Life History Variation and Reproductive Success in the Common Brushtail Possum, *Trichosurus vulpecula*

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Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given

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Preface

Publications arising from this thesis:

Chapter 3 – in review: Isaac, J.L. Life history and demographics in an island possum, *Wildlife Research*.

Chapter 4 – in re-review: Isaac, J.L., Johnson, C.N. Terminal reproductive effort in a marsupial, *Biology Letters*

Chapter 5 – Isaac, J.L., Krockenberger, A.K., Johnson, C.N. (in press) Adaptive sex allocation in relation to life-history in the common brushtail possum. *Journal of Animal Ecology*.

Chapter 6 – Isaac, J.L., Johnson, C.N. (2003) Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. *Behavioral Ecology,* **14** (6): 818-822

Chapter 7 – Isaac, J.L. (in press) Mating season mass loss in male common brushtail possums: implications for age-specific variation in mating strategy. *Journal of Zoology.*

Appendix I – in review: Isaac, J.L. Demographic responses of an arboreal marsupial, the common brushtail possum, to prescribed fire. *Oryx*.

Appendix II – Isaac, J.L., Johnson, C.N., Grabau, P.J., Krockenberger, A.K. (2004) Automated feeders: new technology for food supplementation experiments in mammals. *Wildlife Research,* **31** (4): 437-441

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Abstract

Life history theory aims to describe and explain patterns in the life cycles of organisms and relate these patterns to intrinsic and extrinsic influences. The life history of an organism is commonly defined as a set of co-evolved strategies that relate directly to an individuals genetic fitness, lifetime reproductive success (LRS) and survival. The great majority of research on life history variation in mammals has concentrated on placental mammals, while marsupials have been largely overlooked. This thesis investigates life history variation, and the influence of this variation on reproductive strategy and success, among individuals in an arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula*).

A population of *T. vulpecula* was studied from 2001-2004 on Magnetic Island, north Queensland; the population was censused each month by live-trapping. Demographic changes in the population were modelled using capture-mark-recapture data. The population size remained stable over the study period and there was little temporal variation in recruitment or survival. *T. vulpecula* on Magnetic Island displayed life history traits similar to those reported for other populations of the species. The majority (>80%) of females began to reproduce at the age of two and the main birth period occurred in the autumn months of April and May. Some females went on to produce a second young in the spring, after successfully raising a first. Males became sexually mature at the age of three. Survival, body mass and body condition declined in both males and females after the age of six, although the declines were more pronounced in males.

Variation in life history was strongly related to differences in female reproductive strategy and success. In terms of somatic investment, older females invested significantly more into individual offspring than younger females; older females also gave birth earlier in the season and were more likely to produce a second offspring in the spring birth cohort. Maternal age also influenced the birth sex ratio; young, primiparous females gave birth to

significantly more male offspring than older females, regardless of their condition while older, multiparous females were more likely to give birth to a male offspring when in good condition.

The extent of male biased sexual dimorphism in *T. vulpecula* was extremely variable among 11 populations in northern Australia. Dimorphism was related to seasonality of breeding, being greatest in populations where births occurred all year round. Mean body mass of male possums also decreased with increasing population density, while there was no effect of density on female mass. There was also some evidence that population density influenced the degree of breeding synchrony within populations, particularly in locations with a more seasonal climate.

In the Magnetic Island population, mating effort also varied considerably among male possums and young males lost more mass during the mating period than did older males. There was also some indication that males demonstrated age-specific variation in mating behaviour, which may be related to their size and experience.

The results of my study show that life history traits in both male and female *T. vulpecula* are phenotypically plastic. Age-specific variation in reproductive strategy was found in both male and female possums and is likely associated with the trade-off between current and future reproduction. Increased reproductive effort in older females also appears to entail significant costs in terms of an associated decline in survival, condition and body mass. Variation in body condition also influenced offspring sex allocation in females and is most probably an adaptation to maximise LRS. Male possums displayed a more pronounced decline in survival and condition after the age of five compared to females and this may be a direct cost of increasing mating effort as a young adult.

Table of Contents

Chapter 1: General Introduction

Chapter 2: Description of the study species and site

Chapter 3: Population life-history and demography

Chapter 4: Terminal reproductive investment in females

Chapter 5: Adaptive sex allocation in relation to maternal life history

Chapter 6: Sexual dimorphism and synchrony of breeding: variation in polygyny potential among possum populations in northern Australia

Chapter 7: Mating season mass loss in males: implications for age-specific variation in mating strategy

CHAPTER 1

General Introduction

Life history theory and the concept of fitness

Life history theory is an attempt to bring together some of the major concepts in evolutionary ecology and aims to describe and explain patterns in the life cycles of organisms and relate these patterns to intrinsic and extrinsic influences. The life history of an organism is commonly defined as a set of co-evolved strategies, including morphological, behavioural and physiological adaptations, that relate directly to that individual's lifetime reproductive success (LRS) and survival (Stearns 1992; Ricklefs & Wikelski 2002). Stearns (1992) proposed that the phenotype of an animal consists of a number of interacting demographic traits known as life history traits. Some of the principal life history traits predicted to influence individual reproduction and survival include: age and size at sexual maturity; number, size and sex of offspring; age- and size- specific reproductive investment; age- and size- specific mortality and longevity (Stearns 1992).

The concept of fitness is essential in our understanding of life history theory because it explicitly links the environment, organisms and life history traits to the evolutionary process (Oli & Armitage 2003). Fitness has been defined as 'the relative contribution of an individual to the next generation' (Begon et al. 1996). Individual variation in fitness, and its covariance with particular life history traits, is a necessary requirement for natural selection (Endler 1986; Cam et al. 2002). Thus, the evolution of an individual trait by means of natural selection depends fundamentally upon the relationship between that trait and fitness. The foundations of life history theory, and analysis based on it, must therefore lie in describing and understanding variation and evolution in individual traits (Stearns 1992; Begon et al. 1996).

The role of trade-offs in life histories

A hypothetical organism, perfectly adapted to its environment, should display a life history strategy that maximises its reproductive fitness; thus it would begin breeding at birth, produce many large offspring which all survived, and it would live forever (Partridge & Harvey 1988; Begon et al. 1996). However, in the real world, organisms are subject to ecological and physiological constraints and individuals must compromise, or make trade-offs, in their allocation of available resources to individual fitness components. Life history trade-offs therefore result in benefits to one life history trait being coupled with a cost or decline in an associated trait (Begon et al. 1996). In an evolutionary context, trade-offs constrain the simultaneous evolution of two or more traits (Stearns 1992). By definition, since fitness is implicitly related to reproductive success, trade-offs are inexorably linked to reproductive traits. The most commonly cited trade-offs include those between current and future reproduction, current reproduction and survival, number and quality/size of offspring and reproduction and growth (Stearns 1992).

Mammalian life histories

Mammals span an enormous variety of life histories and early research focussing on life history variation within the Mammalia was initially concerned with body size, which correlates strongly with many aspects of life history across mammalian species (Purvis & Harvey 1995). Larger species are generally characterised by a ‘slow’ life history strategy, typified by delayed sexual maturity; few, large offspring and a long life span, while smaller species demonstrate the reverse pattern - a ‘fast’ life history strategy. However, more recent work established that this slow-fast continuum remains even when variation in body size is accounted for and research suggests that this enduring pattern may be correlated with variation in food resources, intraspecific competition and risk of predation (Partridge & Harvey 1988; Purvis & Harvey 1995).

Intraspecific variation in mammalian life histories

While life history strategies are essentially the product of long-term evolutionary adaptations, individuals can still respond to short-term variation in their immediate environment and life history traits show remarkable plasticity. A variety of short-term influences have been shown to influence life history traits and these fall primarily into two main groups, density dependent and density independent factors.

DENSITY DEPENDENT VARIATION

For the majority of mammals, population density varies considerably, both between and within years, and density is undoubtedly one of the most important factors influencing individual animals in the short-term. Variation in population density has the potential to affect a variety of life history traits through its influence on food availability and other resources that affect individual fitness. High population density has been associated with delayed sexual maturity in females in a wide variety of species (Dobson & Oli 2001; Forchhammer et al. 2001; Ozgul et al. 2004), and this mechanism may help females avoid increased reproductive costs during times of resource scarcity (Kaitala et al. 1997).

A number of studies have observed a male bias in the offspring sex ratio at high population density (Clark 1978; Johnson et al. 2001; Bond et al. 2003). In the majority of mammals, male offspring disperse while females are philopatric, and male biases in the offspring sex ratio are therefore thought to be a maternal adaptation to decrease competition for resources (such as food and nest sites) between mothers and their philopatric female offspring (Clark 1978; Cockburn et al. 2002).

High population density can also have a long-term negative influence on body mass and size in a variety of mammals (Forchhammer et al. 2001; LeBlanc et al. 2001; Bonenfant 2003; Festa-Bianchet et al. 2004). There is evidence that resource scarcity at high population density may constrain the growth of males and females differentially and this can influence the degree of sexual dimorphism and feed back into mating strategy and system (LeBlanc et al. 2001).

DENSITY INDEPENDENT VARIATION

Density independent factors also have the potential to influence life history traits in both the short and long term. In the majority of vertebrate taxa, there is a clear relationship between latitude and body size, and Bergmann (1847) stated that ‘races from warm regions are smaller than races from cold regions.’ A general pattern of increase in body size from south to north is therefore found in the northern hemisphere, and vice-versa in the southern hemisphere. This relationship is thought to be due to the relatively smaller body surface area of larger animals assisting in heat conservation in cooler climates (James 1970; Quin et al. 1996). Bergmann’s Rule has been found to apply not only between species, but also within geographically distinct populations of the same species (Ashton 2000). These clinal variations in size, which are likely to be associated with changes in seasonality and resource availability, may also have divergent consequences for males and females and influence reproductive strategies (Quin et al. 1996; Storz et al. 2001). For species in temperate, seasonal environments, breeding is often constrained by seasonal fluctuations in resource availability and climate and births are likely to be concentrated during favourable periods (Bronson 1989). Variation in breeding seasonality is liable to have a strong impact on maternal investment strategy, male mating strategy and mating system. Climatic conditions at birth have also been shown to influence life history traits, such as body mass and reproductive success, in individuals throughout their lives, giving rise to a ‘cohort effect’ (Albon et al. 1987; Forchhammer et al. 2001). Thus, for species that inhabit a large geographical range, latitudinal and seasonal differences are likely to result in considerable intraspecific variation in life history and ecology.

Variation in predation risk can also influence life history. For example, females in two species of vole (*Microtus agrestis* and *Clethrionomys glareolus*) exhibited delayed sexual maturation under high predation risk from mustelids (Norrdahl & Korpimaki 1995). Adverse consequences on life history traits have also been associated with hunting and exploitation of mammal populations by humans (Palumbi 2001). Selection for smaller rams with reduced horn size, as a response to trophy hunting, has been noted in bighorn sheep, *Ovis canadensis* (Coltman et al. 2003) and an increase in tusk-less African elephants (*Loxodonta africana*) has similarly been suggested as a response to selective ivory poaching (Jachmann et al. 1995).

Maternal factors affecting early development can also have an important influence on offspring. Comparative analysis of life history traits in mammals predicts that maternal state during gestation and lactation will influence offspring success (Stearns 1992; Lindström 1999; Boltnev & York 2001). Such influences are commonly known as maternal effects, and have been classified as ‘a class of phenotypic effects that mothers have on the phenotype of their offspring that are unrelated to the offspring’s own genotype’ (Bernardo 1996). Phenotypic traits often associated with maternal effects are maternal mass and condition, age, dominance rank and breeding experience (Bernardo 1996).

There is also mounting evidence that density independent effects, such as climatic and predation pressures, can be related to, and exacerbated by, high population density (i.e.:Clutton-Brock et al. 1987a; Coulson et al. 2000; Karels et al. 2000).

DEMOGRAPHIC CONSEQUENCES OF LIFE HISTORY VARIATION

The dynamics of all animal populations are affected by the fitness of the individuals within them and the factors that influence individual fitness are of paramount importance when considering population processes. Variation in life history variables among individuals and cohorts can have direct impacts on population structure, growth and dynamics (Cole 1954). For example, phase related changes in life history variables, particularly age at maturity, are the most likely demographic basis of population cycles in small mammals, such as snowshoe hares (*Lepus americanus*) and field voles (*M. agrestis*) (Oli & Dobson 1999; Dobson & Oli 2001; Oli & Dobson 2001).

Differences between individuals, particularly disparity in size and mass between the sexes, can also influence population structure. For example, sex and size specific differences have been found to influence the susceptibility of an individual to predators and parasites (Owen-Smith 1993; Moore & Wilson 2002). Differences in size and body mass between the sexes have also been proposed as the primary cause of sexual segregation in large mammals (Bonenfant et al. 2004).

Marsupial life histories

ARE MARSUPIALS DIFFERENT?

The great majority of research on life history variation in mammals has concentrated on the eutherians, while marsupials have been largely overlooked (Fisher et al. 2001). Compared to eutherian mammals of a similar size, marsupials often have a ‘slower’ life history strategy, and Lee & Cockburn (1985) propose that this reflects a number of characteristics where marsupials are restricted in comparison to eutherians. The most striking difference is that of relative maternal investment at birth; in marsupials, no litter exceeds 1% of the weight of the mother, while in some small eutherians, litter weight can be in excess of 50% of the mother’s mass (Lee & Cockburn 1985). Marsupials also have relatively slow metabolic rates, slow growth rates and demonstrate conservative brain size variation, with large marsupials having relatively small brains (Lee & Cockburn 1985).

Despite this apparent ‘dichotomy’ between marsupial and eutherian life histories (Lee & Cockburn 1985), marsupials still demonstrate a wide range of life history tactics, spanning the slow-fast continuum. Females can range from an adult body mass of <5g (e.g. long tailed planigale, *Planigale tenuiostris*) to >30 kg (e.g. red kangaroo, *Macropus rufus*). They also exhibit a variety of feeding strategies; herbivorous marsupials span a range of feeding guilds including folivores, nectarivores and fungivores, while carnivorous strategies can include insectivory, scavenging and active hunting. Marsupials such as the koala (*Phascolarctos cinereus*) typify the 'slow' end of the spectrum and can live more than 25 years, producing an average of one offspring every two years (Fisher et al. 2001). At the 'fast' end of the continuum are members of the Didelphidae and Dasyuridae, such as *Didelphis marsupialis* - which can produce > 12 offspring per year but has a life span of only a year or two. Like eutherians, the slow-fast continuum appears to be independent of body size in marsupials; an average 1 kg female Virginia opossum (*Didelphis virginiana*) can produce more than 12 offspring a year, but only survives for about 2 years, while a 1 kg common ringtail possum (*Pseudocheirus peregrinus*) can live for up to 5-6 years, but produces an average of only 1.8 offspring annually (Lee & Cockburn 1985).

MARSUPIAL STRATEGIES

Marsupials also display a number of life history traits that are rare, or entirely absent, in the placental mammals. Embryonic diapause, or stasis in embryonic development, is found in a number of species of both marsupial and eutherian mammal. However, what appears to be unique in some marsupials is the ability of the mother to overlap successive litters by pausing the development of the embryo in the uterus, while still lactating the previous offspring/litter in the pouch/at foot (Lee & Cockburn 1985). However, despite much research effort, particularly in the Macropodidae, the adaptive and ecological significance of embryonic diapause in marsupials remains unclear (Lee & Cockburn 1985). Current evidence points to a number of potential roles for embryonic diapause including the ability of the female to space births to coincide with favourable environmental conditions; ensuring females have young when a drought breaks and/or reducing the time to replace a lost pouch young (Lee & Cockburn 1985; Tyndale-Biscoe 1989).

A further typically marsupial life history tactic is that of a very short gestation and a long lactation period. In placental mammals gestation length is positively related to both maternal weight and offspring/litter weight and ranges from <15 days in some rodents, to nearly two years in the Proboscideans (Elephants: Morgan Ernest 2003). This range is much reduced in marsupials, from <12 days in some dunnarts (*Sminthopsis* spp.), up to a maximum of about two months in the honey possum, *Tarsipes rostratus* (Fisher et al. 2001). The relationship between gestation length and weight of young at birth is also absent; no marsupial weighs more than 1g at birth (Lee & Cockburn 1985). By contrast, lactation tends to be extended in the marsupials, ranging from about two months in the western pygmy possum (*Cercartetus concinnus)* up to 20 months in some species of tree kangaroo (*Dendrolagus* spp.) (Fisher et al. 2001). In the placental mammals, lactation ranges from as little as 10 days in some Phocid seals up to 48 months in the short finned pilot whale (*Globicephala macrorhynchus)* (Morgan Ernest 2003). Despite these differences, maternal investment in offspring during the lactation period is similar in marsupials and eutherians (Krockenberger et al. 1998) and there is a positive relationship between maternal mass and the time taken from conception to weaning in both groups (Lee & Cockburn 1985).

Semelparity, the occurrence of only one reproductive event in an organism's lifetime, has not been documented in males in any species of eutherian mammal (Cockburn 1997). However, within the marsupial genera *Antechinus, Parantechinus, Phascogale*, *Dasyurus* and *Dasykaluta*, males live for only one year, reproduce for just one breeding season, and die following the short annual mating period (Lee & Cockburn 1985; Cockburn 1997). This mass post-mating mortality of males is due primarily to stress, which manifests as a variety of, eventually terminal, diseases (reviewed by Lee & Cockburn 1985). While not quite as extreme, the males of some other marsupial species, including members of the Didelphidae, exhibit a similar ‘live fast, die young’ strategy. These observations have led Cockburn (1997) to suggest that patterns of senescence, or age-specific declines in performance and survival, in small–medium sized marsupials differ from those observed in eutherian mammals. Current evidence indicates that the evolution of male semelparity in the Dasyuridae, and also the relatively ‘fast’ life history strategy displayed by other male marsupials, may be due to a number of combined factors including seasonal fluctuations in resource availability, synchronised female oestrus, a prolonged lactation period and high female mortality, all of which result in a restricted window of opportunity in which to mate and reproduce (Lee & Cockburn 1985; Cockburn 1997; Kraaijeveld et al. 2003).

WHY STUDY LIFE HISTORY THEORY IN A MARSUPIAL?

While marsupials demonstrate a variety of life history tactics similar to eutherian mammals, they also exhibit traits that are apparently unique within the Order, making them ideal models with which to investigate some of the key concepts in life history theory. For example, in eutherian mammals, a long gestation period gives offspring an advantage in mother-offspring conflict, as foetal hormones govern the placenta, resulting in manipulation of maternal resources for offspring benefit (Haig 1993; Haig 1996). However, milk supply to offspring during lactation is primarily under maternal control. Thus, the short gestation and long lactation period exhibited by marsupial mothers may allow them greater control in allocating resources into reproduction, making them excellent models to study the trade-off between reproduction and longevity and age-specific reproductive investment. Similarly, the unusual ‘live fast, die young’ strategy of some male marsupials offers a unique opportunity to investigate the trade offs between current and future reproduction and reproductive effort and longevity.

Relevance and aims of this study

The primary aim of this thesis was to investigate life history variation, and the influence of this variation on reproductive strategy and success, among individuals in a marsupial, the common brushtail possum (*Trichosurus vulpecula*). The common brushtail possum is a medium sized marsupial and, like most marsupials, has a relatively slow life history compared to a eutherian of similar size. *T. vulpecula* demonstrate a strategy more comparable to a large ungulate, such as a red deer (*Cervus elaphus*) but unlike most eutherians with a slow life history, are easy to trap and handle allowing repeated measurements to be taken on many life history traits. *T. vulpecula* occur at relatively high densities and have a wide distribution, occurring across most of Australia (see Chapter 2), allowing intraspecific comparisons to be made among geographically distinct populations which are likely to show variation in life history traits. These qualities of *T. vulpecula* therefore make them an ideal species for a study focussing on intraspecific life history variation.

Specifically, my aims for the study were:

1. To determine general life history and demographic patterns in male and female *T. vulpecula* at the Magnetic Island study site.
2. To assess the extent of individual variation in life history traits among female *T. vulpecula* and determine how this impacts on maternal investment strategy through age-specific variation in reproductive effort and offspring sex allocation.
3. To determine how variation in breeding seasonality and population density among *T. vulpecula* populations in northern Australia can influence male body size and the degree of male-biased sexual size dimorphism.

4. To investigate patterns of male reproductive effort, with particular emphasis on age-specific differences in mating strategy.

Thesis Structure

The remainder of this thesis is organised as follows; Chapter 2 gives a general description of *T. vulpecula* and the key life history traits of the species and describes the study site on Magnetic Island. Chapter 3 describes the life history characteristics and demographic traits of the study population. Chapter 4 considers the role of maternal age on variation in reproductive effort in female possums, while Chapter 5 investigates how maternal age and condition influence adaptive adjustment of the offspring sex ratio. Chapter 6 examines the influence of breeding seasonality and population density on male body size and the degree of sexual dimorphism in 11 possum populations from northern Australia. Chapter 7 investigates age-specific variation in male reproductive effort and mating strategy. Chapter 8 provides a general discussion of the results found in this study, summarises the key findings of the thesis and considers their relevance to contemporary theories in evolutionary, behavioural and conservation ecology. Appendix I is a manuscript examining the demographic and life history responses of the study population to a prescribed fire, which burnt half of the study site in 2002. Appendix II details a food supplementation experiment, testing newly developed automated feeding stations, at the study site.

CHAPTER 2

Description of the study species and site

Study Species: the common brushtail possum, *Trichosurus vulpecula*

TAXONOMY AND DISTRIBUTION

The common brushtail possum (family Phalangeridae) is a medium sized, nocturnal marsupial with one of the widest distributions of any mammal in Australia (Fig. 2.1: Kerle 1984; Kerle 2001). However, despite this wide range and the adaptable nature of the species, brushtail possums are currently disappearing from large tracts of central and western Australia. This has been attributed primarily to habitat alteration and clearance and introduced predators (Kerle 2001). Brushtail possums were also introduced into New Zealand in the mid-1800's to establish a fur trade (Clout & Ericksen 2000). They have since become a huge pest in the country, defoliating valuable native forest and impacting on the fragile New Zealand ecosystem (Clout & Ericksen 2000).

GENERAL LIFE HISTORY

Body size and mass

Possums can range in body mass from >3.5 kg (Tasmania) to <1.5 kg (Northern Territory) with the decrease in size following a latitudinal gradient from the temperate south to the tropical north, consistent with Bergmann's rule (Yom-Tov et al. 1986). Possums are commonly sexually dimorphic, with adult males being both larger and heavier than adult females, although the extent of male-biased sexual dimorphism can vary considerably among populations (Isaac & Johnson 2003).

Reproductive behaviour and biology

The breeding season of the brushtail possum ranges from continuous in the north of Australia, where births often occur in every month (Kerle 1984), to

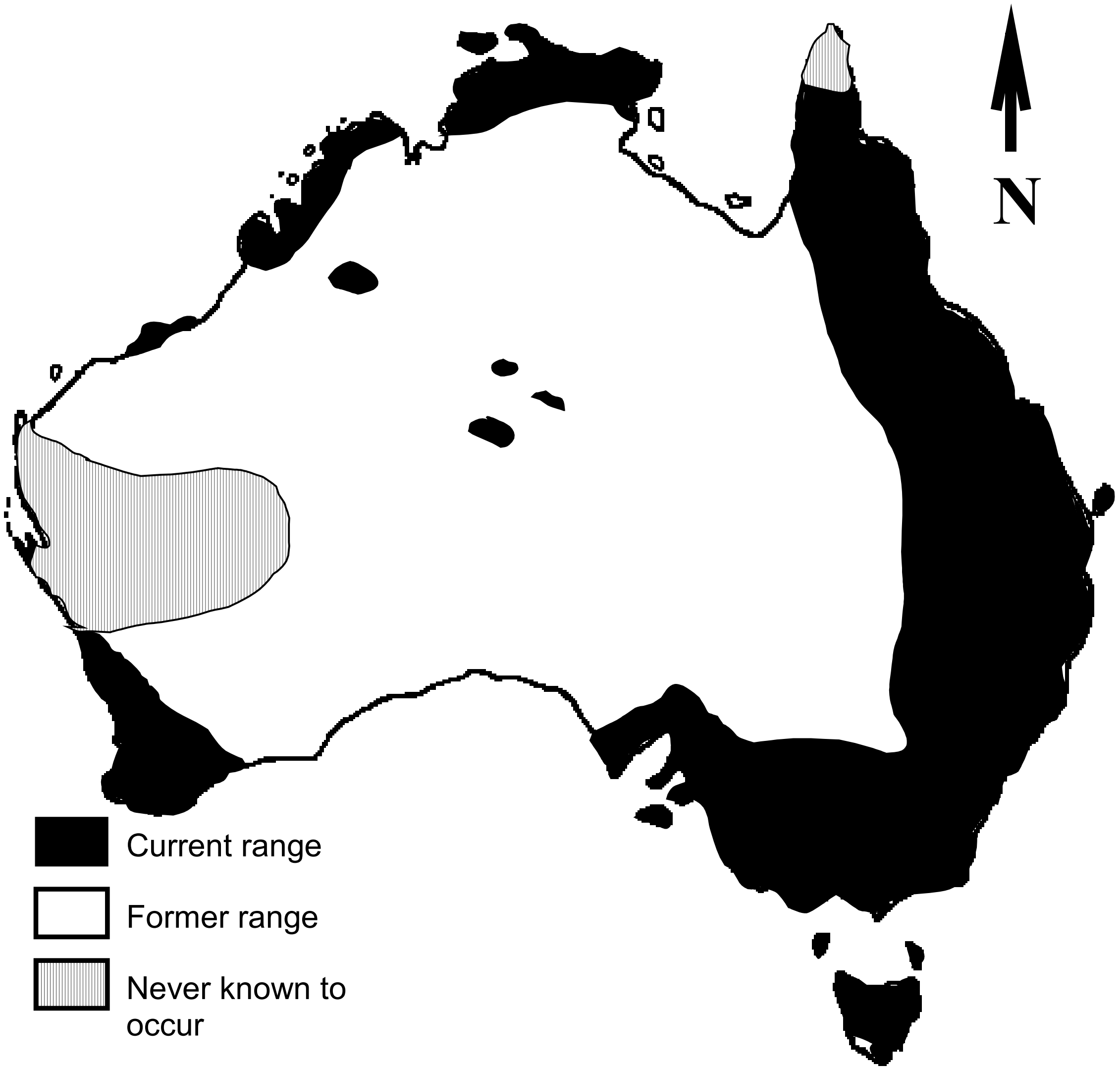

Figure 2.1: Distribution map of *T. vulpecula* across its native range in Australia. Current range is shown in black, former range in white and areas where the species has never been known to occur are hatched. Map adapted from Kerle (2001).

highly seasonal in the south and in New Zealand, with the majority of births occurring during the autumn period of April – May (Kerle 1984). Breeding seasonality in possums has been linked to a number of environmental factors including photoperiod (Gemmell et al. 1993) and seasonality in plant growth (Kerle 1984).

Female possums become sexually mature between 12 and 24 months of age, while males are generally mature by 3 years (Fletcher & Selwood 2000). During the breeding season, adult females are often accompanied by one or more males who may consort with her for 30 – 40 days prior to mating (Winter 1976). Winter (1976) suggests that consort males are usually socially dominant animals and, since these males often mate with several different females each season, the mating system of the brushtail possum has previously been described as polygynous (Day et al. 2000).

Following a gestation period of 17 days, females give birth to a single young which migrates to the pouch and remains there for the duration of lactation (Fletcher & Selwood 2000). Lactation in possums has been loosely divided into three phases by Fletcher & Selwood (2000), the first of which occurs during pregnancy and involves the development of the mammary gland. The second phase follows birth and is characterised by low milk production and slow growth of the pouch young until ~100 days from birth. During the third phase of lactation, high milk production supports rapid growth and development of the pouch young. Figure 2.2 shows a growth curve for offspring during lactation. Lactation lasts for approximately six - nine months and during the final months the offspring rides on its mother's back. Weaning is usually completed by 240 days after birth, when the young becomes an independent juvenile (Fletcher & Selwood 2000). A female can therefore raise an offspring from conception to independence within a 12-month period and previous researchers have noted that some females may give birth to a second young during spring or summer (Kerle 1984). Embryonic diapause does not occur in *T. vulpecula*.

