Ecology of warru (*Petrogale lateralis* MacDonnell Ranges race) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia

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Declaration

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Cover photograph: Warru in the APY Lands wearing a VHF radio-collar. N. Staniford.

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Abstract

Australia has one of the world‟s worst rates of mammal extinctions, accounting for about one third of the mammal species that have become extinct in the world since 1600 (Burbidge and Manly 2002). Most of these documented declines and extinctions have been concentrated towards mammals in the arid-zone of central Australia. In South Australia (SA), one of the arid-zone species that has undergone substantial declines in range and abundance is the black-footed rock-wallaby, *Petrogale lateralis* (MacDonnell Ranges race). Animals are now restricted to the An̲angu Pitjantjatjara Yankunytjatjara (APY) Lands in the state‟s far north-west, where there remain two known metapopulations. The decline of this race, which is known as „warru‟ by Western Desert Indigenous people, is presumed to have been precipitated by introduced predators. However, in order to exclude other potential causes and establish if recovery is feasible, the current project investigated the ecology of warru in the SA APY Lands.

In order to make inferences about the habitat and environmental conditions that best facilitate warru persistence, a modelling approach at multiple spatial scales was used. At a landscape scale, warru presence was correlated to geology, slope, soil type and elevation. At a finer scale, fieldwork established that a number of parameters, including aspect, vegetation, rock complexity and refuges‟ physical characteristics were important determinants of warru presence and use. The work presents the first analysis of *P. lateralis* habitat requirements.

To establish animals‟ use of this preferred habitat, the thesis provides preliminary data on warru home range and movement patterns. Unfortunately, catastrophic failure of Global Positioning System collars meant that data were limited to those from one adult female in one month. Nevertheless, during this time, the animal had a larger than expected home range and undertook a number of long-range movements, including a sojourn off the hill. These results have implications for management, including predator and fire management strategies.

An investigation of the genetic structure of animals in the three largest-known warru colonies indicated that all colonies are genetically diverse, with levels of heterozygosity approximating expected values. All three also exhibited substantial population structuring, with genetic groups correlating to geographic colonies. However, there was also evidence for sub-structuring being present within one of the colonies and for migration occurring into two colonies, with approximately 5% of sampled individuals having mixed ancestry. An analysis of the parentage of offspring indicated that warru have a polygamous mating structure, although one instance of intra- and inter-year monogamy was also established.

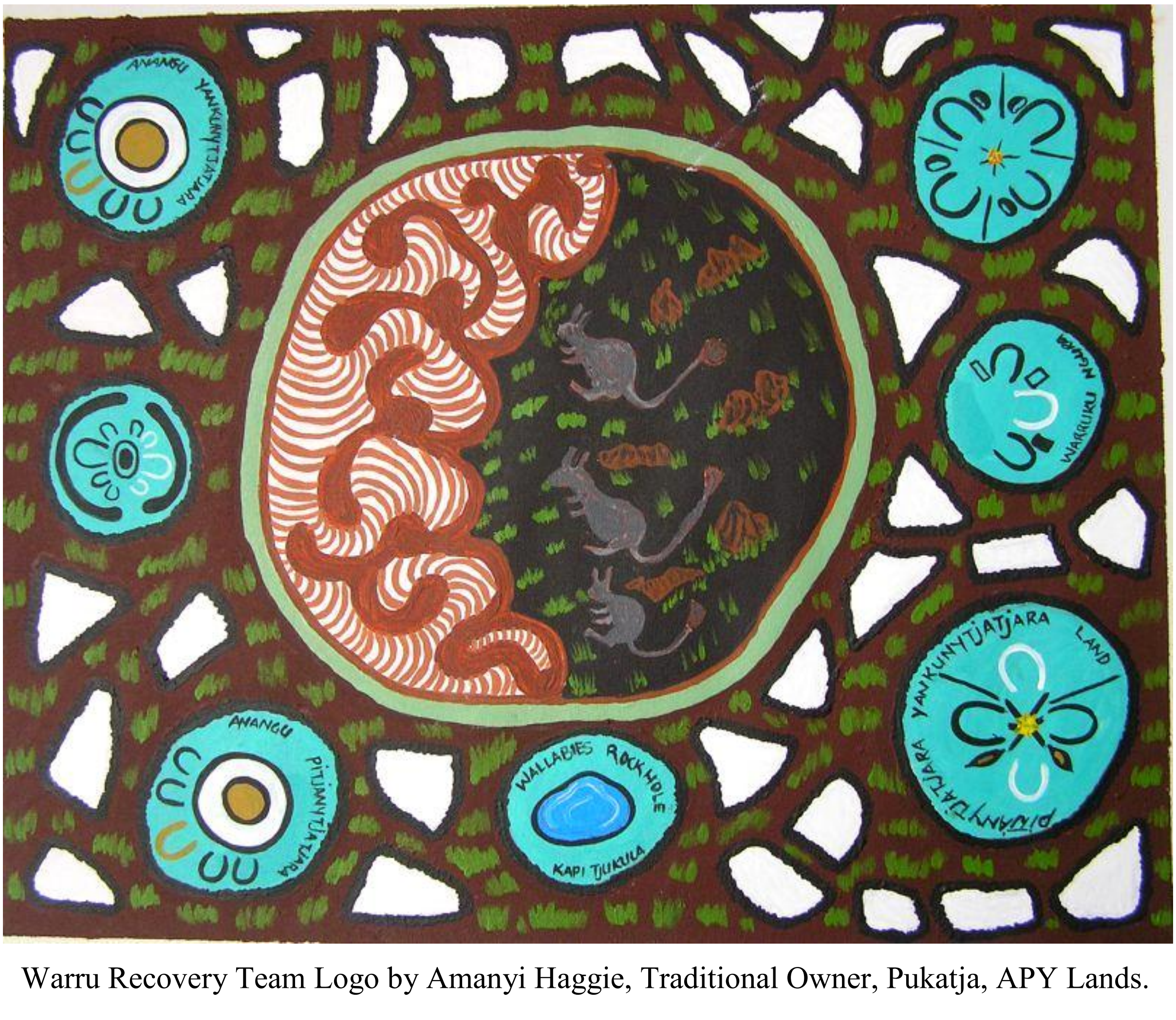
Population modelling was used to provide an estimate of the sizes of each of the three studied colonies. Combined with recent aerial survey data, these data suggested that there are likely to be fewer than 200 warru remaining in SA. However, all three colonies showed signs conducive to potential recovery, including high average reproductive rates, even sex ratios and high adult survivorship (>75%). Juvenile survival, however, was significantly lower (51%) and positively correlated with winter rainfall, indicating that access to water is important during the drier winter months.

The potential for warru recovery was supported by an analysis of warru blood chemistry in both the wild and captive colonies. The latter was established as part of the recovery program and aimed to produce animals for *in-situ* supplementation and reintroduction. In 2009, when blood samples were taken, warru colonies did not manifest with results that are indicative of population-wide disease. However, the biochemical parameters of animals in one of the *in-situ* colonies, „New Well‟, suggested some level of nutritional and water stress. This suggests that managers could consider providing warru at New Well with supplementary food and water during drought, and/or using fire to promote vegetational diversity. The study presents the first detailed haematological reference values for *P. lateralis* and potentially, a methodology for other threatened species recovery programs to follow in order to establish the health of their populations.

The current results have implications for management of both the *in-* and *ex-situ* warru populations. For example, results pertaining to habitat selection can be used to guide selection of appropriate reintroduction sites. Overall, results indicate that although the extant colonies have small population sizes, the animals therein have high reproductive rates, are not suffering the effects of disease and are genetically diverse. The rock-wallabies‟ polygamous mating strategy is also likely to continue to facilitate this genetic diversity. Furthermore, although warru have specific habitat preferences, they have the capacity to disperse to surrounding available habitat. Overall, this suggests that, given appropriate management, warru recovery is feasible. Some of these data may also be pertinent for management of *P. lateralis* in the Northern Territory and Western Australia.

*When conditions were…still virgin…both the mammal fauna and the aboriginal population being virtually undisturbed, (*P. lateralis *MacDonnell Ranges race) was one of the commonest mammals…with swarming populations in many of the rocky outliers of the main ranges.*
Hedley Finlayson, 1961

Warru has been here for a long time, before us, and they should be in our lands because they are Traditional Owners too. Alice Springs are responsible for their warru, we are responsible for ours. We want to see them back in all places where they used to be. And not just warru, we should bring back ninu, mala, stick-nest rat and possum too. All of them.
Frank Young, Traditional Owner, APY Land Management



Warru Recovery Team Logo by Amanyi Haggie, Traditional Owner, Pukatja, APY Lands. The painting depicts warru, the puli and kulpi in which warru live and pir̲anpa scientists and An̲angu working together to conserve warru.

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Glossary

Pitjantjatjara/Yankunytjatjara	**English**
Aṉangu	term used by Indigenous people of the Central Desert to refer to themselves
Aṉangu Pitjantjatjara Yankunytjatjara	traditional land in north-western South Australia that is owned by Aṉangu
kulpi	cave, cavern, shelter
minyma	female Indigenous elders
piṟanpa	white (non-Indigenous) people
Pitjantjatjara	one of the two main Indigenous languages spoken on the APY Lands
puli	hill
tjilpi	male Indigenous elder
warru	black-footed rock-wallaby, *Petrogale lateralis* MacDonnell Ranges race
Yankunytjatjara	one of the two main Indigenous languages spoken on the APY Lands

CHAPTER 1 – General introduction

‘The lower slopes of the ranges are the stations of the short-limbed, broad-chested, sturdy hill kangaroos or euros. And on the craggy tops, where caves and clefts in the weathered rocks afford them shelter, are the beautiful silky-coated rock-wallabies whose sprightly acrobatics amongst the boulders may have given rise on the east coast to an early report that monkeys were to be found in Australia.’

Hedley Finlayson (1936)

Photo: View from New Well, one of the extant warru colonies in the APY Lands, showing perimeter track used for predator baiting. J. Muhic.

Preamble

The impetus for this project was my long-standing interest in threatened species conservation, combined with hearing of the dire situation of mainland *Petrogale lateralis* (MacDonnell Ranges race; „warru‟) in South Australia. In 2006, early-stages recovery efforts were underway but discussions with Department of Environment and Natural Resources (SA) staff highlighted that the cause of the precipitous declines in warru populations was still not clear. It was assumed that, in line with the decline of so many other critical weight range species (Burbidge and McKenzie 1989) in the arid zone, it was caused by predation by introduced species. However, given the remoteness and sheer scale of the APY Lands landscape, research into this was beyond the scope of a PhD. Consequently, it was important to eliminate other potential causes and/or contributors to the decline of warru, namely;

- low habitat availability;
- low dispersal capability;
- inbreeding;
- poor animal recruitment and/or survival; and
- poor health (disease and/or unsuitable nutrition).

Establishing if these factors were contributing to the decline of warru would allow managers to focus recovery efforts appropriately and increase the potential for long-term persistence of warru in South Australia. I hoped that the information garnered on warru in the APY Lands would also be useful for management of black-footed rock-wallabies beyond this region. Lastly, perhaps the „process of elimination‟ utilised in the current study could also provide a model by which the cause of decline of other species could be confirmed.

This dissertation begins with an introduction that reviews the paradigms used by conservationists to manage threatened species, provides an overview of Australian faunal declines and the benefits and challenges of living in rocky habitats and then focuses on rock-wallabies and specifically, *P. lateralis*. It then comprises five data chapters and a discussion. The data chapters are written in a style appropriate for publication in a scientific journal and each data chapter can therefore be read both as an entity in its own right, and as part of a larger study on *P. lateralis*. Two chapters have already been published and one accepted for publication. Due to the intention to submit the remaining chapters close to their current form, some information is unavoidably repeated in individual introductions and methods sections. All cited literature is presented in a separate section at the end of the thesis.

Paradigms for management of threatened species

Stemming declines and fostering recoveries of species has long been part of the relationship between wildlife and people. These efforts became encapsulated within their own discipline – conservation biology – when it acquired a suite of theoretical concepts in the 1980s (Caughley and Gunn 1996). In his seminal review, Caughley (1994) argues that this field contains two overarching paradigms –the declining-population and the small-population paradigms. The former establishes what caused a population to decline and uses this information to design remedial management. In contrast, the latter attempts to understand how low levels of abundance influence a population‟s persistence; as such, questions tend to focus on demographic and environmental stochasticity, inbreeding depression and genetic drift (Caughley and Gunn 1996; Norris 2004). Although both paradigms are often important in saving threatened species from extinction, it is the declining-population paradigm that continues to play a pivotal role in helping managers understand anthropogenic effects on wild populations, and in designing management strategies (Caughley 1994).

The declining-population paradigm encompasses two main areas of theory – the actual causes of extinction and the means by which these are diagnosed (Norris 2004). Caughley and Gunn (1996) are particularly strong proponents of the idea that in order to manage a species, it is imperative to establish surety in the agent(s) of its decline. In particular, they suggest that although it is understandable to encounter feelings of urgency when faced with the last individuals of a species, it is critical to ensure that management decisions are based on unambiguous and defensible information, rather than assumptions. For example, although an agent such as an introduced predator is present, it is not necessarily the culprit in the species‟ decline. An apt illustration is the Aleutian Canada Goose (*Branta canadensis leucopareia*), which breeds in the Bering Sea and winters in Japan, where animals were hunted. Throughout the 20th century, the abundance of geese declined and the attrition was attributed to Arctic foxes (*Alopex lagopus*), which had been released by hunters on islands within the goose‟s nesting range. Although foxes were eliminated from four islands, the decline in geese was not stemmed until hunting ceased in 1975, after which populations started to recover.

To prevent making false assumptions, Caughley and Gunn (1996) espouse the use of a logical series of five steps to diagnose the agents of a species‟ decline;

1. Confirm that the species is in decline, or has previously suffered decline;

2. Study the species‟ natural history and consequently, develop an understanding of the species‟ ecology;
3. Using 2. above, list all the conceivable agents of decline;
4. Identify which of the potential agent(s) is/are the most likely causes of the decline. To do this, determine which agent(s) exist in areas where the species has declined, and do not exist where the species is relatively stable; and
5. Formulate hypotheses and test for causality between the species‟ decline and the potential agent(s).

Testing hypotheses about the cause(s) of decline often involves the use of ecological models. Norris (2004) recently categorised such models into three broad classes; statistical models of habitat use, demographic models and behaviour-based models. Statistical models describe patterns in the distribution of individuals across habitat types, where habitat might include parameters such as vegetation characteristics, abiotic factors (altitude, temperature), predation, disease, competitors and human activities. Demographic models incorporate details on the life history and vital rates of an organism into a population model that can be used to predict extinction risk, population growth or size over a specified future timeframe. In contrast, behaviour-based models focus on processes acting at the level of an individual animal and attempt to derive population parameters such as abundance from an understanding of individual decision-making (Norris 2004).

All three models, and indeed conservation in general, involve intervening during one of the three phases characterised by a declining population (Fig. 1.1; Norris 2004). Phase 1 involves working with a population that is currently secure and quantifying the likelihood that it will decline in the future given a set of specific environmental changes, such as climate change or destruction of key habitat. Phase 2, which focuses on populations that are in the process of declining, and Phase 3, which involves populations that have stabilised to low abundance following a decline, are the milieus on which conservationists have traditionally focused.

For populations in Phases 2 and especially 3, the urgency for action, together with a lack of data, replicate populations and/or resources often preclude managers from following the five steps outlined by Caughley and Gunn (1996). Instead, focus most often turns to how the population can be maintained through the bottleneck. However, in the longer term, it is necessary to analyse of the putative causes of the decline because it is only an address of these that will facilitate the establishment of self-sustaining wild populations (Norris 2004).

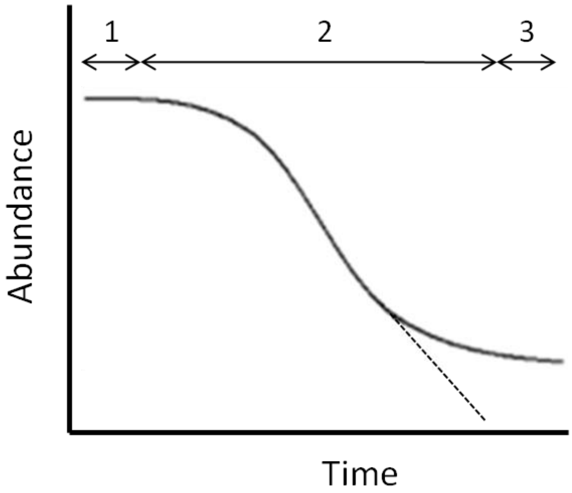


Fig. 1.1 The three phases of population decline, as indicated by arrows and defined in-text. The continuous line alludes to a declining population that is being managed while the broken line indicates a population which, in the absence of conservation, declines to extinction (after Norris 2004).

Declines of Australian fauna

Australia has an evolutionary history dating back to probably the Jurassic (Johnson 2006) and boasts a rich faunal endowment. This bounty has seen it declared as one of the world‟s 17 „megadiverse‟ countries (Department of Sustainability 2010a). However, despite the diversity of its other taxa, it is Australia‟s marsupials that are best known both abroad and by Australians themselves (Kennedy 1992). Unfortunately, part of this reputation relates to Australia‟s rate of mammal extinctions, with 67 of the 340 species of land mammals present 100,000 years ago now lost (Johnson 2006). These extinctions occurred in three waves, with the last happening since European settlement (Johnson 2006) with the loss of ten species and six sub-species of marsupials and nine species of rodent (Department of Sustainability 2010b). This figure accounts for almost half of the worldwide mammal extinctions of the last 200 years (Maxwell *et al.* 1996). A further 94 species/sub-species are currently listed as threatened (Department of Sustainability 2010b) and recent work suggests that the decline is continuing (Woinarski and Milne 2001).

A large number of causes have been proposed to explain this decline. These include disease, competition from introduced herbivores, droughts and climatic change, altered fire regimes, hunting, pastoralism and introduced predators, especially the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*, Morton 1990; Short and Smith 1994; Burbidge 1995). Often, these causes affected populations simultaneously or in close succession (Finlayson *et al.* 2010). For example, between 1883 and 1930 in New South Wales, hunting by European settlers saw 21 million mammals killed; concurrently, there was an influx of predators, competitors and significant land-use changes (Short and Smith 1994). For many species, the relative importance of the factors leading to their decline is still unknown. However, there is growing evidence that, in many cases, fox predation played the decisive role and that foxes continue to act as a multi-species control agent, severely limiting native mammals‟ distribution and abundance (Morton 1990; Burbidge and Manly 2002; Kinnear *et al.* 2002; Johnson 2006).

Australian mammalian extinctions exhibit a heavy bias towards the middle-sized, non-volant (not flying) species. Burbidge and McKenzie (1989) identified this group as the „critical weight range‟ (CWR) mammals, consisting of those between 35 g and 5.5 kg. Species outside of this range have, until recently, remained relatively unaffected (Burbidge and McKenzie 1989). Although the link between body size and risk of extinction has been the focus of recent debate (Cardillo and Bromham 2001), the most recent analysis (Chisholm and Taylor 2007) found strong evidence in favour of the CWR hypothesis at both the continental scale and in the arid zone, although not in the mesic zone. Weight acts as a surrogate for a variety of traits thought to predispose species to becoming threatened, including high population variability, trophic level (herbivores and omnivores) and low density and dispersal ability respectively (Morton 1990; Cardillo and Bromham 2001). Most of the documented declines or extinctions have been concentrated towards CWR mammals in the arid zone. Indeed, since the 1920s, about 33% of all mammal species and 90% of arid-zone CWR mammals have suffered dramatic range contractions or are now extinct (Burrows *et al.* 2003). Macropods in particular have undergone a significant decline, with over 55% of species now listed as threatened (World Wildlife Fund Australia 2008).

One exception to the CWR pattern is that of species which forage and/or dwell in rockpile habitat, defined as massive piles of boulders and rugged scree slopes with innumerable crevices and cavities (Burbidge and McKenzie 1989). Rock-dwelling fauna appears to have escaped the levels of decline evident in compatriots restricted to the ground‟s surface. For example, Western Australia‟s (WA) Pilbara region contains some of the most extensive rockpile habitat in Australia. Eighty percent (4/5) of the Pilbara CWR species that dwell in rockpiles retain stable populations, whereas only 14% (1/7) of the ground-dwelling species are still common (Burbidge and McKenzie 1989). The genus *Petrogale* provides an even more targeted case study, with none of the five species of rock-wallaby found in WA"s semi-arid and arid regions having become extinct, although some are threatened. In contrast, five species within the *Onychogalea, Lagorchestes, Lagostrophus, Bettongia* and *Potorous* genera, which have a similar body size but dwell on soil substrates, have become extinct and a further five are threatened (Burbidge and McKenzie 1989). Many *Petrogale* species outside of this region have also undergone population declines and/or are at risk of extinction. Indeed, although most species of *Petrogale* officially lie outside the CWR, they perhaps should be classified as being within it because their young, which do lie within the CWR, are left alone at rockpiles while their mothers forage (Sharp 1997b) and are therefore exposed to increased risk from introduced predators (Sharp pers. comm.).

Rocky habitat

Mountain ranges, granite outcrops and rocky habitats in general appear with regularity in various parts of the world and their ecological communities are often diverse and rich in endemics (Mares 1997; Illán *et al.* 2010). One of the most well-known effects of rocky habitats is that they facilitate the establishment of micro- and macro-habitats that differ significantly from the surrounding region. In particular, if rocky areas occur within xeric regions, microclimate effects often lead to them becoming more mesic. Such refugia then effectively ameliorate environmental conditions, including decreasing temperature and stabilising humidity, both of which can be extreme in arid environments (Mares 1997). In turn, this, combined with the higher water runoff and/or accumulation seen at such sites, leads to the establishment of higher plant diversity and productivity than that which is present in the surrounding landscape (Freeland *et al.* 1988). For example, Streilein (1982) found that during droughts in Brazil"s semi-arid Caatinga region, rocky habitat, with its green vegetation and occasional pools of water, provided refugia for a variety of small mammals. Vegetation itself also contributes to habitat complexity, stability and microclimate and results in a more predictable supply of food than that which is present in the surrounding environment. In turn, this has implications for the ecology and physiology of rock-dwelling inhabitants. For example, in Australia, the carnivorous, rock-dwelling marsupial *Pseudantechinus macdonnellensis* occupies a relatively small and stable home range. In contrast, sympatric sand-inhabiting dasyurids are highly mobile, undertaking long-range movements to exploit ephemeral food resources (Pavey *et al.* 2003)

Rocky habitats also facilitate shelter in a variety of forms - from wind, rain and sun (Short 1982; Copley and Robinson 1983) and, due to their patchy fuel distribution, from fire (Price *et al.* 2003). They also offer heightened protection from predators (Pople 1989; Spencer 1991), which is consistent with species‟ behavioural patterns, including fleeing to shelter when disturbed and remaining in refuges during perceived danger (Pople 1989; Horsup 1994; Eldridge and Close 1997). Furthermore, since rocky areas are generally unsuitable for agriculture, they are also less likely to have been subject to land clearance and vegetation modification (Burbidge and McKenzie 1989). Crevices also provide shelter, where adults can rest, place nests and/or crèche offspring (Sharp 1997b). For example, Morocco‟s coastal limestone cliffs provide the last refuge for the arid-zone Waldrapp ibis (*Geronticus eremita*), which has been decimated by hunting, pesticides and off-cliff habitat being converted to farmland. The approximately 350 remaining birds are largely protected by the isolation of these coastal cliffs, upon which they build bulky nests (Larson *et al.* 2000).

Clearly then, rocky habitats can provide substantial benefits to their resident fauna. However, cliffs also represent stressful, biologically closed communities where the number of suitable microhabitats is limited and to which resident organisms must adapt „like corks in a bottle‟ (Davis 1951; Larson *et al.* 2000). More specifically, living in such environments affects all aspects of residents‟ ecology, including their morphological, ecological and behavioural traits (Mares 1997; Telfer 2006). Indeed, so profound is the influence that, in a classic example of convergent evolution, rock-dwelling mammals from around the world with entirely disparate phylogenetic histories have developed a host of similar adaptations, including specialised foot structure, general body form, analogous activity periods, alarm calls, communal defaecation and the propensity to form harems (Mares and Lacher 1987). Indeed, rock-dwelling species are often so specialised that they are endemic to such habitat and, since rock formations are spatially isolated, tend to have a patchy distribution. This then impacts on population structure of rock-dwelling species and increases their potential for genetic isolation (Freeland *et al.* 1988). The concept of physical and genetic isolation is particularly relevant in Australia, where rock-dwelling specialists constitute over 14% of the country‟s marsupial and rodent fauna (32 of 223 species, Pavey *et al.* 2003).

The *Petrogale* genus

In the course of the 40 million years that Australia has been isolated from other landmasses, its marsupial fauna has undertaken considerable radiation. In particular, the superfamily

Macropodoidea has become extremely successful, culminating in a total of 72 species of macropods (family Macropodidae) being present before European settlement (Tyndale-Biscoe 2005). Within this family, there are two subfamilies – the Potoroidae and Macropodinae. The latter is the most abundant and includes 61 species occurring in seven groups (Tyndale-Biscoe 2005). Of these 61 species, two within the genus *Macropus* (*M. robustus* and *M. bernardus*) and 16 within the genus *Petrogale* (rock-wallabies) have become rock-specialists (Van Dyck and Strahan 2008).

Distribution and biogeography

Although historically the taxonomic relationship of rock-wallabies was very confused (Tyndale-Biscoe 2005), a total of 16 species and 21 distinct chromosomal races are now recognised. These are all grouped into the genus *Petrogale*, which literally means „rock-weasel‟ (Strahan 1995). This diversity is a classic example of divergence between isolates, with substantial differences in chromosomes, microsatellite and mitochondrial DNA present in different *Petrogale* species, subspecies and even populations (Armati *et al.* 2006). Due to this diversity, *Petrogale* are divided into four species-complexes, which accord with their genetic structure and biogeography - the lateralis, penicillata, xanthopus and brachyotis. The xanthopus complex includes species thought to be nearest to the ancestral stock from which rock-wallabies evolved 3.7 million years ago (Tyndale-Biscoe 2005). The brachyotis complex encompasses species of the monsoon tropics, while the penicillata incorporates eight species extending from Victoria to northern Queensland. The lateralis complex contains the purple-necked (*P. purpureicollis*) and black-footed (*P. lateralis*) rock-wallabies (Tyndale-Biscoe 2005).

The heartland of *Petrogale* distribution is the mainland, with no species found in Tasmania or the Bass Strait islands (Tyndale-Biscoe 2005). However, animals do occur on seven of Australia‟s offshore islands, where, after the islands‟ separation from the mainland, *Petrogale* have developed in isolation. Eight species and/or sub-species of *Petrogale* are listed as being vulnerable under the *Environmental Protection and Biodiversity Conservation Act* 1999 (Department of Sustainability 2010b) and there remain a number for which distribution and status remain poorly known (McCallum 1997; Van Dyck and Strahan 2008). A national recovery plan applicable to five species is currently being prepared (Pearson 2009). Continued threats include predation and competition, habitat alteration, drought, disease and stochastic events such as fires (Delaney *et al.* 2005).

Habitat

Unique amongst the macropodids, rock-wallabies are restricted to rocky places, preferring cliffs, gorges, rocky outcrops and boulder piles near suitable feeding areas (Spencer *et al.* 1997; Sharman and Maynes 2002). Their preference for such habitat means that, compared to other similarly-sized macropods, *Petrogale* have small home ranges and high site fidelity (Horsup 1994; Hazlitt *et al.* 2006a; Telfer 2006). However, dispersal does occur, as evidenced by the fact that, prior to European settlement, animals were found in most suitable mainland habitat, including extremely isolated sites (Eldridge and Close 1997; Sharp 1997a).

Comprehensive studies of *Petrogale* habitat requirements are limited to two species, those of *P. xanthopus* and *P. penicillata* (Short 1982; Lim and Giles 1987; Waldegrave-Knight 2002). These studies have shown that the presence of gullies and gorges, access to water, and shelter from direct sunshine are important for determining habitat occupation (Lim and Giles 1987). For *P. xanthopus*, Gordon *et al.* (1978) and Copley (1983) also found that the vegetation of favoured sites tended to be more abundant, diverse and/or denser than that of unoccupied cliff regions. Occupied sites also tend to have a more rugged topography than surrounding, unoccupied areas (Gordon *et al.* 1978; Short 1982; Sharp 1997b). Although these broad habitat preferences are likely to be applicable to most *Petrogale,* detailed information on habitat choice and utilisation for the other 14 species is almost entirely lacking (Eldridge 1997a). This knowledge gap is particularly relevant because *Petrogale* occurrence tends to be patchy even within areas of continuous rocky habitat, suggesting that fine-scale habitat selection does occur (Briscoe *et al.* 1981; Eldridge and Close 1997). To help fill the existing gap, Chapter 2 presents the first comprehensive analysis of *P. lateralis* habitat preferences.

Population structure and behaviour

Studies of the population structure of *Petrogale* have also been limited, this time to three species (*P. xanthopus, P. penicillata* and *P. assimilis*). Consequently, there is little information on colony size, recruitment or dispersal available for the other 13 species (Piggott *et al.* 2006b). Our current understanding suggests that *Petrogale* colonies can range in size from a single pair to several hundred animals but are limited by the availability of refuge sites (Tyndale-Biscoe 2005). Individuals habituate the same refuges, feeding areas and pathways, although one male‟s territory will usually overlap with those of one or more females (Waldegrave-Knight 2002). Animals are crepuscular and/or nocturnal (Horsup 1994; Eldridge and Close 1997). Trapping studies have generally shown that colonies have a female-biased sex ratio (Delaney 1997a; Jarman and Bayne 1997; Eldridge *et al.* 1999). Biasing towards the non-dispersing sex (Sharp 1997a; Hazlitt *et al.* 2004) may either be a result of, or represent a strategy to manage for, male-led population loss (Piggott *et al.* 2006b).

Information about dispersal between colonies is limited, partly as a result of the logistical difficulties in studying this parameter using traditional methods, namely trapping and radiotracking (Sharp 1997a). Existing studies indicate that animals tend to be relatively sedentary, with infrequent inter-colony dispersal (Piggott *et al.* 2006b). In turn, this suggests that populations are likely to exchange genetic material only occasionally (Spencer *et al.* 1997) and that such isolation may eventually lead to speciation. For example, Pope *et al.* (1996) found that *P. xanthopus* populations that were separated by 10 km of suitable habitat had significant differences in allele frequency at one microsatellite locus, while those separated by 70 km of unsuitable habitat differed substantially in both their mitochondrial and microsatellite DNA. To extend the existing data, the current study presents an analysis of *P. lateralis* movement patterns and genetics.

Reproduction

Macropodidae have a unique reproductive system involving embryonic diapause, which sees an oestrus and mating occurring shortly after the female gives birth. While the newborn young makes its way up to the pouch and attaches to a teat, a fertilised zygote resulting from the mating passes to the uterus. Here, the latter remains in diapause until the pouch is vacated by the suckling pouch young. Should the pouch young be lost early, it can be replaced by the quiescent embryo (Tyndale-Biscoe 2005). Indeed, for *Petrogale,* most mortality occurs either in the early stages of pouch life or just before permanent pouch exit (Delaney 1997b).

In both sexes, sexual maturity is generally attained from 18 months, with adults having a variety of mating systems. *P. xanthopus*, for example, is polygynous, with a dominant male‟s territory encompassing that of several females (Sharp 1997b). In contrast, *P. assimilis* is socially monogamous, although this does not guarantee exclusivity of mating; Spencer *et al.* (1998) found that the consort male fathers only two-thirds of a female‟s offspring. All *Petrogale* are capable of continuous breeding, with non-lactating females rarely being found (Delaney 1997b; Eldridge *et al.* 1999). However, successful reproduction is often dependent on rainfall and the resultant increase in plant biomass (Tyndale-Biscoe 2005). Delaney

(1997b), for example, found that *P. assimilis* population size correlates with annual precipitation. Thus *Petrogale* populations are likely to be predisposed to natural fluctuations of extinction and recolonisation, with infrequent pulses of heavy recruitment followed by years when few young survive (Delaney 1997a; b; Tyndale-Biscoe 2005).

Although these reproductive characteristics apply to all *Petrogale,* species-specific studies have been limited and those that have been conducted have generally used captive populations. Consequently, little is known about *in-situ* colonies and how their reproductive parameters differ from those of their captive counterparts (Poole *et al.* 1985; Delaney and De'ath 1990; Taggart *et al.* 2005). To supplement some existing information on *P. lateralis* reproduction (Jones 2001) and determine if this parameter is limiting recovery, Chapter 5 assesses the fecundity, birth schedule and growth curves of *P. lateralis* (MacDonnell Ranges race) in both captivity and the wild.

Diet

In many herbivorous mammalian taxa, diet correlates to body size, with smaller species selecting high-quality foods that can be quickly digested (browsers), and larger animals consuming abundant, low quality vegetation (grazers; Dawson 1989; Norbury *et al.* 1989; Hume 1999). Although officially defined as browsers, rock-wallabies are actually intermediate between these two groups (Jackson 2003), with a catholic diet of grasses, forbs, trees and shrubs, and, when available, ferns, fruits and flowers (Sharman and Maynes 2002). Their use of, and reliance on, water is unknown. Although most arid-zone species, including *P. xanthopus* and *P. lateralis,* will drink accumulated surface water when it is available, whether this is a limiting resource has not been ascertained (Copley and Robinson 1983). Geelen (1999), for example, hypothesised that *P. lateralis* in the APY Lands can survive using only food-derived moisture. Chapter 6 describes an investigation of the haematology of warru, the results from which can be used to make inferences about the nutritional health of the studied colonies.

***Petrogale lateralis*, especially warru (*P. lateralis* MacDonnell Ranges race)**

Species description

The common names of *P. lateralis* (Gould 1842), those of the black-footed or black-flanked rock-wallaby, allude to its distinguishing morphological features. Specifically, these are its dark brown to black front paws and back feet and a dark brown to black dorsal stripe running from the ears to below the shoulders (Plate 1.1; Eldridge and Close 2002; Sharman and Maynes 2002). There is also a white side-stripe with a wider, dark brown stripe immediately ventral that extends from axillary patch to thigh (Van Dyck and Strahan 2008). Animals also have a distinctly tricoloured head: a dark brown top, whitish or buff cheek stripe to the ear and a grey area below the ear (Menkhorst and Knight 2011). Individuals are medium-sized, with adult females weighing up to 4.5 kg and males up to 6 kg. These morphological features do, however, tend to vary according to geography and animals‟ chromosomal form.

There are five distinct forms of *P. lateralis* – three named sub-species and two unnamed races. These differ in the number and arrangement of their chromosomes, making the species extremely genetically diverse. The MacDonnell Ranges race is distinguished by an acrocentric X-chromosome and a derived acrocentric chromosome 3. Additionally, animals are homozygous for euchromatic short arms on chromosome 1 (Eldridge *et al.* 1992).

Plate 1.1 Black-footed rock-wallaby, *Petrogale lateralis* (MacDonnell Ranges race), showing the distinguishing tri-coloured head, black feet and lateral stripe. Photo: L. Ruykys.

Distribution and conservation status

P. lateralis is Australia‟s most widespread species of rock-wallaby, with colonies in Western Australia (WA), the Northern Territory (NT) and South Australia (SA). In the centre and south of WA, the nominate sub-species, *P. lateralis lateralis,* was formerly widespread and abundant (Eldridge and Close 2002). However, by the 1970s, it had suffered the most precipitous decline of all the forms of *P. lateralis* (Pearson 2009).

In SA, there are two forms – one sub-species and one unnamed race. The former, the endemic *P. l. pearsoni,* occurs on three islands, where it remains common (Eldridge and Close 2002). The latter, *P. lateralis* MacDonnell Ranges race, is found on the mainland and is known as „warru‟ by Western Desert Indigenous Owners. Due to the substantial involvement of Indigenous people in the current project, this nomenclature is utilised for the remainder of this dissertation. Warru is the only species of *Petrogale* found in Australia‟s central ranges. Its distribution is centred in the NT‟s MacDonnell Ranges and extends north to the NT Murchison Ranges, west to WA‟s Warburton region, across northern SA and, previously, as far south as SA‟s Davenport Ranges, which are approximately 50 km west of Lake Eyre (Lundie-Jenkins and Findlay 1997). Within this area, both Indigenous and early explorers‟ records indicate that animals were originally innumerable (Pearson 1992). For example, naturalist H. Finlayson, who surveyed north-western SA, wrote of his first trip in 1931-35 that warru were "one of the commonest mammals…with swarming populations in many of the rocky outliers…" (Finlayson 1961). However, by the 1960s, the race had substantially declined in both range and abundance (Eldridge *et al.* 1992; Pearson 1992), with Finlayson (1961) commenting that it had become "a comparatively rare form". The decline continued and today, outside of the NT, warru populations are highly fragmented and their abundance is limited (Eldridge and Close 2002).

In the NT, with the exception of recent extinctions in the Tanami Desert and at Uluṟu-Kata Tjuta National Park, populations are considered to be stable (Gibson 2000). However, given that the NT does not currently have a monitoring program for the race (Woinarski *et al.* 2007), it is conceivable that a decline is occurring. In WA, warru are now only found in six ranges in the Warburton region. Only at one site are they abundant; elsewhere, individuals are rarely observed and populations are fragmented (Pearson 1992; 2009).

Warru in SA have also suffered precipitous declines and are now considered to be one of the state‟s most endangered mammal species (Copley and Alexander 1997). In 1998, the Davenport Ranges population became extinct, a mere nine years after its discovery. This was attributed to prey switching by foxes and dingos (*Canis lupus dingo)* after the release of rabbit calicivirus disease (Moseby *et al.* 1998). Warru subsequently became restricted to the A<u>n</u>angu Pitjantjatjara Yankunytjatjara (APY) Lands, where, since European settlement, their extent of occurrence and area of occupancy has decreased by 44,896 km^2 and 707 km^2 respectively (Ward *et al.* 2011). Today, animals are known from only two regions (Fig 1.2). The largest metapopulation is located in the north-eastern Musgrave Ranges, between the Indigenous community of Pukatja (Ernabella) and the NT border, and contains seven colonies. A second, smaller metapopulation is located in the Tomkinson Ranges, adjacent to the WA and NT borders. Preliminary genetic analyses on three SA colonies have shown that each has unique mitochondrial DNA haplotypes, with the levels of divergence amongst colonies (most had 3-5% haplotype divergence) being similar to that found between SA animals as a group and those from WA and the NT (Eldridge 2006).

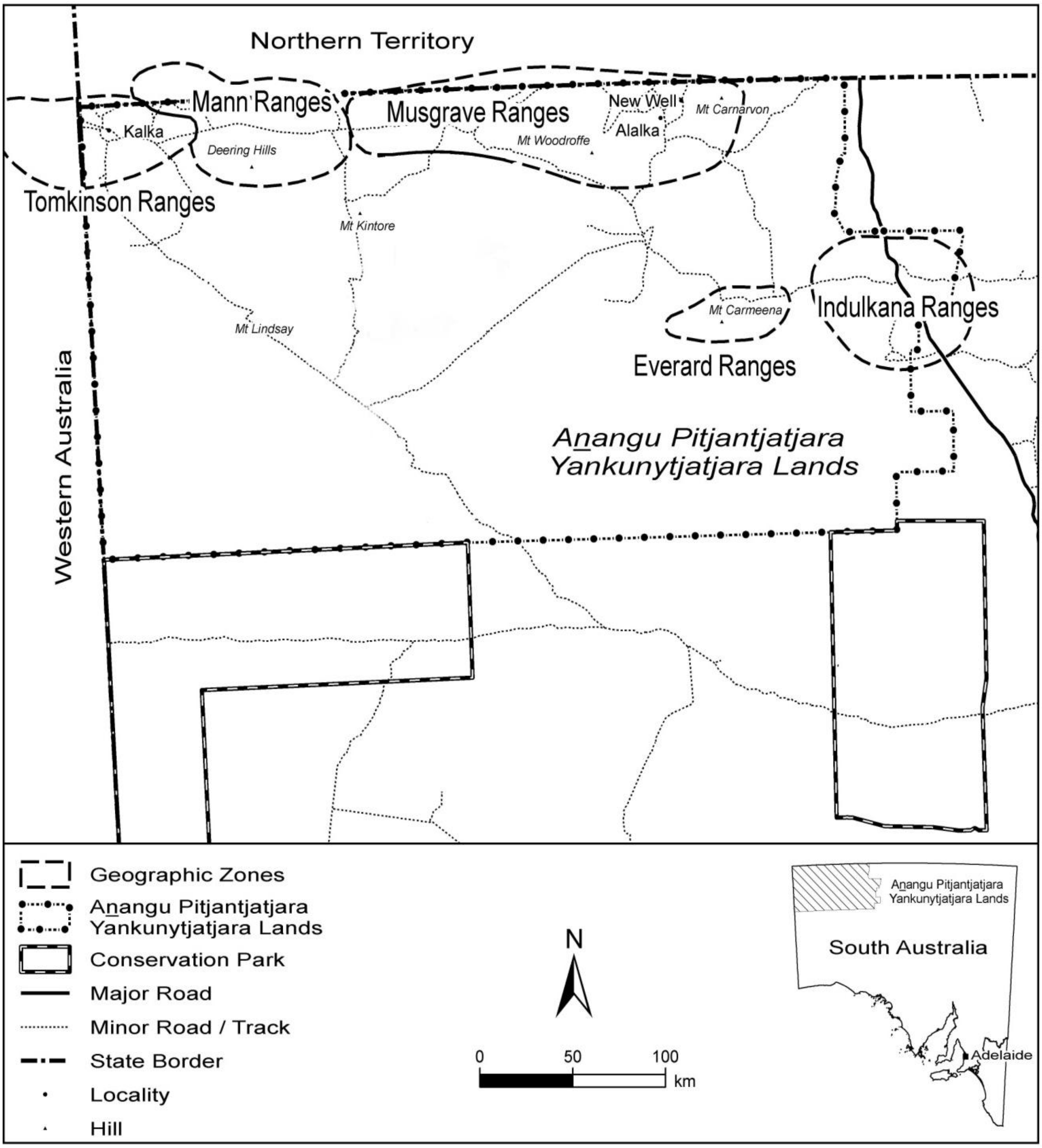


Fig. 1.2 Locational map of the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. The current study‟s three fieldsites, „Alalka‟, „Kalka‟ and „New Well‟, are indicated.
Map produced by R. Urban, Department of Environment and Natural Resources.

