandyte Vet Clinic, Parks Victoria Rangers at Warrandyte State Park, Phillip Island Koala Conservation Centre, Melbourne Zoological Gardens and Healesville Sanctuary all collected koalas that came their way. Viv Turner and Jo Wedgewood provided space for buckets of rotting, smelly skulls. This work was conducted under Department of Natural Resources and Environment permit numbers 10 000 383, 10 001 021 and 10 001 1 584.

**Unpublished data**

Kath Handasyde and Roger Martin generously gave me access to their vast banks of data on many known-age koalas from the Brisbane Ranges, French Island and Phillip Island. The analysis of this data contributed greatly to this thesis and I am very appreciative. Parks Victoria and the Department of Natural Resources granted permission to use the data in the thesis that I collected while employed during koala translocations. Ross Williamson provided invaluable unpublished data on the current koala population abundance on Snake Island. Peter Menkhorst, Alan Crouch and Merril Halley (Department of Natural Resources and Environment) allowed me access to unpublished koala translocation data from Sandy Point and French Island.
Thanks to all the data collectors who were cursing the paper work at the time. I hope it helps that it was very important to someone in the end.

**Statistics, discussions and technical support**

Mick McCarthy, Mick Keough, Rob Day, Margaret Donald, Helena Bender and Graeme Coulson helped me learn more statistical techniques than I knew existed when I began. I am grateful to the Vertebrate Ecology discussion group and the ARCUE (Australian Research Centre for Urban Ecology) lab group, especially Graeme Coulson, Simon Ward, Susan Campbell, Mark McDonnell, Kirsten Paris, Rodney van der Ree and Terry Coates for stimulating discussions and helping to improve conference presentations. I would also like to thank Garry Jolly-Rogers for IT support when computers crashed, patches were needed and viruses were virulent. Thanks to David Paul for taking the photos of the koala teeth.

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## Meanings of abbreviations used in this thesis

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Meaning</th>
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<tbody>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
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<tr>
<td>ANCOVA</td>
<td>Analysis of covariance</td>
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<td>DFA</td>
<td>Discriminant function analysis</td>
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<td>PVA</td>
<td>Population viability analysis</td>
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<tr>
<td>CI</td>
<td>Confidence interval</td>
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<tr>
<td>CV</td>
<td>Coefficient of variation</td>
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<td>s.d.</td>
<td>Standard deviation</td>
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<td>s.e.</td>
<td>Standard error</td>
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<tr>
<td>d.f.</td>
<td>Degrees of freedom</td>
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<tr>
<td>WinBUGS</td>
<td>Windows Bayesian using Gibbs Sampling (software)</td>
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<tr>
<td>MCMC</td>
<td>Markov chain Monte Carlo</td>
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<tr>
<td>GPS</td>
<td>Global positioning system</td>
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<tr>
<td>TWC(s)</td>
<td>Tooth wear class (es)</td>
</tr>
<tr>
<td>mm</td>
<td>Millimetres</td>
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<tr>
<td>kg</td>
<td>Kilograms</td>
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<td>French Island</td>
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<tr>
<td>PI</td>
<td>Phillip Island</td>
</tr>
<tr>
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<td>Koala Conservation Centre (on Phillip Island)</td>
</tr>
<tr>
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<td>Mt Eccles</td>
</tr>
<tr>
<td>Fram</td>
<td>Framlingham</td>
</tr>
<tr>
<td>BR</td>
<td>Brisbane Ranges</td>
</tr>
<tr>
<td>SP</td>
<td>Sandy Point</td>
</tr>
<tr>
<td>DNRE</td>
<td>Department of Natural Resources and Environment, now Department of Sustainability and Environment (DSE).</td>
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Chapter 1 - Introduction

Many parameters contribute to population growth. Knowledge of these, and how they vary between populations, is important in understanding population ecology and predicting population growth. This is especially important in overabundant populations where knowledge of the effects of variation in these parameters on the population growth rate is important for management. Koalas (*Phascolarctos cinereus*) are overabundant at a number of sites in southeastern Australia. This thesis analyses the population ecology of several Victorian koala populations and synthesises this information through the development of a stage-based population model in order to explore the effectiveness of management options for controlling overabundant koala populations.

In this introduction I briefly review the reasons why species become overabundant, the parameters contributing to population growth, the use of mathematical models to predict population growth and responses to management techniques, and finally, current knowledge of overabundant koala populations. I also provide a short outline of the structure of the thesis.

Overabundant vertebrate species


Overabundant or introduced animal populations may have profound impacts upon other species, their own populations or the ecosystem (Caughley 1981). They may do
this directly via competition or predation (e.g. Komak and Crossland 2000) or indirectly through habitat modification such as consumption or destruction of vegetation (e.g. Fenton et al. 1998) or dispersal of weeds (Cowan and Tyndale-Biscoe 1997, Williams et al. 2000). The brown tree snake (Boiga irregularis), accidentally introduced to Guam in the 1950s (Johnston et al. 2002), was directly linked to the extinction of nine endemic bird, two lizard and one bat species (Fritts and Rodda 1998, Clark and Shivik 2002). Overabundant species may modify habitats by, for example, soil erosion and altering the species composition of vegetation communities (Klein 1981, Hone 1994, Mutze and Cooke 1998). For example, grazing and browsing pressure by overabundant macropodid species has led to a significant reduction in the amount of high quality habitat of endangered species such as the eastern barred bandicoot (Perameles gunnii) and the forty-spotted pardalote (Pardalotus quadragintus) (Coulson 1998). The large earth bumblebee (Bombus terrestris), recently introduced to Tasmania, may displace native anthophiles (nectar and pollen feeders) as well as reduce pollination of native plants and increase pollination of weeds (Hingston et al. 2002).

There are a number of reasons why populations of some species become overabundant. Overabundant species are often species that are introduced into novel environments (introduced species) (e.g. Fritts and Rodda 1998, Simberloff 2003). In the marine environment there has been a long history of introductions, typically through ballast water and hull fouling (Cohen and Carlton 1998, Ruiz et al. 2000, Hayes and Sliwa 2003, Ross et al. 2003). The expansion of such populations is thought to be due to escape from natural predators, parasites and competitors, described as ecological release (Torchin et al. 2003). Alternatively, human disturbance, such as habitat reduction and fragmentation and subsequent exclusion of predators or prevention of emigration, may result in species becoming locally overabundant (Caughley 1981, Klein 1981, Walker 1981).
Understanding life histories and demography for population management

Ricklefs and Wikelski (2002) define life history as a collection of evolved strategies that affect reproductive success and survival directly, and include anatomical, physiological and behavioural adaptations. Life history also includes the phenotypic response to environmental variation (Ricklefs and Wikelski 2002). Life histories are therefore made up of a number of components including size at birth, growth rates or patterns, age and size at sexual maturity, age-specific fecundity and mortality, clutch size and offspring size; these vary widely both within and between species (Cole 1954, Roff 1992, Steams 1992). The three basic assumptions in life history theory are that fitness is maximized, there are constraints and trade-offs that limit the possible set of life history trait combinations and there is sufficient genetic variation to achieve the optimal combination (Steams 1976, Roff 1992). Most of the variation in life histories can be considered to be along a continuum. Fast growth, early age at sexual maturity and a short life span are at one end, and slow growth, older age and greater size at sexual maturity and long life span are at the other (Ricklefs and Wikelski 2002). Such variation results from a trade-off between the risk of obtaining sufficient energy to reproduce against that of dying before reproducing (Steams 1977, Charnov 1993, Sinclair and Krebs 2002). Species that exhibit rapid population expansions in novel or changed environments are typically characterised by early age at sexual maturity in combination with production of many large litters and relatively short longevity (Tyndale-Biscoe 1994). However, species that are slow growing, produce only one young per year and are long-lived such as ungulates, elephants (Loxodonta africana) and koalas are also capable of overabundance (Cumming 1981, Klein 1981, Martin 1997, Jensen 2000).

Knowledge of variation of life history traits is essential for predicting population dynamics (Coulson et al. 2000). It is also important in understanding the causes of decline of threatened taxa (Morrison and Hero 2003) and in management of overabundant taxa (Conover 2001). Clutton-Brock and Coulson (2002) demonstrated the variation in life history traits during periods of changing population growth in ungulates. For instance, they demonstrated that fecundity of red deer decreased with increasing population density (Clutton-Brock and Coulson 2002).
In order to understand and control overabundant populations, accurate data on demographics of individual populations facilitates the development of predictive population models. These allow managers to evaluate strategies to reduce or control populations (Goodloe et al. 2000). The abundance and growth rate of a population ultimately results from the interplay of key demographic parameters: births and immigration minus deaths and emigration. To understand the reasons for variation in population size and growth, it is necessary to investigate variation in these parameters and to examine how they alter with extrinsic factors such as environmental conditions and resulting food availability. These parameters are difficult to measure accurately (Brewer and Gaston 2003). Without knowledge of the population growth rate, populations dynamics and density-dependent compensatory mortality and fecundity (Chambers et al. 1999, Twigg et al. 2000, Saunders et al. 2002), it is difficult to reliably predict the effects of population control techniques on population growth (Ramsey et al. 2002).

A number of factors should be considered when choosing methods for controlling overabundant populations, as outcomes are complex. Management techniques (such as lethal population control) may affect density dependent factors such as fecundity, mortality and the recruitment of young. For example, sterilization of females may cause compensatory effects where fecundity increases in non-treated (fertile) females in species with density dependent fecundity (Chambers et al. 1999). Additionally, the juvenile and adult survival rate may increase with the sterilisation of females (Twigg et al. 2000). Thus, it is important to know demographic rates and the effect of population control techniques upon these.

The effect of management techniques on population dynamics and absolute densities must be monitored to assess the effectiveness of the control technique (Bosch et al. 2000). For example, Guillemette and Brousseau (2001) demonstrated that culling of individual predatory gulls (Larus spp.) directly increased the population growth rate of prey species such as common terns (Stern hirundo). The effect of biological control on population dynamics was tested experimentally by Singleton et al. (1995). The nematode parasite Capillaria hepatica was introduced to populations of house mice (Mus domesticus) and although it initially decreased survival it did not affect breeding
success and with the apparent lack of transmission, it failed to have an appreciable effect on population dynamics (Singleton et al. 1995).

Sinclair and Krebs (2002) emphasized the importance of research into the population growth rate and the factors influencing it before making management recommendations. Sibly et al. (2002) distinguished between three alternative paradigms for investigating the factors that cause variation in population growth rates; the mechanistic, density and demographic paradigms. The mechanistic paradigm considers that the population growth rate is affected by external factors such as food availability, predator abundance and climate (Krebs 1995), while the density paradigm considers only the relationship between population density and population growth rate (Sibly et al. 2002). The demographic paradigm concentrates on the correlation between the population growth rate and population parameters such as age-specific schedules of fecundity and mortality (Sibly and Hone 2002). Krebs (2002) cautioned that the density paradigm should not be used without investigation into the ecological processes leading to the changes in the population parameters, thus leading to use of the mechanistic paradigm.

The use of models to assist in understanding population dynamics

Predictive mathematical models are a powerful tool for understanding how changes in demographic parameters affect the population growth (Saether et al. 1996, de Kroon et al. 2000, Saether and Bakke 2000). For managers, these models assist in the evaluation of the effectiveness of different population management techniques (Pople and Cairns 1995, Barlow et al. 1997, Barlow 2000b). For example, Cortes (1998) used demographic models to demonstrate the constraints imposed by life history traits that limit population growth of a number of shark species and thus the restricted capacity of these to sustain commercial exploitation.

Population viability analysis (PVA) is traditionally used to predict population decline, quantitatively assess the risk of extinction and compare management options for increasing the size of the population (Lindenmayer et al. 1993, Possingham et al. 1993). The methods of PVA can also be used to predict population growth, the probability of a population reaching a level that is considered overabundant and to
compare management options for decreasing the population size (McCarthy 1996, Shea 1998). Retrospective testing of PVA models against population trajectories suggests that such models may make unbiased predictions, although any individual prediction may be inaccurate (Ellner et al. 2002). The predictive ability of PVA models relies on the availability and reliability of the biological data on which it is based (Coulson et al. 2001b, McCarthy et al. 2001).

Overabundant koala populations

Koalas are overabundant at a number of sites in Victoria and South Australia. It has been proposed that a combination of habitat fragmentation and reduction in predators has led to overabundance (Martin 1985c, Phillips 1990, ANZECC 1998). This has led to over browsing and defoliation of preferred food trees, and can potentially result in tree death and koala population decline or extinction (Kershaw 1934, Anonymous 1944, McNally 1957, Martin 1985a, Martin 1997). The effects of tree death on the remaining biological community have not been documented. Thus, koalas have the capacity to impact other wildlife species, their own habitat and other koalas within their own population. Clearly, there is a need to manage overabundant koala populations.

Management of overabundant koala populations has been carried out in Victoria since the 1920s (McNally 1960, Martin 1989) usually by translocating individuals (McNally 1960, Martin 1989, Martin and Handasyde 1990b, ANZECC 1996). Culling of koalas was proposed for the Kangaroo Island koala population but was rejected by the Federal Government due to national and international public opposition (St John 1997, Tyndale-Biscoe 1997). Recently fertility control techniques such as surgical sterilization of males, hormonal sterilization of females (Menkhorst et al. 1998) and immunocontraception in females using porcine zona pellucida and recombinant possum ZP3 (Kitchener et al. 2001) have been trialled in Victoria.

The demographics of koala populations at sites of overabundance are largely unknown. Thus, the effectiveness of the above management techniques in reducing overabundant koala populations is difficult to predict. Martin and Handasyde (1990a) and Martin (1997) calculated population growth rates based on population estimates
and Leslie matrices respectively, for Quail Island, Raymond Island and Sandy Point. Koala population dynamics have been modelled based on demographic parameters at sites of low or medium density by Lunney et al. (2002) and Penn et al. (2000). Thompson (2001) states that predictions for regional populations based on single site studies are flawed due to variation in demographic parameters between populations. For instance, fecundity ranges between 0 and 97% in Victorian koala populations (Martin et al. 1988, Martin and Handasyde 1990a).

The present study aims to understand the specific demographics of koalas at sites where koalas are overabundant and how these parameters vary between populations of overabundant koalas in Victoria. Predictive modelling of population dynamics and combinations of control methods will explore changes in koala populations. This will allow predictions of the effectiveness of management programs. It is only with this knowledge that informed decisions can be made that are critical to the success of management strategies (Bayliss and Choquenot 1998, Goodloe et al. 2000).

The parameters that contribute directly and indirectly to the population dynamics of koalas are explored in separate chapters. Due to the fragmented nature of the habitat, migration is not considered at the sites investigated in this thesis. Characteristics of the study sites, habitat and koala populations are described in Chapter 2. The age of individuals is extremely important in predicting their contribution to population growth. Accordingly, previously established growth curves and tooth wear scales are refined and a more accurate correlation between tooth wear and age is determined (Chapter 3). The structure of each population, including sex ratios and sex-specific age structures, is examined in Chapter 4. The relationship between the body condition of koalas and the degree of defoliation of preferred food trees is explored in Chapter 5. This chapter also examines the relationship between the body condition of koalas and the disease status of the population. Chapters Six and Seven examine aspects of the two major population parameters relevant to this study; fecundity and mortality. Information on changes in fecundity with age in populations with and without disease, and the factors influencing the probability of a female producing a young are discussed in Chapter 6. Mortality rates and relative age-specific mortality patterns are presented in Chapter 7. The final chapter draws together the information from the previous chapters and builds predictive mathematical models of population dynamics.
at two Victorian sites where koalas are overabundant. This chapter discusses the potential growth rates of koala populations and the implications of management techniques aimed at reducing such populations.
Chapter 2 - Study sites, koala population and data collection

Abstract

Characteristics of the study areas, koala populations and data collection methods at seven Victorian sites are described. The sites are divided into the main study sites where each individual koala was caught and measured only once (cross-sectional sampling) and the additional study sites where individuals were caught on multiple occasions over a period of time (longitudinal sampling). The history of population establishment at each site, the degree of defoliation of preferred food trees and the Chlamydia-infection status of the populations are described. The main study sites are Snake Island, Framlingham, Mt Eccles and French Island and the additional study sites are the Koala Conservation Centre (KCC) on Phillip Island, the remainder of Phillip Island, and the Brisbane Ranges. There is no evidence of Chlamydia-infection in the French Island and Framlingham populations, whereas populations on Snake Island, Phillip Island, and at the KCC, Mt Eccles and the Brisbane Ranges are Chlamydia-infected. The degree of defoliation of preferred food trees is severe at Framlingham, medium on Snake Island and at Mt Eccles and light on French Island.

Introduction

To investigate the population dynamics of koalas at Victorian sites where koalas are overabundant, study sites were established on Snake Island and French Island and at Framlingham and Mt Eccles (described as the main study sites) which all have abundant koala populations and evidence of food tree defoliation. Individual koalas were sampled only once (cross-sectional sampling) at these sites in order to collect information on population parameters including fecundity, sex ratio and age structure.

In order to determine some population parameters, information on individuals monitored over time is extremely valuable (longitudinal sampling). Therefore, past records (K. Handasyde and R. Martin, unpublished data) of koalas at the Brisbane Ranges National Park, Phillip Island and French Island were analysed. Previously, part of this data was used to analyse factors affecting reproduction (Handasyde 1986), reproductive hormones (Handasyde et al. 1990), Chlamydia-infection and disease (Obendorf and Handasyde 1990) and growth (size - age) curves (Martin 1985b, Martin and Handasyde 1990a). Additionally, I conducted longitudinal sampling
annually at the Koala Conservation Centre (KCC) on Phillip Island. These sites are described as the additional study sites.

In order to avoid confusion, past records of koalas on Phillip Island (K. Handasyde and R. Martin, unpublished data) are termed "Phillip Island" while those I collected from the KCC on Phillip Island are termed the "Koala Conservation Centre (KCC)". Also, data from the past records of koalas from French Island are termed "French Island (1980 – 1985)" (or "French Island (1982-1983)" for the analysis of seasonal variation in mass in Chapter 3) and the data collected during my study on French Island is simply termed "French Island". The physiography of the study sites and characteristics of the koala populations are described in this chapter. The data collection, including the catching methods and personnel involved, the procedure for collecting data from individual koalas (sampling), and the frequency of sampling (sampling regime), are also reported.

Main study sites

Snake Island

Snake Island (38° 46' S, 146° 32' E) is a 3452 ha uninhabited State Faunal Reserve situated within the Nooramunga Marine and Coastal Park approximately 270 km SSE of Melbourne off the South Gippsland coastline, Victoria. The island is 10 m above sea level at its highest point. The soil consists mostly of sand dunes. The climate is relatively mild (11.2°C - 16.3°C, annual mean minimum and maximum daily temperatures, respectively) with an annual median rainfall of 1100 mm in the South Gippsland coastal area (Bureau of Meteorology, site 085096). The open coastal woodland is primarily manna gum (Eucalyptus viminalis), messmate (E. obliqua), saw banksia (Banksia serrata) and coast banksia (B. integrifolia).

Koalas had not been recorded on Snake Island prior to 1945 when 64 French Island and 69 Phillip Island (30 males, 34 females and 5 young) koalas were released (Flora Fauna and Fisheries Unit Yarram 1993). Additional koalas (numbers not recorded) were released onto Snake Island in 1955, 1963 and 1977 (Department of Conservation and Environment Victoria 1991, Department of Natural Resources and Environment
Victoria 1996). The koala population on Snake Island is Chlamydia-infected (Department of Natural Resources and Environment Victoria 1996).

Defoliation of food trees was recognised in 1990, and in 1991 it was recommended that some koalas be removed from the island (Department of Conservation and Environment Victoria 1991). In 1992, eleven percent of the woodland was severely affected by overbrowsing by koalas and koala densities ranged between 1.6 and 7.6 koalas per hectare in manna gum woodland (Flora Fauna and Fisheries Unit Yarram 1993). In 2002, forty percent of the individual manna gums were dead or sick (exhibiting substantial defoliation) (Table 2.1) (Centre for Environmental Management University of Ballarat 2002) (See Appendix A for conversion of different tree condition assessment techniques). Translocations of koalas from Snake Island began in 1992 when 45 koalas were removed from the Island (Flora Fauna and Fisheries Unit Yarram 1993, Department of Natural Resources and Environment Victoria 1996). Further translocations were conducted in 1994, 1997 and 1999-2002. A recent population survey (2000) estimated the population density at approximately 0.65 ± 0.09 (mean ± s.e.) koalas per hectare with a total population of 1680 ± 220 koalas (Morgan 2000b).

Table 2.1 Manna gum (Eucalyptus viminalis) condition on Snake Island and French Island, and at Mt Eccles and Framlingham. The percentage of individual trees, and the percentage of transects where the average condition of the trees was in dead, sick or healthy tree condition categories. Tree condition categories based on Grimes (1988) and Ingeme et al. (1998) where dead = 0-7, sick = 7.5-10, healthy = 10.5+ in Grimes’ (1988) scale. na: data was not available.

<table>
<thead>
<tr>
<th>Site</th>
<th>% individual trees</th>
<th>% transects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dead</td>
<td>sick</td>
</tr>
<tr>
<td>Snake Is¹</td>
<td>32</td>
<td>8</td>
</tr>
<tr>
<td>Framlingham²</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Mt Eccles³</td>
<td>19</td>
<td>65</td>
</tr>
<tr>
<td>French Is⁴</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>

**Framlingham Forest**

Framlingham Forest (38° 15' S, 142° 12' E) is an 1100 ha area 200 km SW of Melbourne in southwest Victoria. The Kirrae Whurrong Aboriginal Corporation has held the free hold title for the area since 1987. The Hopkins River borders the eastern boundary and the surrounding area consists of cleared farmland with a few isolated eucalypts. The climate is mild (8.3°C – 17.9°C, annual mean minimum and maximum daily temperatures, respectively) with a mean annual rainfall of 903 mm (Bureau of Meteorology, site 090172). The open forest consists of manna gum, messmate and swamp gum (*E. ovata*) with river red gum (*E. camaldulensis*) along the Hopkins River.

Thirty-seven koalas were introduced to Framlingham from French Island in 1970 (Martin 1989). Koalas at Framlingham are *Chlamydia*-free (Timms 2000).

In 1991 the local community recognised that some trees were severely defoliated. There was a severe decline in koala abundance prior to 1998 (N. Martin, pers. comm.). At present, many of the manna and swamp gums have been killed or have a substantially reduced crown foliage density due to over-browsing by koalas. All of the manna gums surveyed were sick or dead at Framlingham in 1998 (Ingeme et al. 1998) (Table 2.1). Additionally, the average condition of swamp gums was in the sick or dead categories in 43% of transects (Ingeme et al. 1998). The 1998 translocation of koalas from Framlingham is the only translocation to date. A survey carried out immediately after the removal of 1006 koalas provided an estimate of population density. The remaining mean population density was approximately 0.58 ± 0.06 koalas per hectare, representing a total population of 675 ± 65 koalas (Morgan 1998).

**Mt Eccles National Park**

Mt Eccles National Park (38° 04' S, 141° 55' E) is a 6123 ha park 260 km SW of Melbourne in southwest Victoria. The soil is of volcanic origin and basalt rocks litter the ground. The climate is mild (7.6°C – 19.0°C, annual mean minimum and maximum daily temperatures, respectively) with a mean annual rainfall of 658 mm (Bureau of Meteorology, site 090173). The majority of the park is open manna
gum/blackwood (*Acacia melanoxylon*) woodland that has a varied age structure resulting from a patchy fire history (Parks Victoria 2000). The vegetation also includes silver wattles (*A. dealbata*), cherry ballarts (*Exocarpus cupressiformis*) and a small stand of messmates. The park is surrounded by cleared farmland; however, large plantations of blue gums (*E. globulus*) were planted on private land along the southern boundary of the park in 2000.

In 1973, 30 koalas were translocated from Phillip Island to Mt Eccles National Park. In 1982, a further 46 koalas from French Island were released into the adjoining Stones Flora and Fauna Reserve (Martin 1989). Members of the local community recall a translocation prior to 1973 but the number of koalas released is unknown. The koala population at Mt Eccles National Park is *Chlamydia*-infected having originated from a combination of Phillip and French Island koalas (Martin 1989, Martin and Handasyde 1999). A small sample of koalas at Mt Eccles tested positive to *Chlamydia* using a “Clearview” testing kit at both ocular and urogenital sites (N. McLean, unpublished data). Clinical signs of disease due to *Chlamydia*-infection in the form of both keratoconjunctivitis (“pink-eye”) and dirty-tail (indicative of urinary tract disease) have been observed at Mt Eccles (N. McLean, unpublished data).

Parks Victoria Rangers first noticed koalas defoliating preferred food trees in 1995 at this site. At Mt Eccles in 2000, 19% of individual manna gums that were sampled were dead (Kelly 2000) (Table 2.1). Translocations of koalas from Mt Eccles began in 1999. The estimated woodland population in October 2000 after the removal of approximately 1450 koalas was 1.41 ± 0.12 koalas per hectare giving a total population size of 8480 ± 720 koalas (Morgan 2000a).

**French Island**

French Island (38° 20’ S, 145° 21’ E) is a 17410 ha area of private land and national park situated in Western Port, SSE of Melbourne. The island is 98 m above sea level at its highest point (Parks Victoria 1998). The soil is mostly sandy with small areas of clay (Land Conservation Centre 1994) and the associated low nutrient concentration in the soil affects the growth and form of the eucalypts (Lewis 1934). The climate is similar to that of Phillip Island where the annual mean minimum and maximum daily
temperatures are 10.3°C – 18.8°C respectively, and the mean annual rainfall is 764.5 mm (Bureau of Meteorology, site 086025). The eucalypts include manna gum, swamp gum, messmate and narrow-leaved peppermint (*E. radiata*) (McNally 1957). The vegetation also includes tea-tree (*Laevigatum juniperinum*), austral bracken (*Pteridium esculentum*) and large areas of heathland interspersed with isolated eucalypts (McNally 1957, Mitchell 1990c).

Koalas were introduced to French Island in the 1890s, probably from Corinella on the eastern side of Western Port (McNally 1957). Koalas on French Island are *Chlamydia*-free (McColl *et al.* 1984, Martin *et al.* 1988, Timms 2000). Local residents noted defoliation of preferred food trees in the 1920s (McNally 1957). While most of the manna gums on French Island were recorded as healthy in 2003 (Centre for Environmental Management University of Ballarat 2003) (Table 2.1), there are numerous areas where heavy defoliation is evident (K. Handasyde and N. McLean, pers. obs.). Also, 19% of the swamp gum was in the sick or dead categories (Centre for Environmental Management University of Ballarat 2003) (Table 2.1). Frequent translocations of koalas from the island have occurred since 1923 (McNally 1957, Wameke 1978, Martin 1989). The density of koalas at Redbill Creek, a 9.0 ha area of manna gum woodland, ranged between 0.7 and 6.2 koalas per ha in the early 1980s (Mitchell and Martin 1990). During the present study, koalas were caught from the national park and from remnant manna gum patches on private property and along roadsides.

**Additional study sites**

**Brisbane Ranges National Park**

The Brisbane Ranges National Park (37° 55’ S, 144° 20’ E) is a 7718 ha park, approximately 70 km west of Melbourne. The highest elevation within the park is 440 m (Parks Victoria 1997). The shallow soil is generally of low fertility on a base of sandstone, slates and shales (Trigg and Trigg 2000). The climate is mild (7.7°C – 17.1°C, annual mean minimum and maximum daily temperatures, respectively) with a mean annual rainfall of 691 mm (Bureau of Meteorology, site 087021). The forest
consists primarily of manna gum, swamp gum, messmate, narrow-leaved peppermint, red stringybark (*E. macrorhyncha*), red box (*E. polyanthemos*), silver wattle and silver banksia (*Banksia marginata*) (Hindell *et al.* 1985, Hindell and Lee 1987).

Koalas were introduced from French, Phillip and Quail Island (Western Port) on numerous occasions including 1944, 1945, 1957 and 1977 (Parks Victoria 1997). The koala population at the Brisbane Ranges is *Chlamydia*-infected (Handasyde 1986).

Large-scale defoliation has not been identified at the Brisbane Ranges (C. Worrall, pers. comm.) although heavy defoliation of manna gums occurs locally in small areas (K. Handasyde, pers. comm.). Translocation of koalas from the Brisbane Ranges has not taken place. The population was estimated at approximately 0.7 - 1.6 koalas/ha in the early 1980s (Hindell 1984).

**Phillip Island**

Phillip Island (38° 28’ S, 145° 44’ E) is a 10105 ha area situated in Western Port, SSE of Melbourne. The island predominantly consists of cleared land for agriculture and housing, but koala habitat persists as remnant vegetation on farmland, roadside reserves and specific koala reserves (150 ha) (Martin 1981). The soils are rich red friable loams, dark brown clays or yellow soils with unconsolidated dunes along the Bass Coast (Seddon 1975, Land Conservation Centre 1994). The climate is cool and wet in winter and relatively hot and dry in summer but temperatures are moderated by the island’s proximity to the ocean (10.3°C – 18.8°C, annual mean minimum and maximum daily temperatures, respectively) (Seddon 1975). The mean annual rainfall is 764.5 mm (Bureau of Meteorology, site 086025). The Oswin Roberts Reserve (77 ha) consists of manna gum, swamp gum and blue gum (Martin 1981, Hindell *et al.* 1985).

Koalas were introduced to Phillip Island in the 1870s (Lewis 1954, Martin and Handasyde 1990a). The koala population on Phillip Island is *Chlamydia*-infected (Handasyde 1986).
The koala population on Phillip Island initially increased and translocations were required to control the population growth (Lewis 1954). Over 3000 koalas were relocated from Phillip Island prior to 1978 (Martin 1989). The density in the Oswin Roberts Reserve in 1980 was 3.6 to 5.3 koalas per ha (Handasyde 1986). Koalas are also present at the Koala Conservation Centre (described below). The Phillip Island koala population has declined over the past twenty years (Every 1986, Backhouse and Crouch 1990), and thus, large scale defoliation of preferred food trees is no longer evident on Phillip Island.

**Koala Conservation Centre (KCC)**

The Koala Conservation Centre (38° 28' S, 145° 44' E) on Phillip Island is a 22.5 ha area enclosed within a koala proof fence and is situated in the Phillip Island Nature Park (Reed 1999). The overstorey is a combination of mature manna, swamp and blue gums and younger eucalypts of these species planted as part of a revegetation program.

The KCC was originally stocked in 1991 with seven koalas from South Gippsland. Additional koalas were added later from the Brisbane Ranges, Snake Island and the Strathbogie Ranges. A few koalas have also entered the KCC from the wild Phillip Island koala population. All koalas are tagged and most are of known-age because they were captured when they were less than 14 months of age and their head length was less than 120 mm, allowing their age to be calculated from the growth curves detailed in Chapter 3. The KCC koala population is *Chlamydia*-infected (K. Handasyde, unpublished data).

There are two distinct areas within the KCC. The “free-range area” presently has 19 koalas that are effectively wild as they roam freely within this area. The “close viewing area” has an area of approximately 0.2 ha with raised board-walks for tourists. The five koalas (one male and four females) in the close viewing area are provided with food from a nearby plantation. The koalas in the close viewing area were excluded from analysis of age at sexual maturity as they may have had a different social environment compared with wild koalas.
Koala capture and data collection

On Snake and French Islands and at Framlingham and Mt Eccles I sampled koalas during translocation programs. These programs were conducted by Parks Victoria and the Department of Natural Resources and Environment (DNRE), to reduce over population and relieve browse pressure on koala food trees. At the Koala Conservation Centre I sampled koalas caught by Phillip Island Nature Park staff. Past records on koalas (1992 – 1996, K. Handasyde, R. Martin and A. Reed, unpublished data) from this site are incorporated in the analysis. At the Brisbane Ranges, Phillip Island, and French Island (1980 – 1985) koalas were caught and sampled by Kath Handasyde and Roger Martin as part of other studies (Martin 1985b, Handasyde 1986, Handasyde et al. 1990, Martin and Handasyde 1990a, Obendorf and Handasyde 1990).

Koalas were captured using a noose and an extendable pole (see Martin 1989). The catcher (from the ground or after climbing the tree) placed a rope noose (with a minimum diameter to prevent strangulation) over the head of the koala using an extendable aluminium or fibreglass pole. Holding the rope taught, the catcher waved a flag (a piece of cloth or canvas) above the koala’s head to encourage it to descend the tree. The rope was used to prevent the koala from climbing back up the tree. Additional people on the ground assisted in catching the koala by waving flags on extendable poles above the head of the koala when the koala was within reach. Once on the ground, the koala was immediately placed in a hessian bag. Koalas were then placed in wooden crates with slatted sides.

“Sampling” is the data collected from each koala. The tree species from which the koala was caught and its location were recorded (using a GPS (global positioning system), previously established tree number or relative to the nearest track). Koalas were weighed to the nearest 100 g using 25 kg scales. Head length was measured (to the nearest mm) from the anterior of the nose to the posterior margin of the crest formed between the parietal and supraoccipital bones (i.e. the posterior of the skull) using vernier or spring callipers. The sex and tooth wear class (TWC) (Martin 1981) of all animals were recorded. Details of the tooth wear class criteria are provided in Chapter 3. External clinical signs of Chlamydia-infection, including
keratoconjunctivitis and dirty tail, were noted if present. Internal signs of Chlamydia-infection including adhesions and/or cysts in or adjacent to the reproductive system (reproductive tract lesions) were recorded for female koalas on Snake Island and at Mt Eccles in some years during surgical sterilisation procedures conducted by Parks Victoria. Body condition was assessed (on Snake Island and French Island and at Framlingham and Mt Eccles) using the morphometric (“hybrid”) and muscle condition indices (see Chapter 5). Koalas were tagged using numbered, coloured plastic sheep tags (Leader Products). Female koalas were checked for the presence of young and the condition of the pouch and teats was recorded. Sexually mature females were judged to be in one of four reproductive categories:

Non-reproductive females
- Sexually mature female with no young: no young present, no evidence of recent lactation (both teats small).

Reproductive females
- Female with pouch-young: young still in the pouch.
- Female with back-young/dependent-young: young present on the mother’s back, or in the same or adjacent tree. Mother has elongated teat and may be lactating.
- Female with elongated teat: no young present but evidence of breeding as one teat is elongated and may be lactating.

The sex and head length of accompanying young were recorded. Young were weighed separately if sufficiently large enough to be removed from the pouch. Large young were tattooed or ear tagged.

**Sampling regime**

On Snake and French Islands and at Framlingham and Mt Eccles, sampling was cross-sectional. Attempts were made to catch all koalas located at these sites although the third sample from Snake Island (2000) targeted females. The timing of sampling and the number of koalas sampled at each study site is provided in Table 2.2. At the Brisbane Ranges, Phillip Island, French Island (1980 – 1985) and the Koala Conservation Centre, koalas were sampled longitudinally. At the Brisbane Ranges,
Phillip Island and French Island (1980 – 1985) koalas had been fitted with radio-collars to allow individually known koalas to be located and caught monthly for up to two years. Some of these individuals were caught irregularly between 1979 and 1985 (Table 2.3). Koalas at the Koala Conservation Centre were usually caught and sampled in November each year (1992 – 2002); however, sampling was more frequent in the earlier years.

Table 2.2 The timing of sampling and the number of koalas sampled at the main study sites.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Date of sampling</th>
<th># koalas sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snake Island</td>
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<td>676</td>
</tr>
<tr>
<td>Snake Island</td>
<td>13th October – 9th December 1999</td>
<td>503</td>
</tr>
<tr>
<td>Snake Island</td>
<td>9th October – 8th December 2000</td>
<td>350*</td>
</tr>
<tr>
<td>Snake Island</td>
<td>14th October – 20th October 2001</td>
<td>123</td>
</tr>
<tr>
<td>Framlingham</td>
<td>2nd April – 3rd July 1998</td>
<td>820</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>9th March – 3rd June 1999</td>
<td>1006</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>23rd February – 1st June 2001</td>
<td>1329</td>
</tr>
<tr>
<td>French Island</td>
<td>16th October – 1st November 2000</td>
<td>146</td>
</tr>
<tr>
<td>French Island</td>
<td>1st October – 9th October 2001</td>
<td>137</td>
</tr>
</tbody>
</table>

*Females were targeted during this sampling period and thus, as the sample is biased, it is excluded from most analyses.

Table 2.3 The timing of sampling at the additional study sites.

<table>
<thead>
<tr>
<th>Study site</th>
<th>Catching frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monthly</td>
<td>Irregular</td>
</tr>
</tbody>
</table>
Chapter 3 - Age determination and growth of Victorian koalas

Abstract

Parameters that are important in determining population dynamics, such as fecundity and mortality, often vary with age. In this chapter, the age of Victorian koalas was examined using two methods: the relationship between chronological age and tooth wear, and growth curves based on head length. Aspects of growth, such as size and age at independence from the mother and at physical maturity, were also determined. Tooth wear rates (up to tooth wear class (TWC) III) did not differ significantly between three koala populations or between males and females. The variation in the age of individuals in TWCs increased with age. Growth curves were established for juvenile koalas with a head length of up to 120 mm. The accuracy of predicting age using growth curves decreased with increasing head length such that at head lengths of about 100 mm, the curves allowed age to be calculated within ± two months. Physical maturity, measured by body mass, was quite variable between individuals and occurred between TWC IVA and IVB. Physical maturity as measured by head length was far less variable. The refined methods for the estimation of the age of koalas developed in this study permit the calculation of accurate age-specific fecundity and mortality schedules.

Introduction

Information on the age of individuals and the population age distribution is essential in ecological, behavioural, reproductive and taxonomical studies (Morris 1970). Assessment of age is often important for predicting population growth when fecundity and mortality rates vary with the age of individuals (Garrott 1991, Norton and Fairall 1991, Gaillard et al. 2000, Caswell 2001), as is often the case in vertebrates (Nol and Smith 1987, Cameron et al. 2000, Monson et al. 2000, Orell and Belda 2002, Shi et al. 2002, Cichon 2003). Such data are used in a variety of population studies, for instance, the development of fisheries management plans (Cortes 1998, Gillanders et al. 1999, Brooks 2002, Newman 2002), conservation of rare and endangered species (e.g. Armbruster and Lande 1993) and control of pest populations (e.g. Goodloe et al. 2000, Caswell 2001).

Despite the importance of accurate techniques for determining the age of individuals, these are notoriously difficult to establish for wild animal populations. Many
techniques are used to estimate the age of individuals that have not been monitored since birth (Morris 1972). These methods may be as simple as morphometric measurements (and comparison with growth curves while the individual is still growing) or may require sophisticated histological preparation as with annuli counting in species exhibiting periodic growth (Morris 1972, Campana and Neilson 1985). Different techniques may be more appropriate for determining age in different age classes and taxa. Methods of determining age, which are often indirect, should be validated against specimens of known-age (Morris 1972, Officer et al. 1996, Fowler and Short 1998, Gee et al. 2002) and the assumptions of the techniques should be validated, including measures of accuracy (Garrott 1991, Kimura et al. 1992, Measey 2001, Scroggie 2001).

Determining the age of adults

In species with determinate growth, characteristics other than size must be used to estimate age. These characteristics often include annual marks or wear on hard body structures such as bone, horns or teeth (Morris 1972, Campana and Neilson 1985). Many features of bone have been used to determine age including horn growth, size and shape (Caughley 1966, Spinage 1967, Norton and Fairall 1991, Bender and Spencer 1999), bone density (Guglielmini et al. 2002), the degree of fusion of the epiphysial plates (Kingsmill 1963, DiGiancamillo et al. 1998), annual rings and mass of otoliths (reviewed by Campana and Neilson 1985, Fowler and Short 1998, Newman 2002, Choat et al. 2003) and skeletochronology (Zug et al. 1997, Driscoll 1999, Reaser 2000, Olgun et al. 2001, Scroggie 2001). Additionally, annuli or growth rings on shells and scales and growth increments in vertebrae have been used to determine age (Officer et al. 1996, Officer et al. 1997, Gillanders et al. 1999, Shepherd et al. 2000, Millstein and O'Clair 2001, Simpfendorfer et al. 2002). Due to the need for access to bone to determine the age of individuals, these techniques are usually unsuitable for determining the age of live mammals.

Eye lens mass is another body characteristic that has been used with varying degrees of success to determine the age of individuals (Hall-Martin 1976, Catling et al. 1991, Kramer et al. 1999). As this is a destructive technique, it is also of little use in determining the age of live individuals.
Dental characteristics have been used extensively to estimate the age of mammals (Morris 1978). These include, molar progression (accelerated physiological mesial shift) (Hanks 1972, Sanson and Miller 1979, Lentle et al. 2003), tooth (incisor and molar) eruption (Hall-Martin 1976, Garrott 1991, Delaney and Marsh 1995) and the relative tooth pulp cavity to tooth width ratio (Landon et al. 1998). The latter technique may only be useful to separate juveniles and adults (Knowlton and Whittemore 2001). The most accurate method of determining age using dental characteristics is counting cementum lines (Hamlin et al. 2000, Guglielmini et al. 2002), although the technique is not without limitations as the lines are sometimes indistinct, differences occur in estimates between observers (Norton and Fairall 1991) and the lines may not develop in geographic areas without seasonal changes (Terai et al. 1998).

Cementum lines and the relative size of the tooth pulp cavity are often used in animals from culled or hunted samples where teeth are readily available. In addition, a tooth can be removed and sectioned from a live carnivore (e.g. Troy et al. 1999, Bromley and Gese 2001) but this is not appropriate for herbivorous/folivorous animals (Festa-Bianchet et al. 2002). Nelson (2002) provided evidence that extraction of the incisorform canine tooth does not increase mortality in white-tailed deer (Odocoileus virginianus); however, Clutton-Brock and Albon (1982) found rapid decline in body condition in red deer that had damaged teeth. Thus, the risks associated with reduced condition, survivorship and fecundity would have to be assessed in each species where tooth extraction was proposed as a means of determining age.

In some taxa, instead of removal of teeth, patterns of erosion (tooth wear) through the enamel to the dentine and of the dentine itself are used to allocate live animals into age classes (Martin 1981, Clarke et al. 1992, Harris et al. 1992, Hartman 1995, Landon et al. 1998). However, tooth wear rates may be affected by damage to teeth and jaws, disease, diet, and other regional differences in environmental factors (Scarff et al. 1998, Gipson et al. 2000). Biases in observation of wear may also occur (Garrott 1991). Tooth wear is not a valid technique in species that have continuously growing teeth, such as wombats (Vombatus ursinus) (Triggs 1988).
Tooth wear in koalas

The dentition of koalas follows the standard diprotodont pattern of three incisors, one reduced canine, one premolar and four molars in the upper (adult) jaw (Strahan 1978). Adult dentition erupts by approximately 18 months of age (Martin 1981, Blanshard 1990). The morphology of koala molars has been described by Lanyon and Sanson (1986b, 1986a).

Tooth wear has been the predominant method used to determine the age of koalas. Tooth wear scales for koalas have been developed by Martin (1981), Lanyon and Sanson (1986b) and Gordon (1991). Martin’s (1981) tooth wear class (TWC) scale is a seven-point scale based on the degree of wear on the right premolar of the upper jaw. Martin’s (1981) scale has been expanded at TWC IV (IVA, IVB and IVC) to provide a nine-point scale (R. Martin, pers. comm.) that has been widely used to classify koalas (Brown et al. 1984, Mitchell and Martin 1990, Hirst et al. 1992, Canfield and Spencer 1993, Krockenberger 1993). The resolution of Martin’s scale was increased by Lanyon and Sanson (1986b) who included a description of each molar tooth to form a composite score. This refined scale has not been used extensively in the field, probably due to the detailed description required for each molar tooth and the difficulties of assessing this in live animals (Gordon 1991). Gordon (1991) developed a 10-point tooth wear scale to classify koalas into age groups. Gordon’s scale has been used widely in New South Wales and Queensland (White and Kunst 1990, White and Timms 1994, Dique et al. 2003b).

Little is known regarding the relationship between tooth wear and chronological age in koalas. Young et al. (1996) used the skulls from 13 known-age, captive-raised koalas from Queensland to estimate the relationship of age to tooth wear but concluded that a much larger sample would be required to accurately estimate this relationship. It is possible that tooth wear rates differ between populations but Martin (1981) predicted that between population variation in wear rates would be small and Gordon (1991) found no difference in wear rates between two sites or between koalas with varying diets.
Determining age in juveniles: growth curves

Growth curves relate the size of an individual to its age over time (Kaufmann 1981) and may be represented by plotting age against size, where size may be measured by volume, mass, height, length or girth. Mammalian growth usually follows a sigmoidal curve (Leberg et al. 1989) that can be described by a logistic or Gompertz equation (Kaufmann 1981, Zullinger et al. 1984, Lee and Cockburn 1985, Cockburn and Johnson 1988). There is an initial (usually short) period of slow growth, followed by a period of fast growth, and finally a decrease in growth rate as the individual approaches physical maturity (Russell 1989). Use of growth curves allows comparisons between individuals (Vollestad and Quinn 2003), between litters (Kerle 1984), between individuals within litters (Smith 1979b, Soderquist 1993), and between the sexes (Smith 1979b, Poole et al. 1985, Read et al. 1993). Examination of growth curves enables temporal and spatial (regional) contrasts (Webb et al. 1983, Wood et al. 1983, Boutin and Larsen 1993), provides information on variation of individuals from “typical” growth rates (Hanks 1981, Cockburn and Johnson 1988) and also allows comparisons of populations that have experienced different environmental conditions (O'Donoghue and Krebs 1992).

Most marsupial growth curves have been derived from captive animals, as the date of birth can be accurately ascertained and the young can be measured frequently and regularly (Bach 1998). Growth curves derived from captive marsupials accurately described growth in wild animals for many marsupial species (Shield and Woolley 1961, Sadleir 1963, Delaney and De'ath 1990, Soderquist 1993, Atramentowicz 1995, Jones 2001, Rhind and Bradley 2002). However, it is uncertain whether growth curves from captive animals can be applied to all species in the wild that may have experienced different environmental conditions (Sadleir 1963, Inns 1982, Poole et al. 1982a, Rose and McCartney 1982, Taylor and Rose 1987, Delaney and De'ath 1990).

Many koala researchers have plotted body measurements against age but not calculated an equation to describe these relationships (Smith 1979a, Thompson 1987, Blanshard 1990, 1994, O'Callaghan 1996, Bach 1998, Woods 1999, reviewed by Jackson 2003). Growth equations have been calculated for koalas from Queensland (Krockenberger 1996) and Victoria (Martin 1985b, Lee and Martin 1988, Martin and
Handasyde 1990a). Martin and Handasyde (1990a) calculated quadratic curves for head length against age but the degree of error in different parts of the curve was not reported and they did not account for between-animal variation.