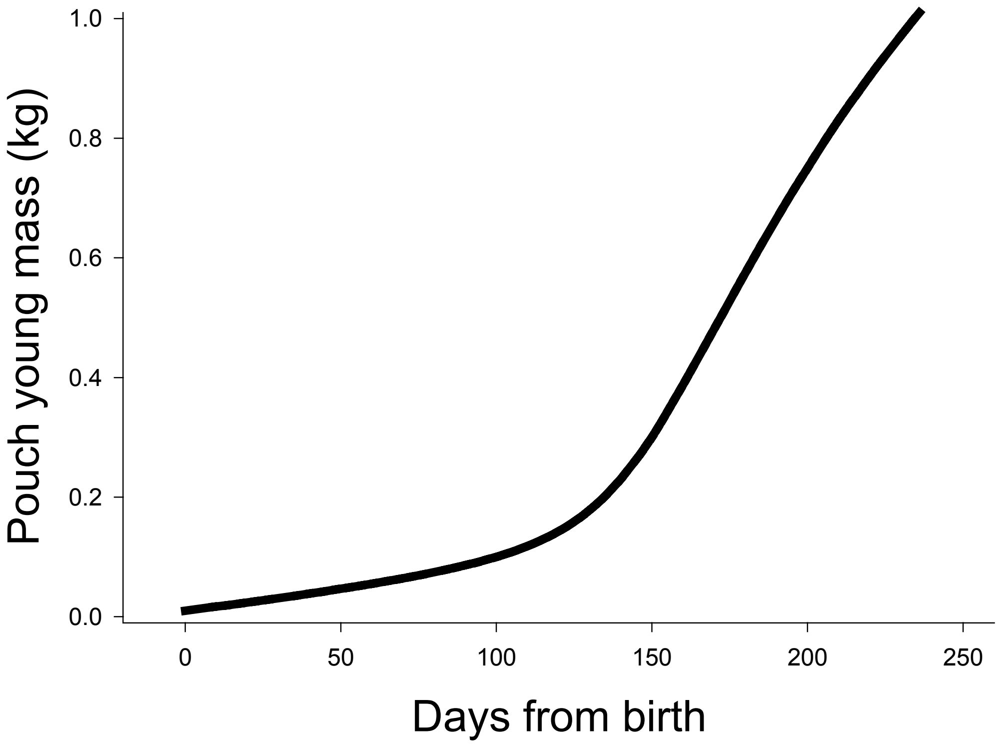

Figure 2.2: Growth curve, in terms of change in body mass (kg), of pouch young from birth to independence in the common brushtail possum (adapted from Fletcher & Selwood 2000).

Brockie et al. (1981) estimated a mean life span of 6.7 years for females in the Orongorongo Valley in New Zealand. Survival analysis by Efford (2000) similarly indicates that probability of survival decreases rapidly following six years of age in both males and females, also in New Zealand. An average female can therefore produce approximately 6 offspring during her lifetime (Fletcher & Selwood 2000).

Social system

Both male and female possums are essentially solitary and spend the majority of their time alone (Day, O'Connor & Matthews 2000). Aside from the mother-juvenile interaction, other social interactions most commonly observed are between adult males and females during the breeding season (Winter 1976). A number of studies have indicated that females are socially dominant to males and that larger, older males are dominant to small, young males (Winter 1976; Jolly & Spurr 1996).

In most populations studied, possums show some territorial behaviour, with defence of the core home range common (Dunnet 1964; Winter 1976; Green 1984). However, the degree of territorial behaviour appears to depend upon resource availability and population density (Green 1984; Kerle 1998). Scent marking and a variety of vocalisations are common and are thought to be important in establishing and maintaining dominance hierarchies and relationships (Winter 1976).

Diet and dietary adaptations

Possums are largely arboreal and folivorous, but show great variation in food preference; the proportion of *Eucalyptus* species in the diet of the brushtail possum can range widely, from up to 100% to as little as 3% (Watson 1998). Possums are opportunistic feeders and have been documented to eat fruit, flowers, fungi and even small invertebrates (Kerle 2001). On Magnetic Island, Dalla Pozza (1993) determined that brushtail possums were able to consume and digest mangrove plant species, while in introduced New Zealand populations, individuals have been observed to prey on eggs, nestlings and even adult birds (Nugent et al. 2000).

Utilising fibrous plant tissue becomes less feasible as body size declines and the brushtail possum, along with most folivorous marsupials, is well below the theoretical weight limit (~10 kg) for a mammal utilising foliage as its main dietary component (Nugent et al. 2000). To compensate, possums have evolved a variety of physiological adaptations in order to cope with their poor quality diet, including an expanded colon and caecum which allow some selective retention of smaller, more digestible particles (Hume 1999). Possums also have a relatively low basal metabolic rate in comparison to other similarly sized placental mammals, allowing them to conserve energy (Cork & Foley 1997). However, the dietary adaptations of the brushtail possum are less specialised than those found in other folivorous marsupials and, as a consequence, possums often require additional high-energy, high-nutrient foods (Nugent et al. 2000). Common brushtail possums are therefore the least folivorous of all the folivorous marsupials (Cork 1994).

Population dynamics

The dynamics and density of possum populations vary considerably, both over their native range in Australia and also in New Zealand. In New Zealand, population densities as high as 25.4 possums per hectare have been recorded, while Australian populations range from <0.1 to ~10 possums per hectare (Efford 2000). Lower population densities in Australia may be attributed to a number of factors, including the presence of large mammalian and avian predators, such as the dingo *Canis lupus dingo* and the powerful owl *Ninox strenua*, and interspecific competition with other folivorous, arboreal marsupials (Efford 2000).

The dynamics of established possum populations are generally stable over time-scales of 10-30 years (Efford 2000). As with most mammal populations, mechanisms of population regulation are not fully understood and regulatory factors, at least in native Australian populations, may include predation, den site availability and food limitation (Efford 2000).

Dispersal in possums is male biased, in accordance with most other mammalian species (Efford 1998; Johnson et al. 2001) and Efford (1998) suggests that dispersal is an integral part of male development and unrelated to density, weather or food shortage. Female offspring are commonly philopatric and often settle adjacent to, or within, their natal home range (Johnson et al. 2001; Kerle 2001).

Study site

The study was conducted over a three year period (May 2001 - May 2004) on a ~10ha site in mixed open eucalypt woodland on Magnetic Island, North Queensland (Fig 2.3a,b: 19˚ 10'S, 146˚ 50'E). Magnetic Island is a high continental island with elevations of up to 540m and an area of approximately 5184 ha. More than half of the island is national park and is dominated by large hills and spurs, covered with extensive granite outcroppings. The climate on Magnetic Island is tropical and highly seasonal, with a dry winter season from May to October and a wet summer season from November to April.

The most common tree species on the island are from the genus *Eucalyptus*, and include bloodwoods, ironbarks and the yellow stringybark. The study site also contained the native yellow kapok tree (*Cochlospermum gillivraei*), *Acacia* spp and *Melaleuca* spp. The hoop pine (*Araucaria cunninghamii*), while abundant elsewhere on the island, was absent from the study site.

Only five native mammal species are currently known to occur on the island - the brushtail possum, allied rock wallaby (*Petrogale assimilis*), echidna (*Tachyglossus aculeatus*), koala (*Phascolarctos cinereus*) and water rat (*Hydromys chrysogaster*). The introduced black rat (*Rattus rattus*) and house mouse (*Mus musculus*) can also be found in low densities in urban areas.

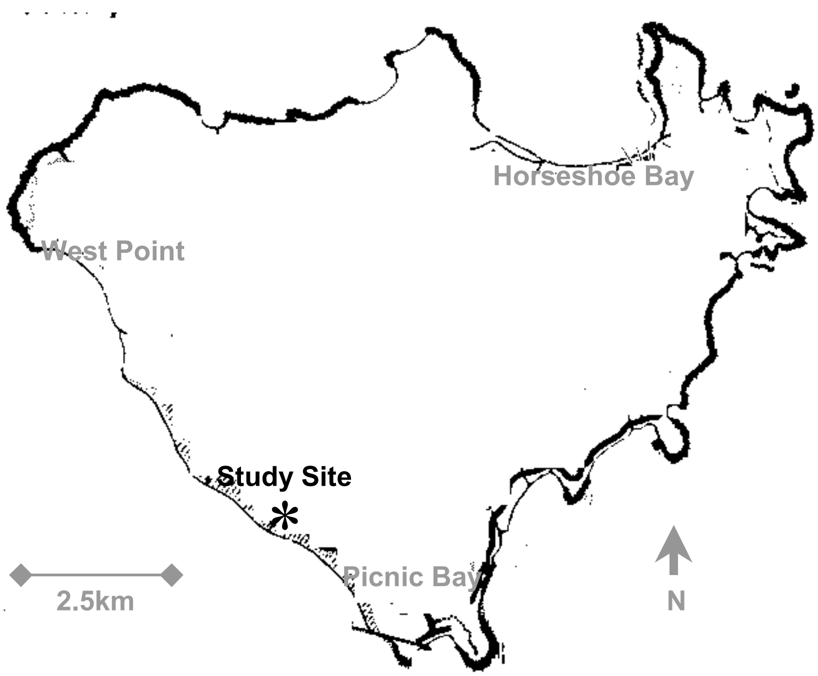

Figure 2.3a: Map of Magnetic Island with the location of the study site shown by the black asterix.

Figure 2.3b: Photograph of habitat typical of the study site (© A. Krockenberger)

There are very few native predators of mammals on Magnetic Island, apart from the boid snakes (*Morelia amethistina, Anteresia maculosa, Morelia spilota*), which are present in low densities. Magnetic Island pythons are smaller than pythons from mainland populations and this may be due to the scarcity of small (<500g) mammalian prey (Fearn 1998). Introduced domestic and feral cats (*Felis domesticus)* and dogs (*Canis canis*) undoubtedly predate native mammals in urban areas, but are unlikely to have a large impact in more remote areas. The barking owl *Ninox connivens* is also increasing in number (personal observation) on the island and may predate small mammals, including possums. A number of raptors are present on the island, but these birds are primarily diurnal hunters and as such are unlikely to have an important impact on the demographics of native island mammals, which are all largely nocturnal or crepuscular.

CHAPTER 3

Population life history and demography

(Submitted for publication [*Wildlife Research*])

Introduction

The question of how life history traits vary among individuals, and how this variation contributes to differences in individual fitness, is a central issue in life history theory (Stearns 1992). Indeed, the evolution of a life history trait through natural selection is governed by the relationship between that trait and its effect on individual fitness (Endler 1986; Stearns 1992)

In developing their theory of *r* and *K* selection, MacArthur & Wilson (1967) proposed that individual life history traits interact with each other to essentially form what is now termed a life history 'strategy', referring to the coordinated evolution of all the life history traits together (Stearns 1992). While the *r* and *K*-selection theory is now thought of as a somewhat simplistic view of the evolution of life histories (Stearns 1992), patterns of covariation between key life history traits are commonly found in individuals in natural populations. For example, body size and mass are known to correlate strongly with many other life history traits across mammalian species (Webster et al. 2004) and variation in survival and reproduction probabilities in relation to both age and body condition have been proposed as key features in life history evolution (Berube et al. 1999).

In order to identify variation and covariation in life history traits, and the evolutionary causes and consequences of this variation, it is essential to describe individual life history traits and be aware of the benefits these traits convey (Begon et al. 1996). Indeed Stearns (1992) proposes that the evolution of life history strategies and their analysis must be based on the evolution of the individual traits and that to fully understand the evolution of life histories, it is necessary to understand the evolution of one trait at a time. McGraw & Caswell (1996) further maintain that to effectively assess the fitness of an individual, a more demographic approach needs to be taken by incorporating as many aspects of life history as possible. Detailed insight into the factors that influence the demographic parameters of a population is also essential for our understanding of population dynamics (Oli & Dobson 2003; Rödel et al. 2004).

In this chapter, I aim to describe and identify life history traits and demographic processes, which will be central to subsequent chapters, in my study population on Magnetic Island. I will also determine which life history traits are subject to variation within the population and evaluate life history differences between the sexes.

Methods

MARK-RECAPTURE DATA

The study was conducted during 2001-2003 at the Magnetic Island study site; details of the study site are given in Chapter 2. A trapping grid was established at the site in May 2001 consisting of 30 trap sites, each with two traps, spaced at approximately 25 m intervals. Trapping sessions were conducted once monthly, for two or three consecutive nights, for the duration of the study; 28 trap sessions were used in the analysis. Standard wire cage traps (60 cm x 20 cm x 20 cm) were baited with oats, honey and peanut butter rolled into small balls. Traps were set at sunset and opened at sunrise. Possums caught during trapping sessions were PIT tagged, measured, weighed and released at the point of capture. On the first capture of each session, the head length of all animals was measured to the nearest 0.1mm using vernier calipers and animals were weighed, to the nearest 20g, with a spring balance. The length of one testis and combined width of both were also measured to the nearest 0.1mm in male possums. Some individuals received food supplements during a field trial of newly developed automated feeding stations (see Appendix II for details). While these animals did gain mass during food supplementation (Appendix II), they did not exceed the natural weight range for *T. vulpecula* in this population and were included along with the rest of the population. During early lactation, female mass was estimated by subtracting the approximate mass of her pouch-young; in late lactation young were removed from the pouch and weighed separately from their mother.

The demographic parameters of the study population were modelled from capture-mark-recapture data using a full Jolly-Seber model for open populations in the program EcoMeth (Krebs 1998). The Jolly-Seber model gives estimates of monthly survival (the probability an animal alive in one trapping session will be alive the following session), recruitment of individuals into the population (incorporating both births and immigration) and population size (number of individuals). The model also calculates capture probabilities, in terms of an estimate of the proportion of the population marked. The Jolly-Seber method does however make four important assumptions about individuals and the population, as follows; every individual has the same probability of being trapped, regardless of whether it is marked or unmarked; every marked individual has the same probability of survival; individuals do not lose their marks, and marks are not overlooked at capture; sampling time is negligible in relation to intervals between samples.

Age-specific survival was calculated separately for males and females and is expressed as the probability of an individual surviving to the next age class, estimated from live-trapping data.

AGE AND CONDITION

Animals first captured as independent juveniles or adults were aged using a tooth wear index developed specifically for *T. vulpecula* by Winter (1980). Tooth wear of the first upper molar was determined by visual inspection during trapping sessions; it was unnecessary to anaesthetise animals for this procedure. Animals were assigned into a tooth wear class from between 1-7, based on the pattern of dentine and pulp exposed as described by Winter (1980). Estimation of age by tooth wear was verified using animals of known age, born during the

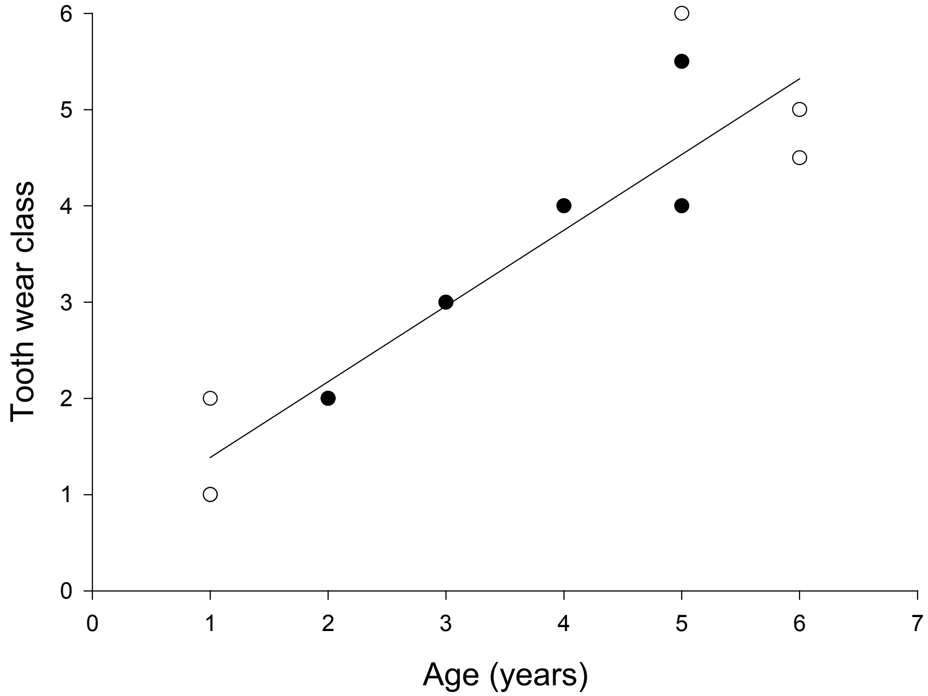

Figure 3.1: The relationship between actual age of a possum, in years, and the tooth-wear class that possum was assigned to. The white open circles denote data from male possums and the filled circles show females. The line is that fitted from a linear regression.

study (n = 7) or marked during earlier trapping in 1999 and 2000 (n = 6). Wear class was found to be a good predictor of actual age in years (Fig. 3.1: $R^2 = 0.86$, $p < 0.0001$, n = 13). While the relationship between tooth-wear class and age does begin to break down in the older age classes, when used in conjunction with other indicators of age including reproductive status (i.e.: pouch status, testes size), body mass and condition, the accuracy of the ageing method was considered very reliable.

A condition index (CI) was calculated for each animal as the ratio of their observed mass to that predicted from a regression of body mass on head length for all animals, as used by Johnson et al. (2003). Morphological indicators of body condition are commonly employed in ecological studies on mammals and while their accuracy and usefulness has been questioned (Hayes & Shonkwiler 2001), a recent study validated their use in the northern brown bandicoot (*Isoodon macrourus*: Parker & Krockenberger 2002). Regression of body mass on head length was calculated for adult male and female animals as follows:

Regression equation for male animals; CI = (actual mass)/ -

1.2334+(0.03559*head length), $R^2 = 0.26$, $p < 0.0001$, $F_{1,\,169} = 60.86$

Regression equation for female animals; CI = (actual mass)/ -

1.2439+(0.03546*head length), $R^2 = 0.23$, $p < 0.0001$, $F_{1,\,234} = 68.83$.

Unless otherwise stated, the age and measurements used for each individual were those taken in the May trapping session of each year.

BREEDING DATA

During trapping sessions, the pouch condition and reproductive status of all females was assessed. Sub-adult females were classed as non-reproductive when their pouch showed no signs of invagination; they were subsequently classed as primiparous when known to give birth to their first offspring. Females first caught as adults with an invaginated pouch were classed as multiparous. An exact reproductive history was known for all females born during the study. The seasonal distribution of births was determined by assigning a date of birth to all unweaned juveniles, defined as dependent pouch-young or young-on-back, captured with their mothers during trapping sessions. Date of birth, in days, was estimated from head length using a growth curve constructed for *T. vulpecula* in north Queensland populations (C. Johnson, unpubs. data). The growth curve for juvenile *T. vulpecula* in north Queensland was estimated by first using the curve published by Lyne & Verhagen (1957) for populations near Sydney as a starting point. It was assumed that this curve would describe accurately the earliest phase of growth but might be unreliable later because *T. vulpecula* grow larger in Sydney than in north Queensland. This curve was used to age north Queensland possums in the first 40 days of life and the curve was completed using animals ($n = 78$) whose birth dates were determined from a measurement during this initial period and who were re-measured later in pouch-life (C. Johnson, unpubs. data).

For pouch young with a head length of ≤25mm in length:

Age (in days) = 2.95*head length (in mm) – 16.82.

For pouch young with a head length > 25mm in length:

Age (in days) = 2.95*head length (in mm) – 18.55.

The first measurement of head length, usually taken when the offspring was still unfurred and permanently attached to the teat, was used in the analysis as the accuracy of this equation declines as offspring grow larger.

In the absence of genetic data to establish paternity, males were classed as sexually mature adults when their testes were full-sized, ≥ 18mm in length, consistent with methodology described in Clout & Efford (1984).

Results

DEMOGRAPHICS

A summary of the demographic parameters estimated by the Jolly-Seber model is shown in table 3.1. During the study, the estimated percentage of the population marked (PIT tagged) was high, ranging from 87% - 98%, with a mean

Table 3.1: Summary of demographic variables estimated in EcoMeth (Krebs 1998) using the Jolly-Seber method for open populations. All values are shown ± standard error of the mean.

Year	Estimated Population Size	Mean monthly survival probability	Mean monthly recruitment
2001	44.7 ± 2.02	0.93 ± 0.18	5.77 ± 1.55
2002	52.3 ± 1.62	0.96 ± 0.15	3.07 ± 0.93
2003	50.2 ± 1.89	0.91 ± 0.19	1.47 ± 0.59
Overall	49.62 ± 6.05	0.94 ± 0.05	3.31 ± 0.66

of 92 ± 0.05%. Estimated population size (from monthly estimates) was significantly larger throughout 2002 than in 2001 (ANOVA: $F_{2, 24} = 4.38$, $p = 0.02$), but did not differ between 2002 and 2003. Although monthly survival probability did decline slightly in 2003, there was no significant difference between the three years of the study ($F_{2, 24} = 2.57$, $p = 0.09$). The number of animals joining the population did not differ between years ($F_{2, 23} = 2.35$, $p = 0.12$). None of the three key demographic variables showed any within year or seasonal variation (ANOVA: $p>0.1$ in all cases).

AGE-SPECIFIC SURVIVAL

Probability of surviving to the next age class was strongly related to age in both male ($R^2 = 0.82$, $p = 0.006$, df = 8) and female ($R^2 = 0.76$, $p = 0.01$, df = 8) possums (Fig. 3.2). Survival increased with age in both sexes, reaching a plateau at age three in males and age four in females. Annual probability of survival declined from age five in both males and females, although the decline was considerably more pronounced in males.

BODY MASS AND CONDITION

Body mass was strongly correlated with age in male ($R^2 = 0.71$, $p = <0.0001$, df = 84) and, to a lesser degree, in female possums ($R^2 = 0.47$, $p = <0.0001$, df= 76). The relationship was best described by a second order polynomial, with mass increasing to a peak, but then declining in old age; however the form of the relationship differed between the sexes (Fig 3.3). Males reached peak adult body mass between 4-6 years of age at a mean mass of 1.87 ± 0.03 kg, while females attained peak body mass at a slightly older 5-7 years, averaging 1.68 ± 0.03 kg. Males were significantly heavier than females at their respective peak masses (ANOVA: $p<0.0001$; post-hoc t-test = -4.6, $p <0.0001$, df = 57). An analysis of covariance, testing for a difference between rate of

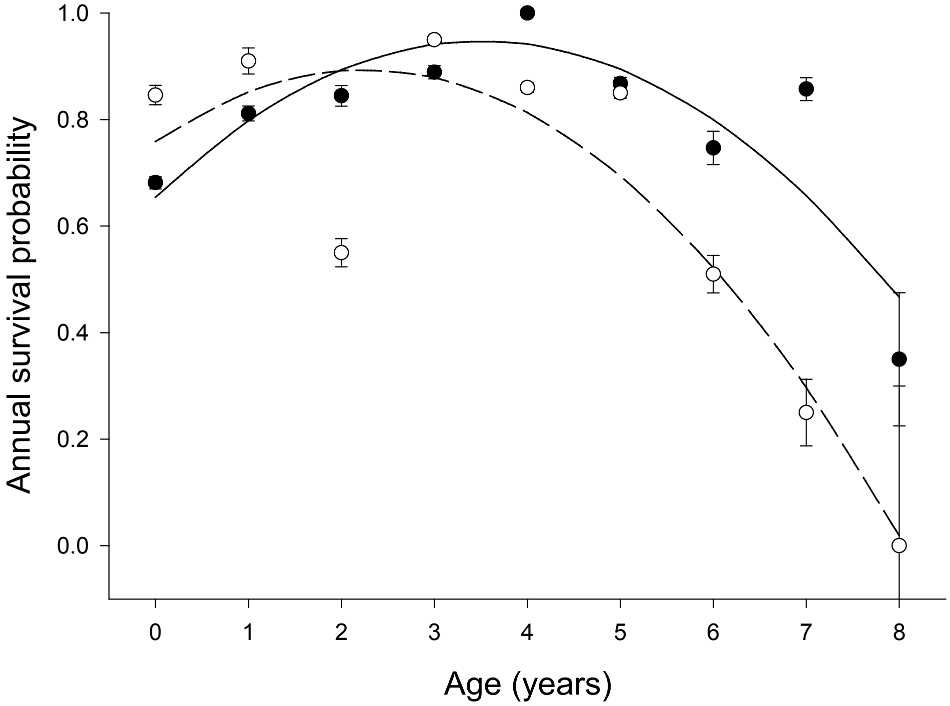

Figure 3.2: Survival probability curves for male (dashed line) and female (solid line) possums at the Magnetic Island study site. Curves are fitted using a second order polynomial regression (see text for statistics). Error bars show standard error of proportion surviving (Zar 1999).

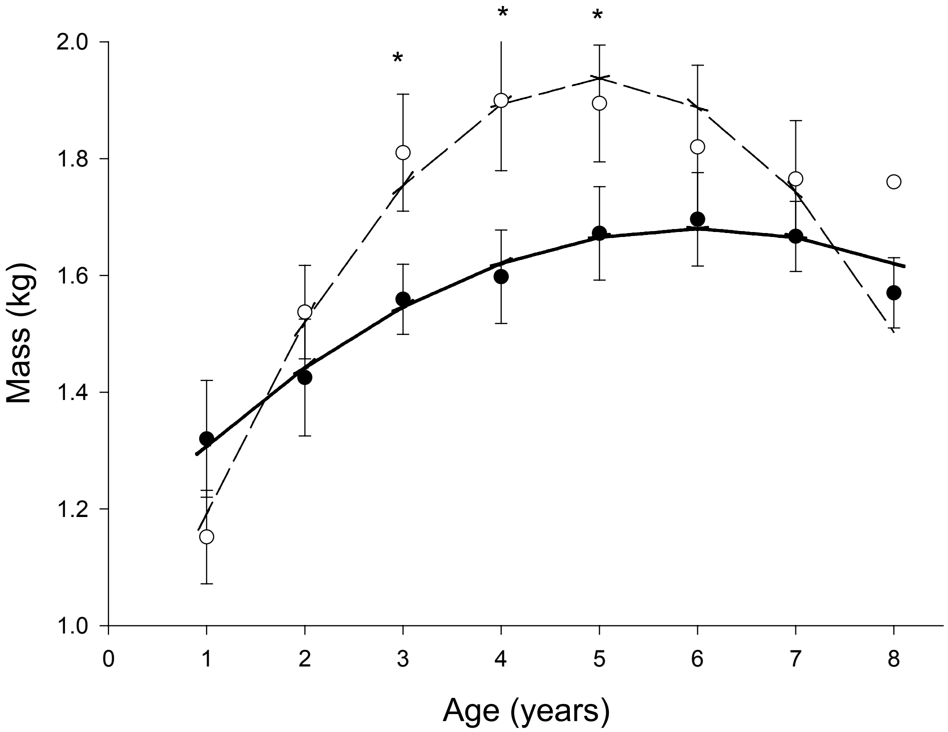

Figure 3.3: Relationship between body mass (kg) and age in male and female possums. Curves are predicted values using a second order polynomial regression. The solid black line shows the curve for females, mean values for each age group by black circles. Male possums are denoted by the dashed line and mean values by open circles. Error bars show 95% confidence limits. Pair-wise comparisons between males and females that are significantly different are denoted by an asterix.

increase in mass to 5 years, found an interaction between sex and age, indicating that the rate of increase in body mass up to the age of five was significantly different between the sexes (Table 3.2; Fig 3.4).

Body condition was also related to age in male ($R^2 = 0.37$, $p < 0.0001$, df = 84) and female ($R^2 = 0.40$, $p < 0.0001$, df = 78) possums. While the relationship was best described by a second order polynomial regression for both sexes, condition showed a steep decline after age five in males, while the decline in females was much less pronounced (Fig 3.5). Due to the large confidence limits, there was no significant variation between the sexes in body condition at any age (ANOVA: $p > 0.1$). The adult sex ratio (animals ≥ 3 years of age) was significantly female biased (46 males: 60 females, Binomial test: p = 0.03).