Threatening processes

The factors that cause extinction are usually complex, seldom documented and often work in tandem (Kinnear *et al.* 1984). Thus, for warru, changed fire regimes, small population size and competition with euros (*M. robustus*) are likely to have had, or will have, an effect that compounds that of predation by introduced species (Kinnear *et al.* 2002).

Finlayson (1961) was the first to notice the threat of predation to *P. lateralis*, commenting on "…the fox and the feral house cat which together have had an effect in certain districts only to be described as catastrophic". Although cats first occupied southern NT and northern SA in 1880-90, and rabbits (*Oryctolagus cuniculus*) were present by 1900, red foxes did not establish in the area until the 1930s (Abbott 2002). However, by 1956, foxes outnumbered dingoes in the SA Mann and Tomkinson Ranges (Finlayson 1961). Foxes are adept, mobile predators with a high search capability. They are readily able to invade areas and are documented as being a surplus killer, meaning that they sometimes kill prey at a rate beyond that which is necessary to supply their immediate food requirements (Short *et al.* 2002). Being capable climbers, they can also hunt prey on cliffs and in their shelters (Rolls 1969). A seminal study by Kinnear *et al.* (1988; 1998; 2010) on *P. lateralis lateralis* in the WA Wheatbelt region implicated foxes as the cause of the precipitous decline in animals" range and abundance. Where baiting continues to be undertaken, populations have rebounded, with animals recolonising vacant rocky areas and, at some sites, even becoming overabundant (Van Dyck and Strahan 2008; Willers *et al.* 2010).

In the APY Lands, the response has not been so clear. Sporadic fox control with 1080 kangaroo meat baits commenced at two colonies in August 2000 and in 2002, baiting intensity was increased (Read and Ward 2011a). The impact of this has been measured using a two-pronged approach. Firstly, one-metre-radius quadrats established by Geelen (1999) at two of the colonies have had their scats counted and removed annually from 2001 to 2010 (Read and Ward 2011a). Quantitative spotlight counts of warru, foxes, dingos, cats and euros have also been conducted around the two colonies" perimeter tracks on the same dates as the scat quadrats were cleared. Both warru scat and spotlight counts declined dramatically from 2001 to the current time. From 2002 onwards, foxes have been recorded only rarely and dingo counts have also remained consistently low. In contrast, cat counts remain highly variable, with no apparent response to the baiting program (Read and Ward 2011a).

Cats are adept hunters that consume animals up to their own body size (Abbott 2002). However, largely due to the difficulties in experimentally manipulating cat numbers, their impact on medium-sized native mammals remains confusing. For example, some fauna reintroductions are believed to have failed due to cat predation (Christensen and Burrows 1994) yet in WA, the „Western Shield‟ fox-baiting program has resulted in faunal recoveries in spite of their presence (Abbott 2002). In a classic mesopredator-release mechanism, cat abundance increases after the removal of foxes and dingoes (Burrows *et al.* 2003; Davey *et al.* 2006). Given that baiting on the APY Lands is currently only targeting the latter two species, this could explain the slow recovery of warru. This is particularly pertinent given that predation by even a few cats can suppress populations of threatened species, including potentially those of *Petrogale* (Spencer 1991). This hypothesis is supported by preliminary results from the Calvert Ranges, where *P. lateralis* populations showed little response to fox-baiting until cats were also baited (Kendrick *et al.* 2010).

Changed fire regimes pose another threat to *P. lateralis.* Historically, Aboriginals‟ extensive and utilitarian use of fire resulted in a mosaic of regenerating vegetation and promoted fire in different seasons (Burbidge *et al.* 1988). With the cessation of desert Aboriginal nomadism, this pattern was replaced by the current „natural‟ fire regime of infrequent but extensive hot summer wildfires, usually started by lightning (Burbidge et al. 1988). In December 2000 for example, 30 000 km^2 of the APY Lands were burnt in a single event (Wilson *et al.* 2004). For *P. lateralis,* this new regime may have decreased the availability and diversity of vegetation, which is used both for shelter and food (Burbidge *et al.* 1988). Whether this has translated into suppression of warru numbers in the APY Lands requires research.

Small population size and isolation thereof are also current threats. These factors can lead to inbreeding and population fragmentation, which, in turn, increase the probability of extinction through genetic, demographic and/or environmental stochasticity (Eldridge *et al.* 1999). For APY Lands warru, isolation is likely to be caused by the prohibitive nature of predation on animals‟ dispersal ability, while in other *P. lateralis* colonies, it is due to animals‟ restriction to a geographic or figurative island (Pearson 2009). Chapter 3 presents an analysis of the magnitude, and thus potential impacts, of population isolation for APY Lands warru.

As a result of European-caused land use changes, competition is now also recognised as being a threatening process. For APY Lands warru, euros are likely to be the major competitor. A common hill-dweller in much of central Australia (Menkhorst and Knight 2011), euros have diets that partially overlap with those of warru, especially in relation to grasses (Capararo 1994; Geelen 1999; Creese 2007). Relative to their historically low densities in the APY Lands (Finlayson 1961), euro numbers have increased substantially and competition for resources may now be impacting on warru (Read and Ward 2011b).

Introduced herbivores, specifically donkeys (*Equus asinus*), horses (*Equus caballus*), camels (*Camelus dromedarius*) and rabbits, may also pose a threat. As well as potentially directly competing with warru for food on the plains adjacent to hills (Chapter 3), their high abundance may alter the latter‟s environment. In the WA Warburton region, for example, Pearson (1992) suggested that rabbits could be degrading habitat by ring-barking trees, reducing seedling recruitment and removing grass and forb biomass (Pearson 1992), as well as providing a key food resource to sustain populations of introduced predators (Read and Bowen 2001). Introduced herbivores can also rapidly deplete the small, ephemeral waterholes that otherwise support native species during droughts (Wilson *et al.* 2004).

Aṉangu Pitjantjatjara Yankunytjatjara Lands

Location, climate, geology and vegetation

Aṉangu is the term that Aboriginal people from central Australia‟s Western Desert region use to refer to themselves. Covering 350,000 km^2, Aṉangu lands cross three state and territory boundaries (SA, WA and NT, Wilson *et al.* 2004). The area is inhabited by 5,000 - 6,000 people who speak six related languages, including Pitjantjatjara and Yankunytjatjara (Baker and Mutitjulu Community 1992; Wilson *et al.* 2004). The SA component, which is named the Aṉangu Pitjantjatjara Yankunytjatjara (APY) Lands, covers 102,650 km^2, or approximately 10 per cent of the state (Robinson *et al.* 2003). Located in SA‟s far north-west corner, the APY Lands extend from the Stuart Highway to the WA border and have a population of 2,230 people across 33 communities and outstations (Australian Bureau of Statistics 2006). In 1981, Aṉangu were granted freehold title and the area is now managed under the *Aṉangu Pitjantjatjara Yankunytjatjara Land Rights Act* 1981.

Climatically, the APY Lands experience a very hot, dry, desert climate with short, cool to cold winters (Robinson *et al.* 2003). Summer temperatures average a maximum 34 degrees

Celsius (°C), while the winter minimum average is 4°C (Burbidge *et al.* 1988). The region receives a low and unreliable rainfall, with a tendency to summer rather than winter precipitation. The highest mean annual rainfall occurs over the Musgrave Ranges, with the Pukatja community (676 m above sea level) annually receiving around 255 mm. However, several years may pass with lower than average precipitation (Robinson *et al.* 2003). Geologically, the APY Lands consist of the crystalline basement rocks of the ~1300-1100 million year old Musgrave Block. In the northern part of the Lands, these form the Musgrave, Tomkinson, Birksgate, Everard and Mann Ranges (Fig. 1.2). The ranges‟ overall orientation is east-west (Robinson *et al.* 2003) and they are highly weathered, containing many caves, fissures and crevices (Geelen 1999). The Musgrave Ranges are of granitic origin and contain the highest point in SA, Mt Woodroffe. The sand plains between ranges are approximately 600 m above sea level (Geelen 1999).

The APY Lands cover the entire Central Ranges and the northern part of the Great Victoria Interim Biogeographic Regionalisation of Australia (IBRA) regions (Robinson *et al.* 2003). Very generally, ranges support *Triodia* communities, while drainage lines contain river red gum (*Eucalyptus camaldulensis*) woodlands and *Melaleuca* shrublands. Floodplains consist of extensive tussock grasslands, while the sand plains support mulga (*Acacia aneura*) and some desert oak (*Allocasuarina decaisneana*) woodlands (Robinson *et al.* 2003). Vegetationally, the area is very diverse, with the Biological Survey of the APY Lands (Robinson *et al.* 2003) recording 719 vascular plant species. The incidence of introduced species was very low, representing only 3.5 per cent of the total flora encountered.

Historical and current management

For approximately 60,000 years, the area now known as the APY Lands was inhabited by three Aboriginal groups – the Pitjantjatjara, Yankunytjatjara and Ngaatjatjara. These people led a nomadic hunting and gathering way of life, moving across the landscape and undertaking traditional land management centred on the production of food, including hunting, dispersal of plant propagules, rockhole cleaning and patch burning. Cleaning rockholes allows them to hold a maximum amount of clean water. Consequently, such sites were a key, reliable water source for many native animals, especially during droughts (Wilson *et al.* 2004). Fire was the major tool used to hunt, gather and promote natural resources and the effect of frequent, small-scale burning was probably most striking in the spinifex grassland landscapes (Morton *et al.* 2011).

The history of Europeans in the APY Lands began in 1873, when explorers first entered the region. While initially focused on finding arable land, they soon realised that the area would not be able to support pastoral or mining developments. Thereafter, it became a *de facto* reserve where Aboriginal culture continued to be practiced. However, due to European policies, this was undertaken with increasing compromises. Substantial changes in traditional ways of life occurred, continuing through to today (Robinson *et al.* 2003). From an ecological perspective, the cessation of Aboriginal fire regimes and introduction of both plants and animals have most likely led to there being larger and more intense wildfires, an increase in woody species and declines of native mammals and some plants (Morton *et al.* 2011).The APY Lands are now managed by Aṉangu Pitjantjatjara Yankunytjatjara, which incorporates various media, health, service, policy and environmental organisations. APY Land Management is responsible for working with Traditional Owners to manage the land according to Indigenous and Western scientific knowledge. Activities include patch burning, rockhole cleaning, threatened species management and feral animal control, all of which help to provide employment and training.

Study sites

The current study has three fieldsites; two in the Musgrave Ranges and one in the Tomkinson Ranges (Fig. 1.2). In the eastern Musgrave Ranges, recent surveys have confirmed that the warru metapopulation has an area of occupancy of approximately 61,000 ha. This is more than likely the largest metapopulation in SA (Read and Ward 2011b). The first fieldsite, „Alalka‟ (Plate 1.2), is located at the north-eastern edge of these ranges, ~16 km north of Pukatja. Alalka‟s landform is that of rugged strike ranges on metamorphics and its geology is that of meta-igneous felsic intrusive rock. It is ~194 ha and, at its highest point, rises approximately 250 metres above the ground. It is contiguous with a large number of surrounding hills.

The second fieldsite, „New Well‟ (Plate 1.3) is located 23 km north-east of Pukatja where the eastern Musgrave Ranges divide into isolated outcrops. As such, New Well is a granite inselberg of ~590 ha that rises 160 m above ground level and has a soil structure of massive earths and sands. The vegetation of both New Well and Alalka is that of emergent low open woodland over *Triodia irritans* grassland (Robinson *et al.* 2003). Warru occupy both the granitic cliff-faces and the piles of boulders at the base of these hills (Read and Ward 2011b).

The third fieldsite is located between the Kalka and Pipalyatjara communities in the Tomkinson Ranges. „Kalka" (Plate 1.4) rises ~350 m above ground and covers about 2,190 ha. The area that warru frequent mainly contains angular granitic or ultra-mafic boulders (Read and Ward 2011b). Vegetation is again dominated by *Triodia,* but this time with an overstorey of *Eucalyptus gamophylla* and *Callitris glaucophylla.*

Plate 1.2 The „Alalka" fieldsite in the South Australian A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands. For a perspective of scale, the circle indicates the location of two people ascending the hill. Photo: M. Ward.

Plate 1.3 The „New Well‟ fieldsite in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Photo: N. Staniford.

Plate 1.4 The „Kalka‟ fieldsite in the South Australian A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands. Photo: L. Ruykys.

Project aims

The decline of SA warru in range and abundance is presumed to have been caused by introduced predators. However, using a process of elimination, the current study aimed to exclude other potential agents of decline by investigating the ecology of *P. lateralis* (MacDonnell Ranges race) in the SA APY Lands. As such, it presents an example of the declining-population paradigm (Caughley 1994) and uses statistical models (Norris 2004) to follow steps 2, 3, 5 and, where possible, 4 of Caughley and Gunn‟s (1996) five-step process to diagnose the agents of a species‟ decline. Specific aims of the study were to determine if the following potential factors are limiting warru recovery:

1. an absence/low availability of preferred habitat;
2. small home range and/or low dispersal capacity;
3. mating system, genetic structure and/or inbreeding;
4. population dynamics, including poor animal recruitment and/or survival; and
5. disease and/or malnutrition.

CHAPTER 2 – Habitat associations of warru at multiple spatial scales

Chief among the difficulties of collecting in the Centre, particularly of mammals collecting, are the hugeness of the area and the obscurity of the factors which determine the distribution of its fauna.
Hedley Finlayson (1936)

Photo: View over the eastern Musgrave Ranges from Aeroplane Hill, APY Lands. N. Staniford.

Chapter 2 - Habitat associations of warru (*Petrogale lateralis* MacDonnell Ranges race) at multiple spatial scales.

Exegesis

Understanding where animals live and what factors have contributed to this distribution is one of the fundamental aspects of ecology. Chapter 2 details an investigation of these two parameters for warru in the APY Lands and indirectly provides an assessment of whether their decline could be due to a lack of suitable habitat. The chapter presents the first analysis of habitat associations for *P. lateralis* (MacDonnell Ranges race) and will hopefully assist with better management of extant sites and selection of appropriate reintroduction sites.

I was responsible for all aspects of the current chapter, including experimental design, planning, fieldwork and data management. A number of volunteers assisted during the fieldwork component. Maxent modelling was completed by me, while the uni- and multivariate analyses were undertaken by Tom Sullivan, a statistician with the University of Adelaide‟s Discipline of Public Health. I then conducted all data interpretation.

The chapter is written in a style appropriate for submission to a scientific journal.

2.1 Abstract

Warru (*Petrogale lateralis* MacDonnell Ranges race) are currently classified as endangered in South Australia and, in order to facilitate better management, an understanding of the dynamics of their distribution and habitat use was required. This study aimed to determine the environmental parameters influencing these factors at four spatial scales – 1) across the whole APY Lands (regional scale); 2) at extinct and extant sites (site scale); 3) at core and non-core areas within hills (hillside scale) and 4) at refuges. Maximum entropy (Maxent) modelling was used for the analysis of data at the regional scale. At the remaining scales, fieldwork was used to collect, and regression modelling to analyse, data. At the regional scale, warru presence was strongly associated with geology, slope, soil type and elevation. At the site scale, aspect, rock abundance and habitat type are likely to have facilitated warru persistence at extant sites. At the hillside scale, aspect, vegetation type and rock complexity are likely to have contributed to the higher warru densities found in core areas. Finally, characteristics including refuge size, exposure and accessibility were significant predictors of the use of shelter sites by warru. This study represents the first multi-scale analysis of *P. lateralis* habitat requirements and is relevant to managing both warru and other species of *Petrogale*.

Keywords: Resource selection functions, multi-scale habitat modelling, habitat preferences.

2.2 Introduction

One of the fundamental aspects of ecology involves understanding the relationship between a species and its habitat, where a habitat is defined as a set of resources and conditions in an area that allow occupancy by an organism (Hall *et al.* 1997). A species‟ habitat needs to provide three core requirements: favourable abiotic (temperature, rainfall etc.) and biotic (e.g. presence of mutualists, absence of serious parasites) conditions, and both current and historical geographic accessibility (Papes and Gaubert 2007). Since these factors all operate at different spatial scales, organisms respond to their environment within a hierarchy of organisational levels. These decrease from a species‟ geographical distribution to their selection of broad habitat types, home ranges within habitat types and choice of food and shelter sites (Le Mar and McArthur 2005; Murray *et al.* 2008).

Traditionally, research and management have only focused on species‟ habitat preferences at the smaller spatial scales (Graf *et al.* 2005). However, multi-scale approaches, preferably within a nested hierarchy, provide a more useful approach (Cushman and McGarigal 2004). Rapidly advancing Geographic Information System (GIS) technology and new powerful statistical tools have ensured that this strategy is becoming more common (Rushton *et al.* 2004). However, due to the cost and time associated with measuring finer-scale parameters, studies combining habitat variables from both GIS (representing coarse-grained landscape data; Gibson *et al.* 2004b) and on-ground sources (finer-scale parameters) remain rare (Loyn *et al.* 2001).

In turn, an understanding of species-habitat relationships can be used to undertake predictive modelling. Known as species distribution models (SDM) or ecological niche modelling (Wisz *et al.* 2008; Elith and Leathwick 2009), such studies generate a map of a species‟ expected distribution using information from the environmental conditions where it is known to occur (Guisan and Zimmermann 2000). SDM has a broad spectrum of applications, including predicting range expansions and highlighting unknown populations (Pearson *et al.* 2007), suitable reintroduction sites (Hernandez *et al.* 2006) and critical habitat (Guisan and Zimmermann 2000). However, despite the clear applicability, there are few examples of SDM being used to inform managers of rare and threatened species (Engler *et al.* 2004), probably due to a paucity of presence data and lack of valid absences (Elith *et al.* 2006). The situation is exacerbated for cryptic species (Müller *et al.* 2009), those at low abundance and/or in inaccessible terrain (Gibson *et al.* 2004a), and when dealing with large spatial scales. Furthermore, while SDM has been conducted on species in artificially fragmented landscapes (Gehrt and Chelsvig 2003; McAlpine *et al.* 2006; Sunde and Redpath 2006), there have been few studies on organisms that naturally occur in fragmented terrain, as exemplified by Australia‟s rock-wallabies (genus *Petrogale*) (Murray *et al.* 2008).

Unlike most medium-sized macropods, rock-wallabies are limited to a habitat that only sporadically occurs in the landscape – that of rugged, steep terrain that has a plethora of outcrops and boulders and is close to suitable feeding areas (Strahan 1995; Sharman and Maynes 2002). Although it is known that such sites are favoured by all *Petrogale*, comprehensive studies of habitat preferences have been almost wholly confined to *P. xanthopus* (Lim and Giles 1987) and *P. penicillata* (Short 1982; Waldegrave-Knight 2002). For the latter, fine-scale modelling has indicated that occupied versus adjacent unoccupied, and extant versus extinct sites differ in a number of parameters, including aspect, slope, size and number of ledges (Short 1982; Waldegrave-Knight 2002). This suggests that habitat selection does occur and infers that fine-scale preferences also probably apply to the other 14 species of *Petrogale.* However, the details of such are currently unknown (Briscoe *et al.* 1981; Eldridge and Close 1997). The black-footed rock-wallaby (*P. lateralis*) is one species for which systematic assessments of habitat requirements are lacking (Davies 2000), with only qualitative descriptions currently being available (Hall and Kinnear 1991; Eldridge *et al.* 1992; Pearson 1992). Known as „warru‟ by Western Desert Indigenous owners, *P. lateralis* (MacDonnell Ranges race) has suffered significant declines in range and abundance across South Australia (SA; Eldridge and Close 2002) and animals are now restricted to the An̲angu Pitjantjatjara Yankunytjatjara (APY) Lands in the state‟s far north-west.

It is important to remember that, given ongoing predation of rock-wallabies by cats (*Felis catus*, Kendrick *et al.* 2010) and red foxes (*Vulpes vulpes*, Kinnear *et al.* 2010), studies investigating habitat associations of Australian native fauna must resort to assessing the characteristics of their refugial, rather than preferred, habitat. This is because, in the absence of effective predator control, native species are associated with habitats that serve as survival niches („refugia‟), which may, or may not, coincide with the species‟ preferred habitat (Kinnear *et al.* 2010). Inevitably, release from predation leads to significant shifts and expansions in habitat use and foraging range (Kinnear *et al.* 1998), making previously-established habitat „preferences‟ moot. Nevertheless, determining the characteristics of refugia remains a valid pursuit because some level of feral predation will undoubtedly continue to be an issue for native populations.

The current study aimed to assess the use of habitat refugia by warru in the APY Lands by answering the following questions;

1. What are the regional-scale habitat associations of warru? and
2. What are their fine-scale (on-ground) habitat requirements?

2.3 Materials and Methods

This study was conducted in the SA APY Lands (Chapter 1) and analyses were conducted at four spatial scales;

1. Across the whole APY Lands („regional scale‟)
2. Extinct and extant colonies („site scale‟)
3. Core and non-core areas within hills („hillside scale‟)
4. Refuge sites („refuge scale‟).

2.3.1 Regional scale

The regional scale encompasses a species‟ geographic range (Murray *et al.* 2008). In this study, this related to the whole APY Lands and involved using SDM. The latter requires two kinds of data; the species‟ occurrence records and environmental variables that may define suitable habitat (Gibson *et al.* 2007; Tinoco *et al.* 2009).

2.3.1.1 Species occurrence records

Warru distribution data for the APY Lands were sourced from the Department of Environment and Natural Resources‟ Biological Database of SA. This contains spatially referenced data on warru dating from 1914 to 2010. However, since the current study aimed to determine environmental parameters that have an influence on *current* warru distribution, which represents the species‟ refugia, records were restricted to those from 1998 to 2010. Within these, only locations with a spatial accuracy ≤100 m were included.

Records were based on two verifiable methodologies – observation (including trapping records), and evidence of fresh scats. For warru, scats comprise the most reliable and repeatable technique for determining the presence of low density populations (Pearson 1992). Freshness can be established by colour, smell and state of deterioration, with fresh scats being shiny black, with odour and compact, and older ones being dull grey-brown, lacking shine and smell and disintegrating (Gibson 2000; Triggs 2004). Although highly dependent on level of exposure, „fresh‟ scats refer to those that are up to approximately 2-3 months of age, while „old‟ scats can persist in the landscape for up to a few decades, especially if they are situated in a position that is protected from the elements (Gibson 2000). Using shape and size, warru scats are easily distinguishable from those of adult euro (*Macropus robustus*) and *M. rufus*, which also occur in the region (Moseby *et al.* 2009). Experienced observers are also able to distinguish between the juvenile scats of these three species.

Both presence and absence data were available from the database. Absence data were not used, however, because of the high likelihood of false negative errors. These could have been caused by insufficient sampling effort and/or the cryptic and nocturnal nature of warru. Furthermore, scats deteriorate in exposed locations and are removed over time by the elements (Geelen 1999; Telfer 2006). Consequently, a lack of scats does not mean that the area was not used by warru. Accordingly, only presence data were extracted for further use.

A total of 286 presence locations were input into ArcGIS ArcMap ver. 9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and spatial autocorrelation examined using Moran‟s index (*I*) via the ArcToolbox Spatial Statistics tool. Initial results indicated that locations were highly clustered so the ArcToolbox „Near‟ tool was used to determine the distance between each location and its nearest neighbour. Data were then filtered so that all presence points were at least 100 m from each other. Moran‟s *I* was then re-run on this decreased number of points, equating to 178 warru presence locations (Appendix 1). Since these points had a random dispersal pattern (Moran‟s $I = 0.03$; z score 1.22 SD; $P = 0.22$), this total was used for further modelling.

2.3.1.2 Environmental variables

A range of environmental variables that represent ecological processes that potentially influence the spatial distribution of warru were obtained (Table 2.1). These variables were selected based on previous studies of warru (Geelen 1999, Read and Ward 2011b), other species of *Petrogale* (Telfer 2006, Waldegrave-Knight 2002) and previous SDM studies (various, e.g. Pearson *et al.* 2007, Müller *et al.* 2009). Using ArcGIS Spatial Analyst and Data Management tools, all layers were clipped to the extent of the APY Lands and resampled to the GDA 1994 geographic coordinate system and a resolution of ~1 km (0.008333 decimal degrees). Climatic parameters were obtained at 30 arc-seconds (~1 km) resolution from the WorldClim database, which characterises average global climates from 1950-2000 using monthly weather station data (ver. 1.4 release 3, Hijmans *et al.* 2005). All 19 available temperature and precipitation variables were considered; however, only those with potential biological relevance to warru were retained for further analysis.

Elevation data were obtained from a ~250 m resolution digital elevation model (GEODATA 9 Second DEM ver. 3, Geoscience Australia) and, using ArcGIS Surface Analysis tools, used to generate slope and aspect layers. Layers that indicated Euclidean distances from Indigenous communities, homelands and water (soaks and springs, drainage) respectively were derived using Spatial Analyst Tools. „Indigenous communities‟ refers to the 11 largest permanent settlements on the APY Lands, while „homelands‟ are family settlements that lie outside of communities but are not necessarily inhabited. „Soaks and springs‟ are areas where water seeps into hollows dug in permeable sediments, often making perennial areas of water storage (Bayly 1999). „Drainage‟ pertains to both perennial and ephemeral watercourses. Fire frequency data were only available for 1999-2009. The „geology‟ layer provided information on broadscale rock type, while „detailed geology‟ was of a finer scale and highlighted the predominant rock types within the general geology.

A high ratio of candidate models to the number of species observations can lead to inclusion of spurious variables (Harrell 2001). Furthermore, multicollinearity between variables creates problems with model selection, interpretation and prediction (Elith and Leathwick 2009). Consequently, the variables that were biologically plausible predictors of warru distribution were tested for multicollinearity. This was done by examining cross-correlations (Pearson correlation coefficient for continuous variables and Spearman‟s rank order correlation for categorical variables) in PASW (PASW Statistics Ver. 17.0.2, March 2009). Where possible, only one variable from a pair of highly correlated variables ($r > 0.85$) was incorporated in the model; which variable to retain was determined by assessing each variable‟s percentage contribution to the model. The final number of predictor variables included in modelling was 16 (Table 2.1). This is in the bounds of the „rule of thumb‟ of Harrell (2001), where no more than $n/10$ variables should be included in the final model, where n is the total sample size (in the current study, 286).

Table 2.1. Environmental parameters used in regional-scale modelling of warru (*Petrogale lateralis*) habitat in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Includes each parameter‟s source: AW NRM – Alintjara Wilu<u>r</u>ara Natural Resources Management Board; DENR – South Australian Department of Environment and Natural Resources; NOAA – National Oceanic and Atmospheric Administration; DEM – Digital Elevation Model; WA – Western Australia.

Environmental parameter	**Layer**	**Source**
Geology	Geology	Data held by AW NRM
	Detailed geology	Geoscience Australia
Soils	Soil type	Data held by AW NRM
Temperature	Annual mean temperature	WorldClim (BIO1)
	Mean temperature of warmest quarter	WorldClim (BIO10)
	Mean temperature of coldest quarter	WorldClim (BIO11)
Precipitation	Mean annual precipitation	WorldClim (BIO12)
Vegetation	Vegetation type	DENR Biological Survey
Distance from settlement	Euclidean distance from Indigenous homelands	Generated from data held by AW NRM
	Euclidean distance from Indigenous communities	Generated from data held by AW NRM
Water	Euclidean distance from soaks and springs	Generated from data held by AW NRM
	Euclidean distance from drainage feature	Generated from data held by AW NRM
Fire	Fire frequency 1999-2009	NOAA satellites via WA Landgate FireWatch
Topography	Aspect	Generated from Geoscience Australia DEM
	Slope	Generated from Geoscience Australia DEM
	Elevation	Geoscience Australia 9 Second DEM

2.3.1.3 Modelling method

The maximum entropy (Maxent) algorithm (Phillips *et al.* 2004; 2006) was used to model the potential distribution of warru at the regional scale. Maxent is a widely-used presence-only method for SDM that is based on a machine-learning approach (Phillips *et al.* 2009; VanDerWal *et al.* 2009; Recio and Virgos 2010). It estimates the probability distribution closest to uniform („maximum entropy") using the species" known occurrences and random background points, subject to the constraints imposed by the known occurrences (Phillips *et al.* 2004; Phillips *et al.* 2006; Elith and Leathwick 2009). Maxent produces mapped predictions in the form of numbers between 0 and 100, representing cumulative probabilities of occurrence (Phillips *et al.* 2004). Maxent was selected for use because, in recent comparisons of SDM methods, it outperformed other presence-only techniques (Elith *et al.* 2006), and even traditional presence-absence methods such as general linear models (Hernandez *et al.* 2006). Furthermore, it can manage model over-fitting and is able to model complex relationships between species and their environments, including interactions between predictor variables (Phillips and Dudík 2008; Elith and Leathwick 2009).

Maxent (ver. 3.3.4) was implemented using the recommended default values for the convergence threshold (10^{-5}), maximum iterations (500) and background points (10,000) (Phillips and Dudík 2008). The latter were selected at random as pseudoabsences from the entire area of the APY Lands (Phillips *et al.* 2009). After experimentation with values of 1, 2, 5 and 10, the regularization, which affects how closely-fitted the output distribution is to the given presence records, was set to 1 (default value) as this was most appropriate for the data. Other parameters used were those of clamping and random seed and, following trials with feature types, the linear, quadratic and product feature types were selected. Potential distribution maps were produced with a 10-fold cross-validation, which holds out 10% of the data as a testing set at each of 10 iterations, and builds the model on the remaining 90% in each iteration (Kearney *et al.* 2010).

The predictive performance of the model was evaluated using the receiver operating characteristic (ROC) curve. The area under this curve (AUC) provides a measure of discriminatory ability, with values close to 0.5 indicating a fit no better than expected by random chance, and 1.0 indicating perfect discriminatory ability. Thus, the AUC is interpretable as the probability that a presence site is ranked above a random background site (Phillips *et al.* 2006; Phillips and Dudík 2008). The jack-knife test was used to evaluate the importance of each environmental variable in the model, where environmental variables with a higher gain provide greater predictive power (Phillips *et al.* 2006). After running Maxent, the resultant map of predictive distribution was integrated into ArcGIS.

2.3.2 Site scale

Site scale work involved undertaking on-ground habitat assessments at three extant and three extinct warru colonies within the APY Lands (Table 2.2). Extant sites were selected on the basis of them being the largest known remaining warru colonies on the APY Lands (Read and Ward 2011b). Extinct sites were based on historical and Indigenous knowledge indicating that they once had robust warru populations. Assessments were undertaken in 2007 and 2008 following the hillside scale procedure detailed below.

Table 2.2. Details of extant and extinct warru colonies assessed for the site scale analysis in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Names in brackets are those of sites‟ alternative titles. Population estimates and year of extinction attained from Read and Ward (2011b), Nesbitt and Wikilyiri (1994) and Indigenous Knowledge from the Watarru Indigenous community.

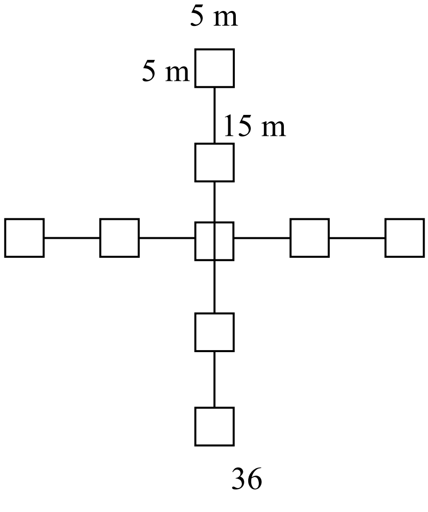
Site	Status	Range	Population estimate	Year of extinction	Assessment undertaken
Alalka	Extant	Musgrave	25	n/a	May 2008
Kalka	Extant	Tomkinson	15	n/a	August 2008
New Well (Atjinyunta)	Extant	Musgrave	25	n/a	June, August 2007
Aeroplane Hill (Anyantanama)	Extinct	Musgrave	n/a	Between ~1944 – 1990	August 2008
Mt Lindsay	Extinct	Birksgate	n/a	Between 1960s-late 1970s	August 2008
Wamitjara (Sentinel Hill)	Extinct	Musgrave	n/a	2006	May 2008

2.3.3 Hillside scale

For the hillside scale assessment, each extant and extinct hill (Table 2.2) was divided into core and non-core areas. Documented Indigenous Knowledge (Robinson *et al.* 2003), information from the on-ground management agency (APY Land Management), Warru Recovery Team information and/or data in Geelen (1999) enabled identification of areas of extinct and extant hills that historically had, or continue to have, a higher density of warru compared to the remainder of the hill. These were termed „core areas‟ and generally contained habitat that was more structurally complex. Aerial photographs of each hill were obtained from the Department of Environment and Natural Resources, georeferenced and, excluding Aeroplane Hill, core areas delineated using ArcMap tools (Appendix 2). Areas outside of this delineated core area were classified as „non-core‟. As such, non-core areas represented areas of the hills which animals may or may not have utilised, but always at a lower „intensity‟ than that of core areas. The ArcMap extension Hawth‟s Analysis Tools (ver. 3.27, 2002-2006) was used to generate seven randomly-located points within each of the core and non-core areas. Consequently, there were 14 points in each of the six hills. Points were set to occur least 200 m apart from each other. No information on core areas was available for Aeroplane Hill so the 14 points were generated across the whole hill and the site was excluded from analyses at the hillside scale.

A point was defined as the centre of a transect and, using transects‟ GPS locations, field assessments were completed at each. Where safety concerns did not allow access to a transect‟s exact GPS location, the transect was moved to a safe position as close as practicable to the original destination. Due to the random selection process, transects ran across both open and restricted areas (eg. over deep crevices, under dense vegetation). Each transect consisted of nine quadrats; five horizontally across the hill and four vertically up and down the hill. Transects were consequently cross-shaped (Figure 2.1). Quadrats were 15 m apart and 5x5 m in diameter, making the entire transect 170 m in length. The number of warru scats present in each quadrat was counted, summed for each transect and then used as the dependent variable. All scats were categorised as either old or fresh. To determine if competition for resources occurs between warru and euros (Read 2006), the euro scats that occurred in quadrats were also counted.

Fig. 2.1. Diagrammatic representation of a habitat assessment transect, made up of nine quadrats. Fourteen transects were completed at each of six hills in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



Habitat parameters were assessed at the level of either a transect or quadrat. Across the transect, assessed parameters were those of slope, aspect, evidence of predators, warru refuges and preferred warru foods. For the slope, a clinometer was used to measure the slope at the western and southernmost quadrats respectively (Fig. 2.1); these measurements were then averaged to provide a slope for the entire transect. Dominant aspect was determined using a compass. Evidence of predators was assessed while walking the length of the transect and counting and, where possible, identifying predator signs (fox, dog, cat). While walking, the number of refuges that were encountered was also recorded and characteristics thereof analysed (see 2.3.4). Lastly, spearbush (*Pandorea doratoxylon)* and fig *(Ficus brachypoda)* plants were also counted as these are favoured warru foods (Geelen 1999).

In each quadrat, assessed parameters were those of vegetation (Appendix 3), geology, habitat type and euro abundance (using scats as a proxy) (Table 2.3). For the vegetation assessments, grasses were defined as those in the Poacea ("true grasses") family, but excluded the sedges (Cyperaceae), which were grouped into the forb/herb/sedge category. Consequently, the latter group was broadly defined as herbaceous plants other than grasses (Kutsche and Lay 2003).

Table 2.3. Environmental parameters assessed at quadrats within hills of the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Veg. – vegetation; FHS – forbs, herbs, sedges. Where options are provided, assessments determined which was most applicable.

Parameter	**Measure**	**Explanation**
Vegetation	%	Total % vegetation. Together with % rock and % bare earth, sums 100%
	% forb/herb/sedge	% forb/herb/sedge out of total % veg. above
	% *Triodia*	% *Triodia* spp. out of total % veg. above
	% other grasses	% non-*Triodia* grass species out of total % veg. above
	% buffel grass	% *Cenchrus ciliaris* in quadrat (if present)
	% shrubs	% shrubs out of total % veg. above
	% trees	% trees out of total % veg. above
	Species richness	Respectively: total number of species; number of FHS; number of grasses
	Vegetation type	Predominantly a) tussock grass b) tussock grass with emergent shrubs c) *Triodia* spp. d) *Triodia* spp. with emergent shrubs e) no vegetation f) mainly shrubs g) FHS with shrubs h) other
Geology	% rock	Total % rock. Together with % vegetation and % bare earth, sums 100%
	% bare earth	Total % bare earth. Together with % vegetation and % rock, sums 100%
	% rocks/stones	Out of total % rock, the % of rocks < 60 cm diameter
	% boulders/outcrops	Out of total % rock, the % of rocks > 60 cm diameter
	Rock complexity	Subjective assessment of a) low b) medium c) high
	Rock dominant size	1) small rocks (<0.5m diameter) 2) large rocks (0.5-1m) 3) Small boulders (1-3m) 4) medium boulders (3-5m) 5) large boulders/cliffs (>5m) 6) large flat slabs of rock („pavement" rock).
Habitat type		a) outcrop b) flat adjacent to outcrop c) hillslope d) hilltop e) ridge/scarp f) other
Competitors	# euro scats	Total number of euro scats counted up to 60; if greater, denoted as > 60
Warru	# of warru scats	Total number, categorised as old or fresh

2.3.4 Statistical analyses for site and hillside scales

Calculations were performed using generalised linear modelling in SAS (ver. 9.2; SAS Institute Inc., Cary, NC, USA). Analyses were conducted using a process of three steps.

The first step involved determining which environmental parameters were significant predictors of warru scats. For this, the number of old, fresh and total scats respectively were modelled against environmental parameters from the site and hillside scales. Scats were separated into these three age categories because this enabled an assessment of whether individual categories revealed different aspects of animals‟ habitat use. For example, old scats, being differentially affected by weather, may not reveal all associations evidenced by fresh scats. Firstly, univariate modelling was undertaken by fitting negative binomial regression models to the data. A generalised estimating equation was used to account for the dependence in measurements from within the same sites. All environmental variables with $P < 0.05$ in the univariate model were then included in the multivariate model (only multivariate results are presented). The latter assessed the influence of an environmental variable on the respective warru scat category while controlling for all other predictor variables in the model.

The second step involved identifying which environmental variables were significant predictors of extant sites and core areas respectively. To achieve this, univariate logistic regression models were fitted to the data, with extant and core areas respectively as the dependent variables. A generalised estimating equation was again used to account for the dependence in measurements from within the same sites.

The third step involved combining the results from steps 1-2. This enabled an analysis of whether the environmental parameters favoured by warru (step 1) were present at extant sites and core areas (step 2) and, consequently, whether these parameters are likely to have influenced the persistence of warru at these two scales.

2.3.5 Refuge scale

Refuges were defined as any shelter-like rock structure which would offer some degree of protection from weather and predators (Waldegrave-Knight 2002; Murray *et al.* 2008). While walking along transects (see 2.3.2), the characteristics of each encountered refuge were assessed (Table 2.4). The number of warru and euro scats both within, and on the immediate outside of, refuges, was counted and used as the dependent variable during analyses.