Stages in growth

Two important stages are recognised in the growth of mammal species that have determinate growth. The first is the age and size at which individuals become independent from their parent(s). In marsupials, dependent animals are juveniles such as pouch- and back-young or young-at-foot; that is, when they are physiologically and behaviourally dependent on the mother (or parents). Independent is defined as not suckling or associated with the mother (and are therefore weaned), and includes both sub-adults and adults. Weaning takes place at approximately one year of age in koalas although there is much variation between individuals (Mitchell 1990c, Blanshard 1994) but little difference between male and female young (Mitchell 1990c). Blanshard (1994) and Mitchell (1990c) determined the age of koalas at independence using known-age juveniles and juveniles where their age was calculated from growth equations. However, the age of juveniles is often unknown and use of growth equations to estimate age involves some error. Thus, it is important to determine the median size (measured as head length) at which juvenile koalas become independent from their mothers. This has not been previously reported for koalas.

The second important stage of growth is the age and size at which physical maturity occurs. Physical maturation is the mass (or size) at which the increase in mass over time is close to zero, that is, cessation of growth. At physical maturation, individuals can allocate all of their energy to maintenance, storage and reproduction rather than growth. Mammals often reach physical maturity after sexual maturity (Charnov 1982, Clutton-Brock 1991, Stamps 1993). Thus, in the time period between sexual and physical maturity there is often a trade-off between growth and reproduction. Handasyde and Martin (1988) considered that female koalas under 3 years and males under 4 years would probably not have attained adult body mass. Eberhard (1972) proposed that physical maturity would occur during or after the fourth year in females and the fifth year in males. Martin and Handasyde (1990a) found the average asymptotic mass of koalas on French Island to be 8.3 kg for females and 11.3 kg for
males. Given these inconsistencies in estimates of physical maturity, it is valuable to determine an accurate estimate of age, mass and head length at physical maturity and describe the variation between individuals.

Aims
The major aims of this chapter are first to refine Martin’s (1981) tooth wear scale used to determine the age of sub-adult and adult koalas and provide a scale that allows the conversion of TWCs to chronological age. Second, to provide an analysis of the growth rates of male and female juvenile (less than 120 mm head length) Victorian koalas from two separate populations. Additionally, two important stages of growth, independence from the mother and physical maturity, are investigated. This will allow the age of adult and juvenile koalas to be determined from tooth wear and head length, respectively.
Methods

Age determination of sub-adult and adult koalas using tooth wear

Tooth wear class data from known-age koalas on French Island (1980-1985), the Brisbane Ranges (R. Martin and K. Handasyde, unpublished data) and the KCC were assessed to determine the relationship between age and TWC. The birth dates of koalas with a head length less than 120 mm at initial capture were estimated from the growth curve regression equation derived in this chapter. The age in months of each individual koala was calculated at each subsequent capture where the koala was recorded as having changed TWC or body mass. Capture frequency varied between regular monthly capture, capture at least once a year and occasional capture over the longer term, such as twice in six years.

Analysis of variance tests (ANOVAs) were used to test whether the age of individuals (when first recorded in a TWC) differed between sites and between the sexes in order to determine if different diets were contributing to different tooth wear rates. However, data were not available in all combinations of sites, sexes and TWCs, thus subsets of ANOVAs were used. As data were scarce in the older TWCs due to lack of access to older known-age koalas, the TWCs of koalas that were first captured as adults (of unknown-age) were also analysed. The period of time between consecutive TWCs in these koalas was used to calculate the duration of time in each TWC. The duration data was compared to the known-age data in TWCs II to IVC with an analysis of covariance (ANCOVA), with TWC as the covariate, to examine possible differences in tooth wear rates between koalas of known- and unknown-age.

Koalas were assessed to determine if there was a pattern of fast or slow tooth wear in consecutive TWCs within individuals. The mean and standard deviation (s.d.) of the duration within each TWC was calculated for all koalas pooled. The duration that each individual spent in each TWC was standardized by subtracting the mean and dividing by the standard deviation. In order to investigate the pattern of time in each TWC relative to the mean and typical variation in the previous stage, the earlier duration was plotted against the subsequent duration for each individual where this was known.
The conversion of TWC to age was calculated from a combination of the age at the start of each TWC from known-age individuals and the duration of individuals of unknown-age in each TWC.

**Growth rates of juveniles and sub-adults: development of growth curves**

Previous growth curves for Victorian koalas used polynomial equations and did not provide estimates of error (Martin and Handasyde 1990a). Since polynomial curves are normally inadequate for describing growth (Vonesh 1992), a new curve was derived allowing for irregularly spaced observations and a combination of longitudinal and cross-sectional data (McRoberts *et al.* 1998, Johnson and Delean 1999). The derivation of the new growth curve used data from juvenile koalas from French Island (1980-1985) and the Brisbane Ranges (R. Martin and K. Handasyde, unpublished data). The study sites and method of data collection are described in Chapter 2. Observations of whether the juveniles were pouch- or back-young or independent of their mother were recorded. Measurements were made monthly for most juveniles until approximately 12 months of age but some individuals were also captured at older stages.

For the development of most growth curves, the date of birth of the animals from which the growth curve was constructed was known to within one week. In the present study, growth curves were derived from juvenile koalas (pouch- and back-young) where the exact date of birth was not known. The maximum possible age of some juveniles could be calculated if the mother had previously been caught without an offspring (e.g. Ward 1990).

The model of juvenile koala growth in the present study was based on the exponential curve, as this family of curves reaches an asymptote and includes the smallest number of parameters possible:

\[ H = a(1 - e^{-bT}) \]

*Equation 3.1*
where $H$ is the head length measured in millimetres, $a$ and $b$ are unknown parameters of the model to be estimated, and $T$ is time (since zero head length, measured in days).

In order to calculate the age at a given head length, Equation 3.1 was transformed:

$$T = \ln \left( 1 - \frac{H}{a} \right) - b$$

Equation 3.2

Age of individual $i$ was then calculated as

$$Age = T(i) - B$$

Equation 3.3

where $B$ is the value of $T$ when head length equals 7 mm (which is assumed to be the head length at birth given it was the smallest head length observed, N. Mclean unpublished data from Mt Eccles and Snake Island), and age is measured in days.

Bayesian analyses using the software WinBUGS (Spiegelhalter et al. 1996) were used to estimate the koala growth curves (e.g. Dey et al. 1997). Bayesian statistics uses prior distributions, based on previous information regarding the parameters to be estimated, in combination with the observed data to produce the posterior distribution of each parameter (Ellison 1996, Hilborn and Mangel 1997, Wade 2000). “WinBUGS” uses Markov chain Monte Carlo (MCMC) procedures (specifically Gibbs sampling) to take samples from the posterior distribution and these samples can be used to approximate the posterior distribution of each parameter (Casella and George 1992, Gilks et al. 1994, Manly 1997). Uninformative prior distributions were used for the parameters $a$ and $b$, and the estimate of age at the time of capture. These were specified as normal distributions with a mean of zero and a standard deviation of 1000. The first 5000 iterations of the model were discarded as a burn in and samples were taken from the subsequent 10000 iterations. The samples appeared to be drawn from a stationary distribution when examined as a time series and on evaluation of the Gelman-Rubin statistics.
The mean, median and 95% Bayesian confidence intervals of the parameters \(a\), \(b\), and age for each possible head length were determined. Hence, the predicted age was determined in two ways. Firstly, the parameters of Equation 3.1 were determined using WinBUGS and then the estimates of age were calculated outside of WinBUGS using the exponential equation. This was termed the growth curve from the equation. Secondly, the age at each head length was estimated within WinBUGS by sampling the posterior distribution of age at each head length. This second method was termed the median growth curve.

Male and female data were analysed separately as koalas are sexually dimorphic (McNally 1957, Nagy and Martin 1985). The fitted growth curves of individuals that spanned a large range of head lengths were plotted against the median growth curve. Growth curves were visually compared between males and females and between koalas from French Island (1980-1985) and the Brisbane Ranges.

**Stages in growth**

The separation of dependent and independent koalas was based on the head length at which most (~90%) individuals became independent from their mother. This was assessed from a total of 175 koalas with head lengths between 85 and 114 mm. These koalas were from Snake and French Islands, Framlingham and Mt Eccles.

The age of koalas at physical maturity (measured by body mass and head length) was assessed from cross-sectional (single sampling of multiple individuals) data of koalas from Snake and French Islands, Framlingham and Mt Eccles and using longitudinal data of known-age individuals from the Koala Conservation Centre (KCC). The relationships between mass and TWC (or age in years at the KCC), and head length and TWC (or age in years at the KCC) were determined separately for males and females at each site using non-linear regression in SPSS 11.5 with the general form of the asymptotic regression equation:

\[
y = b1 - b2 \times \exp(-b3 \times x),
\]

Equation 3.4
where $y$ is body mass (kg), $b_1$, $b_2$ and $b_3$ are unknown parameters of the model to be estimated and $x$ is a code for each TWC (Table 3.1). For example, when $x$ is equal to 5, TWC is equal to IVB.

Table 3.1 Numerical values of tooth wear class (TWC) used for $x$ in Equation 3.4.

<table>
<thead>
<tr>
<th>$x$</th>
<th>TWC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>I</td>
</tr>
<tr>
<td>2</td>
<td>II</td>
</tr>
<tr>
<td>3</td>
<td>III</td>
</tr>
<tr>
<td>4</td>
<td>IVA</td>
</tr>
<tr>
<td>5</td>
<td>IVB</td>
</tr>
<tr>
<td>6</td>
<td>IVC</td>
</tr>
<tr>
<td>7</td>
<td>V</td>
</tr>
<tr>
<td>8</td>
<td>VI</td>
</tr>
<tr>
<td>9</td>
<td>VII</td>
</tr>
</tbody>
</table>

Tooth wear classes where the predicted body mass (or head length) of individuals was greater than 95% of the asymptote for each population were considered to be physically mature. For analysis of the KCC data, all available data were used in the regression but only individuals with more than three measurements are illustrated.
Results

Age determination of adult koalas using tooth wear

Modifications to the tooth wear classes

Modifications were made to the tooth wear scale developed by Martin (1981). As tooth wear often differs between the right and left hand side upper pre-molars, tooth wear on both upper pre-molars was recorded (Young et al. 1996) instead of recording just from the right pre-molar (Martin 1981). If tooth wear differed between the right and left hand side pre-molars by one age class, the higher TWC was used. Differences of a higher magnitude were averaged between the two pre-molars. If tooth wear on each side of the jaw was different because of an injured jaw, estimation of the TWC included additional analysis based on body mass and wear of the molars.

It was difficult to distinguish between Martin’s (1981) TWCs I & II without taking into account the body mass or size of the individual. Hence, Martin’s (1981) TWCs I and II were combined into TWC II. TWC II was therefore defined as all four molars erupted and wear on the premolar varied between none and slight wear on the buccal crest. TWC I was defined as little or no wear on the pre-molar and incomplete eruption of the 4th molar.

It is proposed that TWC VI should be divided into 3 classes (VIa, VIb, VIc) in a manner analogous to the divisions in TWC IV. Thus, TWC VIa was defined as a small indentation in the premolar shape, VIb a moderate indentation, extending approximately half-way through the tooth, and VIc was a nearly complete indentation, just before the wear was so complete that it was a TWC VII (Figure 3.1 and Table 3.2). The division of TWC VI into three categories will be useful in future studies of known-age koalas but due to the small numbers of individuals in TWC VI on Snake Island and French Island, and at Mt Eccles and Framlingham, TWC VIa, VIb and VIc were pooled in this thesis.
Figure 3.1 Patterns of wear on the premolar tooth that were used to allocate koalas into tooth wear classes.

<table>
<thead>
<tr>
<th>Tooth wear class</th>
<th>Corresponding age estimate (years)</th>
<th>TWC description (this study)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>I</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 - 2</td>
</tr>
<tr>
<td>II</td>
<td>II</td>
<td>b, c</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 - 4</td>
</tr>
<tr>
<td>III</td>
<td>III</td>
<td>d</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4 - 5</td>
</tr>
<tr>
<td>IVA</td>
<td>IVA</td>
<td>e</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 - 4</td>
</tr>
<tr>
<td>IVB</td>
<td>IVB</td>
<td>6.5 - 7.5</td>
</tr>
<tr>
<td>IVC</td>
<td>IVC</td>
<td>7.5 - 9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>- 6</td>
</tr>
<tr>
<td>V</td>
<td>V</td>
<td>f</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10 - 12</td>
</tr>
<tr>
<td>VIa</td>
<td>VI</td>
<td>10 - 14*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12+</td>
</tr>
<tr>
<td>VIb</td>
<td></td>
<td>10 - 14*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Medium indent’n - bean shape</td>
</tr>
<tr>
<td>VIc</td>
<td></td>
<td>10 - 14*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Indentation nearly fully through</td>
</tr>
<tr>
<td>VII</td>
<td>VII</td>
<td>14+</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15+</td>
</tr>
</tbody>
</table>

* Note: data were only available for the age and duration of TWC VI as a whole, not the sub-classes TWC VIa, VIb, and VIc.

**Correlation between tooth wear class and age**

There is a strong relationship between TWC and age (Figure 3.2a). The age at eruption of the molars (M1 and M2) is included in Figure 3.2 to enable the determination of age of juveniles from the pattern of tooth eruption. There is larger variation in the oldest TWCs (V - VII) compared with the younger TWCs, due in part to the small sample sizes of known-age animals available in these groups. In order to
increase the sample size in the oldest TWCs, the duration of each TWC was calculated from koalas of unknown-age (Figure 3.2b) (see Appendix B for values of the means, standard errors (s.e.) and range). Error bars should be interpreted with caution, as consecutive TWCs include some repeat sampling of individuals, so they may underestimate the error.

Figure 3.2 Timing of tooth eruption/wear class of koalas. a) Age, in years, at the start of each tooth eruption or tooth wear class (TWC) for known-age animals only. b) Duration, in months, in each tooth eruption or TWC for known-age and not known-age animals pooled. Individuals from French Island (1980-1985), the Brisbane Ranges & the KCC, and males & females were pooled. Numbers above the points indicate sample sizes. Diamonds are the means and error bars represent one s.e.
The age at the start of each TWC from known-age individuals (Figure 3.2a) was combined with the duration of that TWC from females of unknown-age (Figure 3.2b) to convert TWC to age (Table 3.3). Errors are not provided in Table 3.3 due to the combination of the two data types. There is no overlap in age in consecutive TWCs as this table is intended to separate the range of ages in consecutive TWCs as much as the data allowed and provide a working resource for Victorian koala researchers and managers. As an indication of the accuracy of the conversion of TWC to age, the percentage of known-age koalas that were accurately assigned within one TWC (Table 3.3) indicates the accuracy of converting TWC to age. The percentage of known-age koalas accurately assigned to the TWC appropriate to their age, or the TWC above or below that appropriate to the individual's age is illustrated in Figure 3.3. Variation in tooth wear rates is lowest in TWCs I – III and is increasingly variable as age increases. A comparison of the tooth wear scales of different authors and the equivalent age is presented in Table 3.2.

Table 3.3 Scale for converting tooth wear classes (TWCs) to age (years) for Victorian koalas. The data were combined for males and females from French Island (1980-1985), the Brisbane Ranges and the KCC, for all known-age and not known-age individual koalas. Accuracy was calculated as the percentage of known-age individuals within the span of years that were correctly classified within one TWC of the TWC predicted by the table. The numbers in parenthesis are the sample sizes of known-age koalas.

<table>
<thead>
<tr>
<th>TWC</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV A</th>
<th>IV B</th>
<th>IV C</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
</tr>
</thead>
<tbody>
<tr>
<td>Years</td>
<td>&lt;1.25</td>
<td>1.25-3.5</td>
<td>3.5-5.5</td>
<td>5.5-6.5</td>
<td>6.5-7.5</td>
<td>7.5-9</td>
<td>9-10</td>
<td>10-14</td>
<td>14+</td>
</tr>
<tr>
<td>Accuracy</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>91%</td>
<td>50%</td>
<td>83%</td>
<td>80%</td>
<td>100%</td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>(91)</td>
<td>(84)</td>
<td>(35)</td>
<td>(11)</td>
<td>(8)</td>
<td>(6)</td>
<td>(5)</td>
<td>(2)</td>
<td>(0)</td>
</tr>
</tbody>
</table>
Figure 3.3 The percentage of known-age koalas in each tooth wear class (TWC) from Table 3.3 above, classified in the correct TWC (filled bars) according to their age, classified in the TWC below (vertical hatching), classified in the TWC above (diagonal hatching) or classified as two TWCs below the correct TWC (wavy hatching). One individual was assigned to three TWCs below the typical TWC for her age and is not included in the figure. Numbers above the bars are sample sizes. Note: duration data from koalas not of known-age are not included in this figure.

**Individual patterns in rate of tooth wear**

There was little correlation ($r^2 = 0.03$) between the earlier (first) duration (period of time spent in a TWC) and the subsequent (second) duration in TWCs. The low correlation indicates that the length of time in each stage class, relative to the mean and typical variation in each stage, was not strongly correlated over time, and that individuals exhibit a mix of fast and slow tooth wear rates (Figure 3.4).
Figure 3.4 Relationship of the standardised length of time (duration) spent in one tooth wear class (TWC) (First duration) compared with the subsequent TWC (Second duration) for koalas. The data were pooled from French Island (1980-1985), the Brisbane Ranges and the KCC, n = 76, r^2 = 0.03.

Differences in tooth wear rates with sex and site

Sufficient data were available from known-age koalas in TWCs I and II at the Brisbane Ranges, the KCC and on French Island (1980-1985), to compare the age at which koalas entered each TWC at each site. There was no significant difference in the age at which koalas entered a TWC between males and females (F = 0.496, d.f. = 1, P = 0.482), or between sites (F = 0.254, d.f. = 2, P = 0.776). Additionally, the interaction was not significant (F = 1.572, d.f. = 2, P = 0.211). For TWC III, data were available from known-age males and females at the KCC and on French Island (1980-1985). There was no significant difference in the age at which koalas reached TWC III between males and females (F = 3.092, d.f. = 1, P = 0.089) or between sites (F = 0.189, d.f. = 1, P = 0.659). The interaction was not significant (F = 0.077, d.f. = 1, P = 0.784). If real differences between sexes or sites exist, they are likely to be small (Figure 3.5 and Figure 3.6). Therefore, males and females (Figure 3.5) and all sites (Figure 3.6) were combined for further data analysis.
Figure 3.5 Mean age, in months, in tooth wear classes (TWCs) I, II and III for females (horizontal hatching) and males (filled bars). The data were combined for French Island (1980-1985), the Brisbane Ranges and the KCC. Numbers above bars indicate samples sizes. Error bars represent one s.e.

Figure 3.6 Mean age, in months, of koalas in tooth wear classes I, II and III for French Island (1980-1985) (filled bars), the Brisbane Ranges (vertical hatching) and the KCC (diagonal hatching). Males and females were combined. Numbers above bars indicate sample sizes. Error bars represent one s.e.
Tooth wear rate differences between known-age and unknown-age koalas

There was no significant difference in the duration of time spent in each TWC between known-age and animals of unknown-age ($F = 0.191$, d.f. = 1, $P = 0.663$) (Figure 3.7). It is possible that the differences between the known and unknown-age koalas could be large (e.g. TWC III and TWC IVB) but because there is no consistent pattern, and without firm evidence to the contrary, it was assumed there was no difference.

Figure 3.7 Mean duration (in months) that koalas spent in TWCs II, III, IVA, IVB and IVC for known-age (filled bars) and not known-age (diagonal hatching) koalas. Males and females, and French Island (1980-1985), the Brisbane Ranges and the KCC were combined. Numbers above bars indicate sample sizes. Error bars represent one s.e.
Growth curves

Growth equations

Separate growth equations (relating head length to age) for males and females were calculated with data from koalas from French Island (1980-1985) and the Brisbane Ranges using the median parameter values estimated in WinBUGS. The equation to calculate female age up to a head length of 123 mm was:

\[
\text{Age} = \left[ \left( \frac{\ln \left(1 - \frac{H}{135.8} \right)}{-0.033} - 1.6 \right) \times 10 \right]
\]

Equation 3.5

where 1.6 is the female B (birth time), \(H\) (head length) is measured in millimetres and age is measured in days.

The equation to calculate male age up to a head length of 123 mm was:

\[
\text{Age} = \left[ \left( \frac{\ln \left(1 - \frac{H}{158.7} \right)}{-0.024} - 1.9 \right) \times 10 \right]
\]

Equation 3.6

where 1.9 is the male B (birth time), \(H\) (head length) is measured in millimetres and age is measured in days.

As the size of the confidence interval around the age estimate varies with head length, it is inappropriate to report a single error value for the equation. Therefore, the error associated with each possible head length value is given in Appendix C.

Although growth curves are usually represented by head length as a function of age (with age on the x-axis and head length on the y-axis), the growth curves in the present study are intended as a method of determining the age of dependent koalas from their head length. Therefore, age is presented as a function of head length.
Growth curves using two different methods

Estimates of age, and thus growth curves, were obtained using two methods: the median growth curve and growth curves from Equation 3.2 and Equation 3.3. These two approaches yield similar estimates (Figure 3.8) so only the results of median growth curves (estimating the age at each head length in WinBUGS) will be reported.

Figure 3.8 Growth curves of a) females and b) males represented by the median growth curve (pink solid line) and the growth curve from the equation (blue solid line). Black dashed lines: upper and lower 95% prediction intervals.
**Female and male growth curves**

Comparison of female and male median growth curves shows that no sexual dimorphism is evident until a head length of approximately 110 mm (Figure 3.9) or approximately 15 months of age.

![Figure 3.9 Median growth curve of female (grey lines) and male (black lines) koalas. Upper and lower 95% prediction intervals are shown by dashed lines.](image_url)

**Growth of individuals**

The growth curves of most individuals showed fairly close alliance to the median curve although most individuals tended to fall below the median curve between head lengths of 85 and 105 mm (Figure 3.10). Therefore, this area of the curve was further investigated (Figure 3.11). Of the females, all but one individual increased their growth rate with respect to the median curve, between the head lengths of 85 and 105 mm (Figure 3.11a). This corresponds to the period immediately before these young became independent from their mothers. The pattern was similar in males (Figure 3.11b).
Figure 3.10 Median and individual growth curves of a) female and b) male koalas. Black solid line: median growth curve; black dashed lines: upper and lower 95% prediction intervals; each different symbol in a different colour represents the growth curve of a different individual. Nine individuals are shown in each of a) and b).
Figure 3.11 Median and individual growth curves of a) female and b) male koalas with a head length greater than 70 mm. Black solid line: median growth curve; black dashed lines: upper and lower 95% prediction intervals; green symbols: the Brisbane Ranges; blue symbols: French Island (1980-1985). Each different symbol represents the growth of a different individual. Open circles: the head length that the young became independent from its mother (this information is not available for the male individual represented by the green square symbol). Eight individuals are shown in each of a) and b).
Stages in growth

Juvenile koalas at independence

There was a wide range of head lengths at which juvenile koalas were caught independently from their mothers (85 – 112 mm). Of the 175 juvenile koalas caught on Snake Island and French Island and at Mt Eccles and Framlingham with a head length between 85 and 114 mm, 20 individuals became independent before reaching 103 mm and 18 individuals were still dependent after 103 mm (Figure 3.12). Thus, dependent koalas are defined as those koalas with a head length less than 103 mm. Independent koalas are therefore defined as all koalas with a head length greater than 103 mm.

Figure 3.12 Head length (mm) at which individuals became independent from their mother. The data were pooled for Snake & French Islands, Framlingham and Mt Eccles. Dependent young: open bars, \( n = 44 \); independent young: filled bars, \( n = 131 \).
Tooth wear class and mass of koalas at physical maturity

Regression equations of the relationship between TWC and body mass (kg) in koalas from Snake and French Islands, Framlingham and Mt Eccles are:

**Females**
- **Snake Island**: mass = 8.95 - 10.43*exp(-0.88*TWC), \( r^2 = 0.48 \)
- **Framlingham**: mass = 8.82 - 12.16*exp(-0.84*TWC), \( r^2 = 0.73 \)
- **Mt Eccles**: mass = 8.50 - 13.58*exp(-1.09*TWC), \( r^2 = 0.66 \)
- **French Island**: mass = 8.43 - 8.25*exp(-0.92*TWC), \( r^2 = 0.50 \)

Equation 3.7a-d

**Males**
- **Snake Island**: mass = 11.51 - 19.15*exp(-1.01*TWC), \( r^2 = 0.36 \)
- **Framlingham**: mass = 10.72 - 16.41*exp(-0.81*TWC), \( r^2 = 0.69 \)
- **Mt Eccles**: mass = 10.86 - 20.60*exp(-1.11*TWC), \( r^2 = 0.63 \)
- **French Island**: mass = 11.87 - 14.98*exp(-0.65*TWC), \( r^2 = 0.58 \)

Equation 3.8a-d

The 95% confidence intervals for the parameters of the regression equations are listed in Appendix D, Table D.1. Tooth wear classes where the mean koala body mass was greater than 95% of the asymptote for each population were considered to be physically mature (Figure 3.13 and Figure 3.14). Females at all sites were considered physically mature in TWC IVA. Males were considered physically mature in TWC IVA on Snake Island and at Mt Eccles but TWC IVB at Framlingham and on French Island. It is important to note that the difference in mean body mass between TWC III and TWC IVA is quite small in most populations.
Figure 3.13 Range of masses (kg) of female koalas in each tooth wear class at a) Snake Island, b) Framlingham, c) Mt Eccles, and d) French Island. Boxes represent the interquartile range (50% of observations), thick horizontal black lines are the medians, vertical lines extend to the highest and lowest values excluding outliers and extremes, circles are outliers (1.5-3 times the interquartile range from the upper or lower edge of the interquartile range) and asterisks are extremes (3+ times the interquartile range from the upper or lower edge of the interquartile range). Regression lines are from Equation 3.7a-d. Numbers above the boxes are sample sizes.
Figure 3.14 Range of masses (kg) of male koalas in each tooth wear class at a) Snake Island, b) Framlingham, c) Mt Eccles, and d) French Island. Boxes represent the interquartile range (50% of observations), thick horizontal black line is the median, vertical lines extend to the highest and lowest values excluding outliers and extremes, circles are outliers (1.5-3 times the interquartile range from the upper or lower edge of the interquartile range) and asterisks are extremes (3+ times the interquartile range from the upper or lower edge of the interquartile range). Regression lines are from Equation 3.8a-d. Numbers above the boxes are sample sizes.
**Tooth wear class and head length of koalas at physical maturity**

Regression equations of the relationship between TWC and head length (mm) in koalas from Snake and French Islands, Framlingham and Mt Eccles are:

### Females

<table>
<thead>
<tr>
<th>Location</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snake Island</td>
<td>head length = 144.2 – 55.2<em>exp(-0.78</em>TWC), r² = 0.53</td>
</tr>
<tr>
<td>Framlingham</td>
<td>head length = 142.3 – 81.4<em>exp(-0.90</em>TWC), r² = 0.74</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>head length = 143.6 – 102.3<em>exp(-1.12</em>TWC), r² = 0.73</td>
</tr>
<tr>
<td>French Island</td>
<td>head length = 139.2 – 55.4<em>exp(-1.07</em>TWC), r² = 0.51</td>
</tr>
</tbody>
</table>

**Equation 3.9a-d**

### Males

<table>
<thead>
<tr>
<th>Location</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
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<td>Snake Island</td>
<td>head length = 169.3 – 113.5<em>exp(-0.81</em>TWC), r² = 0.53</td>
</tr>
<tr>
<td>Framlingham</td>
<td>head length = 163.3 – 128.9<em>exp(-0.86</em>TWC), r² = 0.73</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>head length = 166.4 – 173.7<em>exp(-1.20</em>TWC), r² = 0.75</td>
</tr>
<tr>
<td>French Island</td>
<td>head length = 164.9 – 89.0<em>exp(-0.69</em>TWC), r² = 0.49</td>
</tr>
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</table>

**Equation 3.10a-d**

The 95% confidence intervals for the parameters of the regression equation for head length are listed in Appendix D, Table D.2. Tooth wear classes where the mean koala head length was greater than 95% of the asymptote for each population were considered to be physically mature (Figure 3.15 and Figure 3.16). Thus, females were considered physically mature based on head length in TWC II on French Island but TWC III at Framlingham, Snake Island, and Mt Eccles. Males were considered physically mature (based on head length) in TWC III at Mt Eccles but TWC IVA at Framlingham, Snake Island and French Island.
Figure 3.15 Range of head lengths (mm) of female koalas in each tooth wear class at a) Snake Island, b) Framlingham, c) Mt Eccles, and d) French Island. Boxes represent the interquartile range (50% of observations), thick black horizontal line is the median, vertical lines extend to the highest and lowest values excluding outliers and extremes, circles are outliers (1.5-3 times the interquartile range from the upper or lower edge of the interquartile range) and asterisks are extremes (3+ times the interquartile range from the upper or lower edge of the interquartile range). Regression lines are from Equation 3.9a-d. Numbers above the boxes are sample sizes.
Figure 3.16 The range of head lengths (mm) of male koalas in each tooth wear class at a) Snake Island, b) Framlingham, c) Mt Eccles, and d) French Island. Boxes represent the interquartile range (50% of observations), thick black horizontal line is the median, vertical lines extend to the highest and lowest values excluding outliers and extremes, circles are outliers (1.5-3 times the interquartile range from the upper or lower edge of the interquartile range) and asterisks are extremes (3+ times the interquartile range from the upper or lower edge of the interquartile range). Regression lines are from Equation 3.10a-d. Numbers above the boxes are sample sizes.
Age, mass and head length of koalas at physical maturity (longitudinal data)

The fitted relationships between age (years) and body mass (kg), and age (years) and head length (mm) in known-age koalas from the KCC are:

female mass = 7.95 - 14.18*exp(-1.01*age), r² = 0.80
male mass = 12.45 - 19.39*exp(-0.72*age), r² = 0.95

Equation 3.11a&b

female head length = 137.10 - 139.31*exp(-1.27*age), r² = 0.92
male head length = 166.95- 163.50*exp(-0.95*age), r² = 0.99

Equation 3.12a&b

The 95% confidence intervals for the parameters of the regression equations for mass and head length are listed in Appendix D, Table D.3. The age that koalas attained 95% of the asymptote was considered to be the age at physically maturity (Figure 3.17 and Figure 3.18). The mass and head length at which the asymptote is approached differs between individual females but is more consistent among males. Based on mass, females were considered physically mature between three and four years of age whereas most males were not adjudged to reach physical maturity (mass) until after five years of age. Female koalas were considered physically mature (based on head length) at approximately three years of age while males were considered to reach physical maturity at four years of age, after which individuals may continue to grow very slowly for a period.

The TWC and age that koalas reached physical maturity as measured by both mass and head length is summarised in Table 3.4. Hence, koalas generally reach 95% of the asymptote of structural size (measured by head length) before they reach 95% of the asymptote of body mass. For comparison of “adult” body mass between populations (Chapter 5), physical maturity of koalas is defined as koalas in TWC IVA and older, by which time most koalas should have attained physical maturity.
Figure 3.17 The mass (kg) of a) female, $n = 12$ and b) male, $n = 10$, individual koalas from the Koala Conservation Centre at years of age. Each symbol represents a different individual. Regression lines are from Equation 3.11a and b.
Figure 3.18 The head length (mm) of a) female, \( n = 10 \) and b) male, \( n = 10 \), individual koalas from the Koala Conservation Centre at years of age. Each different symbol represents a different individual. Regression lines are from Equation 3.12a and b.
Table 3.4 The mass (kg) and head length (mm) that is 95% of the asymptotic value, and the corresponding tooth wear class (or age (years)) at the Koala Conservation Centre (KCC) at which this mass or head length is predicted to be first achieved. Predictions are based on the regression equations 3.7, 3.8, 3.9, 3.10, 3.11 and 3.12 for male and female koalas at Framlingham, Snake Island, Mt Eccles, French Island and the KCC.

<table>
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<th>Male 95% of mass asymptote</th>
<th>Female 95% of head length asymptote</th>
<th>Male 95% of head length asymptote</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mass  TWC/age</td>
<td>Mass  TWC</td>
<td>Head length  TWC/age</td>
<td>Head length  TWC</td>
</tr>
<tr>
<td>Framlingham</td>
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<td>10.2  IVB</td>
<td>135.2  III</td>
<td>155.1  IVA</td>
</tr>
<tr>
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<td>10.9  IVA</td>
<td>137.0  III</td>
<td>160.8  IVA</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>8.1  IVA</td>
<td>10.3  IVA</td>
<td>136.4  III</td>
<td>158.1  III</td>
</tr>
<tr>
<td>French Is.</td>
<td>8.0  IVA</td>
<td>11.3  IVB</td>
<td>132.2  II</td>
<td>156.6  IVA</td>
</tr>
<tr>
<td>KCC</td>
<td>7.6  3-4 yrs</td>
<td>11.8  5 yrs</td>
<td>130.3  3 yrs</td>
<td>158.6  4 yrs</td>
</tr>
</tbody>
</table>

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Discussion

Age determination using tooth wear

The refinement of Martin’s (1981) TWC scale to easily define TWCs I and II and the inclusion of further division of TWC VI into 3 separate classes in the present study provides a more accurate working scale for determining age in koalas. Gordon (1991) states that his scale provides improved resolution compared with Martin’s (1981) scale; however, the classes are very similar in the early and middle age classes. It is only in the oldest TWCs that Gordon’s scale provides a more refined classification by inclusion of a description of wear on the molars (Gordon 1991). In Victoria there are very few animals in these older TWCs (see Chapter 4) and in Chlamydia-infected populations they contribute very little to the growth of the population (see Chapter 6). Therefore, the resolution in this part of the scale is not regarded as essential; however, the simple division of TWC VI into 3 classes has substantially improved the resolution at this end of the scale. As koalas spend the longest duration in TWC VI, it is appropriate to divide this TWC further. In the future, records of known-age individuals in these new TWC divisions may reduce the variation currently recorded for koalas in this TWC.

The conversion of TWCs to age in this thesis is the first to provide information on this relationship for Victorian koalas. This is an important resource for field workers and allows stage-based mathematical models of koala population dynamics to be developed (see Chapter 8), as the model requires data on the amount of time spent in each stage. Although the error in converting TWC to age should be interpreted with caution due to the repeated sampling of individuals (Figure 3.2), the low temporal-correlation in the duration within TWCs in individuals (Figure 3.4) should minimize this source of error.

There was little difference in the age that koalas entered TWC IVA and IVB. This may be due to the difficulty in differentiating between these two TWCs in the field. As both TWC IVA and IVB have relatively short (and similar) durations, the difficulty in distinguishing between them is not of great concern. The variation and overlap in age when entering the older TWCs are shortcomings of these results. This
is due to the unavoidable constraints of the data; in particular, there were very few known-age individuals in the oldest TWCs. The accuracy may be improved with an increased sample size of known-age older koalas, though the variability between individuals may be inherent. Although the confidence in assigning age to koalas in the oldest TWCs is low, there are very few koalas in these older TWCs in the populations (see Chapter 4) and they contribute very little to the overall fecundity of the population (see Chapter 6) and population growth (see Chapter 8). Therefore, it is unlikely that these older koalas greatly influence models of population growth.

Many studies have found large variation between individuals when comparing TWCs of mammals with age, and have argued that only very broad classes, such as juvenile, sub-adult and adult, could be accurately separated (e.g. Erb et al. 1999). For instance, Severinghaus (1949) established a technique for determining the age of white-tailed deer using tooth wear and despite the technique being widely used, it was found to be inaccurate in known-age deer older than two years of age (Gee et al. 2002). Variation between individual assessors may also reduce the accuracy of techniques to determine age from characteristics of teeth (Landon et al. 1998, Gee et al. 2002) and bone (Officer et al. 1996). Van Deelen et al. (2000) found that tooth wear rates differed between male and female white-tailed deer; however, the difference in tooth wear rates between the sexes was less than the variation observed between assessors. The assessments of TWCs of koalas in the present study were made by only three people and the variation between them is unknown. However, the variation is assumed to be minimal as one assessor trained the other two. Further research testing discrepancies between expert and novice TWC assessors, and repeatability over time, would be advantageous in determining the degree of variation between assessors.

The present study found that there was no detectable difference between sites in tooth wear rates of animals in TWCs younger than IVA. Preferred food tree species varied between sites with predominately manna gum and swamp gum on French Island (Martin 1981), blue gum (preferred by some individuals) and manna gum at the KCC on Phillip Island (Hindell et al. 1985, Bednarik 1996) and manna gum and swamp gum at the Brisbane Ranges (Hindell and Lee 1987). Unfortunately, the lack of data in TWCs greater than III does not allow testing between sites in the older TWCs where the variability is the greatest. The similarity in tooth wear rates between sites is
comparable with Gordon (1991) who found that there was no difference in tooth wear rates between Oakey and Springsure (both in Qld) with koalas eating different diets. Swamp gums have significantly higher ash content than manna or blue gums indicating higher silica content (Lithgow 1980). As silica content can be a major contributor to tooth wear in sheep (*Ovis aries*) (Underwood 1977), areas with pure stands of swamp gums could potentially have higher tooth wear rates in koalas (Lithgow 1980). Severinghaus (1949) found increased tooth wear rates in white-tailed deer feeding in areas with increased abrasive substances such as sand and dust. Additionally, Skogland (1988) found increased tooth wear rates in reindeer (*Rangifer tarandus*) in overgrazed areas as lichens were short and animals had a higher rate of soil particle intake. However, Martin (1981) suggested that differences in abrasive substances were unlikely to cause great differences in koala tooth wear rates between his sites. He based this assumption on the similarity in tooth wear in young koalas from different populations where the age of those koalas was estimated from pelage condition and body mass only.

Gordon’s (1991) estimates of age for the three youngest TWCs were slightly higher than those suggested by Martin (1981) (Table 3.2). This may be due to the approximations made by Martin, or alternatively, could have been due to faster wear rates at the Victorian site where koalas are larger, and hence eat a greater absolute amount of leaves, than in Queensland (Gordon 1991). Krockenberger (1993) found Martin’s (1981) scale relatively accurate and consistent when tested against known-age captive animals at Featherdale Wildlife Park; however, variation increased with increasing age. The data presented in this chapter illustrate that despite large variation in tooth wear rates, there is probably little variation between localities in age estimation using TWCs. These results may be applied cautiously to koala in South Australia, New South Wales and Queensland until the relationship between tooth wear rates and age is determined in those areas.

Tooth wear rates may differ between males and females. For example, Van Deelen *et al.* (2000) found that tooth wear rates differed between male and female white-tailed deer and the bias was sufficient to significantly influence trends in population dynamics models. Young *et al.* (1996) suggested that koala tooth wear rates were greater in males than females although this was based on very small sample sizes, and
there were few TWCs with both males and females to substantiate this premise. However, no difference in tooth wear rates was found between male and female koalas in TWCs <IVA in the present study. These results suggest the general applicability of the relationship between age and TWCs across Victorian koala populations.

**Growth**

**Growth curves**

The growth curves in Equation 3.5 and Equation 3.6 provide a valuable method for estimating the age of Victorian koalas up to a head length to 123 mm. As with all regressions, it is important not to extrapolate beyond the range of the original data (Abidi *et al.* 1996). The curves predicted by these equations are not sigmoidal (Gompertz or logistic) with a period of slow growth early in the life of the animal as predicted for most mammalian growth (Lee and Cockburn 1985) but are similar to the Bertalanffy curve (Kaufmann 1981). The age values calculated from the median growth curves produced by WinBUGS are very close to the values of age calculated from the equations. Thus, the equations can reasonably be used to estimate age from head length. The growth curves in the present study are similar to those calculated by Martin and Handasyde (1990a) but the curves in the present study have the advantage of allowing an estimation of the error associated with the prediction of age. Accuracy of predicting age decreases with age. At one year of age there is already considerable variation in head length between individuals. This is consistent with other marsupial growth curves (Johnson 1979, Poole *et al.* 1982a, Delaney and De'ath 1990, Krockenberger 1996, Johnson and Delean 1999).

The growth curves of individuals show the same shape as the median growth curve but with a vertical shift, indicating slightly slower or faster growth. This illustrates that the error around the median curve is largely due to variation between individual growth curves rather than within-individual variation, and is therefore similar to that found by Delaney and De'ath (1990) in allied rock-wallabies (*Petrogale assimilis*). Variation in growth of individuals may be due to differences in condition of their mother (Inns 1982), or differences in diet, local climatic factors, parasite loads and
general health (Lunn et al. 1993). For example, Russell et al. (2002) showed that the growth rate of meerkat pups (Suricata suricatta) was correlated with the number of carers and the carers' body condition.

The rapid decrease in growth rate after permanent pouch exit observed in a range of marsupial species (Lyne 1964, Wood et al. 1981, Poole et al. 1982b, Rose and McCartney 1982) was not observed in the koala. Instead, there was an increase in the growth rate of young koalas immediately prior to independence from their mother. This has also been found in captive Queensland koalas (Blanshard 1994). The growth rate subsequently returns to the median growth rate, and continues to decrease after independence. The start of this period of increased growth rate corresponds with the peak intake of milk components such as solids, lipids, carbohydrates and protein and also with the beginning of leaf intake (Krockenberger et al. 1998). The period of increased growth rate (approximately 290-420 days of age) correlates with the rapid increase in the amount of leaf matter intake (Krockenberger et al. 1998). An increase in growth rate, immediately prior to weaning or independence, has been observed in eutherian species where juveniles are still suckling but also consuming what will be their adult food (van Jaarsveld et al. 1995) but has not previously been reported in marsupials other than koalas.

The increase in growth rate prior to independence indicates the growth curve produced by WinBUGS does not accurately describe growth in this period. Researchers should use caution when estimating the age of juvenile koalas between 85 and 105 mm in head length. The confidence intervals around the higher head lengths of these animals are large (± approximately two months at a head length of about 100 mm, Appendix C) a finding consistent with Gordon (1991). Krockenberger (1996) found that the variation between individual Queensland koalas was greater after a head length of 70 mm but growth curves may still be useful depending on the accuracy required (Wood et al. 1983). Individuals should be measured as young as possible in order to improve the accuracy of the age estimation. When young koalas are measured at a head length of 100-120 mm, growth curves only provide the opportunity to determine the season of birth of the individual rather than an accurate estimate of the birth date.
Information on growth allows the determination of whether greater size of one sex is related to a longer period or greater rate of growth (Stamps 1993, Winship et al. 2001). A comparison of the male and female growth curves did not reveal sexual dimorphism until approximately 110 mm head length or about 15 months of age. This is much younger than the 23 months of age at sexual dimorphism in Queensland koalas found by Smith (1979a) but his analysis was limited to only 8 captive animals.

The present study found there was no difference in the growth curves of juveniles from the Brisbane Ranges and French Island (1980-1985). However, Martin (1985b) reported a difference in koala growth rates between populations. He found that both male and female juvenile koalas at Walkerville (Vic) had significantly lower growth rates than French Island animals and suggested that this was due to the poor condition of the Walkerville animals. This is not consistent with the fact that there was no difference in the mean adult female body mass between the populations, and female body mass did not decline over the study period as trees became further defoliated at Walkerville (Martin 1985b). Neither of the populations at the sites in the present study experienced a shortage of food at the time of the data collection (K. Handasyde, pers. comm.). Gordon (1991) also found that there was no difference in the growth rates of koalas from two different areas in Queensland. However, juvenile koalas from distantly separated populations, such as Queensland and Victoria, do have different rates of growth (Table 3.5). Koalas from Queensland grow at a slower rate than Victorian koalas, and have a lower mean adult body mass than Victorian koalas (Martin and Handasyde 1995). Thus, growth curves need to be developed for separate geographic regions due to the general cline in the adult body mass of mammals with changes in latitude (Bergmann’s Rule, Meiri and Dayan 2003). Additionally, it would be inappropriate to use growth curves developed from koala populations in one geographic region for all koala populations.
Table 3.5 Size and mass (means, s.d. in parentheses for mass) of Victorian and Queensland juvenile koalas at three ages. The ages represent pouch exit (260 days), and completion of weaning (350 days) in Queensland koalas. Queensland data is from Table 5.3.6 Krockenberger (1993).

<table>
<thead>
<tr>
<th>Age (days)</th>
<th>Head length (mm)</th>
<th>Victoria</th>
<th>Queensland</th>
</tr>
</thead>
<tbody>
<tr>
<td>258</td>
<td>81</td>
<td>74</td>
<td>0.95 (0.16)</td>
</tr>
<tr>
<td>299</td>
<td>88</td>
<td>83</td>
<td>1.45 (0.19)</td>
</tr>
<tr>
<td>349</td>
<td>95</td>
<td>92</td>
<td>1.97 (0.29)</td>
</tr>
</tbody>
</table>

The growth rate of koalas is low relative to other marsupial species (Martin and Handasyde 1990a). Russell (1982) also found that the growth and development of koalas from final pouch exit to weaning was slower than in other marsupials. She considered that this may be due to the lower metabolic rate of koalas and that the low mass of young at weaning relative to maternal mass may be due to the arboreal lifestyle. Krockenberger (1998) established that the energy requirements of young koalas were only 60% of the typical energy requirements for marsupials (at permanent pouch exit) and that daily milk-energy production (at peak lactation) was the lowest recorded in any mammal. However, this was compensated for by longer lactation than the combined marsupial and eutherian average, and Krockenberger (1996) suggested this may be due to limitations of their arboreal habit and their poor quality eucalypt foliage diet (Cork and Sanson 1990).

**Stages in growth**

The wide variation in the head length of juvenile koalas at independence (85 – 112 mm) was similar to the variation in age at independence found in koalas from French Island (Mitchell 1990c). This may have been due in part to whether or not the mother gave birth to a new young in the subsequent season (Mitchell 1990c). Mitchell (1990c) found it was difficult to determine the timing of independence of young when the mother did not produce a young in the following season. Independence of these young occurred at an older age than young of females that produced a new young in the next season. The variation may also be due in part to the body condition of the mother and whether she is able to maintain lactation (Lee et al. 1991).
At physical maturity, individuals can allocate all of their energy to maintenance, storage and reproduction rather than growth (Madsen and Shine 2002). Gaillard et al. (1993a) found that physical maturity of roe deer (Capreolus capreolus) was attained at a later age at Chize than Trois Fontaines, France. They concluded that this delay lengthened the period of high mortality risk. As a consequence, the timing of physical maturity may be important in determining mortality rates and population dynamics. Koalas fit the typical mammalian pattern of reaching physical maturity after sexual maturity (Chapter 6) (Clutton-Brock 1991, Stamps 1993, Setchell et al. 2002). Thus, young produced while the female is still growing may incur a substantially greater cost to maintenance and storage of energy to the female than young produced by a physically mature female (Festa-Bianchet et al. 1995). However, in the present study the condition of the young was not correlated with maternal TWC (see below for discussion).