Body mass (Fig 3.6) and body condition (Fig 3.7) also showed seasonal variation in both males and females. Seasonal patterns of change in mass and condition differed between the sexes; compared to January/February, male possums showed a significant decline in mass (t = 2.42, p = 0.02, df = 89) and condition (t = 2.15, p = 0.03, df = 89) in March/April, while females continued to gain mass and condition during this period. Mass (t = 3.07, p = 0.003, df = 102) and condition (t = 2.86, p= 0.005, df = 101) in females declined significantly in September/October, compared to the May/June period, while males remained relatively constant at this time of the year.

REPRODUCTIVE TRAITS

Mean age at first reproduction in female possums was 1.91 ± 0.66 years, ranging from 1-3 years of age. Primiparity occurred at a mean body mass of 1.39 ± 0.06 kg and mean body condition of 0.87 ± 0.03. There was no evidence that females which bred or attempted to breed as yearlings (n = 4) were heavier (t = -0.31, p = 0.7, df = 14) or in better condition (t = 0.11, p = 0.9, df = 11) than one year olds which did not breed (n = 16).

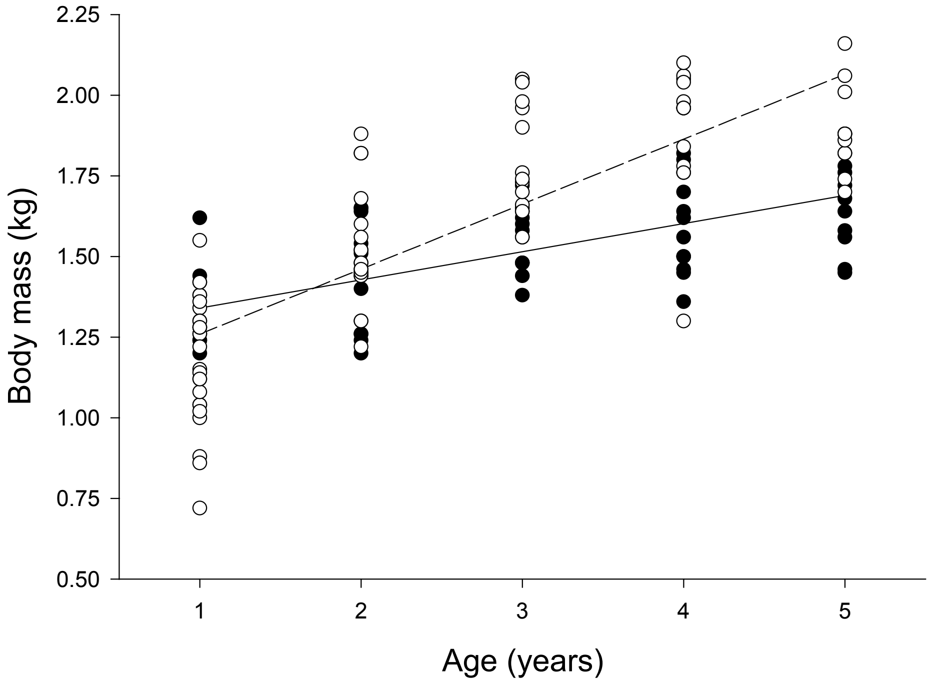

Figure 3.4: The rate of body mass (kg) increase in male (open circles, dashed line) and female (filled circles, solid line) possums up to the age of five. Lines are those fitted from a least-squares linear regression on the sexes separately.

Table 3.2: Results of an analysis of covariance to test for different slopes in increase in body mass in male and female possums.

Source	**df**	**F**	**p**
Age	1	145.45	<0.0001
Sex	1	6.65	0.01
Age*Sex	1	22.74	<0.0001

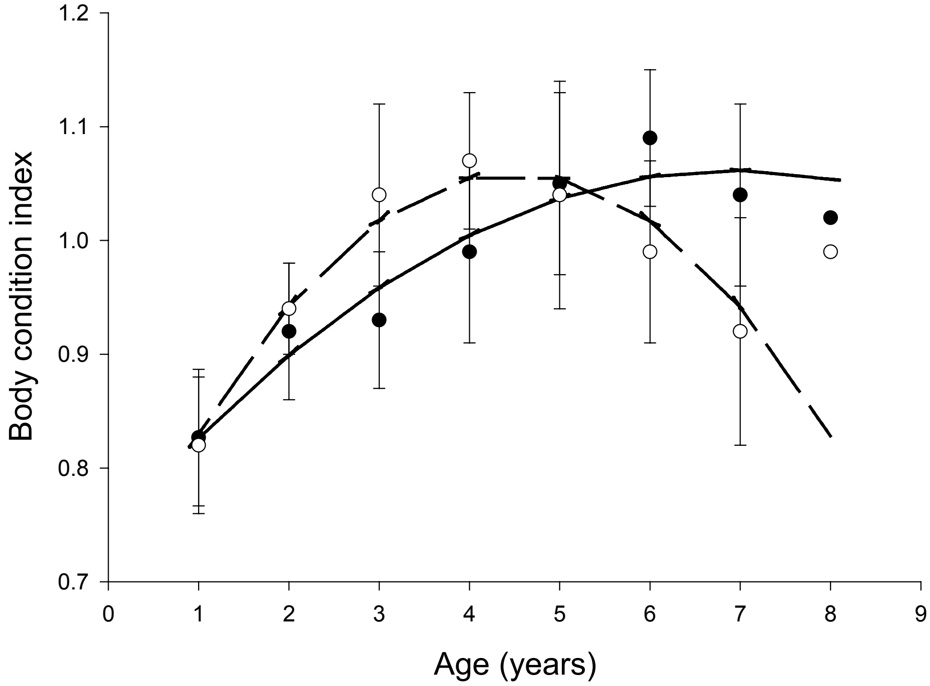

Figure 3.5: Relationship between body condition and age in male and female possums. Curves are predicted values using a second order polynomial regression. Females are shown by a solid black line, mean values for each age group by black circles. Male possums are denoted by the dashed line and mean values by open circles. Error bars show 95% confidence limits.

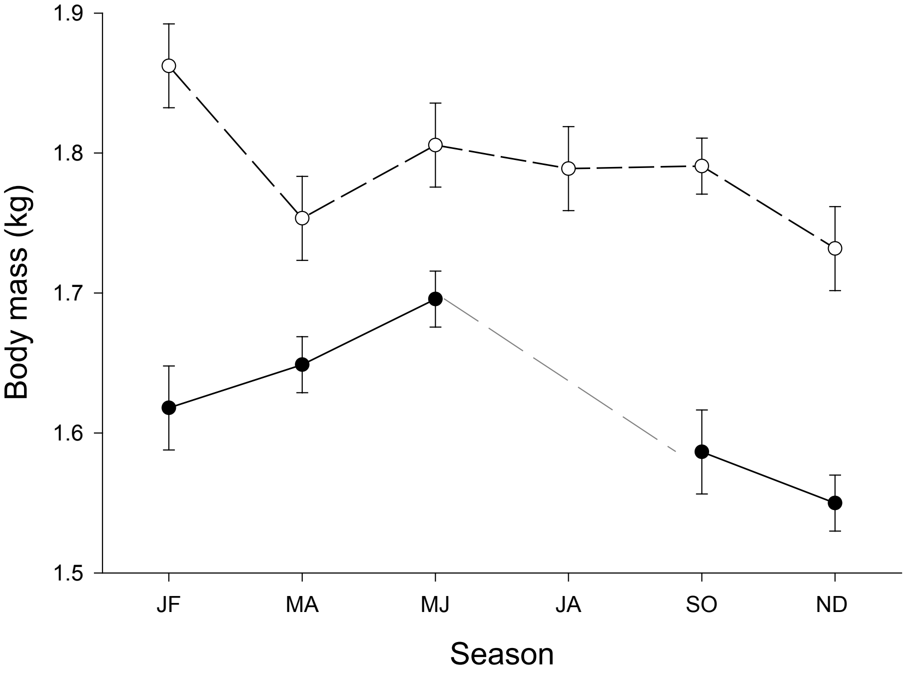

Figure 3.6: Variation in mean body mass during the year in male and female possums. Female possums are shown by the black solid line and filled circles (dashed area = lactation), males are shown by the dashed line and open circles. Error bars show standard error of the mean.

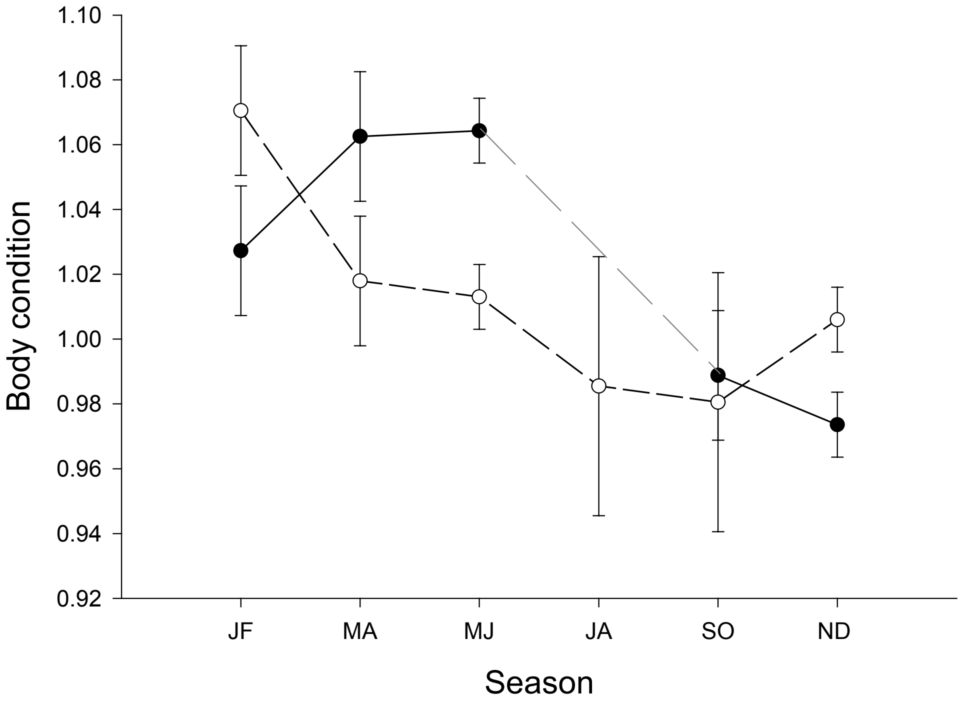

Figure 3.7: Variation in mean body condition during the year in male and female possums. Female possums are shown by the black solid line and filled circles (dashed area = lactation); the dashed line and open circles show males. Error bars show standard error of the mean.

All sexually mature females gave birth to at least one pouch young each year and produced only one offspring per reproductive event. The majority of females were found to give birth to their first offspring in the autumn months of April and May, while a smaller, second peak of births occurring in early spring was found to be due primarily to a few females giving birth to a second young after successfully raising a first (Fig 3.8). During the three breeding seasons, females gave birth to an average of 1.23 ± 0.05 (n = 64) offspring per year, mortality of pouch young during lactation was 17%.

In males, testis length was non-linearly related to age (Fig 3.9: $R^2 = 0.65$, $p < 0.0001$, df = 80), with the majority of males reaching sexual maturity at 3 years of age; testis length was >18mm from 3 years onwards. Beyond three years of age there was no relationship between testis length and age ($R^2 = 0.0002$, $p = 0.75$, df = 43), body mass ($R^2 = 0.02$, $p = 0.35$, df = 55) or condition ($R^2 = 0.01$, $p = 0.35$, df = 56). At sexual maturity (3 years) mean body mass was 1.8 ± 0.05 kg; mean condition was 1.05 ± 0.03. Seasonal variations in testis length were found to correspond broadly with the seasonal pattern of births (Fig 3.10), but were not statistically significant (ANOVA: $p > 0.05$ in all cases).

Discussion

AGE-SPECIFIC MASS, CONDITION AND SURVIVAL

Body mass, body condition and survival showed similar age related patterns and all three declined in animals aged 6 and older, with the decline being more pronounced in male animals. This suggests that, like many long-lived mammals, possums undergo senescence – an increase in age-specific mortality, associated with degenerative changes within an individual (Pistorius & Bester 2002). While the evolutionary causes of senescence are still under debate (Packer et al. 1998), the occurrence of senescence is likely to have important implications for age-specific patterns of reproductive effort in females and mating effort in males.

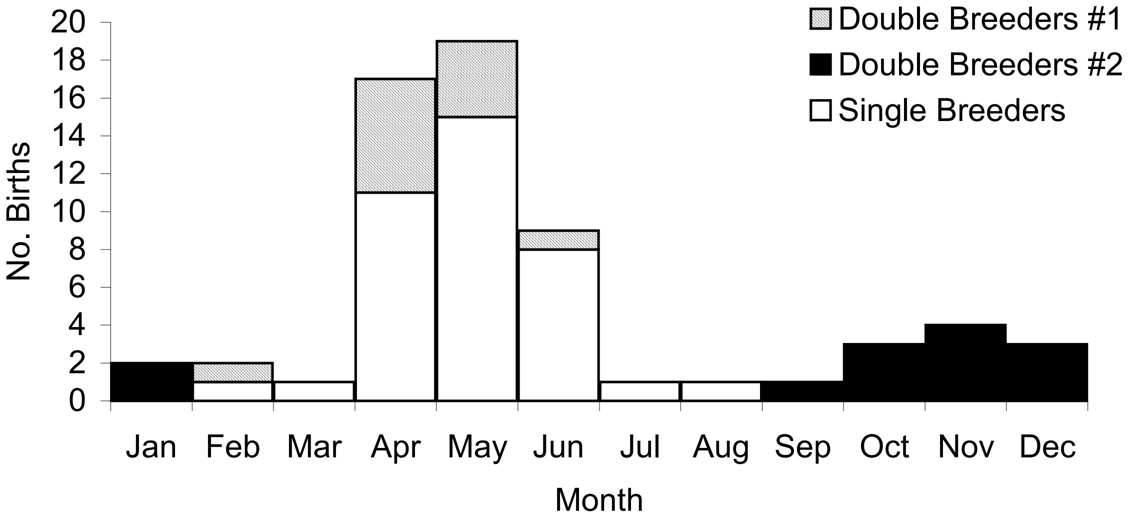

Figure 3.8: The number of births occurring in each month at the Magnetic Island site. Single breeders are shown by open columns, first offspring of double breeders by grey striped columns and second offspring of double breeders by black columns.

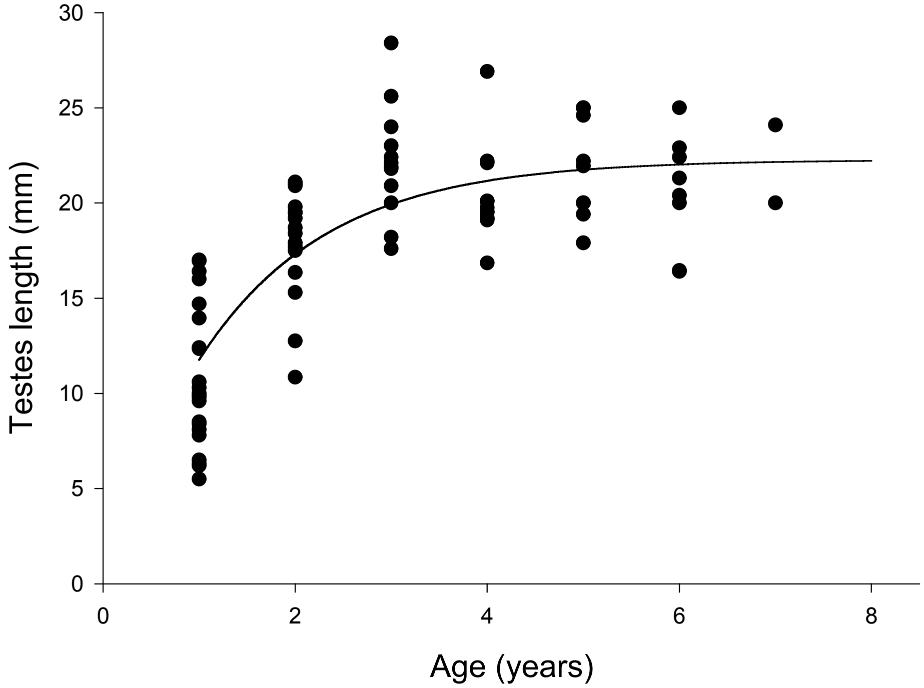

Figure 3.9: The relationship between age and testis length (mm) in male possums. Actual data points are shown by filled circles, the regression line is fitted with an exponential rise to maximum curve (2 parameter).

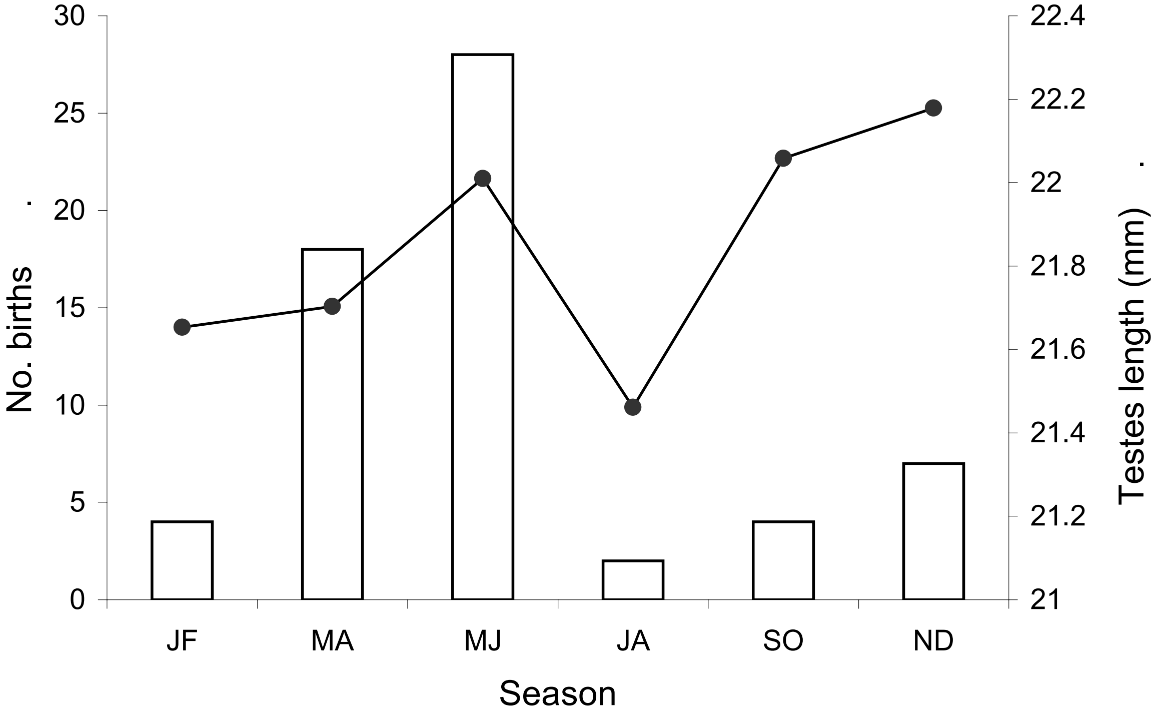

Figure 3.10: Annual variation in testis length (mm) shown by the black line, compared to annual variation in births (open columns) at the Magnetic Island site.

At their peak adult body mass, male possums were significantly heavier than females. Male-biased sexual dimorphism in adult body mass is a common phenomenon among mammalian taxa and is often indicative of sexual selection favouring larger males (Trivers 1972). Dimorphism in body mass suggests that adult males compete for access to receptive females, resulting in a polygynous mating system where disparity in mating success is associated with phenotypic variation among individuals (Krebs & Davis 1981). A polygynous mating system and sexual dimorphism are likely to influence other life history variables such as the offspring birth sex ratio (Trivers 1973) and variation in male reproductive success (Clutton-Brock et al. 1982). In many mammals, male-biased dimorphism appears to develop post weaning due to faster mass gain by males (Festa-Bianchet et al. 1996). This appears to be the case in possums, as the results show that males gained mass at a significantly greater rate than females up to the age of five, resulting in greater adult body mass. Assuming reproductive success is positively associated with body mass, the growth curve suggests that male possums should reach their peak reproductive success at age five. Previous studies have suggested that in sexually dimorphic mammals, there may be a cost to growing to and maintaining a larger body size (Owen-Smith 1993; Key & Ross 1999). The results show some support for this idea as there was a more rapid decline, in comparison to females, in body mass, condition and survival in males older than five, concurring with the observed female-biased adult sex ratio.

Compared to males, female possums showed a slower, less steep gain in mass and condition in relation to age. The mating success (but not necessarily reproductive success) of female mammals is commonly less dependent on body size compared to males and the results of my study are consistent with the prediction that females should adopt a more conservative growth strategy and invest resources into reproduction rather than body growth (Trivers 1972; Clutton-Brock et al. 1982). Yearling females were found to be slightly heavier than males of the same age. Like the majority of mammals, *T. vulpecula* show male biased dispersal, with sub-adult males dispersing from the maternal home range at about six months of age (Clout & Efford 1984). Although the difference in mass was not significant, it may be indicative of a cost of dispersal in young males (Byrom & Krebs 1999). Philopatric female offspring may also benefit from an increased period of maternal care and settling within their natal home range.

SEASONAL VARIATION IN MASS AND CONDITION

Males declined significantly in mass and condition in the two months prior to the onset of the main birth period. Winter (1976) observed that male *T. vulpecula* perform consort behaviour - the persistent following of an oestrus female for up to 30 days prior to mating, and also noted that males often failed to stop and feed during this time. This indicates that males may have to make a trade-off between foraging and reproductive success. Alberts et al. (1996) similarly found that mate guarding behaviour resulted in a decline in foraging activity in male baboons *Papio cynocephalus*.

Contrary to the pattern found in males, females increased in mass and condition prior to the onset of the main breeding season, but lost considerable mass and condition during the lactation period. These seasonal fluctuations imply that possums are capital breeders, acquiring resources in advance of breeding and relying heavily upon body reserves to raise offspring during the lactation period (Jönsson 1997; Andersen et al. 2000). This suggests that, to some degree at least, reproductive success in female possums will be mass dependent and this is supported in recent work by Ramsey et al. (2002), who found that relative body mass was a primary determinant of reproductive success in female possums in New Zealand.

REPRODUCTIVE STRATEGIES

Large variation was found in the age of onset of reproduction in females and, since survival declines after about 6.5 years in female *T. vulpecula*, this is likely to contribute considerably to variation in female LRS and individual fitness. Life history theory predicts that there will be a trade-off between early reproduction and future survival and reproductive success (Stearns 1992; Lambin & Yoccoz 2001). However, while some studies have found support for the costs of early reproduction (Lambin & Yoccoz 2001), others have found no such costs (Neuhaus et al. 2004). In iteroparous species, females should be predicted to delay sexual maturity if further growth and fecundity are associated with an increase in age-specific size and mass, outweighing the advantages of early maturation (Stearns 1992). Sæther & Heim (1993) found that age at maturity was related to body mass in female moose (*Alces alces*). This was not found to be the case in possums and while this analysis did suffer from a very small sample size of primiparous yearling females, Humphries & Boutin (1999) established that reproduction was independent of mass in primiparous eastern chipmunks (*Tamia striatus*). Other constraints on age at primiparity may include resource availability and adverse environmental conditions, resulting in a cohort effect and between-year variation in age at maturity (Becker 1998). Reproductive suppression of young females by conspecifics has been noted in some mammals (Cooney & Bennett 2000; Solomon et al. 2001), but it is currently unknown if this mechanism operates in populations of *T. vulpecula*.

Using testis length as an index of maturity, males appear to become sexually mature slightly later than females, at age 3. After 3 years of age, there was no relationship between age and testis length and little variation in testes size among individuals.

The breeding of female possums on Magnetic Island was highly seasonal, with a large percentage (>50%) of females giving birth in the autumn months of April and May. In seasonal environments, breeding is usually restricted to the part of the year when resources are most abundant and weaning of offspring coincides with a period of good food availability (Bronson 1989). Breeding synchrony can also occur in populations which show breeding seasonality, resulting in a tighter clustering of births than climatic seasonality alone would predict (Ims 1990). A seasonal breeding cycle and oestrus synchrony may have consequences for male reproductive success and the mating system of *T. vulpecula* on Magnetic island. Where females show a seasonal or synchronous breeding pattern, and when individuals are solitary and spatially dispersed, polygyny potential and variance in male reproductive success may be reduced (Emlen & Oring 1977). Smaller males can exploit the fact that more competitive males are involved in consorting and mating with females elsewhere (Say et al. 2001). Preston et al. (2003) also suggest that an advantage of larger testes will be most evident when the number of oestrous females increases, such as during synchronous and/or seasonal breeding. This is supported by the fact that small variations in testes size do seem to relate broadly to the seasonal pattern of births in the population.

Bi-annual breeding appears to be a rare occurrence among mammals and little studied. However, after successfully raising one offspring to independence during the main autumn breeding season, some female possums produced a second young later in the year. Although double breeding in *T. vulpecula* has been noted by a number of other authors (Kerle 1984), the causes and consequences of this behaviour have not been rigorously investigated. It is likely that this strategy will contribute the highest source of variation in LRS in females, since a female can essentially double her annual reproductive output by double breeding. Life history theory predicts that when females invest more in current reproduction, they should show an associated decline in future reproductive success and survival, and double breeders may therefore demonstrate a reduction in future fitness. However, in investigating the fitness costs of double breeding in little penguins (*Eudyptula minor*), Johannesen et al.

(2003) found the converse, instead identifying positive correlations between life history traits and suggesting that their results provide evidence of a quality difference among individual birds.

In conclusion, the results indicate significant variation among individuals with respect to a variety of life history traits and this variation is likely to have important consequences for individual fitness, LRS and population dynamics. In particular, the age-specific patterns of change in body mass, condition and survival identified in both male and female possums are predicted to influence reproductive strategy and success. Differences between the sexes in size, survival and seasonal variation in mass loss are also expected to have implications for mating system and sex-specific reproductive tactics.

CHAPTER 4

Terminal reproductive effort in females

(Submitted for publication [*Biology Letters*], co-authored with Dr. Chris Johnson)

Introduction

For females, reproduction involves the expenditure of maternal energy, which may have negative effects on the mother's own growth, survival and future reproductive success (Stearns 1992). The level of energy investment in any given reproductive attempt should therefore reflect a trade-off between the benefits of reproduction in terms of surviving offspring produced, and the costs in terms of reduced potential for future reproduction. The residual reproductive value (RRV) hypothesis proposes that offspring should become more valuable to a mother as the number of future potential offspring she can produce declines as she ages (Williams 1966). Therefore, as female's age, the trade-off between investment in current and future reproduction should be increasingly resolved in favour of high reproductive effort (RE) in the current breeding attempt and RE should increase steadily with maternal age (Williams 1966; Clutton-Brock 1991; Forslund & Part 1995). If risk of mortality rises abruptly at a particular stage of life, theory predicts a large increase in expenditure in reproduction, and an associated decrease in allocation of resources into somatic reserves, before that age (Pianka 1988; Polak & Starmer 1998).

Predictions for age-specific maternal RE should apply especially well to mammals, because they are iteroparous, undergo terminal senescence (Packer et al*.* 1998) and reproduction involves large expenditures of energy by the female (Clutton-Brock 1991). In addition, because most mammals have determinate growth, the ability of females to transfer energy to offspring is more-or-less constant with age, leaving the trade-off between current and future reproduction as the main determinant (in theory) of RE. However, studies of RE in mammals typically do not show increases with age, with RE often declining slightly in the oldest females (Cameron et al*.* 2000; Côté & Festa-Bianchet 2001; Weladji et al*.* 2002). In some cases, offspring of older females have higher survival rates (Cameron et al*.* 2000; Clutton-Brock 1984), but this may be due to the superior mothering skills of experienced females rather than to greater energy investment in offspring (Cameron et al*.* 2000; McMahon & Bradshaw 2004). Overall, RE is often remarkably constant with age in these studies on eutherians.