Table 2.4. Characteristics assessed for refuges encountered along transects in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Parameter	Measure
Type	Defined as one, or pairing of; cave – has three walls; crevice - has a minimum of two side walls; boulders – rocks formed into a pile; overhang - has a roof; labyrinth - a large jumble of rocks consisting of multiples of all refuge types
Size	Refuge fits a) a person cannot fit b) 1 average person c) 2 average people d) 3 or more average people (after Lobert 1988)
Entrances	Total number
Exposure	Subjective assessment of level of exposure to outside elements; high, medium, low
Accessibility	By human standards, 2) impossible or difficult to climb to 3) safe to climb to 4) can be scrambled to 5) can be walked to.
Altitude	Altitude of refuge (using a GPS)
Height	Height = altitude of refuge - altitude at base of hill

2.3.6 Statistical analysis – refuge scale

Refuge scale data were analysed separately to that of the site and hillside scales and aimed to determine the physical characteristics which increased the likelihood of refuges being used by warru and euros respectively. To achieve this, logistic regression models were fitted to the data. A generalised estimating equation was used to account for the dependence in measurements within the same site. Predictor variables with $P < 0.05$ in the univariate model were included in the multivariate model. Multivariate modelling results indicated what proportion of the variation in scats the variable of interest accounted for, if all other parameters were held at their median.

2.4 Results

2.4.1 Regional scale

The projected potential distribution for warru in the APY Lands is presented (Fig. 2.2). This uses Maxent‟s logistic output, which represents the probability of warru presence based on the modelled environmental variables (Phillips and Dudík 2008). Thus, for each grid cell, the probability of warru presence ranges from 0 to 1.0. Areas of high probability occur in the Musgrave, Birksgate and Tomkinson Ranges. The AUC for the test data was 0.984, indicating that the model had excellent predictive ability (Phillips *et al.* 2006).

Results of a jack-knife test (training data) of variable importance (Fig. 2.3) revealed that the variable with the highest gain when used in isolation was „detailed geology‟, which indicates that it provided the most useful information by itself. When omitted, „distance from Indigenous community‟ decreased gain the most, meaning that it had the most information not present in other variables. The variables with the greatest predictive power, with a gain >1.5, were; detailed geology, slope, geology, soil type and elevation. Probability of warru occurrence was maximised at detailed geology of ultrabasics, metasediments, alluvium and gravel; a slope of 15-25 percent rise; geology of igneous mafic intrusive rock, soil type of massive earths, clays and loams and an elevation between 900 – 1,100 m.

The variables with a medium level of predictive power, with a gain between 0.5 – 1.5, included; distances from homelands, drainage, Indigenous communities, and soaks and springs respectively, annual mean temperature, mean annual precipitation and mean temperature of the coldest quarter. Probability of warru occurrence increased with proximity to Indigenous homelands, drainage, Indigenous communities and soaks and springs. It was also greater at an annual mean temperature of ~16ºC, above which it declined; mean annual precipitation of 300 mm and above; and mean temperature of the coldest quarter of 7.5 - 9 ºC.

The remaining variables, namely aspect, fire frequency, mean temperature of the warmest quarter and vegetation type, were not important in terms of the model‟s predictive power.

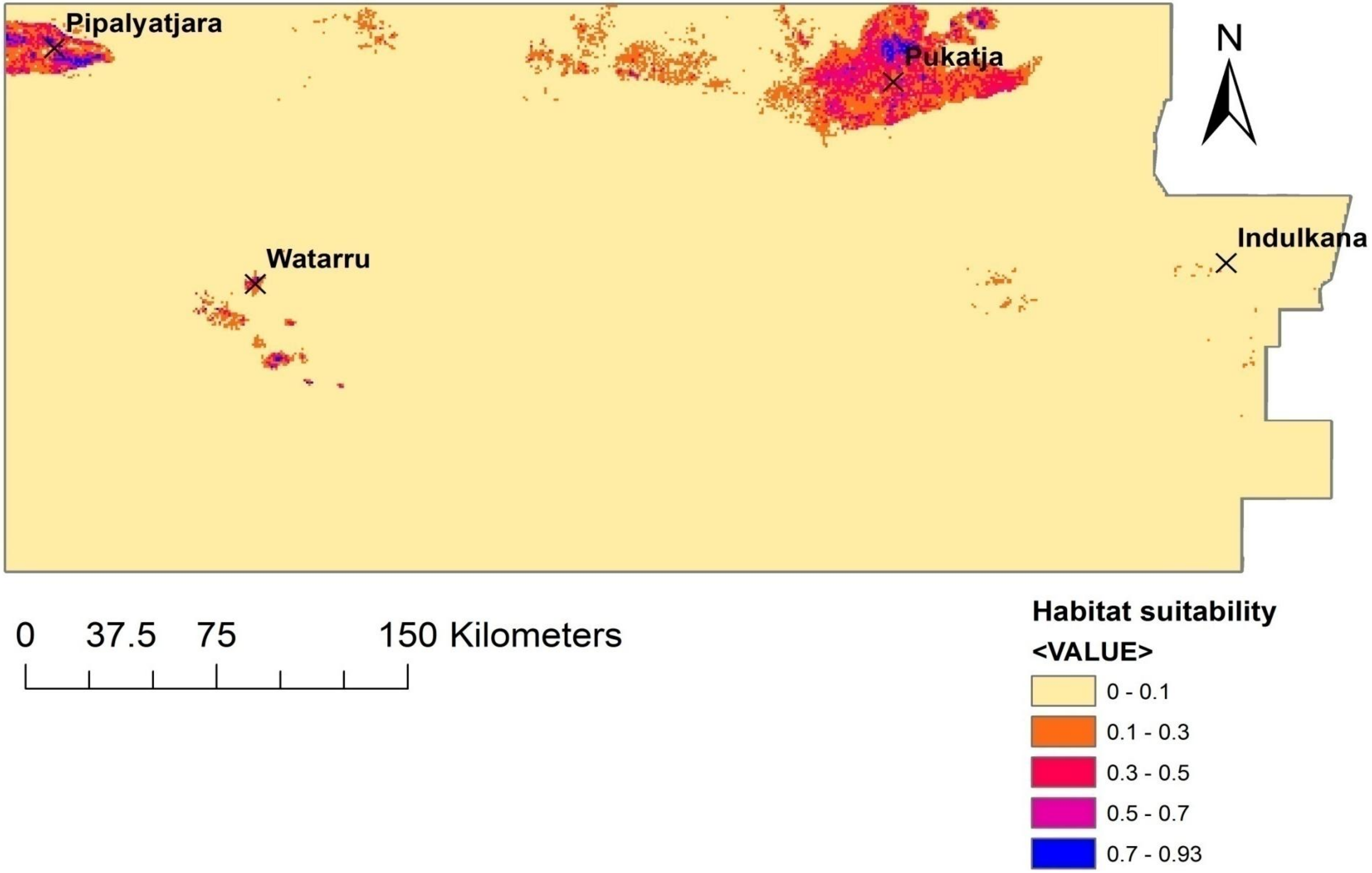


Fig. 2.2 Predicted potential distribution of warru in the Anangu Pitjantjatjara Yankunytjatjara Lands based on the Maxent model, where a higher habitat suitability value equates to a higher suitability for warru. Marked crosses and names are those of Indigenous communities.

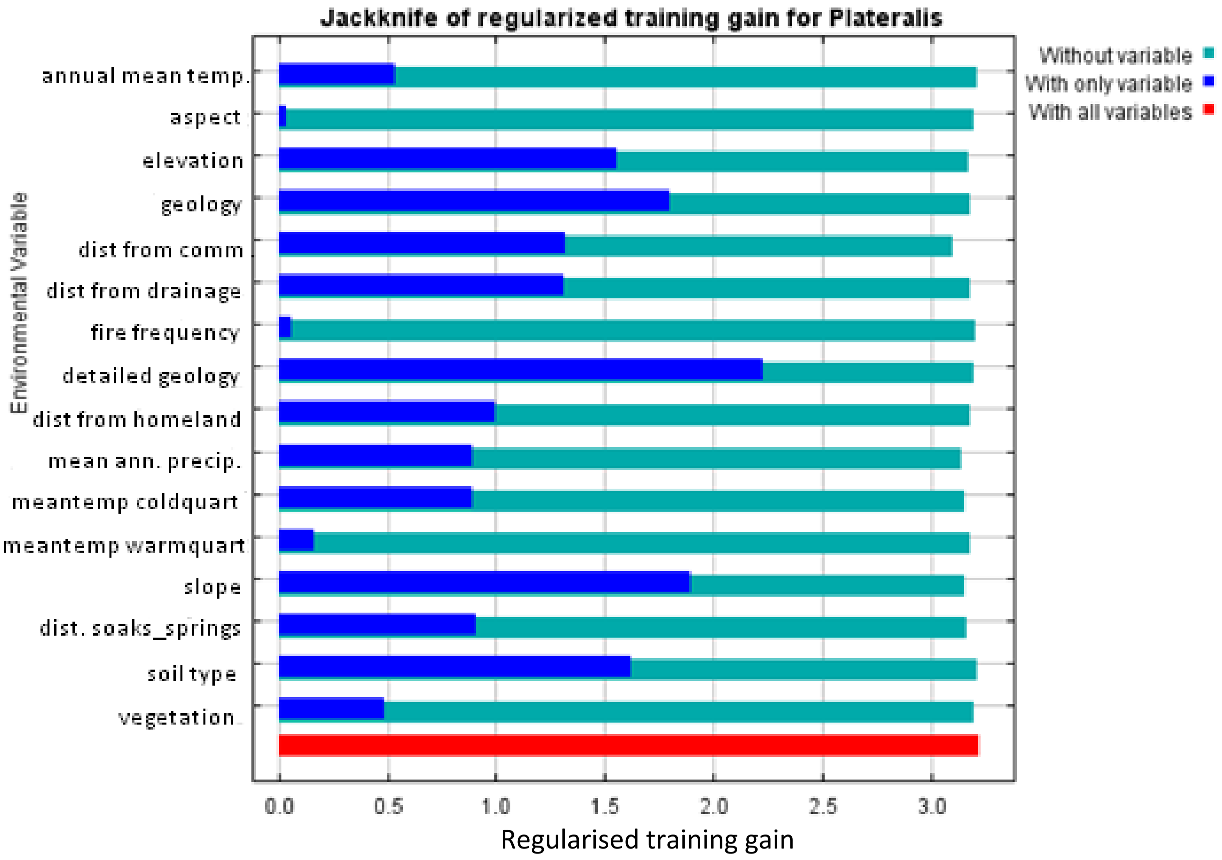


Fig. 2.3. Results of jack-knife tests of variable importance, showing the contribution of each environmental variable (in blue) to the overall gain of the model (in red) while holding all other variables at their mean sample value. Variables are; „annual mean temp"– annual mean temperature, „dist from comm"– distance from Indigenous community, „dist from drainage"– distance from drainage, „dist from homeland"– distance from Indigenous homelands, „mean ann precip"– mean annual precipitation, „meantemp coldquart"– mean temperature of coldest quarter, „meantemp warmquart"– mean temperature of warmest quarter, „dist. soaks_springs"– distance from soaks and springs, „vegetation"– vegetation type.

2.4.2 Site and hillside scales

2.4.2.1 Predictors of warru scats

Environmental variables that were statistically significant predictors of old, fresh and total warru scats at the multivariate level are presented (Table 2.5). During post-hoc analyses, the vegetation types of „mainly shrubs‟, „forbs, herbs, sedges with shrubs‟ and „other‟, and habitat type „other‟ were excluded due to insufficient sample size.

Table 2.5. Significant environmental predictors of old, fresh and total (old + fresh) warru scats in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia, as derived by multivariate modelling. Significant *P* values are highlighted. NM - not modelled, meaning that the variable, not being significant at the univariate modelling level, was not included in multivariate modelling, UM – unable to model due to lack of sample size.

Parameter	Old	Fresh	Total
Site: extant	<.001	UM	<.001
Hill: core	<.001	<.001	<.001
Slope	0.72	<.001	0.96
Aspect	<.001	UM	<.001
% rock	0.004	NM	0.002
% trees	NM	<.001	NM
Vegetation type	<.001	UM	<.001
% boulders/outcrops	0.57	<.001	0.44
Rock complexity	<.001	<.001	<.001
Dominant rock size	0.02	<.001	0.01
Habitat type	<.001	<.001	<.001

For old warru scats, the mean number of scats was 19.8 times higher in extant sites than extinct sites (rate ratio [RR] = 19.77, 95% confidence interval [CI] 4.399, 88.844). Mean number of scats was also 6.09 times higher in core areas than non-core (RR 6.086, 95% CI 3.224, 11.492). Every one unit increase in percentage rock decreased the total number of scats by 2.49% (RR 0.975, 95% CI 0.959, 0.992). For the categorical variables, post-hoc analyses indicated that mean number of scats was highest in areas with a north-easterly aspect, vegetation type of predominantly tussock grass, high rock complexity, a dominant rock size of medium boulders (3-5m) and hillslope habitat type.

For fresh warru scats, the mean number of scats was 3.7 times higher in core areas than non-core (RR = 3.70, 95% CI 2.448, 5.596) and every one unit increase in slope led to a 4.07% increase in scats (RR 1.041, 95% CI 1.031, 1.050). In contrast, every 1% increase in trees and boulders/outcrops respectively decreased mean number of scats by 5.28% (RR 0.947, 95% CI

0.912, 0.984) and 2.55% (RR 0.974, 95% CI 0.967, 0.982). For the categorical variables, post-hoc analyses indicated that mean number of scats was highest in areas with high rock complexity, a dominant size of large boulders/cliffs (>5m) and outcrop habitat type.

For total warru scats, the mean number of scats was 26 times higher in extant sites than extinct (RR 25.96, 95% CI 5.8, 116.21) and 6.76 times higher in core areas than non-core (RR 6.759, 95% CI 3.635, 12.566). Every 1% increase in rock decreased the total number of scats by 2.38% (rate ratio 0.976, 95% CI 0.962, 0.991). For the categorical variables, post-hoc analyses indicated that mean number of scats was highest in areas with a north-easterly aspect, vegetation type of predominantly tussock grass, high rock complexity, a dominant rock size of medium boulders (3-5m) and hillslope habitat type.

2.4.2.2 Site scale

A number of parameters were significant predictors of extant sites (Table 2.6). Specifically, every one percent increase in vegetation and *Triodia* spp. respectively increased the odds of the site being extant by 2.4% and 6.6%. In contrast, every one percent increase in rock, and forbs/herbs/sedges decreased the odds of the site being extant by 1.2% and 5.4% respectively. Post-hoc analyses of the categorical variables indicated that extant sites were also most likely to have an easterly aspect, ridge/scarp habitat type and a dominant size of small rocks.

Table 2.6. Significant predictors of warru extant sites in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia, including parameter means and standard deviations (SD). For categorical variables, odds ratio and confidence intervals are not available; see post-hoc analysis results. CI – confidence interval, FHS – forbs, herbs, sedges.

Parameter	Extant Mean (± SD)	Extinct Mean	Odds ratio	Lower - upper 95% CI	P value
Aspect					<.0001
% vegetation	30.7 (± 17.3)	23.7 (± 17.1)	1.024	1.008 – 1.04	0.0033
% rock	55.8 (± 21.6)	61.8 (± 23.6)	0.988	0.98 – 0.997	0.0074
% FHS	3.9 (± 5.6)	6.2 (± 7.5)	0.946	0.903 – 0.992	0.0207
% *Triodia*	17.9 (± 16.3)	6.7 (± 11.6)	1.066	1.016 – 1.118	0.0089
Habitat type					<.0001
Dominant rock size					<.0001

2.4.2.3 Hillside scale

Modelling indicated a number of parameters were significant predictors of core areas (Table 2.7). The likelihood of the area being core increased by 25.1% with every one unit increase in the number of figs, 235.7% with every unit increase in dog/dingo signs and 0.9% with every one percent increase in outcrops/boulders. Furthermore, the odds of the area being core increased by 9.8% with every one unit increase in slope. Indeed, at extant sites, core areas had an average slope of 31.53 degrees, compared to 13.44 degrees for non-core areas. At extinct sites, core areas had an average slope of 17.9 degrees, compared to 12.32 degrees for non-core areas. A number of parameters led to a decrease in the likelihood of the area being core. Every 1% increase in *Triodia* and rocks/stones decreased the odds of the area being core by 1.7% and 1.3% respectively. Furthermore, every unit increase in euro scats decreased the odds of the area being core by 1.6%. Post-hoc analyses of the categorical variables indicated that core areas were most likely to have a northerly aspect, vegetation type of predominantly tussock grasses, habitat type of outcrops, high rock complexity and dominant rock size of large boulders/cliffs.

Table 2.7. Significant predictors of warru core areas in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia, including parameter means and standard deviations (SD). For categorical variables, odds ratio and confidence intervals are not available; see post-hoc analysis results. CI – confidence interval.

Parameter	Core Mean (± SD)	Non-core Mean (± SD)	Odds ratio	Lower - upper 95% CI	P value
Slope	26.1 (± 15.1)	13 (± 9)	1.098	1.037 – 1.161	<.001
Aspect					<.001
# *Ficus brachypoda*	2.3 (± 3.8)	0.74 (± 1.4)	1.251	1.033 – 1.515	0.02
Dog signs	0.34 (± 0.67)	0.09 (± 0.29)	3.357	1.442 – 7.813	<.01
% *Triodia*	10.3 (± 14.4)	14.5 (± 16.5)	0.983	0.967 – 0.998	0.028
Vegetation type					<.001
% rocks/stones	16 (± 16.7)	19.8 (± 18.5)	0.987	0.979 – 0.996	<.01
% outcrops/boulders	44.5 (± 27.9)	36.7 (± 29.7)	1.009	1.001 – 1.018	0.02
Habitat type					<.001
Rock complexity					<.01
Dominant size					<.001
Euro scats	20 (± 20.8)	28.3 (± 24.2)	0.984	0.978 – 0.989	<.001

2.4.2.4 Combining predictors of warru scats, site and hillside scales

The results of the analyses above (2.4.2.1 – 2.4.2.3) were subsequently combined. At the site scale (Table 2.8), this indicated that the predominantly easterly aspect, lower percentage of rock and hillslope habitat type of extant sites correlates to the preferences of warru (using total scats). It is therefore likely that these parameters have facilitated the persistence of warru at extant sites.

At the hillside scale (Table 2.9), the higher slope, tussock grass vegetation type, high rock complexity and dominant rock size of large boulders and cliffs of core areas correlates to the preferences of warru (using total warru scats). Thus, these parameters are likely to have abetted the higher density of warru in core areas.

Table 2.8 Significant predictors of extant warru sites, warru preferences (using total scats) pertaining to those predictors and therefore, whether the parameters are likely to have abetted warru persistence at extant sites. ↑ = increase; ↓ = decrease; FHS = forbs, herbs, sedges.

Parameter	Extant sites	Warru preference	Affects persistence?
Aspect	East	Northeast	Likely to
% vegetation	↑	None	x
% rock	↓	↓	✓
% FHS	↓	None	x
% *Triodia*	↑	None	x
Habitat type	Hillslope	Hillslope	✓
Dominant size	Small rocks	Medium boulders	x

Table 2.9 Significant predictors of warru core areas, warru preferences (using total scats) pertaining to those predictors and therefore, whether the parameters are likely to have abetted higher warru densities in core areas. ↑ - increase, ↓ - decrease.

Parameter	Core sites	Warru preference	Affects persistence?
Slope	↑	↑	✓
Aspect	North	Northeast	Likely to
# figs	↑	None	x
Dog/dingo signs	↑	None	x
% *Triodia*	↓	None	x
Vegetation type	Tussock grass	Tussock grass	✓
% rocks & stones	↓	None	x
Habitat type	Outcrop	Hillslope	x
Rock complexity	High	High	✓
Dominant size	Large boulders/cliffs	Large boulders/cliffs	✓
Euro scats	↓	None	x

2.4.3 Refuge scale

A number of refuge characteristics were significant predictors of the presence of warru and euro scats (Table 2.10). Altitude results are not presented. For warru, this is because altitude, not being significant at the univariate level, was not modelled at the multivariate level. For euros, although it was significant at the univariate level, it was not able to be modelled at the multivariate.

Results for warru indicated that the odds of finding scats increased by 1.13 (P=0.033) with every one unit increase in number of refuge entrances. For the categorical variables, post-hoc analyses indicated that, using the odds ratios, refuges of a cave-crevice structure that fitted three or more people, were of low exposure and difficult to access were most likely to contain warru scats. However, there was no statistically significant difference between use of cave-crevices and boulder-crevices, labyrinths, crevice-overhangs or boulder-caves.

Results for euros indicated that the odds of finding scats in a refuge decreased by 0.99 for every metre increase in refuge height. For the categorical variables, post-hoc analyses indicated that refuges of a boulders-overhang structure that fitted three or more people and were of medium exposure were most likely to contain euro scats.

Table 2.10 Statistically significant (*P* values highlighted) predictors of the presence of warru and euro scats in refuges. CI – confidence interval, NS – not significant at the univariate level and therefore not included in multivariate modelling. For categorical variables (type, size, exposure, accessibility), odds ratio and confidence intervals are not presented; see post-hoc analysis results.

Parameter	Odds ratio		Lower 95% CI		Upper 95% CI		*P* value	
	Warru	Euro	Warru	Euro	Warru	Euro	Warru	Euro
Type							<.001	<.001
Size							<.001	<.001
Entrances	1.135	NS	1.01	NS	1.275	NS	0.03	NS
Exposure							<.001	<.001
Accessibility		NS		NS		NS	0.01	NS
Height	NS	0.993	NS	0.991	NS	0.996	NS	<.001

2.5 Discussion

2.5.1 Habitat associations

Using the correlates established in the current study, the following presents a hypothetical simulation of the habitat selection process undertaken by warru. Although such choice is obviously influenced by a myriad of factors, including animals‟ historical distribution, dispersal capabilities and previous hunting regimes, the simulation aims to aid interpretation of warru habitat associations.

At the regional scale, warru „choose‟ to live in mountain ranges, with areas of high probability for warru presence in the Musgrave, Birksgate and Tomkinson Ranges. These are analogous to regions of historically high warru abundance (Read and Ward 2011b). Outside of these ranges, there were few areas suitable for warru habitation. The variables driving this choice were geology, detailed geology, slope, soil type and elevation. In particular, warru presence is correlated with areas with igneous mafic (a silicate rock rich in magnesium and iron) intrusive rock and a detailed geology of ultrabasics, metasediments, alluvium and gravel. In contrast, Gibson (2000) found that in the Northern Territory, the race was present on all major rock types. The discrepancy is explained by the fact that in the current study, records from 1998-2010 only were used. By this time in SA, warru had already contracted to only the major ranges, the cores of which consist of intrusive igneous rocks, usually granite mafic rock (Pearson and Kinnear 1997).

Warru also „choose‟ a slope of 15-25 percent rise, which equates to 10-14 degrees, a soil structure of massive earths, clays and loams, or massive earths and sands and elevations between 900-1,100 m. The elevation preference is likely a result of higher areas being steeper, and thus less accessible to predators. Although the result for slope concurs with its pre-eminence in other studies (Short 1982; Waldegrave-Knight 2002), the preference range established for warru is less than that of other *Petrogale* spp. For example, both Joblin (1983 in Jarman and Bayne 1997) and Short (1982) found that *P. penicillata* occupied sites with slopes >45 degrees, while Lobert (1988) recorded values of 70-90 degrees. This discrepancy can probably be explained by the fact that previous researchers measured these slopes during fieldwork in core *Petrogale* habitat. In contrast, the current regional-scale result is for an „average‟ slope for across a whole hill, which is likely to „dilute‟ the value. In support of this, the results for slopes measured during fieldwork (site scale; see later), does accord well with previous research.

Warru then „choose‟ areas close to drainage features, Indigenous communities, homelands and soaks and springs. Given that most creeks in the APY Lands only flow after heavy rain, the first association is probably a result of riparian vegetation providing warru with supplementary feed and/or shelter, rather than being due to the presence of water itself. Similarly, Pearson (1992) found that extant warru colonies in Western Australia‟s (WA) Warburton region were located in areas of mesic vegetation in gullies or along creeklines, but, in this case, most often close to permanent or semi-permanent water. The association with Indigenous communities could be due to the high numbers of camp dogs in these areas acting to suppress fox numbers. However, given that six of the 11 communities included in modelling are located adjacent to hills (defined as areas over 750 m), the result may be an artefact. Similarly, 55% of homelands, and 58% of soaks and springs are located close to hills, again potentially confounding results. Warru also „choose‟ areas of higher mean annual precipitation (300 mm and above) and lower mean annual temperature (~16°C), which would be advantageous for animals‟ food supply and physiological maintenance.

Once in an appropriate mountain range, warru then „choose‟ a hill on which to live. Using total warru scats, modelling from the site and hillside scales indicated that warru prefer: high rock complexity of medium boulders, a north-easterly aspect, tussock grass, a decreased percentage of rock and hillslopes.

The results for rock complexity and dominant rock size concur with a spectrum of *Petrogale* studies, which have found that habitat complexity is a critical predictor of animal presence (Lim and Giles 1987; Jarman and Bayne 1997; Murray *et al.* 2008). The benefits ascribed to rocky habitats are those of enhanced microclimatic conditions (Short 1982; Copley and Robinson 1983; Sharp 1997b), protection from fire and predators (Pople 1989; Sharp 1997b) and high vegetative productivity (Freeland *et al.* 1988). The aspect preference also concurs with previous studies that have suggested that north to east-facing sites are advantageous for animals‟ thermoregulation. This is because such sites are warmed by the sun in the morning, but, during the hotter part of the day, likely to be shaded (Short 1982; Waldegrave-Knight 2002). The preference for tussock-grass dominated vegetation is also unsurprising because warru predominantly eat grasses and forbs (Capararo 1994; Geelen 1999). However, the lack of difference between areas of tussock grass and the other modelled categories (tussock grass with emergent shrubs, *Triodia* spp., and *Triodia* spp. with emergent shrubs) indicates that further research is needed. This could involve determining warru preferences by assessing vegetation availability vs. use. The preference for decreased rock may indicate that in an environment where rocks are not a limiting factor, warru select for more vegetated sites, which can be used as a food resource. Similarly, Gordon *et al.* (1978) found that sites occupied by *P. xanthopus* had greater vegetational diversity. Alternatively, the result may be a modelling artefact, with scats perhaps more likely to persist on soil substrates than on rocks.

Modelling indicated that certain habitat parameters distinguished extant and core areas respectively. Firstly, extant sites had increased percentages of *Triodia*. This could relate to the protective properties of spinifex, with spinifex-clad hills potentially more effective at deterring predators. However, core areas had less *Triodia* than non-core areas, suggesting that, once on a hill that provides sufficient „overall" protection, warru select core areas which contain less *Triodia*, in turn allowing proliferation of other vegetation types. A similar response may be occurring for rocks, with extant sites likely to be dominated by small rocks, which presumably would allow more vegetation to grow. However, core areas had high habitat complexity, suggesting that once they are on a hill that is generally less rocky, warru select areas of high rock complexity. Both extant sites in general, and core areas within extant sites, also had high average slopes. Indeed, the average slope of core areas in extant sites was 31.5 degrees, which is within the preference bounds of 10-40 degrees found by Geelen (1999). A high slope is likely to provide warru with a greater chance of escape from predators. The pertinence of this is highlighted by the higher number of dog/dingo signs in core areas and the fact that fresh warru scats decreased by 76% with every one unit increase in *Canis* signs. This suggests that *Canis* spp. are particularly active in warru core areas, while warru dynamically shift their centre of activity within the colony so as to avoid areas which have had dogs in them.

The other modelled biotic interaction involved euros. Warru had no preference for or against euro scats (as modelled by warru scat abundance). However, there were significantly fewer euro scats in core areas, probably because the latter are less accessible to euros. The mean of 20 euro scats per transect encountered in core areas may be useful for guiding the selection of reintroduction sites that are complex enough to decrease competition between euros and warru. Core areas also had significantly more figs than non-core areas (average of 2.26 per transect *c.f.* 0.74). Since figs are an important component of the diet of warru throughout the year (Geelen 1999), this correlation was unsurprising. More unexpected was the lack of evidence for an increased abundance of spearbush, another favoured food plant (Geelen 1999), in core areas.

Unexpectedly, refuge abundance was also not a significant predictor of extant sites, core areas or old, fresh or total warru scats. This contrasts with results from other *Petrogale* studies (Short 1982; Waldegrave-Knight 2002; Murray *et al.* 2008). Indeed, it is widely accepted that refuges are an important resource for *Petrogale*, with shelter density, rather than general rockiness, supposedly driving animal presence at the local scale (Short 1982; Barker 1990; Jarman and Bayne 1997; Telfer 2006). However, the current study suggests that refuge type is also important. Thus, rather than a high overall quantity of shelter sites, warru may require sufficient refuges of a certain quality. Animals preferentially choose to use large (fits 3 or more people) refuges with low exposure, a higher number of entrances and that are difficult to access (by human standards). Large refuges may be advantageous for several reasons; firstly, they enable more effective retreat from climatic conditions. Secondly, they facilitate greater manoeuvrability from predators and thirdly, allow refuge sharing. For example, Joblin (1983 in Jarman and Bayne 1997) refers to simultaneous refuge use by *P. penicillata*. Refuges of lower exposure provide higher levels of protection from inclement weather. The probability of warru using a refuge also increased as the number of entrances increased, with multi-entranced refuges offering an obvious advantage for the avoidance of predators (Jarman and Bayne 1997). Similarly, Waldegrave-Knight (2002) found that *P. penicillata* core refuges were larger, less exposed and had more than one entrance. Again however, such „preferences‟ must be considered in context of the fact that *Petrogale* are now restricted to habitat refugia. Had a similar analysis been conducted prior to the introduction of cats and foxes, the results would undoubtedly have been very different.

There was no significant difference between use by warru of cave-crevices and boulder-crevices, labyrinths, crevice-overhangs or boulder-caves. This inability to differentiate may be due to the inherent difficulties involved in classifying such topographically complex shelters. It can nevertheless still be surmised that warru prefer refuges with high structural complexity, as supported by the fact that animals were not associated with simple caves or boulders. This is more than likely because animals would be susceptible to predation if cornered in such structures (Sharp 1997b). Telfer and Griffiths (2006) established similar preferences for *P. brachyotis,* with all shelters that were used by animals being complex and containing vertical crevices, horizontal splits and/or boulder-caves. Further research could determine if warru show a preference for shelters with a certain aspect, as has been found for *P. penicillata* (Bulinski *et al.* 1997), and if use is affected by proximity to other refuges (Waldegrave-Knight 2002; Telfer and Griffiths 2006).

There was no evidence of warru „preferring" shelters at or beyond a certain altitude. However, the clear preference for shelters that were difficult to access (by human standards) suggests that warru rely on inaccessibility rather than altitude for protection. This supports the findings of Geelen (1999) for *P. lateralis* and Joblin (1983 in Jarman and Bayne 1997) for *P. penicillata*. The current modelling indicated that euros are most likely to use large refuges of a boulders-overhang structure that have medium exposure and are at lower altitudes. The overlap between euros and warru in preferred refuge size suggests that inter-specific competition may occur for large shelter sites on the lower hillslopes. Since euros may also be competing with warru for food (Capararo 1994), a direct investigation of the nature of the relationship is warranted, especially given that, in recent history, euro abundance in the APY Lands has increased (Read 2006) and euros have been observed as being aggressive towards other *Petrogale* species (Sharp pers. comm.).

2.5.2 Model performance

The current study had two main strengths. The first was that it incorporated all the spatial scales that could logistically be modelled. This minimised the possibility of modelling at an inappropriate scale, which can lead to a loss of discriminative power (Müller *et al.* 2009). The second was that the study used data from both remote-sensing and field surveys. The fact that all four scales yielded novel information about warru distribution supports the suggestion that modelling should be conducted at multiple spatial scales (Martinez *et al.* 2003; McCarthy *et al.* 2005; Murray *et al.* 2008). Limitations of the current study include those relating to SDM, which are summarised in Kozak *et al.* (2008). In particular, since modelling results have their greatest validity in the area where surveying took place (Müller *et al.* 2009), warru habitat associations in the APY Lands do not necessarily apply to *P. lateralis* outside of this region.

Methodological shortfalls include the inability to comprehensively factor in predation. Despite there being a long history of introduced predators on the APY Lands (Finlayson 1961), there remains a dearth of information on their population dynamics. This made it impossible to incorporate warru predation into the regional-scale modelling. At the site and hillside scales, the study attempted to incorporate predation by using fox and dingo scats as indicators of predator abundance. However, since scats are only a proxy for actual predation, future modelling should attempt to incorporate a more robust indicator. Future research should also establish a measure of habitat connectivity, which is likely to be important in explaining warru distribution patterns (Murray *et al.* 2008).

The use of scats in surveys is also associated with several assumptions and biases, which are summarised in Telfer *et al.* (2006) and Geelen (1999). To counter some of these effects, the current study was conducted in winter. Since scats persist longer in cool, dry conditions (Harestad and Bunnell 1987; Telfer *et al.* 2006) which in the APY Lands predominate in winter, the timing of the current study was ideal for counting fresh scats. However, the effect of season on old scats could not be controlled. Further problems can arise because scats can be difficult to distinguish in cryptic locations (Geelen 1999). For example, refuges in which scats were not seen were classified as having no scats; however, given that many shelters were complex, it is possible that some of these records were actually false absences. Although many of these biases and assumptions are large and cannot be controlled or quantified, a recent study (Telfer *et al.* 2006) has shown that scats are an accurate indicator of broad habitat use by rock-dwelling macropods.

2.5.3 Conservation implications

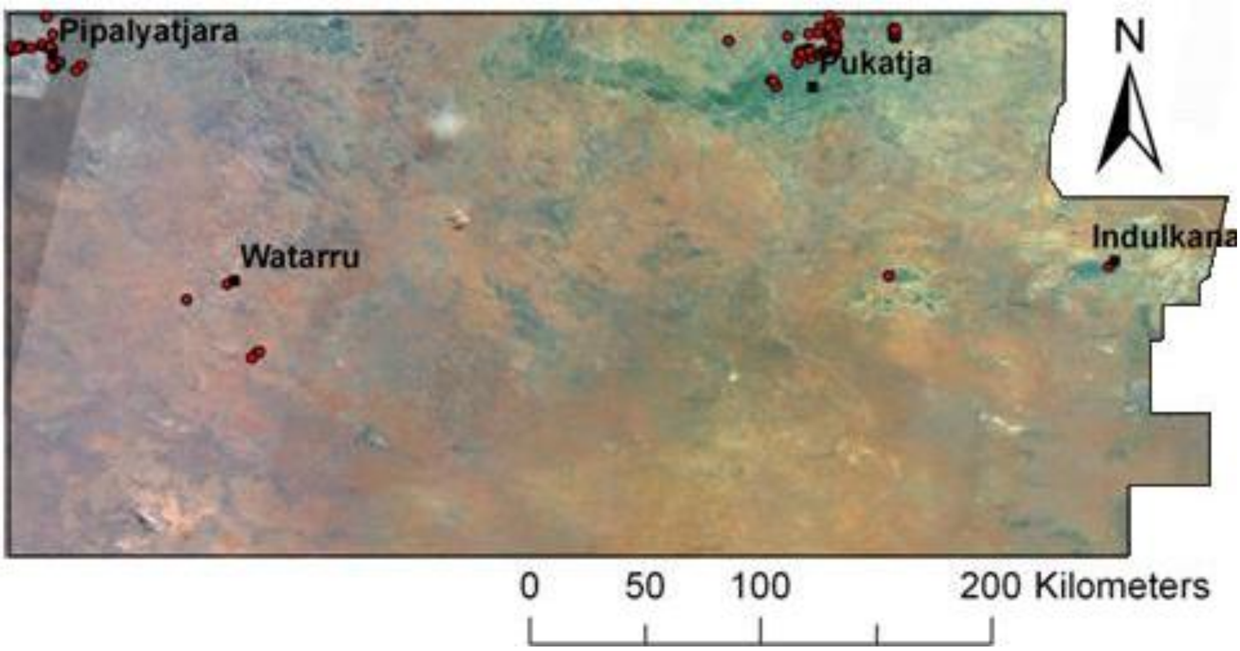
The regional-scale modelling highlighted areas that have similar environmental conditions to those in which warru currently maintain populations (Pearson *et al.* 2007). This information could be used to help target the aerial surveys being conducted by the Warru Recovery Team and thus, accelerate the discovery of unknown colonies.

The site and hillside scale results provide guidance for the selection of appropriate reintroduction sites. Reintroduction of captive-bred warru will occur from 2011 onwards (Read and Ward 2011b) but if animals are released into unfavourable habitat, there will likely be animal attrition through dispersal, predation and/or physiological stress (Waldegrave-Knight 2002). Thus, to select reintroduction sites, the Recovery Team will need to consider both logistical concerns and the ecological parameters specified here. For example, the current study has broadened the scope of potential competition between warru and euros from merely being for food resources (Capararo 1994), to also include shelter sites on the lower hillslopes. This should be considered when selecting reintroduction sites because initially, *Petrogale* tend to remain close to their release site (Molyneux 2011). Thus, to alleviate the potential for naïve, reintroduced warru being out-competed by euros for refuge sites, warru should be released in suitable habitat at higher elevations (ideally, between 900-1,100 m). Honing such details on the APY Lands will hopefully also inform reintroductions at sites beyond the Lands, such as into the SA Davenport Ranges.

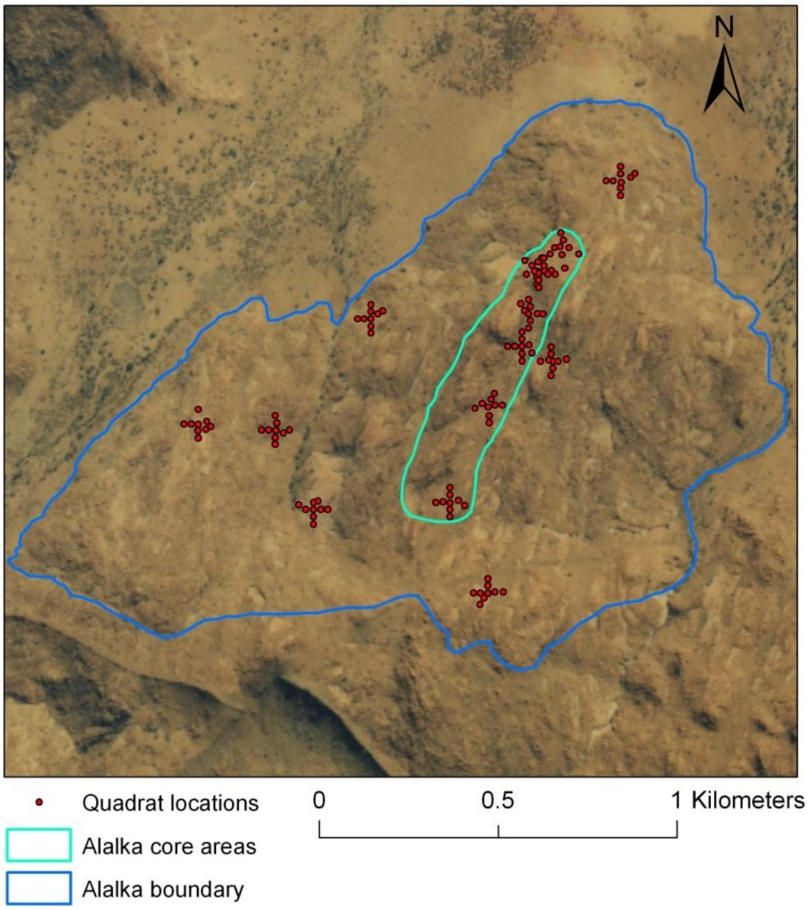
Also of conservation significance was the finding of fresh warru scats at Aeroplane Hill, a site from which warru were considered to be extinct. Since there was only one deposit in one area, it is likely that the scats were from a transient individual, rather than evidence of an established colony. Consequently, this discovery was not considered to negate the status of Aeroplane Hill as an extinct site. However, it supports both the idea of warru moving between extant hills in the context of a metapopulation (Chapters 3 and 4) and the suggestion that lack of suitable habitat is not limiting warru in the APY Lands.

Given that warru populations are more stable in the NT and WA than in SA (Van Dyck and Strahan 2008), undertaking similar habitat assessments in these states could help establish if differences in habitat suitability are contributing to the discrepancies in animals“ status. In the case of WA, where extensive fox and some cat baiting is undertaken (Kendrick *et al.* 2010; Kinnear *et al.* 2010), this could also inform managers as to warru habitat preferences in the absence of feral predators.