Numerous estimates of the age of koalas at physical maturity are present in the literature. Smith (1979a) found that females attain physical maturity after their third year. Whereas Eberhard (1972), Martin and Handasyde (1990a) and Cockram and Jackson (1974) found that females were fully grown after their fourth year and males were fully grown after their fifth year. Martin and Lee (1984) reported that female growth reaches an asymptote at 3 years of age, and males at 4 years of age and Melzer (1995) stated that koalas with a TWC > III are mature, although he found that body mass continued to increase until TWC V (using Gordon’s (1991) TWC scale). The present study found that female koalas at the KCC, Phillip Island, reach physical maturity at 3 to 4 years of age while the mean mass of females from French and Snake Islands, Mt Eccles and Framlingham reached an asymptote at TWC III - IVA which is equivalent to approximately 3.5 – 6.5 years of age. The present study also found that koalas reach 95% of the asymptotic structural size (measured by head length) before they reach 95% of the asymptotic body mass. Male koalas reach physical maturity at an older age than females, which is consistent with the broad patterns generally observed in sexually dimorphic mammals (Charnov 1982, Clutton-Brock 1991, Stamps 1993).

The longitudinal data on the individuals from the KCC is more appropriate for determining the timing of physical maturity as different individuals often have a
different body mass or head length at physical maturity (e.g. Figure 3.16). Such large variation in body mass between individuals resulted in a relatively large 95% confidence interval (of approximately 450 g) around the asymptote compared with a small confidence interval (of less than 3 mm) around the head length asymptote. The relatively small correlation coefficient values for the Snake Island, Framlingham, Mt Eccles and French Island regression equations compared with the high correlation coefficient values for the KCC regression equations were partly due to the categorical nature of TWCs at the former sites and the autocorrelation over time within individuals at the KCC.

**Conclusion**

Without information on age of individuals, results of research may be diluted or invalid (Morris 1972). In this chapter, the development of techniques to determine the age (and associated error) of adult koalas based on tooth wear and juvenile koalas using growth curves based on head length has provided an important tool for researchers investigating the biology of Victorian koalas.
Chapter 4 - Structure of Victorian koalas populations: age structure, and adult and offspring sex ratios

Abstract
Knowledge of the population age structure and sex ratio is important as these influence population dynamics and the effect of population manipulation for management. The age structure and sex ratio of adults and juveniles were investigated in koala populations at Snake Island, Framlingham, Mt Eccles and French Island. The correlations between the offspring sex ratio and maternal variables including age and body condition were investigated in the light of the Trivers-Willard and local resource competition hypotheses. The age structures differed between most sites but all were highly skewed towards the younger age classes with over 50% (range: females 54-80%; males 64-83%) of koalas in tooth wear classes I - III. The adult sex ratio was significantly female-biased on Snake Island and at Framlingham, male-biased at Mt Eccles in 1999 and at parity at Mt Eccles in 2001 and on French Island. At the population-level, the juvenile sex ratio did not differ significantly from parity at any site. However, the offspring sex ratio changed significantly with maternal age and condition but this pattern differed between sites. At Framlingham, younger mothers, and older mothers in poor condition, were more likely to produce female offspring whereas older mothers in relatively good condition were more likely to produce a higher proportion of male offspring. At Mt Eccles, young and old mothers in relatively good condition were more likely to produce a greater proportion of female offspring and middle age mothers were more likely to overproduce male offspring. The converse was true for mothers in relatively poor condition at Mt Eccles. These results were most consistent with the Trivers-Willard hypothesis at Framlingham and with the local resource competition theory at Mt Eccles. These variations in the population structure are likely to have major influences on population dynamics at different sites.

Introduction
In order to gain an insight into the mechanistic processes involved in population dynamics, it is necessary to understand the variation in the demographic structure of the population (Charlesworth 1994, Caswell 2001, Coulson et al. 2001a). The age and sex of an animal may influence its body condition, growth rate, and probability of survival and fecundity (Stearns 1992, Cairns and Grigg 1993). Thus, an understanding of the age structure and sex ratio can be essential to wildlife and game population management (Severinghaus 1949). Although the population sex ratio of vertebrates is
often at parity at birth (Caughley 1977), the birth sex ratio may vary with maternal or environmental variables (Clutton-Brock and Iason 1986).

**Influences of age structure on population dynamics**

The age structure of a population can be used to predict the growth rate of the population (Caughley 1977, Caughley and Sinclair 1994, Boyd et al. 1995) and to estimate many population parameters (Chapman and Robson 1960, Caughley 1967, de Kroon et al. 1986, Udevitz and Ballachey 1998). Additionally, large peaks in recruitment or the lack of recruitment can be detected with analysis of age structures (Delaney and Marsh 1995, Driscoll 1999, Reaser 2000). Factors such as changes in recruitment may result in large temporal variation in population growth (Solberg et al. 1999, Norrdahl and Korpimaki 2002).

Changes in the age structure of populations have been found to drive changes in population dynamics (Tkadlec and Zejda 1998). A population with a high proportion of young individuals typically suggests a rapidly growing population whereas a high percentage of older individuals manifests as slow growth (Alexander 1958, e.g. Wheeler et al. 2003). The variation in the age structure and the relative fecundity and mortality of each age class contribute substantially to changes in the population abundance (Solberg et al. 1999, Albon et al. 2000, Clutton-Brock and Coulson 2002). Zabel and Levin (2002) reported the importance of including accurate information on age structure in fisheries models that predict population growth. They found that when this information was not known, and long-term averages were used instead, the model produced erroneous results including overestimating population growth, which could potentially lead to over-harvesting. Consequently, it is important to use accurate age structures that reflect the current population when modelling population growth rates (Cairns and Grigg 1993, Festa-Bianchet et al. 2003).

The age structure of male and female koalas has been reported for many sites (Martin 1981, Hindell 1984, Martin 1985c, Mitchell et al. 1989, Gordon et al. 1990a, Melzer 1995, Cahill et al. 1999). In highly defoliated sites, Gordon et al. (1988) found a high proportion of young koalas. At a similarly defoliated site Martin (1985c) found a large proportion of older koalas and suggested that larger males may have been actively
defending the remaining food resources. The small sample sizes of most of these studies (except French Island, Martin 1981, 1985c) limits the conclusions that can be drawn. Thus, little is known conclusively about the age structure of koala populations and there is currently no understanding of how the age structure affects population dynamics in this species.

**Influence of adult sex ratio on population dynamics**

Adult sex ratios are of great consequence to population dynamics because of their potential to influence breeding behaviour and thus, fecundity (Jirotkul 1999, Komers and Curman 2000). For example, female-biased adult sex ratios have been shown to decrease fecundity in ungulates (Laurian *et al.* 2000, White *et al.* 2001). Holand *et al.* (2003) found that a highly female-biased sex ratio in reindeer did not cause a decrease in fecundity but did delay the calving dates and this led to reduced survival of juveniles. Adult sex ratios vary widely between species (Berger and Gompper 1999) (Boyd 1981b, Hailey and Willemsen 2000, Ford *et al.* 2003). Adult sex ratios also vary spatially and temporally within species. The adult sex ratio of populations of black-tailed deer (*Odocoileus hemionus*) ranged from female-biased (Krausman and Etchberger 1995, Bowyer *et al.* 1996), to close to parity (McCullough 1993), to male-biased (Relyea and Demarais 1994).

Mammalian sex ratio theory predicts that in sexually size dimorphic species where the males are larger, the adult sex ratio will be biased towards females (Berger and Gompper 1999). Evidence for this has been found in many mammalian taxa including marsupials (Norbury *et al.* 1988), primates (Kappeler 1997) and ungulates (Clutton-Brock *et al.* 1991, Berteaux 1993, Karanth and Sunquist 1995, Bowyer *et al.* 1996, Modafferi and Becker 1997). Biases in adult sex ratios may also be correlated with population density (Boyd 1981a, Clutton-Brock *et al.* 1997). Biased adult sex ratios are the result of a combination of the birth sex ratio and sex-biased dispersal and mortality (Bowyer 1991, Reale *et al.* 1996, Fedigan and Zohar 1997).

In koala populations, adult sex ratios have generally been found to be female-biased (McNally 1957, Hindell 1984, Martin 1985c, Every 1986, Mitchell *et al.* 1989, Martin and Handasyde 1990a, Cahill *et al.* 1999, Thompson 2001). However, the adult sex
ratio was at parity at Redbill Creek on French Island (Mitchell and Martin 1990) and was male-biased at Norwood Creek, Queensland (Melzer 1995). Given the importance of adult sex ratios in population dynamics, and the variation observed in koala populations across Australia, it is critical to determine adult sex ratios of koalas at sites where koalas are overabundant in order to predict population growth at such sites.

**Influence of offspring sex ratio on population dynamics**

Offspring sex ratios are also important in determining population dynamics. An equal sex ratio at birth is favoured when parents invest equally in sons and daughters (Fisher 1930). Skewed sex ratios at birth and differential parental investment in the sexes have been observed in many animal taxa including insects (Wrensch and Ebbert 1993, Hardy 1994), vertebrates in general (Williams 1979), reptiles (Bull and Charnov 1989), birds (Gowaty 1983), mammals (Clutton-Brock and Albon 1982, Clutton-Brock and Iason 1986), ungulates (Hewison and Gaillard 1999), primates (Hiraiwa-Hasegawa 1993) and marsupials (Cockburn 1990). Additionally, many studies have found that while the population sex ratio was close to parity, the sex ratio varied with maternal attributes such as rank, age, mass and condition (Johnson and Jarman 1983, Clutton-Brock *et al.* 1986, Hewison and Gaillard 1999, Arroyo 2002, Maestripieri 2002, Velando 2002) or environmental variables (Johnson and Jarman 1983, Byholm *et al.* 2002).

Sex ratio theory is an interesting and controversial area of evolutionary biology with many adaptive explanations advanced for sex ratio bias (Hardy 1997b). Although the mechanism for sex allocation is yet to be determined (Cockburn 1990), the stage that sex ratio biases are produced has been investigated (see, for example, Hardy 1997b, Davison and Ward 1998, Johnson and Ritchie 2002, Komdeur *et al.* 2002, Krackow *et al.* 2003). Two central theories of offspring sex ratio are the local resource competition theory (Clark 1978, Silk 1983) and the Trivers-Willard hypothesis (Trivers and Willard 1973).

Local resource competition theory predicts that in species with sex-biased dispersal, the philopatric sex (usually females in sexually dimorphic mammals (Greenwood
1980)) will compete for resources with the mother in the future (Smith 1968, Clark 1978, Silk 1983). This theory is often used to predict sex ratio at the population level (Cockburn et al. 1985, Cockburn et al. 2002) but can also be applied at the individual level (Hewison et al. 1999). Therefore, females in good condition could afford to produce the philopatric sex while females in poor condition would reduce future competition with offspring by producing the dispersing sex (see Maestripieri 2002). Similarly, young females would be predicted to produce the dispersing sex because the female would have an extended part of their life in which to compete with the philopatric sex (Hewison et al. 1999).

The Trivers-Willard hypothesis predicts that if one sex has greater variance in reproductive success than the other, and maternal investment affects future reproductive success, mothers in good condition or of high social rank should produce the sex that will benefit most from their mother’s ability to provide additional resources (Trivers and Willard 1973). In sexually dimorphic, polygynous (or promiscuous) species where the females (only) are philopatric, mothers in good condition should produce sons, as good quality (or larger sized) sons should have a reproductive advantage. Mothers in poor condition should theoretically produce daughters, as female reproductive success is less variable. The Trivers-Willard hypothesis assumes that females in good condition will produce offspring in good condition and the condition of offspring will persist to adulthood (Clutton-Brock and Iason 1986, Bercovitch et al. 2000, Carranza 2002).

A number of other theories propose explanations for biased offspring sex ratios. These include the local mate competition theory (Hamilton 1967, Hardy 1992), local resource enhancement (Gowaty and Lennartz 1985, Komdeur et al. 2002), the advantaged daughter hypothesis (Simpson and Simpson 1982, Hiraiwa-Hasegawa 1993, Hewison and Gaillard 1999) and the first cohort advantage hypothesis (Wright et al. 1995, Hardy 1997a). However, these hypotheses do not fit with the social structure or reproductive biology of koalas and thus, are not considered further.

Marsupials are particularly suitable for the investigation of offspring sex ratio as they are born at an altricial stage of development (Lee and Cockburn 1985, Cockburn 1990, Cockburn et al. 2002). In koalas, maternal variables including age, mass and
body condition, and environmental variables such as food availability vary greatly between populations in Victoria (McNally 1957, Martin 1985b, 1985c, 1985a, Handasyde and Martin 1988, Mitchell et al. 1989). Therefore, koalas have the potential to show offspring sex ratio bias. While the offspring sex ratio of koalas has been shown to be close to parity at many sites (McNally 1957, Eberhard 1972, Martin and Handasyde 1990a, Mitchell and Martin 1990, White and Kunst 1990), relationships with maternal or environmental variables have not been investigated.

The level of sex-biased dispersal is an important consideration in offspring sex ratio hypotheses. Dispersal is affected by characteristics of the individual (e.g. age, sex, condition), the population (e.g. density, rate of increase) and the environment (e.g. food supply, connectivity of patches) (Greenwood 1980, Barbraud et al. 2003). The level of sex bias in dispersal of koalas may differ between populations. Male-biased dispersal was found on French Island, Victoria (Mitchell 1990c, Mitchell and Martin 1990) and Inverness, Queensland, (Gordon et al. 1990a). This finding is supported by genetic evidence (Fowler et al. 2000a, Ellis et al. 2002a). In contrast, Ramsay (1999) found that similar numbers of male and female juvenile koalas dispersed.

When considering the offspring sex ratio theories described above and given the general pattern of male-biased dispersal in koalas, the local resource theory (Clark 1978, Silk 1983) would predict for koalas that mothers in good condition (or older females) would produce a greater proportion of female offspring (the more philopatric sex) than mothers in poor condition (or younger females). In contrast, the Trivers-Willard hypothesis (Trivers and Willard 1973) would predict for koalas that mothers in good condition would produce a greater proportion of male offspring than mothers in poor condition.

**Aims**

In this chapter I examine the population age structure and sex ratio at Snake Island, Framlingham, Mt Eccles and French Island. I determine if the age structure is stable and if the severe population decline at Framlingham has differentially affected particular age classes. I also examine offspring sex ratio in koalas and determine if the
offspring sex ratio varies with maternal age and condition and thus, if koala offspring sex ratios fit the available theoretical models.
Methods

Study sites and data collection
The study sites and data collection methods for Snake Island, Framlingham, Mt Eccles and French Island were described in Chapter 2. Male age structures were not analysed from Snake Island in 2000 or French Island in 2000 as sample sizes were inadequate to allow reliable conclusions.

Age structure
The age structure of the population is defined as the proportion of the population within each TWC. The age structures of koalas sampled in different years within sites were compared separately for males and females to establish whether the age structure of each population was stable over time. Age structures were also compared between sites (within sexes). The age structures were compared using the Kolmogorov-Smirnov Z, 2 independent samples tests.

The proportion of koalas in the older TWCs was investigated to provide insights into mortality. “Older koalas” were defined as TWC V and older, and the proportion of koalas in this category was compared between populations using contingency table and adjusted residuals analysis. If the absolute value of the adjusted residuals was greater than 1.96, the adjusted residual was significant at \( \alpha = 0.05 \) (Everitt 1986). The proportion of animals in the oldest TWC (VII) is also reported.

Sex ratio
Adult and juvenile sex ratios were analysed with contingency table and adjusted residuals analysis. Sexually mature adult females were defined as koalas greater than 6 kg in body mass (Chapter 6). Juveniles (offspring) included pouch-, back- and dependent-young. Sub-adults (koalas independent of their mothers and weighing less than 6 kg) were excluded from this analysis. Sampling periods were pooled for each site if there was no significant difference in sex ratios between periods.
Offspring sex ratios were tested using logistic regression for Framlingham and Mt Eccles in 2001. These two sites and sampling periods were chosen as they had the largest sample sizes of offspring and represent populations with and without *Chlamydia*-infection and with different levels of food availability. Additionally, Framlingham and Mt Eccles were sampled in autumn, thus bias in the offspring sex ratio due to differential mortality would be reduced as the peak of the breeding season is in summer (see Chapter 6). In the analysis, the sex of the offspring was the response variable, and the maternal variables morphological condition (see Chapter 5) and TWC (Table 4.1) were continuous explanatory variables (see Hosmer and Lemeshow 2000). Tooth wear class was entered in the regression equation as TWC minus the mean of TWC, and also TWC minus the mean of TWC all squared, as it was considered that the offspring sex ratio might vary non-linearly with TWC. That is, the probability of giving birth to one sex might be low in the youngest TWCs, increase in the middle age classes and then decline with old age. Maternal mass and muscle condition were not included in the model as they were correlated with maternal TWC (Chapter 5). Successive reduction of a term from the full model (which included all variables and interaction terms) and comparison of the change in deviance with a chi-square statistic was used to assess the statistical significance of the variables (Hosmer and Lemeshow 2000). A model that included only statistically significant terms was developed. However, in order to compare between sites, the model with both morphological condition and TWC was used for both sites.

Table 4.1 Numerical values for tooth wear classes (TWCs) in the logistic regression model.

<table>
<thead>
<tr>
<th>TWC</th>
<th>TWC value</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1</td>
</tr>
<tr>
<td>II</td>
<td>2</td>
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<tr>
<td>III</td>
<td>3</td>
</tr>
<tr>
<td>IVA</td>
<td>4</td>
</tr>
<tr>
<td>IVB</td>
<td>5</td>
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<td>IVC</td>
<td>6</td>
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<td>V</td>
<td>7</td>
</tr>
<tr>
<td>VI</td>
<td>8</td>
</tr>
<tr>
<td>VII</td>
<td>9</td>
</tr>
</tbody>
</table>
Results

Age structure

Stability of the age structure

The initial analysis of age structure compared the samples from different years at each site (Figure 4.1 - Figure 4.3). The only significant difference found between samples was between the 1999 and 2001 Mt Eccles male age structures (Z = 2.752, n = 553 and 653, P < 0.001) (See Appendix E for all comparisons), although the differences seem quite small (Figure 4.2b). This indicated that there was not strong evidence for large differences in sex-specific age structures between sampling periods at Snake Island, French Island and within females at Mt Eccles. As a result, samples were pooled within sites for further analysis (except Mt Eccles males).

Age structure and sex

Age structures were compared between the sexes at each site. Significant differences were found between the age structures of males and females at Snake Island (Z = 1.834, n = 1017, 632, P = 0.002), Framlingham (Z = 2.202, n = 434 and 311, P < 0.001), and Mt Eccles in 2001 (Z = 1.921, n = 679 and 653, P = 0.001), but not at Mt Eccles in 1999 (Z = 1.138, n = 454 and 553, P = 0.150), or French Island (Z = 1.249, n = 162 and 101, P = 0.082) (Figure 4.4). TWC III males form the largest proportion of the adult population at Snake Island, Framlingham, and Mt Eccles. Over 50% (range: females 54-80%; males 64-83%) of each of the populations is in TWCs I - III.
Figure 4.1 Age structure of a) female and b) male koalas in each sampling period at Snake Island. 1997: forward diagonal hatching, n = 397 females, 358 males; 1999: filled bars, n = 340 females, 244 males; 2000: horizontal hatching, n = 349 females; 2001: backward diagonal hatching, n = 83 females, 82 males.
Figure 4.2 Age structure of a) female and b) male koalas in each sampling period at Mt Eccles. 1999: forward diagonal hatching, n = 514 females, 627 males; 2001: filled bars, n = 786 females, 764 males.
Figure 4.3 Age structure of females in each sampling period on French Island. 2000: forward diagonal hatching, \( n = 107 \); 2001: filled bars, \( n = 107 \).
Figure 4.4 Age structures of females (horizontal hatching) and males (filled bars) at a) Snake Island, \( n = 1169 \) females, 684 males, b) Framlingham, \( n = 565 \) females, 462 males, c) Mt Eccles 1999, \( n = 514 \) females, 627 males, d) Mt Eccles 2001, \( n = 786 \) females, 764 males, e) French Island, \( n = 214 \) females, 154 males.
Age structure and site

Age structures were compared between sites separately for females and males. Age structures differed significantly between most site comparison combinations in both females and males (Table 4.2 and Figure 4.5). For males, age structures did not differ significantly between Framlingham and Mt Eccles in 1999, between Framlingham and French Island, and the difference between Snake Island and Mt Eccles in 2001 is marginal. For females, age structures also did not differ significantly between Framlingham and French Island.

Table 4.2 Results of Kolmogorov-Smirnov tests comparing age structures within sexes between sites. Samples were pooled within sites except for males at Mt Eccles. SI = Snake Island, Fram = Framlingham, FI = French Island, MtE = Mt Eccles (1999 & 2001 samples ) pooled, MtE99 = Mt Eccles in 1999 and MtE01 = Mt Eccles in 2001.

<table>
<thead>
<tr>
<th>Sites tested</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$K$-$Z$</td>
<td>$n$</td>
</tr>
<tr>
<td>SI &amp; Fram</td>
<td>4.692</td>
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</tr>
<tr>
<td>SI &amp; FI</td>
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<td>1017,162</td>
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</tr>
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<td></td>
<td>2.631</td>
</tr>
<tr>
<td>FI &amp; MtE</td>
<td>2.193</td>
<td>162,1133</td>
</tr>
<tr>
<td>FI &amp; MtE99</td>
<td></td>
<td>2.117</td>
</tr>
</tbody>
</table>
Figure 4.5 Age structures of a) females and b) males in four Victorian koala populations (samples pooled within sites except for males at Mt Eccles). Snake Island (forward diagonal hatching), \( n = 1169 \) females, 684 males; Mt Eccles (horizontal hatching in a), \( n = 1300 \) females, and open bars (sampled in 1999), \( n = 627 \) males, and backward diagonal hatching (sampled in 2001) in b), \( n = 764 \) males; Framlingham (diamond hatching), \( n = 565 \) females, 462 males; and French Island (filled bars), \( n = 214 \) females, 154 males.
**Older animals**

When all sites and samples were combined, 4.4% of all females, and 3.0% of all males were classed as TWC V or older. If similar patterns of mortality occurred across populations, it would be expected that the proportion of older animals would be similar across populations. Framlingham and French Island had a significantly higher proportion of females than Snake Island and Mt Eccles in TWC V and older ($\chi^2 = 93.13$, d.f. = 3, $P < 0.001$). Framlingham and French Island had a significantly higher proportion of males in TWC V or older than Mt Eccles in 2001 ($\chi^2 = 39.11$, d.f. = 4, $P < 0.001$) (Figure 4.6). The percentage of males and females in TWC V or older at Snake Island and Mt Eccles was much lower than in other *Chlamydia*-infected populations (except males at Raymond Island (Table 4.3)).

![Figure 4.6 Percentage of female (horizontal hatching) and male (filled bars) koalas that were in TWC V and older, pooled over samples at each site (except males at Mt Eccles in 1999 (Mt E '99) and at Mt Eccles in 2001 (Mt E '01)). Numbers above the bars are sample sizes.](image-url)
Table 4.3 Percentage (and sample size (n) in parenthesis) of females and males that were in TWC V and older in eleven koala populations.

<table>
<thead>
<tr>
<th>Site</th>
<th>Percentage (n)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Chlamydia-free</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magnetic Island</td>
<td>16.7 (24)</td>
<td>17.7 (17)</td>
</tr>
<tr>
<td>French Island</td>
<td>15.4 (214)</td>
<td>10.4 (154)</td>
</tr>
<tr>
<td>French Island</td>
<td>13.6 (66)</td>
<td>2.1 (48)</td>
</tr>
<tr>
<td>Framlingham</td>
<td>7.6 (565)</td>
<td>4.3 (462)</td>
</tr>
<tr>
<td>Chlamydia-infected</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walkerville</td>
<td>48.7 (39)</td>
<td>23.9 (46)</td>
</tr>
<tr>
<td>Inverness</td>
<td>na</td>
<td>24 (25)</td>
</tr>
<tr>
<td>Norwood Creek</td>
<td>43.8 (16)</td>
<td>36.8 (19)</td>
</tr>
<tr>
<td>Phillip Island</td>
<td>28.2 (39)</td>
<td>na</td>
</tr>
<tr>
<td>Raymond Island</td>
<td>15.7 (51)</td>
<td>2.8 (36)</td>
</tr>
<tr>
<td>Brisbane Ranges</td>
<td>5.9 (17)</td>
<td>16.7 (12)</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>3.1 (1300)</td>
<td>2.1 (1391)</td>
</tr>
<tr>
<td>Snake Island</td>
<td>2.3 (1169)</td>
<td>2.2 (684)</td>
</tr>
</tbody>
</table>

Live koalas in TWC VII were only found on French Island. Of French Island females sampled in 2000 and 2001, 0.6% (n = 162) were in TWC VII, which represents 0.04% of females sampled at all sites (n = 2746). Skulls of animals in TWC VII were found at Snake Island, Framlingham and Mt Eccles, indicating that animals in this class are present at these sites (Chapter 7).

Adult sex ratio

At Snake Island, the 1997 and 1999 samples were pooled after no significant difference in the sex ratio was found between the samples ($\chi^2 = 0.06$, d.f. = 1, $P > 0.80$). The Mt Eccles 1999 and 2001 samples were not pooled, as they were significantly different ($\chi^2 = 9.59$, d.f. = 1, $P < 0.01$) (Figure 4.7). As no significant difference was found between the 2000 and 2001 samples taken from French Island ($\chi^2 = 1.70$, d.f. = 1, $P > 0.10$), the two samples were also pooled.

The adult sex ratio varied between sites (Figure 4.7 and Table 4.4). Although significant differences were found for some populations, the sex ratios were close to
parity, with the observed proportion of females varying between 0.43 and 0.59. There was a significantly higher proportion of females than males in the population at Snake Island ($\chi^2 = 4.36$, d.f. = 1, $P < 0.05$) and at Framlingham ($\chi^2 = 18.81$, d.f. = 1, $P < 0.001$). The adult sex ratio at Mt Eccles in 1999 was significantly different from parity ($\chi^2 = 16.82$, d.f. = 1, $P < 0.001$) with a greater proportion of males, while Mt Eccles in 2001 was at parity ($\chi^2 = 0.0008$, d.f. = 1, $P > 0.95$). The French Island adult sex ratio was not significantly different from parity ($\chi^2 = 1.14$, d.f. = 1, $P > 0.20$) (Figure 4.7).

![Diagram of adult sex ratio at four Victorian koala sites.](image)

Figure 4.7 Adult sex ratio (percentage of females in each population) at four Victorian koala sites. Mt Eccles '99 and Mt Eccles '01 represent Mt Eccles sampled in 1999 and 2001, respectively. Numbers above the bars are sample sizes. The error bars represent the 90% confidence interval.
Table 4.4 Sex ratio (M:F) of adult and juvenile koalas for Snake Island, Framlingham, Mt Eccles and French Island.

<table>
<thead>
<tr>
<th>Year</th>
<th>Adults</th>
<th>Juvenile</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Ratio</td>
</tr>
<tr>
<td>Snake Island</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>619</td>
<td>1:1.07</td>
</tr>
<tr>
<td>1999</td>
<td>472</td>
<td>1:1.23</td>
</tr>
<tr>
<td>2000</td>
<td>304</td>
<td>*</td>
</tr>
<tr>
<td>Framlingham</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>655</td>
<td>1:1.41</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>929</td>
<td>1:0.76</td>
</tr>
<tr>
<td>2001</td>
<td>1189</td>
<td>1:1.00</td>
</tr>
<tr>
<td>French Island</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>124</td>
<td>1:0.97</td>
</tr>
<tr>
<td>2001</td>
<td>129</td>
<td>1:1.35</td>
</tr>
</tbody>
</table>

♦The sex ratio was biased because females were preferentially caught during this sampling period.

Offspring sex ratio

Population-level juvenile sex ratio

Samples were pooled within sites because no significant difference was found between samples. The juvenile sex ratios on Snake Island in 1997, 1999 and 2000 were pooled ($\chi^2=3.05$, d.f. = 1, $P > 0.05$), as were Mt Eccles in 1999 and 2001 ($\chi^2=0.30$, d.f. = 1, $P > 0.50$), and French Island in 2000 and 2001 ($\chi^2=0.33$, d.f. = 1, $P > 0.50$). The juvenile sex ratio was not significantly different from parity at Snake Island ($\chi^2=0.09$, d.f. = 1, $P > 0.70$), Mt Eccles ($\chi^2=1.97$, d.f. = 1, $P > 0.10$), Framlingham ($\chi^2=1.42$, d.f. = 1, $P > 0.20$) or French Island ($\chi^2=0.04$, d.f. = 1, $P > 0.90$). Any real differences were likely to be small (Figure 4.8 and Table 4.4).
Offspring sex ratio and site, sampling period and maternal variables

There was a statistically significant relationship (Table 4.5) between the offspring sex ratio and the mother’s TWC and morphometric condition at both Mt Eccles in 2001 and Framlingham. The regression coefficients and their standard errors are given in Table 4.6:

\[
P(\text{male offspring}) = \frac{\exp(\text{linear predictor})}{[\exp(\text{linear predictor})+1]}\]

Equation 4.1

where \( P(\text{male offspring}) \) was the probability of a mother producing a male offspring and the linear predictor \( = [(0.107*\text{TWC}) + (-0.301*\text{TWC}^2) + (-1.251*\text{condition}) + (0.287*\text{TWC}^2*\text{condition}) + 1.146] \). TWC was given a numerical value (Table 4.1) and normalised by subtracting the mean to avoid correlations between the linear and quadratic terms (Sokal and Rohlf 1981).
Table 4.5 Change in deviance between the full logistic regression model and the reduced model of offspring sex ratio (Equation 4.1).

<table>
<thead>
<tr>
<th>Model</th>
<th>-2 log likelihood</th>
<th>Change in deviance</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full</td>
<td>255.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduced (Equation 4.1)</td>
<td>262.1</td>
<td>6.8</td>
<td>1</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Table 4.6 Results of the logistic regression analysis of the effects of TWC, female condition (morphometric), and the interaction terms on the probability of a female koala having a male offspring at Framlingham, \( n = 277 \), and Mt Eccles in 2001, \( n = 190 \). Tooth wear class (TWC) was given a numerical value (Table 4.1) and TWC was entered as TWC value minus the mean of TWC values, and TWC² was \((\text{TWC value minus the mean value})^2\).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Framlingham</th>
<th>Mt Eccles</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>s.e.</td>
</tr>
<tr>
<td>TWC</td>
<td>0.107</td>
<td>0.126</td>
</tr>
<tr>
<td>TWC²</td>
<td>-0.301</td>
<td>0.359</td>
</tr>
<tr>
<td>Condition</td>
<td>-1.251</td>
<td>1.604</td>
</tr>
<tr>
<td>Condition*TWC²</td>
<td>0.287</td>
<td>0.349</td>
</tr>
<tr>
<td>Constant</td>
<td>1.146</td>
<td>1.693</td>
</tr>
</tbody>
</table>

The pattern of changes in offspring sex ratio (represented as proportion of males in Figure 4.9) with TWC and maternal morphometric condition differed between Framlingham and Mt Eccles. As there was a significant interaction between TWC and condition, the change in the proportion of males with increasing TWC is depicted while morphometric condition is held constant at three different levels: relatively poor (0.9 morphometric condition), average (1.0) and relatively good condition (1.1) (Figure 4.9). At Framlingham, young mothers, whether in good, average or poor condition, were more likely to have female offspring. Older mothers were also more likely to have female offspring if they were in poor condition but were more likely to have a male offspring if in good condition (Figure 4.9a). The pattern at Mt Eccles in 2001 was more complicated. Mothers in good condition were likely to have female offspring when they were young and old but male offspring when they were middle aged. For mothers in poor condition the converse was true. Young and old mothers in poor condition were more likely to have a male offspring, and middle age mothers were more likely to produce female offspring (Figure 4.9b).
Figure 4.9 Logistic regression model of the probability of a mother having a male offspring as a function of tooth wear class (TWC) and morphometric condition for a) Framlingham, $n = 277$, no data for TWC VII, and b) Mt Eccles in 2001, $n = 190$, no data for TWCs $> IVC$. The predicted offspring sex ratio is shown for mothers in relatively good condition (morphometric condition $= 1.1$), average condition (morphometric condition $= 1.0$) and relatively poor condition (morphometric condition $= 0.9$). The crosses represent the observed average offspring sex ratio of females in each TWC regardless of the morphological condition of the mothers. Numbers above symbols are the sample sizes and the error bars represent one s.e.
Discussion

Age structure

The male and female koala age structures at Snake Island, Framlingham, Mt Eccles and French Island were highly skewed to the younger age classes, indicating a rapid growth rate in these populations (Alexander 1958). Overall, the differences between male and female koala age structures seemed to be small and did not vary in a consistent manner with TWC, or site and sampling period. The general koala age structure in the present study was similar to the general pattern of age structures in marsupial populations in temperate environments, as exemplified in eastern grey kangaroos (*Macropus giganteus*) (Quin 1989).

Large peaks or troughs in recruitment can be detected with age structures (Webb *et al.* 1983, Driscoll 1999, Solberg *et al.* 1999). The low proportion of koalas in TWC I at Snake Island compared with French Island, and Mt Eccles compared with Framlingham (sampled in similar seasons) simply reflects the differences in fecundity levels due to *Chlamydia*-infection status (Chapter 6). Comparison of the koala age structures between populations illustrates a deficiency in the proportion of animals in TWC II at Framlingham and French Island. Both sites are *Chlamydia*-free, and have similar levels of fecundity (Chapter 6), and there is a high degree of defoliation at Framlingham (Ingeme *et al.* 1998, Madrau 1999). This may have previously caused a decline in recruitment as these sites.

The population age structure appeared to be stable at Snake Island, French Island and in females at Mt Eccles (within the 2-5 years over which these populations were sampled) as there was no change in the structure between years. A population increasing geometrically that has constant age-specific fecundity and mortality rates will approach an unchanging age structure, termed the stable age structure (Lotka 1922), with the proportion of individuals in each age class not changing over time (Cole 1954, Charlesworth 1994, Udevitz and Ballachey 1998). A population with a stable age structure may be increasing, decreasing or not changing in numbers (Stearns 1992). Krebs (2001) states that natural populations with stable age structures
are not commonly found but Goodloe et al. (2000) found that a population of overabundant feral horses (*Equus callabus*) had a stable age structure and van der Ree's (2002) data suggests that his population of squirrel gliders (*Petaurus norfolcensis*) had a stable age structure.

The stable age distribution at Snake and French Islands was in contrast to island populations of ungulates where the age structure varied widely between years (Clutton-Brock and Coulson 2002). The stability of the age structure of the koala populations in the present study was surprising given the different management strategies that have operated at each site in the past. On French Island, approximately 200 koalas per year have been removed in many years over the previous 80 years (DNRE, unpublished data) while at Snake Island and Mt Eccles removals of koalas began around the time of the first survey. Thus, the population age structure did not change significantly after the removal of a proportion of the population. Overabundant feral horses on islands, which were managed by translocation (similarly to koalas) also showed a stable age structure (Goodloe et al. 2000). The stable age structure in koalas may be evidence that the sample accurately reflects the structure of the population. It is also evidence that removal of a proportion of the population did not open "gaps" in the environment, thus allowing an increase in recruitment. This may suggest that the populations were not at a stage where density dependent mechanisms were acting.

The accuracy of the age structure is only as good as the accuracy of the technique used to determine age (Webb et al. 1983, Hamlin et al. 2000). Additionally, the age structure may be biased due to sampling errors caused by behavioural differences between the sexes (Harkonen et al. 1999) or sampling bias resulting from professional shooters or hunters (Wilson 1975). These limitations probably do not apply to the age structures of koalas discussed in the present study, as koalas do not segregate by sex or age (Mitchell 1990a) and attempts were made to catch all koalas located.

Large sample sizes are required to detect differences in the age structures of koala populations at different sites, because the sample must be divided by nine age classes and the two sexes. Descriptions of age structures of male and female koalas at many sites (other than those investigated in the present study) were generally based on less
than 50 koalas of each sex (Martin 1981, Hindell 1984, Martin 1985c, Mitchell et al. 1989, Gordon et al. 1990a, Melzer 1995, Cahill et al. 1999). Martin and Handasyde (1990a) pooled Victorian sites in order to gain meaningful sample sizes but as shown in the present study, pooling between sites may be invalid. As a result, it is not appropriate to statistically compare the age structures presented in the present study with most koala age structures in the literature. Despite these limitations, Martin (1981, 1985c) found that the koala age structure at Walkerville showed a strong bias towards the older age classes and suggested this was due to population decline. In contrast, the koala age structure on French Island was highly skewed towards younger animals (Martin 1981), similar to that found in the present study, indicative of a high population growth rate (Martin 1985c).

**Older tooth wear classes**

In the present study, a very small percentage of koalas were in TWCs V and older (4.4% of females and 3.0% of males). There was a higher percentage of older animals in the *Chlamydia*-free French Island and Framlingham populations than at *Chlamydia*-infected Snake Island and Mt Eccles populations. The greater proportion of the population in the older TWCs was more closely correlated with disease status of the population rather than the degree of defoliation at the site. This may indicate a deleterious effect on the survival of older individuals in *Chlamydia*-infected populations. These results are contrary to the high proportion of older animals found at the *Chlamydia*-infected koala population at Walkerville (Martin 1981). Martin (1981) suggested this pattern was the result of a low fertility rate over a number of years. Therefore, the low proportion of koalas in the older tooth wear classes may be due to increased mortality, low recruitment of that cohort as juveniles or a combination of these factors.

The percentage of females in the older TWCs was higher than males. This is consistent with the earlier mortality of males found in Chapter 7. It is generally accepted that female koalas live longer, on average, than male koalas (Martin and Handasyde 1999)(Chapter 7). Within females, the proportion of females in the older TWCs ranged between 48.7% at Walkerville in a declining population (Martin 1981, 1985c) and 5.9% at the Brisbane Ranges in a slowly increasing population (Hindell
There was no consistent pattern with the *Chlamydia*-infection status within these populations (Table 4.3). At Walkerville, the koala population was decreasing due to emigration and mortality resulting from defoliation of preferred food trees (Martin 1985c). The proportion of males in older TWCs also varied widely between sites (Table 4.3). Compared with Snake Island and Mt Eccles, koala populations in Queensland had a large percentage of males in the older age classes (Gordon *et al.* 1990a, Melzer 1995). It seems likely that a combination of high population growth and *Chlamydia*-infection in populations equates to a lower proportion of animals in the oldest age classes.

Given the large sample sizes at Mt Eccles and Snake Island it would be expected that live koalas in TWC VII would be detected since they are present in the skull collection (Chapter 7); however, live koalas were not found in TWC VII at these sites. A likely explanation for this is that while the skull of the animal would remain as permanent evidence of the koala, it is probable that the time spent alive in TWC VII is quite short given the advanced degree of tooth wear and the subsequent high likelihood of death. Hence, there would be a greater chance of detecting a skull in TWC VII than a live koala. The percentage of live koalas in TWC VII on French Island found in the present study (0.6%) was similar to that found by Martin and Handasyde (unpublished data) on French Island in 1979 to 1982 (2.3%, *n* = 512). Given the very small percentage of koalas in TWC VII and relatively small percentage of older koalas (TWC V and older), koalas in these TWCs probably contribute very little to population growth.

**Adult sex ratio**

The adult koala sex ratio showed both spatial and temporal variation. The adult koala sex ratio was significantly female-biased at Snake Island and Framlingham, significantly male-biased at Mt Eccles in 1999 and at parity on French Island and at Mt Eccles in 2001. Such spatial variation in the adult sex ratio has been found in many species (Fancy *et al.* 1990, Festa-Bianchet 1991, Tyler 1991, Krausman and Etchberger 1995). For example, adult sex ratios of mountain brushtail possums (*T. caninus*) ranged from female-biased (1:1.4) at Cambarville (Viggers and Lindenmayer 2000) to parity at Clouds Creek in north-eastern NSW (How 1976).
The female-biased adult sex ratios found at Snake Island and Framlingham have also been found in other koala populations (Martin 1985c, Mitchell et al. 1989, White and Kunst 1990) and are similar to the sex ratios reported in some other sexually dimorphic species (Berger and Gompper 1999). The koala populations with female-biased sex ratios had a range of growth rates, koala densities and Chlamydia-infection status (Martin 1985c, Mitchell et al. 1989, White and Kunst 1990). This is contrary to Boyd (1981a) and Glutton-Brock et al. (1991) who found that the proportion of males in the population was positively correlated with the population size. In addition to the male-biased adult sex ratio at Mt Eccles in 1999, male-biased koala adult sex ratios have also been found at Norwood Creek, Queensland (Melzer 1995). The Norwood Creek koala population differs greatly from Mt Eccles in having a very low population density (0.01 koalas per hectare, Melzer and Lamb 1996) and a high mortality rate (Melzer 1995). Hence, the proportion of males in koala populations does not seem to be correlated with population size.

The adult sex ratio varied temporally at Mt Eccles; it was significantly male biased in 1999 and at parity in 2001. A significant variation in the adult sex ratio has not previously been reported in koalas, probably due to low sample sizes. The sex ratio varied (non-significantly) at Walkerville and became progressively more male-biased as the habitat became further defoliated (Martin 1985c). This was possibly due to sex biased dispersal and the exclusion of females from preferred habitat by larger male koalas (Martin 1985c). Such temporally variation in the adult sex ratio may also be due to a combination of differential survival of the sexes in poor conditions and a variable environment (Olsson and van der Jeugd 2002).

The biased adult sex ratio at Snake Island, Framlingham and Mt Eccles in 1999 must be explained by sex-biased dispersal or mortality, or a combination of these, as juvenile sex ratios were at parity. The increasingly female-biased adult sex ratio in red deer (Cervus elaphus) on the island of Rum was due to a combination of male-biased mortality in juveniles and male-biased dispersal (Clutton-Brock et al. 1997). The level of sex bias in dispersal of koalas may differ between populations. Mitchell (1990c) and Mitchell and Martin (1990) found that over twice as many male koalas dispersed (both immigration and emigration) as females, and 83% of the 39 male immigrants
were between two and three and a half years of age when they dispersed into the site at Redbill Creek on French Island. Similarly, Gordon et al. (1990a) found that 90% of males born on site at Inverness, Queensland, dispersed by three years of age. Additionally, the genetic evidence found by Ellis et al. (2002a) and Fowler et al. (2000a) suggested male-biased dispersal in koalas. Furthermore, male koalas were five times more likely than females to escape over the fence at the Koala Conservation Centre on Phillip Island (A. Reed, N. McLean and K. Handasyde, unpublished data). In contrast, at a single site near Nowendoc (NSW), Ramsay (1999) found that similar numbers of male and female juvenile koalas dispersed. It is likely that the dispersal of juvenile koalas in the high density populations at Snake and French Islands, Framlingham and Mt Eccles was more similar (i.e. male-biased) to that at Redbill Creek, French Island, given the high population density at that site (Mitchell 1990c, Mitchell and Martin 1990). Thus, it is likely that male-biased dispersal partially accounts for the female-biased adult sex ratio detected in the current study; however, it is unlikely that sex-biased dispersal is the cause of the skewed sex ratio at Snake Island because the whole island was thoroughly searched for koalas. It is probable that male-biased mortality contributed to the female-biased adult sex ratio at Snake Island as evidenced in the skull collection representing natural mortality (Chapter 7). Similarly, the female-biased sex ratio in Florida key deer (Odocoileus virginianus clavium) was due to male-biased mortality (Lopez et al. 2003). Little is known regarding the mortality schedule at Mt Eccles or Framlingham and thus, it is unclear whether mortality contributed to the biased adult sex ratio at these sites.

Offspring sex ratio

Population-level juvenile sex ratio
The population-level juvenile koala sex ratio at Snake Island, Framlingham, Mt Eccles and French Island was not significantly different from parity. This is consistent with the findings of a number of other studies that have reported juvenile sex ratios for koalas, including Sheldon, southeast Queensland (White and Kunst 1990), Flinders Chase, Kangaroo Island (Eberhard 1972), and in past studies on French Island (McNally 1957, Martin and Handasyde 1990a, Mitchell 1990c, Mitchell and
Martin 1990). However, Martin and Handasyde (1990a) found a slight bias towards males each year on French Island from 1979 to 1982 and suggested this might indicate a male bias among juvenile koalas. The analysis of the timing of births in Chapter 6 shows that males were born significantly earlier than females on French Island. Since Martin and Handasyde (1990a) sampled on French Island in November, this may have introduced a significant sampling bias in analysis of juvenile sex ratio. Such bias is avoided in the present study by sampling over a longer time period. Future studies of juvenile sex ratio could aim to sample late in the breeding season to avoid this bias but such estimates would trade-off the possibility of including some mortality in the juvenile sex ratio.

Sex ratios may differ between populations within species (Cockburn et al. 1985, Johnson and Ritchie 2002). This may result from a combination of environmental factors (Johnson and Jarman 1983) and intrinsic factors such as skewed adult age structures (see below). For example, the juvenile sex ratio became more male-biased in populations with increased rainfall in large macropods (Johnson and Jarman 1983). There is no evidence in the present study, nor found in koala populations in Queensland (White and Kunst 1990) or on Kangaroo Island (Eberhard 1972), that koala juvenile sex biases change between populations with different rainfall levels. This may be due to the different time period that it takes for food resources to be renewed after rain when comparing between grazed and browsed species.

**Variation in the offspring sex ratio in relation to maternal age and condition**

The variation in the koala offspring sex ratio with maternal age and condition was not consistent between sites. At Mt Eccles in 2001, young and old mothers (in better than average condition) produced a greater proportion of female young, while medium age mothers produced a greater proportion of male young. The opposite was true of mothers in poorer than average condition. Numerous studies have found that the offspring sex ratio was correlated with maternal age (Clutton-Brock and Albon 1982, Clutton-Brock and Iason 1986, Heg et al. 2000, Saltz 2001, Hewison et al. 2002, Saltz and Kotler 2003); however, the results were mixed. Young red-necked wallaby (*Macropus rufogriseus*) and northern quoll (*Dasyurus hallucatus*) mothers were more likely to produce male young (Stuart-Dick and Higginbottom 1989, Oakwood 2000)
whereas young mountain goat (*Oreamnos americanus*), eastern grey kangaroo and yellow-footed rock-wallaby (*Petrogale xanthopus*) mothers were more likely to produce female young (Stuart-Dick and Higginbottom 1989, Robinson *et al.* 1994, Cote and Festa-Bianchet 2001). Relationships between maternal body condition and offspring sex ratio have also been detected in marsupials where mothers in better condition produced more male offspring (Sunnucks and Taylor 1997, Fisher 1999).

The direction of the bias in offspring sex ratio in koalas differed between sites. The relationship between maternal body condition and age and the offspring sex ratio was not a simple function as predicted by either the local resource competition theory or the Trivers-Willard hypothesis. Young koala mothers in poor condition were likely to produce a bias towards female offspring at Framlingham but male offspring at Mt Eccles in 2001. Also, old koala mothers in good condition may have had a slight bias towards producing male offspring at Framlingham but a bias towards female offspring at Mt Eccles in 2001. These results are more consistent with the Trivers-Willard hypothesis at Framlingham and more consistent with the local resource competition theory at Mt Eccles in 2001.