In this chapter, I test the prediction that females should show an increase in maternal effort, and an associated decline in somatic investment and survival, with increasing age, in female possums on Magnetic Island. Both this study (Chapter 3) and previous studies (Brockie et al*.* 1981; Efford 2000) have determined that females live to an average age of six and that survival decreases markedly after this age. Any effects of reproductive senescence should therefore be minimal compared to longer lived species, such as ungulates, which often live through a number of senescent years when reproduction is impaired or ceases completely (Berube et al*.* 1999; Packer et al*.* 1998).

Methods

Data were collected during three breeding seasons on Magnetic Island (2001-2003). All females and offspring were weighed, measured and aged as described in Chapter 3. Date of parturition for the first offspring of the year is expressed as days from 1st April in any given year and was assessed by assigning a date of birth to their offspring and growth of pouch young during the lactation period was estimated using measurements of head length (Chapter 3).

Mass change prior to parturition and during the lactation period was calculated for individual possums as change from mass at parturition, standardised to 0 for each female. I used a measure of RE based on relative mass loss, determined as the percentage of mass lost during the lactation period. Pre-breeding body mass was taken the month prior to parturition, post-lactation mass was taken the first month a female was caught without a dependent offspring. If a female was not caught within 4 weeks of estimated offspring independence, her post-lactation mass was not included in the data. RE was also calculated for those individuals that produced an offspring but failed to raise it to independence.

During the study, between 0 – 40% of females each year gave birth to a second young in spring (see Chapter 3) and for analysis involving annual reproductive effort the sum of both reproductive events was used for these mothers. Only females that raised their first young to independence were included. Lactation for second offspring occurred during the summer months of November - March, when all animals increase in mass (Chapter 3). In order to combine RE values from these two periods, I therefore corrected for a 0.09kg mass gain during summer (mean mass gain for non-lactating adult females during November-March). Second offspring were excluded from analysis involving offspring mass at 12 months, due to the potentially confounding effect of them reaching independence during autumn, rather than in spring. Male yearlings were also excluded from this analysis, since the majority of sons had dispersed before they reached 12 months of age; age at dispersal in males can be mass dependent (Holekamp 1984) and those few males that remained at the site (n=5) as yearlings were therefore likely to be a biased sample.

All initial analyses included maternal identity as a random variable to account for repeated observations of females contributing more than one offspring to the data set; 10 females were sampled in all 3 years, 9 females were sampled in 2 years, and 12 were sampled in one year only. All raw data on body mass, maternal age, reproductive effort and date of parturition (of first offspring of the year) conformed to a normal distribution (Shapiro-Wilk W test; $p > 0.1$ in all cases).

I used mixed models incorporating random effects to test for the influence of female age on reproductive effort, date of parturition and the probability of double breeding (SAS 1995).

For some analyses, females were categorised into three age categories; primiparous (1-2 year olds), middle-aged (3-5 year olds) and old (6+), based on observed life span, growth pattern and reproductive parity. Differences in the probability of producing two offspring in a year were analysed with binomial tests; observed probabilities within each maternal age class were compared to that predicted by the population as a whole using Fishers exact test.

Results

During the study, a total of 31 females produced 79 offspring. There was no effect of maternal identity on any of the primary variables (date of parturition: $p = 0.47$; maternal effort: $p = 0.58$; probability of double breeding: $p = 0.23$), and maternal identity was excluded from further analyses.

Individual females changed mass considerably during the breeding season and weighed significantly less at the end of lactation ($\bar{x} = 1.56 \pm 0.04$ kg) than they did at parturition ($\bar{x} = 1.76 \pm 0.04$ kg; paired t-test: $t = 7.98$, $p < 0.0001$, $df = 11$). Rate of mass loss during late lactation coincided with the rapid growth of pouch young during this time (Fig 4.1, see also Chapter 2, Fig. 2.2).

Females lost a mean of 6.59 ± 6.61% of their pre-breeding body mass during lactation. RE, in terms of percent mass loss, differed among female age classes. This relationship was best described by a third order polynomial regression (Fig. 4.2a; $R^2 = 0.27$, $p = 0.002$, $F_{3, 49} = 5.54$). RE was low in females breeding for the first time, stable during the next three years of life, and then increased during the last three years. RE was significantly different between each of the three maternal age groups (Fig. 4.2b; $F_{2, 46} = 46.48$, $p = <0.0001$). RE in females was significantly positively related to the mass of their offspring at 12 months of age (Fig. 4.3; $R^2 = 0.80$, $F_{1, 10} = 35.96$, $p = 0.0002$). There was no independent effect of maternal age on offspring mass ($p > 0.5$) and no evidence that RE as a middle-aged mother influenced the probability of a

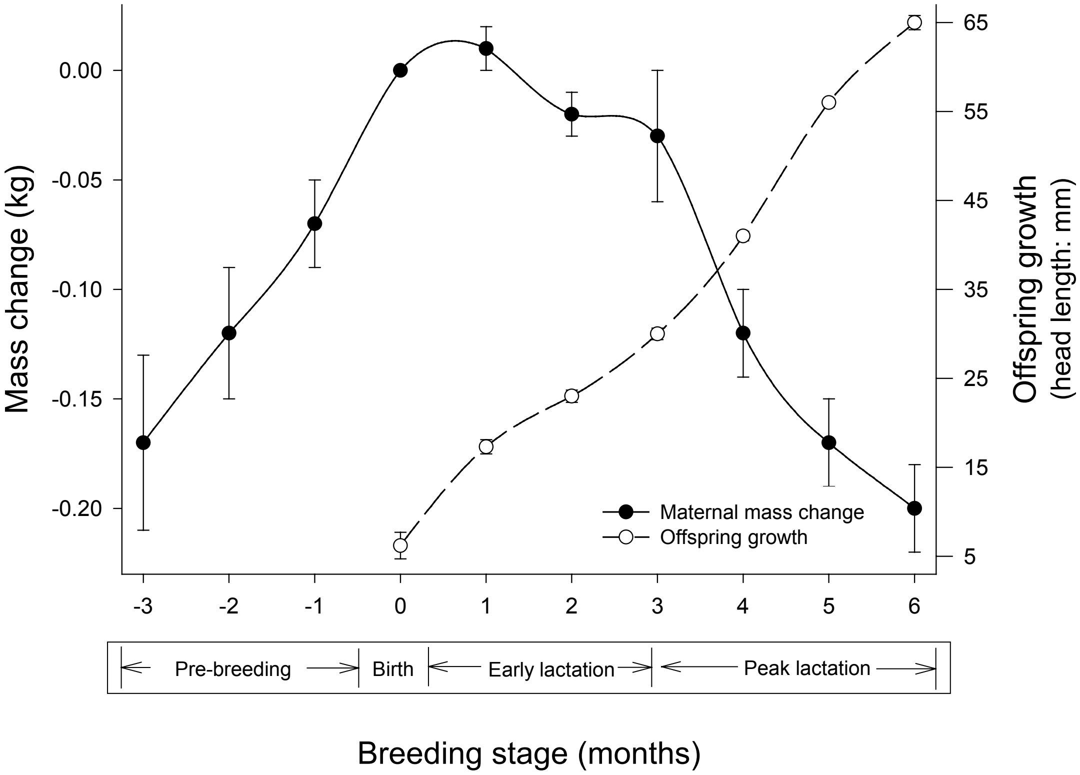

Figure 4.1: Graph demonstrating change in maternal body mass (kg ± SE), and offspring growth (mm ± SE), during the breeding season in *T. vulpecula* on Magnetic Island.

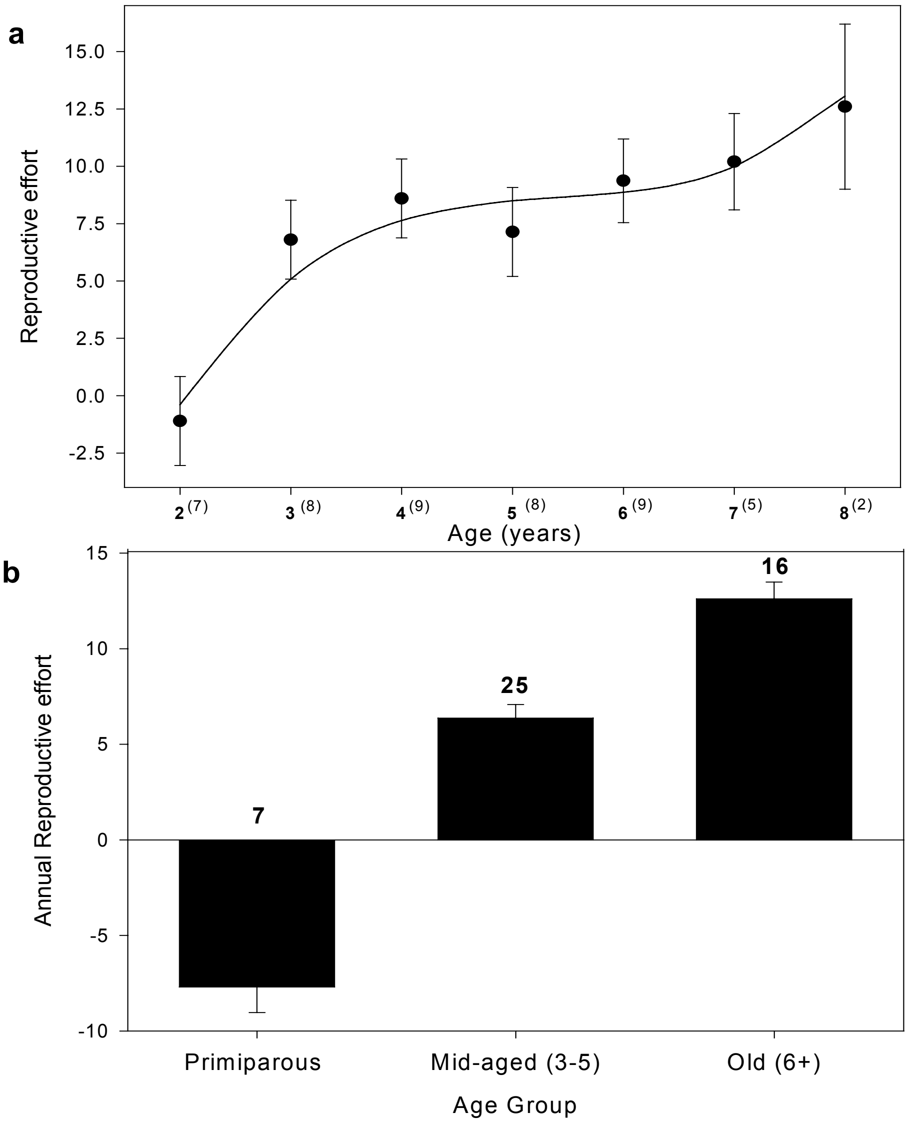

Figure 4.2: **a**, The relationship between maternal age and reproductive effort. Circles show mean RE for each age (±SE), line fit – third order polynomial regression. Samples sizes shown in brackets on x-axis. **b,** Annual reproductive effort for each maternal age group. Columns show mean values (+SE), samples sizes are shown above columns.

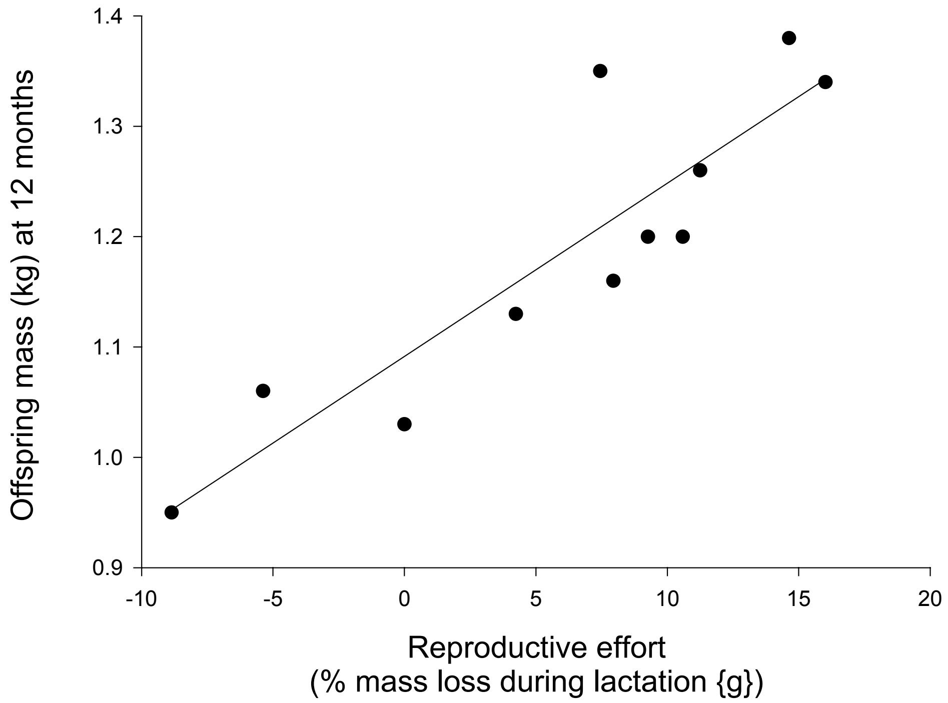

Figure 4.3: Linear regression demonstrating the relationship between reproductive effort and offspring mass at 12 months (in female offspring only, see text). Regression line fitted using a least-squares linear regression model.

female surviving into the old age class (logistic regression: $\chi^2 = 0.87$, $p = 0.35$, d.f. = 1, $n = 22$).

The overall probability of an individual female giving birth to two offspring in any given year was 0.23. The proportion of females that produced two offspring in the old age group was significantly different from that predicted for the overall sample (Fig 4.4; binomial test: p = 0.004). This was not the case for the other two age groups (binomial test: p>0.1 in both cases). RE during the lactation period for the first offspring of year did not differ between single ($\bar{x}$ = 6.77±1.33g, n = 24) and double ($\bar{x}$ = 8.04±1.96g, n =11) breeders (t = -0.53, p = 0.6, df = 33) and double breeders did not vary their maternal effort between first ($\bar{x}$ = 8.3±1.2g) and second ($\bar{x}$ = 7.8±1.2g) offspring (paired t-test; t = 0.27, p = 0.79, df = 7).

Parturition date differed between maternal age groups; older females gave birth significantly earlier ($\bar{x}$ = 17.47±7.94 days, n = 17) in the season than both primiparous ($\bar{x}$ = 68.07±8.75 days, n =14) and mid-aged ($\bar{x}$ = 46.25±6.19 days, n = 28) females (Fig 4.5; ANOVA: F = 9.41, p = 0.0003, df = 58). Parturition dates of primiparous and mid-aged females did not differ significantly. Date of parturition of first offspring of the year tended to be earlier in females which went on to produce a second young ($\bar{x}$ = 27.13+10.14 days), compared to those mothers which produced only a single young ($\bar{x}$ = 48.5± 7.55 days: t = 1.7, p = 0.09, df = 40).

Discussion

MATERNAL MASS LOSS DURING LACTATION

Individual females showed a pattern of mass change through the lactation cycle that indicated that body fat stores were mobilised to meet the energy requirements of reproduction. Females gained mass prior to parturition, body mass was then maintained or declined slightly during the first three months of

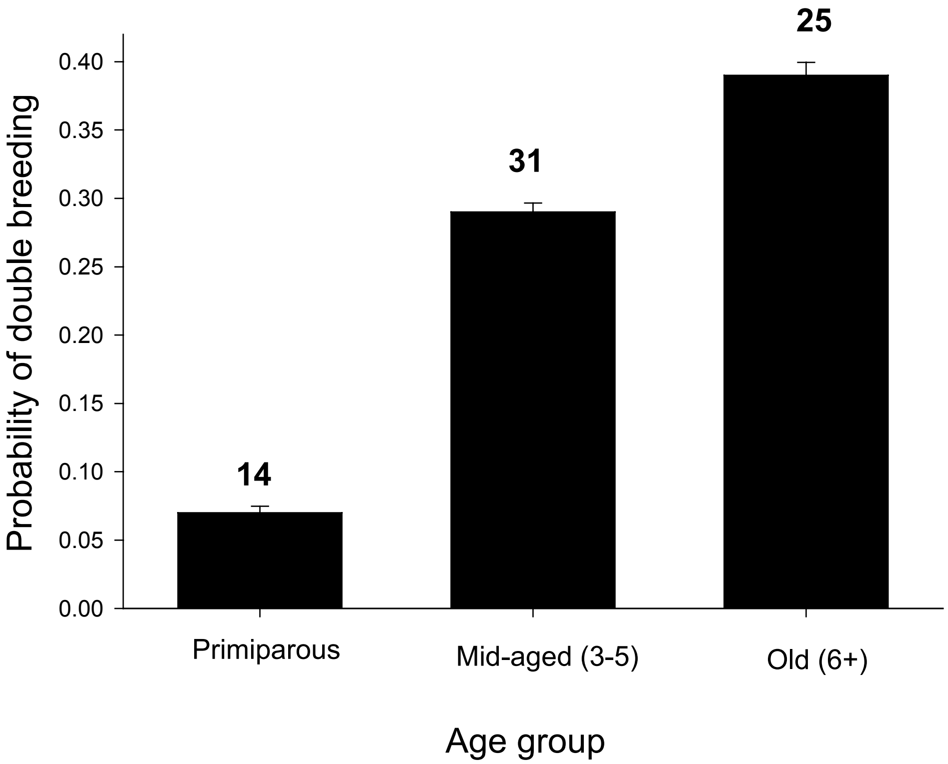

Figure 4.4: The relationship between maternal age group and the probability of double breeding in *T. vulpecula* mothers. Columns show the probability of producing two offspring/year for each age group (+ proportion SE). Samples sizes are shown above columns.

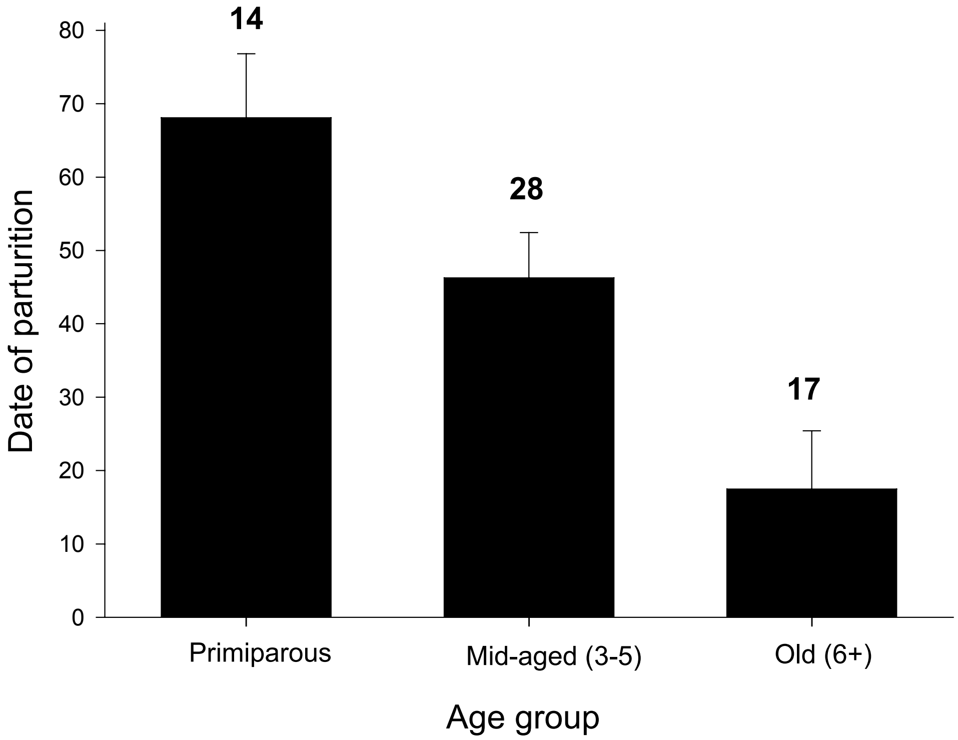

Figure 4.5: The relationship between date of parturition of first offspring (days from 1st April – i.e.: 0 = April 1st) and maternal age group in *T. vulpecula* mothers. Columns show mean values for each age group (+SE). Samples sizes are shown above columns.

lactation. Females lost mass rapidly during the final two or three months of lactation, coinciding with peak energy export in milk and rapid growth of offspring (Tyndale-Biscoe & Renfree 1987).

There was wide variation in the percentage of pre-breeding body mass that was lost by individual females during lactation, and this was closely related to offspring mass at 12 months of age. These data provide strong evidence that mass change during lactation was an accurate index of the effective transfer of energy from mother to offspring; females with the highest rates of mass loss in lactation produced yearling offspring more than 50% heavier than females with minimal mass loss and there is evidence from a variety of mammalian species that heavier offspring often can sustain an advantage throughout their life (Bernardo 1996)

AGE SPECIFIC MATERNAL STRATEGIES

Variation in somatic investment

For females aged 6 or older, reproductive effort increased in an almost linear fashion. Body mass, condition and survival decline in female *T. vulpecula* after the age of six, in both this population (Chapter 3) and others (Efford 2000). Thus, the results are consistent with the terminal reproductive investment hypothesis, which predicts that an increase in reproductive investment in old age should be associated with a decline in somatic investment and survival (Pianka 1988).

Data on changes in RE with age may be confounded by the possibility that older females are larger or more physiologically competent for reproduction, and therefore better able to sustain higher levels of energy transfer to offspring without incurring associated large costs. However, my data demonstrate that while females increased RE in old age, body mass and condition show a general decline after the age of six (Chapter 3). This suggests that old females are no more able to withstand high rates of energy transfer during lactation than young females, and that increased RE produces an underlying decline in body condition. If those females which demonstrated high RE at middle-age were also more likely to survive to old age, this would result in a predominance of these 'high quality' females in the old age group and also provide an alternative explanation for our result. However, I found no evidence to suggest that this occurred in the Magnetic Island population.

While the total amount of energy needed to produce a weaned offspring is similar in marsupial and eutherian mammals (Krockenberger et al. 1998), the costs of gestation are significantly greater for the placental mother (Hsu et al. 1999). Parent-offspring conflict during the eutherian gestation period is thought to favour offspring, as placental hormones are predicted to manipulate maternal resources for foetal benefit (Haig 1993; Haig 1996). Furthermore, in eutherians, an increase in offspring demand during lactation can also result in an increase in milk production (Park & Jacobson 1993), while experiments in macropods have shown that milk production in marsupial mothers is relatively unresponsive to changes in suckling stimulus (Findlay & Renfree 1984; Trott et al. 2003). In placental mothers then, offspring appear to be able to manipulate maternal energy transfer in their favour both during gestation and, to a lesser degree, during lactation. Conversely, marsupial mothers seem have dominant control over both the rate of milk production and milk composition, irrespective of variation in offspring demand (Trott et al. 2003). The difference in the way that energy is transferred from mother to offspring between the two groups may go some way to explaining why previous studies on age-specific RE focussing on eutherian mammals have failed to produce clear conclusions.

Double breeding

The oldest females in the population were also more likely to double breed than young or mid-aged mothers. Females that successfully raised two offspring essentially doubled their annual reproductive output and, for old females whose probability of future survival and reproductive success is rapidly declining, double breeding is likely an important strategy in maximising lifetime fitness. The probability of double breeding (laying two clutches in one year) has also been shown to increase with parental age in little penguins (*Eudyptula minor*: Johannesen et al. 2003). Older mothers were similarly more likely to foal in consecutive years in a population of feral horses (*Equus caballus*: Cameron et al. 2000). However, the authors suggest that in this case, older females invested less in individual offspring and were therefore in better condition to foal the following year (Cameron et al. 2000). This was not the case in our population; females which double bred did not show lower rates of reproductive effort in their first offspring than single breeders, nor did they vary their effort between first and second offspring.

Date of parturition

Old females also demonstrated a significant advance in the date of parturition of their first offspring. There is evidence from eutherian mammals that an early date of birth can benefit offspring, in both the long and short-term, through a number of avenues other than direct energy transfer (Clutton-Brock et al. 1987a; Green & Berger 1990; Green & Rothstein 1993). In this population, there was also some evidence that females which double bred gave birth to their first offspring earlier in the season than those that produced a single offspring and thus in *T. vulpecula*, an early date of parturition may also be an adaptive strategy allowing females to fit a second offspring into a single year. In little penguins, second breeders also gave birth to their first clutch of eggs earlier than pairs that bred only once (Johannesen et al. 2003).

In conclusion, my study shows that a marsupial reveals a high degree of variability in age-specific RE, providing an excellent test of a general theory of adaptive variation in maternal reproductive effort. Females in the oldest age groups appear to combine three strategies to increase their overall maternal effort; first, RE in each breeding cycle increased late in life; secondly, the probability that a female will breed a second time late in the year also increases in old females and third, older females also begin breeding earlier in the year. Thus, old females increased both the number of offspring produced per year and thus their annual reproductive effort, and their level of investment in each individual offspring.

CHAPTER 5

Adaptive sex allocation in relation to maternal life history

(In press [*Journal of Animal Ecology*]; co-authored with Drs. Chris Johnson & Andrew Krockenberger)

Introduction

That natural selection may favour maternal control of offspring sex continues to be a widely debated and controversial topic in evolutionary biology (e.g.: Hewison & Gaillard 1999; Saltz 2001; Cameron & Linklater 2002; Carranza 2002; Hewison et al. 2002; Saltz & Kotler 2003). Fisher (1930) predicted that natural selection should favour an equal sex ratio at birth because if one sex is rare, it gains a frequency dependent mating advantage. However, a critical assumption of Fisher's model - that sons and daughters are equally costly for a mother to produce - is not met in most polygynous mammals where sons are often larger than daughters at the end of lactation (Kojola 1998) and the costs of rearing male offspring are thought to exceed those of rearing a female (Clutton-Brock et al. 1981).

Trivers and Willard (1973) proposed that maternal condition could influence the sex ratio of offspring in dimorphic polygynous mammals. They argued that females in good condition would produce larger offspring which, if male, would have disproportionately high mating success. Thus females who adjusted offspring sex in relation to their own condition could have more grand-offspring. The Trivers Willard (TW) model is dependent upon three key assumptions; 1, offspring condition/phenotype is correlated to the condition/phenotype of its mother; 2, differences in offspring condition endure into adulthood; 3, in polygynous mating systems with high variance in male reproductive success, adult males benefit more than females from an advantage in condition (see reviews in: (Clutton-Brock & Iason 1986; Cockburn 1990; Hewison & Gaillard 1999). Cameron and Linklater (2002) further propose that the TW model makes two explicit predictions; i) that females in good condition should favour male offspring and ii) that mothers in poor condition should produce more daughters.

The local resource competition (LRC) hypothesis (Clark 1978) proposes that competition for resources between mothers and philopatric offspring imposes a cost of producing offspring of the philopatric sex. This hypothesis predicts that when offspring of one sex remain philopatric and the other disperses, females should bias offspring sex ratios toward the dispersing sex to avoid ecological competition with their offspring. The great majority of mammals show female philopatry, while males disperse and therefore, according to the LRC model, if resources are limiting females should be expected to produce a male biased primary sex ratio (Johnson 1988; Cockburn 1990; Dittus 1998).

In the past, the TW and LRC models of adaptive sex ratio adjustment in mammals have often been considered as competing alternatives (Dittus 1998; Saltz 2001) and researchers have attempted to fit their results into the framework of one or the other of these two models. However, while many studies have found strong evidence for either TW or LRC effects (e.g.: Austad & Sunquist 1986; Hewison 1996; Johnson et al. 2001) other results have been more equivocal and conclusions have seldom been straightforward (e.g.: Kruuk et al. 1999; Bonenfant 2003). Furthermore, assumptions that underlie the models are often not addressed in studies that set out to test them (Cockburn et al. 2002).

Recently it has been suggested that it is inappropriate to assume that a single selective pressure is responsible for generating sex ratio biases and it is more likely that several selective pressures may operate simultaneously to produce any particular bias or pattern of bias (Dittus 1998; Cockburn et al. 2002). Thus, results may reflect the sum of those pressures and, as a consequence, are likely to be inherently difficult to interpret (Cockburn et al. 2002).