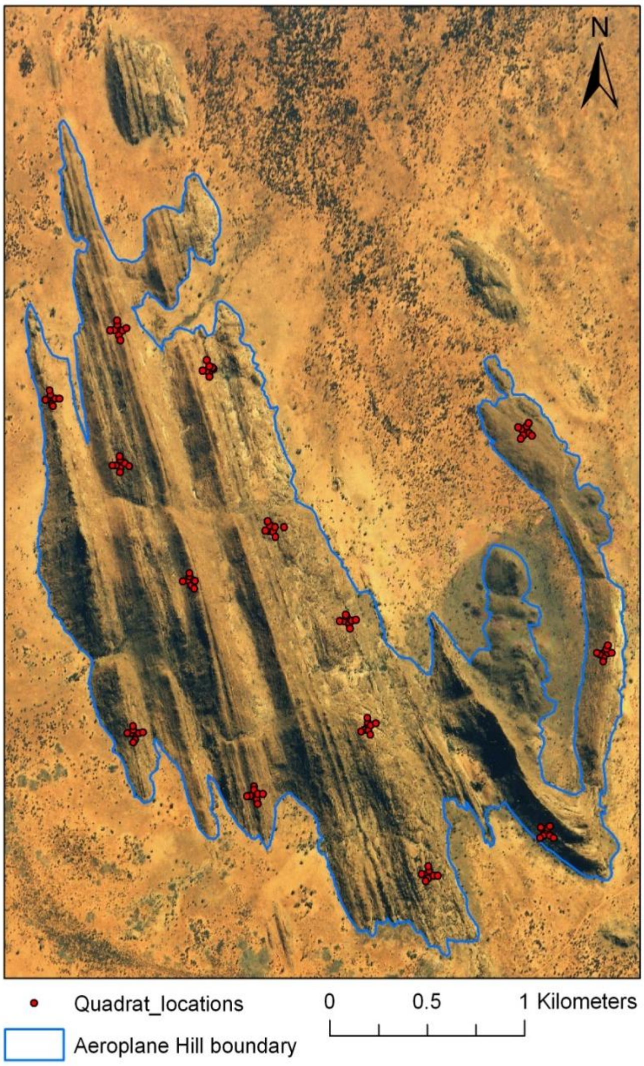
2.6 Appendix



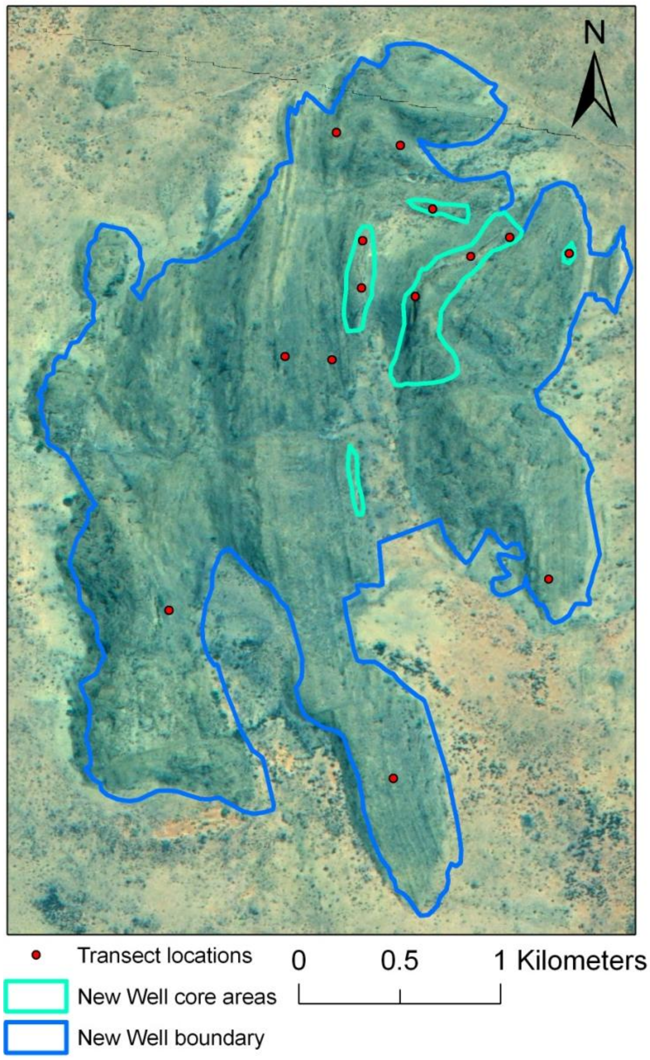
Appendix 1 Warru presence locations used in Maxent modelling for the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



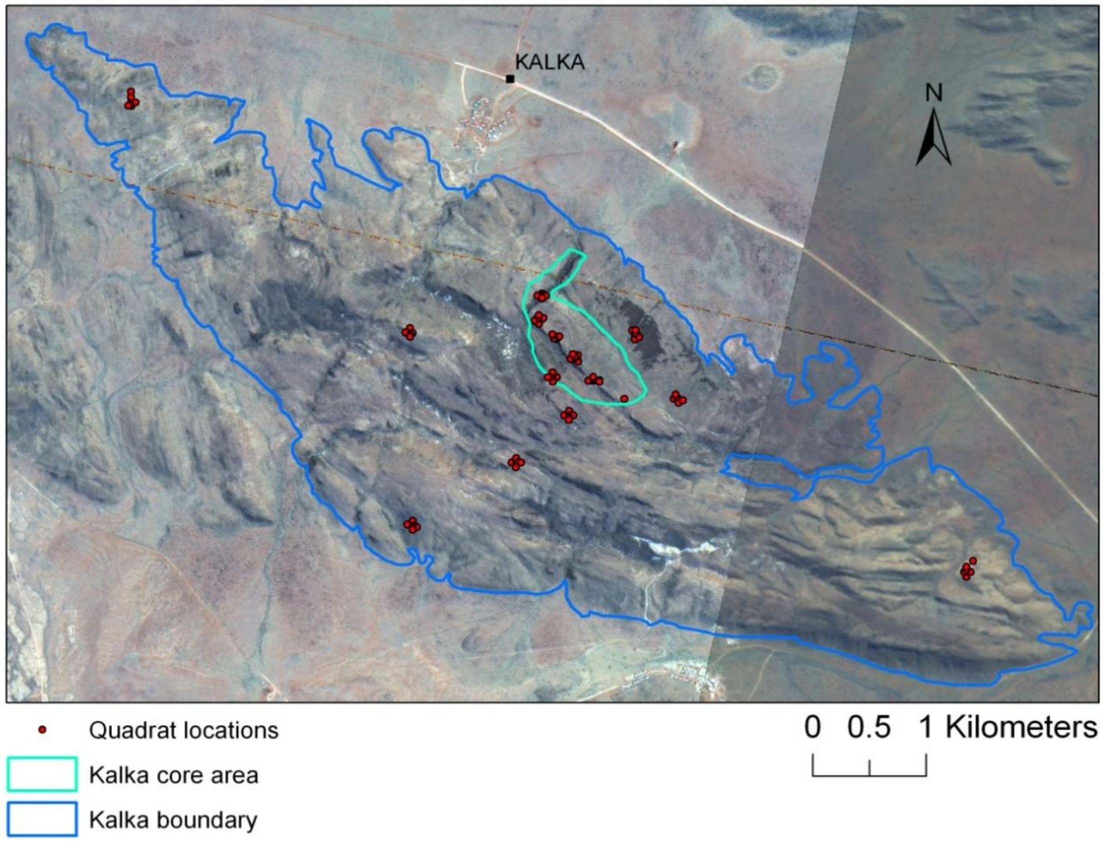
Appendix 2a Transect locations, consisting of 9 quadrats each, within the extant site „Alalka" in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



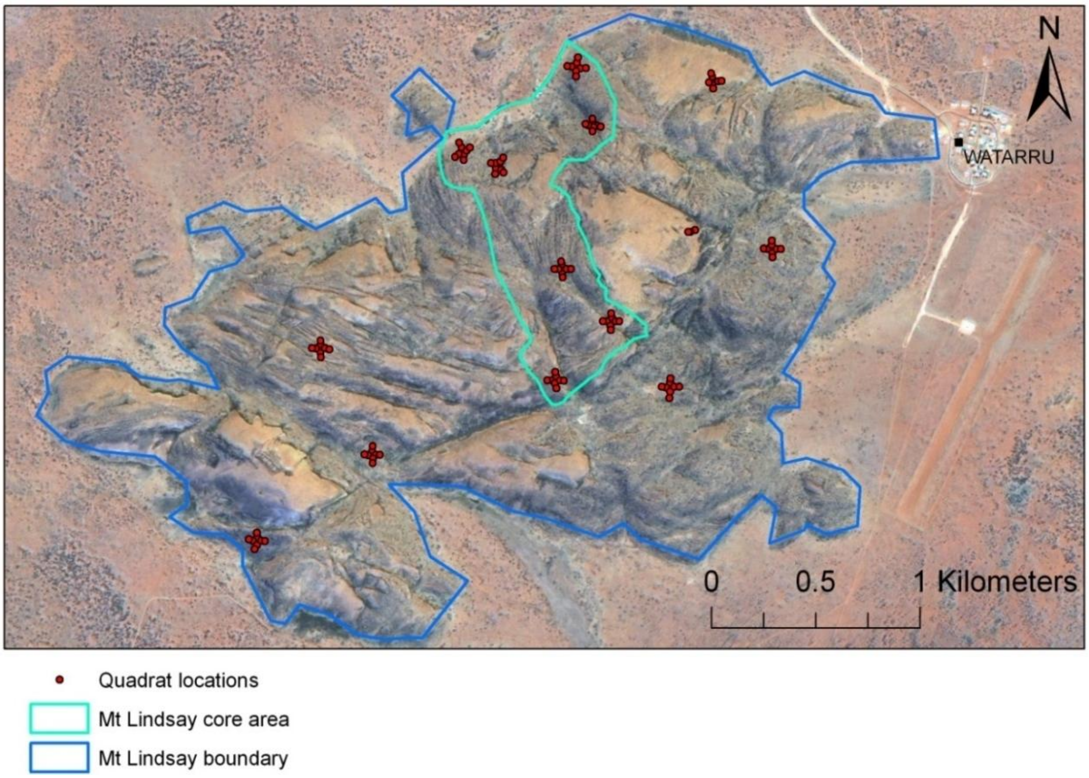
Appendix 2b Transect locations, consisting of 9 quadrats each, within the extinct site „Aeroplane Hill‟ in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



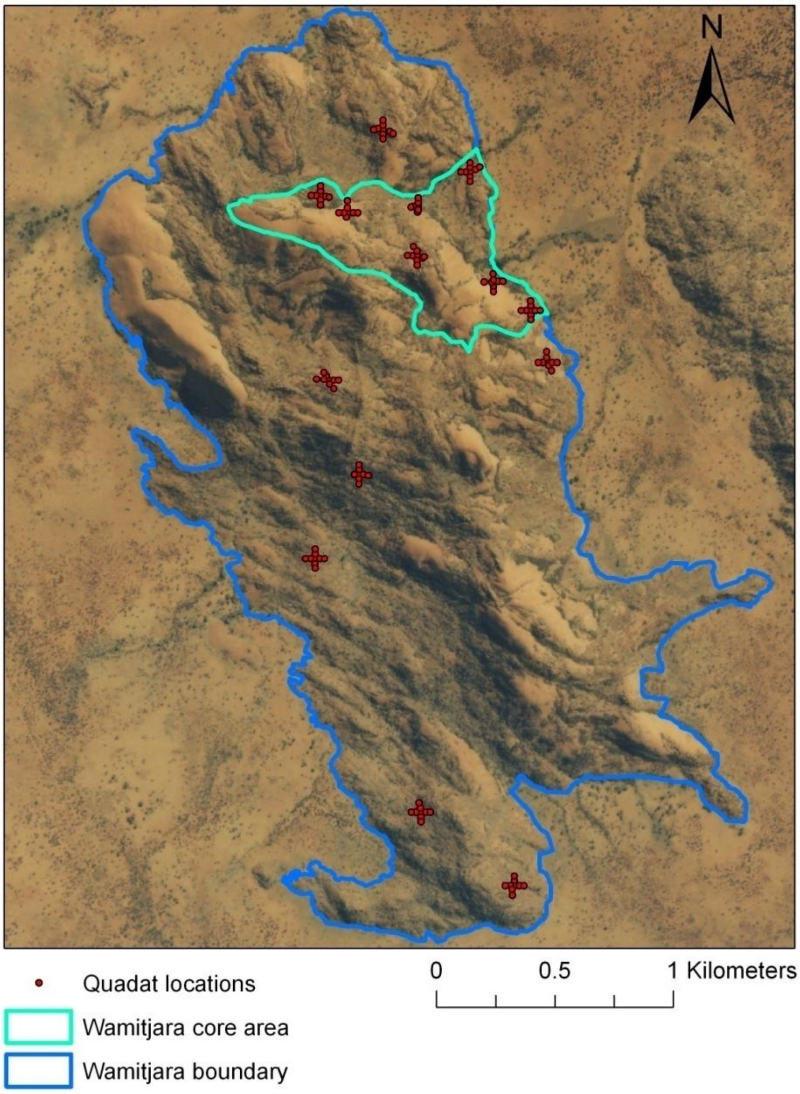
Appendix 2c Transect locations within the extant site „New Well‟ in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



Appendix 2d Transect locations, consisting of 9 quadrats each, within the extant site „Kalka‟.



Appendix 2e Transect locations, consisting of 9 quadrats each, within the extinct site „Mt Lindsay‟ in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia.



Appendix 2f Transect locations, consisting of 9 quadrats each, within the extinct site „Wamitjara‟ in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Appendix 3 Plant species encountered during on-ground field assessments at six locations (Alalka, Kalka, New Well, Aeroplane Hill, Wamitjara and Mt Lindsay) in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Collection site pertains to where the reference specimen was collected and is not a reflection of the species‟ distribution across the six sites.

Scientific name		**Common name**	**Collection site**
Genus	Species		
Abutilon	*leucopetalum*	Desert Chinese lantern	New Well
Acacia	*kempeana*	Witchetty bush	New Well
Acacia	*strongylophylla*	None	New Well
Acacia	*kempeana*	Witchetty bush	New Well
Acacia	*ligulata*	Umbrella bush	Kalka
Acacia	*olgana*	Mt Olga wattle	Alalka
Acacia	*symonii*	Symon's wattle	Watarru
Acacia	*tetragonophylla*	Dead finish	Kalka
Acacia	*basedowii*	Basedow's wattle	Aeroplane Hill
Acetosa	*vesicaria*	Wild hops	New Well
Alyogyne	*pinoniana*	Sand hibiscus	New Well
Amaranthus	*mitchellii*	None	New Well
Amphipogon	*caricinus*	Long grey-beard grass	Kalka
Aristida	? *holathera*	Tall kerosene grass	Aeroplane Hill
Aristida	? *nitidula*	Brush three-awn	New Well
Aristida	*capillifolia*	None	New Well
Aristida	*contorta*	Kerosene grass	New Well
Boerhavia	*coccinea*	Tar vine	New Well
Calandrinia	? *remota*	None	New Well
Calandrinia	*polyandra*	Parakeelya	New Well
Callitris	*glaucophylla*	White cypress pine	New Well
Cenchrus	*ciliaris*	Buffel grass	New Well
Chamaesyce	*australis*	None	New Well
Cheilanthes	*lasiophylla*	Woolly cloak fern	New Well
Cheilanthes	*sieberi*	None	New Well
Chrysocephalum	*apiculatum*	Common everlasting	New Well
Cleome	*viscosa*	Tickweed	Alalka
Codonocarpus	*cotinifolius*	Desert poplar	Kalka
Convolvulus	*remotus*	Australian bindweed	Watarru
Corymbia	*eremaea*	Hills bloodwood	Kalka
Cymbopogon	*ambiguus*	Lemon scented grass	New Well
Cymbopogon	*obtectus*	Silkyheads	New Well
Cyperus	*centralis*	None	New Well
Danthonia	*caespitosa*	Wallaby grass	Watarru
Digitaria	*brownii*	Woolly finger grass	New Well
Dodonaea	*viscosa* spp. *mucronata*	Sticky hopbush	New Well
Dysphania	*melanocarpa*	Black crumbweed	New Well
Enchylaena	*tomentosa*	Ruby saltbush	New Well
Enneapogon	*lindleyanus*	Wiry nineawn	Kalka
Enneapogon	*polyphyllus*	Limestone bottlewasher	New Well

Eragrostis	*laniflora*	Hairy-flowered woollybutt	New Well
Eragrostis	*parviflora*	Weeping lovegrass	Watarru
Eremophila	*elderi*	None	New Well
Eremophila	*latrobei*	Crimson emubush	Aeroplane Hill
Eremophila	*serrulata*	Green fuchsia bush	New Well
Eriachne	*helmsii*	Buck wanderrie	Watarru
Eriachne	*mucronata*	None	New Well
Eucalyptus	? *intertexta*	Gum-barked coolibah	New Well
Eucalyptus	*gamophylla*	Twin-leaf mallee	Kalka
Eucalyptus	*oxymitra*	Sharp-cap mallee	Aeroplane Hill
Euphorbia	*tannensis* spp. *eremophila*	Desert spurge	New Well
Evolvulus	*alsinoides* spp. *villosicalyx*	None	New Well
Ficus	*brachypoda*	Fig	New Well
Glycine	*canescens*	Silky glycine	New Well
Goodenia	*saccata*	Flinders Ranges goodenia	New Well
Gossypium	*sturtianum*	Sturt's Desert Rose	
Hakea	*suberea*	Corkwood	New Well
Halgania	*cyanea*	Rough halgania	Kalka
Haloragis	*aspera*	Rough raspwort	Kalka
Heliotropium	*asperrimum*	Rough heliotrope	Kalka
Hibiscus	*sturtii*	Sturt's / Hill hibiscus	Watarru
? *Hydrocotyle*	sp.		New Well
Indigofera	*leucotricha*	White indigo	Kalka
Jasminum	*didymum* ssp. *lineare*	None	Aeroplane Hill
Leiocarpa	*semicalva*	None	Alalka
Leiocarpa	*leptolepis*	Plover daisy	New Well
Leiocarpa	*tomentosa*	None	
Lysiana	*subfalcata*	Northern mistletoe	New Well
Melaleuca	*fulgens* spp. *corrugata*	Wrinkled honey-myrtle	Watarru
Mukia	*maderaspatana*	Snake vine	New Well
Newcastelia	*spodiotricha*	None	Kalka
Nicotiana	*gossei*	Rock pituri	New Well
Olearia	*ferresii*	None	Alalka
Olearia	*stuartii*	Rock daisy-bush (NT)	New Well
Oxalis	*perennans*	None	New Well
Pandorea	*doratoxylon*	Spearbush	New Well
Panicum	*decompositum*	Native panic grass	New Well
Plectranthus	*intraterraneus*	None	Alalka
Pleurosorus	*rutifolius*	Blanket fern	Alalka
Pluchea	*dentex*	None	New Well
Portulaca	*oleracea*	Common purslane	New Well
Prostanthera	*nudula*	Naked mintbush	Wamitjara
Prostanthera	*striatiflora*	Striated mintbush	Watarru
Pterocaulon	*sphacelatum*	Apple bush	New Well
Ptilotus	*decipiens*	None	New Well
Ptilotus	*gaudichaudii*	Paper foxtail	New Well
Ptilotus	*nobilis*	Yellow tails	New Well
Ptilotus	*obovatus*	Silvertails	New Well
Ptilotus	*polystachyus*	Longtails	New Well
Ptilotus	*sessilifolius*	Crimson fox tail	Kalka

Rhagodia	*parabolica*	Mealy saltbush	Wamitjara
Rulingia	*magniflora*	Rulingia	Alalka
Rutidosis	*helichrysoides*	Grey wrinklewort	Alalka
Salsola	*tragus*	None	Alalka
Santalum	*leptocladum*	Plumbush	Alalka
Santalum	? *acuminatum*	None	New Well
Sarcostemma	*viminale*	Caustic bush	New Well
Senecio	*magnificus*	Showy groundsel	Alalka
Senna	*artemisioides* spp *filifolia*	Desert cassia	New Well
Senna	*artemisioides* spp *helmsii*	Blunt-leaved cassia	New Well
Senna	*artemisioides* ssp. *artemisioides*	Silver senna	Aeroplane Hill
Senna	*glutinosa* ssp. *glutinosa*	Sticky cassia	Kalka
Setaria	*constricta*	None	New Well
Sida	? *cunninghamii*	Ridge sida	Watarru
Sida	*petrophila*	Rock sida	New Well
Sida	*trichopoda*	None	Watarru
Sida	*fibulifera*	Pin sida	Watarru
Sigesbeckia	*australiensis*	None	New Well
Solanum	*ellipticum*	Velvet potato bush	New Well
Solanum	*quadriloculatum*	Tomato bush	New Well
Stemodia	*viscosa*	None	Alalka
Themeda	*triandra*	Kangaroo grass	New Well
Tribulus	*terrestris*	Caltrop	New Well
Trichodesma	*zeylanicum*	Cattlebush	New Well
Triodia	? *basedowii*	Hard spinifex	Kalka
Triodia	*irritans*	Grey spinifex	Aeroplane Hill
Wedelia	*sterlingii*	Sunflower daisy	New Well

CHAPTER 3 – Preliminary study of warru movement patterns and home range

From the general rule of a strong preference for night life, there are only three exceptions amongst the mammals; the red kangaroo, the euro, and the rock-wallaby. On ordinary occasions when one rides, walks or climbs abroad, these are the only species likely to be seen in broad daylight.

Hedley Finlayson (1936)

Photo: Warru fitted with a GPS/VHF radiotracking collar in the APY Lands. S. Nally, Department of Sustainability, Environment, Water, Population and Communities.

Chapter 3 - Preliminary spatial behaviour of warru (*Petrogale lateralis* MacDonnell Ranges race) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Exegesis

Having considered warru habitat requirements in Chapter 2, the current chapter assesses the fine-scale use of suitable habitat by warru. More specifically, it describes the movement patterns and home range of warru using GPS radiotracking technology. The data from the current chapter also feed into subsequent chapters on warru population dynamics and genetic structure.

This chapter was published as a research note in *Australian Mammalogy* vol. 33(2) pp.181-188 and can be accessed via http://www.publish.csiro.au/nid/256/paper/AM10034.htm. I am listed as the primary author. An outline of each author‟s contribution and their permission for inclusion of the work in the current thesis is below.

STATEMENT OF AUTHORSHIP

Ruykys, L. (candidate)

Statement of contribution: Oversaw the design and development of work. Conducted all data analysis and interpretation, wrote manuscript and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

Signed ……. ……………………………………………*Date*…19/1/2011…

Ward, M.J.

Statement of contribution: Supervised development of work and evaluated manuscript.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

Signed … ……………………*Date*…24/1/2011

Taggart, D.A.

Statement of contribution: Supervised development of work and evaluated manuscript.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

Signed .. ……………………*Date*..24/1/2011

Breed, W.G.

Statement of contribution: Evaluated the manuscript.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

Signed …………… …………………*Date*…19/1/2011

3.1 Abstract

This study aimed to determine the home range and movement patterns of *Petrogale lateralis* in the arid-zone A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands in the north-west of South Australia. Ten Global Positioning System radio-collars were attached to animals, with collars programmed to function in 2008-09. Catastrophic collar failure resulted in only 28 days of data, from July 2008, being retrieved from one adult female. During this time, the female occupied a 90% kernel range of 57.9 ha and core (50%) range of 9.3 ha. The animal moved a total of 50.8 km and undertook three journeys of over 1 km. The longest of these was 1.2 km, undertaken in 89 min. The high mobility of the study animal has implications for management, particularly predator baiting and fire management strategies. Future research should assess the validity of these results by increasing sample size and conducting similar work for other arid-zone *P. lateralis*.

3.2 Introduction

Rock-wallabies (genus *Petrogale*) have the most specific habitat requirements of the Macropodidae, preferring rocky habitats such as cliffs, gorges, outcrops and boulder piles near suitable feeding areas (Sharman and Maynes 2002). Such sites ameliorate environmental fluctuations (Short 1982; Van Dyck and Strahan 2008) and provide protection from predators (Burbidge and McKenzie 1989; Telfer and Griffiths 2006). However, this niche specialisation affects all aspects of *Petrogale* ecology, including home range and movement patterns. In particular, the need to return to the perceived safety of resting sites during the day precludes the formation of large home ranges (Lapidge 2001; Laws and Goldizen 2003; Telfer and Griffiths 2006; Sharp 2009). The inhospitable terrain between rock outcrops also ensures that animals are generally relatively sedentary and disperse between colonies only infrequently (Sharp 1997a; Eldridge *et al.* 2001; Piggott *et al.* 2006b). However, long forays have been reported, particularly in semi-arid species (Lim and Giles 1987; Eldridge *et al.* 2001; Lapidge 2001). Indeed, the longest recorded distance travelled by any *Petrogale* is that of the black-footed rock-wallaby (*P. lateralis*), when a female traversed 8 km of agricultural landscape to establish a new colony (Kinnear *et al.* 1988; Eldridge *et al.* 2001).

P. lateralis (MacDonnell Ranges race) is found in three states – South Australia, Western Australia and the Northern Territory. In South Australia and Western Australia, the race has undergone substantial declines in both range and abundance (Eldridge and Close 2002) and in South Australia is now classified as Endangered under the *National Parks and Wildlife Act*

1972 (Schedule 9). Known as „warru" by Indigenous Owners, it is currently restricted to several colonies in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara (APY) Lands in the state"s far north-west (Copley and Alexander 1997; Eldridge and Pearson 2008). These remaining colonies are located on isolated outcrops and information about animals" ability to disperse from these sites into the surrounding habitat is not available. Preliminary VHF radiotracking of 14 warru for six days in one APY Lands colony revealed that most animals, particularly males, used different diurnal dens each day, with a broad activity area away from the site"s most complex habitat (Read and Ward 2007). A more accurate and detailed understanding is required however, if effective fire and predator control strategies are to be implemented.

Using Global Positioning System (GPS) collars, the current study aimed to answer the following questions relating to warru:
1. What are their home ranges and how restricted are these to rock outcrops? and
2. What are their movement patterns and do these facilitate dispersal?

3.3 Materials and Methods

Study site

The arid-zone APY Lands is an Indigenous-owned and managed area that covers 102,650 km^2. It experiences a hot, dry, desert climate with short, cool to cold winters (Robinson *et al.* 2003; Taylor *et al.* 2006). Rainfall is low (average 255 mm at Pukatja) and unreliable, with a tendency for summer rather than winter precipitation. During 2008, the area received below-average rainfall of 190 mm. In July 2008, when data were collected, the „Alalka" fieldsite received 1.6 mm, equating to just 11.5% of the monthly average of 13.9 mm (Bureau of Meteorology 2010).

Fieldwork was undertaken at two hill sites in the eastern Musgrave Ranges – those of „Alalka" (26.137°S, 132.116°E) and „New Well" (26.080°S, 132.215°E). However, since data were only successfully attained from Alalka, details on New Well are not provided. Alalka"s landform is that of rugged strike ranges on metamorphics. It is approximately 194 ha and contiguous with a large number of surrounding hills. The vegetation of the site is that of emergent low, open woodland over *Triodia irritans* grasslands (Robinson *et al.* 2003).

Animal trapping

In June 2008, warru were trapped in nine cage traps supporting a bag of thick, shadecloth-like material. Traps were located in shelter sites (caves, crevices) for which there was evidence of recent warru activity, as indicated by the presence of fresh scats. For at least two days before trapping commenced, traps were wired open and „free-fed‟ using chopped apples and a peanut butter/oat mix. Following „free-feeding‟, traps were set for six nights and checked daily at dawn. Captured warru were removed from traps, placed in hessian sacks and, in an attempt to reduce the incidence of capture myopathy, given an intramuscular injection of Vitamin E at 0.02 mL kg^{-1} (Troy Laboratories Pty. Ltd., New South Wales; Vogelnest and Woods 2008). Animal processing and collar attachment were carried out on-site before animals were released at site of capture. Collars were retrieved by retrapping in July 2009.

Radio-collars

Five Global Positioning System (GPS) / Very High Frequency (VHF) radio-collars (Sigma Delta Technologies, Western Australia) were attached to warru at each of New Well and Alalka (*N*=10). Collars were placed only on adults (> 3 kg), with two collars on males and three on females at Alalka. Collars weighed 80 grams, which constitutes 2% of the average body mass of the warru used in the study (4.4 kg). Collars had an active deployment of 10 months, during which time the VHF component was programmed to operate for 4 h per day (1000-1400 hours). The VHF also had a mortality sensor, whereby hourly movement checks were to be undertaken. If no movement was recorded for 24 h, the VHF pulse frequency was to double in speed so that carcasses could be retrieved and cause of death established.

The collars‟ GPS components were programmed to operate for four months, encompassing two seasons – July-August 2008 (winter) and December 2008 - January 2009 (summer). During active months, the GPS was to „switch on‟ every 1.5 h, with each location attempt lasting until a fix was obtained or for 4 min. Locations were stored on the collar itself for downloading upon retrieval. The VHF and GPS components were mounted on Teflon tubular ribbon and attached around animals‟ necks. The Teflon strands were held together using an epoxy-resin mix and veterinary sutures. To ensure that collars were not too restrictive, a gap of two fingers‟ width was left between the collar and the animal‟s neck.

Data analyses

Data downloaded from GPS collars were those of date, time, location and the estimated accuracy of the locations (positional dilution of precision, PDOP, Merrill *et al.* 1998). The accuracy of all points was assessed using the PDOP value and those with a PDOP > 10 were discarded (D'Eon and Delparte 2005). The remaining fixes were mapped using ArcMap 9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Incremental area analysis (Kenward and Hodder 1996) of the fixes was conducted using the extension Home Range Tools ver. 1.1 (Rodgers *et al.* 2007). Since both diurnal and nocturnal fixes were used, range equates to the warru"s 24-h range.

For range analyses, both Minimum Convex Polygon (MCP) and Kernel analyses were undertaken. The former was completed using the ArcMap extension Hawth"s Analysis Tools (ver. 3.27, 2002-2006) and the latter using Home Range Tools. Fixed kernel analysis was chosen because it produces the least-biased home range areas (Seaman and Powell 1996). Biased cross-validation bandwidth smoothing was chosen as it was more appropriate for the data than least-squares cross-validation, which produced discontinuous isopleths. Simulation studies show that the biased cross-validation method performs quite well in comparison with the least-squares cross-validation and reference bandwidth smoothing methods (Sain *et al.* 1994; Rodgers and Kie 2010). Utilisation plots of 5% kernels did not show any clear slope discontinuity, where the latter is an indication of how many fixes constitute the core area (Kenward and Hodder 1996). Consequently, and based on other *Petrogale* home-range studies (Lapidge 2001; Telfer and Griffiths 2006; Sharp 2009), 50% was chosen as an appropriate core area. Since a utilisation distribution of 95% produced a discontinuous outer isopleth, 90% was used instead as an indication of overall range. MCPs were of 100% range.

To analyse movement patterns, fixes were defined as being diurnal when they occurred from 0600-1800 hours, and nocturnal from 1800-0600 hours. This was based on July sunrise and sunset times at the Pukatja community, which is ~16 km from the study site (Geoscience Australia 2010). Hawth"s Analysis Tools was used to convert consecutive GPS points to paths, with the output being that of the Euclidean distance moved by the warru. To establish distances travelled per hour, each Euclidean length was divided by the time that had elapsed since the last GPS location was taken. These data were separated into the diurnal and nocturnal categories and compared using an independent-samples t-test (PASW Statistics ver. 17.0.2, March 2009).

Since the Euclidean distance does not take into account surface topography, the ArcToolbox 3D Analyst was used to convert the Digital Elevation Model of the area (Geoscience Australia 2008) into a 3D (TIN) projection. The 90% and 50% ranges were then overlaid onto this projection using 3D Analyst Tools („Interpolate Polygon to Multipatch‟). This established the surface area of these ranges. The paths created in the first step of the analysis were also overlaid onto the TIN projection using 3D Analyst Tools („Surface Length‟), providing the actual surface distance travelled. However, as the paths only simulated direct movement between points, which is unlikely in warru behaviour, an accurate measure of movement could not be established. Instead, a proxy measure using the time between each point and the 3D distance (distance/time [metres per hour]) was calculated. Averages were then determined – „Daily average movement index‟ incorporated both diurnal and nocturnal paths, „Diurnal average movement index‟ only diurnal and „Nocturnal average movement index‟ only nocturnal. As the data were heteroscedastic, a non-parametric Kruskal-Wallis test was used to determine whether there was a difference between these groups.

A separate analysis was used to determine whether these movement patterns would enable dispersal to surrounding outcrops. Firstly, to establish the distance the animal could travel in one night, the nocturnal average movement index was multiplied by 12 (1800-0600 hours). Then, using the ArcToolbox, a buffer of this distance was created around the 50% and 90% ranges and the number of accessible hills calculated.

3.4 Results

Collar deployment success

Collar deployment statistics are outlined (Table 3.1). Of the eight retrapped warru, only two retained both their collar and GPS mechanism. Five other animals retained only their Teflon collars, after poor design and manufacturing caused the GPS mechanisms to detach from their collars. Two of these lost mechanisms were found on the ground; one at Alalka and the other at New Well, bringing the number of retrieved mechanisms to four. Of these, only one had successfully logged any data, spanning 28 days (July 2008). Consequently, the results for the current study pertain to just one individual, an adult female at Alalka. At initial capture in 2008, this animal weighed 3.2 kg and was carrying a pouch young that was ~3 months old. While the GPS collar was recording data, this pouch young would have weighed ~185 grams. Given the lack of prior studies on *P. lateralis*, it is not possible to determine whether this young would have affected the dam‟s movement patterns. At recapture in 2009, the female weighed 3 kg.

Table 3.1. GPS radio-collar deployment (*N*=10) success for warru (*Petrogale lateralis* MacDonnell Ranges race) in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia in June 2008 - July 2009.

Parameter	No. of collars
Deployed	10
No. of animals retrapped	8
Of retrapped animals:	
Collar and GPS present	2
Collar only and GPS detached	5
No collar or GPS	1
Total GPS collars:	
Retrieved	4
Successfully logged data	1

A total of 233 fixes was logged by the GPS collar. However, 28 points (12%) were discarded because they had a PDOP > 10. The remaining 205 points were taken at an average of one fix every 193 min (range 86–989 min). Of these fixes, 67% were within 10 min of the programmed logging time (i.e. every 90 min), while the remainder showed significant shifts in duty cycle. As a result, there was an uneven divide between fixes, with 74% (*n* = 151) being diurnal and 26% (*n* = 54) nocturnal. Diurnal fixes were taken, on average, every 198 min and nocturnal every 185 min.

Range

Incremental area analysis of the fixes indicated that 23 days‟ worth of data, equating to 173 fixes, gave a stable estimate of the warru‟s range for July 2008. Using 90% kernel analysis, the female occupied a range of 57.9 ha, and using MCP, 171.4 ha. The core range (50% kernel) was 9.3 ha (Fig. 3.1). When topography was included, the 90% kernel increased to 60.7 ha and core range to 9.7 ha. The core range was located on the ridgeline of Alalka, where habitat complexity is greatest (L Ruykys pers. obs.). In total, 60.9% of diurnal and 70.4% of nocturnal fixes were within the core range, while 95.4% of diurnal and 88.9% of nocturnal fixes were within the 90% kernel.

Movement patterns

Over the 28 days of fixes, the warru moved a total surface (3D) length of 50.8 km. There were multiple fixes each day, with a minimum of 6 m (in 88 min) and maximum of 1.2 km (in 89 min) between points. Using Euclidean distances, the warru moved an average 93.4 m h^{-1} between fixes during the day and 81.3 m h^{-1} during the night. There was no difference between these averages (*t*-test, $t_{203} = 0.776$, $P > 0.05$). Using surface distances, average movement indices were: daily 109 m h^{-1}, diurnal 109 m h^{-1} and nocturnal 101 m h^{-1}, with no difference between these (Kruskal–Wallis $H = 0.337$, χ^2 approximation, d.f. = 2, $P > 0.05$). According to the nocturnal movement index, the female moved an average 1.21 km per night (1800-0600 hours) and, from her core range, could move onto two other rock-faces. From her 90% kernel, the female could disperse to four other major zones of rock and access a rockhole that contains water on an ephemeral basis (Fig. 3.2).

The warru undertook three movements of over 1 km surface length (Fig. 3.3). The longest of these was a nocturnal foray of 1.2 km in 89 min. The other two long movements were conducted as part of a sojourn off Alalka and onto the surrounding plain, with the warru moving 1.0 km on the forward journey and 1.1 km on the return. At the destination, the female was 1.1 km from the centre of her core range and 280 m off the hillside. This sojourn occurred at night and was not repeated. Similar, albeit slightly shorter exploratory movements were also taken from the core range in every other direction. This included trips to the northerly and easterly edges of the hillside, when the animal stopped just short of the plain.

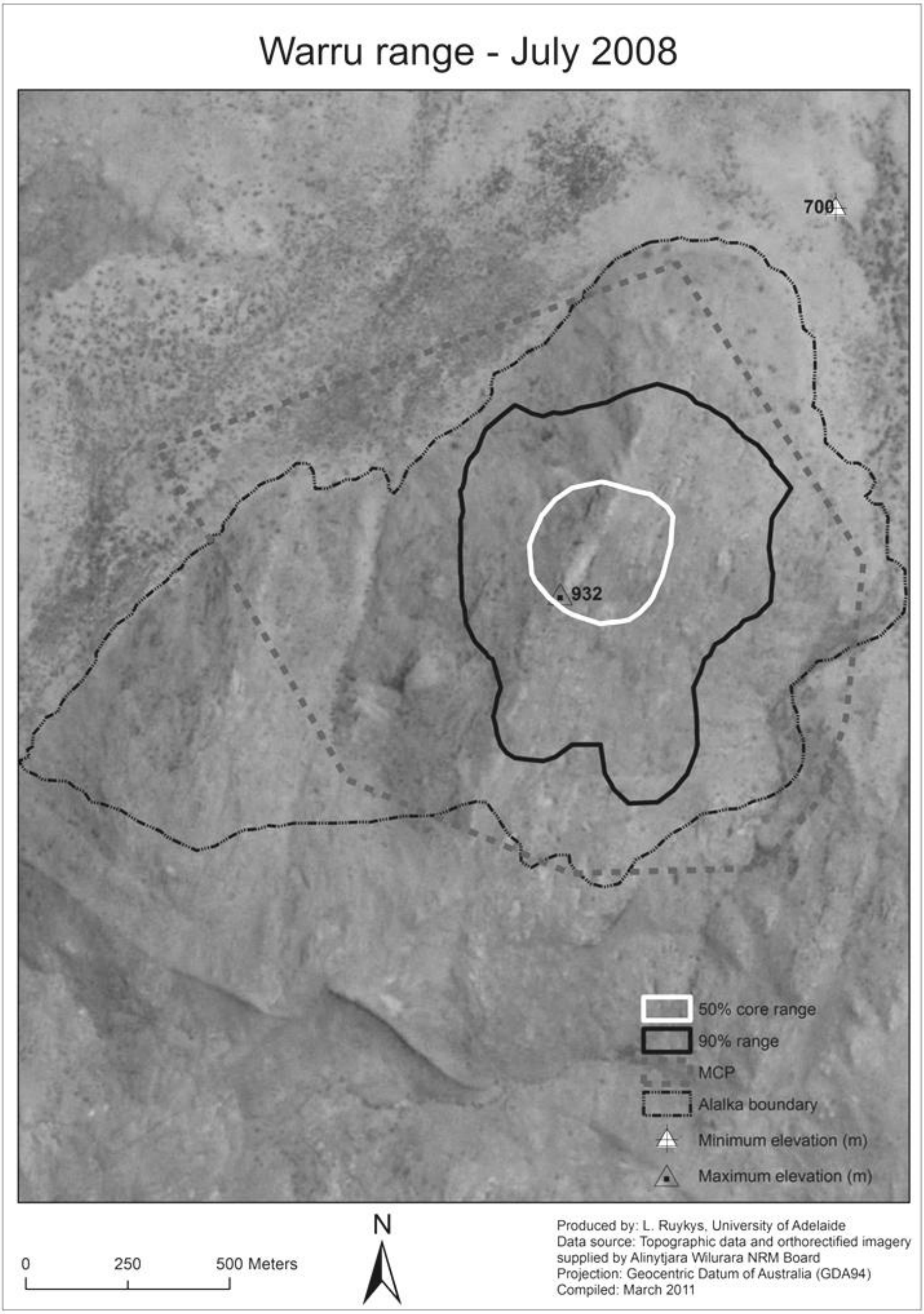


Fig. 3.1 Monthly range of an adult female warru (*Petrogale lateralis* MacDonnell Ranges race) at Alalka in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia, in July 2008, as determined using 90% and 50% kernel and Minimum Convex Polygon (MCP).