Resource availability, such as den site availability and the level of food availability, has been shown to affect offspring sex ratio at both the population and individual level (Austad and Sunquist 1986, Clutton-Brock and Jason 1986, Stuart-Dick and Higginbottom 1989, see also Wright *et al.* 1995, Hardy 1997a, Johnson *et al.* 2001). The variation in the offspring sex ratio in northern goshawks (*Accipiter gentilis*) was correlated with temporal and spatial variation in prey density, with male-biased clutches produced when prey density was high (Byholm *et al.* 2002). Austad and Sunquist (1986) provided additional food resources to an experimental group of common opossums (*Didelphis marsupialis*). The provisioned group produced male-biased litters whereas the control group produced equal numbers of males and females. The provisioned group also produced litters of better condition than the control group and these young in better condition had higher survival as independent juveniles than the young from the control group (see also Dickman 1988). The high level of defoliation of preferred food trees at Framlingham may invoke a high level of competition for food resources. However, the relationship between maternal condition and offspring sex ratio in koalas at Framlingham was very weak. This may be partly
due to the population density, which was very high at Framlingham. Kruuk et al. (1999a) found that previously reported biased offspring sex ratios were not found when the population density was high (see also Hewison and Gaillard 1999).

Many studies have been criticised for not meeting, or even considering, the assumptions of hypotheses regarding offspring sex ratios (Hardy 1997b, Hewison and Gaillard 1999). The predominate assumptions of the local resource hypothesis are that dispersal is sex biased and the philopatric sex competes with the mother (Hewison and Gaillard 1999). The dispersal of koalas has not been studied at Framlingham and Mt Eccles but is likely to be male-biased (see above) and limited (given the high level of agriculture surrounding both forest sites). However, dispersal of males from the natal area is likely to be higher than dispersal of females, and thus, koalas at Framlingham and Mt Eccles are likely to conform to the assumption of sex-biased dispersal. Home ranges of koalas are smaller as population density increases (Mitchell 1990a). Therefore, it is probable that koalas are in competition for the limited food resources at Framlingham and Mt Eccles (Ingeme et al. 1998, Kelly 2000).

The Trivers-Willard hypothesis assumes that the condition of females and offspring is correlated, the condition of the offspring persists until adulthood and males in good condition are more successful breeders than males in poor condition (Hewison and Gaillard 1999). For example, smaller southern snowshoe hares (Lepus americanus) were more likely to be subject to predation and this was a severe consequence of low maternal investment (Wirsing et al. 2002). The final assumption is that there is variance in reproductive output between the sexes (Trivers and Willard 1973). In koalas, adult males vary in size within a population (Chapter 5) and males compete intensively for access to females (Hindell 1984, Mitchell 1990b). Additionally, older, larger males, or males in better condition may be more successful breeders than smaller males (Mitchell 1990b, Martin and Handasyde 1999). As a result, variation in reproductive output is likely to be higher in males than females (Ellis et al. 2002a). Evidence for the assumption that condition of mothers and their offspring is correlated is ambiguous (Chapter 5). There was very little correlation between maternal and offspring condition but it is possible that mothers in good condition are able to promote faster growth in their offspring (see Krockenberger et al. 1998). It is not known whether the condition of koala offspring continues until adulthood; however,
the growth of koalas (Chapter 3) suggests that relatively large animals continue to be larger as they grow. Consequently, it is not clear whether all of the assumptions of the Trivers-Willard hypothesis are met for koalas. However, at least some of the assumptions appear to be met and further research could elucidate the remaining assumptions.

Conclusion

The age structures of the koala populations studied were highly skewed towards younger animals. This is typical of populations with high growth rates. Comparison of the age structures indicates a low recruitment in TWC II at Framlingham and French Island. The adult sex ratio varied spatially and temporally. This variation was not consistent with the population density or the Chlamydia-infection status of the population. The skewed adult sex ratios appeared likely to be due in part to male-biased mortality. Although the population juvenile sex ratio was at parity, there was evidence that it varied with maternal age and condition. The variation in offspring sex ratio was not adequately explained by any of the available theories on sex allocation. The results of the offspring sex ratio were more consistent with the Trivers-Willard hypothesis at Framlingham and with the local resource competition theory at Mt Eccles.
Chapter 5 - Population condition: body condition of koalas in four Victorian populations with differing disease status and degree of habitat defoliation

Abstract

Body condition of mammals is often affected by food availability, environmental conditions and disease. In turn, the body condition of individuals may affect their mating opportunities, and their conception and weaning rates. This chapter examines the relationship between the body condition of koalas in four Victorian koala populations and the habitat condition (degree of defoliation of preferred food trees) and disease status of populations. Body condition was assessed using body mass, a score of relative muscle condition and a size-body mass (morphometric) index. Body mass varied by approximately 3% between seasons in lactating female, non-lactating female and male koalas. Koalas were in better body condition when younger, in populations without *Chlamydia*-infection and at sites with the least defoliation. Also, within *Chlamydia*-infected populations, decreasing muscle condition with increasing age was correlated with an increasing proportion of females with reproductive tract lesions and clinical signs of disease due to *Chlamydia*-infection. Body condition was better in reproductive females than non-reproductive females indicating that the probability of breeding is greater in females with better body condition.

Introduction

Body condition

Body condition has been described as the “well-being” of an animal (Woolnough *et al.* 1997) or as a measure of its energy reserves (usually fat) (Schulte-Hostedde *et al.* 2001). An assumption underlying the concept of “condition” is that individuals in better condition will have greater evolutionary fitness and therefore will live longer, be better able to cope with variable environmental conditions and have offspring in better condition (Caughley 1977, Clutton-Brock *et al.* 1982, Krebs and Singleton 1993). Assessment of body condition allows comparisons to be made between individuals (Dennis and Marsh 1997), seasons (Hulbert and Grant 1983, Guinet *et al.* 1998, Dickman *et al.* 2001), sexes (Luque and Auriol-Gamboa 2001), and populations (Short and Turner 1999, Bradshaw *et al.* 2000). Differences in body condition may be indicative of changes in food availability (Dennis and Marsh 1997),
perceived predator risk (e.g. trade-offs between gaining energy and avoiding predation) (Hik 1995, Hodges et al. 1999) and reproductive status (Reimer and Hindell 1996, Guinet et al. 1998). Body condition may influence population dynamics (Dobson and Michener 1995, Ji et al. 2000, Ramsey et al. 2002, Stienen and Brenninkmeijer 2002) and may in turn be influenced by food availability, habitat condition, and the disease status of animals in the population (Clutton-Brock et al. 1982, McNamara and Houston 1996, Jorgenson et al. 1997).

Habitat condition influences the body condition of individuals (Klein 1968, Barnett et al. 1982, Clutton-Brock et al. 1982), and thus, affects population parameters such as mortality and fecundity (McNamara and Houston 1996). Habitat condition may be affected by a range of factors including availability of consumable (e.g. food) (Klein 1968, Strong and Sherry 2000) and non-consumable (e.g. shelter) resources (Dickman et al. 2001). Additionally, the habitat complexity, species composition and age structure of the vegetation may determine the suitability of habitat for individual species (Wallisdevries 1996, Catling et al. 2001). Habitat condition may be adversely affected by a high density of conspecifics (Klein 1981, Bourgarel et al. 2002) and competitors (Mutze and Cooke 1998). Frequency of catastrophic events (e.g. fire history) (Driessen et al. 1991), global and local climate (Kreuzer and Huntly 2003), processes such as fragmentation (Donovan et al. 1995, Kinley and Apps 2001), and management practices, such as harvesting, may also affect the habitat condition through changes in population density. Habitat condition is frequently measured by assessing the abundance of food (Strong and Sherry 2000). Often rainfall governs the amount of food available, which in turn contributes to the regulation of the condition of individuals and the growth rate of the population (Bayliss 1985a, Cairns and Grigg 1993, Ruthven et al. 1994, Bayliss and Choquenot 2002, Rhind and Bradley 2002).

Disease can impact greatly on the condition of an individual and consequently, its probability of survival or ability to reproduce (Holmes 1995, McCallum 1995, Jorgenson et al. 1997, Tompkins and Wilson 1998, Daszak et al. 1999). Furthermore, disease may differentially affect certain age and sex classes (Cransac et al. 1997, Jorgenson et al. 1997, Coleman and Caley 2000). Parasitism can cause disease and loss of body condition (Singleton et al. 1995, Tripet et al. 2002) but parasites may not always be in sufficiently high abundances to detrimentally affect their hosts or cause
population decline in many populations (Oakwood and Spratt 1999). The effect of
habitat condition and disease may act in combination on the body condition of
individuals (Presidente et al. 1982).

While the most accurate measures of body condition are destructive (Hanks 1981,
Virgl and Messier 1993, Reynolds 2001), many studies, such as behavioural and
ecological research, require non-destructive and non-invasive measures of body
condition. There are a number of non-destructive condition indices (Humphreys et al.
and Krockenberger 2002). However, of these, size–mass indices (Krebs and Singleton
1993, Hayes and Shonkwiler 2001) and combined visual and palpation body condition
scores (Woolnough et al. 1997) (where condition is assessed visually by subjectively
gauging the degree of muscle or fat over a prominent skeletal bone (Wallisdevries
1996)) are very useful for field studies.

Size–mass condition indices aim to remove the influence of structural size from body
mass and are commonly used because they are simple and inexpensive (Virgl and
Messier 1993, Hayes and Shonkwiler 2001). There are three basic types of size mass
indices, the ratio index (ratio of size to mass) (Pitcher et al. 2000, Nilssen et al. 2001,
Tierney et al. 2001), the residual index (residual values of a size-mass regression)
(Jakob et al. 1996, for review see Green 2001, Pople et al. 2001) and the “hybrid”
index (Krebs and Singleton 1993, Hayes and Shonkwiler 2001) which combines the
regression equation of the residual index and the quotient of the ratio index. These
indices have been compared with various measures of body composition across a
range of mammalian species (Bakker and Main 1980, Krebs and Singleton 1993,
al. 2001, Parker and Krockenberger 2002). Of these indices, the hybrid index has
been used successfully to assess body condition in many different mammalian taxa

Body mass is an additional method of determining the body condition of individuals
although it does not account for size differences between individuals. The advantage
of using body mass to assess condition is that differences in average body mass

between populations can potentially indicate past levels of low food availability. Size-mass condition indices may fail to detect this if the affected population is structurally smaller in body size due to a slower growth phase, but is in good body condition due to present high food availability. Therefore, size-mass and muscle (palpation) condition indices and body mass measures are simple, quick, inexpensive methods of assessing condition that do not require destructive sampling and can be widely applied during field studies.

In order to use body mass to assess body condition, any seasonal variation in the body mass must be determined. Seasonal changes in body mass and somatic energy reserves occur in many species and may be due to environmental factors including changing food availability (Bayliss 1985a, van Jaarsveld et al. 1995) and thermoregulatory requirements (Stewart and Barnett 1983, Delgiudice et al. 1992). Behavioural factors such as increased time spent searching for or defending mates (Deutsch et al. 1990, Chabot and Stenson 2002), or physiological factors such as increased energy demands due to lactation (Julienlaferriere and Atramentowicz 1990, Ganzhorn 2002) can also result in seasonal variation in mass.

**Condition of koala habitat and diseases of koalas**

The condition of habitat for koalas will be affected by many variables (Cork et al. 2000). These include the relative abundance and degree of defoliation of preferred food tree species (Martin 1981, 1985b, Gordon et al. 1988), age and chemical structure of the trees (Moore and Foley 2000) and the availability of trace elements in the foliage (McOrist and Thomas 1984, Thomas et al. 1986). The connectivity to other areas of suitable habitat (Phillips 1990), mean annual rainfall (Madrau 1999), and pressure of extrinsic influences, such as urbanisation (Ellis et al. 1993), may also affect the condition of the habitat for koalas. Habitat degradation in the form of severe defoliation of preferred food trees has occurred at many sites where koalas occur in southeastern Australia (McNally 1957, Martin 1985b, 1985a, St John 1997, Martin and Handasyde 1999). Martin (1985b) suggested that the reduced fecundity of females at a severely defoliated site in Walkerville (Vic) was partially due to poor body condition which was attributed to nutritionally induced anaemia.
A range of diseases occur infrequently in koalas (Obendorf 1983, Canfield 1990, Connolly 1999), including diabetes (Shimizu et al. 1989), skin ulcers (Mitchell et al. 1984, Mitchell et al. 1987), pneumonia (McColl and Spratt 1982) and reproductive tract diseases (Canfield et al. 1983). However, the major diseases affecting koala populations are caused by the bacteria *Chlamydia* spp. (Cockram and Jackson 1974, Handasyde and Martin 1988, ANZECC 1996).

Diseases caused by *Chlamydia*-infection include keratoconjunctivitis (Cockram and Jackson 1974), urinary tract infection (Pratt 1937, Dickens 1975, Butler 1978, Hemsley and Canfield 1996) and pathology of the female reproductive tract (Backhouse and Bolliger 1961, Obendorf 1983, Brown et al. 1984, Obendorf and Handasyde 1990). The direct effect of *Chlamydia*-infection on the reproductive tract of female koalas and resulting infertility is discussed further in Chapter 6. The diseases caused by *Chlamydia*-infection may have the potential to seriously impact on the condition of individual koalas; however, the effect on the population will depend upon the prevalence of *Chlamydia* in the population. The prevalence of *Chlamydia*-infection and clinical expression vary greatly between koala populations (0 - 98% and 0 - 39% of individuals in each population, for infection and clinical expression, respectively) (Appendix F). However, the difference in sensitivity between the many techniques used for detecting *Chlamydia* means the prevalence of *Chlamydia*-infection across koala populations cannot easily be compared (Jackson et al. 1999).

**Condition indices used in koalas**

Size-mass condition indices have not previously been reported for koalas. Palpation of the muscle mass over the dorsal spine of the scapula has been used to derive a muscle condition index for koalas (Dickens 1978, Wood 1978, Carrick and Wood 1986). Adaptations of the muscle condition index have been used by veterinarians (Blanshard 1994, Connolly 1999) and in studies of wild koalas (White and Kunst 1990, Prevett 1991, Hasegawa 1995). The koala muscle condition index of Carrick and Wood (1986) (modified from Dickens (1978) and Wood (1978)) was correlated with percent body water, and body water was correlated with body fat (Ellis and Carrick 1992). The body fat of koalas is very low, ranging between 0.87 and 3.72% of total body mass (Ellis and Carrick 1992).
Koalas are sexually dimorphic (McNally 1957, Nagy and Martin 1985). Adult koalas from Queensland are smaller (females, mean = 4.5 kg; males, mean = 6.5 kg) (Smith 1979a) than adult koalas from Victoria (females, mean = 8.3 kg; males, mean = 11.8 kg) (Martin and Lee 1984, Martin and Handasyde 1990a, Martin and Handasyde 1995). Martin (1985b) and Martin and Handasyde (1990a) found variation in adult koala body mass both within and between populations in Victoria and attributed these differences to diversity in both quality and quantity of available food.

Assessing body condition using three techniques, size-mass index, muscle score and body mass, allows for the evaluation of body condition with different assumptions. Koalas provide an excellent model to investigate the effects of disease and poor habitat condition on body condition due to the large variation in habitat condition and differing disease status of Victorian koala populations.

**Aims**

The primary aim of this chapter is to examine the relationship between koala population condition and tree defoliation (habitat condition), and also the relationship between koala population condition and *Chlamydia*-infection status of the population. Further, this chapter aims to ascertain whether condition is correlated with parameters such as fecundity and age; and therefore elucidate its impact on population dynamics. In order to achieve this, a new morphometric condition index is derived for koalas. Possible seasonal variation in body mass of koalas is investigated to ensure that it is reasonable to compare age-specific body mass between populations sampled in different seasons.
Methods

Study sites, koala populations and data collection

Study sites and data collection methods for Snake Island, Framlingham, Mt Eccles and French Island are described in the “Main study sites” section in Chapter 2. The Brisbane Ranges, Phillip Island and the Koala Conservation Centre (KCC) study sites and data collection methods are described in the “Additional study sites” section in Chapter 2. Information on habitat condition at Snake Island, Framlingham, Mt Eccles and French Island was sourced from the Centre for Environmental Management University of Ballarat (2002, 2003), Ingeme et al. (1998) and Kelly (2000).

Mass

It is most appropriate to study seasonal variation in body mass longitudinally, by taking multiple measurements from known individuals across time (Chabot and Stenson 2002). Monthly body masses of tagged adult koalas on French Island (1982 and 1983) and the Brisbane Ranges (1986 and 1987) and of fertile and infertile female koalas from Phillip Island (1982 and 1983) were analysed (K. Handasyde and R. Martin, unpublished data). The masses of individuals over the months October – March were compared using a paired t-test with the corresponding mass for the months April – September 1982. The choice of these time periods was based on the availability of the data throughout the months. The seasonal variation in body mass of males and females was tested separately as koalas are sexually dimorphic.

When comparing adult mass between samples and sites with different disease status and habitat condition, data from physically immature animals (see Chapter 3) were analysed separately. The average body mass of koalas at the KCC was calculated from all the body mass measurements taken after the individual koala was 36 months of age (Chapter 3). The mean of these measurements for each individual represented the average adult body mass for each koala. Data were screened for independence and normality. ANOVA testing only proceeded if box plots were even and Levene’s tests were non-significant. Some samples were not tested due to unequal sample sizes.
(males at Snake Island sampled in 2000 and 2001, and on French Island sampled in 2000 and 2001) but were included in graphs for visual comparisons.

**Body condition**

*Morphometric condition index*

The “hybrid” condition index used linear regression of skeletal size (x-variable) against body mass (y-variable) to predict a mean mass for a particular size (see Krebs and Singleton 1993). The ratio of the observed to the predicted mass describes the condition of each individual. This is termed the morphometric condition of the individual. Head length was used to measure the size of an individual, as this is a repeatable measurement in both adult and juvenile koalas. Regression equations were calculated separately for males and females for all sites and sampling periods combined. Separate regression equations were calculated for dependent (head length < 103 mm) and independent (head length > 103 mm) koalas (defined in Chapter 3). Only dependent koalas that were large enough to be detached from the teat and weighed were included in the analysis.

Individual dependent koalas (caught only once) were only compared for Snake and French Islands as sampling at Framlingham and Mt Eccles in autumn meant that pouch-young were too immature to be removed and weighed. Condition of koalas at different sites and sampling periods was compared with ANOVAs. The morphometric condition of koalas from populations with different *Chlamydia*-infection status was compared with ANCOVAs, controlling for TWC.

Mean head length was compared between sites separately for independent males and females to check whether body size at each site in each sample was similar and therefore ensure that body condition comparisons were not biased.

*Muscle condition index*

Muscle condition was assessed using a subjective three-point index modified from Dickens (1978) and Wood (1978) based on the relative size of the muscle mass (*muscularis trapezius*) compared with size of the dorsal spine of the scapula. In koalas
in good condition the muscle bulged next to the spine of the scapula. In koalas in poor condition the muscle mass was dish shaped and difficult to detect. This condition score was used to assess adults at Snake Island in 1999, 2000 and 2001, Mt Eccles in 2001 and French Island in 2000 and 2001. The proportion of the population in each muscle condition class was compared for independent females and males between populations using contingency tables and adjusted residuals. If the absolute value of the adjusted residuals was greater than 1.96, the adjusted residual was significant at $\alpha = 0.05$ (see Everitt 1986).

**Clinical signs of disease**

Systematic observations of disease in koalas were made at Snake Island in 2000 and Mt Eccles in 1999 and 2001 using observable (external) symptoms. Koalas were recorded as having i) no clinical signs, ii) urinary tract disease resulting in “dirty tail” or a faeces pad adhered near their cloaca, iii) cloudy corneas, or iv) keratoconjunctivitis commonly referred to as “pink-eye” (unilateral or bilateral). Koalas that had both cloudy cornea and pink-eye were classified as having pink-eye and koalas that had both cloudy cornea and dirty-tail were classified as having dirty-tail.

Differences in the frequency of occurrence of clinical signs of disease were compared between 1999 and 2001 at Mt Eccles using a contingency table and adjusted residual analyses. The presence or absence of reproductive tract lesions (unilateral or bilateral cysts and/or adhesions in the reproductive tract observable as changes in the gross morphology using a laparoscope) in female koalas was recorded at Mt Eccles in 2001 during surgery, which was being conducted for management reasons. The level of clinical signs of disease due to *Chlamydia*-infection and reproductive tract lesions was compared between reproductive females and non-reproductive females using contingency tables.
Results

Seasonal variation in mass of koalas

Mean body mass was significantly greater in females in the period April-September than in the period October-March on French Island (1982-1983) \( t = -7.646, \) d.f. = 12, \( P < 0.001 \), Phillip Island \( t = -5.48801, \) d.f. = 7, \( P = 0.001 \) and at the Brisbane Ranges in both 1986 \( t = -2.706, \) d.f. = 11, \( P = 0.020 \) and 1987 \( t = -3.121, \) d.f. = 11, \( P = 0.010 \) (Figure 5.1). The trend was similar in males on French Island (1982-1983) although not significant \( t = -1.897, \) d.f. = 5, \( P = 0.116 \), probably due to the small sample size. The sample size of the Brisbane Ranges males was too small to be tested in either year. The mean difference in mass of females between the two periods was approximately 250 g (Figure 5.1). This represents a difference of about 3% in mass between the two time periods.

![Figure 5.1](image)

Figure 5.1 Mean body mass (kg) of adult female koalas in the period October - March (diagonal hatching) and April - September (filled bars) on Phillip Island and French Island (1982-1983) and at the Brisbane Ranges 1986 and 1987 (K. Handasyde and R. Martin, unpublished data). Numbers above the bars are sample sizes. Error bars represent one s.e.
A similar pattern of decreased body mass in the summer months was observed when fertile and infertile females were examined separately (Figure 5.2a & b).

Figure 5.2 Seasonal variation in a) mean body mass (kg) and b) body mass of individual adult female koalas on Phillip Island in 1982 and 1983 (K. Handasyde and R. Martin, unpublished data). Blue circles are fertile females ($n = 4$) and red triangles are infertile females ($n = 4$). Data were not available for December or July. Error bars represent one s.e.
Effect of habitat condition and disease status on body condition

The effect of habitat condition and disease status on koala body condition is investigated in terms of body mass, morphometric condition and muscle condition.

Comparisons of mass between populations

The mean mass of koalas in TWC I, II and III was significantly less than that of koalas in other TWCs and it was therefore considered that the end of TWC III or the beginning of TWC IVA was equivalent to physical maturity in both females and males (Chapter 3). As a result, koalas in TWCs I, II and III were excluded when comparing the mass of adults between sites.

Females

Adult female mass was not significantly different between samples within sites (Tukey's post hoc tests); therefore, samples were pooled within sites. Adult female mass was significantly different between sites \( (F = 10.874, \text{ d.f.} = 2, \ P < 0.001) \) although the differences were less than 4% of the sample means (the mean adult female body mass with all populations pooled was 8.5 kg). The mass at Mt Eccles (mean = 8.4 kg) was significantly less than at Framlingham (mean = 8.6 kg) and Snake Island (mean = 8.7 kg) (Figure 5.3). The mean mass of French Island females (mean = 8.3 kg) is included in Figure 5.3 for comparison but was not included in the ANOVA due to the disparity in sample sizes. The female with the largest body mass (12.1 kg, TWC IVC) was caught on Snake Island in 1997. Mean female body mass at these sites falls within the range of other Victorian populations (Figure 5.4).
Figure 5.3 Mean body mass (kg) of adult female koalas at Framlingham, Snake Island, Mt Eccles and French Island. Populations are ordered in terms of degree of defoliation of preferred food trees from high defoliation at Framlingham to lower defoliation at Mt Eccles and French Island. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Values of means and ranges are available in Appendix G. Numbers above the bars are sample sizes. Error bars represent one s.e.
Figure 5.4 Mean body mass (kg) of female (triangles) and male (squares) koalas from eight Victorian populations. Blue and black symbols are sites with *Chlamydia*-free and *Chlamydia*-infected populations, respectively. French Island 1 (FI 1), Framlingham (FM), Koala Conservation Centre (KCC), Mt Eccles (Mt E) and Snake Island (SI) data are from the present study; French Island 2 (FI 2), Walkerville (WK) and the Brisbane Ranges (BR) data are from Martin and Handasyde (1990a); and Raymond Island (RI 1 is reproductive females, RI 2 is non-reproductive females) data are from Mitchell *et al.* (1989) (sample sizes and error not provided). The values of means are available in Appendix G. The numbers above and below the symbols are the samples sizes for males and females, respectively. Error bars represent one s.e.

The differences in mean body mass observed between populations in physically mature adults were not reflected in physically immature koalas (TWC III and II). In TWC III, females at Snake Island in 1997 and 1999 were significantly heavier than females from Snake Island in 2000, Framlingham and Mt Eccles in 1999 and 2001 ($F = 13.147$, d.f. = 5, $P < 0.001$). Females in TWC III on French Island were significantly heavier in 2001 than 2000 (Figure 5.5). Due to the timing of sampling, TWC II females would be different ages between sites. Therefore, TWC II koalas were only compared where sampling occurred at similar times of the year. Females from Mt Eccles were significantly heavier than those from Framlingham ($t = -3.048$, d.f. = 274, $P = 0.003$) (Figure 5.5). Females from Snake Island in 1997 were significantly heavier than in 1999 ($F = 5.342$, d.f. = 2, $P = 0.005$) and mass of TWC II females on French Island did not differ significantly between 2000 and 2001, although the actual differences may have been as large as in the other populations (Figure 5.5).
Figure 5.5 Mean body mass (kg) of female koalas at each site in a) tooth wear class (TWC) III and b) TWC II. Sites are ordered in terms of degree of defoliation of preferred food trees from high defoliation at Framlingham to lower defoliation at Mt Eccles and French Island. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Numbers above bars are sample sizes. Error bars represent one s.e.
Males

Adult (TWC IVA and above) mass of male koalas was not significantly different between samples within sites (Tukey’s post hoc tests); therefore, samples from Snake Island 1997 and 1999 were pooled, as were samples from Mt Eccles 1999 and 2001. Male mass was significantly different between sites ($F = 31.613$, d.f. = 2, $P < 0.001$). Males at Snake Island (mean = 11.0 kg) were heavier than Mt Eccles males (mean = 10.4 kg), which were heavier than Framlingham males (mean = 9.9 kg) (Figure 5.6). French Island males (mean = 10.9 kg) are included in Figure 5.6 for comparison but were not included in the statistical analysis due to the inequality in sample sizes. The male with the heaviest body mass (14.3 kg) was caught from Mt Eccles in 2001. The mean adult male body mass for all populations combined was 10.7 kg.

![Figure 5.6 Mean body mass (kg) of adult (TWC IV+) male koalas at Framlingham, Snake Island, Mt Eccles and French Island. Sites are ordered in terms of degree of defoliation of preferred food trees from high defoliation at Framlingham to lower defoliation at Mt Eccles and French Island. Blue bars are sites with Chlamydia-free populations and black bars are sites with Chlamydia-infected populations. Numbers above the bars are sample sizes. Error bars represent one s.e.](image)

TWC III males did not differ in mass between samples within sites but differed significantly between sites, with Snake Island males being heavier than those at Mt Eccles, and Mt Eccles males heavier than those at Framlingham ($F = 35.074$, d.f. = 2, $P < 0.001$) (Figure 5.7a). As with females, males in TWC II were only tested against those that were sampled at a similar time of year. Males in TWC II at Mt Eccles were significantly heavier than males from Framlingham ($t = -6.73$, d.f. = 291, $P < 0.001$),
and males from Snake Island in the 1997 sample were significantly heavier from those sampled in 1999 ($t = 4.276$, d.f. = 184, $P < 0.001$). Mass of TWC II males on French Island was similar in 2000 and 2001 (Figure 5.7b).

![Graph](image_url)

Figure 5.7 Mean body mass (kg) of male koalas in a) TWC III and b) TWC II at each site and sampling period. Sites are ordered in terms of degree of defoliation of preferred food trees from high defoliation at Framlingham to lower defoliation at Mt Eccles and French Island. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Numbers above the bars are sample sizes. Error bars represent one s.e.
Comparisons of morphological condition between populations

The difference in mean adult head length between populations was considered in order to ensure that body size was relatively similar at each site. The difference between sites in the mean female head length was only 1 mm (means: 136 to 137 mm). The largest head length for females (155 mm) was recorded at both Framlingham and Mt Eccles in 2001. The range of adult male mean head lengths between sites was 8 mm (means: 151 to 159 mm). Two males from Mt Eccles had the largest recorded head length of 178 mm. As body size (measured by head length) was relatively similar at each site, it was considered that the morphometric condition index was not biased.

Morphometric condition indices were calculated from separate regression equations for dependent and independent koalas. These were separated on the basis of the head length at which most individuals had become independent from their mothers (for all samples and sites), which was 103 mm (see Chapter 3).

Scatter plots of head length against mass of individuals with a head length over 103 mm revealed an approximately linear relationship for both males and females. However, the residual plots were cone shaped suggesting that the variances were not homogeneous over the range of head lengths. Taking the log of both head length and mass improved the homogeneity of variances. For independent koalas from Snake Island, French Island, Mt Eccles and Framlingham, linear regression was used to estimate the relationship between Ln head length and Ln body mass (Figure 5.8):

Females: \( \ln \text{mass} = 2.800\ln \text{head length} - 11.749, \quad r^2 = 0.796, \quad n = 2352 \)

Males: \( \ln \text{mass} = 2.493\ln \text{head length} - 10.351, \quad r^2 = 0.872, \quad n = 1918 \)
Figure 5.8 Relationship of Ln head length against Ln body mass of independent koalas (individuals with head length greater than 103 mm). a) females, \( n = 2352 \), Ln mass = \( 2.800 \times \text{Ln head length} - 11.749 \), \( r^2 = 0.796 \); and b) males, \( n = 1918 \), Ln mass = \( 2.493 \times \text{Ln head length} - 10.351 \), \( r^2 = 0.872 \).
The morphometric condition of each individual was calculated using the regression equations above. The mean morphometric condition of females was significantly different between sites and sampling periods ($F = 33.31$, d.f. = 7, $P < 0.001$). The mean morphometric condition score of females was greater in 2001 than 2000 at both Snake and French Island (Figure 5.9a). Mean morphometric condition of males was also significantly different between sites and sampling periods ($F = 26.676$, d.f. = 7, $P < 0.001$) (Figure 5.9b). The pattern of morphometric condition between sites and sampling periods was similar between females and males with a large decrease in condition at Snake Island between 1999 and 2000.
Figure 5.9 Mean morphometric condition for each site and sampling period for a) female and b) male koalas. Sites are ordered in terms of degree of defoliation of preferred food trees from high defoliation at Framlingham (Fram) to lower defoliation at Mt Eccles and French Island. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Numbers above the bars are sample sizes. Error bars represent one s.e.
Comparison of muscle condition between populations

Muscle condition differed between sites and sampling periods in both females and males. At Snake Island in 1999 and 2000 there was a significantly lower proportion of females in good condition and a significantly higher proportion of females in average condition than at Snake Island in 2001 and Mt Eccles in 2001. There was a significantly higher proportion of females in poor condition at Snake Island in 2000 than at Mt Eccles in 2001 and French Island in 2000 and 2001 ($\chi^2 = 93.39$, d.f. = 8, $P < 0.001$) (Figure 5.10a). At Snake Island in 1999 and Mt Eccles in 2001 there was a significantly lower proportion of males in good condition and a higher proportion of males in average condition than at Snake Island in 2001 and French Island in 2000 and 2001 ($\chi^2 = 45.12$, d.f. = 8, $P < 0.001$) (Figure 5.10b). Thus, in general, females were in better condition at Snake Island in 2001, Mt Eccles in 2001 and French Island than at Snake Island in 1999 and 2000. Males were generally in better condition at Snake Island in 2001 and French Island than at Mt Eccles in 2001 and Snake Island in 1999.
Figure 5.10 Muscle condition in a) female and b) male koalas at Snake Island in 1999, 2000, and 2001, Mt Eccles in 2001 and French Island in 2000 combined with 2001. Filled bars represent koalas in good condition, open bars are koalas in average condition and diagonal hatched bars are koalas in poor condition. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Numbers above bars represent sample sizes.
Morphometric condition was significantly greater in both female and male koalas from *Chlamydia*-free populations than from *Chlamydia*-infected populations (females: $F = 52.45$, d.f. = 1, $P < 0.001$; males: $F = 26.76$, d.f. = 1, $P < 0.001$) (Figure 5.11).

![Figure 5.11](image)

**Figure 5.11** Mean morphometric condition and *Chlamydia*-infection status of the population of a) female and b) male koalas. *Chlamydia*-infected populations are Snake Island and Mt Eccles; *Chlamydia*-free populations are Framlingham and French Island. Numbers above the bars are sample sizes. Error bars represent one s.e.
Muscle condition and *Chlamydia*-infection status was not compared using statistical tests due to the disparity in sample sizes; however, *Chlamydia*-free populations had a higher percentage of both females (Figure 5.12a) and males (Figure 5.12b) in good condition than *Chlamydia*-infected populations.

Figure 5.12 Percentage of a) female and b) male koalas from *Chlamydia*-free (blue bars) and *Chlamydia*-infected populations (black bars) in each muscle condition class. Females: *Chlamydia*-free *n* = 1347, *Chlamydia*-infected *n* = 161; males: *Chlamydia*-free *n* = 976, *Chlamydia*-infected *n* = 101. *Chlamydia*-infected populations are Snake Island and Mt Eccles; *Chlamydia*-free populations are Framlingham and French Island.
Clinical signs of disease

A small percentage of females (6.4%) and males (3.5%) at Snake Island and Mt Eccles had clinical signs of *Chlamydia* (Figure 5.13). At Mt Eccles, there was no evidence of a difference between 1999 and 2001 in the proportion of females ($\chi^2 = 4.96$, d.f. = 3, $P > 0.90$) or in the proportion of males ($\chi^2 = 6.93$, d.f. = 3, $P > 0.05$) with clinical signs of *Chlamydia*.

In females, the most common clinical sign was dirty tail (2.9%), followed by cloudy corneas (2.6%), and pink-eye (0.9%), whereas in males the most common clinical sign was pink-eye (1.9%). Pink-eye only occurred in 9.5–13 kg males but cloudy corneas were found in males ranging from 2 to 11 kg. Clinical signs were only found in females greater than 6 kg. Forty five percent of females that had clinical signs of disease ($n = 80$) also had reproductive tract lesions. Of the 633 females with no clinical signs at Mt Eccles in 2001, 28.4% had reproductive tract lesions. These were only found in females greater than 5 kg. The percentage of females with reproductive tract lesions increased from 3% of TWC I females to 30% of TWC III and 41% of TWC IVA females (Figure 5.14) (See Appendix H for data).

![Clinical signs of disease](image)

**Site, sampling period and sex**

Figure 5.13 Percentage of female and male koalas from Snake Island in 2000, and Mt Eccles in 1999 and 2001, with clinical signs of *Chlamydia*: dirty tail (filled bars), cloudy cornea or blind (open bars) and pink-eye (diagonal hatching). Numbers above the bars are sample sizes.
Figure 5.14 Proportion of female koalas in each tooth wear class (TWC) that have no sign of *Chlamydia* (filled bars); reproductive tract lesions (diagonal bars); or clinical signs of *Chlamydia* including dirty tail, corneal opacities and pink-eye (vertical bars). See Appendix H for percentages. The data was pooled for Snake Island in 2000 and Mt Eccles in 1999 and 2001. Numbers above bars are sample sizes.

The percentage of koalas with clinical signs of disease increased as muscle condition decreased (Figure 5.15). In the poor muscle condition class there was a similar percentage of females with (7.4%) and without (5.6%) clinical signs of *Chlamydia*. Five percent of males without signs of *Chlamydia* were in the poor muscle condition class compared with 17% of males with clinical signs of disease.

Figure 5.15 Percentage of female (triangles) and male (squares) koalas with clinical signs of *Chlamydia*, in each muscle condition class. The data were pooled for Snake Island in 2000, and Mt Eccles in 1999 and 2001. Numbers above the symbols are sample sizes. Error bars represent one s.e.
Population dynamics and body condition

This section investigates the correlation between the reproductive status of females and body condition and signs of disease, as well as the correlation between age and body condition, and also factors related to the condition of dependent koalas.

The reproductive status of females, body condition and signs of disease

Morphometric condition was significantly greater in reproductive females compared with non-reproductive females ($F = 44.987$, d.f. = 1, $P < 0.001$) (Figure 5.16). Reproductive females had significantly better muscle condition scores than non-reproductive females ($\chi^2 = 7.61$, d.f. = 2, $P < 0.025$) (Figure 5.17). Non-reproductive females had significantly more (almost three times as many) reproductive tract lesions, and greater prevalence of dirty tail than reproductive females (29.9%, $n = 927$; 10.5%, $n = 516$, respectively) ($\chi^2 = 77.79$, d.f. = 4, $P < 0.001$).

Figure 5.16 Mean morphometric condition of reproductive and non-reproductive female koalas, pooled over all sites and sampling periods. Numbers above the bars are sample sizes. Error bars represent one s.e.
The relationship between body condition and TWC

The morphometric condition of both female and male koalas differed significantly with TWC (female: \( F = 2.651, \text{d.f.} = 8, P = 0.007 \); male: \( F = 7.542, \text{d.f.} = 8, P < 0.001 \)); however, Tukey’s test revealed that only TWC I differed significantly from the other TWCs (except TWC VI in males) (Figure 5.18). TWC VII was excluded from the analysis due to the low sample sizes (females: \( n = 1 \); males: \( n = 3 \)). Muscle condition was also related to TWC. In both females and males, younger koalas (TWCs I and II) had significantly better muscle condition scores than middle and older age koalas (TWCs III – VI) (females: \( \chi^2 = 282.20, \text{d.f.} = 8, P < 0.001 \); males: \( \chi^2 = 149.16, \text{d.f.} = 8, P < 0.001 \)) (Figure 5.19).
Figure 5.18 Mean morphometric condition of a) female and b) male koalas in each tooth wear class. Numbers above the bars are sample sizes. Error bars represent one s.e.
Figure 5.19 Percentage of a) female and b) male koalas in each muscle condition class in each tooth wear class. Filled bars represent koalas in good condition, open bars are koalas in average condition and diagonal hatched bars are koalas in poor condition.
Morphometric condition of dependent koalas

A scatter plot of head length against mass of individuals with a head length less than 103 mm revealed that the relationship was not linear. The equation of the curve was estimated using 3 methods: a quadratic equation, taking the log of both axes, and using non-linear parameter estimation in the software SPSS (9.0). The value of the correlation coefficient, normality of the residuals and the suitability of the general shape of the curve determined the log log curve as the most appropriate (Figure 5.20). Thus, the relationship between head length and body mass for dependent koalas from data pooled from Snake Island and French Island is given by the following equation:

\[
\text{Mass} = 1.5 \times 10^{-8} \times \text{head length}^{4.095}, \quad r^2 = 0.868, \quad n = 250
\]

Equation 5.1

Figure 5.20 Relationship (on a log-log scale) between head length (mm) and body mass (kg) of dependent female (red squares) and male (green squares) koalas (head length < 103 mm) from Snake and French Islands, \( n = 250 \).
**Condition of dependent koalas and sex, site and maternal characteristics**

Morphometric condition of dependent koalas was significantly higher for female than male dependent koalas \( (F = 5.087, \text{d.f.} = 1, P = 0.025) \) and varied significantly with site and sampling period \( (F = 3.156, \text{d.f.} = 4, P = 0.015) \) (Figure 5.21). Morphometric condition was significantly higher at Snake Island in 1999 than at Snake Island in 2000 and French Island in 2001. The interaction of sex and sampling period was not significant \( (F = 0.288, \text{d.f.} = 4, P = 0.886) \). The condition of female and male dependent koalas was not correlated with maternal condition (female: \( r^2 = 0.005 \), male: \( r^2 = 0.05 \)), maternal mass (female: \( r^2 < 0.001 \), male: \( r^2 = 0.02 \)), or maternal TWC (female: \( r^2 = 0.006 \), male: \( r^2 = 0.004 \)).

Figure 5.21 Mean morphometric condition of female (hatched bars) and male (filled bars) dependent koalas from Snake and French Islands. Blue bars are sites with *Chlamydia*-free populations and black bars are sites with *Chlamydia*-infected populations. Numbers above bars are sample sizes. Error bars represent one s.e.
Comparison of morphometric and muscle condition indices

There was a relationship between the mean morphometric condition score and the average muscle condition class (Figure 5.22). Females with a poor muscle condition score had a significantly lower morphometric condition score ($F = 7.686$, d.f. = 2, $P < 0.001$). Males with good muscle condition had a significantly higher morphometric condition score than males in average muscle condition, which in turn had a higher morphometric condition score than males in poor condition ($F = 23.332$, d.f. = 2, $P < 0.001$). However, the differences in the mean morphometric condition between good and poor muscle condition are small relative to the variation between individuals within a muscle condition class. Also, due to the large degree of variation in the data (Figure 5.22), there was very little relationship between muscle condition and morphometric condition in individual cases in both females ($r^2 = 0.00$) and males ($r^2 = 0.03$).
Figure 5.22 Boxplots of a) female and b) male koala morphometric condition score for each muscle condition class: good, average and poor. Boxes represent the interquartile range (50% of observations), the thick black horizontal lines are the medians, vertical lines extend to the highest and lowest values excluding outliers (represented as circles). Outliers are defined as 1.5-3 times the interquartile range from the upper or lower edge of the interquartile range. Numbers above the bars are sample sizes. Error bars represent one s.e.
Discussion

Overall, the results of the present study indicate that poor habitat condition (sites with a high degree of defoliation of preferred food trees) and positive disease status of the population are correlated with poorer average body condition of the koala population; however, the results differed between the sexes and between years. In addition, the morphometric (ratio of observed mass to that predicted from a regression of skeletal size against observed body mass) and muscle condition indices produced conflicting results with regard to some variables. In order to consider differences in mass and condition between populations, it is necessary to take into account seasonal variation in body mass. Thus, this discussion begins by examining seasonal variation in body mass before discussing the correlation between the body condition of koalas and their habitat, followed by the correlation between the body condition of koalas in populations with different Chlamydia-infection status. Finally, the effect of body condition on population dynamics is considered.

Seasonal variation in body mass and condition

"Winter fattening" has been observed in many species (Witter and Cuthill 1993, Schultz and Conover 1997, Rozman et al. 2003). Both male and female koalas increased in body mass in winter relative to summer. The 3% seasonal increase in mass of female koalas from the Brisbane Ranges, Phillip Island and French Island (1982-1983) found in the present study is similar to that found in koalas from Queensland by Ellis et al. (1995). Dietary intake of koalas has been found to be higher in winter than summer (Harrop and Degabrielle 1976, Cork 1986, Krockenberger 1993, Ellis et al. 1995). Seasonal variation in body mass may be due to a number of reasons including thermoregulatory requirements and changes in reproductive activities, including lactation and greater movement in searching for mates. Animals may change their behaviour seasonally in order to reduce thermoregulation costs (Arnold et al. 1988, Holloway and Geiser 2001, Thomas and Cuthill 2002). The similar degree of seasonal variation in body mass in non-lactating female koalas suggests that environmental factors, such as climate, have a large impact on variation in body mass.
Reproductive activities during the breeding season may lead to a decrease in body mass (Sand et al. 1995, Ganzhorn 2002). The koala breeding season occurs during the summer months (Chapter 6) and most back-young are usually weaned in October and November. In females, lactation may result in a decrease in body mass (Millis and Bradley 2001). However, in the present study, infertile Phillip Island female koalas (non-lactating) decreased in mass in a similar manner to fertile female koalas. This implies that a heavy lactation load and corresponding energy demand (Krockenberger et al. 1998) is not the only reason for the decrease in body mass. There may be compensation for the increased energy demands given that lactating female koalas eat more than non-lactating females (Krockenberger 1993, Logan and Sanson 2003). This has also been found in other herbivorous species (Ruckstuhl and Festa-Bianchet 1998, Neuhaus and Ruckstuhl 2002). Additionally, activities such as searching and competing for mates may cause a decrease in body mass during the breeding season (Ryser 1992). Energy expenditure is increased in male koalas during the breeding season with increased ranging behaviour and fighting between males (Mitchell 1990a). For animals on a very low energy budget (Cork and Sanson 1990), this increase in activity may cause the observed decrease in mass during the breeding season. Thus, the increase in body mass of male koalas and fertile and infertile female koalas in the colder months may be due to a combination of increased thermoregulatory requirements and a decrease in energy expenditure relative to the breeding season.

**Body condition and habitat condition**

The seasonal variation in mass of koalas (controlling for sex and age) would imply that animals at Framlingham and Mt Eccles (sampled in Autumn/Winter) should be heavier than Snake and French Island koalas (sampled in Spring/Summer). Conversely, the Mt Eccles and Framlingham male koalas were found to be lighter than the Snake Island koalas, indicating that the effect of differences in body mass is actually stronger but is partially masked by seasonal variation in mass.

Low body mass of adult, TWC III and TWC II male koalas occurred at sites with severe defoliation of preferred food tree species. Defoliation was severe at Framlingham, medium at Snake Island and Mt Eccles and light on French Island (see
The food trees were severely defoliated, with the average condition of all of the transects (containing manna gums) classified as dead at Framlingham (Ingeme et al. 1998), 32% of individual trees dead at Snake Island (Centre for Environmental Management University of Ballarat 2002), 19% dead at Mt Eccles (Kelly 2000) and 6% dead or exhibiting severe defoliation on French Island (Centre for Environmental Management University of Ballarat 2003). At Mt Eccles there was also reduced mean foliage cover compared with control sites (Madrau 1999). The mean foliage cover of manna gums at Framlingham was less than one fifth of that at Mt Eccles (Madrau 1999). Male body mass differed between sites; koalas with the smallest age-specific body mass and head length were found at Framlingham where defoliation was the most severe. This suggests that koalas at Framlingham were experiencing a food shortage. The morphometric body condition index did not, however, indicate that male koalas from Framlingham were in the poorest condition compared with the other sites. Since koalas from Framlingham were smaller, this may imply that growth of koalas at Framlingham was impaired due to the high degree of defoliation of preferred food trees. The mean mass of adult male koalas at Framlingham was lower than at all other populations in Victoria, other than Walkerville (Martin and Handasyde 1990a) (Figure 5.4). The degree of defoliation at Framlingham was similar to that at Walkerville where 40% of the preferred food trees were dead (Martin 1985b). Martin (1985b) found that male koalas at Walkerville were smaller in both head length and body mass than on French Island. He attributed the poor condition of the Walkerville koalas to the severe food shortage that resulted from over browsing (Martin 1985a). Gordon et al. (1988) found that body mass of koalas (controlling for head length) was lower at sites with severe leaf-fall (as a consequence of drought) than at sites with normal crown cover. This is consistent with the notion that the small body mass (mean body mass of 9.9 kg) and structural size (mean head length of 151 mm) of adult male koalas at Framlingham may have been due to a shortage of food throughout the growth period.