The TW hypothesis considers sex ratios at the level of the individual while the LRC model is usually considered to be a process that operates at the level of populations or species (Ward 2003). However, LRC can also shape sex allocation through life history variation in individual females, as the duration of mother-daughter competition is influenced by maternal age (Dittus 1998; Cockburn et al. 2002). It might be predicted then that patterns of sex ratio bias will be influenced by age-related shifts in the importance of TW and LRC effects. LRC effects are expected to be more pronounced in young, primiparous females (Ward 2003), who are predicted to show a male bias in order to avoid the potential for lifetime competition with a philopatric daughter. A consequence of this may be that after producing a male bias early in life, females should show a shift or reversal in their sex ratio (Ward 2003). Older mothers might also be expected to produce more females, as they are less likely to live to compete with a surviving daughter (McShea & Madison 1986; Cockburn 1994). Maternal condition should also affect offspring sex ratios, particularly among older females who should be more likely to produce sons when in good condition.

In this chapter, I test these predictions in possums on Magnetic Island. Brushtail possums meet assumptions inherent of both the TW and LRC hypotheses; they have a polygynous mating system (Smith & Lee 1984) in which males compete for access to oestrus females (Winter 1976). There is male-biased sexual dimorphism (Isaac & Johnson 2003) and in Australian populations larger males have higher reproductive success (Clinchy et al. 2004). A number of studies have also shown that dispersal in *T. vulpecula* is male biased, while daughters are philopatric and settle in a home range which often overlaps or is adjacent to that of their mother (Winter 1976; Clout & Efford 1984; Johnson et al. 2001). Females produce only a single offspring at each reproductive event, so there are no complications due to effects of multiple offspring and mixed sex litters (Cockburn et al. 2002). Previous research on variation in offspring sex ratios among populations of *T. vulpecula* has shown that facultative adjustment of the sex ratio occurs when resources (den sites) are limiting, consistent with the predictions of the LRC model (Johnson et al. 2001) and that biases in offspring sex ratios are established prior to birth (Johnson & Ritchie 2002).

Methods

The study was conducted over three breeding seasons (2001 - 2003) on the Magnetic Island study site (see Chapter 2). The majority of offspring were sexed while still pink and permanently attached to the teat; the remainder were sexed prior to weaning, while still riding on their mother's back. Second births of females that were known to give birth to two offspring during the same year were not included in the analysis unless specified.

Condition scores, measurements and ages of females were recorded as described in Chapter 3; condition was taken for each female the month prior to birth as this best reflected condition at conception (Cameron 2004). Age and maternal condition were positively correlated (Chapter 3) and therefore, to avoid potentially confounding results, I used the residuals of maternal condition on age in all analyses except when looking at the raw data. Sample sizes vary, since not all information was available for all mother-offspring pairs.

I used a nominal logistic regression model with random effects to test for the effects of maternal age and condition on offspring sex (SAS 1995). Maternal identity and year were entered into the model as random variables to account for repeated observations of females contributing more than one offspring to the data set and any between year variation in pouch young sex. Observed sex ratios were compared to an expected random (binomial) distribution with a mean of 0.5 using Fishers exact test. Sex ratios were expressed as the proportion of males (males/(males + females)) in all cases.

I checked observed relationships between offspring sex ratio and reproductive stage of the mother (primiparous vs. multiparous) and maternal body condition using data from six mainland populations at the same latitude as Magnetic Island (Johnson et al. 2001; Johnson & Ritchie 2002). Detailed data on age of females was not available for these populations, so analysis could not be extended to age-specific effects as it was for the Magnetic Island population.

Results

MATERNAL AGE AND OFFSPRING SEX RATIOS

For the Magnetic Island study population a total of thirty-four individual breeding females were sampled and fifty-three pouch-young were sexed and used in the analysis.

The overall sex ratio, including all females, in 2001-2003 did not differ from parity (25 males: 28 females, $p = 0.1$, $n = 53$). I found a significant difference in offspring sex ratios for primiparous and multiparous mothers. At Magnetic Island, females breeding for the first time produced more sons than daughters, and at subsequent reproductions females produced more daughters than sons. There was a similar direction of change in offspring sex ratio in the mainland populations, although in the mainland sample the sex ratio of offspring born to multiparous mothers was still male-biased. The birth sex ratio in primiparous females was significantly male biased on Magnetic Island, the mainland population and a pooled sample (Table 5.1). The proportions of male and female offspring born to multiparous and primiparous females differed significantly in the Magnetic Island sample and in a pooled sample including Magnetic Island and the mainland populations. This trend was present, but not significant, in the mainland populations alone (Table 5.1).

MATERNAL CONDITION AND OFFSPRING SEX RATIOS

The raw data (Fig 5.1) show a positive relationship between maternal condition and the proportion of male offspring in females aged ≥ 3 years of age. However, this relationship was not evident for primiparous females (aged ≤ 2 years). There was no effect of either maternal identity or year on offspring sex and these factors were excluded from all further analyses. On Magnetic Island,

Table 5.1: Comparison of proportions of male and female offspring produced by primiparous and multiparous females in mainland populations, on Magnetic Island, and a combined sample. Binomial probability values show the probability that the observed proportion differs from that predicted by an expected random (binomial) distribution. Chi-square results test for a difference between the number of male and female offspring produced by multiparous and primiparous mothers.

Source	Reproductive status	Male offspring	Female offspring	Proportion males	Binomal Probability *p*	χ^2	p
Mainland	Primiparous	11	4	0.73	0.04		
	Multiparous	41	31	0.56	0.05	1.39	0.23
Magnetic	Primiparous	9	3	0.75	0.05		
Island	Multiparous	15	25	0.37	0.04	5.25	0.02
Combined	Primiparous	20	7	0.74	0.006		
	Multiparous	56	56	0.50	>>0.1	5.09	0.02

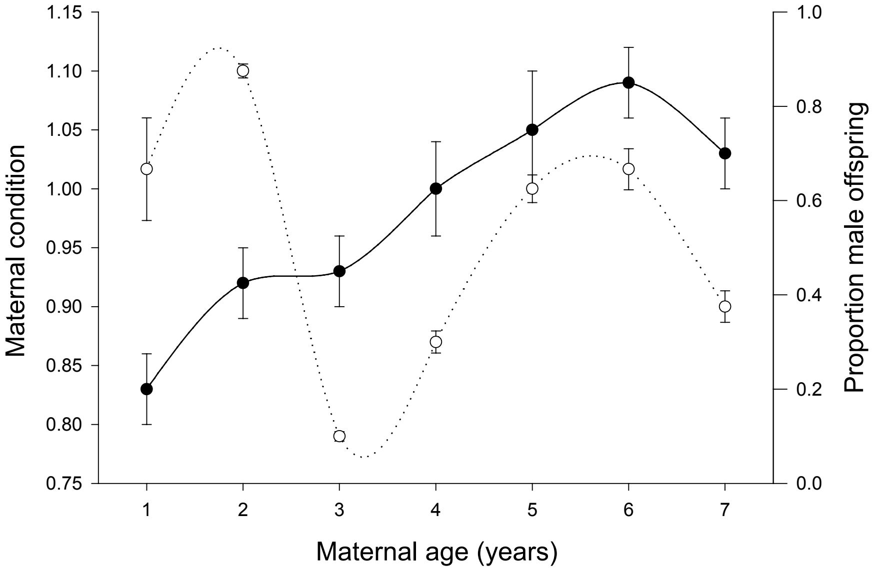

Figure 5.1: For each age class, the proportion of male offspring produced (±SE, dashed line, open circles) and mean condition index (uncorrected for age, ±SE, solid line, black circles) for females on Magnetic Island.

Table 5.2: The effects of maternal age and condition on the offspring sex ratio in female brushtail possums on Magnetic Island.

	Model estimates ± SE	Wald statistic	P
Maternal Age	-0.46 ± 0.27	2.87	0.09
Maternal Condition	-6.93 ± 3.60	3.71	0.04
Constant	3.11± 1.53		

condition was found to be the best predictor of offspring sex (Table 5.2); females in better condition were more likely to have sons (Fig. 5.2). The effect of maternal age was not significant in multiparous females after the effect of condition was removed. The proportion of male offspring produced by females in the mainland populations was also positively related to maternal condition (logistic regression: $\chi^2 = 4.45$, $p = 0.03$, $n = 153$).

Offspring sex in individual, multiparous females on Magnetic Island was also related to between year shifts in maternal condition; females who gained in condition from one year to the next were more likely to give birth to a male offspring in the second year (Fig. 5.3: logistic regression: $\chi^2 = 4.53$, $p = 0.03$, $n = 17$). Between year variation in maternal condition was not influenced by the sex of offspring born in the preceding year ($t = -1.67$, $p > 0.05$, $df = 13$).

For those females that gave birth to males, offspring mass at five months was correlated to maternal condition (Fig. 5.4, $R^2 = 0.54$, $p < 0.05$, $df = 10$), however no relationship was found between maternal condition and mass of female offspring (Fig. 5.4, $R^2 = 0.11$, $p > 0.05$, $df = 17$).

Females which produced two offspring within a single breeding season produced a female biased sex ratio in both cohorts, although the bias did not differ significantly from parity in either cohort (Table 5.3). There was no evidence that these double breeders produced a different sex ratio bias between cohorts (Table 5.3).

Discussion

The results show evidence that TW effects are operating in multiparous females in *T. vulpecula*, since females in relatively good condition were found to produce more sons. However, given that the TW model is based on individual

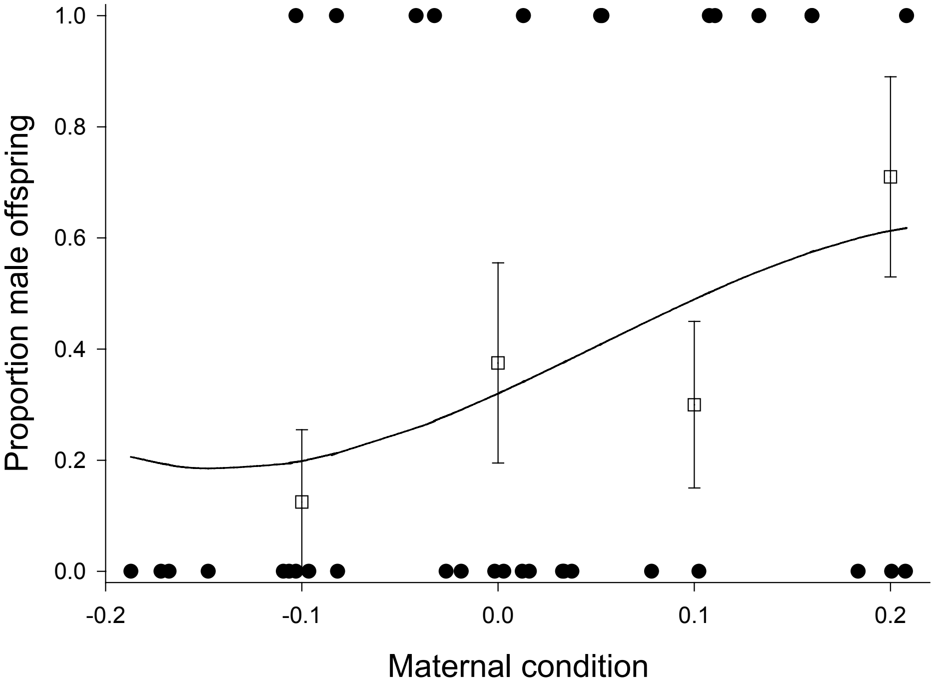

Figure 5.2: Proportion (±SE) of male offspring produced (open squares) according to maternal condition by multiparous female brushtail possums on Magnetic Island. The regression line is generated from the logistic model including maternal age as a fixed effect. Black circles show the actual numbers of sons and daughters produced.

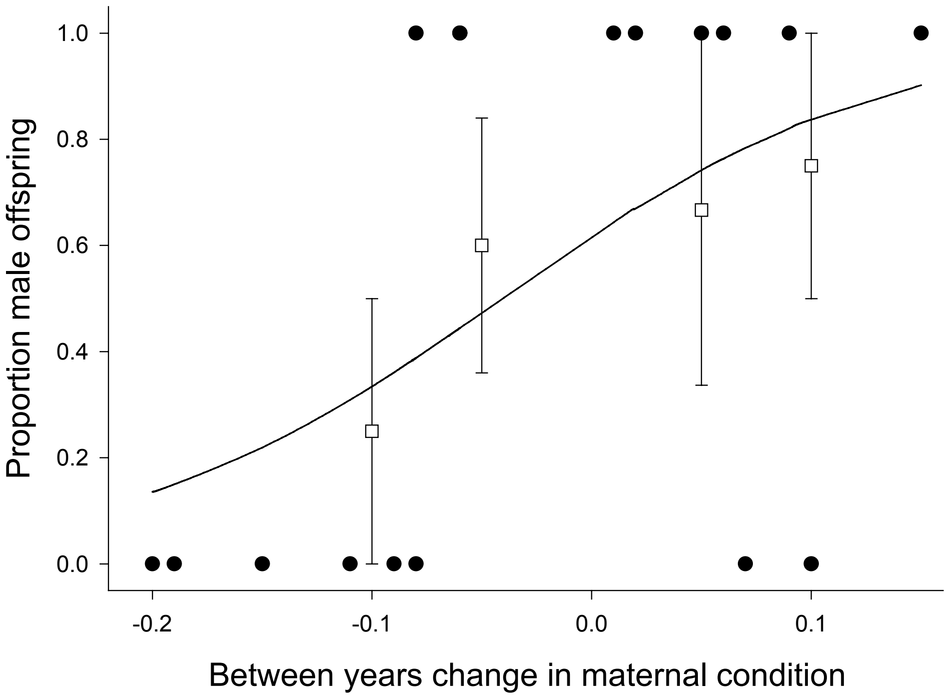

Figure 5.3: Relationship between the proportion of male offspring produced and between years change in maternal condition. Proportions of male offspring produced (+SE) are shown by open squares, black circles indicate actual numbers of male and female offspring produced. The regression line is generated from a simple nominal logistic model.

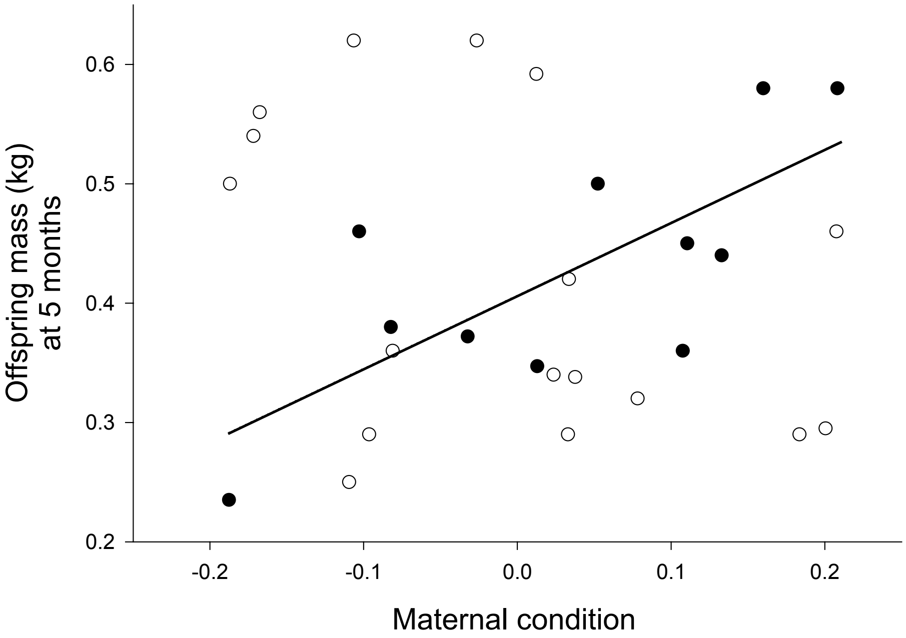

Figure 5.4: Linear regressions of mass in males and female offspring at 5 months against their mothers' pre-birth condition index. Male offspring are shown as black circles with a solid regression line, female offspring as open circles (relationship not significant – see text for statistics).

Table 5.3: Comparison of the proportion of male and female offspring produced in the first and second cohort by females which double-bred within an annual breeding season.

Cohort	Male	Female	Proportion Male	Binomial probability p
First	4	10	0.29	0.06
Second	6	8	0.43	0.18
				$\chi^2 = 0.43$
				$p = 0.62$

life history strategy, a more important result is perhaps that individual females were found to adaptively adjust their sex ratio between years according to shifts in maternal condition. Similar results have been found in another marsupial, the bridled nailtail wallaby (*Onychogalea fraenata*), where females that lost weight following drought were more likely to produce daughters (Fisher 1999).

Data also meet, in as far as they are able, assumptions 1 and 3 of the TW model. However, since all male offspring but two dispersed from the site, I was unable to verify assumption 2, predicting that differences in offspring condition endure into adulthood. In accordance with assumption 1 - that offspring phenotype and maternal phenotype will be related, I found that mass of male offspring at five months, just prior to independence, was positively correlated with maternal condition.

In *T. vulpecula*, sons begin to disperse away from their natal range at approximately six months of age (Cowan & Clout 2000; Johnson et al. 2001) and it is probable that selection will favour phenotypic adaptations, such as an increased early growth rate, that will result in improved first year survival and dispersal success in males. Females however remain close to their mothers for a much longer period and characteristically settle in a home range which overlaps or is adjacent to that of their mothers and thus early growth rate is likely to be a less important strategy in female offspring. This result also implies indirect evidence for assumption 3 of the TW model; that sons will benefit more than daughters in lifetime reproductive success by an advantage in condition. Clutton-Brock (1984) points out that when male lifetime reproductive success increases with body size, early growth rates are likely to exert an important effect on breeding success as an adult. Hewison & Gaillard (1999) also suggest that this assumption is probably valid in most species where male mating success increases with body size. Paternity analysis in the Magnetic Island population is currently ongoing, but recent molecular work by Clinchy et al. (2004) indicates that, in Australian populations at least, larger heavier males do have greater reproductive success. Since I am currently unable to show conclusive evidence that maternal investment has a differential effect on the reproductive value of sons and daughters, females could still be biasing sex ratios in line with the cost of reproduction hypothesis (Myers 1978; Cockburn et al. 2002), rather than demonstrating TW effects. The cost of reproduction hypothesis proposes that females in poor condition may be unable to produce a given sex because it is more costly and may impact on their future reproductive potential. There are many examples, particularly among the ungulates, which indicate that rearing a male offspring can have a detrimental effect on subsequent maternal fitness in mammals (e.g.: Clutton-Brock et al. 1981). However, this study found no effect of offspring sex on maternal condition the following year, suggesting that the cost of reproduction hypothesis does not explain sex ratio bias in this population.

Preliminary data found no evidence that females that produced two offspring in a single breeding season adjusted their sex ratio bias between cohorts. This result contradicts the predictions of the first-cohort advantage hypothesis (Wright et al. 1995), which proposes that females should increase their fitness by producing more males than females in their first litter. This is proposed because first-cohort males are expected to have an advantage over second-cohort males by being larger in their first year of reproduction (Wright et al. 1995; Ward 2003). Most studies which have found support for the first-cohort advantage hypothesis (FCAH) have been carried out on species which have a short life-span and often reproduce for one year only, such as *Didelphis virginiana* (Wright et al. 1995) and *Microtus canicaudus* (Wolff et al. 2003). However, Hardy (1997) found no cohort effect in *D. marsupialis*. I propose that the FCAH may be less applicable to species where males have multi-year opportunities to reproduce, as second cohort males will have time to ‘catch-up’, in terms of mass and condition prior to mating. However, my data on FCAH suffers from a small sample size as double breeding occurred in only two years of my study. Further long-term data will be required in order to fully understand the fitness benefits, and costs, to double breeding in *T. vulpecula*.

According to the LRC hypothesis of sex ratio bias, biases should be related to the potential for resource competition between related females. Although LRC is predicted to affect sex ratio at the level of the population, Cockburn et al. (2002) highlight a number of circumstances where predictions of population-wide sex ratio bias need not be fulfilled in order to meet the requirements of the LRC model. For example, the potential for competition between related individuals is predicted to be highest under conditions of resource scarcity and Johnson et al. (2001) found that the offspring sex ratio in eight populations of *T. vulpecula* in Australia was related to den availability; in populations where den sites were limiting, females showed a male-biased sex ratio. This is supported in the results since multiparous mothers showed a male-bias in the mainland sample. However, this explanation cannot be applied to the Magnetic Island population since, unlike the populations used by Johnson et al. (2001), *T. vulpecula* at the Magnetic Island study site den almost exclusively in rock crevices which are abundant. Population density is however high in comparison to mainland populations (Chapter 6) and individuals given food supplements have been shown to increase in mass considerably (Isaac et al. 2004 [Appendix II]), suggesting that food limitation may constrain individuals in terms of life history.

The potential for LRC effects is also predicted to be high early in the reproductive life of young females and this was supported in the results as young primiparous mothers were found to bias their offspring sex ratio toward males, the dispersing sex. Cockburn et al. (1985) found similar results in populations of *Antechinus* spp. In iteroparous species of *Antechinus* (i.e. *Antechinus swainsonii*), females were likely to survive to breed twice and mothers were found to bias their first litter toward sons. However, in more semelparous populations (i.e. *Antechinus agilis*), females rarely breed more than once and produced female-biased litters. A consequence of this may be that after producing a male bias early in life, females should show a shift or reversal in their sex ratio (Ward 2003). This prediction was also upheld, at least for the Magnetic Island population, since the sex ratio of multiparous mothers was female biased. Similar results have been shown in the northern quoll *Dasyurus hallucatus* (Oakwood 2000) and iteroparous populations of *Antechinus swainsonii* (Cockburn et al. 1985). However, females of both these species breed only twice in their lifetime and thus the adaptive significance behind this shift in *T. vulpecula* is likely to have a more complex explanation. Primiparous females with intrinsically high residual reproductive value may essentially take a bet-hedging strategy and produce a low quality male without incurring the costs associated with producing a daughter early on in life through LRC. However, the prediction of the LRC model that older females close to the end of their breeding life should over-produce daughters was not met as the female bias found in multiparous females was independent of maternal age.

In conclusion, this study supports the prediction that both TW and LRC effects can operate simultaneously within a population to produce differing patterns of bias among mothers according to variation in maternal condition and reproductive status. Further long-term monitoring of this population and ongoing paternity analysis will be imperative in elucidating the influence of maternal condition on the LRS of male offspring.

CHAPTER 6

Sexual dimorphism and synchrony of breeding: variation in polygyny potential among possum populations in northern Australia

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Introduction

Most mammals have a polygynous mating system in which males compete for access to breeding females (Krebs & Davis 1981; Clutton-Brock 1989). Sexual selection is expected to favour adaptations, such as large body size, that enhance reproductive success in males during combat (Trivers 1972; Clutton-Brock et al. 1979; Schulte-Hostedde et al. 2001). However, the mating success of females is less dependent on body size and females are likely to adopt a more conservative growth strategy and invest resources into the production and provisioning of offspring, rather than growth (Trivers 1972; Reeve & Fairbairn 2001; Schulte-Hostedde et al. 2001). Thus, due to differences between the sexes in life history strategy and reproductive investment, the majority of mammals show male-biased sexual dimorphism (SD), with adult males being larger and/or heavier than adult females (Krebs & Davis 1981; Weckerly 1998). However, recent studies have also associated SD in mammals with population density (LeBlanc et al. 2001), diet quality and selection (Clutton-Brock et al. 1987c; PerezBarberia & Gordon 1998), latitude and climatic variables (Quin et al. 1996; Storz et al. 2001), disease (Pontier et al. 1998) and habitat use (Clutton-Brock et al. 1987c), in addition to reproductive strategy (McElligott et al. 2001).

When females show a seasonal breeding pattern, and where individuals are solitary and spatially dispersed, polygyny potential and variance in male reproductive success may be reduced (Emlen & Oring 1977). Smaller males can exploit the fact that more competitive males are involved in consorting and mating with females elsewhere (Say et al. 2001). If large, dominant males are unable to control access to large numbers of females, there will be less benefit to allocating energy into additional growth. Therefore we can predict that levels of SD will be lower in populations with seasonal reproduction. Conversely, when breeding occurs continuously throughout the year, large dominant males may potentially sire a greater proportion of offspring (Say et al. 2001) and the degree of SD should be higher. Few studies have previously investigated the influence on mammalian male mating strategies of the distribution of receptive females in time, while a great deal of research effort has centred upon the effects of the distribution of receptive females in space (review in: Clutton-Brock 1989). This may be because many of the most intensively studied mammals have highly seasonal breeding patterns and thus do not provide the variation in seasonality needed to reveal potential effects on reproductive strategies of males and SD. Thus, little is known of the extent to which differences in breeding seasonality between populations can influence the development of SD within a species.

Density dependent factors may also exert an influence on breeding seasonality through their effect on breeding synchronisation. Ims (1990) defines reproductive synchrony as ‘a phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone’. Breeding synchrony can occur in populations which show breeding seasonality, resulting in a tighter clustering of births than climatic seasonality alone would predict (Ims 1990). However, reproductive synchrony can also occur in the absence of breeding seasonality, in relatively aseasonal, tropical regions, and a variety of studies have demonstrated that oestrus synchronisation between sexually mature females can be socially induced by external, olfactory cues (Ims 1990; Johannesen et al. 2000). Therefore, if high population density results in increased contact between individuals, this may stimulate ovarian activity and synchronise oestrus between females.

The common brushtail possum is an ideal model animal with which to investigate the interactions between sexual dimorphism, breeding seasonality and population density. While possums have a predominantly polygynous mating system, the degree of polygyny varies considerably between populations (Day et al. 2000). Males often have overlapping home ranges and compete for access to oestrus females; both males and females are generally solitary (Winter 1976). In Australia, large, dominant males reportedly consort with females for 30 – 40 days prior to mating (Winter 1976) and this behaviour could put a severe limit on the number of females any one male could mate with during a seasonal or synchronous breeding cycle. Population density and levels of sexual dimorphism are also variable among Australian populations (see below). Breeding seasonality is broadly related to latitude, with a short breeding peak during the early autumn characteristic of the temperate south, often with a smaller, more variable breeding peak in the early spring. The spring birth peak was previously attributed to females in good condition giving birth to a second young (Kerle 1984, but see Chapter 4). Year round breeding is commonly found in the tropical north. This latitudinal pattern is thought to be due to environmental cues, such as photoperiod, climatic variation and food availability, influencing the onset of reproduction (Kerle 1984). However, in the tropical north of Australia, breeding season can range from highly seasonal to year round over relatively small geographic distances, suggesting that breeding seasonality is not constrained by climatic seasonality alone and that other factors must contribute to the degree of breeding seasonality in these populations.

In this chapter, I use data from 11 possum populations located in the north of Australia to investigate how variation in breeding seasonality between populations influences SD. I also address the power of population density to influence SD, both in respect to its potential effect on the ability of males to find multiple mates within their home range, its relationship with individual body mass of adult males and females, and also its possible influence on breeding seasonality itself, through increasing oestrus synchrony within a seasonal breeding pattern. I predict that seasonality of breeding will be negatively correlated to levels of male-biased SD and that increasing population densities may result in a higher level of reproductive synchrony within populations.