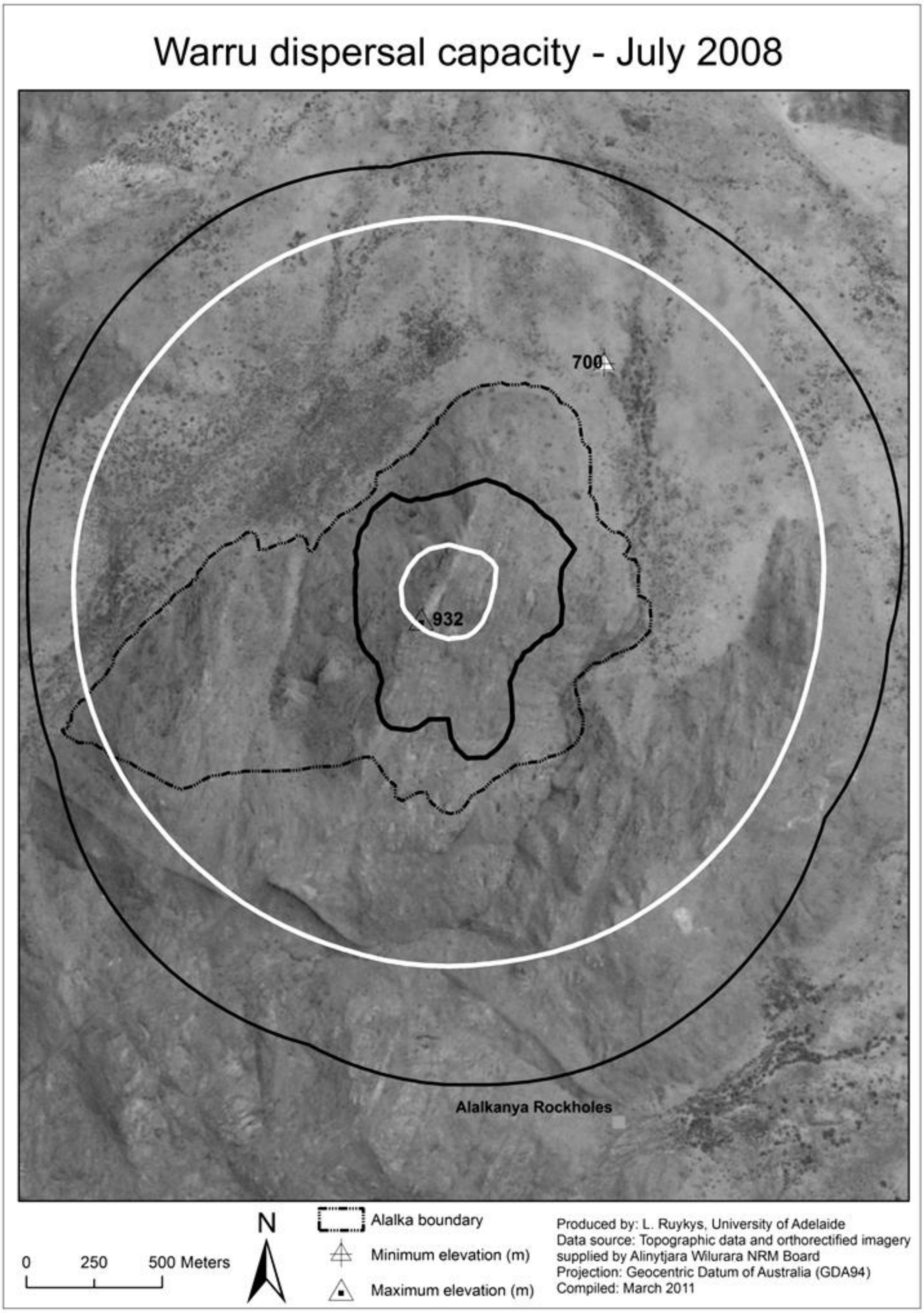


Fig. 3.2 Dispersal capacity of a female warru at Alalka in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Dispersal capacity from the animal‟s core home range (inner white, 50% kernel) is indicated in the outer white circle (1.21 km), and from the 90% kernel home range (inner black) in the outer black circle. The Alalka rockhole is also indicated.

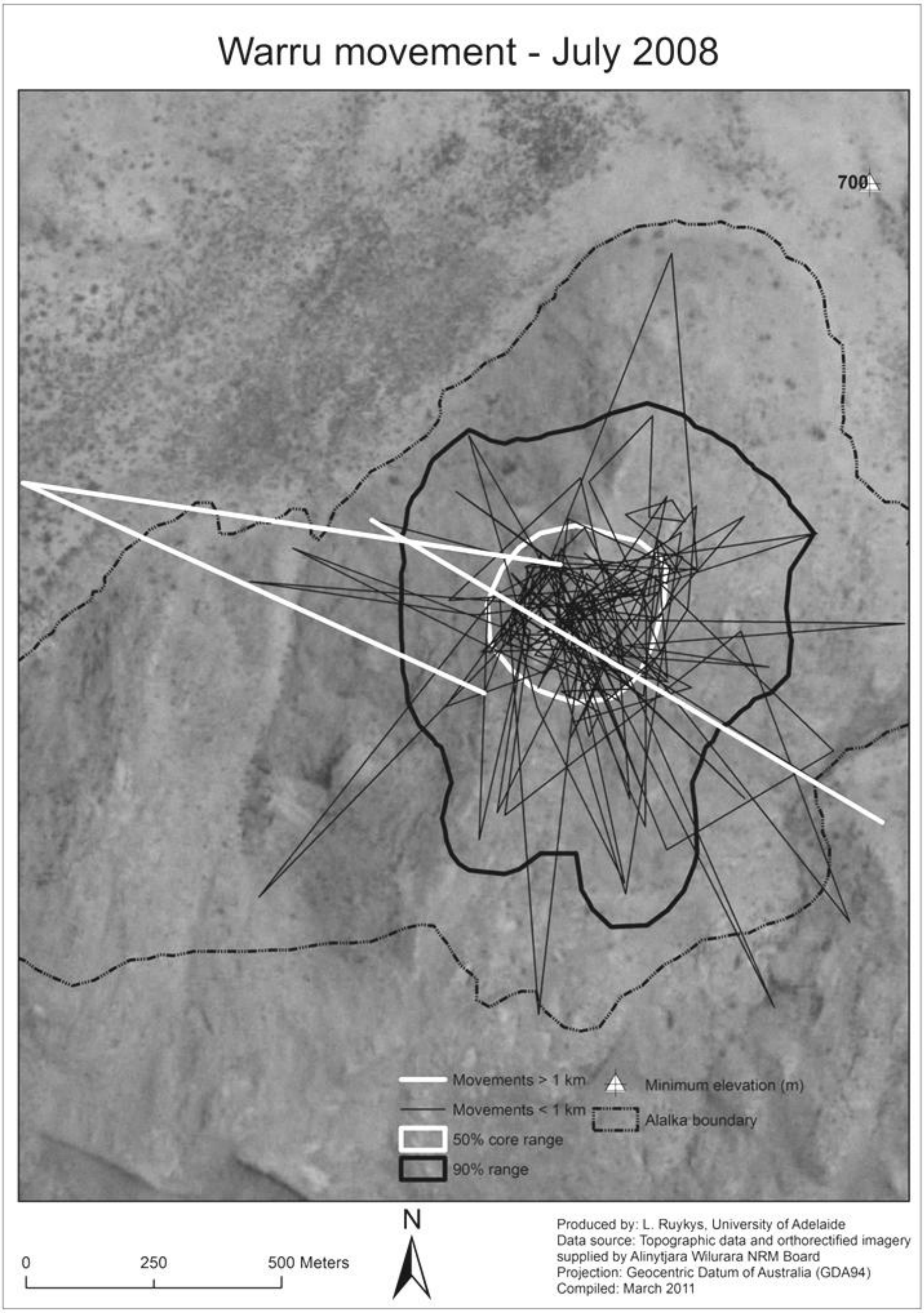


Fig. 3.3 Movement paths, including those over 1 km (in white), of a female warru (*Petrogale lateralis* MacDonnell Ranges race) at Alalka in the A̲nangu Pitjantjatjara Yankunytjatjara Lands, South Australia in July 2008. Distances are surface lengths, which includes topography. Individual lines represent single movements conducted over different durations.

3.5 Discussion

Due to the mass failure of GPS radio-collars, the current study is severely limited and, specifically, pertains to only one individual"s behaviour in July 2008. As such, the results should be interpreted with caution and are by no means a reliable representation of the home range or movement patterns of all warru in the Alalka colony, in the APY Lands, or of *P. lateralis* as a whole. Instead, they should be seen as preliminary data that require supplementation through further research. However, the results may be useful for management of this threatened species, while the lessons learnt from the current GPS collar deployment, which is only the second published documentation of the use of such technology on a macropod species (Hayward *et al.* 2011), may be of interest to other researchers.

Home range

The current study"s first aim was to establish the home range of warru. In July 2008, the female"s 90% kernel range was 57.9 ha and her core range was 9.3 ha. This is substantially larger than the ranges established in most other *Petrogale* studies (3-26 ha: Laws and Goldizen 2003; Telfer and Griffiths 2006; Sharp 2009). The only similarly large result is that of Lim (1987), who documented a home range of 170 ha for *P. xanthopus*.

The current study also aimed to determine how restricted warru are to rock outcrops. The female"s two ranges were strongly tied to the hillside, with her 90% range covering areas of *Triodia* spp. on hillslopes, and her core range in particular located in the most structurally complex area of Alalka. Although the current study was unable to determine the nature of activities undertaken in these areas, rocky outcrops are known to be a critical shelter resource for *Petrogale,* while the surrounding plains are often used for foraging (Barker 1990; Jarman and Bayne 1997; Stirrat 2003b).

Movement patterns

The collared warru had a high degree of fidelity to the Alalka hill, with her activity generally restricted to the outcrop. Since the female was recaptured in 2009 at the study site, her movements did not culminate in migration or dispersal. Other species of *Petrogale* are also known to have high levels of philopatry (Lim and Giles 1987; Robinson *et al.* 1994; Telfer 2006). Indeed, most other studies of *Petrogale* spp. suggest that rock-wallabies are relatively sedentary and that movement between colonies is infrequent (Robinson *et al.* 1994; Jarman and Bayne 1997; Sharp 1997a; Piggott *et al.* 2006b). In contrast, the female warru ranged across a wide area of Alalka, a surface length of 50.8 km over 28 days. This high mobility suggests that once population pressures stimulate it, Alalka warru are capable of undertaking dispersal. Indeed, from her 90% range, the female could move to four other rock complexes on the basis of just her average nocturnal movement index. Such dispersal capacity is supported by information from Indigenous consultants in the Warburton region of Western Australia, who reported seeing warru tracks up to 4 km from the nearest rockpile (Pearson 1992). It is also corroborated by the current study, which showed that warru do move off hillsides and onto the surrounding flats. The female undertook one such foray, culminating in her being 280 m off the hill. Read and Ward (2007) recorded similar behaviour for New Well warru, although here animals crossed only ~100 m. Previous *Petrogale* studies have also documented off-hill movement, usually for foraging purposes (Batchelor 1980; Pearson 1992; Jarman and Bayne 1997) or to attain water (Lim and Giles 1987; Sharp 2011). However, given that the off-hill sojourn documented in the current study was an isolated event, it is likely that the female predominantly foraged on Alalka and potentially used the flats for occasional food supplementation. Water was unlikely to be a motive for the movements because there is no known free water at the destination. It is also improbable that it was a reaction to capture because the journey was completed a month after collar attachment and disturbance by humans was also unlikely to have been the cause as no people are known to have been climbing the site on the appropriate dates.

Despite the nocturnal habits of *Petrogale* (Van Dyck and Strahan 2008), the Alalka female was not stationary during the day, with diurnal fixes ranging from being 15 m to 1.2 km apart (Euclidean distance). It is possible that, as with *P. x. xanthopus* (Lim 1987), warru will move between den sites during the day in winter for thermoregulatory reasons, but, in summer, are more likely to remain sedentary. In the current study, the lack of difference in movement patterns between night and day is likely due to the low sample size of nocturnal fixes (n=54). In relation to speed, the studied warru had a nocturnal movement index of 101 m h^{-1}. This is less than the 187 m h^{-1} reported by Lim *et al.* (1987) for female *P. x. xanthopus*, but substantially higher than Horsup‟s (1994) result for *P. assimilis,* which only moved a mean 88 m between fixes 2 h apart.

Lessons learnt from current GPS collar deployment

The first lesson pertains to ensuring that there is a within-deployment communication link between the GPS units carried by study animals and the researcher. For example, GPS collars can indicate whether the last fix attempt was successful by having a particular sequence of VHF „beeps" (Merrill *et al.* 1998; Millspaugh and Marzluff 2001). Without such an arrangement, it is impossible to determine whether collars are operating properly until animals are recaptured. However, in remote areas, recurrent recapture often cannot be undertaken and, by the time researchers realise that the units are malfunctioning, resolving and/or repeating the work may not be possible.

A second lesson pertains to having the GPS component actually „switching on" prior to attachment to the study animal. This provides an opportunity for test deployment and download. In the current study, collars were attached to warru in June 2008, before they were actually programmed to start taking fixes (July 2008). This meant that we were unable to ensure that the GPS was functioning correctly and instead relied on the manufacturer"s testing, which undoubtedly, would have been conducted in different conditions to those in the field. We also suggest that GPS collars should always be supplemented with data from VHF radiotracking; this would provide back-up should the GPS fail. Unfortunately, this was not possible in the current study as the VHF component also failed. Lastly, given that GPS collars for wildlife require a specialised understanding of animal behaviour, field conditions and terrain, we suggest that researchers ensure that their chosen manufacturer has had experience in making collars for the required conditions and/or taxon.

Management implications and future research

The current study"s result, although preliminary, may have implications for several facets of management, including predator baiting. In particular, given that the female ranged off Alalka, it is possible that other individuals conduct similar movements. Thus, should ground-based predator baiting be established at Alalka, baits should be placed at an appropriate distance from the base of the hill. Failing to provide such a buffer would mean that predators are being enticed into areas that warru potentially utilise for resources and/or dispersal (Saunders and McLeod 2007). Given the high mobility evident at both Alalka and New Well (Read and Ward 2007), it may also be prudent to establish similar buffer zones at other *P. lateralis* sites where ground-based predator baiting is undertaken.

The movement patterns exhibited by the female are also relevant for fire management. The APY Lands Fire Management Plan (Paltridge and Latz 2009) suggests that small burns on the upper slopes adjacent to warru colonies would promote more palatable plant species. The current results suggest that warru would indeed be capable of moving the distances required to take advantage of such resources. However, warru ranging off-hill also has bearing on any fuel-reduction burns undertaken in the tussock grasslands at the base of ranges. In particular, a series of small burns rather than a single, large fire would be preferable because the latter could decimate the food resources warru are seeking, and/or shelter resources they are using during their off-hill sojourns.

The current results also contribute to a more holistic understanding of the Alalka colony in the context of the eastern Musgrave Ranges metapopulation. During recent aerial surveys, fresh warru scats were found in numerous colonies up to 20 km away from Alalka (Ward *et al.* 2010). Given the current evidence of Alalka warru undertaking long-distance movements, it is possible that exchange occurs between the closer satellite colonies. It also suggests that successful broad-scale predator control could facilitate the establishment of new populations through natural dispersal (Sharp 1997a; Eldridge *et al.* 2001).

Further research, with an increased sample size, on warru home range and movement patterns is required to validate the current results. Such data would enable comparisons between the home ranges of *P. lateralis* and other species of *Petrogale,* and inform managers about warru habitat use, frequency of inter-colony exchange, social structure and foraging behaviour. We suggest that future researchers again attempt to use GPS technology but that they follow the recommendations on GPS collars provided herein.

CHAPTER 4 – Population structure, genetic diversity and mating system of warru

I found no solace in the fact that the Davenport Ranges' wallabies were but one variety of black-footed rock wallaby and that other populations of the same species survived elsewhere. Hugh Possingham's students had confirmed the importance of populations. Varieties are the base from which natural selection upon individuals is made. Even Charles Darwin… concluded that in an evolutionary sense, 'there is no fundamental distinction between species and varieties'.

John Read (2003), *Red sand, green heart* p. 288

Photo: Cross-fostered warru siblings at Monarto Zoological Park sourced from the APY Lands. M. Post.

Chapter 4 – Population structure, genetic diversity and mating system of *Petrogale lateralis* (MacDonnell Ranges race) in South Australia.

Exegesis

The current chapter presents an investigation of the genetic diversity, population structure and mating system of warru at the three extant colonies in the APY Lands, and, as relevant, the captive population. Since genetic structure is directly related to animals‟ habitat requirements (Chapter 2), fine-scale habitat use (Chapter 3) and population dynamics (Chapter 5), the chapter complements data presented in other sections of the thesis.

I was responsible for the experimental design, planning and laboratory analyses required for the current chapter. Some genotyping was completed by Dr Justyna Paplinska from the University of Melbourne in a paid arrangement. However, I undertook all data analysis, interpretation of results and chapter writing. The chapter is written in a style appropriate for a scientific journal.

4.1 Abstract

In South Australia (SA), warru (*Petrogale lateralis* MacDonnell Ranges race) once occupied virtually all suitable habitat within the arid zone of the Central Ranges. However, only two metapopulations now remain in the state, both in the Anangu Pitjantjatjara Yankunytjatjara (APY) Lands. To establish if genetic factors such as inbreeding have contributed to the race‟s decline, the current study used six polymorphic microsatellite loci to examine the population structure, genetic diversity and mating system of warru in the three largest-known remaining colonies. Bayesian and frequency-based assignment tests revealed substantial population structuring, with genetic groups strongly correlating to geographic colonies. However, there was also some evidence for migration into two colonies, with approximately 5% of sampled individuals having mixed ancestry. Allelic diversity, allelic richness, heterozygosity and F_{IS} values suggested that two of the three colonies were genetically diverse. A low F_{IS} for the third colony provided evidence of inbreeding. Data on the mating system suggests that warru are polygamous, although a small number of animals had persistent pairings both within- and between-years. These findings have implications for the management of both the *in-* and *ex-situ* warru populations.

Keywords: Macropod, inbreeding, captive wildlife management, molecular ecology.

4.2 Introduction

Genetic diversity is one of the three fundamental levels of biodiversity (with the others being species and ecosystem diversity) and is defined as the extent of genetic variation in a population (Hunter and Gibbs 2007). It is critical to the conservation of species because it both enables animals to evolve and adapt to environmental change, and prevents inbreeding and a reduction in reproductive fitness (Frankham *et al.* 2002). Maintaining a species‟ genetic diversity is therefore a key focus in conservation genetics and involves two facets; maintenance of genetic variation in the wild and production of outbred captive individuals for future reintroductions (Robert 2009).

The importance of genetic diversity is highlighted by a classic study of black-footed rock-wallabies (*Petrogale lateralis*) in Western Australia (WA), where Barrow Island population has the lowest recorded level of diversity of any vertebrate (Eldridge *et al.* 1999). Isolated from the mainland for about 1,600 generations, animals have clearly survived stochastic events. Nonetheless, the population suffers from inbreeding depression, including reduced female fecundity and increased levels of fluctuating asymmetry. The latter refers to an organism‟s deviation from bilateral symmetry and is believed to measure the ability of the genome to successfully achieve a „normal‟ phenotype under imperfect environmental conditions (Waddington 1957). Eldridge *et al.* (1999) concluded that inbreeding depression, which is increasingly being identified in small, isolated wildlife populations, is one of a multitude of interacting factors that threaten population viability and should be taken into account in recovery programs for threatened species (Eldridge *et al.* 2010).

One of the main processes affecting genetic diversity is dispersal (Dieckmann *et al.* 1999), which is defined as the permanent movement of an individual away from its home area to another population (Scott Mills 2007). Study of this parameter has been advanced by the development of assignment tests, which assign an individual to the population where its multi-locus genotype is most likely to occur (Paetkau *et al.* 1995; Cornuet *et al.* 1999; Pritchard *et al.* 2000). Dispersers are therefore allocated to their natal population, rather than the one in which they were sampled (Eldridge *et al.* 2001). Assignment tests have provided insight into sex-biased dispersal (Hazlitt *et al.* 2006b; Piggott *et al.* 2006a), the source of animals responsible for colonising new habitat (Eldridge *et al.* 2001) and the appropriate geographical scale for managing populations (Roach *et al.* 2001). In turn, such information can have significant implications for species‟ conservation. For example, Cegelski *et al.* (2003) detected reduced levels of gene flow among wolverine populations in Montana, USA compared to those in Alaska and Canada. This was due to human-induced habitat fragmentation in Montana and had actual implications for wolverines‟ reproductive rates, re-colonisation of vacant habitat and harvesting levels. The study supports the hypothesis that species with continuous distributions will have higher genetic connectivity than those with disjunct distributions, and that the latter‟s genetic patterns are likely to reflect their fragmentation (Storfer *et al.* 2007; Smit *et al.* 2010).

In Australia, this process is particularly evident for the genus *Petrogale* (rock-wallabies). Unlike other members of the marsupial family Macropodidae (kangaroos and relatives), *Petrogale* are fundamentally tied to their preferred habitat of steep slopes and rocky outcrops (Strahan 1995; Sharman and Maynes 2002). Since such habitat is patchy, animals persist in aggregated densities in discreet colonies (Eldridge *et al.* 1999; Hazlitt *et al.* 2004). Effective dispersal is generally limited, even if colonies are geographically close (e.g. 0.5-8km; Pope *et al.* 1996; Eldridge *et al.* 2001). Consequently, although individual colonies display high levels of among-population differentiation (Spencer *et al.* 1997), *Petrogale* as a whole have substantially lower levels of genetic diversity than do other macropods, which usually have much higher levels of landscape connectivity (Eldridge *et al.* 2010).

The second main process affecting genetic diversity is a species‟ mating system (Briton *et al.* 1994). Studies of *Petrogale* suggest that animals undertake persistent pairings, although females switch breeding partners when their mates disappear and/or purposely breed with a male other than their social consort (Spencer *et al.* 1998). This conclusion, however, is based on studies of just two species - *P. assimilis* and *P. penicillata* (Eldridge *et al.* 2010); consequently, for the other 14 *Petrogale* spp., there remains a substantial knowledge gap. The latter is exacerbated by the fact that, due to the disparate ecosystems in which rock-wallabies live, it is unreliable to extrapolate information between species. This lack of information, combined with the trend for high genetic diversity, means that individual *Petrogale* colonies often need to be regarded as independent management units that are susceptible to extinction (Eldridge *et al.* 2010).

P. lateralis (MacDonnell Ranges race), known as „warru‟ by Indigenous Owners, is one threatened race of rock-wallaby for which colony-specific management strategies may need to be implemented. Classified in South Australia (SA) as Endangered, warru have suffered precipitous declines across northern SA and are now only found in the Aṉangu Pitjantjatjara Yankunytjatjara (APY) Lands in the state‟s far north-west (Copley and Alexander 1997; Read and Ward 2011b). An active recovery program has involved both *in-* and *ex-situ* conservation initiatives, including baiting of introduced predators (dogs and foxes). Although baiting appears to have led to a decrease in the numbers of foxes, but not cats, at two colonies (Read and Ward 2011b), there has been no evident increase in warru abundance (Read and Ward 2011b). Based on the unequivocal, positive effect of similar management on *P. lateralis* colonies in the WA Wheatbelt region (Kinnear *et al.* 1988; 1998; 2010), an increase was, however, expected. To ascertain if genetic factors are hampering warru recovery in SA, a detailed analysis of their genetic diversity, structure and mating systems was required.

Preliminary analyses of APY Lands warru conducted by Eldridge (2006) using mitochondrial DNA indicated that the remaining populations are genetically unique. Indeed, Eldridge (2006) concluded that most colonies in SA are as different from each other (most had 3-5% haplotype divergence) as they are as a group from colonies in the Northern Territory and

WA, and that each sampled colony was therefore worthy of conservation. To advance this knowledge, the current, more detailed study used microsatellite markers to examine the genetic characteristics of SA warru. Microsatellites are hypervariable tandem repeats of short (1-6) nucleotides found at high frequency in the nuclear genomes of most taxa (Selkoe and Toonen 2006). Possessing high mutation rates, they have become the marker of choice in population genetic studies over the past decade (Eldridge *et al.* 2010).

The study aimed to answer the following questions pertaining to extant warru colonies;

1. What is their inter- and intra-colony population structure?
2. What level of gene flow occurs between them?
3. What are their levels of genetic diversity? and
4. What are their mating systems?

4.3 Materials and Methods

4.3.1 Study site and sample collection

This study was undertaken in the APY Lands, the landscape, tenure and management of which are discussed in Chapter 1. Fieldwork was undertaken at three colonies; two in the eastern Musgrave Ranges – „Alalka‟ (26.137°S, 132.116°E) and „New Well‟ (26.080°S, 132.215°E), and the third, „Kalka‟ (26.137°S, 129.160°E), in the Tomkinson Ranges. The landform, soil structure and vegetation of these sites are also addressed in Chapter 1.

Wild warru were sampled over multiple trapping sessions from 2005 to 2009 (Chapter 5). Briefly, trapping was conducted on an annual basis at New Well and Alalka, although in 2007, it was undertaken biannually. At Kalka, trapping occurred in 2005 and then annually from 2008. At each site, animals were caught, processed and aged as pouch young, juveniles, sub-adults or adults (Chapter 5). Amongst other procedures, processing involved using a hole-punch to take ear biopsies of 3 mm diameter from each sub-adult, adult and, if possible, juvenile warru. These samples were stored in 90% ethanol. For a small number of animals, a portion of the blood samples taken for health assessments (Chapter 6) were also used as a genetic sample. For one adult, a decayed tooth extracted by a veterinarian was used for the latter purpose. For pouch young that were too small for ear biopsies, sampling of both tail tips and skin swabs was trialled. However, since tail-tipping led to tail bleeding, only four samples were collected this way. Swabs were unsuccessful.

In 2007 and 2008, in order to establish a captive colony, some pouch young from all three *in-situ* colonies were cross-fostered from their wild warru mothers to yellow-footed rock-wallaby (*P. xanthopus*) surrogates at Monarto and Adelaide Zoos (Chapter 5). Once these animals became sub-adults, genetic samples (ear biopsy, blood or fur) were collected and again stored in 90% ethanol.

4.3.2 DNA extraction and microsatellite analysis

Total cellular deoxyribonucleic acid (DNA) was extracted from skin and fur samples using the Qiagen QIAamp DNA Mini Kit and from blood samples using the QIAamp DNA Blood Mini Kit protocol (Qiagen, Melbourne, Australia). For the tooth sample, DNA was extracted by filing off 1g of bone powder and decalcifying the powder in 4 ml of 0.5M EDTA at 4°C on a rotating mixer for three days, changing the EDTA daily. The decalcified sample was then washed twice in distilled water and the entire washed pellet used in a Qiagen DNA Mini Kit extraction.

Previous analyses of *P. penicillata* DNA have identified a number of potential microsatellites that could also be used for warru (Hazlitt *et al.* 2004; Paplinska 2007). Twelve of these markers were tested on five warru samples. Four (Me14, Me15, Pa595y, G20.2b) were monomorphic or displayed significant stutter; consequently, only eight were chosen for further analysis. Of these loci, three were derived from an allied rock-wallaby (*P. assimilis*) library (Pa297, Pa385, Pa593; Spencer *et al.* 1995), four from a tammar wallaby (*Macropus eugenii*) library (Me16, Me17; Taylor and Cooper 1998, T32-1; Zenger and Cooper 2001a and Il51; Hawken *et al.* 1999) and one from the eastern grey kangaroo (*M. giganteus* G26.4; Zenger and Cooper 2001b) library.

For all individuals, microsatellite loci were amplified via polymerase chain reaction (PCR) using fluorescently-labelled microsatellite markers in two multiplexes (multiplex 1 – Pa297, Pa385, G2.64, Me16; multiplex 2 – Pa593, Pa597, Me17, Il51) and one singleplex (T32-1). Multiplexes were constructed such that there was no overlap in the size range of loci within each. After initial amplification of DNA, individual primer concentrations were adjusted such that the peak intensity of the product of each marker within the multiplex was balanced. Polymerase chain reactions (PCRs) were set up using Qiagen Multiplex PCR kits (Qiagen, Melbourne, Australia), with Qiagen Multiplex PCR Master Mix to a final concentration of 3mM $MgCl_2$, 2.5 µL Q-solution, 0.5µM reversed primer and 10ng/µL template DNA and made up to 25µL by adding distilled water. Each singleplex and multiplex reaction included a negative control. To check for genotyping and laboratory errors, a small proportion of individuals were re-screened.

After amplification, PCR products were diluted 1 in 10 with distilled water and 1µL of the diluted product mixed with 0.3µL GeneScan Liz 500 size standard and 8.7µL HiDi formamide (both Applied Biosystems, Foster City, USA). The solution was then denatured at 95°C for 3 minutes. PCR products were visualised on an Applied Biosystems 3730xl DNA analyser (Applied Biosystems, Foster City, USA) and alleles scored manually using GeneMapper (ver. 4.0, Applied Biosystems, Foster City, USA).

4.3.3 Data screening

Since some loci were isolated from distantly-related species, MicroChecker (ver. 2.2.3; Van Oosterhout *et al.* 2004) was used to check for microsatellite null alleles and scoring errors. To confirm MicroChecker results, an allele frequency analysis was conducted using the program CERVUS (ver. 3.0.3, Marshall *et al.* 1998). This was undertaken at a colony by colony level and estimated the null allele frequency for each locus. The same program was also used to find mismatches between the genotypes of mothers and their known offspring. Since CERVUS provides output indicating if the mismatch could be explained by a null allele, this output was amalgamated with the MicroChecker results. Both programs highlighted the loci Me17 and G26.4 as potentially having low-frequency null alleles. To establish the effect of excluding these two loci, the program Arlequin (ver. 3.5.1.2; Excoffier *et al.* 2005) was used to determine pairwise F_{ST} values (Weir and Cockerham 1984) with and without the loci. Pairwise F_{ST} measures genetic differentiation between sampled populations, where the lower the value, the more genetically similar are the populations (range 0-1). Tests were conducted to the significance level of $\alpha=0.05$ using 1,000 permutations. Excluding the two loci did not appear to substantially reduce the resolving power of the loci; however, retaining them could potentially be problematic for parentage analysis (Kalinowski *et al.* 2007). Consequently, they were excluded from further analyses.

4.3.4 Population structure

The program STRUCTURE (Pritchard *et al.* 2000) was used to determine the number of genetic groups present and to establish if these concurred with the known colonies. STRUCTURE uses a Bayesian model-based clustering method to find population groupings that mimimise Hardy-Weinberg and linkage disequilibrium (Pritchard *et al.* 2000). It does not require *a priori* geographic information; rather, it assigns individuals according to their genotypes. All age classes were included in the analysis. Parameters used were those of the admixture ancestry model with correlated allele frequencies, a burn-in length of 25,000 iterations and a run length of 100,000 iterations. To ensure that the burn-in length was adequate, the program"s in-built time-series plot was used to check for the convergence of key parameters. To test that the run length was appropriate, several runs were conducted at each *K* and checked for consistency, as recommended by Pritchard *et al.* (2010). Although the final number of genetic groups (*K*) was expected to be less than five, to be cautious, a model of *K*=1-10 was tested. To check for consistency of log probability values, each run of K=1-10 was replicated five times and the average taken. ΔK scores were calculated using the program Structure Harvester (http://taylor0.biology.ucla.edu/struct_harvest/). As suggested by Evanno *et al.* (2005) and Pritchard *et al.* (2010), the highest ΔK score was used to select the model of best fit.

STRUCTURE assigns individuals to defined population clusters based on the degree of their ancestry (*Q*) that can be attributed to a given subpopulation (Pritchard *et al.* 2000). In the current study, an individual was assigned to the population for which it had the highest estimated membership fraction. Whether the inferred populations corresponded to the population from which animals were sampled was then manually examined. To establish whether any intra-population structure was present, each of the genetic groups was also re-analysed separately using STRUCTURE. Parameters were as above.

4.3.5 Genetic diversity

Using the program GENEPOP (ver. 4.0: Rousset 2008), the genetic groups established through the STRUCTURE analysis were tested for linkage disequilibrium. Conformance to Hardy-Weinberg equilibrium for each microsatellite locus was also tested using GENEPOP. For both tests, parameters were those of the Markov chain method with 1,000 iterations. When performing comparisons, *P* values were adjusted using the sequential Bonferroni procedure (Rice 1989).

Observed heterozygosity (H_O), expected heterozygosity (H_E) and allelic diversity (A) were calculated using the program Arlequin. Mean allelic richness (A_R; allelic diversity corrected for sample size) per genetic group was calculated using the program FSTAT (ver. 2.9.3.2:

Goudet 1995). FSTAT was also used to examine inbreeding levels (F_{IS}) at each locus for each genetic group. Differences in H_E, A_R and F_{IS} between groups were tested with Kruskal-Wallis one-way ANOVAs in PASW (PASW Statistics ver. 17.0.2, March 2009).

4.3.6 Dispersal

The program STRUCTURE assumes that an individual"s true population of origin has been sampled. However, given that there are multiple colonies within the Musgrave Ranges metapopulation (Ward *et al.* 2011), this is not necessarily true in the current study. This, along with the high level of differentiation between colonies, could lead to STRUCTURE performing false clustering and not detecting migrants. The program GeneClass 2 (ver. 2.0.h: Piry *et al.* 2004) was therefore used to test for first generation migrants and their likely population of origin. Unlike STRUCTURE, GeneClass provides the option of detecting migrants without all populations having been sampled.

GeneClass is an assignment-based approach that uses the allele frequencies within populations to compute the likelihood of each individual"s genotype arising in a sampled population. It then compares these likelihoods against simulated genotypes to provide a „probability of belonging" (*P*) for each individual (Paetkau *et al.* 1995; Manel *et al.* 2002). The frequency-based algorithm of Paetkau *et al.* (2004) with a significance threshold of $P<0.01$ and partial Bayesian method (Rannala and Mountain 1997) was used. Observed allele frequencies were used to simulate a population of 10,000 genotypes, to which individual likelihoods were compared (Walker *et al.* 2008). All age classes were included in the analysis. Animals were assigned to a population if their probability of belonging was $P \geq 0.10$ (Cegelski *et al.* 2003; Hazlitt *et al.* 2006a). Individuals that were excluded from all colonies according to this criterion were considered to be immigrants from unsampled colonies.

4.3.7 Parentage and mating system

The parentage assignment program CERVUS was used to assign parentage to warru weighing < 3 kg, which incorporates pouch young, juveniles and sub-adults. All adults known to be alive in the relevant colony at the time of the relevant offspring"s birth were included as candidate parents.

CERVUS assigns parentage to a candidate parent based on a number of parameters, including if the log-likelihood ratio for that parent is large relative to the likelihood ratios of alternative candidates (Kalinowski *et al.* 2007). For each of the three wild populations (with their respective cross-fostered animals included), parentage analysis was conducted in two steps. Firstly, for the offspring whose dams were known from capture data (i.e. in pouch or caught in same trap as dam), CERVUS was used to confirm maternity and then to assign paternity. Secondly, for offspring that were caught by themselves and whose dams were therefore unknown, „parent-pair analysis‟ was used to establish dams and sires. Simulations were based on 100,000 cycles and parameters set as 65% of candidate parents sampled, 96% of loci typed and the standard error rate of 0.1. For the Alalka analysis, the number of candidate mothers and fathers respectively was set to 20. For New Well, it was set to 30, while at Kalka it was 15. These figures were based on estimated population sizes at each of the colonies (Chapter 5) and inflated to avoid over-confident assignments. Strict (>95%) and relaxed (>80%) levels of confidence were used to assign parentage (Hazlitt *et al.* 2006b).

Parentage information was used in two ways. Firstly, the familial relationship of captive animals was established by manually comparing their respective dams and sires. Secondly, it was used to assess mating patterns across the five year study. Specifically, the parentage of offspring and the sequence of parents‟ matings were used to make inferences about each sex‟s mating strategy. Male breeding output was established by comparing the number of males known to have successfully sired pouch young to the number of animals of breeding age (adults and sub-adults) that were known to be alive each year (Chapter 5).

4.4 Results

4.4.1 Sample sizes

There were a total of 22 captive warru. Together with the 100 samples from wild warru, this amounted to a total of 122 genetic samples (Table 4.1).

Table 4.1 Number of genetic samples from warru (*Petrogale lateralis*) in three colonies (Alalka, Kalka, New Well) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. „Captive offspring‟ refers to warru that were transferred to Monarto Zoo, while „wild offspring‟ pertains to pouch young, juvenile and sub-adult warru sampled *in-situ*.

	Alalka	Kalka	New Well	Total
Adult	16	7	26	49
Wild offspring	22	11	18	51
Captive offspring	7	5	10	22
Total	45	23	54	122

4.4.2 Hardy-Weinberg equilibrium and linkage disequilibrium

STRUCTURE analysis (4.4.3) indicated that four warru caught at Alalka should be grouped with New Well animals because the majority of their Q value correlated with the latter site. The resulting genetic groups conformed to Hardy-Weinberg equilibrium at most loci. MicroChecker results indicated that the loci that were outside of Hardy-Weinberg equilibrium had a general excess of homozygotes. There was no evidence of linkage disequilibrium ($P > 0.05$).

4.4.3 Population structure and dispersal

All pairwise F_{ST} values were both high and significantly different ($P<0.001$), indicating considerable genetic differentiation among the three sampled populations (Table 4.2). Kalka was most genetically dissimilar from Alalka and then from New Well.

Table 4.2 Genetic differentiation (pairwise F_{ST}) between *Petrogale lateralis* at three sampled colonies in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia.

	Kalka	Alalka
Alalka	0.278*	
New Well	0.141*	0.122*

*Statistically significant difference

Based on the criterion of the highest ΔK (Evanno *et al.* 2005; where ΔK is the second order rate of change of the likelihood function with respect to K), STRUCTURE results indicated that the true number of genetic clusters (K) in the dataset was three (Fig. 4.1).

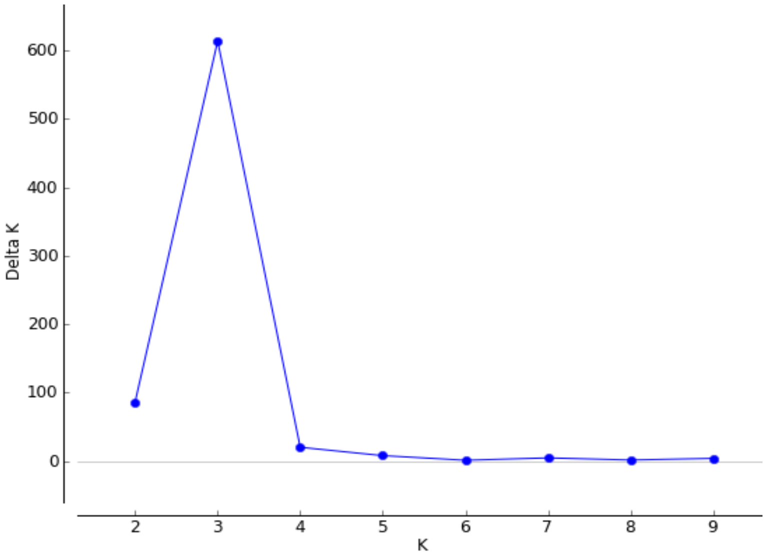


Fig. 4.1 The estimated number of populations (K) plotted against ΔK using Structure Harvester. The highest ΔK was at K=3, suggesting that this was the model of best fit (Evanno *et al.* 2005).

Based on the assumption that K=3, STRUCTURE strongly assigned the majority of individuals to their sampled population (Figs 4.2 - 4.3). Indeed, the program assigned 91.8% of all individuals to their sampling site with a posterior probability of $Q \geq 0.90$. Of the ten individuals not assigned at this probability, three had *Q*-values greater than 0.80, which is still a relatively high level of membership (Hazlitt *et al.* 2006a). None of the individuals with low *Q*-values for their sampled population were assigned to any other known population with a high probability. However, there were at least four individuals in the Alalka population that appeared to have mixed ancestry, with *Q*-values between 0.53 and 0.71 for belonging to New Well. Two of these animals were likely to be father and offspring. The results indicated that each of the three populations is genetically distinct but that a low level of migration is likely to have occurred between New Well and Alalka.

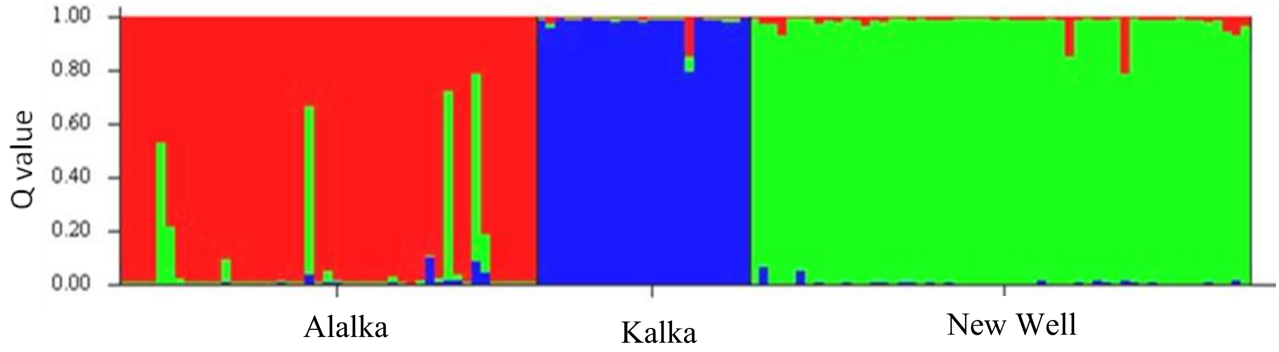


Fig 4.2 Estimates of *Q* (membership coefficient for each individual) for warru (*P. lateralis*) in the A̲nangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Each warru is represented by a single vertical line partitioned into coloured segments. These represent the animal‟s membership fraction of the estimated number of populations = 3, where red = Alalka, blue = Kalka and green = New Well.