The variation in body mass observed in males between populations was different from that observed in females. For example, adult females at Framlingham were heavier on average than females at Mt Eccles, whereas males at Framlingham were lighter than males in other populations. Mean body mass of adult females at the sites examined in this study fell well within the range found at other sites (Figure 5.4). Thus, it seems
that males are affected by severe defoliation to a greater degree than females despite the large energy demand that lactation places on females (Krockenberger 1996). Martin (1985b) also found that the female koalas with limited access to food at Walkerville were similar in body mass to females from French Island. The greater susceptibility of males to changes in resource availability has been shown in other mammalian species (Leberg and Smith 1993, Bourgarel et al. 2002). Males may be more vulnerable to food shortages due to the larger body size of males compared with females, with higher nutritional requirements necessitating a greater absolute quantity of resources (Clutton-Brock et al. 1982). In addition, female koalas may have greater access to food resources compared with males as females can feed further towards the extremities of the canopy due to their smaller body size (Martin 1985b). The differences between the sexes may also be due to the differences in growth period as females reach physical maturity at an earlier age than males; and thus, may then allocate resources between reproduction and storage while males are continuing to allocate resources to growth (Fedigan and Zohar 1997). Interestingly, a comparison of females at Framlingham and Mt Eccles showed that TWC II females were on average 500 g lighter at Framlingham. In TWC III, the mass of females was similar at the two sites, and in the adult category (physically mature), females were slightly heavier (200 g) at Framlingham. This pattern may indicate that the growth of females in highly defoliated habitat is affected but the female koalas still manage to attain a similar adult body mass as female koalas in lightly and non-defoliated habitats.

To be practical for use in the field, condition measures need to be quick, easy and inexpensive to conduct, repeatable between observers and have low measurement error. Condition measures should also be comparable between different sized animals and between populations and should be responsive to small changes in condition (Speakman 2001). Finally, a change in condition should indicate a change in the chance of survival, fecundity or future reproductive success of an individual or its offspring (Boltnov et al. 1998). Morphometric condition indices have been criticised for being ill-defined and for not measuring an aspect of the population’s evolutionary fitness, such as the chance of survivorship or probability of fecundity (Hayes and Shonkwiler 2001). Additional criticism has suggested that these indices do not measure the “fatness” of an animal (Martin 1985b). Knowledge of body fat may not provide information on nutritional quality/condition if the animal cannot use all of the
stored fat (Pond 1978). In the present study, the morphometric condition index is simply intended to represent a measure of the mass (that is, a measure of the resources available to the animal) while controlling for size (measured as head length). Compared with other methods of assessing koala body condition such as haematological parameters, the morphological condition index is simple, inexpensive, non-invasive, and time efficient. It also provides a less subjective assessment of body condition than the muscle condition score and it is highly repeatable between observers. Given the ease of assessment of both the morphometric and muscle condition indices, it is valuable to assess both. For programs such as koala translocations in Victoria, the morphometric body condition index provides a technique for assessing the suitability of an individual for translocation, perhaps in conjunction with other measures of condition such as blood parameters (Parks Victoria 2003).

The pattern of differences in body condition of both males and females between populations was difficult to interpret as it differed between the morphometric and muscle condition indices and also varied between years at sites. The correlation between the morphometric condition index and the muscle condition classes was very low due to the large degree of variation in the data (Figure 5.22). Head length would not be expected to affect the interpretation of comparisons between populations of the morphometric condition index in females as the mean head length differed by only 1 mm. In males, Framlingham koalas had a smaller mean head length than koalas at Snake Island or Mt Eccles, but the mean difference in head length between Mt Eccles in 1999 and 2001 (3 mm) did not cause a difference in morphometric condition between those two samples.

**Body condition and disease status**

A low percentage (less than 6%) of koalas exhibited clinical signs of *Chlamydia*. These results are similar to those found by Martin et al. (1988) and Handasyde (1986) in several southern Australian koala populations where pink-eye and dirty tail were detected in less than 5% of individuals in *Chlamydia*-infected populations. Varying rates of disease due to *Chlamydia* between infected populations may also be due to infection with different *Chlamydia* species, *C. pneumoniae* and *C. pecorum* (Glassick
et al. 1996, Jackson et al. 1997). Jackson et al. (1999) proposed that different levels of infection and clinical disease between populations are probably attributable to environmental or host factors. As the presence of the bacteria does not necessarily result in expression of clinical disease, it has been suggested that other factors such as stress, destruction of habitat or over-crowding may increase the manifestation of clinical disease (Strahan 1985, 1986, Canfield 1990, Ellis et al. 1993, White and Timms 1994).

The percentage of koalas with clinical signs of Chlamydia-infection was relatively constant across all TWCs; however, the percentage of koalas with reproductive tract lesions increased consistently from TWC I to TWC IVA and then remained reasonably constant in TWC IVB and IVC before decreasing in TWC V and VI. Gordon et al. (1990b) found that survivorship was lower in koalas with clinical signs of Chlamydia than in disease-free koalas. Thus, female koalas with clinical signs of Chlamydia were probably under-represented in TWC V and VI as they may have suffered higher mortality than females without clinical signs.

Due to the low numbers of male koalas with clinical signs of disease, it is difficult to draw conclusions about the prevalence of the disease in different demographic groups. Nonetheless, pink-eye, the most common clinical sign of disease in males, only occurred in males that were heavier than 9 kg. This may indicate that physical injury, acquired during fights over access to females (Mitchell 1990b), may aggravate pink-eye. Males with clinical signs of Chlamydia-infection were more likely to be in the poor muscle condition class than males without clinical signs and a comparable pattern was found in female koalas. These results are similar to the findings of White and Kunst (1990). Whether this is cause or effect is unknown.

Male and female koala body condition (measured using both the morphometric and muscle condition indices) was higher in Chlamydia-free populations than in Chlamydia-infected populations except at Snake Island (Chlamydia-infected) in 1999 where koalas were in better body condition than at Framlingham (Chlamydia-free) (Figure 5.11 and Figure 5.12). Also, body condition varied with site and the year of the sample. Due to the low level of clinical expression of disease, the average condition of the population will not necessarily be seriously decreased by Chlamydia-
infection. Although, infection with *Chlamydia* may sufficiently compromise the health of koalas such that other debilitating factors such as food shortage have a greater effect than they would on a population without *Chlamydia*-infection. The degree of defoliation of preferred food trees at the site seemed to override the effect of disease at a population level. For instance, the mean body mass of males at Framlingham was less than at Snake Island. Disease in the form of parasitism and viruses have been found to decrease body mass (Loison *et al.* 1996, Khokhlova *et al.* 2002) and body condition (Newman *et al.* 2002). For example, wombats with severe sarcoptic mange were in poor body condition, had low levels of subcutaneous fat and haematological parameters consistent with anaemia and starvation (Skerratt *et al.* 1999). Although Handasyde (1986) found that individual koalas with serological evidence of *Chlamydia*-infection were able to maintain body mass over a mean period of 2 years, in the present study both morphometric and muscle condition were generally higher in *Chlamydia*-free populations (French Island and Framlingham) than in *Chlamydia*-infected populations (Snake Island and Mt Eccles). A limitation of this finding was that only the chlamydial status of the population, not the individual, was known.

**Additional factors possibly affecting body condition**

In addition to food availability and population disease infection status, a number of factors including soil nutrients and deficiency of trace elements, rainfall patterns and genetic differences may also affect koala body mass and condition.

**Soil nutrients**

Deficiencies in trace elements may affect body condition of mammals (Barker 1961b). Shortages of trace elements such as copper can cause depletion of somatic energy reserves as seen in sheep where it manifests as keratinisation of the wool (Underwood 1977). Limited copper in the plants on Rottnest Island (Barker 1961a) may induce copper depletion and limit body condition in quokkas (*Setonix brachyurus*) (Barker 1961b). Soil fertility can have a large impact on the abundance and distribution of koalas (Cork *et al.* 1990, Norton and Neave 1996). Trace element levels have been measured in koalas and eucalyptus browse (Ullrey *et al.* 1981,
McOrist and Thomas 1984). Copper levels were deficient in some koalas at Raymond Island (Vic) (Thomas et al. 1986) and this has been proposed as the cause of lower body mass in this and other coastal island koala populations including French Island (Martin and Handasyde 1990a). Given that Framlingham koalas are direct descendents of French Island koalas (Martin 1989) and the present study found that male koalas are smaller at Framlingham than French Island, the suggestion that food shortage at Framlingham was the cause of the lower body mass is strongly supported.

**Rainfall patterns**

Rainfall may be a significant factor influencing body condition or population density due to its large influence on the availability of food. Population densities of African herbivores increase with rainfall and co-vary with soil nutrient status (Georgiadis et al. 2003). Preliminary predictive modelling of koala densities in Victoria found that of the site, vegetation and population characteristics, mean annual rainfall was the best predictor of population density (Madrau 1999); however, rainfall did not predict koala population density at Inverness, Queensland (Gordon et al. 1990b). At Springsure (Qld), there was evidence of a negative relationship between population density and rainfall and Gordon et al. (1990b) suggested this was due to koalas dispersing in good seasons but favouring the study site in poor seasons.

There may be a time lag associated with the effect of rainfall on body condition or population response as vegetation takes some time to respond to changes in precipitation (Caughley et al. 1984, Bayliss 1985b, Cairns and Grigg 1993, McCarthy 1996). Increases in population density, may occur within a generation (Lande et al. 2002) but changes in body condition may be considerably quicker. Short et al. (1998) found that the condition of western barred bandicoots (*Perameles bougainville*) increased with high rainfall over the previous two months and red kangaroo population densities increase with rainfall with a time lag (Cairns and Grigg 1993).

In the present study, adult male body mass (and body mass of males in TWC III) was significantly greater at Snake Island than Mt Eccles. It may have been expected that koalas would be in better condition at Mt Eccles than at Snake Island due to the richer volcanic soil at Mt Eccles compared with the sandy soils of Snake Island (Braithwaite
1993) and the lower degree of defoliation and number of dead trees at Mt Eccles (Kelly 2000, Centre for Environmental Management University of Ballarat 2002). However, mean annual rainfall at Snake Island is one and a half times that at Mt Eccles (Bureau of Meteorology) and this may have compensated for the effects of soil nutrients and defoliation. There may be an extended time lag in the response of eucalypt foliage to changes in rainfall; and thus, it may be difficult to detect changes in koala body mass and condition in response to changes in local rainfall.

Interestingly, the body mass (in TWC II and III), morphometric condition and muscle condition of both males and females differed between years at Snake Island. Morphometric and muscle condition scores were higher in 2001 than in 2000 at both Snake Island and French Island. This may be related to the rainfall in both the year of measurement and the previous year as annual rainfall increased at both Snake Island and French Island by approximately 100 mm from 1999 to 2000 and by the same amount from 2000 to 2001 (Bureau of Meteorology). Other possible explanations for changing body mass and condition include the wildfire at Snake Island (in January 2000) that may have promoted new foliage growth. Increasing body condition with decreasing density of koalas is consistent with the koalas at Snake Island in 2001 being in better condition than those in 2000, and those in 2000 being in better condition than those in 1999. The changes in body condition are probably not due to demographic causes as the population age structure was stable between the years (Chapter 4).

Genetic differences

Differences in body size and body mass may also be attributed to genetic differences between populations. Despite small sample sizes prohibiting controlling for age, Melzer (1995) considered that significant differences in the morphology of two koala populations in central Queensland might represent separate genetic populations. Due to a combination of koala population decline in the late 1900s (Martin and Handasyde 1995) and the translocation program in Victoria, there is an extremely low level of genetic diversity between populations (Houlden et al. 1996, Houlden et al. 1999). Consequently, it is unlikely that differences in morphology between Victorian koala populations are due to genetic differences.
Body condition and population dynamics

Female fecundity

The body condition of females may affect population dynamics via its impact on fecundity (Guinet et al. 1998). The results of the present study show that this is the case in koalas. Both the morphometric condition index and the muscle condition index indicated that reproductive female koalas had better body condition than non-reproductive females. It might be expected that only females with sufficient energy reserves could afford to attempt to wean a young (e.g. Guinet et al. 1998). Conversely, it may be predicted that reproductive females would be in relatively poor condition as they would have a heavy lactational load. Lactation drained body reserves and caused poor body condition in red deer (Clutton-Brock et al. 1982); however, there was no decrease in either body mass or condition with the increasing demands of lactation in eastern barred bandicoots (Reimer and Hindell 1996). Additionally, parental body condition may influence population dynamics through survival and recruitment of juveniles. Body condition and survival of snow petrel chicks (Pagodroma nivea) were correlated with the body condition of parents (Tveraa and Christensen 2002). Survival until fledging of sandwich tern chicks (Sterna sandvicensis) was strongly affected by the mother’s body condition (Stienen and Brenninkmeijer 2002). Thus, body condition of females may affect not only whether young are produced, but also whether they are weaned/fledged. This may be especially pertinent in marsupials where the young at birth is extremely altricial (effectively young are cheap to produce) and most of the resources are provided during lactation (Tyndale-Biscoe and Renfree 1987).

The present study demonstrates that non-reproductive females had significantly more reproductive tract lesions and clinical signs of Chlamydia than reproductive females and that the proportion of females with reproductive tract lesions increased with age. Over a quarter of the females at Mt Eccles in 2001 that did not have external clinical signs of Chlamydia, had reproductive tract lesions. The results of the present study showed that these pathologies did not always cause infertility in females, as there were some reproductive females with lesions. Additionally, there were non-
reproductive females present that did not have similar pathologies. These results were consistent with the findings of Obendorf and Handasyde (1990) and Brown et al. (1984). Infertility in individual females may be due to the extent and severity of lesions in the reproductive tract (Obendorf and Handasyde 1990). It has been argued that a *Chlamydia*-infected population may exhibit relatively low levels of clinical signs of disease, but if stressed by processes such as increased habitat clearing (White and Kunst 1990, Ellis *et al.* 1993), high population densities (Canfield 1990), or urbanisation (Hall 1994), then the level of clinical expression increases. There was no evidence that the high koala population density and defoliation of food trees (and presumed subsequent stresses) increased the prevalence of clinical signs of *Chlamydia* at Mt Eccles or Snake Island.

**Age structure**

Body condition may also affect population dynamics through changes in the age structure. This may be due to the effects of body condition on fecundity and survival in different age classes. Muscle condition (but not morphometric condition) declined with age in a similar pattern in female and male koalas. Clutton-Brock *et al.* (1982) and Mysterud *et al.* (2001) showed a similar trend in female red deer after 7 years of age; however, many studies have insufficient sample sizes or group animals into a limited number of classes and thus, are unable to demonstrate trends of changing condition with age.

The consistent decline in the proportion of koalas in good condition with age may be due to increased tooth wear. Tooth wear results in reduced mastication efficiency and production of larger sized food particles, which affects digestibility (Lanyon and Sanson 1986b). Logan and Sanson (2002) found that koalas with a high level of tooth wear spent longer feeding and chewed a greater number of leaves each day compared with younger individuals. These results suggest that many koalas with increasing tooth wear may not fully meet the energy requirements required to achieve peak body condition. This has also been found in other herbivores (Kojola *et al.* 1998). Decreasing muscle condition with increasing age was also correlated with an increasing proportion of females with reproductive tract lesions. Decreased body
condition as a result of age and disease in older tooth wear classes may make it increasingly difficult for females to successfully reproduce.

**Condition of juveniles**

It might be expected that the body condition of juveniles would be affected by the body condition of their mothers, and therefore, would be an additional factor that would influence population dynamics. However, the morphometric condition of dependent koalas was not correlated with any maternal characteristics tested; morphometric condition, body mass or TWC. The condition of dependent koalas may only be affected subsequent to weaning and there was not a sufficiently large sample of juveniles over this time period to elucidate any trends. Mitchell (1990c) found that the mass of koala young at independence was correlated with the body mass of their mother. Despite the absence of a correlation between morphometric condition of dependent koalas and their mother in the present study, the mean morphometric condition of both dependent and independent young was significantly greater in Snake Island in 1999 than 2000. Thus, condition of juveniles and adults may follow similar temporal patterns.

Mean morphometric condition of dependent koalas was lower in males than females. The energy content of milk is quite variable between individual female koalas (Krockenberger 1996); hence, dependent koalas with greater resource availability may allocate the additional energy to growth rather than storage and the observed trend may be due to different strategies between the sexes. That is, males may allocate all extra resources into growth as larger males are likely to gain more mating opportunities, whereas females in good condition may have a greater chance of successfully weaning young.

**Conclusion**

Many factors affected the condition of koalas, and males appeared more susceptible to changes in resource availability than females. In particular, body condition was better in *Chlamydia*-free populations, at sites with the least defoliation and in younger koalas. Also, within *Chlamydia*-infected populations, decreasing muscle condition
with increasing age was correlated with an increasing proportion of females with reproductive tract lesions and clinical signs of *Chlamydia*. Body condition was better in reproductive females than non-reproductive females indicating that reproductive fitness is greater in females with better body condition. At sites with the same disease status, the degree of defoliation may affect the fitness of individuals.
Chapter 6 - Reproduction and fecundity of Victorian koalas

Abstract

This chapter investigates relationships between aspects of fecundity of koalas and the disease status of the population, and the age and health of individuals. At sexual maturity female koalas had a mean age (& 95% confidence interval) of 24.4 months (23.5 – 25.3), a mean head length of 125 mm (124 – 127) and a mean body mass of 6.6 kg (6.3 – 6.8). On the basis of this analysis, females were considered sexually mature if they were greater than 6 kg, with only 7.4% of independent females having young when they weighed less than 6 kg. In comparison, 73.6% (n = 534) of females greater than 6 kg at Framlingham and French Island had young. At Framlingham and Mt Eccles 85% and 91% of births, respectively, occurred between December and March. The breeding season was relatively extended at Snake and French Islands where only 46% and 53% of births, respectively, were recorded in the same period. Overall fecundity was higher in the Chlamydia-free populations (65.6 – 81.1%) than in the Chlamydia-infected populations (32.3 – 38.8%). There was little temporal variation in fecundity within all sites except Sandy Point. This variation was probably due to the severe defoliation of preferred food trees. Fecundity declined with age at all sites after peaking at tooth wear class (TWC) II at Snake Island and Mt Eccles, TWC III at Framlingham and TWC IVA on French Island. Females in good body condition had a greater probability of having a young than females in poor body condition. Despite having lower fecundity, Chlamydia-infected koala populations, such as those at Snake Island and Mt Eccles, still have the potential to become overabundant.

Introduction

Mammal species exhibit a great diversity of reproductive strategies (Cole 1954, Williams 1966a, Tyndale-Biscoe 1979, Roff 1992, Ranta et al. 2002). Many aspects of fecundity differ between and within species and contribute to the overall fecundity (the percentage of reproductive females) and growth of the population (Lack 1954, Williams 1966b). These include the timing of sexual maturity (Nol and Smith 1987) and reproductive senescence (Gaillard et al. 2000), timing of births and the length of the breeding season (Lunn and Boyd 1993, Tkadlec and Zejda 1998), consistency of breeding in consecutive seasons, and the age schedule of fecundity (Cole 1954). Differences in age-specific fecundity have been found in many long-lived vertebrate species where the pattern of fecundity resembles an inverse U-shape as it increases early in life, reaches a maximum around the middle of life and then declines in old age (Clutton-Brock 1988a, Reid et al. 2003). Several factors may influence allocation of resources to reproductive events in individuals (Skutch 1948, Lack 1956, Williams...
1966b). These include age, body size, and condition (Wauters and Dhondt 1995) where condition may comprise fat or protein reserves (Schulte-Hostedde et al. 2001), nutritional status (Delgiudice et al. 1992), territory quality (Potti 1993), parasite load or disease status (McCallum 1995), and the state of the immune system (McNamara and Houston 1996, Boyd 2000).

Age-specific fecundity is a combination of age at sexual maturity, fecundity during the "prime-age" period of life and reproductive senescence, and is an important aspect of population dynamics. The age at which an individual reaches sexual maturity is a trade-off between maximizing lifetime reproductive success and minimizing the risk of mortality (Stearns 1976, Takada and Caswell 1997, Boyd 2000, Haugen 2000). Age at sexual maturity may differ between populations (e.g. How 1976, Viggers and Lindenmayer 2000), perhaps due to the effects of density dependence (Baharav 1983, Tkadlec and Zejda 1998, Dobson and Oli 2001, Oli and Dobson 2001), altitude and latitude (Morrison and Hero 2003), social rank (Setchell et al. 2002), or food abundance and correspondingly, body mass or condition (Green and Rothstein 1991, Jorgenson et al. 1993, Saether and Heim 1993, Gaillard et al. 1998, Laaksonen et al. 2002).

Fecundity often peaks during "prime-age" (Gaillard et al. 2000) and many studies do not distinguish further classes within "prime-age" (e.g. Sydeman et al. 1991, Cameron et al. 2000). This may be due to the difficulty of accurately determining the age of the individuals of many mammal species (Gee et al. 2002), or alternatively, it may be because vital rates, such as fecundity and mortality, do not vary substantially between age classes within the "prime-age" category (Caswell 2001). It is important to know whether fecundity varies with age within the "prime-age" category (Lima and Paez 1995) and include this variation in models of population dynamics (Caswell 2001).

Reproductive senescence (Packer et al. 1998, Kirkwood and Austad 2000), the decline in fecundity with increased age, has been reported in many iteroparous mammalian species (Boyd et al. 1995, Gaillard et al. 2000, Fedigan and Pavelka 2001, Broussard et al. 2003) but may be absent in other similar species (Schwartz et al. 1998, Bales et al. 2001, Pistorius and Bester 2002). In marsupials, reproductive senescence may be the failure to successfully wean young as opposed to a reduction
in the birth rate, as marsupials are very small at birth (compared with eutherians) and much of the energetic cost of producing a marsupial is in the latter stages of lactation (Tyndale-Biscoe 1979, Tyndale-Biscoe and Renfree 1987, Tyndale-Biscoe and Janssens 1988). For example, older female mountain brushtail possums continued to breed but did not successfully wean the young (Viggers and Lindenmayer 2000).

In mammals, the distribution of births may be spread over the year (continuous breeding) or may be concentrated within a shorter period of time, known as the breeding season (a seasonal breeding pattern) (Lack 1954, Caughley 1977, Gaillard et al. 1993b). The length of the breeding season is one of the critical parameters that determine population dynamics in mammals (Tkadlec and Zejda 1998). Some mammalian species have highly synchronous breeding seasons and parturition dates within (Oakwood 2000, Renfree and Shaw 2000) and between populations (Soderquist 1993), whereas others have asynchronous breeding seasons (Gaillard et al. 1993b). The length and timing of the breeding season may differ between geographically isolated populations (Bowyer 1991, Pitcher and Stutchbury 1998) or between habitats (Baharav 1983, Kreuzer and Huntly 2003). The timing of the birth of the young within the breeding season may influence the subsequent quality or survival of the young (Smith 1976, Lunn and Boyd 1993, Young 1994, Boltnev et al. 1998), the number of young produced (Stefan and Krebs 2001) or the age of the young at sexual maturity (Clark et al. 2002). The season of births may also differ between male and female juveniles. The “Early Bird” hypothesis suggests that mothers breeding early in the season should produce males as these individuals have more time to grow before they first reproduce the following year (Daan et al. 1996, Smallwood and Smallwood 1998). Mothers breeding later in the season should produce female young as there is no relationship between timing of birth and probability of breeding in the following year in females.

The fecundity of many species varies significantly over time and between populations with intrinsic population factors such as the population age structure (Tkadlec and Zejda 1998), body condition (Newsome 1977), disease status and density (Kruuk et al. 1999b, Forchhammer et al. 2001). Fecundity may also vary with extrinsic factors such as latitude (Skutch 1948, Henmi 1993, Young 1994), environmental conditions...
Kirkpatrick and McEnvoy 1966, Kruger and Lindstrom 2001) and food supply (Clutton-Brock et al. 1982).

Lifetime breeding effort and success is very important in investigating life-history theory (Wauters and Dhondt 1995, McNamara and Houston 1996, Pomeroy et al. 1999, Arroyo 2002). Reproduction imposes costs on females that may be so considerable that individuals do not have sufficient energy reserves to breed in the subsequent season (McNamara and Houston 1996, Velando 2002). Two broad reproductive strategies are distinguished. Females of the species either do not breed every year due to physiological or ecological constraints (Rismiller and McKelvey 2000, Jouventin and Dobson 2002) or most of the females breed every year but some females fail to breed due to poor body condition (Gaillard et al. 1992, Boyd et al. 1995, Loison et al. 2002, Ramsey et al. 2002).

**Koalas**

Most reports on the age of sexual maturity in female koalas indicate that they mature between 2 and 3 years of age (Eberhard 1972, Dickens 1975, Smith 1976, White and Kunst 1990). McNally (1957) and Handasyde (1986) found a “threshold” body mass of approximately 6 kg for sexual maturity. The findings of these previous studies suggest that mass at sexual maturity, combined with tooth wear, is an appropriate measure to assess sexual maturity in koalas where age is unknown. Reproductive senescence in koalas has been reported for French Island where the fecundity of the oldest age class was half that of middle age females (Martin and Handasyde 1990a). However, little is known regarding reproductive senescence in *Chlamydia*-infected populations.

Koalas are seasonal breeders with little variation in the distribution of the timing of births over the geographical range (White and Kunst 1990). The Victorian koala breeding season has been determined on French Island and at the Brisbane Ranges (McNally 1957, Martin and Handasyde 1990a) with births occurring between October and May, with a peak (over 50% of births) between November and January. Little is known about the timing of dates of births in relation to different geographic locations within Victoria, sex of the young or maternal characteristics such as age and body
condition in koalas. The "Early Bird" hypothesis (Daan et al. 1996, Smallwood and Smallwood 1998) may account for patterns of births of koalas given the extended breeding season (described below) and male-biased sexual dimorphism; however, the extended time period between birth and sexual maturation in males may mask this influence.

Fecundity estimates of many koala populations reported in the literature vary between populations and within populations over time (Gall 1980, Gordon et al. 1988, Martin et al. 1988, Gordon et al. 1990b, White and Timms 1994, Thompson 2001). This variation may be partly due to the different methods used to determine the fecundity estimates (Appendix I). Fecundities of Victorian koala populations ranged from 0% at the Grampians (Martin et al. 1988), to 97% on French Island (Martin and Handasyde 1990a). Long-term fecundity data demonstrate large variation within individual koala populations over time. Fecundity of koalas on Phillip Island varied over time, ranging between 9 and 40% (Martin 1981). However, the fecundity of koalas on French Island, where the population has been intensively managed, has remained stable over many years, ranging between 58 and 66% (calculated as the percentage of all independent females breeding) from 1955 to 1981 (Martin 1981, 1983, McColl et al. 1984). Due to the large degree of variation both between and within populations, and the variation in methods used to estimate fecundity, accurate, site-specific information is required on fecundity to predict population dynamics.

A number of different factors appear to influence the fecundity of koala populations. Koala fecundity may vary with altered environmental conditions such as variation in food abundance owing to over-browsing in Victoria and South Australia (Martin 1981, 1985c) or drought in Queensland (Gordon et al. 1990b). Fluctuations in the fecundity of koala populations may also be due in part to variation in the incidence of reproductive tract disease caused by *Chlamydia*. (Brown et al. 1980, Martin 1981, McColl et al. 1984, Gordon et al. 1990b). Infection with *Chlamydia* can cause reproductive tract disease and subsequent infertility in some female koalas (Obendorf and Handasyde 1990), hence potentially lowering the fecundity of the population. *Chlamydia*-free populations in southeastern Australia had consistently higher fertility than *Chlamydia*-infected populations (Martin et al. 1988). However, the fertility levels of *Chlamydia*-infected populations could not be entirely explained by levels of
Chlamydia-infection as infection does not always result in disease (see Obendorf and Handasyde 1990). Weigler et al. (1988) compared clinical signs of disease with infection rate and fertility in koalas at the Redland Shire, Queensland. While Chlamydia was isolated from 71% of 65 koalas, only 9% had clinical signs of disease, and 67% of females were infected but 82% had young. Serological evidence of Chlamydia-infection has been found in clinically normal koalas (Cockram 1978, McColl et al. 1984, Canfield et al. 1991) and conversely, Chlamydia-infection was not detected in a proportion of koalas exhibiting clinical signs of disease (Brown and Carrick 1985, Canfield et al. 1991, Girjes et al. 1996). White and Timms (1994) postulated that not all female infertility could be attributed to chlamydial infection, as infection could not be detected in 44% of the non-parous females they surveyed. Additionally, Chlamydia-infection may have varying effects on fecundity in different age classes (Martin 1981, Obendorf and Handasyde 1990).

Koalas generally produce one young per year, however it is not known whether all females consistently breed each year (Martin and Handasyde 1995). Koalas may fail to breed due to poor body condition or reproductive tract disease (Martin 1981, 1985b, Gordon et al. 1988, Obendorf and Handasyde 1990). On French Island and Flinders Chase, Kangaroo Island, female koalas bred each year (McNally 1957, Eberhard 1972, 1978). In an area close to Brisbane it was suggested that female koalas may fail to breed one year in three (Tyndale-Biscoe and Renfree 1987) but Martin and Handasyde (1990a), after reviewing the French Island data of Handasyde (1986), concluded that most sexually mature females in Chlamydia-free populations bred each year. This finding did not resolve the question of breeding in consecutive years in Chlamydia-infected populations.

Aims
My principal aim is to investigate aspects of the fecundity of koala populations at Snake and French Island, Framlingham and Mt Eccles. Specifically, I aim to determine the mean female age at sexual maturity. Secondly, I aim to compare fecundity between populations, and between different age classes, and to investigate temporal variation in fecundity in populations with different densities. Additional aims are to determine the factors that affect the probability of females producing a
young and to examine breeding in individuals over time. I will also compare breeding seasons between populations and determine whether male and female young have different seasons of birth and if maternal characteristics affect the season of birth of the young.
Methods

Study sites, koala populations and data collection

The study sites, sample sizes and data collection methods for Snake Island, Framlingham, Mt Eccles, French Island, the Brisbane Ranges, Phillip Island and the (KCC) are described in Chapter 2. Data from koalas caught and translocated from Sandy Point (1985-1999, DNRE unpublished) are also analysed in this chapter. Sandy Point is part of HMAS Cerberus Naval Base, Western Port, and twenty Chlamydia-free (Handasyde and Martin 1988) koalas were introduced from French Island in 1972 (Martin 1989). The vegetation has been described by Backhouse and Crouch (1990). Defoliation of food trees was noted in the early 1980's (Backhouse and Crouch 1990) and a population crash had commenced in October 1988 (Martin 1997).

Sexual maturity

The age of females at sexual maturity was determined from French Island (1980-1985), the Brisbane Ranges (K. Handasyde and R. Martin, unpublished data), and known-age females from the KCC that were observed until the birth of their first young. The age of the young upon first capture was calculated from growth curves (Chapter 3). The age of the mother at sexual maturity (birth of the first young) was calculated by subtracting the age of the young from the age of the mother. A number of criteria were assessed to determine if the observed young was the female’s first young. These were the regularity and number of the captures prior to sexual maturity, the mass of the mother prior to and after the birth of the young in combination with the time difference between them.

The estimation of the head length and mass of females at sexual maturity is important because the age of animals is often not known. Therefore, indices of both mass and head length at sexual maturity were devised based on the measurement before and after the birth of the first young, the time difference between the two measurements, and the age of the young at the first measurement after birth. The age, head length and mass at sexual maturity were compared between koalas from the Brisbane Ranges, French Island (1980-1985) and the KCC with one-way ANOVAs if tests for
heterogeneity of variances among sites did not reveal significant differences. The mean and 95% confidence intervals (CI) are reported.

**Breeding season**

The birth date of each dependent young with a head length of less than 120 mm, from Snake Island, French Island, Framlingham and Mt Eccles, was calculated from the growth curves derived in Chapter 3. Distributions of birth dates were compared between sampling periods within sites, between sites and between the sexes using Kolmogorov-Smirnov Z, 2 independent sample tests. These tests were also used to assess the difference between the distributions of birth dates of offspring of younger females (TWC II and III) and older females (TWC IVA*). However, due to the inherent problems of performing multiple tests, analysis was restricted to Framlingham as this site had the largest sample of dependent young.

**Fecundity**

Overall fecundity at Snake Island, French Island, Framlingham and Mt Eccles was calculated as the proportion of sexually mature females with young (reproductive females) in each sample. The accuracy of the comparisons of the timing of births and overall fecundity between sites is reduced by the sampling schedule (Table 2.2). However, the combination of low juvenile mortality and employing the procedure of recording the proportion of females with elongated teats should minimise possible biases in overall fecundity (Martin 1981). The difference in fecundity levels between populations was analysed with contingency tables and adjusted residuals with the null hypothesis that fecundity would be equal between populations. If the absolute value of the adjusted residuals was greater than 1.96, the adjusted residual was significant at \( \alpha = 0.05 \) (Everitt 1986). French Island was not included in the between sites analysis of fecundity due to the disproportionately smaller sample sizes.

In order to investigate the effect of a dramatic population decline on fecundity in *Chlamydia*-free populations, long-term data from French Island and Sandy Point (DNRE, unpublished data) were examined. Due to limitations of the data sets, for example, the lack of age data for individuals, fecundity was calculated as the number
of reproductive females divided by the total number of independent females i.e. inclusion of sub-adults (e.g. Allen et al. 1997, White et al. 2001). A comparison of the temporal variation in fecundity between French Island and Sandy Point was analysed using maximum likelihood estimation (Kendall 1998). The mean fecundity and 95% confidence intervals of the coefficient of variation (CV) are reported. Age-specific fecundity was calculated as the percentage of reproductive females divided by the number of sexually mature females in each TWC.

The factors affecting the probability of having a young were examined with multiple logistic regression (e.g. Boyd et al. 1995, Quinn and Keough 2002). Possible explanatory variables included maternal mass, TWC, morphometric or muscle condition (see Chapter 5), Chlamydia-infection status of the population, and the site of capture. Maternal mass and TWC were correlated (Chapter 5) so only TWC was included (as a continuous explanatory variable) (Tabachnick and Fidell 2001) (Table 6.1). A quadratic term for TWC was included because the probability of having a young might vary non-linearly with TWC. That is, the probability of having a young might be low in the youngest TWCs, increase in the middle age classes and then decline with old age (e.g. Ramsey et al. 2002). Morphometric condition was chosen over muscle condition, as it was a continuous variable. The site and Chlamydia-infection status of the population were correlated, therefore, only the latter was included in the model. Hence, TWC, Chlamydia-infection status of the populations and morphometric condition were included in the multiple logistic regression. Successive reduction of a term from the full model (including all variables and interaction terms) and comparison of the change in deviance with a chi-square statistic was used to assess the statistical significance of the variables (Hosmer and Lemeshow 2000). The model described includes only statistically significant terms.
Table 6.1 Numerical values given to the TWCs for the logistic regression model.

<table>
<thead>
<tr>
<th>TWC</th>
<th>TWC value</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1</td>
</tr>
<tr>
<td>II</td>
<td>2</td>
</tr>
<tr>
<td>III</td>
<td>3</td>
</tr>
<tr>
<td>IVA</td>
<td>4</td>
</tr>
<tr>
<td>IVB</td>
<td>5</td>
</tr>
<tr>
<td>IVC</td>
<td>6</td>
</tr>
<tr>
<td>V</td>
<td>7</td>
</tr>
<tr>
<td>VI</td>
<td>8</td>
</tr>
<tr>
<td>VII</td>
<td>9</td>
</tr>
</tbody>
</table>

In order to investigate long-term breeding patterns in individuals, data were analysed from the Brisbane Ranges (K. Handasyde and R. Martin, unpublished data) and the KCC and reanalysed from French Island (from Appendix 6, Handasyde 1986). Female koalas were defined as “breeding in non-consecutive seasons” if they bred in one season, did not breed in the next season but resumed breeding in a subsequent season.
Results

Sexual maturity

In order to investigate when sexual maturity occurs, sites were pooled as there was no compelling evidence for a significant difference in age \((F = 2.187, \text{ d.f.} = 2, 29, P = 0.130)\), head length \((F = 2.621, \text{ d.f.} = 2, 21, P = 0.096)\) or mass \((F = 1.261, \text{ d.f.} = 2, 22, P = 0.303)\) at sexual maturity between sites (Table 6.2). The mean age at sexual maturity was 24.4 months of age \((95\% \text{ CI} = 23.5 – 25.3 \text{ months}, n = 32)\). The mean head length within 4 months of sexual maturity was 125 mm \((95\% \text{ CI} = 124 - 127 \text{ mm})\). Only one female \((4\%, n = 24)\) had given birth at a head length under 120 mm. The mean mass within 4 months of sexual maturity was 6.6 kg \((95\% \text{ CI} = 6.3 - 6.8 \text{ kg}, n = 25)\). Eighteen percent \((n = 28)\) of known-age females were under 6 kg when they first bred.

Table 6.2 Mean, standard deviation (s.d.) and sample size \((n)\) for age (months), head length (mm) and body mass (kg) of female koalas at or within 4 months of sexual maturity on French Island (1980-1985), the Brisbane Ranges and the Koala Conservation Centre (KCC) on Phillip Island.

<table>
<thead>
<tr>
<th>Site</th>
<th>Age (months)</th>
<th>Mean</th>
<th>s.d.</th>
<th>n</th>
<th>Head length (mm)</th>
<th>Mean</th>
<th>s.d.</th>
<th>n</th>
<th>Body mass (kg)</th>
<th>Mean</th>
<th>s.d.</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>French Island</td>
<td>25.3</td>
<td>2.3</td>
<td>16</td>
<td>126.4</td>
<td>3.7</td>
<td>12</td>
<td>6.5</td>
<td>0.5</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brisbane Ranges</td>
<td>23.4</td>
<td>1.5</td>
<td>7</td>
<td>123.8</td>
<td>3.5</td>
<td>6</td>
<td>6.5</td>
<td>0.3</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KCC, Phillip Is.</td>
<td>23.1</td>
<td>3.3</td>
<td>9</td>
<td>126.8</td>
<td>2.9</td>
<td>6</td>
<td>6.4</td>
<td>1.1</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All sites pooled</td>
<td>24.4</td>
<td>2.6</td>
<td>32</td>
<td>125.6</td>
<td>3.7</td>
<td>24</td>
<td>6.5</td>
<td>0.6</td>
<td>28</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

At Snake Island, French Island, Framlingham and Mt Eccles, 7.4% of all independent females under 6 kg \((n = 323)\) had young. The lowest mass of a female with young was 4.2 kg. Two percent of all reproductive females were less than 6 kg (Figure 6.1). As females breeding at a mass of less than 6 kg were possibly those that would attain a mass of 6 kg towards the end of the breeding season, the dates of birth of the young of females less than 6 kg were calculated from growth curves (see Chapter 3). Eighty percent of the females that were less than 6 kg when they bred conceived before March (Figure 6.2).
Figure 6.1 Reproductive female koalas in mass classes above and below 6 kg, pooled for Snake Island, French Island, Framlingham and Mt Eccles populations over all sampling periods. Numbers above bars are sample sizes.

Figure 6.2 Cumulative percentage of birth dates of young of female koalas less than 6 kg, pooled for Snake Island, French Island, Framlingham and Mt Eccles over all sampling periods, $n = 20$. 

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On the basis of the preceding results, females will be classified as sexually mature in a particular breeding season if they had attained a mass of 6 kg during that breeding season (defined as December to April, see below). Fecundity will be based on this definition of sexually mature females; however, the actual fecundity of a population may be slightly higher. The two methods of calculating fecundity, including females under 6 kg with young and excluding females under 6 kg with young, were assessed for each site at each sampling period. The mean difference between the two methods of assessing fecundity was 0.87% (s.d. = 1.44%) so the results were not particularly sensitive to the method of calculating fecundity.

**Breeding season**

Data were analysed to ascertain whether there were any correlations between the timing of births and variables such as site and sampling period, the sex of the young and maternal variables such as age and body condition.

**Timing of birth dates at different sites and sampling periods**

Births were recorded in each month of the year at Snake Island. The distribution of births was compared between years within sites. As there was no significant difference between 1999 and 2000 at Snake Island ($Z = 0.644, n = 81, 88, P = 0.801$) or between 2000 and 2001 on French Island ($Z = 0.880, n = 46, 61, P = 0.421$), these samples were pooled within sites. There was a significant difference between 1999 and 2001 at Mt Eccles ($Z = 1.661, n = 125, 203, P = 0.008$) with females breeding earlier in 1999. Comparing between sites, Framlingham and Mt Eccles had similar distributions of birth dates, as did Snake and French Islands (Figure 6.3). Thus, data from Framlingham was pooled with Mt Eccles, and similarly, data from Snake Island was pooled with French Island. Births were earlier at Snake and French Islands than at Framlingham and Mt Eccles. At Framlingham and Mt Eccles 85 and 91% of births respectively were recorded in the four-month period from December to March, whereas at Snake and French Islands only 46 and 53% of births respectively were recorded in the same period.
Timing of birth dates and sex of young

The distribution of birth dates of female young was significantly different from male young at both Snake and French Islands (pooled data, $Z = 1.488$, $n = 152, 143$, $P = 0.024$) and Mt Eccles and Framlingham (pooled data, $Z = 1.802$, $n = 250, 288$, $P = 0.003$) with male young being born earlier in the season (Figure 6.4). For Snake and French Island pooled data, 50% of males were born by the end of November whereas 50% of females were not born until the end of December.
Figure 6.4 Cumulative percentages of birth dates of female and male dependent young. Squares: French Island and Snake Island pooled, open: males, \( n = 143 \), closed: females, \( n = 152 \); triangles: Mt Eccles and Framlingham pooled, open: males, \( n = 288 \), closed: females, \( n = 250 \).

**Timing of birth dates and maternal age and muscle condition**

At Framlingham, the distribution of dates on which young sexually mature females (TWC II and III) gave birth was similar to that of offspring of older (TWC IVA+) females \((Z = 0.901, n = 34, 64, P = 0.392)\) with 95-97% of births between November and March, and 61-62% of births between January and February in both categories. The distribution of dates on which females gave birth (pooled from Snake Island in 1999, 2000 & 2001 and French Island in 2000 & 2001) was similar for females in good and average muscle condition \((Z = 0.602, n = 97, 176, P = 0.862)\) with 90% of births between September and April for both classes.
Fecundity

Overall fecundity

Overall fecundity was lower in *Chlamydia*-infected populations (32.3 – 38.8%) compared with those that were *Chlamydia*-free (65.6 – 81.1%) (Figure 6.5). There was no significant difference in fecundity between the sampling periods at Snake Island ($\chi^2 = 0.47$, d.f. = 2, $P > 0.70$). There was no significant difference in fecundity between the sampling periods at Mt Eccles ($\chi^2 = 0.18$, d.f. = 1, $P > 0.50$). There was a significant difference in fecundity between 2000 and 2001 on French Island ($\chi^2 = 5.04$, d.f. = 1, $P < 0.05$) with greater fecundity in 2001. There was no significant difference in overall fecundity between Snake Island and Mt Eccles ($\chi^2 = 2.88$, d.f. = 1, $P > 0.05$). Examination of adjusted residuals showed that fecundity at Framlingham (*Chlamydia*-free) was significantly higher than at Snake Island and Mt Eccles (*Chlamydia*-infected) ($\chi^2 = 145.93$, d.f. = 2, $P < 0.001$) (Figure 6.5). There was no significant difference in overall fecundity (calculated as the number of reproductive females divided by all independent females) between French Island (in 2000 and 2001, 66%, $n = 162$), Framlingham (66%, $n = 432$) and Sandy Point (in 1993-95, 67%, $n = 61$) (peak fecundity from Figure 6.6) ($\chi^2 = 0.02$, d.f. = 2, $P > 0.98$).

Figure 6.5 Overall koala fecundity at each site during each sampling period. Black bars represent *Chlamydia*-infected populations; blue bars represent *Chlamydia*-free populations. Fram = Framlingham Forest. Numbers above bars are sample sizes.

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Temporal variation in fecundity: effect of an extreme population decline on fecundity

There was much greater temporal variation in the fecundity at Sandy Point compared with French Island (French Island 1989-1999: mean fecundity = 0.584, 95% CI of CV = 0.079, maximum likelihood estimate = 55.08; Sandy Point 1985-1999: mean fecundity = 0.485, 95% CI of CV = 0.23, maximum likelihood estimate = 77.59). The change in fecundity between the maximum and minimum on French Island was 11%. The decline in fecundity at Sandy Point during the period of the dramatic population decline between 1985 and 1989 was 31% (Figure 6.6). There were three samples of koalas from Sandy Point in 1989, in May (n = 21), October (n = 26) and November – December (n = 77). There was not a significant difference in fecundity between the May (62%) and October (58%) sampling periods ($\chi^2 = 0.09$, d.f. = 1, $P > 0.80$) and they were pooled.

Figure 6.6 Overall koala fecundity (reproductive females divided by the total number of independent females). Diamonds: French Island; horizontal lines: Sandy Point. Data source: DNRE, unpublished data. Numbers above the lines are the sample size for each year from French Island and numbers below the lines are sample sizes for each year from Sandy Point.
**Age-specific fecundity across populations**

There was a general trend of declining fecundity with increasing age at each site (Figure 6.7). Fecundity peaked in TWC II at Snake Island and Mt Eccles, in TWC III at Framlingham and in TWC IVA on French Island. The slight increase in observed fecundity in TWC VI at Snake Island and Mt Eccles may be due to the small sample size in this TWC (n = 5 and 15, respectively).

![Fecundity (%) vs Tooth wear class](image)

Figure 6.7 Age-specific koala fecundity at each site. Squares: Snake Island, n = 847; triangles: Mt Eccles, n = 997; circles: Framlingham, n = 383; and diamonds: French Island 2000 & 2001, n = 135. Note: There were no sexually mature females in TWC 1 and no live females in TWC VII.

**Factors correlating with the probability of having a young**

There was a statistically significant relationship (Table 6.3) between the probability of a female koala having a young and TWC and morphometric condition. The regression coefficients and their standard errors are given in Table 6.4.

\[
P(F_{\text{young}}) = \frac{\exp(\text{linear predictor})}{[\exp(\text{linear predictor})+1]} \]

Equation 6.1
where $P(F_{\text{young}})$ was the probability of a female having a young, and the linear predictor = $[(-0.063 \times \text{TWC}) + (0.107 \times \text{TWC}^2) + (-1.853 \times \text{Chlamydia status}) + (-4.752 \times \text{morphometric condition}) + (0.458 \times \text{TWC} \times \text{Chlamydia status}) + (-0.130 \times \text{TWC}^2 \times \text{Chlamydia status}) + 5.404]$

where TWC was given a numerical value (Table 6.1) and normalised by subtracting the mean to avoid correlations between the linear and quadratic terms (Sokal and Rohlf 1981).

Table 6.3 Change in deviance between the full logistic regression model and the reduced model of the probability of producing a young (equation 1.1).