Methods

Data were collected from field studies of five possum populations in the Mt. Fox region (18°50'S, 145°46'E), one population at Herveys Range (19°23'S, 145°26'E) as well as the Magnetic Island population (Fig. 6.1), providing a total of 7 north Queensland populations. The Mt. Fox and Herveys Range raw data were collected by C. Johnson, and analysed along with the Magnetic Island data. Data from two other Magnetic Island sites were taken from a study by Pieters (1985). Further data were taken from studies conducted in Brisbane, Southern Queensland (27°32'S, 152°53'E; Winter 1976) and Jabiluka in the Northern Territory, 12°28'S, 132°15'E (Kerle & Howe 1992; Kerle 1998). Possums at each of the 7 North Queensland sites were live-trapped using wire mesh traps over a period of at least 12 months in order to determine the distribution of births throughout no less than one full breeding season. The five Mt. Fox populations were trapped on average four times per year, over a period of at least three years. Individual possums were not found to travel between any of the Mt. Fox populations over the period of the study, thus they were considered to be five independent sites. The three Magnetic Island sites and the Herveys Range site were trapped once monthly for a period of one year. Each animal was also weighed, to the nearest 20g, with a spring scale during each trapping session. Population size was calculated as the minimum number of animals known to be alive (Krebs 1998), per hectare, determined from live-trapping data for all sites except Brisbane. For the Brisbane site, the number of animals known to be alive

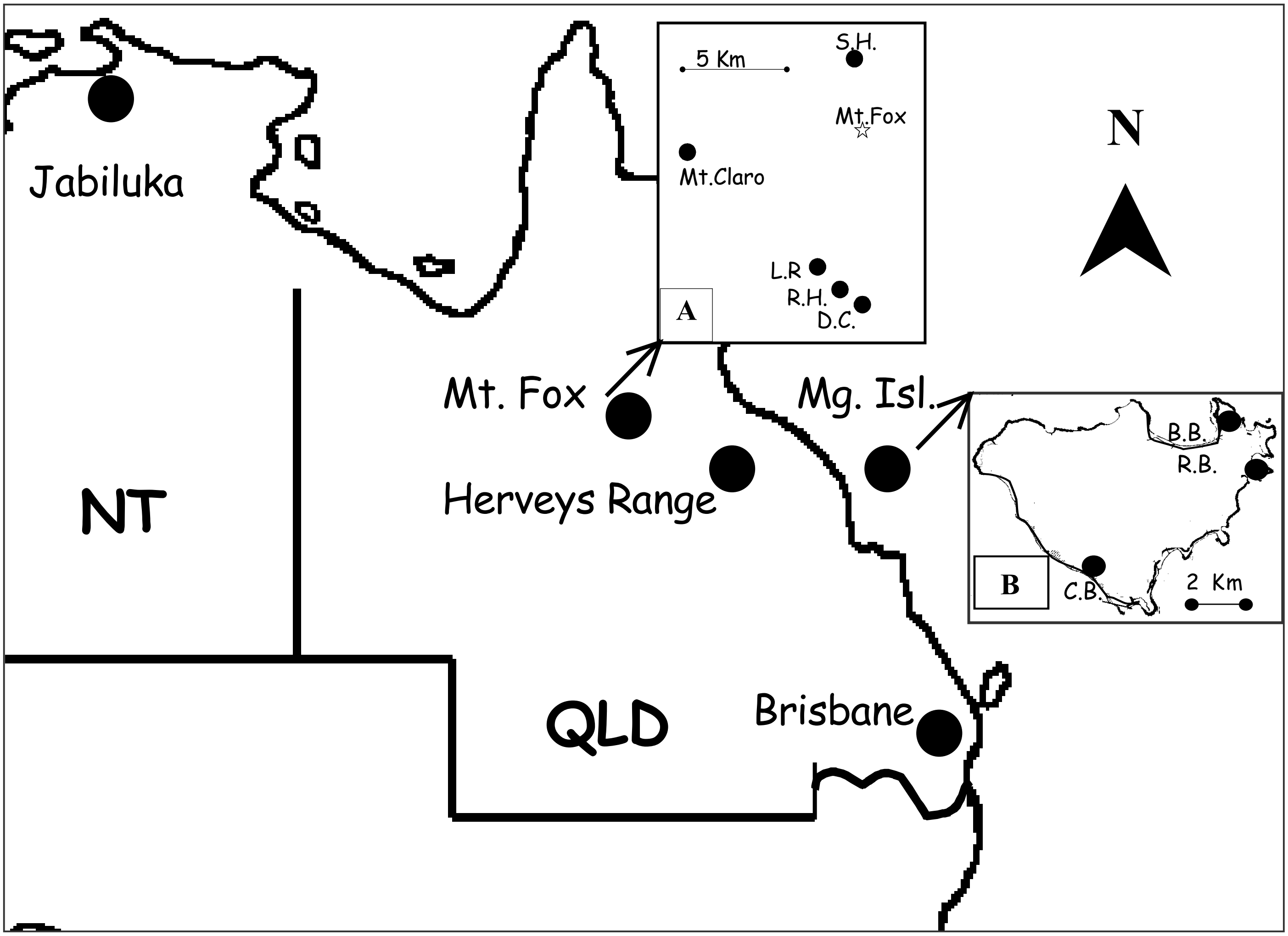

Figure 6.1: The location of the 11 study populations. Inset A show the five Mt. Fox sites signified as S.H.– Schoolhouse, Mt. Claro, L.R.- Loading Ramp, R.H.-Rocky Hollow and D.C.-Dingo Creek. Inset B shows Magnetic Island, with the location of the three study sites; C.B.-Cockle Bay, R.B.- Radical Bay and B.B.-Balding Bay.

was estimated by a spotlighting transect method (Winter 1976). The five Mt Fox sites and the Herveys Range site were *ca*. 40 ha, the three Magnetic Island sites were *ca.* 10 ha., the Jabiluka site was *ca*. 5 ha and the Brisbane site was 17 ha.

Breeding seasonality was determined by assigning a date of birth to all unweaned juveniles, as described in Chapter 3, and was expressed as the percentage of births occurring in the peak two months, whether these months were consecutive or not, for each population. Populations with a more continuous, year round breeding pattern therefore had a lower value of this index than those with a pronounced seasonal breeding peak. Relationships between variables were analysed using least squares linear regression. Population densities and measures of sexual size dimorphism (expressed as male body mass (kg) divided by female body mass (kg)) were log transformed prior to analysis. All raw data and log transformations were normally distributed (Shapiro-Wilk W Test; $p>0.5$ in all cases). Sexual dimorphism values refer to sexually mature adults, i.e. breeding females, indicated by an invaginated pouch, and males with full-sized testes (length $\geq$ 18.0mm; Clout and Efford 1984; Kerle and Howe 1992). In the Brisbane population, Winter (1976) classed adult possums as those individuals aged over 2 years and determined age from tooth wear. Temperature and rainfall data came from Australian Bureau of Meteorology records (1995).

Results

The distribution of births, levels of SD and population density were found to vary considerably within the 11 populations (Table 6.1).

None of the key variables were found to be significantly related to latitude (°S) (breeding seasonality: $F_{1, 9} = 1.05$, $p = 0.33$, $R^2 = 0.11$; sexual dimorphism:

Table 6.1: Summary of the key variables for the 11 study populations; MI = Magnetic Island site, MF = Mt. Fox site. Breeding seasonality is expressed as the percentage of births occurring in the peak two months. Sexual dimorphism values are male body mass (in kg) / female body mass (in kg).

Site	Years Data Collected	Population Density n/ha	Breeding Seasonality (no. births: peak two months)	Mean Male Body Mass kg ± sd (n)	Mean Female Body Mass kg ± sd (n)	Sexual Dimorphism
Jabiluka	1979-1981	3.1	23.00 (39:Jan/Jul)	1.57± 0.18 (70)	1.36± 0.2 (107)	1.15
Cockle Bay (MI)	2001	7.2	79.00 (17:Apr/May)	1.67± 0.22 (34)	1.66± 0.18 (26)	1.01
Radical Bay (MI)	1985	4.96	71.00 (27:Apr/May)	1.58± 0.16 (48)	1.61± 0.25 (26)	0.98
Balding Bay (MI)	1985	2.84	96.00 (26:Apr/May)	1.60± 0.17 (42)	1.65± 0.19 (36)	0.97
Brisbane	1965-1968	2.14	58.13 (43:Mar/Apr)	2.51 ± 0.35 (21)	2.11 ± 0.23 (18)	1.19
Schoolhouse (MF)	1996-2001	1.51	71.00 (154:Apr/May)	1.86 ± 0.18 (140)	1.72 ± 0.17 (101)	1.08
Dingo Creek (MF)	1996-2000	0.32	68.98 (29:Apr/May)	2.06 ± 0.21 (29)	1.91 ± 0.19 (15)	1.08
Loading Ramp (MF)	1997-2000	1.15	59.70 (67:Apr/May)	1.93 ± 0.19 (41)	1.79 ± 0.18 (28)	1.08
Mt. Claro (MF)	1996-2000	0.09	42.00 (10:Jan/Aug)	2.23± 0.22 (14)	1.96 ± 0.22 (8)	1.14
Rocky Hollow (MF)	1997-2000	0.26	49.99 (9:Apr/May)	2.05 ± 0.19 (16)	1.77 ± 0.23 (28)	1.16
Herveys Range	2000	0.57	63.33 (11:Apr/May)	1.84± 0.25 (33)	1.78±0.24 (27)	1.03

0.005), mean annual rainfall (mm) (breeding seasonality: $F_{1,\ 9}$ = 3.25, p = 0.12, R^2 = 0.35; sexual dimorphism: $F_{1,\ 9}$ =0.43, p = 0.53, R^2 = 0.07; population density: $F_{1,\ 9}$ = 1.84, p = 0.22, R^2 = 0.23) or mean maximum temperature (°C) (breeding seasonality: $F_{1,\ 9}$ =1.39, P = 0.29, R^2 = 0.18; sexual dimorphism: $F_{1,\ 9}$ =0.06, p = 0.80, R^2 = 0.01; population density: $F_{1,\ 9}$ = 1.11, p = 0.33, R^2 = 0.16).

The level of male-biased SD within possum populations was significantly related to breeding seasonality (Fig. 6.2: $F_{1,\ 9}$ = 16.64, p = 0.002, R^2 = 0.65). Populations with a more continuous breeding season had a greater degree of SD than those with a short, seasonal peak. A standard least squares multiple regression determined that there was no significant interactive effect of population density and breeding seasonality on SD ($F_{1,\ 9}$ = 0.15; p = 0.7) and no effect of population density on SD that was independent of the relationship between breeding seasonality and SD ($F_{1,\ 9}$ = 2.23; p = 0.17).

There was a trend for an increase in breeding seasonality with increasing population density ($F_{1,9}$ = 1.95, p = 0.19, R^2 = 0.18). The Northern Territory population was found to be a significant outlier in this analysis using the Jacknife Distance (Mahalanobis) method and when this population was removed from the analysis, the relationship between reproductive seasonality and density became significant (Fig. 6.3: $F_{1,\ 8}$ = 8.72, p = 0.02, R^2 = 0.52). This population was not found to be a significant outlier in any of the other analyses. An increase in population density also resulted in a decrease in the mean male body mass ($F_{1,9}$ = 5.55, P = 0.04, R^2 = 0.38), however no such relationship was found between density and female body mass ($F_{1,9}$ = 3.01, p = 0.11, R^2 = 0.25).

Discussion

SEXUAL DIMORPHISM AND BREEDING SEASONALITY

The data support the prediction that male-biased SD in brushtail possums is significantly more pronounced in populations with a more continuous breeding pattern. Substantial differences in SD and seasonality were observed between

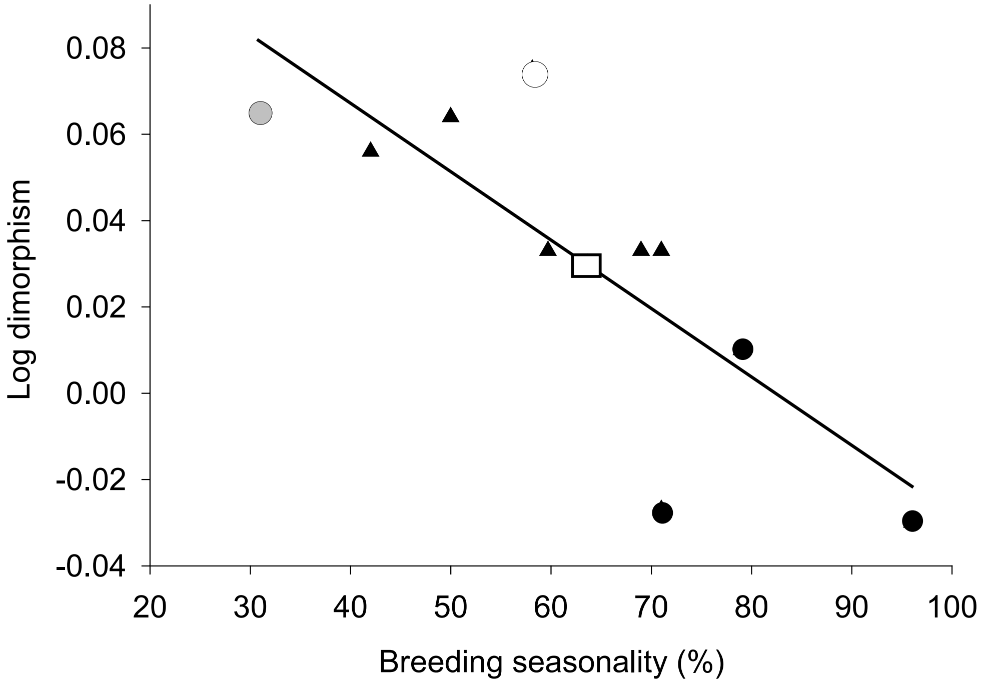

Figure 6.2: Sexual dimorphism values, the log of male body mass/female body mass (kg), for *T. vulpecula* populations in tropical Northern Australia, plotted against breeding seasonality, in terms of the percentage of births occurring in the peak two months. Magnetic Island sites are denoted by filled black circles, Mt. Fox sites by filled black triangles, the Herveys Range site by an open square, the Brisbane site by an open circle and the Jabiluka site by the filled grey circle.

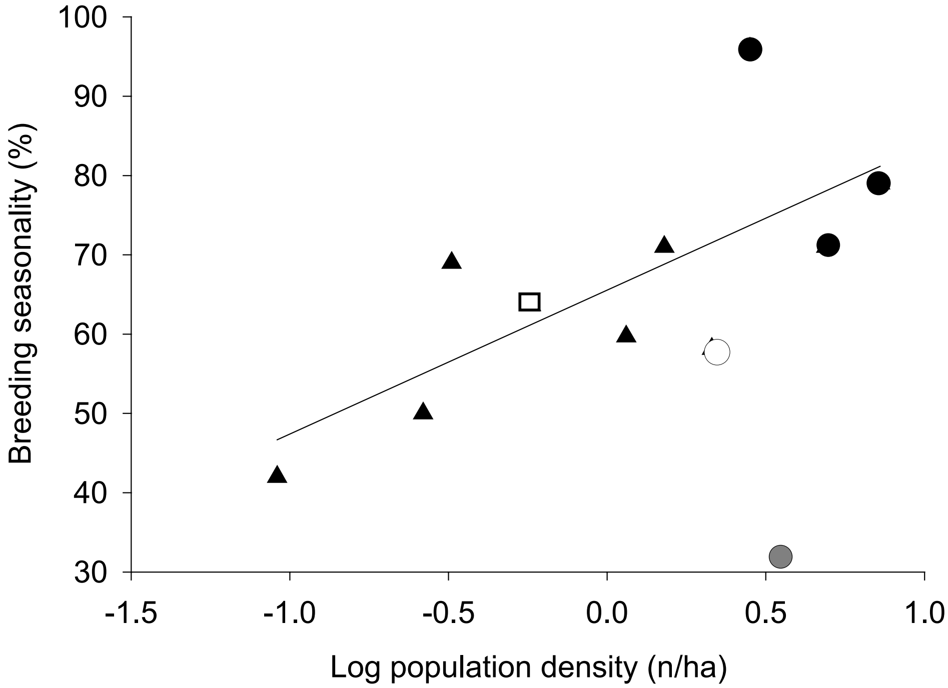

Figure 6.3: Breeding seasonality, in terms of the percentage of births in the peak two months, of *T. vulpecula*, plotted against population density. The Northern Territory population was found to be a significant outlier and was not included in the regression analysis, but is shown on the figure as a filled grey circle. Magnetic Island sites are shown by filled black circles, Mt. Fox sites by filled black triangles, the Herveys Range site by an open square and the Brisbane site by an open circle.

populations which were geographically very close to one another and the results confirm that these differences were not the result of latitudinal or climatic effects.

According to the sexual selection hypothesis of SD, levels of male-biased dimorphism in mammals should be correlated to the degree of polygyny within a population (Boonstra et al. 1993). Aseasonality of breeding can influence the operational sex ratio of a population by increasing the number of receptive females per male, resulting in greater polygyny potential (Emlen & Oring 1977).

Say et al. (2001) recently investigated the effects of reproductive synchrony on the degree of polygyny in the domestic cat (*Felis catus*) and found that variance in male reproductive success was four times greater in years when females bred asynchronously, compared to years where females bred synchronously. To our knowledge, the present study is the first on a mammal to clearly correlate levels of SD with variation in breeding seasonality among populations. However, the results do concur with those of a recent study on a socially monogamous seabird, the brown booby (*Sula leucogaster*), where it was found that males showed a significantly greater degree of sexually dimorphic plumage in populations where birds bred year round (Tershy & Croll 2000). However, in populations where breeding occurred within a short 90-day period, there was little male sexual dimorphism in plumage (Tershy & Croll 2000). The authors suggest that further data will reveal that breeding synchrony prohibits sequential polygyny, resulting in reduced male-male competition and a consequent decrease in the need for sexually dimorphic traits (Tershy & Croll 2000).

POPULATION DENSITY AND BREEDING SEASONALITY

The data also indicate that population density influences breeding seasonality. This may suggest that high population density results in an increase in reproductive synchrony among females, within a seasonal breeding pattern. In the north Queensland study areas, the possum populations are from a relatively small geographical area and variations in seasonality were not explained by differences in climatic seasonality or latitude. Density in these populations is primarily related to soil fertility (Johnson et al. 2001). In seasonal environments, breeding is usually restricted to the part of the year when resources are most abundant (Bronson 1989). Kerle and Howe (1992) have suggested that the continuous breeding cycle of possums in the Northern Territory can be directly related to their tropical environment, where there are no annual periods of food shortage, allowing year round breeding regardless of population density. This may, in part, explain why the Northern Territory population was found to be a significant outlier in our analysis. However, breeding synchrony has also been observed in tropical, aseasonal regions and has been linked to a number of ecological and sociobiological processes (Ims 1990). Research has shown that pheromonal signals, often secreted in urine, from individuals of the same species can stimulate ovarian activity and synchronise oestrus within a population (Rekwot et al. 2001). Furthermore, a recent study found that the presence of males significantly increased the incidence of ovulation in female brushtail possums, following the removal of pouch young (Crawford et al. 1998). If high density results in increased exposure to such signals, either from males and/or other females, the breeding cycles of individual females are more likely to be entrained with their neighbours (Johannesen et al. 2000), possibly resulting in population-wide breeding synchrony.

The results also suggest that population density may affect the individual body mass of adult male possums. Similar relationships have also been found in ungulates such as bighorn sheep (*Ovis canadensis*: LeBlanc et al. 2001)), roe deer (*Capreolus capreolus*: Vincent et al. 1995) and red deer (*Cervus elaphus*: Clutton-Brock et al. 1982), where results indicated that body growth of males was limited by resource availability at high density. In bighorn sheep and roe deer, it was also suggested that females were able to undergo compensatory growth later in life, resulting in a lower degree of SD (Vincent et al. 1995; LeBlanc et al.

2001). This explanation could also be highly applicable to possums, which consume a low quality, high biomass diet comparable to that of ungulates (Nugent et al. 2000) and is supported by the fact that our results found no relationship between density and a decrease in female body mass. Greater breeding synchrony in higher density populations could also contribute to the observed lower body male body mass through reduced selection for large male body size.

In conclusion, this study provides evidence that breeding seasonality can influence patterns of sexual dimorphism in brushtail possums. This result implies that life history traits including aspects of the reproductive behaviour of males and patterns of male-male contact will also vary substantially between populations. Recent studies on the mating system of *T. vulpecula* have found inconsistent results; Taylor et al. (2000) found no relationship between male age or mass on mating success in *T. vulpecula* in New Zealand farmland, while Clinchy et al. (2004) found a clear positive association between male body mass and mating success in possums in old-growth *Eucalyptus* forest in southern Australia, suggesting a more polygynous mating system.

CHAPTER 7

Mating season mass loss in males: implications for age-specific variation in mating strategy

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Introduction

Life history theory predicts trade-offs between current and future reproduction in order to balance current energy expenditure against any negative effects on future growth, survival and reproductive success (Stearns 1992). The residual reproductive value hypothesis proposes that, as individual's age, they should progressively increase their expenditure into reproduction as their number of future potential reproductive events declines (Williams 1966; Clutton-Brock 1989). This increase may be more marked toward the end of an organisms life, as the probability of surviving to the next reproductive bout rapidly decreases (Pianka 1988).

In polygynous mammals, male reproductive success is largely dependent upon male-male competition for access to breeding females (Clutton-Brock 1989). Reproductive expenditure in males is therefore most likely to be directed towards behaviours such as mate-guarding and male-male combat (Shuster & Wade 2003). However, while a variety of studies have investigated age-specific variation in reproductive effort in female mammals (see Chapter 5), few have concentrated on male reproductive expenditure and those that have are largely restricted to ungulates with a highly polygynous, harem mating system (i.e.: Yoccoz et al. 2002; Mysterud et al. 2003).

The priority-of-access model (Altmann 1962; Weingrill et al. 2003) proposes that, in species with a hierarchical social system, high-ranking males should monopolise matings when at least one female is receptive. In long-lived mammals, social hierarchies are often age-related and established prior to the breeding season (Clutton-Brock et al. 1982). Older, high-ranking males are likely to get priority-of-access to receptive females, with younger males conceding during male-male interactions. Thus, contrary to the pattern predicted by the residual reproductive value hypothesis, males may actually need to invest relatively less into reproduction as they age.

In this chapter, using repeated monthly measurements of body mass, I test these predictions in an arboreal marsupial, the common brushtail possum (*Trichosurus vulpecula*). Male *T. vulpecula* demonstrate an age related, almost linear, dominance hierarchy, often have overlapping home ranges and compete for access to oestrus females; both males and females are generally solitary (Winter 1976). In their native range in Australia, dominant males consort with receptive females for 30 – 40 days prior to mating (Winter 1976). Dominant males are also able to exclude subordinate males from access to females (Winter 1976) and molecular analysis has shown that larger, older males have higher reproductive success (Clinchy et al. 2004). Annual survival declines rapidly after about the sixth year of life in both male and female possums (see Chapter 3).

Methods

Data were collected at the Magnetic Island study site during the breeding seasons of 2002 and 2003. Adult males were weighed, measured and aged as described in Chapter 3.

The majority (79%) of females gave birth between January and June (see Chapter 3), after a gestation period of 17 days (see Chapter 2). I therefore took the months of January-May as the main mating period for males. The percent of conceptions known to occur in each of these months was calculated from offspring birth dates, described in Chapter 3. It was not possible to directly determine numbers of receptive females; some females may been receptive and not conceived, or lost a pouch young early on. Mass change in males was expressed as the change from mass in the January trapping session of each year (i.e.: mass in January standardised to 0 for each male). Total reproductive somatic expenditure was calculated as relative mass loss (% change from pre-mating period mass) from January to May for adult males aged 3 years (n = 4), 4 years (n = 11), 5 years (n = 5), 6 years (n = 2) and 7 years (n = 3).

I used a linear mixed model with random effects to test for the influence of male age on mass loss (JMP; SAS Institute 1995). Male identity was included as a random variable in initial analyses; 21 individuals were sampled, 4 individuals contributed twice to the data set (in 2002 and 2003). Paired t-tests (using paired observations from the same individual) were used to test for a difference in mass from the beginning of the mating period (January) to the end of the main mating period (May). Variation in the pattern of mass loss between young and old males was examined using analysis of variance. Males were categorised into two age categories for this analysis, young (3-4 years of age) and old (≥ 5 years old). Monthly mass changes were calculated for each individual as the change in mass between the four-weekly trapping sessions. Not all information was available for all individuals and consequently sample sizes vary among analyses.

Results

MASS LOSS DURING THE MATING PERIOD

There was no influence of male identity on mass loss (p = 0.63) and therefore male identity was excluded from further analysis. Male possums changed mass considerably during the main breeding season (Fig. 7.1) and individual males weighed significantly less in May ($\bar{x}$ = 1.77 ± 0.04 kg) than in January ($\bar{x}$ = 1.85 ± 0.04 kg; paired t-test: t = 3.93, p = 0.0008, df = 20). Females gain mass during this period (see Chapters 3 & 4). The decline in mass in males during the breeding season was broadly associated with an increase in the number of oestrous females available; oestrus synchrony increased considerably during April and May, with more than 50% of all conceptions occurring in these two months alone (Fig. 7.1).

AGE-SPECIFIC MASS LOSS

Relative mass loss during the mating season was negatively related to male age (Fig. 7.2: $R^2 = 0.26$, $F_{1,\ 23} = 5.81$, p = 0.008). Using absolute mass loss did not significantly alter the results ($R^2 = 0.24$, $F_{1,\ 23} = 4.6$, p = 0.01). Mass loss was highest in younger males.

Males lost a mean of 4.16 ± 4.5 % of their pre-breeding body mass during the mating period. Young males (aged 3-4) lost significantly more relative mass ($\bar{x}$ = 5.67 ± 1.07%, n = 15) than old males (age ≥ 5; $\bar{x}$ = 1.91 ± 1.31%, n = 10) during the main mating season (t = 2.21, p = 0.04, df = 24). The monthly pattern of relative mass loss also differed between the two age groups; old males lost significantly more mass in May compared to the other months (Fig. 7.3: ANOVA; $F_{3,\ 28} = 7.27$, p = 0.001) while there was no difference between months for young males (Fig. 7.3: ANOVA; $F_{3,\ 35} = 1.11$, p = 0.36).

Discussion

This study provides one of the first assessments of male reproductive expenditure in a non-ungulate mammal and is, to the best of my knowledge, the only such investigation focussing on a male marsupial. In contrast to patterns found in red deer (*Cervus elaphus*: Yoccoz et al. 2002) and reindeer (*Rangifer tarandus*: Mysterud et al. 2003), and to the predictions of the residual reproductive value hypothesis, male possums decreased their reproductive expenditure as they aged. The percentage of body mass lost by male possums is much less than that found in most cervids; red deer stags have been shown to lose an average of 40% of their body mass during the rut (Bobek et al. 1990). However, Pelletier (2004) determined that bighorn rams (*Ovis canadensis*) lose only up to 16% of their pre-rut mass. However, male *T. vulpecula* lose a

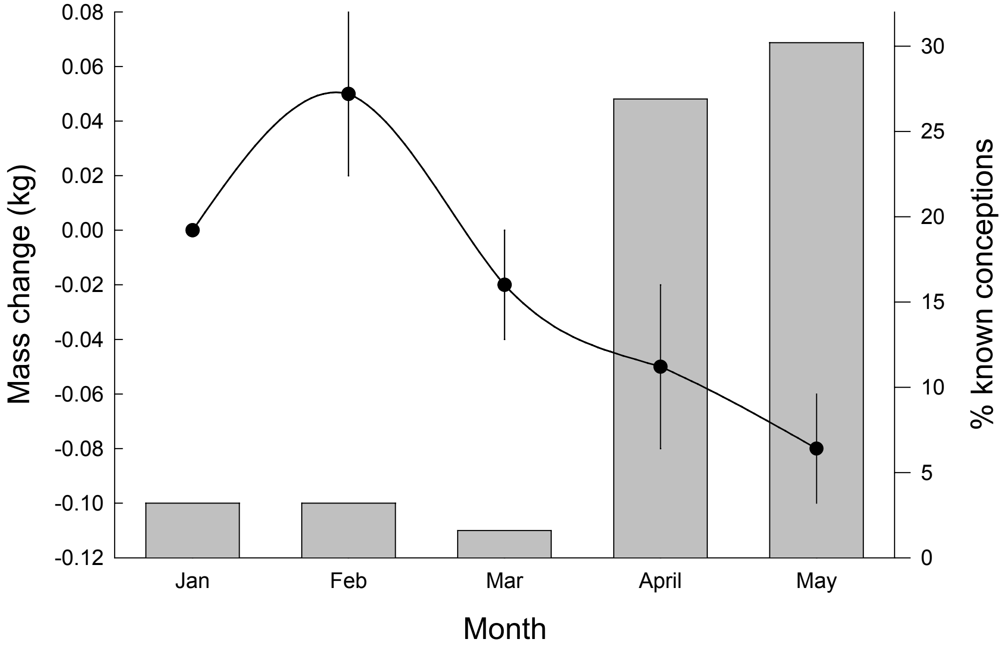

Figure 7.1: Absolute change in mass in male possums over the main breeding season (solid line), plotted against the percentage of known conceptions at the study site each month (shaded columns). Change in body mass each month was calculated for individual males and the means (kg ± standard error) are shown. Masses were standardised to account for variation among individuals at the start of the breeding season, thus mass of all males is 0 in January.