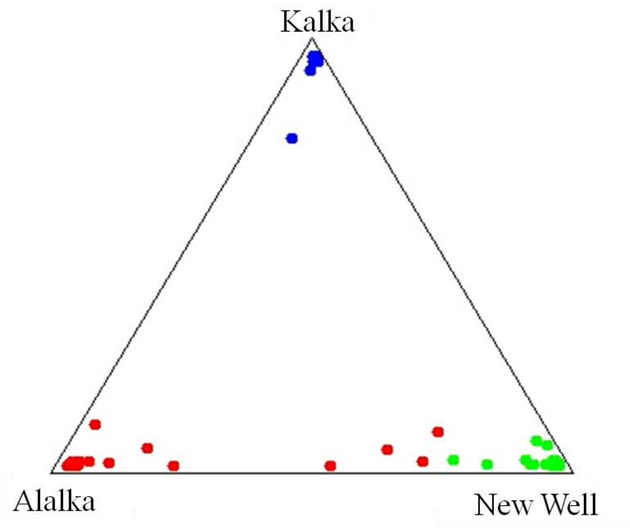


Fig 4.3 Triangle plot of *Q* showing clustering of individual warru based on their genotype. The dots represent each warru while the colours represent the population of origin, where red =Alalka, green = New Well and blue= Kalka, from the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Four warru sampled at Alalka are clustering with animals from New Well.

There was no genetic division (i.e. within-population sub-structuring) evident at Kalka or Alalka. However, at New Well, there was evidence for two genetic groups being present (ΔK = 12.98; Fig. 4.4), with only a small proportion of New Well individuals being admixed.

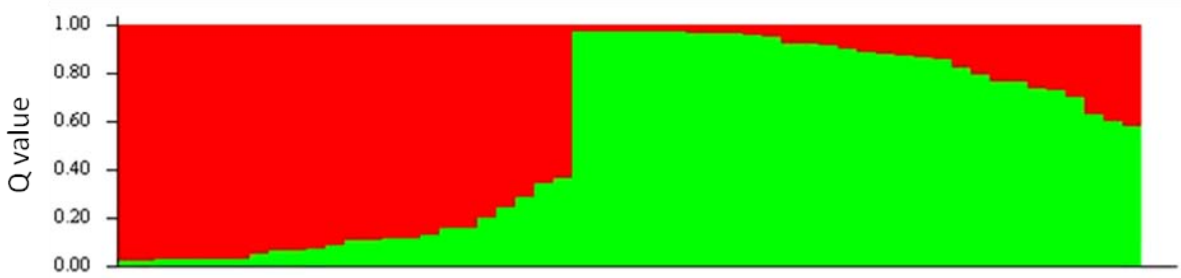


Fig 4.4 Estimates of *Q* (membership coefficient for each individual) for warru (*Petrogale lateralis*) in the New Well colony of the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Each warru is represented by a single vertical line which is partitioned into coloured segments (red and green) that represent its membership fraction of the estimated number of populations (K) = 2.

GeneClass2 allocated all but two of the sampled animals to their population of origin with a *p* ≥ 0.10. The two unassigned warru were sampled from Alalka (female) and New Well (male) respectively and were both excluded from all sampled populations. The female was also highlighted by STRUCTURE as being a migrant into the colony, although STRUCTURE assigned her as being from New Well.

4.4.4 Genetic diversity

Mean measures of genetic diversity are presented (Table 4.3). Mean observed heterozygosity was high within each population (range 0.67 – 0.71). There was no significant difference in expected (H_E) or observed heterozygosity (H_O) between populations (*P*>0.05). Both allelic diversity and allelic richness were highest at New Well and lowest at Kalka. However, the difference in allelic richness between sites was not significant (*P*>0.05). Inbreeding levels (F_{IS}) were not significant at Alalka or Kalka. However, for New Well, both the overall F_{IS} value ($F_{IS} = 0.115$) and the locus-specific F_{IS} values across all but two of the loci were high, potentially indicating inbreeding. However, there was no significant difference in F_{IS} values between populations (*P*>0.05).

Table 4.3 Mean (± standard deviation) measures of genetic diversity for *Petrogale lateralis* at three colonies in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. *N* = number of samples, H_E = expected heterozygosity, H_O = observed heterozygosity, A = mean number of alleles per locus (allelic diversity), A_R = allelic richness (mean number of alleles corrected for sample size), F_{IS} = inbreeding levels.

Site	*N*	Mean heterozygosity		A (± S.D)	A_R (± S.D)	Mean F_{IS}
		H_E (± S.D)	H_O (± S.D)			
Alalka	45	0.66 ± 0.12	0.67 ± 0.16	6.5 ± 3.45	5.68 ± 2.4	-0.011
Kalka	23	0.71 ± 0.14	0.69 ± 0.22	5.5 ± 1.64	5.5 ± 1.6	0.04
New Well	54	0.8 ± 0.06	0.71 ± 0.06	9.0 ± 2.53	7.89 ± 2.0	0.115

4.4.4 Parentage and mating system

On average across the three colonies, maternity was confirmed and/or determined for a total 64% of offspring, paternity for 24% and trio (parent-offspring relationship given the known parent) for 36% (Fig. 4.5). There was a higher success rate for establishing both maternity and trio relationships at Kalka than at Alalka and New Well. This is probably because of the lower level of migration evident at Kalka (see 4.4.2). For the 22 captive warru, maternity was confirmed and/or determined for 100% and paternity for 77% of animals. Amongst the captives, there were two sets of direct siblings, three half-siblings on the maternal side and two half-siblings on the paternal side.

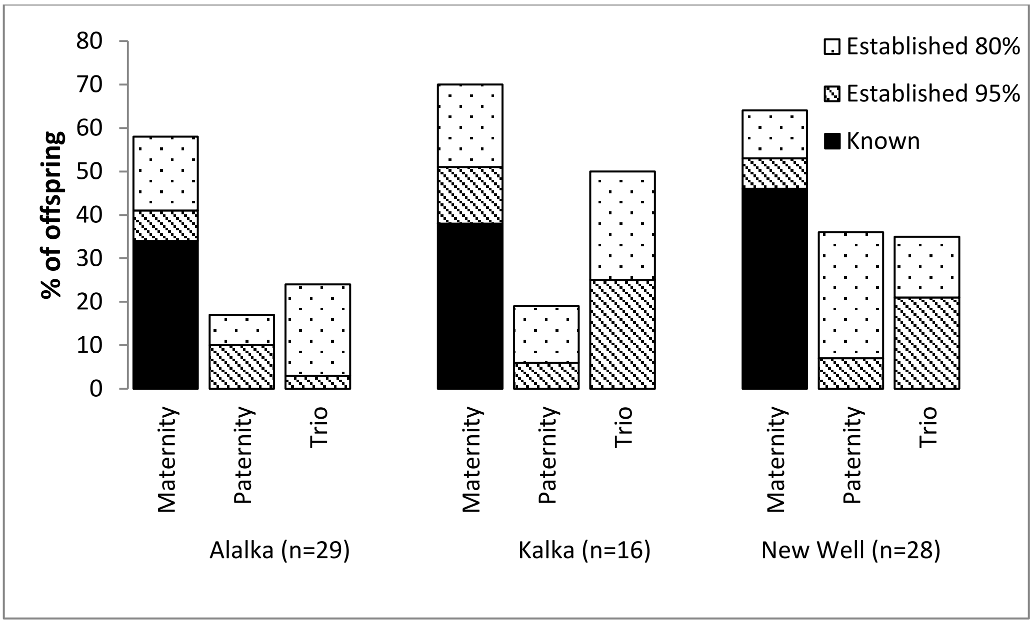


Fig. 4.5 Success rates for establishing maternity, paternity and trio relationship for warru (*Petrogale lateralis*) offspring at three colonies (Alalka, Kalka and New Well with respective captives incorporated into their colony of origin) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Total number of offspring from each colony is indicated.

An analysis of mean reproductive success for males (Table 4.4) indicated that, across all colonies, an average of 32% of the males annually known to be alive successfully sired young (range = 30-80%). However, this figure should be seen as a minimum since it was only based on the 24% of offspring for which paternity was successfully established. This proportion would have been higher if the offspring which were not genotyped, and the offspring for which paternity was not established, could have been incorporated. Most males only sired one known offspring over the five (three at Kalka) study years; however, one male was genotyped as siring four offspring over three years (Fig. 4.6). Due again to the lower success rates for establishing paternity, it is difficult to translate the number of offspring sired by males into absolute breeding success.

Table 4.4 Mean reproductive success for male warru (*Petrogale lateralis*) at three colonies (Alalka, Kalka, New Well) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. KTBA = known to be alive and includes only breeding (adult and sub-adult) animals, NA = not available due to an absence of trapping events.

	Alalka		Kalka		New Well	
	No. males KTBA	No. breeding (%)	No. males KTBA	No. breeding (%)	No. males KTBA	No. breeding (%)
2005	1	0	1	0	6	0
2006	0	0	NA	NA	8	0
2007	5	4 (80)	NA	NA	10	6 (60%)
2008	5	2 (40)	7	3 (43)	7	4 (57%)
2009	7	3 (43)	5	3 (60)	10	3 (30%)
Average	3.6	1.8 (33)	4.3	2 (34)	8.2	2.6 (29%)

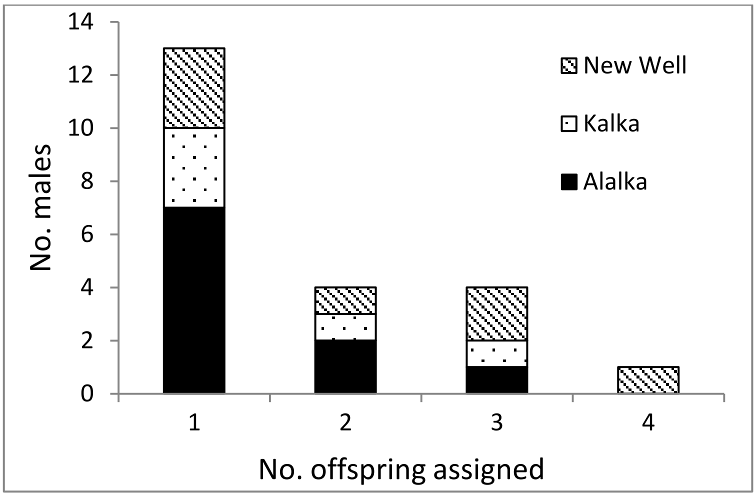


Fig. 4.6 Number of warru (*Petrogale lateralis*) offspring assigned to males at three colonies in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia from 2005-2009 (NB. due to an absence of trapping events, parentage not established for Kalka in 2006 and 2007).

An assessment of mating strategies indicated that males are polygynous, siring offspring with different females both within- and between-years (Table 4.5). The single exception was that of a male at New Well (M6), who appeared to persistently produced offspring with just one female (F4) both between- and within-years. Males bred with an average of 1.75 females both within one year, and between years.

Using the six dams which had the paternity of their offspring established across multiple seasons, females appeared to have a polyandrous mating strategy. There was just one instance of within-year, and two of inter-year persistent pairings (Table 4.6). Females bred with an average of 1.75 males within one year, and 1.5 between years. The three instances when a female had a different partner within one year all coincided with the female „losing‟ the previous offspring due to cross-fostering (in one instance, the offspring was a young-at-foot). Of the two instances when a female had a different partner between years, one coincided with the female losing the pouch young for cross-fostering. Of the two instances of apparent inter-year monogamy, one female maintained her partner despite losing her pouch young and the other lost a young-at-foot rather than a pouch young to cross-fostering.

Table 4.5 Mating strategy of male warru (*Petrogale lateralis*) in three colonies (Alalka, Kalka and New Well) in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Birth year refers to the year of birth of offspring for which dam and sire were genotyped. „F‟ and „M‟ denote individual female and male warru respectively, the „polygyny‟ and „persistent pairing‟ columns denote incidence thereof in the respective year. „UK‟ indicates that it is unknown if the incidence occurred.

Site	Sire	Birth year	Dam	Polygyny		Persistent pairing	
				Within-year	Inter-year	Within-year	Inter-year
Alalka	M9	2007	F7	1	UK	0	UK
		2007	F8				
	M10	2007	F9	UK	1	UK	0
		2009	F10				
Kalka	M3	2008	F11	UK	1	UK	0
		2009	F2				
	M11	2008	F12	1	UK	0	UK
		2008	F13				
New Well	M4	2007	F3	UK	1	UK	0
		2009	F14				
	M5	2007	F5	1	UK	0	UK
		2007	F6				
	M6	2007	F4	0	0	1	1
		2007	F4				
		2008	F4				
Total				3	3	1	1

Table 4.6 Mating strategy of female warru (*Petrogale lateralis*) in three colonies (Alalka, Kalka and New Well) in the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Birth year refers to the year of birth of offspring for which dam and sire were genotyped. „F‟ and „M‟ denote individual female and male warru respectively, the „polyandry‟ and ‚persistent pairing‟ columns denote incidence thereof in the respective year. „UK‟ indicates that it is unknown if the incidence occurred and * that the dam „lost‟ the offspring to cross-fostering.

Site	Dam	Birth year	Sire	Polyandry		Persistent pairing	
				Within-year	Inter-year	Within-year	Inter-year
Alalka	F1	2008	M1	1*	UK	0	UK
		2008	M2				
Kalka	F2	2008	M3	0	UK	UK	1*
		2009	M3				
New Well	F3	2007	M4	0	1	0	0
		2008	M5				
	F4	2007	M6	0	0	1	1*
		2007	M6				
		2008	M6				
	F5	2007	M7	1*	1*	0	0
		2007	M8				
		2009	M5				
	F6	2007	M5	1*	UK	0	UK
		2007	M8				
Total				3	2	1	2

4.5 Discussion

4.5.1 Population structure and dispersal

Warru in the APY Lands have a substantial level of population structuring, with almost all individual animals assigned to their genetic cluster with a high certainty ($q \geq 0.90$). In turn, these genetic clusters strongly correlate to the known geographic arrangement of colonies. There are also highly significant pairwise F_{ST} values among all three populations. These values reflect colonies‟ geographic proximity, with Kalka, which is over 300 km from Alalka and New Well, being the most genetically dissimilar. Overall, these results suggest that there is restricted gene flow among colonies, with increasing distance leading to increasing genetic difference. The current conclusion is congruent to findings from other *Petrogale* studies; for example, Hazlitt *et al.* (2006a) found that *P. penicillata* colonies located only 2-4 km apart within relatively continuous habitat exhibited considerable levels of colony differentiation. *P. xanthopus* have also been found to have significant differences in allele frequency between populations separated by 10 km of suitable habitat (Pope *et al.* 1996; 1998).

Although the warru colonies assessed in the current study were highly differentiated, evidence for at least some dispersal was available, with mixed ancestry for four warru sampled at Alalka. STRUCTURE inferred that these animals shared ancestry with warru from New Well. Since this program assumes that all colonies have been sampled, this conclusion may not be accurate. However, GeneClass2 results corroborated those from STRUCTURE, highlighting one warru in each of New Well and Alalka as probable first- or second-generation migrants, each from an unsampled colony. This suggests that these two colonies act as part of a broader Musgrave Ranges metapopulation. A metapopulation is defined as a group of spatially-separated populations that interact at some level through the process of dispersal (Scott Mills 2007). This hypothesis is supported by a preliminary mitochondrial DNA (mtDNA) analysis of SA warru (Eldridge 2006). The study found two quite different haplotypes at Alalka (4.3% sequence divergence), with one of these very similar to the haplotype found at New Well (0.1%), suggesting some historical maternal gene flow. Overall, in the current study, approximately 5% of sampled individuals had mixed ancestry. This figure is identical to that identified for *P. penicillata* in New South Wales (Piggott *et al.* 2006b) and suggests that, while still rare, *Petrogale* perhaps undertake inter-colony dispersal more frequently than what is generally inferred from trapping and telemetry studies (Piggott *et al.* 2006b). In contrast, all Kalka warru had extremely high *Q*-values and there was no evidence of immigration. Given that this site is geographically isolated, this result was unsurprising. Eldridge (2006), however, found two different mtDNA haplotypes at Kalka (3.3% sequence divergence), with one of these being similar to that found in animals from the Bell Rock Range in Western Australia (WA). This again suggests some historical maternal gene flow, albeit one undetected by the current study due to a lack of sampling of WA warru.

Since there was a high degree of population structuring amongst all three studied APY Lands colonies, each should be managed as a unique unit worthy of individual conservation. Indeed, an investigation of whether the Musgrave and Tomkinson Ranges populations constitute separate Evolutionary Significant Units (Moritz 1994) is warranted. As there was some evidence for dispersal within the Musgrave Ranges metapopulation, management initiatives such as aerial baiting should continue to be conducted across the entire area. The current results provide support for the hypothesis that, since warru have the capacity to move between adjacent sites of suitable habitat (Chapter 3; Eldridge *et al.* 2001), gene flow is likely limited by intrinsic factors such as behaviour and social structure, rather than dispersal capability. Similar conclusions have been reached for *P. penicillata* (Hazlitt *et al.* 2006a). For warru, this means that, if afforded appropriate management, animals are likely to be capable of recolonising sites that are currently vacant.

4.5.2 Genetic diversity

All three studied colonies were genetically diverse, with the level of diversity similar to that observed in other *Petrogale* colonies (reviewed in Eldridge *et al.* 2010). For example, the reported value for *Petrogale* allelic diversity ranges from 1.2 - 11.6 (current study average = 7.0), while for average heterozygosity (H_E) values, it is between 0.05 and 0.86 (current study average = 0.72; Spencer and Marsh 1997; Eldridge *et al.* 1999). The highest levels of both allelic diversity and heterozygosity in *P. lateralis* were established for animals in the Northern Territory‟s MacDonnell Ranges (Jones 2001). APY Lands warru had the second-highest values for these parameters, followed by those of *P. lateralis lateralis* in Exmouth, WA (Eldridge *et al.* 1999) and then those in the WA Wheatbelt (Eldridge *et al.* 1999; Jones 2001). This was followed by *P. pearsoni* on three of SA‟s islands (Pearson North and Mid-South and Wedge; Jones 2001), with those on Barrow Island in WA (Eldridge *et al.* 1999) having the lowest values. This pattern clearly exhibits the effect of isolation on genetic diversity, with the warru populations in the MacDonnell Ranges considered to be secure and well-connected (Jones 2001; Woinarski *et al.* 2007). Similarly, and excluding the presence of feral predators, both the APY Lands and Exmouth animals live in a relatively undisturbed landscape, with those in Exmouth in particular being found in many gorges through the area (Pearson 2009). For the APY Lands warru, the result suggests either that there has not yet been enough time since colony isolation for losses of genetic diversity to have accumulated, or supports the hypothesis that the Musgrave colonies are part of a broader metapopulation that is able to maintain its genetic diversity. In contrast, the Wheatbelt populations are highly fragmented and/or established via translocation (Kinnear *et al.* 2010), while the four islands separated from the mainland between 8,000-10,500 years ago, substantially increasing their degree of isolation (Eldridge *et al.* 1999; Jones 2001).

There was no evidence of inbreeding detected at Alalka and Kalka. The New Well colony, however, showed evidence of homozygote excess, potentially providing evidence of inbreeding. The explanation for this may lie with the STRUCTURE results, which indicated that there are two genetic groups within the colony. Thus, although overall genetic variation is high, colony segregation may be leading to the observed homozygote excess. There are two potential reasons for such a division; geographic and/or social isolation. The core study area at New Well contains two opposing cliff-faces divided by a large gully. Trapping records (Chapter 5) indicate that warru are capable of moving across the gully, with individuals trapped on different cliffs on successive days. However, during trapping, animals are likely to disrupt their natural population structure so as to access free food. Furthermore, the presence of humans, in this case the trapping team, is also likely to result in animals undertaking aberrant movements. In contrast, preliminary VHF radiotracking (Read and Ward 2007) suggests that, although animals generally roam across a broad area of New Well, most animals tend to stay on one cliff-face. This may help explain the genetic sub-structuring, and potentially, homozygote excess, evident within New Well.

The current results suggest that each colony‟s inbreeding values should be monitored and, if required, population supplementation undertaken to compensate for any increase. Such supplementation should ideally only involve intermixing of animals from within the same metapopulation (i.e. keep the Musgrave and Tomkinson Range metapopulations separate). However, since all three colonies are presently generally diverse, recovery of APY Lands populations, unhindered by factors such as those seen in *P. lateralis* on Barrow Island (Eldridge *et al.* 1999), is feasible. Further studies could involve using genetic relatedness to determine whether the intra-colony grouping seen at New Well is due to family structuring.

4.5.3 Parentage and mating system

There was a high success rate for confirming and establishing the maternity (64%) of warru pouch young, but lower success for determining paternity (24%). This discrepancy can be explained by the fact that dams were already known for 40% of offspring, while sires were available for none. Furthermore, although not conclusive, studies suggest that dispersal for macropodoids is usually male-biased (Eldridge *et al.* 2010). Consequently, males, and thus potential sires, may not have been as well-sampled as females. The lower success for establishing paternity, combined with incomplete sampling of wild offspring, meant that interpretation of results was somewhat limited. For example, it is likely that substantially more males than that presented (32%) actually succeed in siring young. Similarly, the number of males producing two or more offspring is likely higher than established. Indeed, it would be plausible for male warru to have reproductive rates as high as those of *P. penicillata,* which sire multiple offspring per year and breed successfully for 2-4 years (Hazlitt *et al.* 2006b). The current results nevertheless provide preliminary data which, until further research is undertaken, can be seen as a minimum.

The current results suggest that warru have a polygamous mating system. Males sired offspring with multiple females both within- and between-years, with just one instance of genetic monogamy, between Male 6 and Female 4. An investigation of home ranges (Read and Ward 2007) found that in 2007, both of these individuals resided in a similar area of New Well and shared three of their four „night zones" (geographic radiotracking zones across the rock complex). Since these zones also contained a number of other resident females and are in core rather than marginal habitat, the reason for this apparent monogamy cannot be provided. Given the low success rates for establishing paternity and the presence of unsampled offspring, the monogamy apparently evidenced by this pair may, however, be misleading. Nevertheless, the mating system of male warru appears to contrast that of the polygynous *P. penicillata*, which have individual males overseeing a spatially clustered group of related females (Hazlitt *et al.* 2006b). A lack of comprehensive home range data for warru meant that it was not possible to establish if male *P. lateralis* establish a similar mating strategy; however, the data for females suggests that they do not.

Female warru tended to have a polyandrous mating strategy, producing offspring with an average of 1.75 males within one year and 1.5 between years. This contrasts with results from *P. assimilis* and *P. penicillata* (Eldridge *et al.* 2010). Specifically, *P. assimilis* are behaviourally monogamous (Spencer *et al.* 1998), while female *P. penicillata* have a pattern of serial mate fidelity across years, seemingly only changing mates when their breeding partner disappears from the colony (Hazlitt et al. 2006b). The latter trend did not appear to apply to female warru. In contrast, three female warru changed their breeding partner when they lost their pouch young to cross-fostering, although two others did not (albeit one of those lost a young-at-foot, rather than a pouch young). Similarly, Spencer *et al.*"s (1998) study found that female *P. assimilis* were more likely to have an offspring fathered as a result of extra-pair copulation if their previous young had failed to survive to pouch emergence. Thus, as with *P. assimilis,* the partner changes exhibited by warru may be attributable to females seeking new mates in an attempt to improve their breeding success. However, given the relatively low samples sizes, the current, somewhat unclear result requires validation through further research.

Understanding species" mating systems is important because breeding group dynamics can minimize inbreeding and positively influence genetic diversity within populations (Hazlitt *et al.* 2006b). The polygamous mating strategy established in the current study suggests that warru mating systems have, and will continue to, assist in the maintenance of gene flow within the extant populations. It also suggests that managers need to retain sufficient numbers of males and females in both the *in-* and *ex-situ* colonies for individuals to be able to maintain this mating system. For the same reason, reintroductions should involve relatively equal numbers of males and females. Results relating to the parentage of captive animals were provided to Monarto Zoo, enabling establishment of appropriate pairings. It is recommended that similar genetic studies be undertaken for other species in which animals are brought into captivity and where management of the *in-situ* population is required.

4.5.4 Future research

The current study presents the first analysis of warru genetic structure and diversity using microsatellites. However, only three of the six markers used in the current study were congeneric to warru (those from *P. assimilis*). Allele amplification success rates increase if the markers used for the study species are from a closely related species (Selkoe and Toonen 2006). Consequently, to establish information on warru pedigrees or sibling relationships, future researchers should develop a suite of markers specific to *P. lateralis.* Such markers, combined with an increased number thereof, would be able to further the current study‟s results and establish a more accurate understanding of male reproductive success, the mating strategy of both sexes and the impact of cross-fostering on females‟ mate choices.

CHAPTER 5 – Population dynamics and reproduction of warru in the APY Lands

Ecology is…to discover the reasons for the distribution and numbers of animals in nature.
Charles Elton (1927)

The pattern for warru is that they will live as husband and wife. When they have kids, the kids will follow the parents around and see what they eat. As they have [more] children, they will then spread out between shelter sites…they are not like families who stay together. Warru are not conscious of family ties.
Jacob Puntaṟu, Aṉangu Traditional Owner in Geelen (1999).

Photo: Captive-bred warru joey in the pouch of a warru that was herself cross-fostered from the APY Lands. M. Post.

Chapter 5 - Population dynamics and reproduction of *Petrogale lateralis* (MacDonnell Ranges race) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia

Exegesis

Chapter 5 details an assessment of warru population dynamics in three colonies in the APY Lands, attained during six years of animal trapping. The chapter links to the current thesis through the fact that a species‟ population dynamics has a direct effect on its home range, genetics and fitness parameters.

The chapter is divided into two sections – population parameters and reproduction. For the population parameters component, I participated in all trapping trips conducted in 2007-2010, including free-feeding sites in 2008-2010. From 2009-2010, I was primarily responsible for updating the Microsoft Access database used for managing trapping records. Also, I undertook all analyses and data interpretation except those relating to POPAN modelling. For the reproductive component, I was responsible for all data analysis and interpretation.

The population parameters and some of the reproduction data were published in *Australian Mammalogy* vol 33(2) pp. 142-151 and can be accessed via http://www.publish.csiro.au/nid/256/paper/AM10055.htm. Dr Matthew Ward is listed as the manuscript‟s primary author because trapping trips were organised by him. Although I am only listed as the secondary author, the chapter/manuscript is included in this thesis because I was responsible for the work outlined above. Each author‟s contribution and their permission for inclusion of the work in this thesis is outlined below.

STATEMENT OF AUTHORSHIP

Status of warru (*Petrogale lateralis* MacDonnell Ranges race) in the Anangu Pitjantjatjara Yankunytjatjara Lands of South Australia: 2. Population dynamics. *Australian Mammalogy*. Submitted on 16 December 2010.

Ward, M.J.

Statement of contribution: Contributed to design and implementation of work. In collaboration with L. Ruykys, conducted data analysis (except that which undertaken by S. de Little) and interpretation. Evaluated manuscript. Acting as corresponding author.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

Signed . ……………………………Date…24/1/2011

Ruykys, L. (candidate)

Statement of contribution: Contributed to implementation of work. In collaboration with M.J. Ward, conducted data analysis (except that which undertaken by S. de Little) and interpretation. Wrote manuscript.

I hereby certify that the statement of contribution is accurate.

Signed ……. ……………………………………………………Date…24/1/2011

van Weenen, J.

Statement of contribution: Contributed to design and implementation of work.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

Signed …. ………………….Date….1/3/2011

de Little, S.

Statement of contribution: Analysed data and evaluated manuscript.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

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5.1 Abstract

In order to inform management and better understand aspects of its conservation ecology, the population dynamics of warru (*Petrogale lateralis* MacDonnell Ranges race) were studied in the An̲angu Pitjantjatjara Yankunytjatjara (APY) Lands of South Australia (SA). Capture-mark-recapture between 2005 and 2010 at the three largest known remaining colonies, followed by POPAN modelling, indicated that population sizes were 23 at „New Well‟ and 24 at „Alalka‟ in the Musgrave Ranges, and 14 at „Kalka‟ in the Tomkinson Ranges. Taking into account recent aerial survey results, the study confirmed that warru are endangered in SA. However, there were signs for potential recovery of the race, including high average reproductive rates (in the Musgrave Ranges, 90% of reproductively active females had pouch young), even sex ratios and high adult survivorship (>75%). Juvenile survival (51%), however, was significantly lower than that of adults. Given that red fox (*Vulpes vulpes*) numbers are low at these sites, the latter is possibly due to predation by feral cats (*Felis catus*), although this needs further investigation. Juvenile survival was also positively correlated with winter rainfall, indicating that access to water is important during the drier winter months. In light of these observations, it is proposed that management of remaining warru colonies focus on cat control and consider providing access to free water during winter.

Keywords:

Black-footed rock-wallaby, demography, reproduction, growth curves.

5.2 Introduction

An accurate knowledge of demographic parameters, such as population size, sex ratios and recruitment rate, is critical for threatened species recovery programs because it facilitates an understanding of a species‟ biology, assessment of its conservation status and helps to forecast future population trends (Caughley and Gunn 1996; Clancy and Close 1997; Piggott *et al.* 2006b). Furthermore, information on the extrinsic drivers of these dynamics, such as predation and rainfall-driven resource availability (Krebs 2009), is essential for implementing appropriate recovery and management strategies (Eldridge 1997a).

Due to the inherent difficulties of working with rare or elusive species (Piggott *et al.* 2006a), information on population dynamics is often difficult to attain, limiting many recovery programs (Delaney 1997a; Sharp *et al.* 2006). This is particularly the case for rock-wallaby (*Petrogale*) species because of their nocturnal habits, elusive nature and the inaccessible and often remote habitat in which they live. Reflecting this, knowledge of the population dynamics of *Petrogale* is scant (Delaney 1997a), with work focusing on just four of the 16 described species (Eldridge 1997b; Van Dyck and Strahan 2008), specifically the brush-tailed (*P. penicillata*; Batchelor 1980; Piggott *et al.* 2006a; 2006b), yellow-footed (*P. xanthopus*; Robinson *et al.* 1994; Lethbridge 2004; Sharp *et al.* 2006), allied (*P. assimilis*; Delaney 1997a; Delean 2007) and black-footed rock-wallabies (*P. lateralis*; Eldridge *et al.* 1999).

The importance that understanding population dynamics can have for species recovery is exemplified by the seminal studies of Kinnear *et al.* (1988; 1998; 2010), who demonstrated that predation, particularly by the introduced red fox (*Vulpes vulpes*), was the primary driver in suppressing, and in some cases driving to extinction, *P. lateralis* populations in the Western Australian (WA) Wheatbelt region. This information subsequently influenced the implementation of the WA „Western Shield‟ predator abatement program (Possingham *et al.* 2003), which led to the translocation and recovery of several species, including *P. lateralis*. Similarly, an ongoing population monitoring study in the WA Calvert Ranges has preliminary data which suggest that feral cats (*Felis catus*) may limit *P. lateralis* juvenile survival and thus population growth. The implementation of cat baiting is demonstrating promising initial results (Kendrick *et al.* 2010).

Whilst predation is a strong driver of *Petrogale* population dynamics, rainfall-driven resource availability can also have a major influence on macropods (Lethbridge 2004; Sharp and McCallum 2010). For example, kangaroo abundance increases with food resource availability (Caughley *et al.* 1984; Clancy and Croft 1992), and biomass itself is generally related to rainfall, meaning that it may be possible to model the correlation between species‟ population dynamics and rainfall. For example, the annual growth rates of several *P. xanthopus* colonies in South Australia are correlated with short-term rainfall patterns (Lethbridge and Alexander 2008). This highlights the need to investigate potential abiotic drivers when interpreting population monitoring data.

A better understanding of the population dynamics of *Petrogale* species and their drivers has been identified as a high priority for management of the genus across Australia. For example, there has long been a call to clarify the distribution, population status and reproductive biology of *P. lateralis*, including the establishment of techniques that allow easy ageing of animals in the field (Eldridge 1997a). This need is particularly pertinent given that in South

Australia (SA), *P. lateralis* (MacDonnell Ranges race) has suffered substantial declines in range and abundance (Finlayson 1961) and is now only known from the Indigenous-owned and managed A<u>n</u>angu Pitjantjatjara Yankunytjatjara (APY) Lands in the far north-west. Termed „warru" by Western Desert Indigenous Owners, animals are restricted to two metapopulations encompassing three primary colonies; „New Well" and „Alalka" in the Musgrave Ranges and „Kalka" in the Tomkinson Ranges. Accordingly, a substantial recovery program has been implemented (Read and Ward 2011a). This is based on the acceptance that the extensive decline in warru across SA is correlated with the spread of exotic predators across central Australia (Finlayson 1961). However, given the arid nature of the APY Lands and the small size of the remaining populations, managers needed to gain an understanding of the influence of rainfall on warru recovery, as well as greater clarity on the size of the largest-known remaining colonies. This would both enable managers to set appropriate recovery targets and better understand the minimum population sizes which might trigger the need to supplement wild populations with captive stock.

The present study on warru therefore aimed to:
1. Clarify the race"s status in SA by estimating the size and structure of the three largest known, extant colonies.
2. Model survival probabilities for adults and juveniles.
3. Establish the influence of rainfall on survival.
4. Understand their reproductive and developmental parameters.

5.3 Materials and Methods

5.3.1 Study site

This study was conducted in SA APY Lands, which experience a hot, dry, desert climate with short, cool to cold winters. Rainfall is low and unreliable, with a tendency for summer rather than winter precipitation (Robinson *et al.* 2003). Geologically, the area is extremely complex, with the northern third of the APY Lands containing extensive range systems, including the Musgrave, Tomkinson and Mann Ranges. These generally support *Triodia* hummock grasslands, supplemented with tussock grasses and herbs and an overstorey of tree and shrub species of considerable diversity, including *Acacia olgana, Ficus brachypoda* and *Pandorea doratoxylon* (Robinson *et al.* 2003).

Fieldwork was conducted at three study sites; „New Well‟ and „Alalka‟ in the eastern Musgrave Ranges, 15-20 kilometres north and north-west of the Indigenous community of Pukatja (26°16'43.08"S, 132°8'2.13"E), and „Kalka‟ in the Tomkinson Ranges, near the community of Kalka (26°7'5.18"S, 129°9'2.91"E). These are the largest-known warru colonies in SA (Read and Ward 2011b). Alalka‟s landform is that of rugged strike ranges on metamorphics. It is 194 ha and contiguous with a large number of surrounding hills. In contrast, New Well is a granite inselberg of 590 ha located where the eastern Musgrave Ranges divide into isolated outcrops. The two sites are 11 km apart. Kalka is adjacent to the SA, WA and Northern Territory (NT) borders in the Tomkinson Ranges, where warru are primarily associated with extrusions of angular granitic or ultra-mafic boulders (Moore 1970; Read and Ward 2011b). Approximately 2,190 ha, Kalka rises 350 m above ground and has a vegetation type dominated by *Triodia* with a sparse overstorey (Robinson *et al.* 2003). Kalka is the only one of the three field sites which contains a known water supply. This is in the form of a perennial spring at the base of the site. Minor camera-surveillance has indicated that it is occasionally visited by warru (APY Land Management unpubl. data). However, no empirical data are available on the frequency of this use. Furthermore, the spring sits at the bottom of the very large Kalka outcrop and may, in fact, have minor influence compared with the availability of surface waters following rain. The spring‟s importance to the population dynamics of warru at Kalka cannot therefore be determined in this study.

A fourth, „pseudo-population‟ was that of the captive warru. These animals were sourced as pouch young from all three APY Lands colonies during trapping in 2007-2009. At this time, they were either cross-fostered (Taggart *et al.* 2005) to surrogate yellow-footed rock-wallaby (*P. xanthopus*) dams, or hand-reared. A total of 22 animals (New Well *n* =10, Alalka *n* = 7, Kalka *n* = 5) survived to weaning and have since been held at Monarto Zoological Park, SA, which is located around 60 km east of Adelaide on the eastern side of the Mt Lofty Ranges.

5.3.2 Animal trapping and processing

At New Well and Alalka, trapping was conducted annually between 2005 and 2010. In 2007, trapping was conducted biannually (May and August) with the aim of sourcing pouch young for the captive population. At Kalka, trapping occurred in 2005 and then annually between 2008 and 2010. At all sites, trapping occurred between May and October, which coincides with the coolest and driest weather conditions on the APY Lands (Robinson *et al.* 2003).

Animals were caught in cage traps (33 x 36 x 80 cm) supporting a bag of thick, shadecloth-like material. Traps were located in shelter sites (caves, crevices) with evidence of recent warru activity. Traps were only able to cover a small proportion of each respective hill; however, they were placed in areas considered to be core habitat. At Alalka, the total number of traps was increased from five in 2005 to nine in 2008. At New Well, traps were increased from 11 in 2005 to 20 in 2007. At both sites, new traps were placed at the extremities of the original trapping area, yet still in good quality habitat, so as to increase the trapping area. At Kalka, traps were increased from five in 2005 to 12 in 2008, and then 13 in 2009. Traps were placed in good quality habitat. For two to three days before trapping commenced, traps were wired open and „free-fed‟ by placing bait (chopped apples and a peanut butter/oat mix) inside and outside the traps. Following „free-feeding‟, traps were set for four to six nights and checked at dawn.

Captured animals were removed from traps, placed in hessian sacks and, in an attempt to reduce the incidence of capture myopathy, given an intramuscular injection of Vitamin E at 0.02 mL kg^{-1} (Troy Laboratories Pty. Ltd., New South Wales; Vogelnest and Woods 2008). Processing involved implanting microchips and individually coloured eartags, attaining morphometric data, checking animals‟ reproductive status and taking blood samples. Pouch young were sexed, morphometric (head and pes length as a minimum) and developmental data collected and, if their size permitted (generally from 5 months of age), microchipped. All animals were aged according to categories established using growth curves for the race (see 5.3.3.2 and Table 5.5). Even if their morphometric measurements suggested that they fitted into the juvenile age class, young females that were breeding were classified as sub-adults. If a pouch young was thrown during the trapping process, it was stitched back into the dam‟s pouch using dissolvable stitching in a „purse-string‟ arrangement. After processing, trapped animals were released at site of capture.

5.3.3 Data analysis

5.3.3.1 Population parameters

Data from the two trapping sessions conducted in 2007 at New Well and Alalka were amalgamated within sites to ensure that 2007 results were comparable to those from the other years‟ annual trapping. A range of data were calculated for each site and trapping period, including total number of animals caught, capture rates, sex ratios (proportion of females trapped / total animals trapped; Sharp *et al.* 2006) and percentage of females breeding.

A population size for each colony was estimated using two techniques. Firstly, a tally of the number of animals known to be alive (KTBA) was calculated. This included all animals (pouch young, juvenile, sub-adult and adult) which were tagged upon capture; pouch young that were too small to be marked were not included. The KTBA estimates were adjusted to include animals that had avoided capture for one or more trapping sessions, but which were subsequently recaptured (Kinnear *et al.* 1988). They did not incorporate untagged adult animals trapped in a session and who, by virtue of their age, were hypothetically present in the colony during the preceding trapping event. This is because such animals may have immigrated into the colony; in such a scenario, the timing of their entry is unknown.

Secondly, each colony‟s annual population abundance and an estimate of mean population size were estimated using POPAN models (Schwarz and Arnason 1996) in the program MARK 5.1 (White and Burnham 1999). These estimates took into account variation in trapping effort and the differing intervals between trapping sessions.

The program MARK was also used to estimate warru survival (φ) and recapture probabilities (p) using live-recaptures-only models for Alalka, and combined live-recaptures and dead recoveries models for Kalka and New Well (because mortality was recorded at these two sites, Burnham 1993). Survival and recapture estimates took into account the degree of dispersion within the data, animal mortality, variation in trapping effort and the differing durations between trapping sessions. Survival was determined for both juvenile and adult animals, where „juvenile‟ warru were defined as non-breeding animals (pouch young and juveniles), and „adults‟ as breeding animals (sub-adults and adults). Survival for any particular year was calculated as survival from the trapping period of that year up until the trapping date of the following year (i.e. survival over an extended „summer‟ period).

To investigate the impact of rainfall on warru survival, a candidate set of survival and recapture models for combined mark-recapture data from Alalka and New Well were used. Kalka was not included in this analysis because the dataset was too small. The modelling included testing for the separate influence of annual, summer (October – March) and winter (April – September) rainfall on juvenile and adult survival, as well as annual rainfall time-lag effects of one and two years. For the Musgrave Ranges, annual rainfall (Fig. 5.1) was compiled from monthly data from the Pukatja weather station, which is nearest to the New Well and Alalka fieldsites (approx. 16 km, Bureau of Meteorology 2010). For the Tomkinson

Ranges, monthly rainfall data from the Pipalyatjara weather station, which is 2.3 km from the fieldsite, is recorded only sporadically. Consequently, these data were used where possible but supplemented preferentially with data from the Kanypi (94 km away), Docker River (142 km) and Giles Meteorological Stations (152 km) respectively.