<table>
<thead>
<tr>
<th>Model</th>
<th>-2 log likelihood</th>
<th>Change in deviance</th>
<th>d.f.</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full</td>
<td>2515.22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduced (Equation 4.1)</td>
<td>2534.45</td>
<td>19.23</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 6.4 Results of logistic regression analysis of the effects of TWC, Chlamydia-infection status of the population (Chlamydia), female morphometric condition, and the interaction terms on the probability of a female koala having a young when censused, $n = 2097$.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>s.e.</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>TWC</td>
<td>-0.0643</td>
<td>0.091</td>
<td>0.480</td>
</tr>
<tr>
<td>TWC$^2$</td>
<td>0.1065</td>
<td>0.032</td>
<td>0.001</td>
</tr>
<tr>
<td>Chlamydia</td>
<td>-1.8527</td>
<td>0.150</td>
<td>0.001</td>
</tr>
<tr>
<td>Morphometric condition</td>
<td>-4.7517</td>
<td>0.563</td>
<td>0.001</td>
</tr>
<tr>
<td>TWC*Chlamydia</td>
<td>0.4583</td>
<td>0.102</td>
<td>0.001</td>
</tr>
<tr>
<td>TWC$^2$*Chlamydia</td>
<td>-0.1297</td>
<td>0.041</td>
<td>0.002</td>
</tr>
<tr>
<td>Constant</td>
<td>5.4036</td>
<td>0.576</td>
<td>0.001</td>
</tr>
</tbody>
</table>

As the interaction with the Chlamydia-infection status of the population was a significant term in the logistic regression model, the results are shown separately for populations with and without Chlamydia-infection (Figure 6.8). The probability of having a young increased by approximately 20% between relatively poor (0.9) and relatively good (1.1) condition females (across all TWCs) in both Chlamydia-infected and Chlamydia-free populations (Figure 6.8). In Chlamydia-free populations, the probability of having a young increased with TWC but declined in the oldest TWCs (Figure 6.8a). The pattern was quite different in Chlamydia-infected populations.
where the probability of having a young was greatest in the earliest TWCs and declined with increasing TWC (Figure 6.8b). Females with the highest probability of having a young are those in good morphometric condition, of TWCs III to IVB and from *Chlamydia*-free populations.

Figure 6.8 Logistic regression model of the probability of a female koala having a young as a function of tooth wear class (TWC) for a) *Chlamydia*-free, and b) *Chlamydia*-infected populations. The predicted probability of having a young is shown for mothers in relatively good condition (morphometric condition = 1.1), average condition (morphometric condition = 1.0) and relatively poor condition (morphometric condition = 0.9). There are no data for TWC VII. The crosses are the observed fecundity rates for each TWC (± 1 s.e.) averaged across females regardless of body condition. Numbers above bars are sample sizes.
Consistency of breeding in consecutive seasons

None of the females in the *Chlamydia*-free French Island (1980-1985) population failed to breed in a season and then resumed breeding, whereas a percentage of the females at the *Chlamydia*-infected populations at the Brisbane Ranges (K. Handasyde and R. Martin, unpublished data) and the KCC did so (Figure 6.9). In the latter two populations, three of the four females that were monitored for five or more breeding seasons, bred in non-consecutive breeding seasons. The pattern of breeding in non-consecutive years varied between individuals but included one female from the KCC that bred every second year over six years.

![Figure 6.9 Percentage of female koalas breeding in consecutive (filled bars) and non-consecutive (diagonal hatching) breeding seasons on French Island (1980-1985) (FI), and at the Brisbane Ranges (BR) (R. Martin and K. Handasyde, unpublished data) and the Koala Conservation Centre (KCC), when monitored for 3, 4 or 5+ consecutive breeding seasons. Numbers above the bars are sample sizes.](image)

Twenty-six percent of females at the KCC that were monitored from less than one year of age failed to produce a young (*n* = 27). Eighteen percent had one young then failed to breed subsequently and 55% of females had more than one young (Figure 6.10). Six individual females that bred more than once were still breeding at an old TWC (TWC IVC") (Table 6.5).
Figure 6.10 Patterns of breeding in individual koalas at the Koala Conservation Centre. Open bars are sexually mature females that did not produce any young, filled bars are females that produced only one young; wavy horizontal hatching is females that produced only two young; vertical hatching is females that produced 2 young and then were not monitored further; diagonal hatching is reproductive females in consecutive seasons, horizontal hatching is females breeding in non-consecutive seasons, \( n = 27 \).

Table 6.5 Number of years that older females (\( \geq \) TWC IVC) at the KCC failed to breed before death or the present (Dec, 2003) (females that bred in 1+ seasons).

<table>
<thead>
<tr>
<th>Animal</th>
<th># years failed to breed before death/the present</th>
<th>TWC when ceased breeding</th>
<th>Present Status</th>
<th>Reason for failure to breed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.5</td>
<td>V</td>
<td>Dead</td>
<td>Sick</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>V</td>
<td>Dead</td>
<td>Unknown</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>VII</td>
<td>Dead</td>
<td>Unknown</td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>V</td>
<td>Alive</td>
<td>Unknown</td>
</tr>
<tr>
<td>5</td>
<td>4</td>
<td>VI</td>
<td>Alive</td>
<td>Unknown</td>
</tr>
<tr>
<td>6</td>
<td>8</td>
<td>V</td>
<td>Dead</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

The percentage of females that discontinued breeding during the period of observation was greater at the *Chlamydia*-infected populations (the Brisbane Ranges, Phillip Island and the KCC) than at the *Chlamydia*-free French Island (1980-1985) population (Table 6.6).
Table 6.6 The number of female koalas at French Island (1980-1985), the Brisbane Ranges, Phillip Island (K. Handasyde and R. Martin, unpublished data) and the KCC that discontinued breeding during the period of observation.

<table>
<thead>
<tr>
<th>Site</th>
<th>% of females that discontinued breeding</th>
<th>( n )</th>
<th># years observed at site</th>
</tr>
</thead>
<tbody>
<tr>
<td>French Island</td>
<td>6.6</td>
<td>15</td>
<td>Up to 4</td>
</tr>
<tr>
<td>Brisbane Ranges</td>
<td>33.3*</td>
<td>15</td>
<td>Up to 4</td>
</tr>
<tr>
<td>PI, non KCC</td>
<td>66.6</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>PI, KCC</td>
<td>72.2</td>
<td>18</td>
<td>Up to 10</td>
</tr>
</tbody>
</table>

* The percentage of females that discontinued breeding at the Brisbane Ranges is probably under-represented due to the targeting of fertile females in this sample.
Discussion

Sexual maturity

The sexual maturation of female koalas at approximately two years of age was consistent with previous findings (McNally 1957, Eberhard 1972, Dickens 1975, Smith 1979a, Martin 1981, White and Kunst 1990). Additionally, the present study found no difference between sites in the age, head length or body mass of koalas at sexual maturity. The small degree of variation around the age at sexual maturity suggests that the timing of sexual maturity is not plastic in female koalas. Therefore, individual female koalas may have limited ability to reduce the age at sexual maturity in order to increase lifetime reproductive effort. Alternatively, the benefits of reproducing at an earlier age may be outweighed by the benefits of delaying reproduction (in terms of future survival and reproductive success) (Stearns 1992, Lunn et al. 1994).

The mean mass at sexual maturity of 6.6 kg was in agreement with Handasyde (1986) and McNally (1957). A good working definition of sexual maturity was provided by defining females greater than 6 kg in the breeding season as being sexually mature. However, a small percentage (7.4%) of females that were less than 6 kg bred successfully. This pattern in the koala is consistent with data for many female herbivores which must reach a threshold body mass before they can reproduce (Gaillard et al. 1992, Bon et al. 1993, Gaillard et al. 1998). Female moose (Alces alces) reached sexual maturity at 2.5 years old instead of 3.5 years if they were of sufficient body mass (Saether and Heim 1993).

In the present study, the youngest koala to give birth was a 4.2 kg and 17 month of age (95% prediction interval 14-20 months, 114 mm head length, Chapter 3) koala from Mt Eccles but she did not raise her young to independence. Thus, female koalas may occasionally unsuccessfully attempt breeding at a very young age or small body size, as has been found in bighorn sheep (Ovis canadensis) (Festa-Bianchet et al. 1995) and Antarctic fur seals (Arctocephalus gazella) (Lunn et al. 1994).
Breeding season

The breeding season at Snake and French Islands was longer than at the Brisbane Ranges (Martin and Handasyde 1990a), and at Framlingham and Mt Eccles (the present study). The differences in the breeding seasons at these sites may be due to environmental differences such as abundance, diversity and health of preferred food trees, climate, soil type and koala density. The timing of the breeding season usually means that peak lactation occurs, or young are weaned, when there is high availability of food and beneficial climatic conditions (Tyndale-Biscoe 1979, Bowyer 1991). Influences on the length and timing of the breeding season have been found in other mammals. For instance, the breeding season was earlier when population densities were high in Soay sheep (*Ovis aries*) (Forchhammer *et al.* 2001). The breeding season of the mountain brushtail possum was restricted at Cambarville in the Central Highlands of Victoria where the winters are cool and wet with occasional snow (Viggers and Lindenmayer 2000), but was extended in some years at Clouds Creek in north-eastern New South Wales where the winters were milder (How 1976). The breeding season of the eastern grey kangaroo was extended in Queensland (Kirkpatrick 1965) but sharply focused on the warmer months in Tasmania, resulting in young leaving the pouch at a time of peak grass availability (Pearse 1981). Snake and French Islands have Mediterranean climates (Chapter 2), moderated by their proximity to the coast (Seddon 1975), whereas Framlingham and Mt Eccles are further inland and experience colder winters and more frequent frosts (mean annual number of days where the minimum daily temperature was \( \leq 2^\circ \text{C} \) was 0.4, 4.4, 15.9 and 33.9 days, respectively (Bureau of Meteorology)). This may explain the extended breeding seasons at the island sites whereas the breeding season starts later and finishes earlier at Framlingham and Mt Eccles. The milder weather at the island sites may mean that koalas have to allocate less energy to thermoregulation and can instead allocate energy to reproductive activities such as lactation and searching for mates (Withers 1992). Alternatively, the different weather patterns may affect the patterns of leaf chemistry in preferred food trees, thus affecting the availability of palatable food (Moore and Foley 2000). The breeding season on French Island was longer in 2000-2001 (the present study) than was found in previous studies (McNally 1957, Martin and Handasyde 1990a). The reasons for this temporal difference are unclear.
Life-history theory predicts that in species with male-biased sexual dimorphism, females with greater resource availability should produce male offspring (Trivers and Willard 1973). There is some evidence for this in koalas (Chapter 4). However, the present results suggest that male offspring are produced earlier in the season than female offspring, perhaps in order to allow a longer period of investment in males, which ultimately attain a greater size than females (see Daan et al. 1996, Smallwood and Smallwood 1998). Krockenberger (1996) found that although koalas produce low energy milk relative to other marsupials, they lactate for a substantially longer period of time, which ensures adequate energy transfer to the young. Earlier births of males within the breeding season have also been found in a number of other mammal species (Clutton-Brock and Albon 1982).

The results of the present study showed that neither maternal age nor muscle condition had a detectable effect on the timing of births. In a number of mammalian species, primiparous or younger females give birth later in the breeding season than previously parous or older females (How et al. 1984, Lunn et al. 1994, Ratcliffe et al. 1998, San Jose et al. 1999). Cransac et al. (1997) found that primiparous females gave birth later in the season than older (or multiparous) females and suggested that the younger females did not reach the body mass threshold until later in the season. Smith (1976) proposed similar reasons to explain female koalas attaining sexual maturity at a small body mass. However, the female koalas in the present study were not just attaining breeding body mass towards the end of the breeding season, as 50% of females that were less than 6 kg when they bred gave birth before March.

**The effect of Chlamydia-infection on fecundity**

The overall fecundity at Framlingham and French Island was approximately double that at Snake Island and Mt Eccles, probably due to *Chlamydia*-infection at the latter sites. The difference in fecundity between sites with different chlamydial-infection status, such as between Mt Eccles and Snake Island, and Framlingham and French Island, has been demonstrated in many studies of Victorian and South Australian koala populations (Table 6.7). Thus, it is likely that *Chlamydia*-free populations will require greater levels of management than *Chlamydia*-infected populations. There is considerable variation in the level of fecundity in *Chlamydia*-infected and *Chlamydia*-
free populations in Queensland. This difference in the effect of *Chlamydia* on the fecundity of koala populations may be due to environmental factors or different variations of *Chlamydia*.
Table 6.7 Koala fecundity estimates in Australian populations, summary of Appendix I. T.S. = The number of times sampled. Fec = Fecundity estimate. The full definition for each estimate is given in Appendix I but the fecundity estimate is calculated from *sexually mature females only, ** all independent females and *** unknown definition of fecundity. Chl. = Chlamydia-infection status of the population, Inf. = Chlamydia-infected, and Free = Chlamydia-free.

<table>
<thead>
<tr>
<th>Location</th>
<th>Years</th>
<th>T.S.</th>
<th>Fec.</th>
<th>n</th>
<th>Chi.</th>
<th>Reference:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Victoria</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Is.</td>
<td>1954-95</td>
<td>15</td>
<td>50*-97*</td>
<td>14-278</td>
<td>Free</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10</td>
</tr>
<tr>
<td>Sandy Pt.</td>
<td>1986</td>
<td>1</td>
<td>56**-67*</td>
<td>27-32</td>
<td>Free</td>
<td>9, 10</td>
</tr>
<tr>
<td>Tower Hill</td>
<td>1998</td>
<td>1</td>
<td>94*</td>
<td>18</td>
<td>Free</td>
<td>7</td>
</tr>
<tr>
<td>Walkerville</td>
<td>1977-80</td>
<td>4</td>
<td>11**-36**</td>
<td>22-44</td>
<td>Free</td>
<td>2, 3, 11</td>
</tr>
<tr>
<td>Brisbane R.</td>
<td>1983-87</td>
<td>2</td>
<td>45**-61*</td>
<td>23-29</td>
<td>Inf.</td>
<td>9, 10, 12</td>
</tr>
<tr>
<td>Grampians</td>
<td>1983-87</td>
<td>2</td>
<td>0*-40***</td>
<td>34</td>
<td>Inf.</td>
<td>9, 10</td>
</tr>
<tr>
<td>Phillip Is.</td>
<td>1945-83</td>
<td>15</td>
<td>9**-41**</td>
<td>18-338</td>
<td>Inf.</td>
<td>2, 4, 5, 9, 13</td>
</tr>
<tr>
<td>Raymond Is.</td>
<td>1980-85</td>
<td>2</td>
<td>38*-42*</td>
<td>24-51</td>
<td>Inf.</td>
<td>10, 14</td>
</tr>
<tr>
<td>Sth. Gipps.</td>
<td>1987</td>
<td>1</td>
<td>56**-62*</td>
<td>25-29</td>
<td>Inf.</td>
<td>9, 10</td>
</tr>
<tr>
<td>Stony Rises</td>
<td>1987</td>
<td>1</td>
<td>36**-38*</td>
<td>21-22</td>
<td>Inf.</td>
<td>9, 10</td>
</tr>
<tr>
<td>South Australia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleland</td>
<td>1981</td>
<td>1</td>
<td>33*</td>
<td>6</td>
<td>Free</td>
<td>15</td>
</tr>
<tr>
<td>Flinders Ch.</td>
<td>1966-81</td>
<td>6</td>
<td>45*-83*</td>
<td>5-21</td>
<td>Free</td>
<td>15, 16</td>
</tr>
<tr>
<td>Kangaroo Is.</td>
<td>1986</td>
<td>2</td>
<td>59**-79*</td>
<td>27-39</td>
<td>Free</td>
<td>9, 10, 17</td>
</tr>
<tr>
<td>New South Wales</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tucki Tucki</td>
<td>1972-76</td>
<td>8</td>
<td>50*-100*</td>
<td>8-12</td>
<td>NA</td>
<td>18, 19</td>
</tr>
<tr>
<td>Queensland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Koala Coast</td>
<td>1996-7</td>
<td>2</td>
<td>33*-91*</td>
<td>12-22</td>
<td>Inf.</td>
<td>20</td>
</tr>
<tr>
<td>Magnetic Is.</td>
<td>1997-98</td>
<td>2</td>
<td>35*</td>
<td>24</td>
<td>Free</td>
<td>21</td>
</tr>
<tr>
<td>Mungalalla</td>
<td>1980</td>
<td>2</td>
<td>57*-91*</td>
<td>11-14</td>
<td>Inf.</td>
<td>22</td>
</tr>
<tr>
<td>Mutdapilly</td>
<td>1989-90</td>
<td>2</td>
<td>42*-48*</td>
<td>21-26</td>
<td>Inf.</td>
<td>23</td>
</tr>
<tr>
<td>Oakey</td>
<td>1971-82</td>
<td>13</td>
<td>27*-62*</td>
<td>16-38</td>
<td>Inf.</td>
<td>24</td>
</tr>
<tr>
<td>Redland</td>
<td>1987</td>
<td>2</td>
<td>67*-82*</td>
<td>33-54</td>
<td>Inf.</td>
<td>25, 26</td>
</tr>
<tr>
<td>Springsure</td>
<td>1975-81</td>
<td>7</td>
<td>72*-92*</td>
<td>21-26</td>
<td>Inf.</td>
<td>24</td>
</tr>
</tbody>
</table>

In many mammalian species the combined effects of low reproductive success in younger (sexually mature) females (Nol and Smith 1987, Festa-Bianchet et al. 1995, Monson et al. 2000) and reproductive senescence in older females (Packer et al. 1998) may produce a characteristic inverse U-shaped (quadratic) relationship between fecundity and age (Clutton-Brock 1988a, Boyd et al. 1995, Ramsey et al. 2002). Such a relationship was observed in the present study in Chlamydia-free populations of koalas (Framlingham and French Island) (Figure 6.7 and Figure 6.8). An increase in fecundity with age may occur due to increased breeding experience (Harvey et al. 1988, Ratcliffe et al. 1998, Cichon 2003), increased access to high quality territories (Part 2001) and increased foraging skills (Sydeman et al. 1991) or a combination of these factors (Forslund and Part 1995). It is unlikely that koala fecundity increases with age due to increased access to high quality patches of habitat or increased foraging skills when food is not limited. The increased fecundity with age may be explained by the failure of some koalas to reach the body mass threshold required to breed until they reach TWC III.

The observed decline in fecundity with age in koalas from the French Island and Framlingham populations suggests the occurrence of reproductive senescence in Chlamydia-free koala populations (see also Martin and Handasyde 1990a). Evidence of reproductive senescence has been found in birds (Forslund and Part 1995, Ratcliffe et al. 1998, Saino et al. 2002) and domestic (Mysterud et al. 2002b) and wild mammals (Lima and Paez 1997, Berube et al. 1999, Viggers and Lindenmayer 2000, Fedigan and Pavelka 2001, Broussard et al. 2003). Muscle condition decreased with increasing age in koalas (Chapter 3) and perhaps a proportion of older koalas become too poor in body condition to successfully raise a young. Decreasing fecundity with age may also be due to changes in the proportion of breeding individuals as a result of differential mortality rates rather than changes in individuals' fecundity (Nol and Smith 1987, Boyd et al. 1995, Forslund and Part 1995, Laaksonen et al. 2002, Reid et al. 2003). For example, individuals that are not breeding successfully are of poor quality, have a higher probability of death or emigration prior to the next breeding season, and this changes the fecundity of older animals at a population level (Reid et al. 2003). Unfortunately, insufficient longitudinal data are available to detect reproductive senescence in individual koalas in Chlamydia-free populations.
In contrast to the pattern of age-specific fecundity in the Chlamydia-free sites, fecundity declined with age from the earlier peak of TWC II at the Chlamydia-infected populations at Snake Island and Mt Eccles (Figure 6.7). Fecundity may decline with increasing age in Chlamydia-infected populations because the disease caused by Chlamydia ascends the reproductive tract and causes infertility in an increased proportion of older individuals (Obendorf and Handasyde 1990). This was consistent with the increase in the proportion of females with reproductive tract lesions with increasing age (Chapter 5).

**Consistency of breeding in consecutive seasons**

Female koalas studied in the Chlamydia-free French Island (1980-1985) population bred consistently in consecutive years. This has been found in previous studies of Chlamydia-free populations (McNally 1957, Eberhard 1972, 1978, Martin and Handasyde 1990a). Therefore, female koalas can gain sufficient resources from their energy-poor, folivorous diet to consecutively wean one young per year, despite the significant costs incurred during lactation (Krockenberger 1996). In contrast, at the Chlamydia-infected koala populations at the Brisbane Ranges and the KCC, some females failed to breed in one year and then bred in subsequent years. This has also been reported in koalas from Tucki Tucki, NSW (Gall 1980). It is unlikely that koalas do not breed in Chlamydia-infected populations due to factors such as the level of defoliation, koala density or rainfall at the site, as these parameters vary widely across both Chlamydia-infected and Chlamydia-free sites. Gustafsson et al. (1994) found a strong negative correlation between the immune response to parasitism and fecundity in collared flycatchers (*Ficedula albicollis*). It is possible that Chlamydia-infection not only reduces fecundity in koalas by causing infertility but also imposes a cost in terms of immune response that may reduce breeding in consecutive seasons.

The probability of a female koala having a young increased with morphometric condition in both Chlamydia-infected and Chlamydia-free populations. Condition affects fecundity in many species (see Chapter 3). For example, during drought, female red kangaroos with young had a heavier average body mass than females without young, within similar age classes (Newsome 1977) and fecundity declined in
drought years in ring-tailed lemurs (*Lemur catta*) (Gould *et al.* 2003). Body mass or condition explained variation in pregnancy rate in Crabeater (*Lobodon carcinophagus*) and Grey seals (*Halichoerus grypus*) (Boyd 2000), and breeding success in red deer (Albon *et al.* 1983) and common brushtail possums (*T. vulpecula*) (Ramsey *et al.* 2002). Additionally, body condition is correlated with litter mass in Richardson’s ground squirrels (*Spermophilus richardsonii*) (Dobson and Michener 1995). Poor body condition in females may be due to low food availability. Ramsey *et al.* (2002) found that over 80% of female common brushtail possums bred each year in populations in New Zealand but the probability of breeding decreased as body condition declined with low food availability.

**Density dependent declines in fecundity**

The fecundity of koalas declined with a severe population decline caused by food shortage at Sandy Point (Figure 6.6). There was a large decrease in fecundity from 1985 to 1989 at Sandy Point (66.7 - 36%), by which time the habitat was severely defoliated. This decline in fecundity at Sandy Point was associated with a period where food was not limited in 1984, through to a period corresponding with a large population decline culminating with a severe crash in 1988/89 due to starvation (Martin and Handasyde 1990a, Martin 1997, Martin and Handasyde 1999). The second decline in fecundity at Sandy Point from 1995 to 1999 (Figure 6.6) may have been linked to the defoliation of a second, separate habitat patch (K. Handasyde, pers. comm.). In contrast, there was very little variation in fecundity over time on French Island, which did not experience a severe population decline during that time period. Temporal variation in fecundity has been found in other koala populations. At Springsure (Qld) the fecundity ranged between 72 and 92%, whereas at Oakey (Qld) the variation was larger, 27-55% (Gordon *et al.* 1990b). At Walkerville, defoliation of preferred food trees was so severe that the koala population decreased (mostly through dispersal) from 3.0 to 0.7 koalas/ha between 1978 and 1980 and fecundity decreased from 36% to 13% over a similar time period (Martin 1981, 1985c, 1985a). Also, fecundity declined in koalas in Queensland as drought combined with a heat wave reduced the level of available browse (Gordon *et al.* 1988). Fecundity, especially that of younger females, has also been found to decrease with increasing population density in other mammalian herbivore species (Skogland 1985, 1986,
Clutton-Brock et al. 1987) but it may not decline until the population is close to starvation (Peterson 1999).

The two sampling periods at Sandy Point in 1989 provide an opportunity to investigate two hypotheses regarding the cause of the decreased fecundity during periods of population decline. Observed fecundity may be reduced by lower rates of conception or by lower juvenile survival rates. The absence of a difference in fecundity levels between May and October suggests either that mortality occurred before May, or that fecundity was low compared with other years due to a decreased conception rate. Sandy Point juveniles would most likely be 4-6 months of age in May and 9-11 months of age in October (calculated from the French Island breeding season, Martin and Handasyde 1990a). Krockenberger (1996) found that the time of highest energy content of milk is when koala young are 6-9 months of age. The absence of difference in the fecundity levels between May and October indicates that young at Sandy Point have very high juvenile survivorship through the period that is most energetically stressful to their mother even though their habitat was severely degraded.

The relationship between population density and fecundity was investigated at Snake Island, Mt Eccles and Framlingham to detect influences of density dependence on fecundity. At Framlingham the density in preferred habitat was estimated at 1.10 ±0.19 (mean ±s.e.) koalas per ha (Morgan 1998) whereas density ranged from 0.91 ±0.10 to 1.73 ±0.10 koalas per ha at Snake Island and Mt Eccles (Morgan 1998, 1999a, 1999b). Yet the fecundity at the former site was up to double that at the latter sites. Density was also reported to change between years at Snake Island (Morgan 1999b, 2000b) whereas fecundity remained constant. This may be due to biases in the population estimates (Morgan 2000a); however, it may be that the change in density was not sufficient to affect fecundity. There was also no evidence that the high degree of defoliation at Framlingham impacted upon the overall fecundity of the population in 1998, as the fecundity was similar to that on French Island (Figure 6.5) and in past studies (McNally 1957, Martin 1981), where there was little evidence of defoliation at present (Centre for Environmental Management University of Ballarat 2003). It is possible that there was a decrease in the fecundity at Framlingham prior to 1998 associated with the severe population decline (N. Martin, pers. comm.). Similarly, on
Raymond Island there was no decline in fecundity associated with defoliation of preferred food trees (Mitchell et al. 1989). Density-dependent decreases in female fecundity have been detected in red deer (Kruuk et al. 1999b) and sheep (Forchhammer et al. 2001). Additionally, fecundity of female Soay sheep is correlated with body mass, which in turn, is correlated with habitat condition and population density (Clutton-Brock et al. 1996). Thus, koala populations are affected by density-dependent factors but fecundity did not decrease at Sandy Point until the koalas were starving and the fecundity increased remarkably quickly after the main population crash. Thus, it may require a high population density and severe degree of defoliation and subsequent starvation of koalas before fecundity is substantially decreased.

Conclusion
The disease status of the population has a larger effect on the overall fecundity of the population than the degree of defoliation. Density dependent effects may not occur in koala populations until defoliation is severe, such as at Sandy Point in 1988. The effect of *Chlamydia*-infection on the age-specific fecundity of populations has the potential to alter the dynamics of the population. The breeding success of individuals, both in terms of the probability of having a young, and the ability to produce a young in subsequent seasons, is affected by a combination of body condition or nutritional status and the presence of *Chlamydia* in the population. Although *Chlamydia*-infection causes infertility in some females and reduces fecundity through decreasing body condition, it does not regulate populations, as illustrated by the high population densities and degree of defoliation at Snake Island and Mt Eccles, *Chlamydia*-infected populations.
Chapter 7 - Mortality rates and relative age- and sex-specific mortality patterns in Victorian koalas

Abstract
Aspects of the age structure, sex ratio, body condition, and fecundity of koala populations were investigated in previous chapters with the overall aim of determining how these factors affect population dynamics. An additional major factor influencing population dynamics is mortality, or its converse, survival. Juvenile and adult mortality rates were investigated by analysing available data from the literature, and patterns of sex and age-specific mortality (or longevity) were examined using collections of koala skulls. Annual juvenile mortality rates were variable (mean: pouch-young = 18%; back-young = 12% mortality per annum) but relatively low compared with other marsupials. Estimates of mortality rates of independent koalas varied with the method of data collection. The annual mortality rate at the Koala Conservation Centre (7.8%), where the most reliable data were collected, was comparable with other herbivores. Ninety-five percent of the skulls from Snake Island (both males and females) were in tooth wear classes (TWCs) I–IVC whereas 95% of the skulls from all other populations combined were in TWC I–VI (males) and TWC I–VII (females). Koalas exhibited sex-biased mortality with males dying at a younger age than females. This is similar to other sexually dimorphic mammal species. The low adult juvenile and mortality rates of koalas probably contribute to the rapid population growth of some populations.

Introduction
Variation in rates of mortality is one of the central determinants of population dynamics (Caughley 1966, Saether et al. 1996, Gaillard et al. 2000). However, accurate estimates of mortality rates, and how they vary with factors such as population density and environmental conditions, are difficult to determine (Hiby and Mullen 1980, Eberhardt 1985, Lebreton et al. 1992, Zens and Peart 2003). Furthermore, mortality rates of wild populations of long-lived vertebrates are difficult to measure given the long period of monitoring required (Jorgenson et al. 1997) and the difficulty of keeping track of known individuals (Lack 1954). Mortality will be over-estimated if it is assumed that emigrating individuals have died (McMahon et al. 2003). Therefore, it is advantageous to monitor individuals using radio-telemetry so that disappearance of animals can be confirmed as either death or emigration (Fedigan and Zohar 1997, Kenward et al. 1999). The difficulty of obtaining information on mortality often limits knowledge of population dynamics of many species. It also
means that data on mortality must often be obtained indirectly (Lima and Paez 1997). Mortality rates may differ between age classes and the sexes and may also vary temporally and spatially (Jorgenson et al. 1997, Sibly et al. 1997, Gaillard et al. 2000).

Age-specific mortality
Mammalian mortality rates often vary with age (Deevey 1947, Sibly et al. 1997, Shi et al. 2002). Age-specific mortality has a very important influence on strategies to maximize lifetime reproductive success (Clutton-Brock 1988b); and thus, is an important determinant of life history traits (Stearns 1976, Promislow and Harvey 1990, Stearns 1992). Age-specific mortality data are difficult to obtain (Brewer and Gaston 2003) and consequently, relatively few studies have reported accurate information on age-specific mortality and variation over time for wild mammal populations (Cransac et al. 1997, Jorgenson et al. 1997, Pistorius and Bester 2002). Long-term studies have been carried out and mortality rates determined for some primate species, although many of these studies relied on assumptions explaining the reasons for the absence of individuals (from death or emigration) (Furuichi et al. 1998, Watts 1998, Nakagawa et al. 2003, Nishida et al. 2003, Cheney et al. 2004). Additionally, as mortality rates may vary temporally and spatially, studies of population dynamics require understanding of this variation (Gould and Nichols 1998, Gould et al. 1999, Gaillard et al. 2000). Populations are often divided into broad age categories such as juveniles, sub-adults and adults. Adults may be divided further into "prime-age" where mortality rates are relatively low, and older animals where mortality rates may increase (senescence) (Promislow 1991, Sibly et al. 1997, McElligott et al. 2002). "Prime-age" has been defined as 2-7 years of age in large-bodied herbivores but the age range will differ between taxa (Loison et al. 1999, Gaillard et al. 2000).

Age-specific mortality greatly influences the capacity of a population to increase. In many mammal species, population growth is often more sensitive to changes in adult mortality than juvenile mortality (Eberhardt 1985, Coulson et al. 2001a, Clutton-Brock and Coulson 2002, Hebblewhite et al. 2003). However, relatively small variation in adult mortality may mean that variation in population growth rates are
primarily due to temporal variation in juvenile mortality (Gaillard et al. 1998, Gaillard et al. 2000). Juvenile mortality is frequently higher than adult mortality in mammals (Caughley 1966, Sibly et al. 1997) and is often affected to a greater extent by environmental factors than adult mortality rates (Jorgenson et al. 1997).

Determining age-specific mortality

Age-specific mortality rates can be determined using three main methods (Lack 1954, Caughley 1966). The most accurate method is to directly observe survivorship in a cohort using capture-mark-recapture (Caughley 1966, 1977, Lebreton et al. 1992, Lebreton 1995, Krebs 2001). The cohort should be observed at frequent intervals until the last individual is dead and differences in detectability should be accounted for (Owen-Smith 1993, Gaillard et al. 2000). While accurate, these methods are difficult to conduct and are expensive in terms of time and effort, especially in long-lived, wild mammals (Caughley 1967, Gaillard et al. 2000).

The second method is to determine mortality rates from the age structure of a population (Caughley 1977, Eberhardt 1985). This method is used frequently in fisheries management and called catch curve analysis (Chapman and Robson 1960, e.g. Choat et al. 2003). The relative abundance of an older age class is divided by the relative abundance of a younger age class to obtain the survivorship between the two age classes. This method assumes that the population size and survival rate in each age class is constant over time and that the age distribution is stable (Eberhardt 1985, 1988). Accuracy in determining the age of individuals is also assumed (Caughley 1967, 1977). Unfortunately, the data required to evaluate these assumptions are rarely available (Udevitz and Ballachey 1998). Additionally, Gaillard et al. (2000) warned that this was an unreliable method as it is affected by large sampling errors and changes in the survival (or detectability) of either age class would alter the survival estimate.

The third method is to observe the age at death of individuals within a population; for example, by determining the age at death of a collection of skulls or carcasses (Spinage 1972, Monson et al. 2000, Gonzalez and Crampe 2001). This method assumes that the population size and the age-specific fecundity and mortality rates remain constant (Caughley 1966, Murphy and Whitten 1976). Also, the probability of
skull deterioration and finding skulls in each age class should be equal (Spinage 1972, Bartmann 1984).

Occasionally a combination of these methods is used when a single method does not meet the assumptions in all age classes (Spinage 1972, Eberhardt 1985). For example, Sinclair (1977) found that the probability of finding skulls in the youngest age classes of African buffalo (*Syncerus caffer*) was low as the skulls were more fragile and easily crushed by carnivores and scavengers. Therefore, Sinclair (1977) directly observed the mortality rates of juveniles but calculated mortality rates of adults from skull collections.

**Sex-specific mortality**

Mortality rates differ not only due to differences in age but also differences in sex. The sex ratio of many mammal species is approximately equal at birth but becomes progressively female-biased in older age classes (e.g. Rogers *et al.* 1997). Sex-biased mortality occurs in many mammal species of all body sizes from moles (*Scalopus aquaticus*) (Hartman 1995) to elephants (Moss 2001). It has been proposed that earlier mortality of males of sexually dimorphic species may be due to their larger body size, the type of mating system or male-biased dispersal (Clutton-Brock *et al.* 1982, Clutton-Brock *et al.* 1985b, Promislow and Harvey 1990).

Sex-biased mortality is commonly detected in sexually dimorphic but not monomorphic mammal species. Male-biased mortality has been found in many sexually dimorphic species (Clutton-Brock *et al.* 1982, Skogland 1985, McCrorquodale *et al.* 1988, Quin 1989, Bowyer 1991, Promislow *et al.* 1992, Owen-Smith 1993, Moss 2001, Lopez *et al.* 2003, McMahon *et al.* 2003). Male-biased mortality was not detected in monomorphic species such as the isard (*Rupicapra pyrenaica*) (Gonzalez and Crampe 2001) or the alpine marmot (*Marmota marmota*) (Farand *et al.* 2002). The larger body size of males in many sexually dimorphic mammals means they have larger absolute energy requirements; thus, in food limited environments males may be more vulnerable to starvation (Clutton-Brock *et al.* 1985a, Toigo and Gaillard 2003). Fedigan and Zohar (1997) suggested that in sexually dimorphic species, males are more susceptible to nutritional shortages as...
they grow for a longer time period and the authors termed this the "fragile male" hypothesis. Contrary to the evidence supporting the sexual size dimorphism sex-biased mortality hypothesis, male-biased adult mortality has been detected in some sexually monomorphic species (Gaillard et al. 1993a, Loison et al. 1999) and failed to be detected in some sexually dimorphic species (Cransac et al. 1997, Toigo et al. 1997).

The degree of sexual dimorphism is highly correlated with polygyny (Jarman 1983, Cockburn and Johnson 1988). Thus, it is difficult to separate the effects of larger body size from the type of mating system. Sex-biased mortality may be due to the type of mating system and extent of male-male competition (Clutton-Brock et al. 1982). Male-biased mortality may occur in polygynous species where males expend large amounts of energy searching for sexually receptive females. The consequent competition for mating opportunities can lead to death from fighting (Clutton-Brock et al. 1982, Owen-Smith 1993, Yoccoz et al. 2002). Promislow (1992) found that mortality in monogamous mammal species was mostly non-biased or female-biased while mortality was male-biased in non-monogamous species (but see Owen-Smith 1993, Loison et al. 1999).

Sex-biased dispersal has also been suggested as an explanation for sex-biased mortality (Clutton-Brock et al. 1985b). As the males of many mammal species disperse further and more frequently than the females (Greenwood 1980), costs associated with dispersal such as increased energy expenditure and increased risk of predation may lead to male-biased mortality (Clutton-Brock et al. 1985b, but see Owen-Smith 1993). Sex-biased mortality due to increased susceptibility to road trauma has been documented in some mammalian species (Coulson 1997, Dique et al. 2003b). Fedigan and Zohar (1997) formalised this as the "high-risk, high-gain" hypothesis and proposed that males that disperse are at higher risk of predation and disease and have lower security of food availability than non-dispersing animals, but they have a higher probability of increased mating success with unrelated females.
Mortality in koalas

Koalas are thought to live to between 10 and 20 years of age in southern Australian populations (Eberhard 1978, Martin and Handasyde 1990a) but only to a maximum of 10 years in Queensland populations (Melzer 1995). Martin and Handasyde (1990a) estimated that one female koala was 17.5 years of age. As with most long-lived (greater than 5 years of age) mammals, little is known about mortality rates in koalas despite the importance of this parameter for population dynamics (Melzer and Houston 2001). Many estimates of loss of koalas from wild populations do not separate mortality from emigration (Martin 1985c, Gordon et al. 1988, Gordon et al. 1990b, Mitchell and Martin 1990, Middleton et al. 2003). Most information regarding mortality rates of koalas is incidental or relies upon small sample sizes or short time periods (Gall 1978, White and Kunst 1990, Hasegawa 1995, Thompson 2001). Annual mortality was estimated to be 5.6% (n = 22) in northern New South Wales (Ramsay 1999), and 35% (n = 20, females aged 36 months and over) on the Koala Coast (Dique et al. 2003a).

Apart from the differences in mortality rates between the major life stages (juvenile, sub-adult and adult), little is known about age-specific mortality patterns in koalas (Melzer and Houston 2001). Limited information on age-specific mortality patterns of adults based on koala skulls was provided by Melzer (1995) and Gowans et al. (2000). The information from Melzer (1995) was used by Penn et al. (2000) to predict growth of Queensland koala populations. Mortality rates may be high for dependent koalas in some populations (29%, n = 42 Ramsay 1999, 14.3%, n = 126 Dique et al. 2003a). Annual mortality rates of sub-adult koalas (one to three years old) ranged between 9% and 25% (Mitchell 1990c, Ramsay 1999, Dique et al. 2003a). More accurate information regarding age-specific mortality rates in koalas is required as mortality has such a profound influence on population dynamics.

Very little is known about sex-specific differences in koala mortality except for the suspected greater maximum longevity in females compared with males (Martin and Handasyde 1999). Recent evidence from Dique et al. (2003a) suggested that mortality rates of two to three year old male and female koalas is similar. Koalas potentially fit the sex-biased mortality hypotheses of sexual size dimorphism, sex-biased dispersal...
and a polygynous mating system discussed above. Adult koalas are sexually dimorphic (McNally 1957, Nagy and Martin 1985) where male koalas are, on average, 1.3 times the body mass of females (Chapter 5). Male koalas disperse at approximately two years of age in high density populations (Mitchell and Martin 1990) but do not reach physical maturity until after four years of age (Chapter 3). Young males are thought to experience greater mortality rates than other age/sex classes due to the increased risks encountered during dispersal (Eberhard 1978, Gordon et al. 1990a, Mitchell and Martin 1990). However, mortality of koalas was highest in the post dispersal period on the New England Tablelands in New South Wales (Ramsay 1999) and high mortality rates were not found in young dispersing males on French Island (Mitchell 1990c), where the influence of cars and domestic dogs was negligible. Koalas are regarded as polygynous and males compete for access to females and sometimes sustain fatal wounds (Hindell 1984, Mitchell 1990b, see also Ellis et al. 2002a). Additional evidence for a polygynous mating system comes from the home range sizes, where the home ranges of males are usually larger than those of females (Mitchell 1990a, reviewed by Melzer and Houston 2001, Ellis et al. 2002b) and may overlap the home ranges of several (up to nine) female koalas (Mitchell 1990a). Furthermore, adult males moved more often during the breeding season than the non-breeding season (Mitchell 1990a). Thus, males probably have an increased chance of mortality due to both fighting and increased energy expenditure during the breeding season. Hence, sexual dimorphism, male-biased dispersal and/or a polygynous mating system suggest that mortality in koalas will be male biased.

Aims

The aims of this chapter are to determine koala mortality rates at the KCC and compare these with data extracted from the literature. I investigate evidence of differential mortality between the sexes in koalas and determine survivorship of juveniles. I also aim to determine relative age-specific mortality patterns.
Methods

Mortality rates

Average mortality rates for wild juvenile, sub-adult and adult koalas were calculated from information in the literature, from koalas that were radio-collared for up to 3.5 years at the Brisbane Ranges, French Island (1980-1985) and Phillip Island (K. Handasyde and R. Martin, unpublished data) and from koalas at the KCC monitored for up to ten years. The proportion of the total number of koalas alive and dead were compared between populations separately for pouch-young and back-young using contingency tables and adjusted residuals. If the absolute value of the adjusted residuals was greater than 1.96, the adjusted residual was significant at \( \alpha = 0.05 \) (Everitt 1986). Sub-adult and adult mortality rates were not compared statistically between populations due to small sample sizes and the different methods used to calculate the mortality rates. Mortality rates were not calculated from the population age structure in this chapter as this is covered in Chapter 8.

Information on mortality derived from skulls

Skull collections

Koala skulls were opportunistically collected from Victorian koala populations (Appendix J). These skulls are referred to as “pick-up skulls”. Skulls collected from Snake Island, Framlingham and Mt Eccles were assumed to have resulted from natural mortality, as road traffic and predation by domestic dogs are considered negligible at these sites. Skulls from other populations were allocated a cause of death including natural mortality, death resulting from road trauma or unknown cause of death. Koalas were presumed to have died from road trauma if the carcass was found in close proximity to a road. Koalas were allocated to the unknown cause of death category if there was no information regarding collection details. Skulls from collections held at Museum Victoria and the Departments of Zoology at the University of Melbourne, Monash University and La Trobe University were included in the sample.
**Skull measurements**

In order to compare age-specific mortality patterns separately in males and females, skulls were measured to determine the sex. Tooth wear class was recorded following the criteria described in Chapter 3. Three skull measurements (recorded to the nearest millimetre) were made using vernier calipers. "**Maximum width**" was the maximum distance across the zygomatic arches while maintaining the calipers perpendicular to the midline of the skull. As many skulls had damage to the nasal/premaxillae bones, two measures of length were recorded. Length was measured from the posterior margin of the crest formed by the junction of the parietal and supraoccipital bones to:

1) the junction between the anterior of the premaxillae bones and the anterior part of the upper incisors (termed "**skull length**") and,

2) the anterior margin of the nasal bones (termed "**dorsal length**"), see Figure 7.1.
Figure 7.1 Measurements of maximum width (the maximum distance across the zygomatic arches), skull length (the distance between the posterior of the skull and the anterior edge of the premaxillae bones) and dorsal length (the distance between the posterior of the skull and the anterior margin of the nasal bones).
Determining the sex of skulls

The sex of the pick-up skulls was unknown. In order to determine the sex of the pick-up skulls, skulls where the sex of the individual was known were measured at museums and additional skulls were collected from koalas that died as a result of road trauma and from veterinary surgeries. Known-sex skulls were used to obtain a function to predict the sex of skulls for which the sex was unknown. Two methods were trialled to predict the sex of skulls: logistic discrimination and discriminant function analysis (DFA).

Logistic discrimination incorporated skull length, dorsal length and maximum width as continuous explanatory variables. TWC was entered as a categorical explanatory variable. All interactions were also included. Statistical significance of variables and interaction terms were assessed by comparing the change in deviance with a chi-square distribution (at $P < 0.05$). Only variables that were significant were included in the results.

Discriminant function analysis has been used to determine whether there were differences in skull morphology between geographically isolated populations (Rhind et al. 2001) and to distinguish between the sexes (McCloskey and Thompson 2000). Data for the DFA were screened for normality, outliers, multivariate outliers (using Mahalanobis distances) and homogeneity of variance-covariance matrices (assessing Box's M test at a increased $P$-value as this test is overly sensitive (Tabachnick and Fidell 2001). DFA was only proceeded with if Wilk's lambda was significant ($<0.05$). Prior probabilities were set at "all groups equal" and predictor variables were entered together instead of stepwise (Quinn and Keough 2002). Skull length, dorsal length, maximum width and TWC were entered in the DFA along with the interaction of skull length with TWC. As classification results may be biased if based on the cases that are then used to test the functions, all classification results reported are jackknifed (cross-validated). The classification success of the two methods was compared.
Increasing the accuracy of determining the sex of skulls

In order to improve the classification success of the discriminating equations, the sample size of known-sex skulls was increased by estimating the skull length of live koalas. This was done via correlation of the head length with the skull length in individual fresh koalas killed on roads (road kills). The head length of each road kill animal was measured before the head was removed and cleaned. Cleaned skulls from these individuals were then measured in the same manner as the pick-up skulls. The head lengths of the fresh road kill koalas were regressed against the skull lengths, dorsal lengths and the maximum skull widths. Using this regression, the mean difference between the head and skull length of the road kill koalas was subtracted from the head lengths of live animals to estimate the skull length of the live (known-sex) koalas from Framlingham, Mt Eccles, and Snake and French Islands. The estimated skull lengths of the live koalas from Framlingham, Mt Eccles and Snake and French Islands were then used in the discriminant function analysis.

Relative pattern of age-specific mortality based on skulls

The frequency distribution of pick-up skulls across TWCs was assessed in order to compare age and sex-specific mortality patterns. Due to the low sample sizes from many sites (Appendix J), distributions were not compared between all sites. Skulls were divided into those from Snake Island and those from all other sites. The TWC distributions of skulls were compared between males and females, and natural, road trauma or unknown cause of death for Snake Island and the pooled sites using Kolmogorov-Smirnov Z, 2 independent samples tests. A pattern of natural mortality was calculated from the skulls from Snake Island, as this was a large sample that was collected over a relatively short time period. This distribution was compared with distribution of live koalas at Snake Island (Chapter 4). The distribution of skulls from koalas that died as a result of road trauma was examined for patterns in the age and sex of the koalas killed.
Results

Mortality rates

Mortality of koalas in wild populations

The adult mortality rates derived from data in the literature varied between 0.75 and 39.6% per year (Table 7.1). Within the radio-collared adults, three natural and one unnatural death were recorded from a sample of 41 koalas over a mean of 1.9 (s.d. = 0.68) years on French Island (1980-1985), Phillip Island and at the Brisbane Ranges (K. Handasyde and R. Martin, unpublished data) giving a mean annual mortality rate of 4.5% (Table 7.1). There were insufficient data to separate “prime-age” mortality rates from older koala mortality rates. The mortality rate of sub-adults at the Brisbane Ranges (3.7% per year) (Table 7.1) was due to the road trauma death of one female.