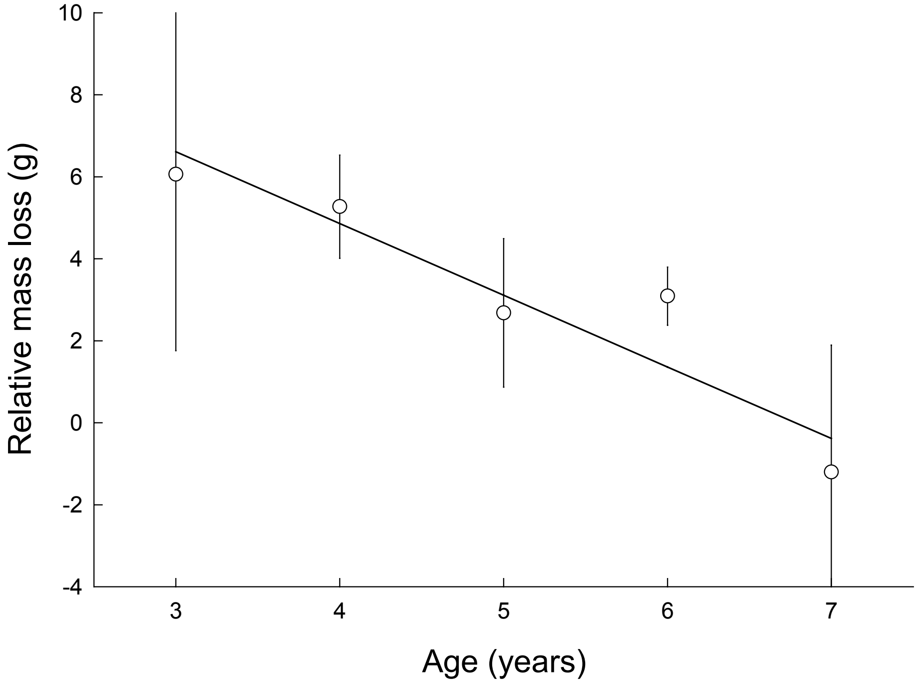

Figure 7.2: The relationship between relative mass loss (% mass lost from January – May) during the breeding season and male age. Circles indicate means for each age class (± standard error). The line is that predicted from a least-squares linear regression on all data (see text).

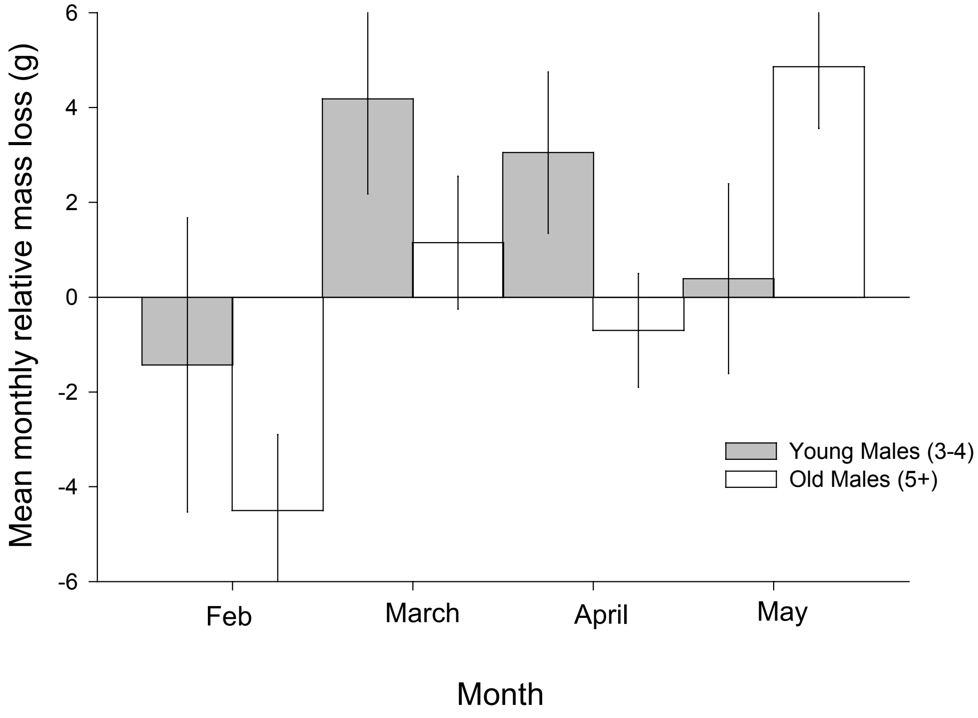

Figure 7.3: Mean (+ standard error) monthly relative mass loss for old males (open columns) and young males (grey columns).

comparable amount of body mass during the breeding season as females do during the energetically expensive period of lactation (Chapter 4).

FORAGING VERSUS REPRODUCTION

The results demonstrate that most adult males lose some mass during the breeding season, suggesting that foraging behaviour is traded-off against mating behaviour during the breeding period. Winter (1976) observed that male possums often failed to feed when in consort with a female. Coltman et al. (1997) similarly found that male harbour seals (*Phoca vitulina*) lost mass when making shallow dives associated with mating behaviour. Alberts et al. (1996) also determined that mate-guarding and consortship behaviour constrained foraging activity in wild baboons (*Papio cynocephalus*).

AGE-SPECIFIC REPRODUCTIVE EXPENDITURE: IMPLICATIONS FOR MATING STRATEGY

The observed pattern of age-related reproductive expenditure in male possums is quite different to that found in ungulates, where reproductive effort (similarly measured as mass loss) increases up to prime-age and then decreases in very old individuals (Kojola 1985; Yoccoz et al. 2002; Mysterud et al. 2003). This pattern has been explained in terms of harem holders (peak-age males) experiencing a higher somatic cost compared to the lower cost ‘sneaker’ strategy exhibited by males unable to hold a harem (Yoccoz et al. 2002). The mating system and strategy of *T. vulpecula* differs markedly from that of the temporary harem polygyny displayed by many cervids. Female possums are solitary and spatially dispersed year round, making it difficult for one male to control large numbers of females (Isaac & Johnson 2003; Chapter 6). It is probable then that dominant male possums will try to successively consort with receptive females as they come into oestrus. In support of this idea, Winter (1976) observed that male possums switch their consorting behaviour from one female to another immediately following mating.

According to the priority-of-access model, older, dominant males should gain priority of access to receptive females when other males are present (Fisher & Lara 1999). The pattern of reproductive expenditure shown here suggests that older, more dominant individuals may have to invest less time in finding and gaining access to receptive females, while younger males may have to search and compete for females to a much greater degree resulting in a higher somatic cost. Previous studies on *T. vulpecula* have suggested that not only are dominant males able to exclude subordinate males from receptive females (Winter 1976), but also that females may ‘choose’ dominant sires (Day et al. 2000). In another solitary marsupial, the bridled nailtail wallaby (*Onychogalea fraenata*), priority of access to oestrous females was primarily influenced by male body mass, which was closely correlated to age (Fisher & Lara 1999). These results are also in support of a recent study where, contrary to predictions from previous ungulate studies, older bighorn rams which employed a tending (mate-guarding) mating tactic did not lose more mass during the rut, and were observed foraging more often, than younger males which used the alternative coursing strategy (Pelletier 2004).

‘TARGETED’ EFFORT IN OLDER, WISER MALES?

Winter (1976) determined that the home ranges of male brushtail possums could be separated into two groups based on age; older males, those in at least their fourth year, had established home ranges that changed very little over time. Younger males, however, were in the process of establishing themselves and often shifted their centre of activity. Similar results have been found in roe deer bucks, with prime aged males showing high home range stability while young males ranged widely (Rossi et al. 2003). Older male possums that are long-term residents of the site may therefore benefit from having an established territory which overlaps that of a number of females, making it easier for them to serially consort with, and guard, consecutive females over the breeding season. In arctic ground squirrels (*Spermophilus parryii plesius*), more than 90% of monitored females mated with the male upon whose territory they resided. Moreover, these males were also most likely to gain first access to neighbouring females as they came into oestrus (Lacey & Wieczorek 2001). By contrast, younger males may travel extensively, employing a roaming strategy, to find receptive females (Sandell & Liberg 1992).

Older males may also have prior information about the reproductive status of the resident females that overlap their home range, allowing them to concentrate their mating behaviour during a shorter, but more productive, period with each female. Support for this theory comes from chacma baboons (*Papio hamadryas ursinus*); high-ranking males were found to consort less often, and for fewer days, than expected but consorted more often with females during their conceptive cycle than their nonconceptive cycle (Weingrill et al. 2003). The authors suggest that males with longer residency have more information about the reproductive state of females (Weingrill et al. 2003).

There was evidence that older males increased their reproductive expenditure late in the mating season, while younger males did not. As oestrus synchrony increases during April and May, younger, subordinate males may exploit the fact that more competitive males are involved in consorting and mating with females elsewhere and as a result gain greater access to receptive females (Say et al. 2001; Isaac & Johnson 2003). In racoons (*Procyon lotor*), an increase in oestrus synchrony has been shown to result in greater access to receptive females for subordinate males (Gehrt & Fritzell 1999). Thus, older males may target their reproductive effort, by increasing costly behaviours such as mate-guarding and direct conflict, toward later in the mating season as the number of receptive females increases. Ongoing paternity analysis in the

Magnetic Island populations will be crucial in ascertaining how these patterns of mass loss relate to actual mating success.

CHAPTER 8

General Discussion

Aims of the thesis

My study sought to investigate life history variation and reproductive success in a marsupial, the common brushtail possum, in tropical northern Australia. Specifically, the work contained in this thesis addressed the following aims:

1. To determine general life history and demographic patterns in male and female *T. vulpecula* at the Magnetic Island study site.
2. To assess the extent of individual variation in life history traits among female *T. vulpecula* and determine how this affects maternal investment strategy through age-specific variation in reproductive effort and offspring sex allocation.
3. To determine how variation in breeding seasonality and population density among *T. vulpecula* populations in northern Australia influence male body size and the degree of sexual size dimorphism.
4. To investigate patterns of male reproductive effort, with particular reference to potential differences in age-specific mating strategy.

In this chapter I will summarise the key findings of this thesis and discuss their relevance to contemporary theories in evolutionary and behavioural ecology. I will also assess the value of my results to conservation and management issues and identify promising areas for further research.

Life history of Magnetic Island possums

In general, the life history traits of *T. vulpecula* on Magnetic Island were similar to those identified for the species elsewhere (i.e.: Winter 1976; Kerle & Howe 1992; Kerle 1998; How & Hillcox 2000). The majority of females produced their first offspring at two years of age and continued to produce at least one offspring each year during their life (Chapter 3). The main breeding season occurred during autumn, but births were observed in all months during the study and a second smaller birth peak occurred in spring when a number of, generally older, female possums produced a second young (Chapters 3 and 4). Females produced an average of 1.23 offspring per year (Chapter 3). Survival remained high for females until their sixth year of life, when it declined rapidly, concurring with results found in New Zealand populations of *T. vulpecula* (Brockie et al. 1981; Efford 2000). Thus, an average female on Magnetic Island, maturing at 2 years of age and living to 6.5 year of age, could be expected to produce 6 or 7 offspring during her lifetime. This result is similar to that proposed by Brockie et al. (1981) who estimated that a typical female in New Zealand could produce 6 offspring in her lifetime. However, in the Northern Territory, females produce an average of 1.7 young/year, and thus in this population, assuming females show a similar age specific schedule of fecundity and survival, each female could produce seven or eight young during her life (Kerle 1998). Kerle (1998) suggests that higher fecundity in these possums is likely due to year round food availability allowing continuous breeding in females.

Female possums exhibit a slow life history relative to that of similar sized herbivorous eutherian mammals such as the snowshoe hare (*Lepus americanus*), which can become sexually mature by four months of age, produce an average of 8 young per year and live for up to 5 years (Sinclair et al. 2003). However, many primates demonstrate a slow life history in comparison to other mammals (Richard et al. 2002) and female *T. vulpecula* show a life history strategy which is remarkably similar to some of the comparably sized folivorous, arboreal lemurs. The relatively low basal metabolic rates and slow life history characterised by many folivorous, arboreal mammals is suggested to be due to both the low available nutrient content of foliage and low activity levels associated with an arboreal lifestyle (McNab 1995). Thus, female possums appear to be constrained by their largely folivorous diet and arboreal existence to relatively low fecundity.

The life history strategy of male *T. vulpecula* on Magnetic Island differed from that of females. Males became sexually mature at the slightly later age of 3 years (Chapter 3) and these results concur with those of Clinchy (2000), who similarly used testis length as an indicator of maturity, but on a much smaller sample size of known age males. Males also demonstrated a faster age-specific growth rate than females and as a result were heavier than females as adults (Chapter 3). These results agree with the general prediction that in polygynous mammals selection should favour phenotypic adaptations, such as a rapid growth rate and larger body size, that enhance the ability of a male to prevail in male-male contest for females (Clutton-Brock et al. 1982). However, in contrast to other populations of *T. vulpecula* in Australia, levels of sexual dimorphism on Magnetic Island were relatively low and I propose that this is due to breeding seasonality influencing the potential for polygyny among populations (Chapter 6). Patterns of age-specific reproductive effort also differed between the sexes. Females increased their reproductive effort with age, consistent with the general predictions of the residual reproductive value hypothesis (Chapter 4). However, older male possums lost less mass during the mating season, suggesting that they decreased their reproductive effort as they aged and I argue that this pattern may reflect age-specific differences in mating strategy between young and old males (Chapter 7).

The study site was estimated to contain about 50 resident individuals (Chapter 3) at approximately 7 possums ha^{-1} known to be alive at any time (Chapter 6). This is considerably higher than densities previously reported for most Australian populations, however densities as high as 25 possums per hectare have been reported in New Zealand podocarp-broadleaf forest (Efford 2000). The high densities found in New Zealand have been attributed to a suite of interacting factors, including a lack of large predators, absence of interspecific competition and access to relatively high quality food resources (Efford 2000). These factors are also likely to contribute to the observed densities on Magnetic Island, which has none of the large predators known to predate possums on the mainland (Chapter 2) and only one other arboreal folivore, the koala. On the mainland, at the Mount Fox study sites (Chapters 4 and 6), the number of suitable den trees was found to be a limiting resource for the population (Johnson et al. 2001). On Magnetic Island possums den in rock crevices, which are highly abundant, and this may also go some way to explaining why the Island can sustain such high population densities. There was no evidence from my study to suggest that possum numbers, or population processes, at the study site were influenced by season (Chapter 3) and there was little variation in numbers over the three years of the study (Chapter 3). These results agree with those of Efford (2000) who found that the dynamics of possum populations are generally stable through time and fluctuate within fairly narrow boundaries.

Do possums show life history trade-offs?

A central premise of life history theory is that resource limitation will result in trade-offs between life history traits, whereby an increase in allocation of resources into one trait will result in constraints on an associated trait (Stearns 1992). During a food supplementation experiment (Isaac et al. 2004 [Appendix II]), possums were found to gain mass in direct relationship to the amount of supplemental food they consumed. Furthermore, following a fire that burnt half of the study site in 2002, there was an increase in both recruitment and population size in the burnt area, suggesting that regeneration of vegetation resulted in an increase in food quality and quantity following the fire (Appendix I). These results indicate that, to some degree at least, the individuals and the population on Magnetic Island may be constrained by food availability. In support of this suggestion, young females were found to bias the sex ratio of their offspring towards males, indicating that the potential for resource competition with philopatric offspring influences life history (Chapter 5). Further, sex of offspring in older mothers depended on maternal condition, which should reflect access to resources (Chapter 5). Females also increased their allocation of somatic resources into reproduction progressively as they aged and this appeared to result in a decline in body mass and condition (Chapters 3 and 4), indicative of a trade-off between current and future reproduction and survival (Stearns 1992).

I also found evidence that male possums made life history trade-offs. My results suggest that male possums may have only three breeding seasons in which to reproduce; based on testis length, males became sexually mature at 3 years of age (Chapter 3) and body mass, condition and survival declined rapidly in males older than five years (Chapter 3). Furthermore, assuming a polygynous mating system where reproductive success is at least partly influenced by mass and size, reproductive success as a 3 year old is unlikely to be high. While not as extreme as the semelparous strategy of some male didelphids and dasyurids, male possums still appear to demonstrate a short reproductive lifespan compared to other similarly sized mammals. Reproduction, in terms of mass loss during the breeding season, was found to be particularly costly for young males and there is also some evidence males may trade-off foraging in favour of mating behaviour (Chapter 7). The age-specific pattern of reproductive effort in possums (Chapter 7) suggests that, like some other marsupials, males may adopt a ‘live-fast, die-young’ life history strategy whereby increased reproductive effort as a young adult results in early onset of senescence.

It has also been suggested that growing to, and maintaining, a larger body size can result in costs to the larger sex in dimorphic species (Key & Ross 1999) and male possums could incur further costs that may be associated with their larger size. Costs associated with larger size have been suggested to include accelerated tooth-wear due to increased food demand (Owen-Smith 1993), pressure of maintaining larger body size during periods of reduced food availability (Powell & King 1997) and an increased parasite load (Moore & Wilson 2002).

Intraspecific variation in possum life history traits

I found considerable density independent variation in life history traits both among individual possums and among geographically distinct populations. Age at first breeding in females varied among individuals; while the majority of females produced their first young at 2 year of age, some females successfully bred as yearlings (Chapter 3). Variation in age at maturity can have important implications for population growth, dynamics and life history (i.e.: Oli & Dobson 2001). Date of parturition and number of offspring produced per year also varied among individual females and the source of this variation had a strong age-specific component in both cases (Chapter 4). Offspring born to older mothers (Chapter 4) and mothers in good condition (Chapter 5) had a relatively greater mass compared to other offspring, indicating that maternal effects operate in possums. There is evidence that both date of birth and mass as a juvenile can influence offspring in the long term, resulting in life history variation among individuals as adults (Albon et al. 1987; Clutton-Brock et al. 1987b; Gaillard et al. 1993; Festa-Bianchet et al. 2000).

In males, I identified variation in reproductive effort that may be reflective of differences in age-specific mating strategy among individuals (Chapter 7). There was also variation in the extent of male-biased sexual dimorphism among populations, which appears to relate to differences in mating system (Chapter 6). I also found some evidence of a density dependent influence on male life history; in high-density populations males had a lower body mass, suggesting that intraspecific competition may constrain growth in males (Chapter 6).

Implications for conservation and management

Many mammal populations are now the targets of management programs and there are numerous reasons why we would want to manage a particular species; for human exploitation, either as a resource or for sport hunting; because it is a pest; or because the species and/or its habitat is endangered or threatened (Festa-Bianchet & Apollonio 2003). In the past, management programs have been based primarily upon population counts, which have low precision and can lead to erroneous assessments of population trends (Gaillard et al. 2003). The life history of a species may largely determine the relative importance of the intrinsic and extrinsic factors that contribute to population growth and dynamics and knowledge of a species' life history is now considered essential for effective management of target species (Gaillard et al. 2003; Lande et al. 2003). The addition of life history variables into realistic demographic models can provide accurate predictions of population growth rates and estimates of population parameters (Gaillard et al. 2003). Knowledge of reproductive behaviour can also significantly alter the predictions made in management models for species (Côté 2003). Côté (2003) further highlights a number of ways in which information on life history and reproductive behaviour can be used to contribute to the conservation and management of a particular species, including predicting the effects of habitat loss, the effects of exploitation and the risk of extinction.

In Australia, more than 20 species of mammal have become extinct since European settlement, while many more have suffered declines in range and abundance (Short & Smith 1994). Those with intermediate body-size and low reproductive rates have been identified as the most intrinsically extinction-prone (Johnson 2002; Johnson et al. 2002). While patterns of mammal extinction and decline have previously been most evident in the arid zone (Burbidge & McKenzie 1989), declines are now extending into the north and the mammals of the wet-dry tropics can no longer be assumed secure (Woinarski et al. 2001).

Although *T. vulpecula* is currently one of Australia's most widely distributed native mammals, it is thought to be in decline in a number of regions including the Northern Territory, Cape York peninsula and Western Australia (How & Hillcox 2000; Kerle 2001). For populations in decline, population viability analysis (PVA) can provide a useful tool for predicting population trends under different scenarios (Beissinger & Westphal 1998). However, the power of PVA to accurately predict extinction risk is dependent upon the reliability of data entered into the population model (Coulson et al. 2001). Recent studies have determined that complex, age-structured models, incorporating traits such as mating system (Sæther et al. 2004), social system (Grimm et al. 2003) and sex-specific survival (Gaillard et al. 2003) are likely to give the most accurate predictions. The effects of habitat loss on food and den availability, and the influence of predation, should also be considered in models investigating PVA in possums.

The results of this study could also be usefully applied in management plans to control, and eventually eradicate, *T. vulpecula* in New Zealand. As mentioned previously, *T. vulpecula* occurs at very high densities across New Zealand and causes widespread damage to the fragile New Zealand ecosystem by defoliating native forests, predating endangered native birds and their eggs and is also a reservoir of bovine tuberculosis (Coleman & Caley 2000). As a result, *T. vulpecula* is listed by the IUCN as one of the 100 worst invasive species (IUCN 2003a). Recent research has shown that populations and individuals can respond quickly, in terms of their life history, to the pressures of hunting, exploitation and control by humans (Jachmann et al. 1995; Coltman et al. 2003). Thus, population reduction by culling in New Zealand may result in a cascade of compensatory effects including a decline in age at maturity, reduced interspecific competition for resources and a potential increase in individual breeding success, and perhaps the percentage of females that double breed. Sarre et al. (2000) also propose that the polygynous mating system displayed in their study population should facilitate the spread of an immunocontraceptive agent within

New Zealand populations. However, this study demonstrates that the degree of polygyny among populations can be highly variable and should therefore be an important consideration in future management plans focussing on immunocontraception.

In Tasmania, *T. vulpecula* has been commercially exploited for it's meat for many years. However, an important development that may impact negatively on Tasmanian possums is the recent confirmed introduction of the red fox (*Vulpes vulpes*) to Tasmania. Life history and demographic data should thus be employed in future management plans to assess the responses of possum populations and individuals to the combined pressures of commercial harvesting and fox predation, in order to ensure a safe future for Tasmanian possums. Gaillard et al. (2003) stress that incorporating sex specific differences in mortality into management models can produce significantly lower estimates of population size and propose that where sex-biased survival is likely to occur, as it appears to in possums (Chapter 3), management must be based on sex structured models to prevent overexploitation. Given the wide variation in life history and demography among possum populations across their native and introduced range, it seems vitally important that any attempt to model population responses, either for control or conservation purposes, should use life history and demographic data specific to the target population.

In a broader context, the results of my study could also be used in management plans for similar marsupials which lack such detailed life history data. Compared to other groups of Australian mammals, nocturnal, arboreal mammals appear to have fared relatively well, in terms of extinctions and declines, to date (Johnson 2002). However, a number of arboreal, folivorous marsupials are classified as nationally vulnerable or endangered, including Leadbeater's possum (*Gymnobelideus leadbeateri)*, the mahogany glider (*Petaurus gracilis*) and the western ringtail possum (*Pseudocherius occidentalis*) (IUCN 2003b). The koala (*Phascolarctos cinereus*) is classed as vulnerable in

New South Wales (Lunney et al. 2002) and a number of other species are declining across their range (Woinarski et al. 2001). *T. vulpecula* has many traits which make it a good general ecological model for management plans involving lesser studied marsupials. Possums range in body mass from >3.5 kg to <1.5 kg and have a relatively low reproductive rate for their body mass, life history traits which typify taxa that have suffered the most serious declines or extinctions in Australia (Johnson et al. 2002), and also share many life history traits with other arboreal, folivorous marsupials. In terms of habitat and diet requirements, the common brushtail possum is one of the most adaptable of arboreal marsupials. Thus the species could also be used to predict the response of more specialised species to anthropogenic factors such as habitat disturbance and prescribed burning regimes, as any negative effects would likely be amplified in species with more specialist diets and habitat requirements.

Directions for future research

Continuing studies on the Magnetic Island population and long term monitoring of individuals with known life histories will provide a valuable extension of this study. For example, further data could reveal the adaptive benefits, and potential costs in terms of future survival and reproductive success, of early breeding in those females that bred as yearlings. By continuing the study into the long term, a comparison of lifetime reproductive success between the sexes could be made, which could establish what factors contribute to sex-specific differences in survival. It would be interesting, for instance, to combine paternity analysis with data on survival and condition among individual males to determine whether male possums exhibit the ‘life fast, die young’ strategy identified in other marsupials. As well as identifying the life history parameters that influence paternity success in males, molecular techniques could further be employed to establish the nature of philopatry and matrilineal structure among females. Investigating the ‘cohort effect’ also requires considerable long-term data, which could reveal the effects of shorter-term environmental factors, such as fire and drought, on individuals and the population. Further research could also help identify the influence of life history variation on long-term population dynamics and growth.

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APPENDIX I

Demographic responses of an arboreal marsupial, the common brushtail possum, to prescribed fire

(Submitted for publication [*Oryx*])

Abstract Changed fire regimes have been implicated as an important factor in the recent rapid decline of many Australian mammals and, as a consequence, prescribed burning is now used as a conservation tool in a number of species-specific management plans. However, information regarding the effects of fire on arboreal marsupials is scarce. In this study I use the common brushtail possum (*Trichosurus vulpecula*) as a model, medium-sized arboreal marsupial to look at changes in population processes and individual life-history traits before and after a prescribed fuel reduction burn on Magnetic Island, tropical north Queensland. Possums were live-trapped every month for 12 months pre-fire and 12 months post-fire in both the burnt and unburnt site, measurements of individuals were taken each month and population parameters were modelled using capture-mark-recapture data. Recruitment into the population at the burnt site increased significantly following the fire, which resulted in higher population densities that persisted for at least 12 months post-fire. There was no apparent influence of the fire on immediate or long-term survival, body condition or female reproductive success of possums at the burnt site. The results are discussed in terms of their relevance to future plans incorporating fire management in the preservation and conservation of Australian mammals.

INTRODUCTION

More than 20 species of mammal have become extinct in Australia since European settlement, while many more have suffered declines in range and abundance (Short & Smith 1994; Wilson & Friend 1999). Early research suggested that most at risk were those species within what has been termed the ‘critical weight range’ (Burbridge & McKenzie 1989) of between 35 – 5500g. However, more recently species with intermediate body-size, particularly from non-forested habitats, and those with low reproductive rates have been identified as being most intrinsically extinction-prone (Johnson 2002; Johnson *et al.* 2002). While patterns of mammal extinction and decline have previously been most evident in the arid zone (Burbridge & McKenzie 1989), declines are now extending into the north and the mammals of the wet-dry tropics can no longer be assumed secure (Woinarski *et al.* 2001).

A suite of, often interacting, factors have been implicated in mammal declines in Australia, including introduced predators, land clearance, habitat fragmentation and modification and changes in fire regime (Wilson & Friend 1999). Pre-European settlement, Aboriginal burning patterns created a mosaic of vegetation which provided a diversity of habitats, with unburnt areas suitable for shelter and regenerating areas thought to provide more food resources (Wilson & Friend 1999; Letnic 2002). Mosaic burning has therefore been proposed to play an important role in facilitating mammal populations and encouraging a diverse mammalian fauna (Letnic 2002). A lack of regular, active fire management can also result in a higher frequency of wildfires, which often encompass very large areas and are of high intensity, resulting in a decline in vegetation structure and floristic diversity (Wilson & Friend 1999; Letnic 2003). As a consequence, fire management, and particularly fire mosaics, are now commonly used and promoted as management tools to increase biodiversity (Letnic 2002; Wilson & Friend 1999). Indeed, species-specific conservation plans for a number of native Australian mammals now include the reintroduction of traditional mosaic-burning regimes (Vernes 2000; Wilson & Friend 1999).