To rank and weigh models, Akaike‟s information criterion corrected for small samples (AIC_c) was used as an estimate of Kullback-Leibler information loss (Burnham and Andersen 2002). The difference between the model‟s AIC*c* value and the top-ranked model ($\Delta\mathrm{AIC}_c$), and the relative model weights ($w\mathrm{AIC}_c$), were calculated (Burnham and Andersen 2002). Thus, the strength of evidence ($w\mathrm{AIC}_c$) for any particular model varies from 0 (no support) to 1 (complete support) relative to the entire model set. So as to include model selection uncertainty in the estimates of parameter precision, survival, recapture and population size estimates were model-averaged using model weights ($w\mathrm{AIC}_c$) (Buckland *et al.* 1997).

NOTE:
This figure is included on page 115
of the print copy of the thesis held in
the University of Adelaide Library.

Fig. 5.1 Annual rainfall during the study period (2005 – 2010) for the Musgrave and Tomkinson Ranges in the A̲nangu Pitjantjatjara Yankunytjatjara Lands, South Australia. The mean given for each mountain range is for 1997 – 2010 (Bureau of Meteorology 2010).

5.3.3.2 Reproduction

Birth rates were ascertained by determining, and comparing between colonies, the percentage of female adult and sub-adult warru breeding each year. To establish if there was a relationship between females‟ reproductive rates and rainfall (total annual in previous year, total in current year, total summer in current year), linear regression was undertaken using

PASW (PASW Statistics ver. 17.0.2, March 2009). Since both rainfall and breeding data from Kalka were limited, this analysis was undertaken only for the Musgrave Ranges; for this, data from the New Well and Alalka colonies were combined.

Observations on the development of wild and captive pouch young included details on the eyes, ears, body, pouch status and capacity to vocalise. These data were used to establish a developmental timeline. For this, age of pouch young was estimated using Delaney and De‟ath‟s (1990) exponential equation. This equation was chosen because Jones *et al.* (2004) found that it provided a high level of explanation (r^2 = 99.5%) for the variation in headlength observed in eight captive *P. lateralis* (MacDonnell Ranges race) pouch young. Delaney and De‟ath‟s (1990) equation was re-arranged such that;

$$\text{Age} = \frac{\ln(1\text{-HL}/111.88)}{-0.0051} - 9.24$$

where HL = headlength of pouch young.

Growth curves of the respective relationships between age and bodyweight, and age and pes length, were then established. For this, the calculated ages of both captive and wild pouch young were plotted against their weight and pes length measurements. For the captive warru, the need to prevent maternal stress, and thus the expulsion of pouch young, precluded scheduled measurements. However, pouch young were monitored and serially measured whenever practicable, including at pouch emergence. The seven hand-reared warru were measured at up to weekly frequency. Although Jones (2001) has already provided data for the age-pes relationship, this was based on only eight animals in captivity. As such, the current data was used to confirm the validity of those results.

To determine the timing of breeding, a birth schedule was established. Using Delaney and Death‟s (1990) equation, birth dates of pouch young and juveniles were calculated by subtracting animals‟ estimated ages from the trapping date. To examine the influence of seasonality, birth dates were then plotted across time (Sharp *et al.* 2006). Results from all three colonies were combined because this enabled seasonality to be more easily determined.

Age categories were established using morphological and behavioural data from Jones (2001) and developmental data from wild animals in the APY Lands and captives at Monarto Zoo. Data used included scrotal and cloacal measurements, testis index (>30 mm^3 to delineate adult males; Jones pers. comm. and as per Delaney‟s [1997b] equation) and times to weaning and commencement of breeding. Given that Jones‟ data pertains to NT animals, the age categories established in the current study are applicable to *P. lateralis* (MacDonnell Ranges race) in both SA and the NT.

5.4 Results

5.4.1 Population parameters

5.4.1.1 Census results

The total number of warru captures (including annual recaptures) at the three colonies broadly approximated total trapping effort for each site (Tables 5.1-5.3). Thirty eight animals were caught at Kalka (248 trap nights), 72 at Alalka (244) and 102 at New Well (637). However, the maximum number of warru known to be alive (KTBA_{max}) was not proportional to trapping effort. Thus, despite the substantially higher trapping effort at New Well, the site had a KTBA_{max} of 24 in 2010, only one more than Alalka‟s KTBA_{max} of 23 in 2009. Although annual trends in KTBA_{max} and POPAN population estimates demonstrated some increases in colony size between 2005 and 2010, this is most likely an artefact of there being an increase in trapping effort and area in 2007, as well as it only being the early stages of the trapping program, when a large proportion of animals were unmarked. Population estimates as calculated by POPAN models (Tables 5.2-5.4) were similar to the KTBA_{max} estimates, except at Alalka where POPAN estimates were higher. A population of 14 warru was estimated for Kalka (95% Confidence Intervals [CI] = 4 – 24), 24 at Alalka (95% CI=7 –36) and 23 at New Well (95% CI=14 – 32).

At all sites, the re-trap rate generally increased over the early years of the trapping regime, indicating that an increasing proportion of the colony had been marked (Tables 5.1-5.3). The capture rate of new animals fluctuated at all three sites, and there was no distinguishable pattern across all six years of trapping. Between 2009 and 2010, however, all three showed increases, from 0.03 to 0.05 new animals per trap night for Kalka, 0.15 to 0.25 for Alalka and 0.09 to 0.17 for New Well. The juvenile and sub-adult capture rates generally increased across all trapping years at New Well and Kalka, but no distinguishable pattern was evident for Alalka (Tables 5.1-5.3). The oldest individual detected was greater than six years of age – a male caught in 2005 at New Well, already as an adult, and retrapped each year to 2010. Across all sites, adult males averaged 4.63 kg (±SD 0.8, range 2.9 - 6 kg), while females averaged 3.52 kg (± SD 0.56, range 2.3 - 5.9 kg).

The sex ratio of captured warru varied between sites, with a higher proportion of males at Kalka (1:0.9 M:F) than at the other sites. However, sex ratios at Kalka did not differ significantly from parity ($P > 0.05$, $\chi^2 = 0.105$, d.f. = 1). At Alalka and New Well, there was a slight skew in favour of females (1:1.32 and 1:1.04 respectively); however, again the ratios did not differ significantly from parity (for Alalka, $P > 0.05$, $\chi^2 = 1.39$, d.f. = 1; for New Well, $P > 0.05$, $\chi^2 = 0.04$, d.f. = 1).

Table 5.1 Summary of warru (*Petrogale lateralis* MacDonnell Ranges race) trapping at the Kalka fieldsite, A̲nangu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Parameter	2005	2008	2009	2010	Total
Trapping parameters					
Total no. trap nights	20	72	78	78	248
Population information					
All animals					
Total no. caught[#]	3	13	9	13	38
Sex ratio	0.67	0.38	0.67	0.38	0.47
% females breeding	50	50	100	100	75 (mean)
New animals					
Number	3	11	5	6	24
Sex ratio	0.67	0.36	0.8	0.17	0.46
No. juveniles	0	1	1	2	4
No. sub-adults	0	2	2	3	7
No. adults	3	8	2	1	13
Population estimates					
Known to be alive animals*	3	13	11	15	NA
POPAN model	2.3	13.2	14.2	16.9	13.7
Capture rates					
Capture rate (new animals/trap night)	0.15	0.15	0.06	0.08	0.15
Juvenile capture rate (no. new juveniles/trap night)	0	0.01	0.01	0.03	0.02
Sub-adult capture rate (no. new sub-adults/trap night)	0	0.03	0.03	0.04	0.03
Retrap rate (previous session retraps/trap night)	0	0.03	0.05	0.09	0.05

[#] Does not include same session retraps or pouch young

*Known to be alive – sum of new animals, previous session retraps and animals that went „missing" in one year but were recaptured in future trapping sessions

Table 5.2 Summary of warru (*Petrogale lateralis* MacDonnell Ranges race) trapping at the Alalka fieldsite, An̲angu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Parameter	2005	2006	2007	2008	2009	2010	Total
Trapping parameters							
Total no. trap nights	20	20	60	54	54	36	244
Population information							
All animals							
Total no. caught[#]	3	5	16	14	18	16	72
Sex ratio	0.67	0.8	0.69	0.5	0.55	0.44	0.57
% females breeding	100	100	89	100	87.5	100	96.1 (mean)
New animals							
Number	3	5	12	7	8	9	44
Sex ratio	0.67	0.8	0.67	0.43	0.5	0.33	0.55
No. juveniles	1	1	2	3	4	1	12
No. sub-adults	0	0	5	1	0	5	11
No. adults	2	4	5	3	4	3	21
Population estimates							
Known to be alive animals*	3	5	16	16	23	16	NA
POPAN model	5.2	10.9	28.2	24.6	30.5	31.0	23.6
Capture rates							
Capture rate (new animals/trap night)	0.15	0.25	0.2	0.13	0.15	0.25	0.18
Sub-adult capture rate (no. new sub-adults/trap night)	0	0	0.08	0.02	0	0.14	0.05
Juvenile capture rate (no. new juveniles/trap night)	0.05	0.05	0.03	0.06	0.07	0.03	0.05
Retrap rate (previous session retraps/trap night)	0	0	0.07	0.13	0.19	0.19	0.11

[#] Does not include same session retraps or pouch young

*Known to be alive - sum of new animals, previous session retraps and animals that went 'missing' in one year but were recaptured in future trapping sessions

Table 5.3 Summary of warru (*Petrogale lateralis* MacDonnell Ranges race) trapping at the New Well fieldsite, An̲angu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Parameter	2005	2006	2007	2008	2009	2010	Total
Trapping parameters							
Total no. trap nights	44	44	229	120	120	80	637
Population information							
All animals							
Total no. caught[#]	12	10	20	16	21	23	102
Sex ratio	0.5	0.5	0.45	0.44	0.57	0.56	0.51
% females breeding	83	100	89	100	100	82	92.3 (mean)
New animals							
Number	12	8	9	5	7	10	51
Sex ratio	0.5	0.62	0.44	0.2	0.71	0.6	0.53
No. juveniles	0	0	1	4	3	4	12
No. sub-adults	0	0	0	0	2	4	6
No. adults	12	8	8	1	2	2	33
Population estimates							
Known to be alive animals*	12	14	20	18	22	24	N/A
POPAN model	12.9	25.4	22.4	21.2	22.3	26.7	22.9
Capture rates							
Capture rate (new animals/trap night)	0.27	0.18	0.04	0.04	0.06	0.13	0.08
Juvenile capture rate (no. new juveniles/trap night)	0	0	0.004	0.033	0.025	0.05	0.019
Sub-adult capture rate (no. new sub-adults/trap night)	0	0	0	0	0.017	0.05	0.009
Retrap rate (previous session retraps/trap night)	0	0.045	0.048	0.092	0.117	0.16	0.082

[#] Does not include same session retraps or pouch young

*Known to be alive - sum of new animals, previous session retraps and animals that went 'missing' in one year but were recaptured in future trapping sessions

5.4.1.2 Survival

Survival of adult warru was relatively high and very similar for each site, with a mean proportional survival over the trapping period of 0.76 at Kalka (Lower Confidence Interval [LCI]) = 0.12, Upper Confidence Interval [UCI] = 0.98), 0.78 at Alalka (LCI = 0.37, UCI = 0.95) and 0.75 at New Well (LCI = 0.58, UCI = 0.87, Fig. 3). The wide confidence intervals are probably the result of low sample sizes. In contrast to the adult survival rates, juvenile survival differed considerably among sites (Fig. 5.2), being highest at Kalka, followed by New Well and lowest at Alalka. However, a small sample size ($N = 5$) at Kalka suggests that the result for this site should be interpreted with caution. At New Well and Alalka (combined), the mean proportional survival rate of juveniles (0.51 ± 0.06) was significantly lower than that of adults (0.77 ± 0.06, $F = 10.1$, d.f. = 1, 20, $P = 0.005$). This was demonstrable both across the study period and on an annual basis (Fig. 5.2). Model selection criteria indicated that there was strong evidence for annual and age-specific variation in survival, and that trap effort influenced recapture probability (Table 5.4). Due to insufficient data, it was not possible to establish the exact nature of the annual (time dependent) survival. For the age-specific variation, there was higher survival for adults than juveniles. Increased trapping effort led to an increase in captures.

Model selection also found substantial evidence for the effect of winter rainfall on juvenile survival (ΔQAICc = 1.23, Table 5.4). This is highlighted in a plot of the model-averaged, predicted estimates of annual juvenile and adult survival (Fig. 5.2). The model incorporating the effect of winter rainfall on annual juvenile survival accounted for greater than 20% of model weights (*w*QAICc = 0.213), and winter rainfall accounted for 1.24% of the deviance in juvenile survival. Taking into account modelled survival and winter rainfall periods, this indicates that a juvenile‟s survival during a trapping period is correlated with the winter rainfall in the year in which it was caught.

Table 5.4 Ranking for models estimating age-specific survival and recapture probability of warru in the Aṉangu Pitjantjatjara Yankunytjatjara Lands, South Australia. Effects of time (**t**), winter rainfall (**winter**) with lags of 1 and 2 years (**winter1**,**winter2**) and age (**age-juvenile/adult**) on the probability of survival (φ) and trapping effort (**trap**) on recapture (*p*) of warru from a combined dataset from two colonies, New Well and Alalka. Models are ranked according to their Akaike weights (*w*QAIC$_c$), the relative change in AIC$_c$ score (ΔQAIC$_c$), and number of parameters (*k*) based on an inflation factor ($\hat{c}$) of 1.3328. % QDE is the % deviance explained.

Model	QAIC$_c$	ΔQAIC$_c$	*w*QAIC$_c$	*k*	% QDE
φ (**age-t/t**) *p*(**trap**)	176.56	0	0.395	8	54.83
φ (**age-winter/t**) *p*(**trap**)	177.79	1.236	0.213	8	56.07
φ (**age-winter2/winter2**) *p*(**trap**)	178.64	2.080	0.140	5	63.58
φ (**age-winter/winter**) *p*(**trap**)	180.21	3.653	0.064	5	65.15
φ (**age-winter2/t**) *p*(**trap**)	180.26	3.703	0.062	8	58.53
φ (**age-winter1/t**) *p*(**trap**)	180.35	3.797	0.059	8	58.63
φ (**age-./.**) *p*(**trap**)	181.18	4.627	0.039	4	68.28
φ (**t**) *p*(**t**)	191.40	14.842	<0.001	10	65.05

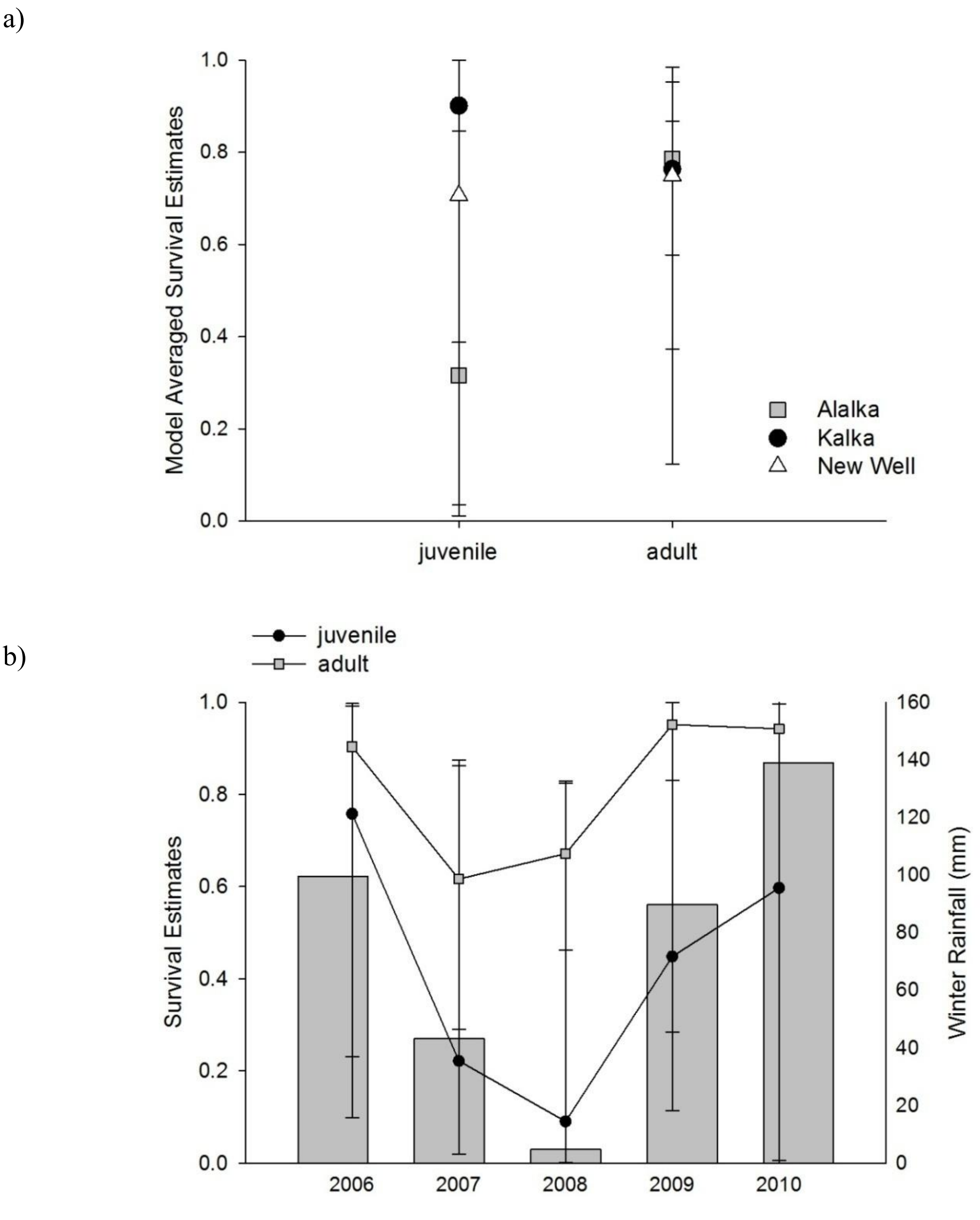


Fig. 5.2 a) Juvenile (pouch young and young-at-foot) and adult (sub-adult and adult) survival estimates for warru averaged across six years of trapping at Alalka, Kalka and New Well in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. b) Relationship between annual juvenile and adult survival estimates and winter (April – September) rainfall between 2006 and 2010 for New Well and Alalka (combined). As an example, survival for 2007 is calculated as survival from October 2007 until August 2008, and rainfall for the period April 2008 – September 2008. Error bars are indicated.

5.4.2 Reproduction

5.4.2.1 Birth rates and schedule

Reproductive rate was generally very high (Tables 5.1-5.3). Across all years, Alalka and New Well had the highest average per cent of adult females with pouch young, 96% and 92% respectively, while Kalka had the lowest, 75%. The lowest annual value (50%) occurred at Kalka in 2005 and 2008; however, as only two and four females were caught at these times respectively, it is not a representative sample of the whole colony"s reproductive output. At New Well/Alalka, there was no statistical relationship between the per cent of females breeding and rainfall (total in the current year, total in previous year or total summer in current year; all *P*>0.05).

Across the three study sites, a total of 89 pouch young and young-at-foot were encountered during trapping (Alalka *n*=29, New Well=47, Kalka=13). Births occurred throughout the year at Alalka and New Well and in all but three months at Kalka (Fig. 5.3). However, across all years, there was a peak in births in autumn-winter, with Kalka recording the highest percentage of total births in March (31%, *n*=4), Alalka in April (24%, *n*=7) and New Well in June (22%, *n*=10). Across all sites, an average of 80% of births occurred between March and July, compared to 10% in the summer months (Dec.-Feb.).

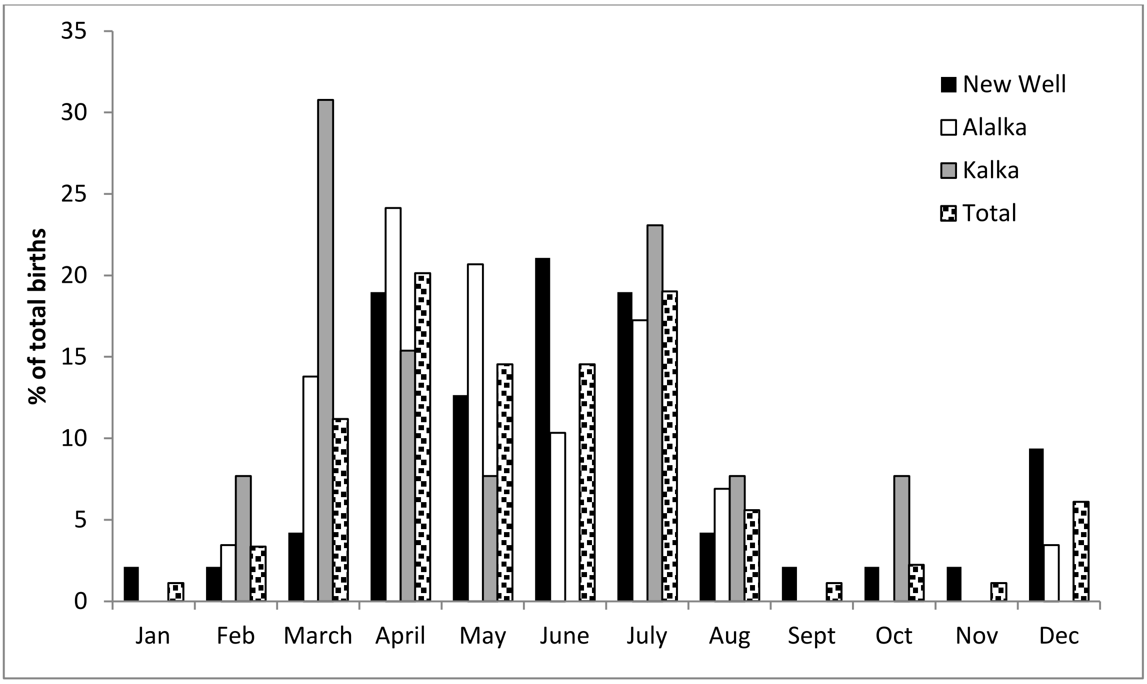


Fig. 5.3 Percentage of total known wild warru births (*N*=89*)* between 2005 and 2010 across months at New Well, Alalka and Kalka in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. Total = % births across all three warru colonies between 2005 and 2010.

5.4.2.2 Age categories, growth curves and development

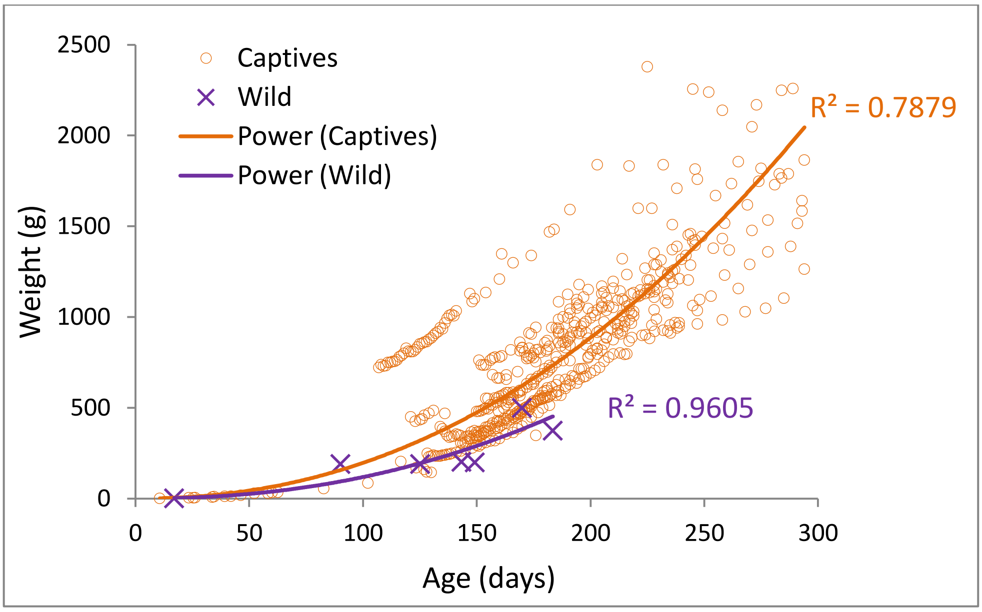
Age categories for warru are presented (Table 5.5). Juveniles were generally caught in the presence of their dams, while sub-adults were independent. Sub-adults were capable of breeding, with multiple sub-adult females found with pouch young in the wild, and a 15 month old male known to have sired in captivity. However, the distinction between sub-adults and adults was made because the former were of a visibly smaller size than adults. The latter is supported by data on the relationship between age and bodyweight of warru (Fig. 5.4). A strong power relationship is visible for both captive ($y = 0.0089x^{2.1721}$) and wild ($y = 0.0045x^{2.2118}$) warru up to 300 days. After 300 days, from which time animals were classified as sub-adults, the relationship plateaus and is best represented by a logarithmic curve ($y = 1.6622 \ln(x) - 7.7414$).

Compared to wild warru, pouch young on *P. xanthopus* foster dams showed accelerated development in both bodyweight and pes length (Fig. 5.5). However, due to small sample size, the age-bodyweight relationship for wild warru should be interpreted with caution.

Table 5.5 Categories used for ageing warru (*Petrogale lateralis* MacDonnell Ranges race) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia.

Age category	Headlength (mm)	Body weight	Days (months)	Description
Pouch young	0 - 70	0 - 620 g	0 - 186 (0-6)	Until permanent pouch exit
Juvenile	70.1 - 85	621 g - ~ 2 kg	187 – 295 (6-9)	Young at foot; not weaned, not fully grown and not sexually mature.
Sub-adult	85.1 – 90	~2 kg - 3.0 kg	296 – 460 (9-15)	Weaned but not fully grown. Independent and may be breeding.
Adult	Males ≥ 97.1; females ≥ 90	≥ ~ 3.0 kg	≥ 461 days (≥ 15)	Fully grown and sexually mature.

a)



b)

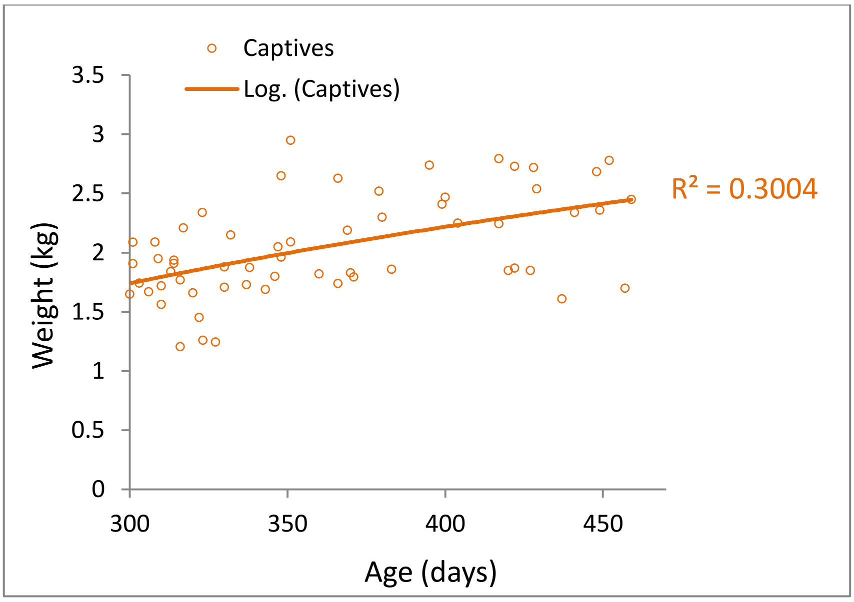


Fig. 5.4 Changes in bodyweight with age for a) pouch young and juveniles and b) sub-adults of *Petrogale lateralis* (MacDonnell Ranges race). Growth curves are separated for young reared by their natural mothers („wild"), *c.f.* those cross-fostered onto *P. xanthopus* dams („captives"). Trend lines (power and logarithmic [log.]) with R^2 are indicated.

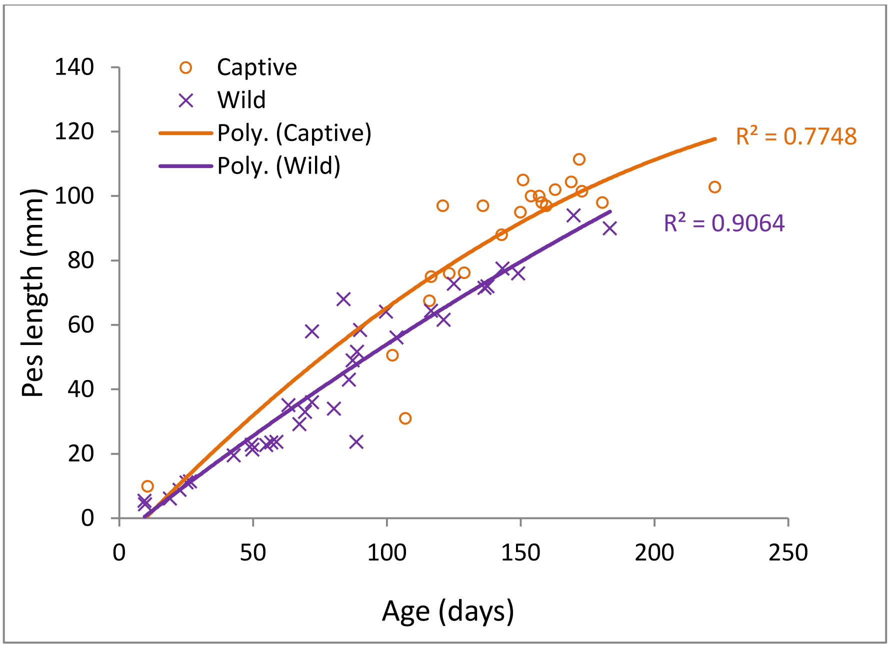


Fig. 5.5 Changes in pes length with age for pouch young and juvenile *Petrogale lateralis* (MacDonnell Ranges race). Growth curves are separated for pouch young and juveniles reared by their natural mothers („wild"), *c.f.* those cross-fostered onto *P. xanthopus* („captives"). Trend lines (polynomial [poly.]) with R^2 are indicated.

Development parameters for captive and wild pouch young (combined) are summarised (Fig. 5.6). At birth, pouch young had closed eyes and ears that were flattened and fused to the head. The body was initially pink, with thin, almost translucent skin; however, at around 35 days, animals attained a tinted snout. Colouration then progressed such that the nose became grey at around 55 days, at which point pouch young also had claws. At around 70 days, animals" noses turned black, there was pigmentation around the muzzle and the soles of the feet were grey. From 65-90 days, a pouch young"s body became pigmented; this developed into fine, and then thicker fur. Lower incisors were present before upper, with top incisors erupting at around 125 days. Using data from warru cross-fostered onto *P. xanthopus* at Monarto Zoo, pouch young were observed with their head out of pouch at an average of 131 days (±SD 17.3, range 81-146 days). Permanent pouch emergence occurred at an average of 176 days (±13.6, range 155-194). No data were available as to how long young-at-foot remain with their mothers.

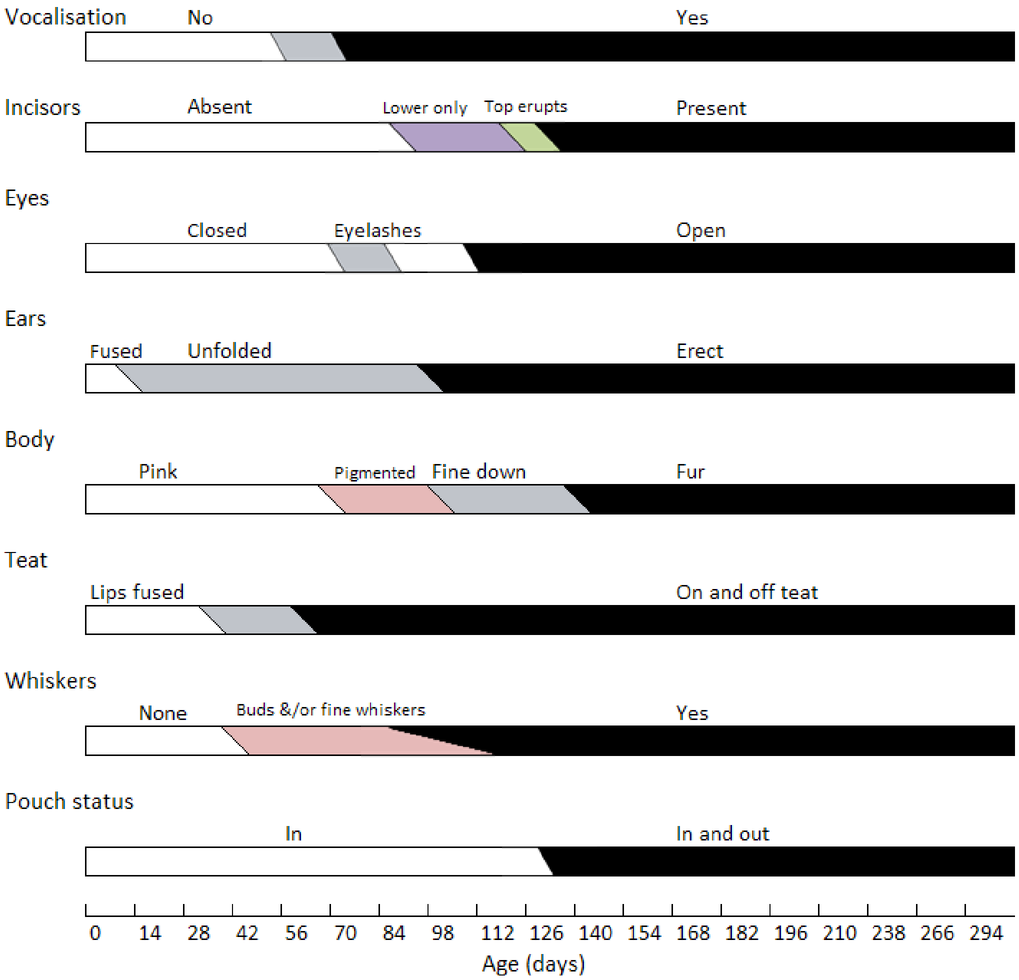


Fig. 5.6 Developmental timeline for *Petrogale lateralis* (MacDonnell Ranges race) pouch young (*N*=41), measured in days.

5.5 Discussion

5.5.1 Population parameters and survival probability

Modelling indicated that only 23, 24 and 14 animals remain at New Well, Alalka and Kalka respectively. It is possible that these may be slight underestimates because trapping may not necessarily pick up dispersing animals, was generally only undertaken annually and may only represent the trappable, rather than the true, population (Sharp and McCallum 2010). Such small colony sizes are not in themselves unusual for *Petrogale* spp., which can occur in colonies that range in size from a single pair to several hundred animals (Tyndale-Biscoe 2005). However, in this case, the result is concerning because the studied populations represent the largest known colonies of warru in SA (Read and Ward 2011b) and concurs with the conclusion that, without ongoing management of threats, warru in SA are at risk of extinction. This conclusion has been reached based on warru spotlighting results and biannual scat accumulation counts (Read 2010), aerial survey results (Ward *et al.* 2011) and historical evidence (Finlayson 1961).

The present study has, however, also provided some grounds for optimism for population recovery. Prior to undertaking trapping and aerial surveys, it was estimated that the total known population of warru in SA was between 50 and 70 animals (Read and Ward 2011b). With the recent discovery, via aerial survey, of fresh scats at 83 locations in the Musgrave Ranges (Ward *et al.* 2011), combined with the estimate of 46 animals at New Well and Alalka, it is estimated that the Musgrave Ranges warru metapopulation may actually contain ~100-150 animals. Furthermore, surveys in the Tomkinson Ranges found evidence of fresh warru scats at an additional 27 locations (Ward *et al.* 2011). Thus, together with the estimate of 14 warru at Kalka, the total Tomkinson metapopulation may contain up to 50 animals. Overall, this provides a population estimate of 150-200 animals in SA.

Additional encouragement for the potential of recovery of warru comes from the demographic parameters calculated in the present study. In particular, there was no evidence of a significant sex bias at any of the three studied colonies. This is consistent with results for *P. penicillata* (Piggott *et al.* 2006b) and *P. xanthopus* (Sharp *et al.* 2006) colonies in New South Wales, although obviously these may vary through time with changing environmental conditions. The sex ratios at Alalka (1:1.32) and New Well (1:1.04) were also similar to those observed for mainland *P. lateralis* in Western Australia (WA, 1:1.5, Eldridge *et al.* 1999). Sex bias may result in lower fecundity and, in contrast to animals in both the APY Lands and mainland WA, highly inbred *P. lateralis* on Barrow Island, WA have both a skewed sex ratio of 1:2.5 and low fecundity (52% of females with pouch young) (Eldridge *et al.* 1999).

The current study‟s estimates of adult survival for warru are also encouraging. POPAN modelling indicated that at all trapping sites, mean adult warru survival was high, averaging 76%. This is analogous to that observed for populations of *P. xanthopus* in both Queensland (76%, Sharp 2002) and SA (63 - 71%, Robinson *et al.* 1994), both during fluctuating rainfall conditions, but lower than that demonstrated in New South Wales (97%, Sharp *et al.* 2006). This high survivorship indicates that adult warru are less vulnerable than juveniles to what appear to be the primary drivers of *Petrogale* population dynamics, namely predation (1988; Kendrick *et al.* 2010; Kinnear *et al.* 2010) and rainfall (Lethbridge and Alexander 2008; Sharp and McCallum 2010). Supporting this, warru survival monitoring through radiotelemetry and predator (fox, dog, cat) abundance monitoring have respectively demonstrated high adult warru survivorship and very low abundances of foxes, albeit moderate to high numbers of cats (Read and Ward 2011a).

In contrast, juvenile survival rates at New Well and Alalka (excluding Kalka due to low sample size) were low (51%), which is likely to be suppressing warru population growth in these colonies. This low survival may be due to a combination of juveniles being more susceptible to predation and, as indicated by the POPAN modelling, more affected by fluctuations in rainfall. Empirical evidence for the impact of predation on juveniles was unavailable in the current study; however, previous studies have hypothesised on its significance (Higginbottom 1991; Sharp *et al.* 2006). For example, Kinnear *et al.* (1988) considered the effects of fox predation and/or drought on juveniles to be substantial contributors to the declines of *P. lateralis* seen in WA. Although both Alalka (aerial) and New Well (aerial and ground) were fox baited for the duration of the study, baiting effort was not equivalent between sites, and furthermore, did not target cats. Cats have been speculated to focus predation on juvenile *Petrogale* (Spencer 1991) and may be capable of suppressing rock-wallaby recovery even when foxes and/or dingos are controlled (Kendrick *et al.* 2010). Indeed, there is growing focus on the mesopredator release hypothesis (Crooks and Soule 1999; Hayward and Somers 2009; Richie and Johnson 2009), which postulates that when populations of apex predators (in the current study, foxes and dingos) are reduced (such as through the current baiting program), previously suppressed mesopredator populations (cats) substantially increase. Supporting this, predator monitoring using track transects around New Well has demonstrated low fox and dog abundance, but moderate to high numbers of cats (Read and Ward 2011b).

POPAN modelling indicated that rainfall was also a driver of warru survival. In particular, juvenile survival was positively associated with winter rainfall of the same year in which an animal was caught. In the APY Lands, winter generally corresponds to the driest period of the year (Robinson *et al.* 2003). As such, rainfall during this period could both improve the forage quantity and/or quality available to warru, and potentially provide access to water through accumulations on rock. This, in turn, may improve the success of a dam"s lactation period and increase the survival chances for the warru pouch young and young-at-foot. Similarly, Delaney (1997a) found that rainfall influenced the survival of *P. assimilis* pouch young and hypothesised that adequate rainfall would lead to an increase in recruitment and net increase in population size. Should predation by introduced species be adequately managed, a similar pattern may also manifest for warru.

5.5.2 Reproduction

In the current study, warru bred throughout the year (a smaller sample size [max no. animals caught=13] was likely to be responsible for the absence of births seen at Kalka in November-January). Continuous breeding is often seen in wild populations living in environments with unpredictable climatic conditions, including in the arid zone, where rainfall is irregular (Sharman *et al.* 1966; Lee and Cockburn 1985). However, the pattern of births seen in the current study also reflected the potential impact of winter scarcity, with a reproductive peak in autumn-winter at all three colonies. Such timing enables pouch young to spend the most resource-deficient time, namely winter, in pouch (up to 6 months), and emerge during summer, when resources are likely to be more abundant. Similarly, Willers (2011) found that *P. lateralis lateralis* in the WA Wheatbelt bred throughout the year. However, highlighting the capacity of rock-wallabies to adapt to local conditions, Willers (2011) found that animals had two reproductive peaks – in autumn and late winter/spring.