The mortality rate of pouch-young (Table 7.1) was significantly higher at Walkerville (33%) than French Island (1980-1985) (14%) or the Brisbane Ranges (4%) ($\chi^2 = 9.79$, d.f. = 4, $P < 0.05$). Similarly, the mortality rate of back-young (Table 7.1) was significantly higher at Walkerville (37.5%) than on French Island (4%) ($\chi^2 = 12.99$, d.f. = 3, $P < 0.01$).
Table 7.1 Number (n) of pouch-young, back-young, sub-adult and adult koalas monitored (mean study duration ± one standard deviation (s.d.) in years) and the number of deaths, resulting annual mortality rate and corresponding average age at death (in years) for koala populations in Victoria and South Australia. Method denotes the style of data where “radio-collar” represents radio-collared individuals (or the mother of dependent young) monitored over time, “Ear tags” represents animals with individually recognisable ear tags observed over time, and “Road kill” represents a study of the number of koalas killed by road trauma and estimates of the number of live animals in the population.

<table>
<thead>
<tr>
<th>Site</th>
<th>Method</th>
<th>n</th>
<th>Mean study duration ± s.d. (years)</th>
<th># of deaths</th>
<th>Mortality rate (%/year)</th>
<th>Av. age of death (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pouch-young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Island&lt;sup&gt;a&lt;b&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>56</td>
<td>8 ± 14.3</td>
<td>8</td>
<td>3%</td>
<td>14 ± 3</td>
</tr>
<tr>
<td>Kangaroo Island&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>14</td>
<td>3 ± 21</td>
<td>3</td>
<td>7.7%</td>
<td>5 ± 2</td>
</tr>
<tr>
<td>Nth Walkerville&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Ear tags</td>
<td>24</td>
<td>8 ± 33.3</td>
<td>8</td>
<td>37.5%</td>
<td>3 ± 2.5</td>
</tr>
<tr>
<td>Brisbane Ranges&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>25</td>
<td>1 ± 4</td>
<td>1</td>
<td>12.5%</td>
<td>1 ± 0.5</td>
</tr>
<tr>
<td>Phillip Island&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>8</td>
<td>3 ± 37.5</td>
<td>3</td>
<td>14.3%</td>
<td>1 ± 2</td>
</tr>
<tr>
<td>Back-young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Island&lt;sup&gt;a&lt;b&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>48</td>
<td>2 ± 4</td>
<td>2</td>
<td>4%</td>
<td>3 ± 1</td>
</tr>
<tr>
<td>Kangaroo Island&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>13</td>
<td>1 ± 7.7</td>
<td>1</td>
<td>7.7%</td>
<td>5 ± 2</td>
</tr>
<tr>
<td>Nth Walkerville&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Ear tags</td>
<td>16</td>
<td>6 ± 37.5</td>
<td>6</td>
<td>37.5%</td>
<td>3 ± 2</td>
</tr>
<tr>
<td>Brisbane Ranges&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>24</td>
<td>3 ± 12.5</td>
<td>3</td>
<td>9.1%</td>
<td>2 ± 1</td>
</tr>
<tr>
<td>Sub-adults&lt;sup&gt;f&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Island&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>11</td>
<td>1.1 ± 3.7</td>
<td>1</td>
<td>3.7%</td>
<td>2 ± 0.7</td>
</tr>
<tr>
<td>Brisbane Ranges&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>18</td>
<td>1.1 ± 3.7</td>
<td>1</td>
<td>3.7%</td>
<td>2 ± 0.7</td>
</tr>
<tr>
<td>Adults</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Island&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Ear tags</td>
<td>152</td>
<td>3.5 ± 3.5</td>
<td>3&lt;sup&gt;l&lt;/sup&gt;</td>
<td>0.75%</td>
<td>0.75 ± 0.3</td>
</tr>
<tr>
<td>French Island&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>9</td>
<td>1.6 ± 0.3</td>
<td>0</td>
<td>0%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>Nth Walkerville&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Ear tags</td>
<td>98</td>
<td>3.0 ± 5.4</td>
<td>16</td>
<td>5.4%</td>
<td>0.75 ± 0.3</td>
</tr>
<tr>
<td>Brisbane Ranges&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>21</td>
<td>1.6 ± 0.5</td>
<td>3</td>
<td>8.9%</td>
<td>10 ± 2</td>
</tr>
<tr>
<td>Phillip Island&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Radio-collar</td>
<td>11</td>
<td>2.6 ± 0.7</td>
<td>1</td>
<td>3.5%</td>
<td>3 ± 0.5</td>
</tr>
<tr>
<td>Phillip Island&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Ear tags</td>
<td>117</td>
<td>3.5 ± 5.6</td>
<td>23</td>
<td>5.6%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>Phillip Island&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Road kill</td>
<td>234</td>
<td>62 ± 26.5</td>
<td>62</td>
<td>39.6%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>1986 Road kill</td>
<td></td>
<td>177</td>
<td>70 ± 39.6</td>
<td>70</td>
<td>39.6%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>1987 Road kill</td>
<td></td>
<td>131</td>
<td>44 ± 33.6</td>
<td>44</td>
<td>33.6%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>1988 Road kill</td>
<td></td>
<td>133</td>
<td>44 ± 33.1</td>
<td>44</td>
<td>33.1%</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>Sum radio-collared adult koalas</td>
<td>Radio-collar</td>
<td>31</td>
<td>1.9 ± 4.5</td>
<td>4</td>
<td>4.5%</td>
<td>2 ± 1</td>
</tr>
</tbody>
</table>

References: <sup>a</sup> Handasyde (1986), <sup>b</sup> Martin and Handasyde (1990a), <sup>c</sup> Eberhard (1972), <sup>d</sup> Martin (1985c), <sup>e</sup> Mitchell (Table 10.5, 1990c), <sup>f</sup> R. Martin and K. Handasyde, unpublished data, <sup>g</sup> Mitchell and Martin (1990), <sup>h</sup> Every (1986), and <sup>i</sup> Backhouse and Crouch (1990). <sup>j</sup> Sub-adults on French Island were monitored.
observed from (approximately) 30 to 42 months of age, and sub-adults at the Brisbane Ranges were observed (on average) from 13 to 28 months of age. Includes juveniles, plus one juvenile female died. Calculated using the equation, average age of death = 1/(1-s), where s is survival, and survival is assumed constant over time (Kendall 1949, Johnson and Kotz 1969). Note: the average age at death is included to illustrate the potential inaccuracy of the mortality rates, not as a true estimation of the average age of death of koalas.

**Mortality of semi-captive koalas at the Koala Conservation Centre**

Mortality at the KCC averaged 7.8% per year (s.d. = 4.99, 69 individual koalas) between 1991 and 2002 but ranged widely between 0 and 16% in different years (Figure 7.2). Of the 47 koalas monitored between birth and one year of age, 8.5% died and of the 43 koalas monitored from one to two years of age, 4.7% died (Figure 7.3, Note: the sex was not known for all young). Male koalas died at an earlier age than female koalas (Figure 7.3). All known-age koalas died before 13 years of age.

![Figure 7.2 Percentage mortality (known and not known-age koalas) in the years between 1991 and 2002 at the Koala Conservation Centre. Numbers above the symbols are sample sizes.](image)

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Figure 7.3 The percentage of known-age female (hatched bars) and male (filled bars) koalas that died in each age at the Koala Conservation Centre between 1991 and 2002. The numbers above the bars are sample sizes for females and males.

**Determination of the sex of skulls**

**Determining the sex of skulls using known-sex skulls**

Three hundred and ninety-seven skulls were measured where the sex of the koala from which the skull was derived was known. However, 37 of these skulls were damaged precluding some measurements from being taken. The sex of skulls was determined using two statistical methods: logistic discrimination and discriminant function analysis (DFA). The logistic discrimination based on 360 known-sex skulls produced the following equation to classify skulls by sex:

$$Pm = \frac{\exp \text{(linear predictor)}}{[\exp \text{(linear predictor)} + 1]}$$

Equation 7.1
where $P_m$ is the probability of the koala being male, and the linear predictor = $\Sigma(\text{Variable}*\text{Coefficient}) - \text{constant}$, see Table 7.2.

If $P_m > 0.5$, then the skull was classified as a male.

Table 7.2 Values for the coefficients and standard error (s.e.) of the coefficient for each variable in the logistic discrimination equation derived from 360 Victorian koala skulls of known-sex (Equation 7.1).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>s.e. of coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>TWC I</td>
<td>8.669</td>
<td>1.51</td>
</tr>
<tr>
<td>TWC II</td>
<td>4.422</td>
<td>1.10</td>
</tr>
<tr>
<td>TWC III</td>
<td>3.673</td>
<td>1.08</td>
</tr>
<tr>
<td>TWC IVA</td>
<td>2.435</td>
<td>1.01</td>
</tr>
<tr>
<td>TWC IVB</td>
<td>1.886</td>
<td>1.05</td>
</tr>
<tr>
<td>TWC IVC</td>
<td>1.258</td>
<td>1.02</td>
</tr>
<tr>
<td>TWC V</td>
<td>-2011.82</td>
<td>7072.5</td>
</tr>
<tr>
<td>TWC VI</td>
<td>-2038.53</td>
<td>7693.2</td>
</tr>
<tr>
<td>Dorsal length</td>
<td>-0.233</td>
<td>0.09</td>
</tr>
<tr>
<td>Skull length</td>
<td>-0.032</td>
<td>0.10</td>
</tr>
<tr>
<td>Width</td>
<td>-0.011</td>
<td>0.07</td>
</tr>
<tr>
<td>Dorsal*Skull length</td>
<td>0.002</td>
<td>0.0003</td>
</tr>
<tr>
<td>TWC V*Skull length</td>
<td>14.642</td>
<td>51.46</td>
</tr>
<tr>
<td>TWC VI*Skull length</td>
<td>0.505</td>
<td>11.89</td>
</tr>
<tr>
<td>TWC VI*Dorsal length</td>
<td>10.859</td>
<td>43.08</td>
</tr>
<tr>
<td>TWC VI*Width</td>
<td>6.837</td>
<td>26.78</td>
</tr>
<tr>
<td>Constant</td>
<td>0.072</td>
<td>3.69</td>
</tr>
</tbody>
</table>

In the discriminant function analysis TWC I skulls were excluded to improve normality and homogeneity of variance. The full DFA was performed with all terms and the interaction of skull length with TWC but this interaction had a non-significant Wilk's lambda value ($P > 0.05$) and was excluded. Dorsal length and maximum width were highly correlated with skull length ($r^2 = 0.952$ and 0.790, respectively) and also had low (absolute) standardized canonical discriminant function coefficients indicating that they contributed relatively little to the discriminant function (Table 7.3). Therefore, dorsal length and maximum width were excluded, and the DFA was based only on TWC and skull length.
Table 7.3 Standardized canonical coefficients of each variable in the discriminant function analysis for known-sex skulls.

<table>
<thead>
<tr>
<th>Variable in DFA</th>
<th>Standardized canonical coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>TWC</td>
<td>-6.37</td>
</tr>
<tr>
<td>Skull length</td>
<td>0.909</td>
</tr>
<tr>
<td>Dorsal length</td>
<td>0.064</td>
</tr>
<tr>
<td>Maximum width</td>
<td>0.169</td>
</tr>
</tbody>
</table>

The DFA produced the following equations to calculate the discriminate score (D):

\[ D_F = [-1.899 \times \text{TWC} + 1.807 \times \text{skull length} - 110.131], \]
\[ D_M = [-2.696 \times \text{TWC} + 2.139 \times \text{skull length} - 151.103]. \]

Equation 7.2

In order to classify each skull with regard to sex, the measurements for each skull were inserted into both equations and the skulls were classified as male if \( D_F < D_M \), and female otherwise.

When TWC I skulls were excluded, the logistic discrimination correctly predicted the sex of 94% of female and 88% of male skulls (91.1% overall) while the discriminant function analysis correctly predicted 97% of female and 87% of male skulls (91.9% overall). The percentage of females and males correctly classified in each TWC is shown in Figure 7.4. Both classification techniques had similar success in TWCs greater than TWC IVA but the logistic discrimination was slightly more accurate for classifications of male skulls. For females in TWC III, the DFA had higher accuracy while in TWC II logistic discrimination had higher classification success than DFA. Figure 7.5 shows how both techniques classified skulls with respect to TWC and skull length. Although the range of head lengths of female koalas in TWC I was similar to that of males (Figure 7.5a), logistic discrimination classified the half with the largest skull length as males and the half with the smallest skull length as females (Figure 7.5b). This indicated that neither method could accurately separate male from female skulls in TWC I.
Figure 7.4 Percentage of a) female and b) male koala skulls classified correctly by logistic discrimination (hatched bars) and discriminant function analysis (filled bars). Numbers above bars are sample sizes.
Figure 7.5 Skull length (mm) regressed against tooth wear class for females (triangles) and males (squares) where sex is a) the observed sex, \( n = 390 \); b) predicted from logistic discrimination, \( n = 360 \); and c) predicted from discriminant function analysis, \( n = 359 \).
**Increasing the accuracy of determining the sex of skulls**

In order to increase the accuracy of the classifications, the sample size of known-sex skulls was augmented by estimating the skull length of live koalas via correlation with head length in road kill koalas. Head length of road kill koalas was regressed against skull length \( (r^2 = 0.989) \), dorsal length \( (r^2 = 0.976) \) and maximum width \( (r^2 = 0.904) \) of the cleaned skull (Figure 7.6a, b, c). Skull length was chosen for analysis as it had the highest correlation coefficient. Skull length was related to head length by the following equation:

\[
\text{Skull length} = 0.97 \times \text{head length} - 6.64
\]

Equation 7.3

Equation 7.3 was applied to the head lengths of live koalas from Mt Eccles, Framlingham and Snake and French Islands to obtain an estimate of each individual’s skull length. The estimated skull lengths of live koalas from these sites were analysed using DFA. The variables included in the DFA were the log of TWC and estimated skull length (from Equation 7.3).

The overall classification result of 92.9% correct allocation of sex (female 96.9%; male 88.0%) was not greatly improved beyond the DFA classification results from the smaller sample of known-sex skulls (91.9%). Therefore, the estimated skull lengths of live koalas were not used to improve the discriminant functions. Instead they were used as an independent test of the discriminant function derived from the known-sex skulls. The overall classification success for the estimated skull lengths was 83.8% \( (n = 4022) \), which was much lower than the classification success from the known-sex skulls used to derive the discriminant functions. Classification success was low for females \( (75.7\%, n = 2199) \) but high for males \( (93.6\%, n = 1706) \) (Figure 7.7). Both males and females in TWC II had a low classification success of <83% and females in TWC III and IVA had classification success under 68%. The apparently low classification success of males in TWC VII may be due to the low sample size.
Figure 7.6 Regression of the head length (mm) of road kill koalas on a) skull length (mm), \( n = 60 \); b) dorsal length (mm), \( n = 58 \); and c) maximum skull width (mm), \( n = 55 \). Triangles represent females and squares represent males.
Tooth wear class

Figure 7.7 Percentage of live female (hatched bars) and male (filled bars) koalas from Framlingham, Mt Eccles, Snake and French Island classified correctly (allocated to the correct sex on the basis of skull length) using the discriminant functions derived from the known-sex skulls. Numbers above the bars are sample sizes.

This suggested that a sample of skulls not used to derive the classification equations were classified with lower success using DFA than those skulls used to derive the equations, even using jackknifed classification. The live koalas with estimated skull lengths were not used to independently test the classification success of the logistic discrimination as the regression of head length on maximum skull width had a lower regression coefficient ($r^2 = 0.904$) and the estimation of the maximum skull width of the live animals would not be as accurate as the estimation of the skull length. Therefore, to test the logistic discrimination with skulls not used to derive the function, the logistic discrimination was performed with 25% of cases randomly removed from the initial sample and these cases were then used to test the success of the classification equation. The new classification equation (using 75% of the original cases) correctly classified 87.7% of all skulls (90.1% success for females, $n = 131$; 85.4% success for males, $n = 127$) that were used to derive the equation. This classification equation had similar if not better success in classifying the skulls not
used to derive the equation (93.5% success for all skulls, \( n = 92 \); 94.5% success for females, \( n = 55 \); 91.9% success for males, \( n = 37 \)).

To assign a sex to the "pick-up" skulls where sex was unknown, both the equations from the DFA and the equation from the logistic discrimination were used:

If \( TWC \geq IVA \) then sex of the skull is predicted by Equation 7.1;
If \( TWC = III \) then sex of the skull is predicted by Equation 7.2;
If \( TWC = II \) then sex of skull is predicted by Equation 7.1;
If \( TWC = I \) the sex of the skull cannot be accurately predicted;

If the skull was missing measurements for some variables required for the logistic discrimination then Equation 7.2 was used to predict the sex of the skull, provided the animal was older than \( TWC \) I.

**Relative pattern of age- and sex-specific mortality based on skulls**

One thousand and two skulls were measured; however, many had damage to their length or teeth or their sex could not be estimated, leaving 839 useable skulls from 132 Victorian localities (Appendix J). Eleven sites had more than ten skulls collected from them. Distributions of both male and female skulls across TWCs were different between Snake Island and the other sites but similar among the other sites. Therefore, all sites except Snake Island were pooled and the analysis was conducted separately for Snake Island and the pooled sites.

**Patterns of age-specific mortality in males and females**

All skulls from Snake Island were from animals that probably died from natural causes. No skulls were found in TWC I. Mortality occurred at an earlier age in males than in females. Median mortality was TWC IVB in females and TWC III in males (44.7% of males died in TWC III) (females, 7 y.o.; males, 5 y.o.; see Chapter 3). Ninety-five percent of skulls from both males and females were in TWC II - IVC. The TWC distribution of male skulls was significantly different from the distribution of female skulls (\( Z = 2.170, n = 46, 132, P < 0.001 \)) (Figure 7.8a). In January 2000 a
large fire burnt a proportion of Snake Island. To determine whether this fire might have affected the pattern of age-specific mortality at Snake Island, the skulls that were found after this date in the area of the fire, were excluded from the data (Figure 7.8b). A visual comparison of Figure 7.8a and Figure 7.8b shows that there is little difference between the distributions.

Age distribution: live and dead koalas

The age distributions of dead koalas (from skulls) were significantly different from that of the live population at Snake Island in 1997 (Chapter 4) for both females ($Z = 2.989, n = 46,342, P < 0.001$) and males ($Z = 2.705, n = 132,305, P < 0.001$) with TWC II animals under-represented in the skull collection. This suggests that mortality is lower in younger TWCs.
Figure 7.8 Percentage of female (hatched bars) and male (filled bars) koala skulls from Snake Island in each tooth wear class. a) Full data set, $n = 46$ female, 132 male skulls; b) skulls from koalas that could possibly have been killed by fire were excluded, $n = 31$ female, 89 male skulls.
For sites where data on skull age were pooled, mortality due to road trauma was spread over all TWCs greater than TWC I in females and TWC II in males (Figure 7.9). Of the individuals that were presumed killed by road trauma, 39% of females and 17% of males were in the older TWCs (V – VII combined). Only 2.5% of all koalas that were presumed killed by road trauma were in TWC II. The overall sex ratio of 1:1.35 (17 males: 23 females) for koalas presumed killed by road trauma was not significantly different from parity ($\chi^2 = 0.9$, d.f. = 1, $P > 0.05$).

Figure 7.9 Frequency of female (hatched bars), and male (filled bars) koala skulls from all sites pooled (except Snake Island) in each tooth wear class that were presumed killed as a result of road trauma.

In the pooled sites there was little evidence of a difference in the pattern of age-specific mortality of male koalas that died of natural causes compared with unknown causes ($Z = 0.522$, $n = 89, 231$, $P = 0.948$), or natural causes compared with road trauma ($Z = 0.607$, $n = 89, 17$, $P = 0.855$), or unknown causes compared with road trauma ($Z = 0.762$, $n = 17, 231$, $P = 0.607$). Therefore, males were pooled over all causes of death for all sites except Snake Island. Similarly, there was little evidence of a difference in these same comparisons for females from pooled sites (natural and unknown: $Z = 0.694$, $n = 81, 225$, $P = 0.722$; natural and road trauma: $Z = 0.479$, $n = 81, 23$, $P = 0.976$; road trauma and unknown: $Z = 0.283$, $n = 23, 225$, $P = 1.000$).
Therefore, females were pooled for all three causes of death for all sites except Snake Island.

Age-specific mortality patterns differed significantly between females and males for the pooled sites \((Z = 2.374, n = 335, 346, P < 0.001)\) (Figure 7.10). The median age of the pick-up skulls at death was TWC IVC in females and TWC IVB in males. This was two TWCs older than the Snake Island males. Ninety-five percent of skulls from females were in TWC I - VII while 95% of skulls from males were in TWC I - VI.

![Figure 7.10](image)

Figure 7.10 Percentage of female (hatched bars), \(n = 335\), and male (filled bars), \(n = 346\), koala skulls from all sites pooled (except Snake Island) in each tooth wear class (pooled over all causes of death).

**Comparison of age-specific mortality patterns between Snake Island and pooled sites**

Female and male age-specific mortality patterns were significantly different between Snake Island and all other sites pooled (female: \(Z = 2.609, n = 46, 335, P < 0.001\); male: \(Z = 3.539, n = 132, 346, P < 0.001\)) (Figure 7.11). Mortality curves (cumulative mortality as a function of age) for adults from Snake Island and the pooled sites, where adults are defined as older than TWC I are shown in Figure 7.12. Juveniles could not be included in the mortality curves due the differences in the methods of data collection. Both females and males tended to die at a younger age on Snake
Island compared with the other sites. Seventy-eight percent of female skulls from Snake Island were in TWCs IVA, IVB and IVC whereas only 39% from the pooled sites were in these TWCs. Only 4% of female skulls at Snake Island were in TWCs greater than IVC but 45% of female skulls at the pooled sites were in these classes. Forty-five percent of Snake Island male skulls were in TWC III compared with 17% at the pooled sites. Five percent of male skulls at Snake Island were in TWCs greater than TWC IVC, compared with 35% at the pooled sites.
Tooth wear class

Figure 7.11 Age-specific mortality distributions based on koala skulls from Snake Island (open bars) and all sites (excluding Snake Island) pooled (hatched bars): a) females, Snake Island, $n = 46$, pooled sites $n = 335$; and b) males, Snake Island $n = 132$, and pooled sites $n = 346$. 
Figure 7.12 Relationship between cumulative mortality and tooth wear class based on koala skulls for females (triangles) and males (squares) for Snake Island (filled symbols) and all sites (excluding Snake Island) pooled (open symbols). Females: Snake Island, $n = 46$, pooled sites, $n = 335$; males: Snake Island, $n = 132$, pooled sites, $n = 346$. None of the skulls collected were in TWC I.
Discussion

Mortality Rates

Low adult mortality rates

The average mortality rate at the KCC (7.8% per year) is probably the most representative of actual mortality rates among wild koala populations as the population was monitored over a long time period. Although the koalas at the KCC are semi-captive, they occasionally climb the fence, therefore deaths caused by road trauma are included in the data. However, the mortality rate may be lower than the true mortality rate of wild koalas as veterinarians treat sick and injured animals, and the population density and composition is managed at the KCC. Another line of evidence that mortality at the KCC might be lower than in truly wild populations is the higher survival of TWC VI and VII individuals at the KCC compared with sites such as Snake Island and Mt Eccles (Chapter 4). Unfortunately sample sizes were insufficient to compare temporal variation in mortality rates at the KCC and there were insufficient data to separate mortality rates of “prime-age” adults and older adults in the senescent phase (see Jorgenson et al. 1997, Gaillard et al. 2000). Despite these limitations, these data provide the only reasonably direct estimate of mortality rates of adult koalas in Victoria.

Annual mortality rates of Victorian adult koalas, of 4.5% per year (calculated from radio-collared koalas) and 0.75-5.6% per year (data extracted from studies of tagged animals) (Table 7.1), were very low. In non-urban environments natural mortality may only currently occur through avian predators and old age. Avian predators include raptors such as wedge-tailed (Aquila audax) and white-bellied sea eagles (Haliaeetus leucogaster) and powerful owls (Ninox strenua), although these predators may only cause substantial mortality in juveniles (Eberhard 1978, Phillips 1990). However, there was no evidence of an increase in the mortality rates of koala back-young compared with pouch-young on French Island (1980-1985), Kangaroo Island, Nth Walkerville or the Brisbane Ranges.

Mortality rates may be very low in long-lived species when food is not limited (Olsson and van der Jeugd 2002). Mortality rates in adult koalas at the KCC
resembled those in recently established populations of Alpine ibex (*Capra ibex ibex*), where plentiful resources led to very high survival rates (Toigo *et al.* 1997). Gaillard *et al.* (2000) reviewed annual mortality in adult female herbivore populations with and without large predators, and found that mortality was generally very low (mean of 57 studies = 13% per year) with little temporal variation. Stubsojen *et al.* (2000) also found low temporal variation in adult moose survival rates. Although insufficient data existed to separately analyse the mortality rates of adult male and female koalas, the adult mortality rate in all Victorian populations was generally similar to that found for large-bodied carnivores such as black bears (*Ursus americanus*) (16%) (Hebblewhite *et al.* 2003) and large-bodied female herbivores (Gaillard *et al.* 2000). For example, adult female mortality of bighorn sheep monitored for twenty years was 5% (Jorgenson *et al.* 1997), similar to adult koala mortality at North Walkerville and Phillip Island. The low adult mortality rates of koalas probably contributes to the rapid population growth in some populations (Martin 1997).

**Variation in mortality rates between populations**

Adult mortality rates in Victorian koala populations vary widely between populations (0.75 – 39.6% per year, Table 7.1) although comparisons are weakened by the limitations of the data (see below). Additional information on adult mortality comes from studies of koala populations in southern Queensland and northern New South Wales. Seventeen percent of radio-collared koalas (*n* = 60) died over one year in southeast Queensland (Thompson 2001) and the mortality rate of females over 3 years of age in that population was 35% (Dique *et al.* 2003a). Seven of 99 marked koalas died at Sheldon, near Brisbane (White and Kunst 1990). At Point Halloran in southeast Queensland, 6 of 12 radio-collared individuals died over the 13 month study (Hasegawa 1995) and at Tucki Tucki three adult males (*n* = 12) died during an 18-month period (Gall 1978).

Analysis of data from the literature showed that the mortality rates of pouch-young varied between wild Victorian and South Australian koala populations with the greatest mortality rate on Phillip Island (37.5%) and the lowest rate at the Brisbane Ranges (4%). The mortality rates of back-young varied over a similar range from 4% on French Island (1980-1985) to 37.5% at North Walkerville. The reliability of the
mortality data for dependent young (young not yet weaned) is probably greater than for adult koalas as the stage is relatively brief, and as a result, dependent young were usually observed for the whole period.

Natural mortality rates are likely to differ between koala populations due to differences in koala density and mortality factors such as density of roads, degree of urbanization, number of predators and stochastic events such as fire and drought. In urban southeast Queensland the major causes of mortality were disease, dog attack and road trauma (Nattrass and Fiedler 1996, Thompson 2001, Dique et al. 2003a). Smith and Smith (1990) also found that historically, dog attack was the major cause of mortality of koalas on Barrenjoey Peninsula, NSW. The majority of reports on the causes of mortality of koalas are based on records from koala hospitals and autopsies. These reports are probably biased towards urban causes of death such as road trauma, dog kills and disease and may under represent natural causes of death (Backhouse and Bolliger 1961, Butler 1978, Obendorf 1983, Canfield 1987, Weigler et al. 1987, Connolly 1999, Jones 2000b).

Adult mortality rates were likely to be high at North Walkerville as this population experienced a high degree of defoliation of preferred food trees and many koalas had dispersed from the site by the end of the study period (Martin 1985c, 1985a). Koala deaths in Victoria have been associated with koala overabundance and a decline in food availability (Kershaw 1934, Barrett 1937, Anonymous 1944, Braithwaite et al. 1980, Martin 1985c, Martin 1997). Extraordinary koala mortality occurred during an extreme weather event of continued drought and a heat wave where many of the eucalypt trees dropped their leaves (Gordon et al. 1988). Some koalas survived in trees along the river where leaf loss was less severe (Gordon et al. 1988). In the more temperate southeastern koala populations, drought may not produce such a high mortality rate as the leaves of eucalypts are less likely to wilt and die (Costermans 1994).

Much of the variation in mortality rates between populations may be due to the methods used to collect the data, in addition to variable age structures, habitat quality and mortality factors between sites. Accordingly, the quality of the data for estimating natural mortality rates varies greatly. For example, the mortality rate on Phillip Island
was likely to be high as much of the remaining koala habitat was along roadsides and therefore, mortality due to road trauma was high at this site (Backhouse and Crouch 1990, Reed 1999). Error in the estimate of mortality on Phillip Island may be inflated as individual koalas were not monitored. The size of the live population was estimated by censusing the population and this may include a large degree of error. In contrast, the number of dead animals (mostly from road kills) was estimated with greater accuracy (Backhouse and Crouch 1990). Additionally, the mortality rate on Phillip Island derived from the data of Backhouse and Crouch (1990) is up to seven times higher than that derived from the data of Every (1986). Hence, measurement error may be large in the estimate of the mortality rate of koalas on Phillip Island and the estimate derived from Backhouse and Crouch (1990) is not considered further.

Juvenile mortality may be variable between populations and may increase with population density (Skogland 1985, Mahoney and Schaefer 2002). For example, weaning success of sea otters (*Enhydra lutris*) was 50% higher in an expanding population than in a high-density population (Monson *et al.* 2000). Data analysed during the present study showed that the mortality rates of both pouch- and back-young were significantly higher at Walkerville (>33%) than French Island (1980-1985) (<14%). At the time of data collection there was severe defoliation at Walkerville and the koala population declined from 3.0 koalas per hectare in 1978 to 0.7 koalas per hectare in 1980 as adult koalas dispersed into the surrounding forest (Martin 1985c). In contrast, the low mortality rate of dependent young on French Island (1980-1985) was probably because part of the population was actively managed due to high growth (Martin 1989, Mitchell 1990c). The mortality rates of dependent young on French Island (1980-1985) were similar to those at the Koala Coast in Queensland (14.3%) where preferred food trees are not defoliated (Dique *et al.* 2003a). Therefore, it seems likely that the food shortage and perhaps the quality of food (see McOrist and Thomas 1984) at Walkerville contributed to the higher mortality rate of dependent young. This may result from reduced maternal milk supplies, as Martin (1985b) showed that females at Walkerville exhibited nutritionally induced anaemia. Furthermore, dependent young and sub-adult koalas at Walkerville (Martin 1985b) had lower growth rates than koalas on French Island (1980-1985) (analysed in the present study).
The mortality rate of pouch-young on Phillip Island was 37.5% (Table 7.1) and defoliation of food trees was not severe at the time of data collection (K. Handasyde, pers. comm.). This mortality rate was much greater than at the similarly Chlamydia-infected Brisbane Ranges population (4%), so it is unlikely that the Chlamydia-infected status of the Phillip Island population was the reason for the high mortality rate of pouch-young. Additionally, the mortality rate of pouch-young on Phillip Island (Table 7.1) was much higher than at the semi-enclosed Koala Conservation Centre on Phillip Island (8.5%). Thus, it is difficult to explain the high juvenile mortality rate on Phillip Island although sample sizes were small ($n = 8$) and further research may elucidate reasons for these differences.

Survivorship of juvenile koalas appears to be appreciably higher than in juveniles of other marsupials (Frith and Sharman 1964, Johnson 1989, Oakwood 2000) and eutherian (10 – 800 kg) herbivores (mean of 46 studies = 36%) (Gaillard et al. 2000). This high survivorship of juvenile koalas may contribute to the rapid population growth in some populations (Russell 1982, Martin 1997).

**Mortality and dispersal**

Differences in mortality have been correlated with dispersal in a range of taxa (Hartman 1995, Bonnet et al. 1999, Hubbard et al. 1999). Eberhard (1978) proposed that dispersing sub-adult (male and female) koalas suffered high mortality. However, the mortality rates of sub-adults on French Island (Mitchell 1990c) and the Brisbane Ranges (Table 7.1) were less than 10%.

Mortality rates of sub-adults were lower in the data analysed for French Island (1980-1985) and the Brisbane Ranges (3.7 – 9.1%) than those found in northern NSW by Ramsay (1999) and those found in southeast Queensland by Dique et al. (2003a). Ramsay (1999) found that 15% ($n = 13$) of female and 23% ($n = 13$) of male koalas died as sub-adults (between one and three years of age). None of the koalas died during the actual dispersal phase and mortality was highest in the immediate post dispersal period (Ramsay 1999). Similarly, Dique et al. (2003a) found that 11.5% ($n = 26$) of females and 18.2% ($n = 22$) of males died as sub-adults (between one and two years) but mortality was much greater in dispersing (30.0%, $n = 22$) compared with
philopatric individuals (3.6%, \( n = 26 \)). Also, Dique et al. (2003a) found that the mortality rate of two to three year old koalas averaged 25.5% (females: 33.3%, \( n = 30 \); males: 14.3%, \( n = 21 \)). The difference in mortality rates of sub-adult koalas between the Victorian populations and southeast Queensland is probably because the latter population is located in urban areas and dispersing koalas have a high risk of mortality due to cars and dogs (Dique et al. 2003a), although firm conclusions are limited by small samples sizes.

**Limitations of the data**

A number of limitations imposed by the data restrict the strength of conclusions regarding mortality rates in koalas. The low mortality rates reported in the present study indicate that the average age of death in koalas is approximately 22 years (Table 7.1). The skull and tooth wear data show that this is not the case (Chapter 3). Average longevity at Snake Island based on the skull data was 7 years of age in females and 5 years of age in males. This illustrates the inaccuracy of some of the mortality rate estimates. The mortality rate on French Island was extremely low (Mitchell and Martin 1990), but koalas were not radio-collared in this study and individuals that disappeared were only recorded as deaths if the carcass was found; consequently, it is unlikely that most deaths were detected. Many of these studies were also limited by low sample sizes and short durations. Although there was some evidence of variation in mortality rates of adult koalas between populations, the important assertion is that all mortality rates were very low.

In a review of large-bodied herbivores in populations both with and without predators, Gaillard et al. (2000) found that the majority of pre-weaning mortality occurred within one month of birth (e.g. Kunkel and Mech 1994) and advised that several studies may have underestimated juvenile mortality as marking of juveniles did not occur immediately after birth. This potential source of error is unlikely to greatly affect the estimates of juvenile koala mortality on French Island (1980-1985) because juveniles were recorded at a young age (less than a month old) and a large proportion of the females were carrying young (Martin and Handasyde 1990a).
Determining sex of skulls

A new method was developed in the present study to determine the sex of koala skulls in order to investigate sex-specific mortality patterns in koalas. The most accurate method for determining the sex of koala skulls was to combine logistic discrimination and discriminant function analysis. This demonstrated the usefulness of trialling multiple statistical techniques. The decline in classification success when tested with new skulls, similar to that found by Poole et al. (1980), illustrates the value of examining the equation with skulls not used to derive the equation, in addition to using jackknifed techniques. Classification success of higher than 85% was similar to that found in determining the sex of culpeo fox (Pseudalopex culpaeus) skulls (Travaini et al. 2000). Other techniques such as measuring the cementum thickness in incisors may be a successful technique for determining the sex of koala skulls in older TWCs (Young et al. 1996); however, using morphometrics proved to be a simple, quick, inexpensive and relatively accurate method to determine the sex of these skulls.

Neither method used in this study succeeded in accurately classifying TWC I skulls. Growth curves of male and female koalas illustrate that there is not a high divergence in head length at this stage (Chapter 3). The limited ability to discriminate between males and females in TWC I was not of importance as no skulls were found from koalas that died from natural causes in TWC I and there was quite high survivorship of koalas in this age class (Table 7.1). Skulls from young animals have the potential to get crushed and carried away by predators and scavengers more easily than skulls from older animals, as the sutures have not had time to fully calcify (Sinclair 1977). Consequently, mortality of juveniles was estimated using other methods such as direct observations (Sinclair 1977). Skulls from animals in TWC II may also be more fragile than adult skulls and could also be underrepresented in the mortality schedule.

Relative pattern of age- and sex-specific mortality

Mortality due to natural causes

The relative pattern of mortality determined from the pick-up skulls showed that koala mortality was sex-biased, specifically, male koalas died at a younger age than female koalas. Early male mortality was more pronounced at Snake Island, where most of the
mortality was from natural causes, than in the pooled sites. Average longevity at Snake Island was 7 years of age in females and 5 years of age in males. Male-biased mortality may be due to the larger body size of males, male-biased dispersal or the type of mating system (Clutton-Brock et al. 1982, Clutton-Brock et al. 1985b, Promislow and Harvey 1990).

The larger body size of males, and hence, higher nutritional requirements, may lead to higher mortality rates in environments where food is limited (Clutton-Brock et al. 1982). Sex-biased mortality has been found in eastern grey kangaroos (Quin 1989) and in many ruminants, especially where food abundance is low (Clutton-Brock et al. 1982, Clutton-Brock and Coulson 2002). The larger body size of male koalas in an environment with a large degree of defoliation of preferred food trees (Centre for Environmental Management University of Ballarat 2002) may have been partly responsible for the male-biased mortality on Snake Island.

Male-biased dispersal may lead to higher mortality due to increased energy expenditure and greater risk of predation (Clutton-Brock et al. 1985b, Fedigan and Zohar 1997, Dique et al. 2003a). Mortality was higher in male dispersing koalas than in female dispersing koalas in NSW (Ramsay 1999). In contrast, at Redbill Creek on French Island, Mitchell (1990c) did not find high mortality rates among dispersing males, probably due to low occurrence of cars and dogs and natural predators. Although koalas cannot disperse from the population at Snake Island, the risk of mortality may be higher for sub-adults leaving the general natal area than for those remaining within the natal home range due to non-familiarity with the area. Thus, dispersal from the natal home range may be a factor in the male-biased mortality detected in the present study. However, dispersal is likely to occur at an earlier age than the majority of the mortality detected from the pick-up skulls (TWC III, 4-5.5 years of age, Chapter 3) at Snake Island.

The earlier mortality of male koalas may be related to the mating system, which is probably polygynous with males fighting for access to females (Hindell 1984, Mitchell et al. 1987, Mitchell 1990b). Additionally, males have larger home range sizes, move more than females and are likely to have higher energy requirements (Mitchell 1990a). It has been suggested that male koalas may be sexually mature at
two years of age but may not have the opportunity to mate until they attain adult body size at four to five years of age (Handasyde et al. 1990, Martin and Handasyde 1990a, Mitchell 1990b). Male mammals experience increased mortality when they become sexually mature (Clinton and Leboeuf 1993, Jorgenson et al. 1997). The median age at death of males in TWC III at Snake Island corresponds to the age that males are approaching physical maturity (Chapter 3). It may be that the large amount of energy expended by males in the breeding season detrimentally affects male survival when males have to divide limited energy supplies between growth, maintenance and reproductive activities. Therefore, the combined effects of larger body size in males, dispersal and the competition which occurs with a polygynous mating system, probably contribute to the high level of mortality in male koalas in TWC III (4-5.5 years of age, Chapter 3), especially in areas of low food availability such as Snake Island.

Patterns of mortality derived from analyses of skulls have previously been found to be different to those derived from observations of marked individuals (Festa-Bianchet 1989, Murphy et al. 1990, see also Gonzalez and Crampe 2001). This may be due to a number of biases in skull collection studies. Survival of juveniles may be overestimated as small skulls and carcasses are more likely to be broken or hidden by scavengers (Murphy and Whitten 1976, Sinclair 1977, Bartmann 1984, Jorgenson et al. 1997). Also, skulls from smaller animals may be less likely to be detected than skulls from larger animals (Festa-Bianchet 1989). It is also likely that skulls from young koalas (TWC I and II) deteriorate at a faster rate than skulls from older koalas, thus skulls from older koalas are found at a disproportionately higher rate.

As the sex ratio at birth is generally close to parity in koala populations (Chapter 4) (Martin and Handasyde 1990a), the male-biased mortality observed at Snake Island accounts for the female-biased adult sex ratio. The sex-biased mortality pattern demonstrates the importance of determining the sex of skulls in calculating the mean age at death and mortality rates for populations. This allows the exclusion of male skulls from mortality schedules used in female-only models of population growth.
Mortality due to road trauma

Mortality due to road trauma can have large negative effects on populations of wild animals (e.g. Dufty 1994, Jones 2000a, Hebblewhite et al. 2003, Lopez et al. 2003). Road trauma is known to impact on some koala populations (Backhouse and Crouch 1990, Thompson 1996). Mortality due to road trauma may be greater in age/sex classes that have high dispersal rates or increased activity levels (Bonnet et al. 1999, Inbar and Mayer 1999). For example, Coulson (1989) found that 48% of road killed eastern grey kangaroos were 1 to 2 years of age, and males were more likely to be hit than females in five species of macropods, possibly due to greater ranging behaviour (Coulson 1997). A high proportion of ungulate road traumas are also related to dispersal and breeding behaviour (Groot Bruinderink and Hazebroek 1996).

In the present study, a similar proportion of male and female skulls were collected beside roads and these were spread relatively evenly over all TWCs. Additionally, koalas presumed killed on the road had a similar age distribution to those that died of natural causes in both males and females in the present study. This differs from Weigler et al. (1987) and Dique et al. (2003b) who found that mortality due to road trauma was male-biased in koalas in Queensland. The results of the present study also contrast with Canfield (1991) who found that young to middle-aged male koalas are highly represented in road trauma incidents, especially during the mating period. This variation is possibly due to differences in population density and road and traffic differences between the koala populations.

Comparison of mortality patterns between populations

Both male and female koalas at Snake Island suffered higher mortality compared with individuals from the pooled populations. Mortality patterns have been found to differ between populations of both bighorn sheep and roe deer, although mortality of prime-age animals (2-7 years) was similar despite differences in predation pressure (Gaillard et al. 1993a, Jorgenson et al. 1997, Loison et al. 1999). It is possible that the difference in koala mortality patterns between Snake Island and the pooled populations reflects the live population structure or may be due to the different sampling intensities between the two groups. Additionally, early koala mortality on Snake Island may result from poor body condition or starvation due to the relatively
high koala population density and the high proportion of dead trees (Morgan 1999b, Centre for Environmental Management University of Ballarat 2002). Unfortunately, strong conclusions cannot be drawn regarding the differences in mortality patterns between the pooled sample and Snake Island as little is known about the density and age structure of koalas, degree of defoliation or intensity of mortality factors (including cars) in the 131 populations in the pooled sample.

**Conclusion**

Survivorship of juvenile koalas appears to be substantially higher than in other marsupials and survivorship of juvenile and adult koalas is high in populations with few predators or human induced mortality. This may contribute to the rapid population growth in some populations. On average, adult male koalas die at a younger age than female koalas and this may be due to a combination of larger body size, male-biased dispersal and competition that results from a polygynous mating system. I have a high degree of confidence in the relative patterns of age- and sex-specific mortality reported in this chapter as they are based on large data sets. The mortality rates reported in this chapter provide an extremely important synthesis of data for wild koala populations. Information regarding these mortality patterns and rates is essential in modelling koala population dynamics.
Chapter 8 - Koala population growth and models for management

Abstract
Koalas are overabundant in some populations in southeastern Australia. Currently, two management techniques are used to reduce the population size: translocation and sterilisation. In order to understand the dynamics of the population and investigate the consequences and effectiveness of different management strategies, predictive population modelling is required. The population parameters determined in previous chapters were used to model the population growth of female koalas in one *Chlamydia*-infected (Snake Island) and one *Chlamydia*-free (French Island) population. The model was parameterised using Bayesian techniques and the population projection was modelled in “RAMAS Metapop”. The predicted finite growth rate ($r$) was 1.04 on Snake Island and between 1.17 and 1.25 on French Island giving estimated doubling times of 20 years and 3.2-4.5 years, respectively. Translocation produced a more rapid reduction in the population size than a reduction in fecundity. Sterilisation of approximately 200 females and subsequent translocation of 200 females was predicted to reduce the Snake Island population size to low numbers in eight years. On French Island, annual translocation of approximately 140 – 250 females was predicted to be sufficient to maintain a stable mean population size. The models predicted that postponement of management actions for only three years would greatly increase the number of koalas that would have to be translocated to return the French Island population to its current size. These koala population growth models can provide help to guide management of overabundant koala populations in Victoria.

Introduction
Overabundant species may impact negatively on themselves, other species, communities and human livelihood (Caughley 1981). For example, overabundant, introduced species, such as the common brushtail possum, is both an economic and environmental pest in New Zealand (Montague 2000). Common brushtail possums are predators of many vulnerable bird and invertebrate species (Nugent *et al.* 2000, Payton 2000), cause millions of dollars of damage to agriculture (Butcher 2000, Coleman and Caley 2000) and are reservoir hosts for bovine tuberculosis, threatening beef, dairy and venison markets (Coleman and Caley 2000). Koalas are overabundant in some populations in southeastern Australia and have severe negative impacts on their own habitat, other species and communities (Menkhorst *et al.* 1998, Martin and Handasyde 1999). This
chapter uses population modelling to investigate the growth of overabundant koala populations in Victoria and predict the effectiveness of different management regimes to control them.

techniques depend on development of appropriate delivery systems. In addition, the control of populations of long-lived animals will also require additional techniques that increase mortality (Cowan and Tyndale-Biscoe 1997).

Due to a need to evaluate the most effective method of population management, population growth predicted by modelling is becoming increasingly popular (Lindenmayer and Possingham 1996, Punt and Hilborn 1997, Ferreras et al. 2001, Watola et al. 2003). Models assist scientists and managers to understand the biological system and predict future changes in the population size (Cairns 1989). Demographic models use data on demographic parameters of stage or age classes to project future population size (Caswell 2001, Coulson et al. 2001b). An assumption of these models is that individuals within classes are more similar in their demography than between classes (Caswell 2001).

Models allow investigation of how changes in demographic parameters affect population growth (Saether et al. 1996, de Kroon et al. 2000, Saether and Bakke 2000). Modelling dynamics of wildlife populations is becoming more prominent in management of threatened species (Possingham et al. 1993) and commercially and recreationally exploited wildlife populations (Pascual and Hilborn 1995, White and Lubow 2002). Modelling is also used to determine optimal management strategies in order to control overabundant wildlife populations (Gross 2000). Models predict what can happen given a set of assumptions but do not predict what will happen (McCallum 1995). There will be a compromise between the complexity of the model required to represent the intricacy of the biological system and the simplicity of the model required by paucity of available data (White and Lubow 2002). The variability, reliability and accuracy of predictions generated by population models must be considered before the predictions can be used to guide management actions (Coulson et al. 2001b, McCarthy et al. 2001, Ellner et al. 2002, McCarthy et al. 2003).