However, Pardon *et al.* (2003) caution that mammals can be vulnerable to poor fire management and even low-medium intensity fires can have unfavourable effects on mammal populations. Immediate effects of fire may include direct mortality as a result of flames or smoke (Silveira *et al*. 1999) and increased predation risk due to a reduction in ground cover immediately following fire (Christensen 1980; Vernes 2000). Other effects may include a decline in food resources in burnt areas, which may have an indirect impact on other areas of the behaviour and ecology of a species.

Previous studies investigating the effects of fire on native Australian mammals have been strongly biased toward small-bodied and/or ground dwelling species (Claridge & Barry 2000; Vernes 2000; Letnic 2002; Letnic 2003; Pardon *et al*. 2003), whereas few studies have addressed larger mammals and in particular, as noted by Wilson & Friend (1999), research on the effects of fire on arboreal mammals is scarce (but see Lindenmayer & Possingham 1995; Van der Ree & Loyn 2002). Furthermore, while a number of studies have looked at the influence of fire on survivorship, distribution and abundance (Claridge & Barry 2000; Vernes 2000; Pardon *et al.* 2003), little is currently known of how fire can influence individual life-history traits, such as body condition and reproductive performance, which have the potential to influence population growth and dynamics.

Body condition has been related to female reproductive success in a wide-variety of mammalian species (Festa-Bianchet 1998; Boyd 2000; Ramsey et *al.* 2002), with females in relatively good condition having greater reproductive success. Indeed, studies have found that if females fall below average body condition they may fail to breed at all (Ramsey *et al.* 2002). Thus, if fire results in a decline in food availability, and a consequent decrease in body condition in individuals, this could be critical for endangered mammals, particularly in small, isolated populations which are inherently more vulnerable to disturbance factors (Lunney *et al.* 2002).

Nocturnal, arboreal mammals are often considered to be less at risk from disturbance factors than other mammals and this is thought to be due to their ability to shelter in tree hollows and other den sites (Johnson *et al.* 2002; Wilson & Friend 1999). However, while Lindenmayer & Possingham (1995) found that populations of Leadbeater's possum (*Gymnobelideus leadbeateri*) were vulnerable to intensive wildfires, few other studies have investigated the potential effects of fire on arboreal mammals. In this study, I use the common brushtail possum (*Trichosurus vulpecula)*, a medium sized, arboreal marsupial, as a model native Australian mammal to investigate the effects of a prescribed fire on demographic processes, body condition and female reproductive success. *T.*

vulpecula is currently one of Australia’s most widely distributed native mammals (Kerle 2001) but despite this wide-range and the adaptable nature of the species, brushtail possums are currently thought to be in decline in the arid zone (Kerle *et al*. 1992), Cape York peninsula (Winter & Allison 1980) and Western Australia (How and Hillcox 2000). Kerle (1998) has also suggested that fire may result in unfavourable conditions that could impact negatively on possum populations in the Northern Territory. Brushtail possums range in body mass from >3.5 kg (Tasmania) to <1.5 kg (Northern Territory) and also have a relatively low reproductive rate for their body mass - traits which typify taxa that have suffered the most serious declines or extinctions (Johnson *et al.* 2002). Reproductive success in female possums is also condition dependent (Ramsey *et al*. 2002)

METHODS

Study site, study species and fire

Possums were studied for a total of 23 months (July 2001 – June 2003) on a ~10ha site in mixed open eucalypt woodland on Magnetic Island, North Queensland (19˚10’S, 146˚50’E). Magnetic Island is a high continental island with elevations of up to 540m and an area of approximately 5184 ha (Fig. 1a). More than half of the Island is National Park and is dominated by large hills and spurs, covered with extensive granite outcroppings. The climate on the Island is tropical and highly seasonal, with a dry winter season from May to October and a wet summer season from November to April. The most predominant tree species on the island are from the genus *Eucalyptus*; the study site also contained the native yellow kapok tree (*Cochlospermum gillivraei*), *Acacia* spp and *Melaleuca* spp.

Possums occur at densities of ~7 possums/ha at the study site (Isaac & Johnson 2003) and have been observed to den primarily in rock crevices (J. Isaac, unpublished data). There are very few native predators of mammals on

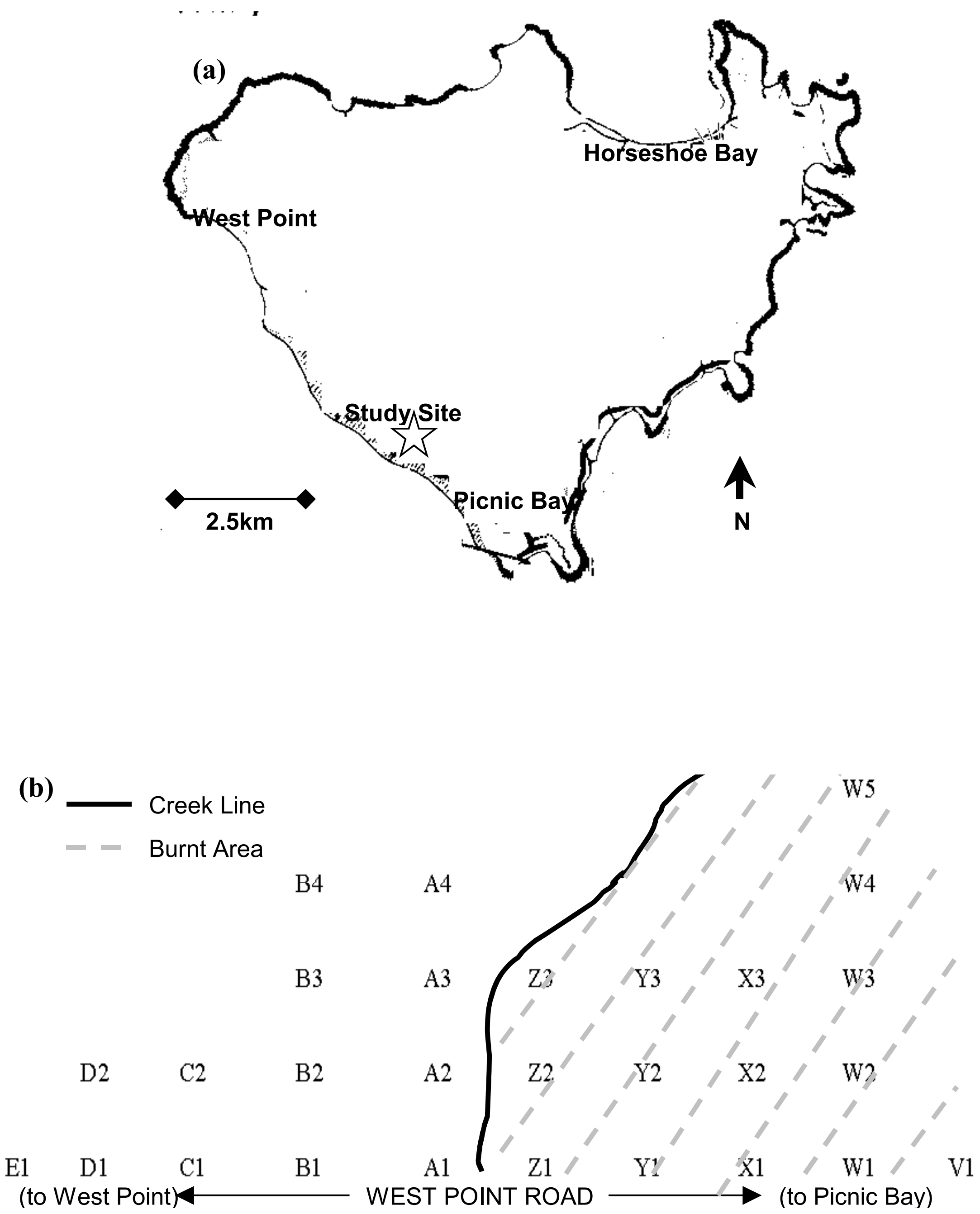

Figure 1: Maps of the study area and site. (a) Map of Magnetic Island; the star shows the location of the study site. (b) Diagram of the trapping grid at the study site, individual trap sites (each with 2 traps) are labelled by a letter and number. The area which burnt during the fire is indicated by the grey shading.

the Island, apart from the boid snakes (amethystine python: Morelia amethistina, carpet python: Morelia spilota) and Fearn (1998) has suggested that these species are present only at low density. A trapping grid was established at the site in 2001 consisting of 28 trap sites, with two traps per site, spaced at approximately 25m intervals. Possums were live-trapped at the site once monthly, for two or three consecutive nights, during the study period. Possums caught during trapping sessions were PIT tagged, measured, weighed and released at the point of capture.

A fire burnt through approximately half the study site in July 2002 (early-mid dry season) as part of an Island-wide fuel reduction burn organised by Queensland Parks and Wildlife Service. The fire was of low-medium intensity and generally removed only ground cover in most areas. In the burnt area of the site, >90% leaf litter was consumed and approximately 50% logs, while the canopy was left mostly intact. There were areas of unburnt vegetation present within the burnt area (mosaic pattern). A total of 13 trap sites (26 traps) were located in the unburnt, control area and 15 (30 traps) in the burnt area. A creek (dry at the time) in the centre of the grid acted as a fire-break (Fig. 1b).

Estimation of demographic parameters

Demographic responses of the populations inhabiting the burnt and unburnt area were modelled separately from capture-mark-recapture data using a full Jolly-Seber model for open populations in the program EcoMeth (Krebs 1998). The Jolly-Seber model gives estimates of monthly survival (the probability an animal alive in one trapping session will be alive the following session), recruitment of individuals into the population (incorporating both births and immigration) and population size (number of individuals). Animals known (from live-trapping data) to move between the burnt and unburnt areas of the grid were allocated to the unburnt area for analysis.

Life-history parameters

A condition index (CI) was calculated for each adult (males: testis length ≥ 18mm, females: invaginated pouch) animal during the study period as the ratio of their observed mass to that predicted from a regression of body mass on head length for all animals. Regression of body mass on head length was calculated separately for male and female animals:

Males: CI = (actual mass)/-1.2334+(0.03559*head length)

Females: CI = (actual mass)/ -1.2439+(0.03546*head length)

In terms of reproductive success, sexually mature (invaginated pouch) females were classed as successful if they reared an offspring to independence and unsuccessful if they lost an offspring during the lactation period (determined from monthly live-trapping sessions). All mature females attempted to breed in all years.

Statistical analysis

An initial comparison (using a Students t-test) was made between the burnt and unburnt areas incorporating data collected from all 23 months in order to determine if any intrinsic differences in the demographic and life-history variables measured were evident. Data was categorised into three time periods in order to compare the population pre-fire, immediately post-fire, and 5-10 months post-fire; time period 1 was therefore the 12 months prior to the fire (July 2001 – June 2002), period 2 was the 5 months immediately post-fire (August 2002 – Dec 2002) and time period 3 the following 5 months (Jan 2003 – June 2003). Analysis of variance (ANOVA) was then used to investigate any immediate and delayed effects on the population post-fire.

For analysis involving body condition I included only data from five adult males and five adult females, from each site, which were present during the entire study period. These animals were matched, as far as possible for initial body mass, condition and age between the burnt and unburnt sites. Change in condition over the study period was calculated as any change from initial condition, in order to account for the fact that repeated measurements were taken for each individual; initial condition was that taken in July 2001, standardised to 0 for each animal.

RESULTS

Demographic responses

During the 2 years of the study, recruitment did not differ between the burnt and control sites (Fig. 2a: T = 1.29, P = 0.2, d.f. = 42) and recruitment into the control area did not differ between the three time periods of interest, pre- and post-fire (ANOVA: $F_{2,\,21} = 2.22$, P = 0.13, n = 22). However, recruitment into the burnt site increased during time period 2, immediately post-fire, and was significantly higher during this time compared to periods 1 and 3 (ANOVA: $F_{2,\,21} = 4.84$, P = 0.02, n = 22). Results indicate that recruitment of both male and female individuals contributed to this increase (Fig. 2b).

Estimated population size was significantly higher in the control ($\bar{x}$ **=** 28.3 $\pm$ 0.71) area than in the burnt ($\bar{x}$ **=** 22.5 $\pm$ 0.71) site over the study period (Fig. 3: T = -5.7, P < 0.0001, d.f. = 42). In the burnt area, population size was significantly greater in periods 2 and 3 – post-fire, compared to period 1 – pre-fire (ANOVA: $F_{2,\,21} = 15.28$, P < 0.0001, n = 22). At the control site, there was some evidence that population size declined during period 3, in comparison to periods 1 and 2, although this results was significant only at the 10% level (ANOVA: $F_{2,21} = 3.04$, p = 0.07, n = 22).

Monthly survival probability did not differ between the burnt and unburnt sites during the study (T = 0.087, P = 0.93, d.f. = 42), nor did survival probability change over the period of the study within either site (ANOVA: P > 0.2 in both cases).

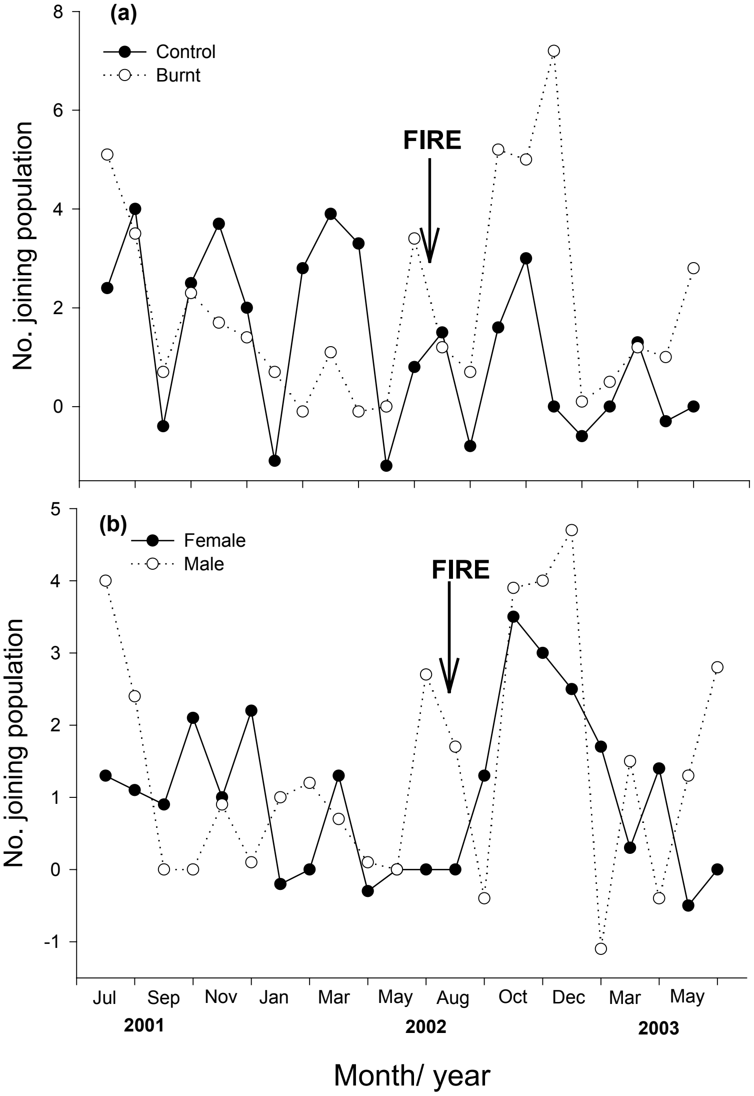

Figure 2: **(a)** Patterns of recruitment in the burnt and control areas during the study. The burnt area is shown by the dashed line and open circles, the control area by the solid line and filled circles. **(b)** Recruitment of male and female individuals into the burnt area during the study; males are shown by the dashed line and open circles, females by the solid line and filled circles. Timing of the fire is labelled on both graphs, standard errors have been omitted for clarity.

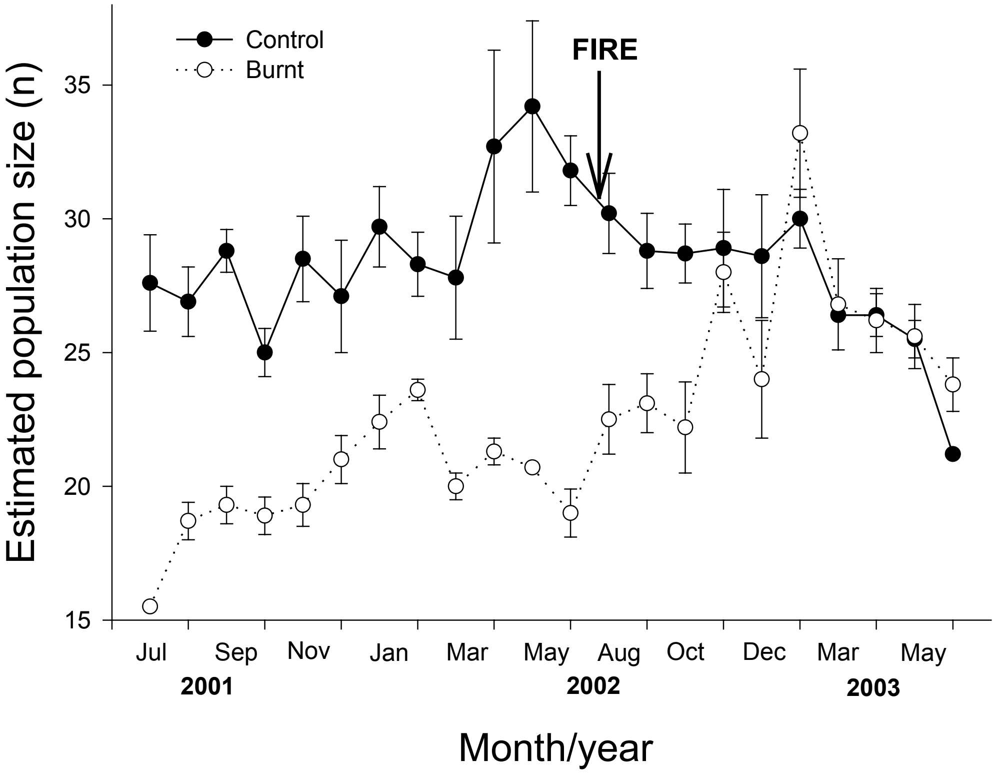

Figure 3: Changes in estimated population size in the burnt and control areas during the study. The burnt area is shown by the dashed line and open circles, the unburnt area is shown by the solid line and filled circles. Error bars show standard errors calculated by the Jolly-Seber model for open populations (Krebs 1998).

Life-history responses

An intrinsic difference in body condition was found between the burnt and unburnt areas; during the study female (T = -3.15, P = 0.003, d.f. = 41) and, to a lesser degree, male (T = -1.72, P = 0.09, df = 41) animals in the burnt area were consistently in poorer condition than those in the unburnt area. All females showed a decline in condition following the lactation period (May-Nov). However, there was no evidence that mean body condition changed over the study period within either site for males or females (Fig. 4a, 4b: ANOVA: P > 0.2 in all cases).

During the three breeding seasons included in the study, females in the burnt site were more likely to lose offspring during lactation (32%) than those in the control (10%) area (χ^2 **=** 2.5, P = 0.04). However, there was no evidence that the fire exacerbated this pattern; during the breeding season in which the fire occurred (2002), 1 female from each site lost a pouch young and both these females were older than average (J. Isaac, unpublished data).

DISCUSSION

Demographic consequences of the fire

Prior to the fire, population size in the burnt site was consistently lower than in the unburnt site. Following the fire however, the number of both male and female animals joining the population increased in the burnt area, resulting in a higher population size, which persisted into the following year. Recruitment did not vary over time in the unburnt site, and the number of individuals estimated to be in the population decreased slightly in 2003, resulting in population size being similar at each site by the end of the study, 12 months post-fire. These results suggest that regeneration of vegetation following the fire resulted in an increase in food quality and quantity at the burnt site and concur with those found by Moreno & Villafuerte (1995), who found that rabbit (*Oryctolagus cunniculus*) abundance (estimated by pellet counts) increased

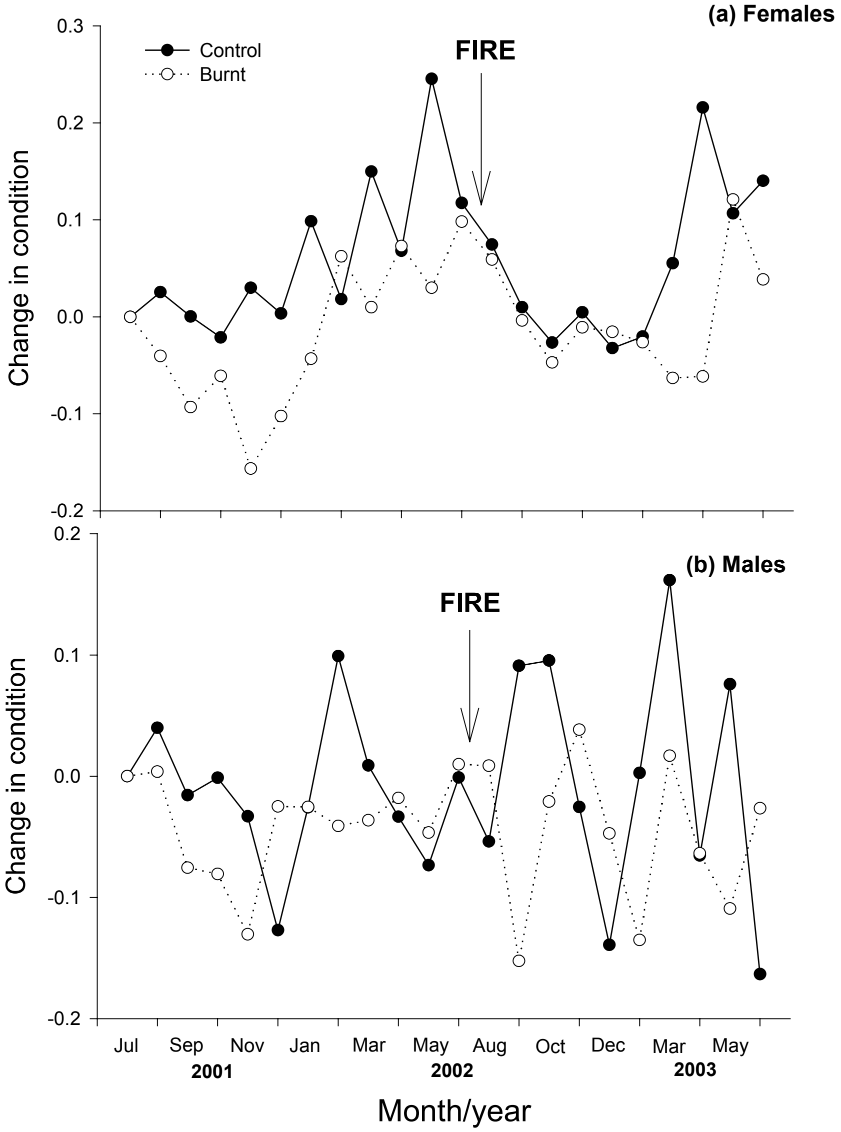

Figure 4: Changes in body condition in **(a)** adult male possums and **(b)** adult female possums during the study period in the burnt (dashed line, open circles) and control (solid line, filled circles) sites. Timing of the fire is shown on both graphs, standard errors have been omitted for clarity.

significantly after fire in dry scrubland in Spain. The authors similarly suggest that an improvement in habitat quality following fire may have resulted in the rapid rise in rabbit numbers (Moreno & Villafuerte 1995).

There was no evidence that the fire had any effect, either immediate or long-term, on possum survival. These results correspond with those of Vernes (2000) who found that post-fire survival of northern bettongs (*Bettongia tropica*) was high following a low-medium intensity fire in Queensland. Similarly, while Silveira *et al.* (1999) report finding a number of dead anteaters (*Myrmecophago tridactyla*) and other mammals following a high-intensity wildfire in Emas National Park in Brazil, no such mortalities were found when a low-intensity fire burnt through the same site the following year. On Magnetic Island, brushtail possums den almost exclusively in rock crevices and this behaviour would have protected them from direct mortality as the fire burnt through the site. Furthermore, the increase in predation noted by other authors immediately following fire (i.e.: Christensen 1980) is unlikely to occur on Magnetic Island, which has very few predators of native mammals.

Consequences of fire on life-history traits

This study is one of the first to consider changes in body condition in relation to fire in a mammal. I found no evidence that the fire had any influence, either negative or positive, on body condition for individuals resident in the burnt area. Given that the canopy remained relatively intact and the mosaic pattern of the fire left large areas of vegetation unburnt, it is unsurprising that the fire had no demonstrable negative effect on body condition. Moreno & Villafuerte (1995) speculated that increased use of burnt areas by rabbits following fire could reflect higher quality forage, which may result in an improvement in condition, benefiting survival and reproductive success. However, I found no evidence for this, as both male and female individuals were consistently in poorer condition in the burnt area, both before and after the fire.

I also found no evidence that the fire had any detrimental effect on female reproductive success, despite occurring during the period that coincided with mid-lactation in 2002. While I could find no previous studies that investigated the effects of fire on reproductive success in a mammal, the results do concur with those found in avian studies. Bond *et al.* (2002) recently concluded that wildfire had little short-term effect on reproductive success in the endangered spotted owl (*Strix occidentalis*). Similarly Artman and Downhower (2003) found no evidence that reproductive success in the wood thrush (*Hylocichla mustelina*) was influenced by a prescribed fire in a mixed oak forest in Ohio.

Conclusions

Compared to other groups of Australian mammal, nocturnal, arboreal mammals appear to have fared relatively well in terms of extinctions and declines to date (Johnson 2002). However, a number of arboreal marsupials are currently classified as nationally vulnerable or endangered, including Leadbeater's possum, the mahogany glider (*Petaurus gracilis*) and the western ringtail possum (*Pseudocherius occidentalis*) (IUCN 2003). The koala (*Phascolarctos cinereus*) is also classed as vulnerable in New South Wales (Lunney *et al.* 2002), while a number of other species are declining across their range (Kerle 2001, Woinarski *et al.* 2001). Thus, the findings of this study have important implications for conservation initiatives and recovery plans aimed at such species.

The results of this study indicate that a low-medium intensity prescribed burn, during the early-mid dry season, resulted in an increase in recruitment and population size in an arboreal, folivorous marsupial in tropical north Queensland. However, wildlife managers should be cautious when deciding how best to implement fire management in species conservation plans. In particular, the timing of prescribed burns should be a priority; seasonal timing of fire has been shown to be crucial to bandicoot (*Isoodon macrourus*) survival in the Northern Territory (Pardon *et al*. 2003). The results of this study support the conclusions of Pardon *et al.* (2003) who suggest that in the wet-dry tropics, burning in the early dry season may be the most the favourable approach for mammals.

While this study did not find any negative effect of the fire on body condition, if animals are already in relatively poor condition, due to other factors influencing resource availability, this could be exacerbated by fire and consequences could be devastating, particularly in the isolated populations which are typical of many declining species. Kerle (1998) has suggested that while possums can readily recover from short periods of unfavourable conditions, such as a low-intensity fire, perturbations such as repeated annual burning may be more difficult to overcome. A greater impact on body condition could negatively impact on female reproductive success, which could have substantial impacts on marsupial species that already have intrinsically low fecundity rates. Furthermore, the common brushtail possum is the most adaptable of arboreal marsupials in terms of diet requirements and has been documented to also eat fruit, flowers, fungi and even small invertebrates (Kerle 2001). Thus, negative effects on food availability caused by fire would likely be amplified in more specialist folivores, such as the koala and western ringtail.

The potential for direct mortality as a result of fire should also be taken into account in other populations of arboreal marsupial. Mainland arboreal marsupials are more likely to be directly affected by fire as they shelter in tree hollows, rather than the rock crevices favoured by possums on Magnetic Island. Furthermore, the possibility of an increase in avian predation following fire, due to reduced foliage cover, should also be considered in mainland populations where predators such as powerful owls (*Ninox strenua*) can have an important impact on arboreal mammals. Thus, management plans incorporating the use of fire in conservation initiatives should take into account previous environmental conditions or disturbance factors, including the intensity and frequency of previous fires, which may have already adversely affected animals. The habitat and dietary requirements of the species involved should also be considered.

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