Some knowledge of the growth rate and the magnitude of the response of the population to the management technique is important (Sibly and Hone 2002). For example, great cormorant (Phalacrocorax carbo sinensis) populations in northern Europe have doubled
to over 100,000 pairs in the last 20 years and conflict with aquaculture and fisheries industries (Frederiksen et al. 2001). Density-dependent population modelling predicted that even large annual culls of over 30,000 birds would not reduce the population sufficiently to lessen conflicts with industry (Frederiksen et al. 2001).

In southeastern Australia, koala populations at sites such as French Island, Phillip Island, Sandy Point, Quail Island, Wilson’s Promontory and recently Kangaroo Island, Framlingham, Snake Island, Tower Hill and Mt Eccles increased to such an extent that they defoliated their preferred food trees. These populations either experience a massive population decline or require ongoing active management (Kershaw 1934, Barrett 1937, Braithwaite et al. 1980, Backhouse and Crouch 1990, Martin and Handasyde 1990a, Martin 1997, St John 1997, Menkhorst et al. 1998). Many southeastern Australian populations are effectively isolates and as a result there was no emigration. In combination with limited predation, these populations have expanded to fill the available habitat and further population growth has led to overabundance and habitat destruction.

In Victoria, overabundant koala populations historically have been managed by large-scale translocation of individuals and more recently by a combination of translocation and sterilisation of females (Menkhorst et al. 1998). Trials on hormonal contraception (Middleton et al. 2003), immunocontraception (Kitchener et al. 2001) and surgical sterilisation of male koalas (Menkhorst et al. 1998) have also been conducted. The effects of these management techniques on the dynamics of overabundant koala populations have not been investigated, although preliminary modelling of koala demographics at sites with low koala densities was carried out by Penn et al. (2000). Predictive population models using accurate estimates of population parameters such as age structure, sex ratio, age-specific fecundity and mortality schedules, and fecundity and mortality rates (from previous chapters) are required to improve current management regimes. Analysis of these models will indicate targets for management that are necessary to control the population size.
Aims

In this chapter I aim to model growth of koalas populations at sites where they are overabundant. I also aim to determine the effect of translocation and sterilisation on population growth for control of overabundant koala populations and forecast the effect of delaying management actions on population size.
Methods

The model

A stage-based matrix model of population growth (see Caswell 2001) was developed with TWCs defining the stages. Only females were modelled because they are thought to be the sex that limits population growth (Cole 1954, Mysterud et al. 2002a). Additionally, data from the previous chapters illustrate that males are similar to females with the exception that mortality occurs at an earlier age. However, there are probably always sufficient males available to fertilise all females (in populations where koalas are overabundant) and therefore, only females were modelled. Density dependence was ignored because the model aimed to predict population abundance prior to the impact of overabundance on population growth. It was assumed that the population was censused immediately prior to breeding.

The parameters of the model were obtained using Bayesian statistics in WinBUGS (see Chapter 3) following the method of McCarthy and McLean (in prep) in order to model population growth at Snake Island and French Island. Data included the average duration in each TWC (Chapter 3), the age structure and juvenile and adult sex ratio (Chapter 4), age-specific fecundity rates (Chapter 6) and mortality rates and age-specific mortality patterns (Chapter 7). Back-young were assumed to be one year of age and thus the age structure on French and Snake Islands includes dependent young (mostly back-young, censured before the breeding season). Published adult mortality rates ranged from 0.75 to 33% and the problems associated with these estimates are discussed in Chapter 7. Of the mortality rate estimates calculated in this thesis, 7.8% at the KCC seems the best approximation of actual rates (Chapter 7) and these data were used to help estimate mortality rates. The skull age structure was assumed to represent the age structure of individuals that die, therefore representing the product of the population structure of the live animals and the relative mortality in each TWC. The Snake Island skull age structure was used for predictions at Snake Island, while the age structure of skulls from the other sites (pooled sites) was used to determine the relative mortalities for French Island. The prior for lambda at Snake Island was based on the population growth of females from
1945 (founding population size) to 1993 when the population was estimated at approximately 5000 koalas (R. Williamson, unpublished data; lambda ~ 1.09). The prior for lambda at French Island was based on growth rates for similarly *Chlamydia*-free koala populations at Quail Island and Sandy Point (lambda between approximately 1.2 and 1.4) (Martin *et al.* 1987, Martin 1997). The first 5000 iterations of the parameterisation model were discarded and samples were taken from the subsequent 10000 iterations. The predicted age structure and age-specific fecundity rates of each population were compared using Chi-square values (where the smallest value is the better fit) against the observed values to check the fit of the parameterisation although it is acknowledged that while different models may give an equally good fit, this may result in quite different management outcomes (Pascual and Hilborn 1995, Pascual *et al.* 1997).

**Predicting population growth**

The parameters estimates from WinBUGS were put in the stage matrix to project population growth in RAMAS Metapop (Akcakaya and Root 1998) which is based on matrix population models (see Caswell 2001). Age-specific fecundity was multiplied by the survivorship of young to obtain the proportion of young, produced by females in each adult TWC that survived until one year of age. Population growth was predicted over a relatively short time period (ten years on French Island and twenty years at Snake Island). The model was run for 100 iterations and the results are presented as the mean and standard deviation population projection of those iterations at each time step.

Management actions that were simulated in RAMAS Metapop were translocation and sterilisation. These were the only two management options investigated as culling of koalas is not a politically acceptable method of control and sterilisation of males is not effective for large populations as a very high percentage of males must be sterilised to reduce fecundity (Menkhorst *et al.* 1998). Translocation was simulated as “harvesting”, with a specified proportion of the population removed (from all TWCs) at each time step of the model (words in parenthesis represent the term used by RAMAS Metapop). The reduction in fecundity was simulating by reducing the “relative fecundity”, which
entailed an immediate reduction in fecundity in all TWCs by the specified percentage, and then maintenance of fecundity at that reduced level for the remaining years of the population projection. In order to simulate the sterilisation of part of the population and the subsequent translocation of some of those sterilised females the following year at Snake Island (i.e., replication of current management actions), the total female population was divided into two sub-populations. In the first, previously uncaught sub-population, a number of females were “translocated” to the second sub-population. This second sub-population had a relative fecundity of zero to represent sterile females but otherwise had the same age structure and age-specific mortality rates as the first sub-population. In the following year, a number of sterile females were “harvested” to represent translocation off Snake Island.

Population size (and population growth) targets must be set by managers who consider the carrying capacity of the habitat, the resources available for management, the objectives for the population and political realities. In the absence of published targets for population sizes, I have made reasonable guesses at sensible targets by considering past management actions, presumed objectives for each population, and the desire by management agencies to reduce required management. I estimated that a population size of less than 100 and 50 females (for different management actions) at Snake Island, and a population size similar to the current level at French Island, were reasonable targets.
Results

Goodness of fit of the parameters

The age structures predicted from WinBUGS were a good fit ($\chi^2 = 7.66$) to the observed age structures for Snake Island (Figure 8.1). The predicted and observed age-specific fecundities for Snake Island also matched closely ($\chi^2 = 85.17$) (Figure 8.2). As the growth rate on French Island was not known precisely, the WinBUGS code was run three times with identical data for age-specific fecundity, age structure, age-specific mortality patterns and mortality rates but with the prior for the mean of lambda set at 1.20, 1.30 and 1.40. The predicted age structures for French Island fitted the data better when the prior for the mean of lambda was 1.2 rather than when 1.3 or 1.4 ($\chi^2 = 36.61, 44.87$ and 45.86 for lambda of 1.20, 1.30 and 1.40, respectively) (Figure 8.3a-c). The predicted age-specific fecundities for French Island fitted the data better when the prior for the mean of lambda was 1.2 and 1.3 than when 1.4 ($\chi^2 = 165.28, 169.70$ and 175.01 for lambda of 1.20, 1.30 and 1.40, respectively) (Figure 8.4). Given this, the effects of management actions were analysed in the following sections for growth rates with a prior for the mean of lambda on French Island was 1.2 and 1.3.
Figure 8.1 The observed (black bars), $n = 397$, and WinBUGS-predicted (hatched bars) koala age structures for Snake Island.
Figure 8.2 The observed (black bars), $n = 847$, and WinBUGS-predicted (hatched bars) koala age-specific fecundities for Snake Island.
Figure 8.3 The observed (black bars), \( n = 241 \), and WinBUGS-predicted (hatched bars) koala age structures for French Island where the prior for the mean of lambda was equal to a) 1.20, b) 1.30 and c) 1.40.
Figure 8.4 The observed (black bars), \( n = 241 \), and WinBUGS-predicted (hatched bars) koala age-specific fecundities for French Island where the prior for the mean of lambda was equal to a) 1.20, b) 1.30 and c) 1.40.

**Population growth**

The population growth rate (that produced the best fit of the observed to the predicted age structures and age-specific fecundities) was higher on French Island (\( \lambda = 1.17 \) and \( \lambda = 1.25 \) for priors for the mean of lambda set at 1.20 and 1.30, respectively), than on Snake Island (\( \lambda = 1.04 \)) (Figure 8.5). This gives an approximate doubling time of 20 years at Snake Island, 4.5 years on French Island (with a prior for the mean of lambda of 1.2) or 3.2 years on French Island (with a prior for the mean of lambda of 1.30).

The growth rate of the population can also be estimated from initial and recent population size estimates and the time interval (Table 8.1). The predicted population growth rate for Snake Island (\( \lambda = 1.041 \)) was lower than that estimated from the initial and the most recent estimates of population size (\( \lambda = 1.09 \)) (Table 8.1). The population growth rates determined for French Island (see above) were similar to the growth rate estimated from population size estimates for Quail Island (*Chlamydia*-free) but lower than those for Sandy Point (*Chlamydia*-free).
Figure 8.5 Projection of population growth modelled in RAMAS for Snake Island (crosses), and French Island where lambda was equal to 1.17 (triangles) and 1.25 (squares). Lines without symbols represent ±1 s.d. for each population projection.

Table 8.1 Growth rates and doubling times for Victorian koala populations estimated from initial population sizes and the most recent population size estimates.

<table>
<thead>
<tr>
<th>Population</th>
<th>Initial size</th>
<th>Most recent estimate</th>
<th>Time between estimates (years)</th>
<th>Growth rate</th>
<th>Doubling time (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snake Is.</td>
<td>48</td>
<td>2750</td>
<td>47</td>
<td>1.09</td>
<td>8</td>
</tr>
<tr>
<td>Raymond Is.</td>
<td>42</td>
<td>196</td>
<td>27</td>
<td>1.06</td>
<td>12</td>
</tr>
<tr>
<td>Sandy Point</td>
<td>20</td>
<td>2000</td>
<td>16</td>
<td>1.33</td>
<td>2.5</td>
</tr>
<tr>
<td>Quail Is.</td>
<td>45*</td>
<td>1347</td>
<td>14</td>
<td>1.18</td>
<td>4.3</td>
</tr>
</tbody>
</table>

Data were obtained from \(^a\) analysis from the present study, \(^b\) Martin and Handasyde (1990a) and Martin et al. (1987), \(^c\) Martin (1997) and \(^d\) Martin et al. (1987). For Snake Island, the population estimates are for females only (based on the current sex ratio), the initial population estimate is from Martin (1989) and the recent estimate is from R. Williamson (unpublished data). \(^*\)The initial population size at Quail Island was 45 koalas but an additional 120 koalas were added to the population in the following three years.
Effects of different management techniques on population growth

The effects of translocating a percentage of the population each year from Snake Island (Figure 8.6) and French Island (Figure 8.7) illustrate that an annual translocation of 5% of the population at Snake Island is sufficient to cause a decline in the population size but an annual translocation of 15% or greater (depending on which potential growth rate is assumed) is required on French Island for the same result. A reduction of approximately 20% in fecundity is required at Snake Island to cause a decrease in the population size (Figure 8.8) compared with a 60% or greater reduction in fecundity on French Island to achieve a similar decline (Figure 8.9).

Figure 8.6 The effect of translocation on koala population growth at Snake Island. Squares represent no management, crosses represent a translocation of 5% of the population each year, triangles represent a translocation of 10% of the population each year and circles represent a translocation of 20% of the population each year. Lines without symbols represent ±1 s.d. for each population projection.
Figure 8.7 The effect of translocation on koala population growth on French Island where lambda was equal to a) 1.17 and b) 1.25. Squares represent no management, crosses represent a translocation of 5% of
the population each year, triangles represent a translocation of 15% of the population each year and circles represent a translocation of 30% of the population each year. No standard deviations represent presented to aid visual clarity of the effects of the varying management options.

![Figure 8.8](image)

Figure 8.8 The effect of a reduction in fecundity on koala population growth at Snake Island. Squares represent no management, triangles represent a 10% reduction in fecundity, circles represent a 20% reduction in fecundity and asterisks represent a 50% reduction in fecundity. Lines without symbols represent ±1 s.d. for each population projection.
Figure 8.9 The effect of a reduction in fecundity on koala population growth on French Island where lambda was equal to a) 1.17 and b) 1.25. Squares represent no management, crosses represent a 20% reduction in fecundity, triangles represent a 40% reduction in fecundity, circles represent a 60% reduction.
in fecundity and diamonds represent an 80% reduction in fecundity. No standard deviations represent presented to aid visual clarity of the effects of the varying management options.

Simulations that mirrored current management actions on Snake Island were run (Figure 8.10a). At present, there are approximately 830 previously uncaught “fertile” female koalas and approximately 600 previously caught, sterilised females (R. Williamson, unpublished data). The model simulates previously uncaught females being caught and sterilised, thus adding to the sterilised female sub-population. For the model, this latter sub-population was then hypothetically reduced by translocating females from Snake Island in the subsequent year. The total female population size would be reduced to less than one hundred females in approximately seven years if current management actions continued. This assumes that the same number of females can be found and treated in subsequent years as the population size declines. Due to the potential for insufficient suitable locations to which koalas can be translocated, projections were also run for management that included only sterilisation of females (without translocation off Snake Island) (Figure 8.10b). In this case the total female population size is only reduced by mortality and the model predicted that it would take twice as long (14 years) to reduce the population to below 100 females compared with management that included translocation.

Simulations that mirrored recent management actions on French Island were run (Figure 8.11). When lambda was 1.17, modelling the recent management actions on French Island predicted that the population would be maintained between its current size and a slightly increasing size. An increase in the number of females translocated from 102 to 138 predicted maintenance of a stable mean population size. However, if the actual growth rate was closer to 1.25, then the model predicted that the French Island population would continue to increase with recent levels of management action (Figure 8.11). The number of koalas translocated would have to be increased by 247% to maintain a stable population size if lambda was 1.25.

Simulations were also run for French Island with management similar to Snake Island, where previously uncaught females were caught and sterilised but not translocated until
the following year (but the numbers of females caught were the same as recent levels of management on French Island). The total population size on French Island was predicted to increase relatively slowly if lambda was 1.17 (Figure 8.12) and more quickly with a lambda of 1.25 (Figure 8.13).
Figure 8.10 Koala population projection at Snake Island with a) sterilisation and removal one year later, and b) only sterilisation (at the current rate). Squares represent the total female population, crosses represent the previously uncaught sub-population and triangles represent the previously caught, sterile
female koala sub-population. Lines without symbols represent the standard deviations for each population projection.

Figure 8.11 Koala population projection on French Island with the current management actions (translocation of approximately 102 females per year) where lambda was equal to 1.17 (triangles) and 1.25 (squares). Lines without symbols represent the standard deviations for each population projection.
Figure 8.12 Koala population projection on French Island where lambda was equal to 1.17 and management consisted of a) sterilisation and removal one year later, and b) sterilisation only (at the current rate). Squares represent the total female population, crosses represent the previously uncaught sub-
population and triangles represent the previously caught, sterile female koala sub-population. Lines without symbols represent the standard deviations for each population projection.
Figure 8.13 Koala population projection on French Island where lambda was equal to 1.25 and management consisted of a) sterilisation and removal one year later, and b) only sterilisation (at the current rate). Squares represent the total female population, crosses represent the previously uncaught sub-population and triangles represent the previously caught, sterile female koala sub-population. Lines without symbols represent the standard deviations for each population projection.

Simulations were also carried out to investigate the effect of postponing management actions. At Snake Island, the time taken to achieve a total abundance of less than 50 female individuals was 50% greater if the management began after four years (Table 8.2). On French Island, the level of translocation required to reduce the population to the same level as at year zero increased greatly for each year that management was delayed (Table 8.3). For instance, if management were delayed for three years (and lambda was 1.17), 246 females would have to be translocated each year for ten years (2.46 times recent translocation effort) to reduce the population size to the initial level.

Table 8.2 The effect of postponing current management action on projected koala population abundance at Snake Island.

<table>
<thead>
<tr>
<th>Start management in time step</th>
<th>Year in which koala abundance is predicted to be less than 50 individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>4</td>
<td>12</td>
</tr>
</tbody>
</table>

Table 8.3 The level of management required over 10 years to reduce the projected koala abundance at French Island to its current size (approximately 640 females) if management continues or is delayed.

<table>
<thead>
<tr>
<th>Management action</th>
<th>Translocated (females/yr)</th>
<th>* present effort</th>
<th>Abundance in 10 yrs since management began</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lambda</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.17</td>
<td>102</td>
<td>1</td>
<td>1101 (± 169) 3723 (± 290)</td>
</tr>
<tr>
<td>1.25</td>
<td>102</td>
<td>1</td>
<td>1101 (± 169) 3723 (± 290)</td>
</tr>
<tr>
<td>1.17'</td>
<td>1.25</td>
<td>3.29</td>
<td>633 (± 130) 626 (± 221)</td>
</tr>
<tr>
<td>1.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Present action</td>
<td>102</td>
<td>1</td>
<td>1101 (± 169) 3723 (± 290)</td>
</tr>
<tr>
<td>Management delayed</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 year</td>
<td>168</td>
<td>1.65</td>
<td>637 (± 161) 645 (± 230)</td>
</tr>
<tr>
<td>2 years</td>
<td>198</td>
<td>1.98</td>
<td>637 (± 161) 645 (± 230)</td>
</tr>
<tr>
<td>3 years</td>
<td>246</td>
<td>2.46</td>
<td>654 (± 202) 644 (± 265)</td>
</tr>
</tbody>
</table>

250
Present effort is the number of females that need to be translocated relative to the current level of effort.
Discussion

Population growth

There was a much lower population growth rate at Snake Island than on French Island due to infertility caused by *Chlamydia*-infection. The predicted population doubling time at Snake Island (20 years) was greater than reported for the similarly *Chlamydia*-infected Raymond Island population (Martin and Handasyde 1990a). Likewise, the doubling time for French Island (3.2 – 4.5) was greater than that reported for Sandy Point (Martin 1997) but similar to doubling time reported for Quail Island (Table 8.1) (Martin *et al.* 1987). This variation in growth rates between populations with the same *Chlamydia*-infection status is probably driven by differences in fecundity rates between *Chlamydia*-infected populations (e.g. Martin and Handasyde 1990a) but the reasons for differences in doubling times between *Chlamydia*-free populations are unclear. Additionally, different methods were used to calculate the growth rates in different studies. In the present study, the growth rate at Snake Island was estimated as 1.04 using the posteriors from WinBUGS, even though a value of 1.09 was used as the mean of the prior, based on the initial and recent population size estimates. Previous predictions of the growth rates at Sandy Point and Raymond Island were also based on estimates of the initial and current population sizes (Martin and Handasyde 1990a, Martin 1997). Such calculations require assumptions regarding the relative contributions of the fecundity and mortality of different age classes to the population growth rate but sometimes this information is unavailable (Table 8.1). Therefore, when information on age structure is available, it is likely that the stage-structured model in the present study gives a more reliable estimate of population growth rates in *Chlamydia*-infected and *Chlamydia*-free populations. Furthermore, calculating the population growth rate from initial and recent population estimates assumes that the accuracy and precision of the two estimates is similar. The accuracy of the growth rate calculated in this manner is decreased if this assumption is invalid.
Population dynamics and regulation

Koala populations without *Chlamydia*-infection, such as on French Island and at Framlingham, have high growth rates which were similar to other herbivores (see Garrott *et al.* 1991). The high growth rate in koalas is probably due to few opportunities for emigration, high fecundity (Chapter 6) and low adult and juvenile mortality (Chapter 7). This combination of parameters has led to over population and defoliation of preferred food trees at a number of sites in southeastern Australia (Martin and Handasyde 1999). The 70 to 80% fecundity recorded for adult female koalas at Framlingham and French Island (*Chlamydia*-free populations) is similar to the level of fecundity in other herbivores (Gaillard *et al.* 2000, Loison *et al.* 2002, Ramsey *et al.* 2002). Thus, high levels of female fecundity are not unusual in mammal populations in areas where sufficient food is available. For example, the values of the demographic parameters of a population of mouflon (*Ovis gmelini*) on a protected reserve in France (Cransac *et al.* 1997) were very similar to koala demographics on French Island. The female mouflon reach sexual maturity at 2 years of age and there is approximately 90% fecundity. The juvenile survival is very high and the natural mortality rate was estimated at approximately 10-15%, as there are no predators on the reserve. Further, the population is maintained below a level of resource depletion due to annual removal of an additional 10-15% of the animals for live export. Hence, the need for management of herbivore populations in the absence of predators is not limited to koalas.

Overabundant koalas have undergone severe population declines at a number of sites in Victoria (Kershaw 1934, Anonymous 1944, McNally 1957, Braithwaite *et al.* 1980, Martin and Handasyde 1990a). Koala populations at Wilson’s Promontory reached high population densities, defoliated and killed a large proportion of their preferred food trees and many of the koalas died of starvation (Kershaw 1934). Subsequently, the vegetation community was changed at Wilson’s Promontory with the loss of preferred food trees in some areas, however, koalas persisted in the area at low densities. This suggests that the current mechanisms of population regulation of koalas in southeastern Australia are insufficient to maintain koala numbers below the carrying capacity of the habitat and that
long-term management of such populations is essential if the priority of management authorities is to preserve current vegetation communities.

**Effectiveness of management**

In terms of reducing population size, the model predicts that translocation will be relatively successful. At Snake Island, translocation of only 5% of the population per annum was sufficient to slow population growth over twenty years. On French Island, translocation of a higher percentage of the population was required to reduce the population size due to the higher population growth rate. Translocation may be expensive (Conover 2001, Beringer et al. 2002), spread disease (e.g. Jenkins and Winkler 1987), cause a high degree of capture related mortality (Coulson 1996, Beringer et al. 2002), and relocated animals may return to the site of capture (Conover 2001). Historically, translocation of koalas has been successful with the reintroduction of koalas to many parts of their former range (Martin and Handasyde 1990b, Menkhorst et al. 1998). Translocation of koalas to habitat with novel food trees was also successful (Lee and Martin 1988, Lee et al. 1990); however, recent research into the combination of translocation and surgical sterilisation has demonstrated occasional high mortality rates (Parks Victoria 2003). In addition, costs of management programs and alternative management actions can be extensive (up to $130 per koala on Kangaroo Island, A. Duffy, pers. comm.) and need to be considered by managers. Thus, translocation may not be a feasible management option for reducing overabundant koala populations in the future.

The models that included translocation predicted a more rapid reduction in koala abundances than a reduction in fecundity (see Barlow et al. 1997, Davis and Pech 2002). However, given the possibility that translocation of koalas may not be a management option in the future, fertility control may be the only remaining way of reducing population size. The reduction in fecundity required to reduce the population size was 20% at Snake Island and between 60 and 80% on French Island (depending on which estimate of the growth rate is used in the model). This level of reduction in fecundity
required at French Island to reduce koala population growth is similar to that required for population control in rabbits (Twigg and Williams 1999). In the initial simulations fecundity was reduced to the target level from year one (Figure 8.8 and Figure 8.9). That is, in the simulation of an 80% reduction of fecundity, it is assumed that this reduction is achieved in the first year and maintained for the remainder of the simulation. This is not likely to represent the reduction of fecundity that could be attained in practice. It is more likely that the reduction of fecundity would progress gradually over time. Gradual reduction in fecundity is represented in the simulations that mirror the current management at Snake Island (Figure 8.10a). These results indicate that current management at this site should reduce the population size to low numbers in seven or eight years, assuming that the current numbers of koalas are treated each year. This assumption is perhaps unrealistic but once an estimate of the decline in the efficiency of finding new, untreated koalas is known, it could be factored into the model to produce a revised estimate of the rate of population decline.

If the translocation component of the current Snake Island management was discontinued, the population would reach approximately 600 females in eight years time (Figure 8.10b). It is unknown whether the current level of defoliation of preferred food trees would sustain this population size for this time period. A future extension of the model to include the population dynamics and growth of the foliage of food trees would provide some insight into this. A holistic model such as this could include all factors limiting tree growth and recruitment such as variation in rainfall patterns, herbivores grazing seedlings and insect damage to canopies.

Sterilisation of wild female rabbits (*Oryctolagus cuniculus*) was found to lead to a compensatory response of increased survivorship (Twigg and Williams 1999, Twigg *et al.* 2000). Hence, the potential effect of decreased fertility and the possibility of increased survival on population dynamics must be demonstrated (Tyndale-Biscoe 1994, Sinclair 1997). The implications for increased survival of infertile females is not currently known for koalas. There is some evidence that management actions may increase the mortality of treated koalas remaining in the population rather than a compensatory increase in
survival (Middleton et al. 2003). Without knowledge of compensatory mortality implications on population dynamics (Chambers et al. 1999, Saunders et al. 2002), it is difficult to accurately predict the effects of population control techniques on population growth (Ramsey et al. 2002).

The models presented in the present study represent a limited number of combinations of management actions. With further clarity of the objectives of koala population management, projections could be simulated to estimate the consequences of alternative management actions. For instance, the recent management on French Island of an annual translocation of approximately one hundred females was projected to maintain the population at a relatively stable but slowly increasing size (Figure 8.11); however, these levels of management would be required for many years. If the management objective were to maintain a stable population at approximately the current abundance, an annual translocation of approximately 138 to 252 females would be required depending on the actual growth rate on French Island. If the objective was to lower the population size, the model could be used to predict the number of females that would have to be translocated each year. The model could also project the effects of a very large translocation event in the first year, and the subsequent regeneration of the population. Alternatively, the model could estimate the level of translocation required if management is delayed for a number of years due to logistic or budget problems (Table 8.2 and Table 8.3). For example, on French Island, if management were delayed for three years then translocation would have to increase from 102 females per year to between 246 (lambda = 1.17) and 552 females per year (lambda = 1.25) to maintain a relatively stable population size.

It is probable that the results of the predictions for the Snake Island population can be used to generalize to other Chlamydia-infected populations at sites where koalas are overabundant (such as Mt Eccles) given the similarity of the age structures and age-specific fecundity schedules (Chapters 4 and 6). Similarly, it is likely that the results of the French Island model are applicable to other Chlamydia-free populations such as Framlingham, although determination of the variation in population parameters between sites with the same Chlamydia-infection status is vital for accurate predictions. Future
research into the temporal and spatial variation in parameters such as growth rates and mortality rates will improve these models and permit site-specific modelling of population growth.

**Limitations of the model and future research**

It is often true that some parameters are well known for a population whereas others require assumptions (Pascual and Hilborn 1995). The data on age structure, sex ratio, age-specific fecundity, age-specific mortality patterns (at Snake Island) and juvenile mortality that were used in the model came from large samples, which increased the reliability of the model. However, the data for mortality rates, population growth rates and age-specific mortality patterns (at other sites) were less robust. Future research into age-specific mortality patterns and mortality rates by radio-collaring a large number of koalas at a number of sites would increase the reliability of the mortality data, although this procedure would be expensive and time consuming (e.g. Stubsjoen *et al.* 2000). Improved monitoring of koala population abundances and the pattern of change over time would also improve the predictive capability of the models.

The model in the present study was relatively simple, as it did not include density dependence or environmental stochasticity. Environmental stochasticity had relatively little effect on fecundity on French Island (see Chapter 6) but its influence on mortality is unknown. Similarly, little is known regarding density dependence in koalas but high koala densities at Sandy Point did not reduce fecundity levels or juvenile survival until koalas were starving (Chapter 6). The ability of koalas to sustain population growth for several years even when habitat conditions decline suggests that environmental stochasticity in mortality is low. Future study may elucidate the effects of environmental variation and density dependence on mortality rates.

**Conclusion**

The models of population growth and the predicted effects of management actions generated in the present study provide substantial advantages for directing both policy
and management. The models are intended as a guide to what may happen, within certain boundaries, if certain management practices are adopted. Some of the parameters in the model are known imprecisely and other parameters, such as the possible change in survival of sterilized females, may not be known for many years. Thus, future research can only improve the usefulness of these models. Despite these limitations, the models are built from very large data sets, which are rarely obtained for long-lived mammals. The models produced in the present study allow the determination of the level of management required to reduce the population to the density deemed suitable for the available habitat.

The determination of the relationship between tooth wear classes and chronological age (Chapter 3) makes an important contribution to the model as the variation in demographic parameters can be incorporated. The information on density dependent changes in fecundity (Chapter 6) demonstrates that fecundity does not decline until the koala population is near starving. Hence, it is appropriate that density dependent factors were not included in the model which projected population growth over a short time period. The age-specific mortality patterns derived from skulls of koalas (Chapter 7) provide the first available information on this parameter in koalas. The compilation of koala mortality rates was an essential consolidation of this information. Additionally, the fitting of the demographic parameters using Bayesian statistics in WinBugs allows a transparent and repeatable method which substantially increases confidence in the population projections. These factors afford greatly increased accuracy of the models. The koala population growth models generated in this study will help to guide improved management of overabundant koala populations in Victoria.
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## Appendix A

Table A.1 Comparison of the scales used to measure tree condition at Snake Island, Mt Eccles, French Island and Framlingham. Based on categorization from Ingeme et al. (1998), Grimes (1988), Centre for Environmental Management University of Ballarat (2002), Centre for Environmental Management University of Ballarat (2003), Kelly (2000). The relationship of Grimes (1988) crown condition score to CEM (2002) and Kelly’s (2000) defoliation scores was based on Figures 3.4 and 3.5 from Centre for Environmental Management University of Ballarat (2002). Score for the Crown condition score is a composite score based on assessment of crown size, crown density, dead branches and epicormic growth. Description for the Defoliation score is the % of the crown cover/density remaining.

<table>
<thead>
<tr>
<th>Condition Score</th>
<th>Description</th>
<th>Grimes Score</th>
<th>Defoliation Score, CEM Score</th>
<th>Defoliation Score, Kelly Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead 3</td>
<td>Dead</td>
<td>-1</td>
<td>Dead</td>
<td>Dead</td>
</tr>
<tr>
<td>Dead 4</td>
<td>Mostly dead</td>
<td>0</td>
<td>Recently dead</td>
<td>0</td>
</tr>
<tr>
<td>Dead 6</td>
<td>Maybe some epicormic growth</td>
<td>6.5</td>
<td>Very few leaves</td>
<td>1</td>
</tr>
<tr>
<td>Sick 7.5</td>
<td>Sparse leaf clumps, &amp; epicormic growth</td>
<td>7.5</td>
<td>Many dead branches</td>
<td>2</td>
</tr>
<tr>
<td>Sick 8</td>
<td>Many dead branches</td>
<td>8</td>
<td>Av. density clumps, some dead branches</td>
<td>3 &amp; 4</td>
</tr>
<tr>
<td>Healthy 10.5</td>
<td>No epicormic growth, dense uneven clumps</td>
<td>10.5</td>
<td>Crown wide &amp; deep, no dead branchlets</td>
<td>6</td>
</tr>
<tr>
<td>Healthy 11</td>
<td>Some faults in crown</td>
<td>11</td>
<td>75-90%</td>
<td>7</td>
</tr>
<tr>
<td>Healthy 12.5+</td>
<td>Crown wide &amp; deep, no dead branchlets</td>
<td>12.5+</td>
<td>90-100%</td>
<td>5</td>
</tr>
</tbody>
</table>

Note: Due to the different methods used to include epicormic growth in the condition scales, the scales cannot be directly compared. However, this table provides an approximate comparison of the different scales used to measure tree condition at Snake Island, Mt Eccles, French Island and Framlingham.
### Appendix B

Table B.1 Data presented in Figure 3.1a: Age, in years, at the beginning of each tooth eruption/wear class of known-age male and female koalas pooled from French Island, Phillip Island and the Brisbane Ranges.

<table>
<thead>
<tr>
<th>TWC</th>
<th>mean</th>
<th>s.e.</th>
<th>n</th>
<th>min</th>
<th>max</th>
</tr>
</thead>
<tbody>
<tr>
<td>1M</td>
<td>0.6</td>
<td>0.01</td>
<td>26</td>
<td>0.6</td>
<td>0.8</td>
</tr>
<tr>
<td>2M</td>
<td>0.8</td>
<td>0.01</td>
<td>75</td>
<td>0.7</td>
<td>1.0</td>
</tr>
<tr>
<td>I</td>
<td>1.2</td>
<td>0.02</td>
<td>91</td>
<td>0.8</td>
<td>1.5</td>
</tr>
<tr>
<td>II</td>
<td>1.8</td>
<td>0.03</td>
<td>89</td>
<td>1.2</td>
<td>2.4</td>
</tr>
<tr>
<td>III</td>
<td>4.0</td>
<td>0.14</td>
<td>36</td>
<td>2.3</td>
<td>5.7</td>
</tr>
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<td>0.34</td>
<td>19</td>
<td>3.3</td>
<td>7.4</td>
</tr>
<tr>
<td>IVB</td>
<td>5.9</td>
<td>0.46</td>
<td>11</td>
<td>3.8</td>
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<td>IVC</td>
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</tr>
<tr>
<td>V</td>
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Table B.2 Data presented in Figure 3.1b. Duration, in months, in each tooth eruption/wear class for known-age male and female koalas and for koalas of unknown age pooled from French Island, Phillip Island and the Brisbane Ranges.

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<th>s.e.</th>
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<th>min</th>
<th>max</th>
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<td>1M</td>
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<td>56</td>
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Appendix C

Table C.1 Head length and age of female and male koalas under 123mm head length. Median age is the age for each head length determined in “WinBUGS”. Lower and upper CIs represent the 95% confidence intervals. Age is measured in days.

<table>
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<th>Female Upper CI</th>
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## Appendix D

Table D.1 Lower and upper asymptotic 95% confidence intervals of each parameter ($b_1$, $b_2$, and $b_3$) in the asymptotic regression equation relating body mass (kg) to tooth wear class for male and female koalas at Snake Island, Framlingham, Mt Eccles and French Island.

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Table D.2 Lower and upper asymptotic 95% confidence intervals of each parameter ($b_1$, $b_2$, and $b_3$) in the asymptotic regression equation relating head length (mm) to tooth wear class for male and female koalas at Snake Island, Framlingham, Mt Eccles and French Island.

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<th>French Island</th>
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Table D.3 Lower and upper asymptotic 95% confidence intervals of each parameter ($b_1$, $b_2$, and $b_3$) in the asymptotic regression equation relating mass (kg) to age (years) and head length (mm) to age (years) for male and female koalas at the Koala Conservation Centre at Phillip Island.

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### Appendix E

Table E.1 Kolmogorov-Smirnov 2-Independent samples tests comparing age distributions between samples within sexes at Snake Island, Mt Eccles and French Island. Female koalas: Snake Island: 1997 \( n = 347 \), 1999 \( n = 308 \), 2000 \( n = 308 \), 2001 \( n = 72 \), Mt Eccles: 1999 \( n = 454 \), 2001 \( n = 679 \), French Island: 1979 \( n = 52 \), 1980 \( n = 64 \), 1981 \( n = 103 \), 1982 \( n = 134 \), 2000 \( n = 84 \), 2001 \( n = 78 \); Male koalas: Snake Island: 1997 \( n = 308 \), 1999 \( n = 212 \), 2000 \( n = 39 \), 2001 \( n = 73 \), Mt Eccles: 1999 \( n = 553 \), 2001 \( n = 653 \), French Island: 1979 \( n = 29 \), 1980 \( n = 40 \), 1981 \( n = 89 \), 2001 \( n = 59 \).

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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000 &amp; 2001</td>
<td>0.332</td>
<td>0.999</td>
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</tr>
</tbody>
</table>

Note: male age distributions were not analysed from French Island in 1982 or 2000 due to the low sample sizes. * Denotes the only significant difference in age structure between samples.
### Appendix F

#### Table F.1

*Chlamydia*, clinical signs and infection prevalence and fertility of Australian koala populations reported in the literature. CFT = Complement Fixation Test, Gene = Gene Probe, n = sample.

<table>
<thead>
<tr>
<th>Site</th>
<th>Clin %</th>
<th>Infect %</th>
<th>Fert %</th>
<th>Test</th>
<th>Reference</th>
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<td><strong>Victoria</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bris. Ranges</td>
<td>2</td>
<td>78</td>
<td>52</td>
<td>51</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
<td>Grampians</td>
<td>2</td>
<td>84</td>
<td>0</td>
<td>50</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
<td>French Is</td>
<td>0</td>
<td>0</td>
<td>97</td>
<td>64</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
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<td>7</td>
<td>66</td>
<td>66</td>
<td>87</td>
<td>CFT (McColl et al. 1984)</td>
</tr>
<tr>
<td>Phillip Is</td>
<td>5</td>
<td>83</td>
<td>17</td>
<td>53</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
<td>Phillip Is</td>
<td>98</td>
<td>15</td>
<td>15</td>
<td>30</td>
<td>CFT (McColl et al. 1984)</td>
</tr>
<tr>
<td>Raymond Is</td>
<td>Few</td>
<td>86</td>
<td>38</td>
<td>50</td>
<td>CFT (Mitchell et al. 1989)</td>
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<tr>
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<td>4</td>
<td>86</td>
<td>42</td>
<td>50</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
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<td>0</td>
<td>67</td>
<td>62</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
<td>Sth Gippsland</td>
<td>4</td>
<td>56</td>
<td>62</td>
<td>50</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
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<td>0</td>
<td>82</td>
<td>38</td>
<td>34</td>
<td>CFT (Martin et al. 1988)</td>
</tr>
<tr>
<td><strong>South Australia</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Kangaroo Is</td>
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<td>0</td>
<td>74</td>
<td>60</td>
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</tr>
<tr>
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<td>79</td>
<td>63</td>
<td>CFT (Robinson et al. 1989)</td>
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<tr>
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<td>39</td>
<td></td>
<td></td>
<td>18</td>
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</tr>
<tr>
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<td>0</td>
<td></td>
<td>10</td>
<td>(Timms 2000)</td>
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<td></td>
<td></td>
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<tr>
<td>Mutdapilly</td>
<td>15-20</td>
<td>39-61</td>
<td>45</td>
<td>57</td>
<td>Cell Cui. (White and Timms 1994)</td>
</tr>
<tr>
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<td>17</td>
<td>85</td>
<td></td>
<td>33</td>
<td>PCR (Jackson et al. 1999)</td>
</tr>
<tr>
<td>Oakey</td>
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<td>41</td>
<td>41</td>
<td>20-50</td>
<td>CFT (Gordon et al. 1990)</td>
</tr>
<tr>
<td>Redland Shire</td>
<td>9</td>
<td>71</td>
<td>71</td>
<td>65</td>
<td>CFT (Weigler et al. 1988)</td>
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<td>85</td>
<td></td>
<td>85</td>
<td>68</td>
<td>Gene (Girjes et al. 1989)</td>
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<tr>
<td>Redland Shire</td>
<td>12</td>
<td>67</td>
<td>67</td>
<td>54</td>
<td>(White and Kunst 1990)</td>
</tr>
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<td>0-12</td>
<td>84</td>
<td>84</td>
<td>20-40</td>
<td>(Gordon et al. 1990)</td>
</tr>
<tr>
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<td></td>
<td>15</td>
<td>PCR (Ellis et al. 1993)</td>
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<tr>
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<td>73</td>
<td>73</td>
<td>20</td>
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</tr>
<tr>
<td>Ney Rd</td>
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<td>91</td>
<td>91</td>
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<td>(Thompson 2001)</td>
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<td>Gravel Res.</td>
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<td>33</td>
<td>33</td>
<td>21</td>
<td>(Thompson 2001)</td>
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Note: Brown *et al.* (1984) examined the presence of clinical signs of reproductive tract disease using radiographs.
Appendix G

Table G.1 Mean adult (>TWC III) female and male koala body mass from seven Victorian populations. Body mass is mean ± s.d. and sample size in parenthesis. The range of body mass is provided for sites from this thesis. Data source 1 is the present thesis, 2 is Martin and Handasyde (1990) and 3 is Mitchell et al. (1989). French Island 1 is 2000 and 2001, and French Island 2 is 1979-1981. The definition of “Adult” from the present thesis is koalas in TWC IVA – VII. The analysis of the average age of koalas from the KCC (Koala Conservation Centre) is described in the methods. The definition of “Adult” from Martin and Handasyde (1990) was not reported. ^ is females with young, B is females without young.

<table>
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<th>Females</th>
<th>Males</th>
<th>Data source</th>
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<td></td>
<td></td>
</tr>
<tr>
<td>French Island (1)</td>
<td>8.3 ± 0.9 (85)</td>
<td>11.4 ± 1.3 (37)</td>
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<tr>
<td></td>
<td>(5.9 – 11.4)</td>
<td>(7.6 – 13.6)</td>
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</tr>
<tr>
<td>French Island (2)</td>
<td>8.3 ± 0.8 (141)</td>
<td>11.3 ± 1.1 (86)</td>
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<tr>
<td>Framlingham</td>
<td>8.6 ± 0.8 (258)</td>
<td>10.2 ± 1.1 (134)</td>
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</tr>
<tr>
<td></td>
<td>(6.0 – 10.8)</td>
<td>(7.7 – 13.1)</td>
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</tr>
<tr>
<td>Chlamydia-infected</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Walkerville</td>
<td>7.7 ±0.8 (22)</td>
<td>9.6 ± 1.0 (21)</td>
<td>2</td>
</tr>
<tr>
<td>Phillip Island (KCC)</td>
<td>8.1 ± 1.0 (16)</td>
<td>11.2 ± 0.9 (9)</td>
<td>1</td>
</tr>
<tr>
<td>Mt Eccles</td>
<td>8.4 ± 0.9 (437)</td>
<td>10.6 ± 1.2 (389)</td>
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</tr>
<tr>
<td></td>
<td>(4.4 – 11.4)</td>
<td>(6.5 – 13.5)</td>
<td></td>
</tr>
<tr>
<td>Snake Island</td>
<td>8.7 ± 0.9 (331)</td>
<td>11.3 ± 1.1 (147)</td>
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</tr>
<tr>
<td></td>
<td>(6.0 – 12.1)</td>
<td>(8.0 – 14.1)</td>
<td></td>
</tr>
<tr>
<td>Brisbane Ranges</td>
<td>9.1 ± 0.8 (20)</td>
<td>11.2 ± 1.0 (14)</td>
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</tr>
<tr>
<td>Raymond Island</td>
<td>8.6^A (~20)</td>
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<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.3^B (~20)</td>
<td></td>
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</table>
Appendix H

Table H.1 Percentage of female koalas in each tooth wear class (TWC) with clinical signs of *Chlamydia*. Pooled for Snake Island and Mt Eccles.

<table>
<thead>
<tr>
<th>TWC</th>
<th>No clinical sign</th>
<th>adhesions</th>
<th>dirty tail</th>
<th>corneal</th>
<th>pink eye</th>
<th>n</th>
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<tr>
<td>I</td>
<td>95.9</td>
<td>2.7</td>
<td>0.0</td>
<td>1.4</td>
<td>0.0</td>
<td>73</td>
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<tr>
<td>II</td>
<td>84.1</td>
<td>9.8</td>
<td>0.0</td>
<td>4.5</td>
<td>1.5</td>
<td>132</td>
</tr>
<tr>
<td>III</td>
<td>64.1</td>
<td>30.3</td>
<td>4.3</td>
<td>0.9</td>
<td>0.4</td>
<td>234</td>
</tr>
<tr>
<td>IVA</td>
<td>48.6</td>
<td>40.4</td>
<td>5.5</td>
<td>2.8</td>
<td>2.8</td>
<td>109</td>
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<td>IVB</td>
<td>55.6</td>
<td>41.3</td>
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<td>63</td>
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<td>IVC</td>
<td>37.0</td>
<td>40.7</td>
<td>7.4</td>
<td>9.3</td>
<td>5.6</td>
<td>54</td>
</tr>
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<td>V</td>
<td>81.8</td>
<td>9.1</td>
<td>9.1</td>
<td>0.0</td>
<td>0.0</td>
<td>11</td>
</tr>
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<td>VI</td>
<td>83.3</td>
<td>16.7</td>
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<td>0.0</td>
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<td>VII</td>
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</table>
Appendix I

Table I.1 Fecundity of Australian koala populations. Obs\(^1\) Definition of Observation of fecundity: 1=Caught koalas; 2=3=combination of catch and observation of tagged koalas; 4=information not available. Juv Incl\(^2\) Definition of juveniles used in back young; 2=pouch or back young, or evidence of lactation; 3=pouch young only; 4=back young only; 5=information not available. Females used in fecundity estimate: 1=adult females; 2=total females; 3=females of breeding condition; 4=-independent female. Adult\(^4\) Definition of an adult female: 1=older than one year; 2=older than one and a half years; 3=older than two years; 4=sexually and tooth wear class; 6=based on weight; 7=based on age; 8=based on tooth wear class; 9=information not available.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Season</th>
<th>% fec.</th>
<th>n</th>
<th>Obs(^1)</th>
<th>Juv Incl(^2)</th>
<th>Fecund(^3)</th>
<th>Adult(^4)</th>
<th>Chlamydia</th>
<th>Refere</th>
</tr>
</thead>
<tbody>
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<td>Victoria</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French Is</td>
<td>1954</td>
<td>Aug-Oct</td>
<td>73</td>
<td>236</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>9</td>
<td>Negative</td>
</tr>
<tr>
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<td>278</td>
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<td>1</td>
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<td>2</td>
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<td>(Martir)</td>
</tr>
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<td>(Martir)</td>
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</tr>
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<td>2</td>
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330
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<th>Incl</th>
<th>Fecund</th>
<th>Adult</th>
<th>Chlamydia</th>
<th>Referee</th>
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<td>(Martir)</td>
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<tr>
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<td>44</td>
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<td>24</td>
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<td>2</td>
<td>2</td>
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<td>(Martir)</td>
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Appendix J

Table J.1 Number of skulls collected from each Victorian locality. Skulls measured from collection of author, Victorian Museum, Department of Zoology museums from the University of Melbourne, Monash University and La Trobe University and Parks Victoria offices at Brisbane Ranges National Park and Wilsons Promontory National Park.

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References for Appendices


Thompson, J. (2001) The role of research in koala management: Case studies from South-East Queensland. In The research and management of non-urban koala populations (eds K. Lyons, A. Melzer, F. Carrick and D. Lamb). Central Queensland University publishing unit, Rockhampton.


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