In the current study, rainfall (in current year, previous year and current year‟s summer) did not affect warru reproductive rate, with the latter being high across the studied sites, even during what constituted a period of primarily below-average rainfall. During the study, an average of 92% and 96% of females carried pouch young at New Well and Alalka respectively. The lower rate at Kalka (75%) may have been an artefact of small sample size, particularly given that all adult and sub-adult females caught in 2009 and 2010 were breeding. Given the well-established positive effect of rainfall on arid-zone fauna (Masters 1993; Dickman *et al.* 1999a; 1999b), the lack of a relationship between breeding and rainfall was surprising. It also contrasts data from *P. lateralis* in the WA Wheatbelt, where Willers (2011) found a strong positive relationship between total winter rainfall in the previous year and females‟ autumn reproductive rates (R^2=0.87). However, the current absence of a relationship is likely explained by the fact that, given warru reproductive rates were already extremely high, there was little room for an increase even when more rainfall occurred. Such high and stable reproductive rates support the notion that it is juvenile survival, rather than female breeding, which is limiting population growth in the APY Lands. Given the reproductive rates observed in the current study are higher than those of other *Petrogale* populations which have demonstrated recovery, they also suggest that warru recovery is feasible. For example, Kinnear *et al.* (1988) found that an average of 49% of female *P. lateralis* had pouch young at two fox-baited colonies in the WA Wheatbelt, while Sharp *et al.* (2006) reported a rate of 76% for *P. xanthopus* in New South Wales.

The developmental timeline provided concurs with details on the development of eyes, ears and body presented by Jones *et al.* (2004) for warru pouch young from the NT. However, the current result should be interpreted with some caution because, due to there not being enough data available to have separate graphs, the timeline incorporates information from both captive and wild warru. However, warru cross-fostered onto *P. xanthopus* have accelerated development when compared to those on their natural mothers. The effect can be seen in, for example, animals in the current study undertaking permanent pouch emergence at an average of 176 days. In contrast, Jones (2001) noted that pouch young reared by their natural mothers emerged between 186 and 200 days. This is also supported by the current study‟s bodyweight and pes growth curve data, which show that cross-fostered warru pouch young developed faster than those in the wild. This acceleration is probably due to captive animals being under less environmental stress (e.g. *ad libitum* food and water) and is therefore also highly likely to manifest in earlier development of captive animals‟ eyes, ears and bodies.

5.5.3 Conservation implications

The survival data indicate that warru recovery is likely to be dependent on improving juvenile survival rates. This is because even minor positive changes in juvenile survival can translate into substantial impacts on population size (Gaillard *et al.* 1998). Given the potentially substantial impact of cats on juveniles, even in the presence of fox and dog baiting (Kendrick *et al.* 2010), establishing an effective cat control program is recommended, particularly during summer when there is a peak in juveniles. Alternatively, it may be more cost-effective and practical in the long-term to adjust the fox and dog control program such that cats are kept at lower densities. Provision of supplementary water may improve juvenile survival rates, although care must be taken that such sites do not serve as a focal point for predators. It is also recommended that studies similar to the current one be initiated for *P. lateralis* (MacDonnell Ranges race) in the NT and WA. This would help to identify sites of population decline, the causes thereof and clarify the race‟s national status.

CHAPTER 6 – Blood parameters

To the student of mammals the plant is always of interest as it determines quite definitely the distribution of some of the most interesting herbivorous mammals of the Centre.

Hedley Finlayson (1936)

Photo: Adelaide Zoo veterinarian Dr David McLelland (right) taking a blood sample and Laura Ruykys (left) measuring pes length from a sub-adult warru in the APY Lands. N. Staniford.

Chapter 6 - Haematology and biochemistry parameters of warru (*Petrogale lateralis* MacDonnell Ranges race) in captivity and the wild.

Exegesis

Having considered habitat availability, animal mobility, genetic diversity and population dynamics as potential explanatory factors for the decline of warru populations, this chapter examines disease and food and water availability. This is undertaken indirectly through the use of blood chemistry parameters.

Three types of blood analyses were undertaken – general haematology, general biochemistry and protein electrophoresis. I completed the laboratory work for the general haematology analysis (excluding differential leukocyte counts), while volunteers at Adelaide Zoo conducted the investigations on general biochemistry. Gribbles Pathology Pty Ltd completed the protein electrophoresis analyses. I was responsible for all data analyses, interpretation and writing.

The data contained in this chapter was submitted to *Australian Veterinary Journal* and, at thesis submission, had been resubmitted following revisions. As such, the chapter (excluding references) is written according to the journal‟s requirements. An outline of each author‟s contribution and their permission for inclusion of the work in this thesis is provided.

STATEMENT OF AUTHORSHIP

Haematology and biochemistry parameters of warru (*Petrogale lateralis* MacDonnell Ranges race) in captivity and the wild. *Australian Veterinary Journal.*

Ruykys, L. (candidate)

Statement of contribution: Oversaw the design and development of work and collected samples from the field. Completed statistical analysis of data and interpretation of results. Wrote manuscript and acted as corresponding author.

I hereby certify that the statement of contribution is accurate.

*Signed …. ……………………………………….Date…*25 May 2011

Rich, B.

Statement of contribution: Supervised development of work, participated in laboratory analyses of samples, assisted with interpretation of results and evaluated manuscript.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

*Signed ……… ……………………Date…*3/6/2011

McCarthy, P.

Statement of contribution: Participated in laboratory analyses of samples and assisted with interpretation of results.

I hereby certify that the statement of contribution is accurate and that permission is given for the inclusion of the paper in the thesis.

*Signed …. …………………………….Date…*3/6/11*……*

6.1 Abstract

Objective Using haematology, biochemistry and protein electrophoresis analyses, establish reference values for, and describe the health status of, wild and captive colonies of critically endangered warru (black-footed rock-wallaby, *Petrogale lateralis* MacDonnell Ranges race).

Methods Blood samples were taken from warru in three wild colonies (Alalka, Kalka, New Well) in the Anangu Pitjantjatjara Yankunytjatjara Lands in the north-west of South Australia (SA), and from captive animals at Monarto Zoo, SA. General haematology, serum biochemistry and protein electrophoresis analyses were conducted on all samples and results used to establish reference ranges. For the parameters that are indicative of a population"s health, comparisons amongst the four study sites were completed using ANOVAs.

Results General haematology results suggested that warru were not experiencing chronic anaemia, while protein electrophoresis values indicated that colonies were not suffering from population-wide disease. However, the lower superoxide dismutase, retinol, total carotenoids and ascorbic acid values of New Well warru suggested that animals here had a lower plane of nutrition than did those at Kalka and Alalka. Higher average urea concentrations in New Well and Alalka warru could reflect the absence of reliable free water at these sites.

Conclusion The results have implications for the management of *in-situ* colonies, including potentially using supplementary feeding to improve nutrition, and suggest that animals were not suffering from disease. The study presents the first detailed blood reference values for *P. lateralis* and potentially, a methodology for other threatened species recovery programs to follow in order to establish the health of their populations.

Keywords Biochemistry; blood; clinical pathology; haematology; *Petrogale lateralis*; population health.

6.2 Introduction

Understanding the factors that contribute to the dynamics of animal populations is a core concern of conservation biology (Caughley and Gunn 1996). Two such factors, disease and starvation, have been identified as particularly important causes of declines in animal populations (Young 1994; Cunningham 1996). For example, during a one-year drought, Caughley *et al.* (1985) documented a decline in kangaroo (*Macropus* spp.) abundance of approximately 40% across over one million square kilometres of inland eastern Australia. If the populations involved in such declines are those of a threatened species, this can be of conservation concern. For example, high mortality has been documented in Tasmanian devils (*Sarcophilus harisii*) as a result of devil facial tumour disease, leading to a population decline of 53% and the listing of the species as endangered by the International Union for the Conservation of Nature (McAloose 2009).

Clearly then, monitoring both the nutritional and disease status of animals is required. This can be conducted using a proxy – their blood parameters, which incorporate analyses of general haematology, general biochemistry and protein electrophoresis. General haematology results can elucidate animals‟ disease status, while general biochemistry analyses provide information on changes in organ function and thus animals‟ nutritional status (Vogelnest and Woods 2008). Protein electrophoresis results can give insight into chronic infections and immune-mediated diseases (Wilkins 1979). Individual parameters within the three analyses can establish information at two levels – that of an individual animal and/or its population (Hanks 1981; Barnes *et al.* 2008). For example, elevated levels of the biochemical parameter creatine kinase can be used as an indication of capture myopathy in an individual animal (Schultz *et al.* 2011) while the levels of retinol, a-tocopherol, ascorbic acid and total carotenoids found in individuals are related to animals‟ diets and can therefore be used to establish the nutritional health of a population (Rich *et al.* 2007). To facilitate monitoring at both levels, it is necessary to establish reference values and understand the variation of such under different conditions. This allows an individual‟s observed value to be compared to an „average‟ for its relevant group (e.g. species, sex, method of restraint) (Solberg 1987) and for anomalies to be recognised and managed. To date, however, there are few baseline data available on the haematology of free-living Australian fauna (Barnes *et al.* 2008). For example, of the 16 species of rock-wallabies (genus *Petrogale*), detailed studies have been limited to brush-tailed (*P. penicillata*, Close *et al.* 1988; Barnes *et al.* 2008) and allied rock-wallabies (*P. assimilis*, Spencer and Speare 1992), with limited data available for *P. inornata, P. persephone* and *P. xanthopus* (Vogelnest and Woods 2008).

One *Petrogale* for which the lack of information is hampering recovery efforts is *P. lateralis* (MacDonnell Ranges race) in South Australia (SA). Known as „warru‟ by Anangu Indigenous Owners, animals have undergone substantial declines in range and abundance and are now being intensively managed as one of the state‟s most endangered mammals (Read and Ward 2011b). Warru are restricted to two metapopulations encompassing three primary colonies in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara (APY) Lands in the state‟s far north-west (Ward *et al.* 2011). A substantial recovery program has been implemented, including baiting of foxes (*Vulpes vulpes*) and dogs/dingos (*Canis lupus dingo*) around extant colonies and the establishment of a captive population (Read and Ward 2011a). However, *in-situ* colonies have been slow to respond to the former and managers needed to know if nutritional deficiencies and/or disease were contributing to this (Read and Ward 2011b). This question is particularly pertinent given that in recent history, the abundance of euros (*Macropus robustus*), which have diets that partially overlap with those of warru (Capararo 1994; Geelen 1999), has increased (Read and Ward 2011b). Specifically, grasses constitute an important part of the diet of both species, although warru also consume various species of browse and forb (Robinson *et al.* 2003). The current study used general haematology, biochemistry and protein electrophoresis parameters to answer the following questions about warru;

1. What are their blood reference values, and
2. What is the nutritional and disease status of wild and captive colonies?

6.3 Materials and Methods

6.3.1 Study sites

The study was conducted in SA APY Lands, which experience a very hot, dry, desert climate with short, cool to cold winters. Geologically, the area is extremely complex, with the northern third of the APY Lands containing extensive range systems, including the Musgrave, Tomkinson and Mann Ranges. These generally support *Triodia* hummock grasslands supplemented with tussock grasses and herbs, and an overstorey of tree and shrub species of considerable diversity (Robinson *et al.* 2003).

Fieldwork was conducted at three *in-situ* warru colonies; „New Well‟ and „Alalka‟ in the eastern Musgrave Ranges, 15-20 km north and north-west of the Indigenous community of Pukatja (26°16'43.08"S, 132°8'2.13"E), and „Kalka‟ in the Tomkinson Ranges, near the community of Kalka (26°7'5.18"S, 129°9'2.91"E). These are the largest-known warru colonies in SA (Read and Ward 2011b). Alalka is 194 ha and contiguous with a large number of surrounding hills. Its landform is that of rugged strike ranges on metamorphics. In contrast, New Well is a granite inselberg of 590 ha that is located where the eastern Musgrave Ranges divide into isolated outcrops. The two sites are 11 km apart and the vegetation of both hills is that of emergent low, open woodland over *Triodia irritans* grasslands. Kalka is approximately 2,190 ha and lies adjacent to the SA, Western Australia and Northern Territory borders. The hill rises 350 m above ground and its vegetation is dominated by *Triodia* and a sparse overstorey of *Eucalyptus gamophylla* and *Callitris glaucophylla* (Robinson *et al.* 2003). Kalka is the only one of the three field sites which contains a known water supply, in the form of a perennial spring at the base of the site. Minor camera-surveillance has indicated this is occasionally visited by warru (unpublished data, APY Land Management). However, no empirical data are available on the frequency of such use. It is also difficult to quantify food availability at each of the study sites, both because vegetative cover is highly dependent on irregular rainfall events and because only a preliminary investigation of the diet of warru in this region has been undertaken (Geelen 1999). Competition for food at the sites most likely comes from euros, for which abundance data are unavailable, and potentially rabbits (*Oryctolagus cuniculus*), although the latter tend not to penetrate into the hills themselves, but to occur on the plains. Predators include low numbers of foxes and dogs/dingos and variable but generally higher numbers of cats (*Felis catus*) (Read and Ward 2011a).

A fourth study group was that of the captive warru, which were sourced as pouch young from all three APY Lands colonies during trapping in 2007-2009. At this time, animals were either cross-fostered to surrogate yellow-footed rock-wallaby (*P. xanthopus*) dams, or hand-reared. A total of 22 warru (New Well *n* =10, Alalka *n* = 7, Kalka *n* = 5) survived to weaning and have since been held at Monarto Zoo, located approximately 60 km from Adelaide on the eastern side of the Mt Lofty Ranges. The site has a Mediterranean climate with hot, dry summers and cool, wet winters; the annual average rainfall is 346 mm (Bureau of Meteorology 2010). Animals were fed a diet of lucerne hay and kangaroo cubes or pellets (Barastoc, Ridley AgriProducts Australia; Furney‟s Stock Feeds, Australia) and had water available *ad libitum.*

6.3.2 Animal trapping

Warru at all three wild colonies were trapped in late July 2009, which coincides with the coolest and driest weather conditions (Robinson *et al.* 2003). Animals were caught in cage traps that supported a bag of thick, shade cloth-like material and which were located in shelter sites (caves, crevices) with evidence of recent warru activity. For two to three days before trapping commenced, traps were wired open and „free-fed‟ by placing bait (chopped apples and a peanut butter/oat mix) inside and outside the traps. Following „free-feeding‟, traps were set for four to six nights and checked at dawn. Captured animals were removed from traps, placed in hessian sacks and, in an attempt to reduce the incidence of capture myopathy, given an IM injection of Vitamin E at 0.02 mL kg^{-1} (Troy Laboratories Pty. Ltd., Smithfield, New South Wales) (Vogelnest and Woods 2008). Processing involved implanting microchips and individually coloured eartags, attaining morphometric data, checking animals‟ reproductive status and taking blood samples. After processing, trapped animals were released at site of capture.

Captive warru were caught and blood samples taken in early August 2009. Capture involved cornering animals in their enclosure and grasping them by the base of their tails. Animals were then placed into a hessian sack for blood sampling. No Vitamin E was administered.

6.3.3 Blood sampling

Following capture, warru at Kalka, New Well and in captivity were all anaesthetised using 2-3% isoflurane (Attane, Pharmtech, Australia) in oxygen. Alalka warru were not anaesthetised as the steepness of the site limited logistics. Each animal was only sampled once, with blood being taken from the jugular or lateral caudal (tail) vein. A few drops were immediately used to make two smears on microscope slides, which were then air-dried. The remainder of the blood was placed in a 1 mL EDTA tube and, using ice packs in insulated cooler-bags, kept cool for a maximum of 4 hours until processing could be undertaken at the field base. Blood from captive animals was processed immediately. Processing involved taking off 250 microlitres (µL) of whole blood, placing it into an eppendorf for general haematology and refrigerating the sample. The remaining EDTA solution was centrifuged and some of the resultant red cells pipetted into an eppendorf for analyses of superoxide dismutases (SOD; 50 µL). The plasma was separated into blood tubes for protein electrophoresis (100 µL) and biochemistry (500 µL), and eppendorfs for thiobarbatric acid-reducing substances (TBAR; 50 µL) and ascorbic acid (AA; 50 µL) analyses. Each sample was stored at -50°C until laboratory analyses were performed.

Haematological analyses were completed using an automated veterinary Coulter Counter T660 analyser (Beckman Coulter Inc., Florida, USA) for the following variables: haemoglobin (Hb), red blood cell count (RBC), haematocrit (Hct), mean corpuscular volume (MCV), mean corpuscular haemoglobin (MCH), mean corpuscular haemoglobin concentration (MCHC), platelets and white blood cell count (WBC). Blood slides were fixed in 70% ethanol, stained with a Diff-Quik stain set and examined under light microscopy

(Olympus BH2) at 400x magnification for differential leukocyte counts (*n*=100 cells). Cells were counted using a battlement counting system.

Biochemical analyses were performed using Roche Diagnostic kits and a Cobas Bio analyser (Roche Diagnostics, Switzerland) for the following parameters; glucose, urate, creatinine, urea, alanine aminotransferase (ALT), aspartate aminotransferase (AST), creatine kinase and cholinesterase. Retinol and alpha-tocopherol (a-toc) were both analysed using the method of Catignani and Bieri (1983) and modified as described in Schultz *et al.* (2011), total carotenoids using the method of Khachik *et al.* (1992) and again modified as per Schultz *et al*. (2011), AA using Omaye *et al.*‟s (1979) procedure and the ferric reducing ability of plasma (FRAP) utilising Benzie and Strain‟s (1996) protocol. SOD analyses were conducted as per the methods of Misra and Fridovich (1972) and TBAR using those of Esterbauer and Cheeseman (1990). Protein electrophoresis samples were shipped to a commercial laboratory (Gribbles Veterinary Pathology) for analysis.

6.3.4 Data analysis

Data were used in two ways. Firstly, parameters were compared amongst all four study sites (where possible; if data for captive animals were unavailable, then comparisons were made amongst wild colonies only). Comparisons were conducted for the parameters that are indicative of the health of a population, as opposed to those that only relate to an individual animal‟s health. For example, a reference value (see later) for glucose is provided. However, because glucose values are only relevant at the level of an individual animal (where an increase is linked to capture stress, Wesson *et al.* 1979), inter-site differences are not presented.

To conduct these inter-site comparisons, the program PASW (PASW Statistics Version 17.0.2, March 2009) was first used to assess data for normality and, using Levene‟s test of equality of error variances, homoscedasticity. If data were normal and homoscedastic, comparisons were made using a one-way ANOVA and post-hoc Tukey HSD tests. If data were abnormally distributed and/or heteroscedastic and transformation did not rectify the situation, the program „R‟ (R Development Core Team 2009) was used to complete a non-parametric Kruskal-Wallis one-way ANOVA, with pairwise post-hoc comparisons conducted using the Wilcoxon rank sum test and the *P* value adjusted using the Bonferroni correction. Assessing differences between animals of different sexes, ages and sampling techniques was beyond the context of the study; however, it is acknowledged that these are likely to have significant effects on the results. For example, depressed values for a number of parameters have been recorded in anaesthetised compared to manually restrained animals (Wesson *et al.* 1979; Kuttner and Wiesner 1987) and differences between the sexes have been established for at least two species of *Petrogale* (Spencer and Speare 1992; Barnes *et al.* 2008).

The second use of data involved generating reference values (mean, s.d. and the central 0.95 fraction) for every haematology, biochemistry and protein electrophoresis parameter using the technique recommended by Solberg (1987). For variables that differed amongst sites, results are presented separately; otherwise, combined data are provided.

6.4 Results

6.4.1 Inter-site differences

For general haematology, comparisons of inter-site differences (Table 6.1) were undertaken for all parameters except eosinophils and basophils, which both had too low a sample size. Captive animals had significantly higher RBC counts than did New Well warru ($F_{3,54} = 3.8$, $P = 0.014$), but lower MCH ($F_{3,54} = 7.18$, $P < 0.001$) and MCV values (Kruskal-Wallis H=18.61 χ^2 approximation, d.f.=3, P<0.001) than Alalka and New Well animals. Alalka animals had the lowest monocyte values of all the wild sites (H=7.88 χ^2, d.f.=2, P=0.02).

For general biochemistry (Table 6.2), comparisons of inter-site differences were relevant for all parameters except glucose, creatinine, ALT, AST, creatine kinase and TBAR. There were significant differences amongst sites for ascorbic acid ($F_{3,59} = 4.47$, $P < 0.07$), with captive warru presenting with the lowest average value. There were also significant differences amongst sites in SOD values (H=39.2 χ^2 approximation, d.f.=3, P<0.001), with average values substantially higher in captivity than at each wild site, as well as at Alalka compared to New Well and Kalka. New Well warru had lower values of retinol (H=19.2 χ^2 approximation, d.f.=2, P<0.001), total carotenoids ($F_{2,46} = 74.5$, $P < 0.001$) and alpha-tocopherol ($F_{2,36} = 11.0$, $P < 0.0001$) than those at Kalka and Alalka. Kalka animals had lower values of urea (H=12.27 χ^2 approximation, d.f.=2, P<0.001) and FRAP (H=8.15 χ^2, d.f.=2, P=0.003) than New Well and Alalka warru, as well as lower values of ChE (H=7.44, d.f.=2, P=0.02) than New Well warru.

For protein electrophoresis (Table 6.3), inter-site differences were assessed for all parameters. Kalka animals had lower values of total protein (H=87.2 χ^2, d.f.=2, P<0.001), albumin ($F_{3,\,54} = 15.58$, $P < 0.001$) and total globulins (H=19.5 χ^2, d.f.=3, P<0.001) than the other sites. Captive warru had a higher average A/G ratio ($F_{3,\,54} = 4.8$, $P < 0.005$) than both Alalka and New Well animals.

6.4.2 Reference values

Reference values for general haematology (Table 6.4), biochemistry (Table 6.5) and protein electrophoresis (Table 6.6) are presented. It should be noted that Solberg (1987) suggests that at least 40 values are required for the reliable determination of reference intervals. In many cases in the current study, small population sizes precluded this minimum from being reached. The parameters for which this is applicable generally had large variation in reference values. As such, the latter should be seen as being of a preliminary nature only.

Table 6.1 Means, statistical significance and post-hoc comparisons of differences in haematology properties of warru *(Petrogale lateralis*) from four sites – in captivity and at three wild colonies; Alalka, Kalka and New Well (NW) in the An̲angu Pitjantjatjara Yankunytjatjara Lands, South Australia. *comparison made using one-way ANOVA and post-hoc Tukey HSD test; #comparison made using Kruskal-Wallis one-way ANOVA and post-hoc Wilcoxon rank sum test. RBC, red blood cell count; MCV, mean corpuscular volume; MCH, mean corpuscular haemoglobin; MCHC, mean cell haemoglobin concentration; WBC, white blood cell count.

Variable	Captives		Alalka		Kalka		New Well		Statistical comparisons						
	n	Mean	*n*	Mean	*n*	Mean	*n*	Mean	Overall	Captives vs Alalka	Captives vs Kalka	Captives vs NW	Alalka vs Kalka	Alalka vs NW	Kalka vs NW
RBC (x10^{12}/L)*	16	6.7	13	6	8	6.4	21	5.9	0.01	NS	NS	0.014	NS	NS	NS
Haemoglobin (g/L)*	16	15.7	12	16	8	15.4	21	14.8	NS	-	-	-	-	-	-
Haematocrit (L/L)*	16	49.5	13	47.7	8	49.3	21	46.3	NS	-	-	-	-	-	-
MCV (fL)#	16	72.6	13	79.2	8	77	21	78.1	<0.001	<0.001	NS	0.001	NS	NS	NS
MCH (pg)*	16	23.5	13	25.8	8	24	21	25	<0.001	<0.001	NS	0.01	NS	NS	NS
MCHC (g/L)#	16	32.1	13	32.6	8	31.2	21	32.1	NS	-	-	-	-	-	-
Platelets (x10^{9}/L)*	16	229.8	13	106.2	8	189.9	21	118.2	<0.001	<0.001	NS	0.002	0.025	NS	NS
WBC (x10^{9}/L)#	16	4.7	13	8.9	8	4.5	21	6.2	<0.001	<0.005	NS	0.03	0.01	NS	NS
Neutrophils (x10^{9}/L)*	0	NA	13	59.5	8	63.7	20	61.9	NS	NA	NA	NA	-	-	-
Lymphocytes (x10^{9}/L)#	0	NA	13	36.6	8	33.6	20	33	NS	NA	NA	NA	-	-	-
Monocytes (x10^{9}/L)#	0	NA	13	2.6	8	4.4	19	4.2	0.02	NA	NA	NA	0.01	NS	NS

Table 6.2 Means, statistical significance and post-hoc comparisons of differences in biochemical properties of warru *(Petrogale lateralis*) from four sites – in captivity and at three wild colonies; Alalka, Kalka and New Well (NW) in the An̲angu Pitjantjatjara Yankunytjatjara Lands, South Australia. *comparison made using one-way ANOVA and post-hoc Tukey HSD test; #comparison made using Kruskal-Wallis one-way ANOVA and post-hoc Wilcoxon rank sum test. a-tocopherol, alpha-tocopherol; TEAC, trolox-equivalent antioxidant capacity; FRAP, ferric-reducing ability of plasma; SOD, superoxide dismutase; Carot, total carotenoids.

Variable	Captives		Alalka		Kalka		New Well		Statistical comparisons						
									Overall	Captives vs Alalka	Captives vs Kalka	Captives vs NW	Alalka vs Kalka	Alalka vs NW	Kalka vs NW
	n	Mean	*n*	Mean	*n*	Mean	*n*	Mean							
Ascorbic acid (µM/L)*	16	105.6	14	140.6	8	168.9	22	169.3	0.007	NS	NS	0.006	NS	NS	NS
Retinol (mg/L)#	0	NA	10	0.11	7	0.14	20	0.08	<0.001	NA	NA	NA	NS	0.02	0.003
a-tocopherol (mg/L)*	0	NA	10	5.2	7	6.3	20	3.7	<0.001	NA	NA	NA	NS	0.02	<0.001
Urate (µM/L)#	0	NA	10	44.3	7	23.9	20	20.4	0.009	NA	NA	NA	NS	0.01	NS
Urea (mM/L)#	0	NA	10	14.4	7	10.9	20	17.5	<0.001	NA	NA	NA	0.01	NS	0.007
Cholinesterase (U/L)#	0	NA	10	1508	7	1070	20	1570	0.02	NA	NA	NA	NS	NS	0.03
TEAC (mM/L)#	0	NA	10	2.3	7	2.3	20	2.4	NS	-	-	-	-	-	-
FRAP (mM/L)#	0	NA	10	0.87	7	0.6	20	0.9	0.003	NA	NA	NA	0.02	NS	0.04
SOD (U/gHb)#	16	4503	14	2133	7	538	19	714	<0.001	0.01	0.001	<0.001	0.01	<0.001	NS
Carot. (mg/L)*	0	NA	10	1.3	7	1.6	21	0.4	<0.001	NA	NA	NA	NS	<0.001	<0.001

Table 6.3 Means, statistical significance and post-hoc comparisons of differences in protein electrophoresis properties of warru *(Petrogale lateralis*) from four sites – in captivity and at three wild colonies; Alalka, Kalka and New Well (NW) in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands, South Australia. *comparison made using one-way ANOVA and post-hoc Tukey HSD test; #comparison made using Kruskal-Wallis one-way ANOVA and post-hoc Wilcoxon rank sum test. A/G ratio, albumin/globulin ratio.

Variable	Captives		Alalka		Kalka		New Well		Statistical comparisons						
									Overall	Captives vs Alalka	Captives vs Kalka	Captives vs NW	Alalka vs Kalka	Alalka vs NW	Kalka vs NW
	n	Mean	*n*	Mean	*n*	Mean	*n*	Mean							
Total protein (g/L)#	15	74.8	14	69.1	8	55	21	68.9	<0.001	NS	0.003	NS	0.01	NS	<0.001
Pre-albumin (g/L)#	15	0.83	14	0.51	8	0.56	21	0.53	<0.001	<0.001	0.02	<0.001	NS	NS	NS
Albumin (g/L)*	15	44	14	38.7	8	31.7	21	37.7	<0.001	0.007	<0.001	0.001	0.003	NS	0.01
Alpha 1 globulins (g/L)*	15	4.3	14	4.1	8	3.4	21	4.4	NS	-	-	-	-	-	-
Alpha 2 globulins (g/L)*	15	3.2	14	2.8	8	2.2	21	3.1	<0.001	0.03	0.02	NS	NS	0.04	0.04
Beta 1 globulins (g/L)*	15	6.6	14	4.6	8	4.2	21	5.6	<0.001	<0.001	0.001	0.002	NS	0.02	0.03
Beta 2 globulins (g/L)*	15	6.7	14	6.8	8	5.8	21	6.2	NS	-	-	-	-	-	-
Fibrinogen (g/L)*	15	4.7	14	6.1	8	3.8	21	5.8	0.003	NS	NS	NS	0.01	NS	0.02
Gamma globulins (g/L)*	15	4.4	14	5.4	8	3.2	21	5.6	0.001	NS	NS	NS	0.01	NS	0.01
Total globulins (g/L)#	15	30.8	14	30.4	8	23.4	21	31.3	<0.001	NS	0.003	NS	0.001	NS	<0.001
A/G ratio*	15	1.4	14	1.3	8	1.4	21	1.2	0.005	0.03	NS	0.004	NS	NS	NS

Table 6.4 Reference values for haematology of warru in captivity and at three wild colonies in the Anangu Pitjantjatjara Yankunytjatjara Lands. Reference intervals are calculated as the central 0.95 fraction (Solberg 1987). RBC, red blood cell count; MCV, mean corpuscular volume; MCH, mean corpuscular haemoglobin; MCHC, mean cell haemoglobin concentration; WBC, white blood cell count.

Variable	*n*	Mean	s.d.	Reference interval
Captivity				
RBC (x1012/L)	16	6.7	0.61	5.5-7.7
MCV (fL)	16	72.6	5.02	61.4-78.8
MCH (pg)	16	23.5	1.39	21.4-26.9
Platelets (x109/L)	16	229.8	123	61-640
WBC (x109/L)	16	4.7	2.3	2.8-11.0
Alalka				
MCV (fL)	13	79.2	1.46	77-81.2
MCH (pg)	13	25.8	1.7	23.5-30.6
Platelets (x109/L)	13	106.2	68.3	33-279
WBC (x109/L)	13	8.9	3.9	3.6-15.9
Monocytes (x109/L)	13	2.6	1.8	1-8
Kalka				
Platelets (x109/L)	8	189.9	78.5	94.5-291.5
WBC (x109/L)	8	4.5	0.8	3.3-5.5
Monocytes (x109/L)	8	4.4	1.3	2-6
New Well				
RBC (x1012/L)	21	5.9	0.72	4.6-7.7
MCV (fL)	21	78.1	4.31	72-85.9
MCH (pg)	21	25	1.6	22.8-27.4
Platelets (x109/L)	21	118.2	53.7	32.5-228
WBC (x109/L)	21	6.2	2.5	3.6-12.6
Wild combined				
RBC (x1012/L)	42	6	0.82	3.4-7.8
MCV (fL)	42	78.3	3.3	72-85.9
MCH (pg)	42	25.1	1.6	22.8-30.6
Eosinophils (x109/L)	6	1.7	0.5	1-2
Basophils (x109/L)	12	1.6	0.9	1-4
Neutrophils (x109/L)	40	61.5	13	22-90
Lymphocytes (x109/L)	40	34.3	12.9	7-75
All combined				
Haemoglobin (g/L)	57	15.4	1.6	11.7-19.0
Haematocrit (L/L)	58	47.9	6.1	26-59.2
MCHC (g/L)	58	32.1	2.1	29.8-41.4

Table 6.5 Reference values for biochemistry of warru in captivity and at three wild colonies in the A<u>n</u>angu Pitjantjatjara Yankunytjatjara Lands. Reference intervals are calculated as the central 0.95 fraction (Solberg 1987). AA, ascorbic acid; SOD, superoxide dismutase; a-toc, alpha-tocopherol; FRAP, ferric reducing ability of plasma; ChE, cholinesterase; ALT, alanine aminotransferase; AST, aspartate aminotransferase; TEAC, trolox equivalent antioxidant capacity; TBAR, thiobarbatric acid-reducing substances. ^ parameter only relevant at the individual level.

Variable	*n*	Mean	s.d.	Reference interval
Captivity				
AA (µM/L)	16	105.6	62.6	46.4-279.2
SOD (U/gHb)	16	4503	2404	1,503-9,644
Alalka				
Retinol (mg/L)	10	0.11	0.02	0.09-0.16
a-toc (mg/L)	10	5.2	1.3	2.9-6.9
Urate (µM/L)	10	44	23	10-85
Urea (mM/L)	10	14.5	2.2	8.8-17.1
FRAP (mM/L)	10	0.87	0.06	0.81-0.98
SOD (U/gHb)	14	2133	1310	543-5,540
Total carotenoids (mg/L)	10	1.25	0.4	0.8-1.9
Kalka				
Retinol (mg/L)	7	0.14	0.04	0.09-0.21
a-toc (mg/L)	7	6.3	1.9	3.4-9.2
Urea (mM/L)	7	10.9	2.4	6.7-13.7
ChE (U/L)	7	1070	276	683-1,525
FRAP (mM/L)	7	0.63	0.13	0.53-0.87
SOD (U/gHb)	7	538	322	123-1,082
Total carotenoids (mg/L)	7	1.58	0.58	1.0-2.5
New Well				
AA (µM/L)	22	169.3	54.7	102.3-318.9
Retinol (mg/L)	20	0.08	0.03	0.04-0.2
a-toc (mg/L)	20	3.7	1.2	1.3-6.7
Urate (µM/L)	20	20	12	5-44
Urea (mM/L)	20	17.5	4.8	11.0-27.7
ChE (U/L)	20	1571	488	975-2,532
FRAP (mM/L)	20	0.89	0.27	0.55-1.53
SOD (U/gHb)	19	714	340	225-1,571
Total carotenoids (mg/L)	21	0.41	0.13	0.2-0.7
Wild combined				
AA (µM/L)	44	160.1	54.4	50.7-318.9
Glucose (mM/L)^	37	14.5	2.5	6.8-17.9
Creatinine (µM/L)^	37	133	30	96-258
ALT (U/L)^	37	58	58	15-335
AST (U/L)^	37	237	386	25-2,350
Creatine kinase (U/L)^	37	24,559	27,262	457-136,991
TEAC (mM/L)	37	2.35	0.04	2.25-2.51
All combined				
TBAR (µM/L)^	60	0.9	0.61	0.04-3.19

Table 6.6 Reference values for biochemistry of warru in captivity and at three wild colonies in the A͟nangu Pitjantjatjara Yankunytjatjara Lands. Reference intervals are calculated as the central 0.95 fraction (Solberg 1987). A/G ratio, albumin/globulin ratio.

Variable	*n*	Mean	s.d.	Reference interval
Captivity				
Total protein (g/L)	15	74.8	6.8	65-87
Pre-albumin (g/L)	15	0.8	0.2	0.5-1.2
Albumin (g/L)	15	44	4.4	36.2-52.9
Alpha 2 globulins (g/L)	15	3.2	0.5	2.6-4.4
Beta 1 globulins (g/L)	15	6.6	0.7	5.5-7.4
Total globulins (g/L)	15	30.8	3.4	23.1-38
A/G ratio	15	1.4	0.16	1.1-1.8
Alalka				
Total protein (g/L)	14	69.1	4.3	59-76
Albumin (g/L)	14	38.7	3.6	32.2-45.6
Alpha 2 globulins (g/L)	14	2.8	0.4	2.1-3.4
Beta 1 globulins (g/L)	14	4.6	0.9	3.6-6.5
Fibrinogen (g/L)	14	6.1	1.4	4.7-9.1
Gamma globulins (g/L)	14	5.4	1.2	3.5-7
Total globulins (g/L)	14	30.4	1.9	26.8-33.4
A/G ratio	14	1.3	0.13	1.1-1.5
Kalka				
Total protein (g/L)	8	55	3.7	51-62
Albumin (g/L)	8	31.6	3.6	26.2-37.1
Alpha 2 globulins (g/L)	8	2.2	0.71	0.7-2.9
Beta 1 globulins (g/L)	8	4.2	1.1	1.8-5.1
Fibrinogen (g/L)	8	3.8	1.4	1.8-6.5
Gamma globulins (g/L)	8	3.2	1.4	0.9-4.9
Total globulins (g/L)	8	23.3	2.1	18.9-24.9
New Well				
Total protein (g/L)	21	68.9	6.7	57-80
Albumin (g/L)	21	37.6	4.7	30.2-46.3
Alpha 2 globulins (g/L)	21	3.1	0.3	2.3-3.8
Beta 1 globulins (g/L)	21	5.6	0.8	4.2-7.6
Fibrinogen (g/L)	21	5.8	1.6	3.2-8.5
Gamma globulins (g/L)	21	5.6	1.7	2.7-8.9
Total globulins (g/L)	21	31.2	3.9	25.4-37.2
A/G ratio	21	1.2	0.19	0.9-1.5
Wild combined				
Pre-albumin (g/L)	43	0.53	0.14	0.3-0.9
A/G ratio	43	1.3	0.2	0.9-1.8
All combined				
Alpha 1 globulins (g/L)	58	4.2	1	2.4-5.9
Beta 2 globulins (g/L)	58	6.4	2.2	2.5-12.9

6.5 Discussion

Obtaining reliable haematological measurements from wild animals is notoriously difficult (Wells *et al.* 2000) and, when interpreting values, factors such as sample collection method, season, animal age, sex and reproductive condition can have an effect (Vogelnest and Woods 2008). For example, platelet counts are particularly affected by the collection process, with any platelet aggregation incited during collection leading to a spurious decrease in the results (Clark 2004). Since in-field blood collection is particularly problematic, this is the most likely explanation for the lower platelet count seen in wild compared to captive warru. The current study‟s inability to assess factors such as sex and age is likely to be reflected in the standard deviations presented but does not invalidate results because it is season (which, in the current study, was held constant) which appears to have the most pronounced effect on blood results (Spencer and Speare 1992). Furthermore, although factors such as capture stress could not be controlled, the current study followed standard macropod trapping protocols, meaning that results should be comparable to both past and future studies.

6.5.1 General haematology

There were significant differences between sites in a number of parameters, including a difference in red blood cells (RBCs) between captive and New Well warru. However, this result must be interpreted in the context of haemoglobin (Hb) and haematocrit (Hct) values, with a decrease in all three parameters below a species‟ defined range termed „anaemia‟ (Clark 2004). Consequently, the absence of differences in Hb and Hct between sites meant that, at the population level, chronic anaemia was not evident in any of the colonies. This is supported by the mean corpuscular haemoglobin (MCH) index, which is a measure of the amount of haemoglobin per erythrocyte (Clark 2004). While captive warru had lower MCH values than did those at Alalka and New Well, results from all sites were within reference values provided for *P. penicillata* (Schultz *et al.* 2011), suggesting that animals‟ Hb production is sufficient (Clark 2004). Since RBCs and Hb have both been positively associated with post-release survival and longevity in at least one species (European water vole, *Arvicola terrestris*, Mathews *et al.* 2006), and haemoglobin levels probably reflect general body condition (Algar *et al.* 1988), this is a positive sign for the health of wild and captive warru.

Mean corpuscular volume (MCV) provides an indication of average erythrocyte „size‟ and can be associated with food availability. For example, in both quokkas (*Setonix brachyurus*) and agile wallabies, MCV decreases commensurate with seasonal reductions in food availability (Shield 1971; Stirrat 2003a). In the current study, all values were proximate to those provided for *P. penicillata* (Barnes *et al.* 2008), suggesting that no colony was chronically malnourished. However, captive warru unexpectedly had lower MCV than did those at Alalka and New Well. Further research should assess if there are any seasonal differences in MCV and thus clarify whether captive warru, which have food and water provided *ad libitum* and are thus theoretically better-nourished, do indeed have lower values than wild animals.

White blood cells accumulate at sites of inflammation and initiate tissue defence (Clark 2004). In brushtail possums (*Trichosurus vulpecula*) for example, Wells *et al.* (2000) noted significant increases of neutrophils, monocytes, basophils and eosinophils during winter and hypothesised that this may represent seasonal infections, inflammatory and/or detoxification challenges. In the current study, although Alalka warru had the lowest monocyte counts, there was no difference among sites in neutrophils and lymphocytes. Since all three parameters need to differ before an effect is interpretable at the population level (Clark 2004), this suggests that no warru colonies were experiencing similar challenges to those postulated by Wells *et al*. (2000).

6.5.2 General biochemistry

The use of biochemical parameters as indicators of nutritional and health status is confounded by large environmental variation. Not only does forage quality vary between locations, seasons and years, but factors such as disease, age, reproduction and weather may also contribute to variation in animals‟ blood chemistry (Algar *et al.* 1988; Stirrat 2003a). Nevertheless, if caution is used, a number of the parameters established in the current study can be used to provide insight into the nutritional health of animals.

The first of these, ascorbic acid (AA), or vitamin C, is an organic acid with antioxidant properties that can be biosynthesised by most mammals, most likely including *Petrogale*. Although this means that AA is not an essential nutrient, if present in the environment, animals are likely to absorb a surplus and utilise it (Burtis and Ashwood 1994). The results for warru suggest that in 2009 (when blood samples were taken), none of the colonies had deficiencies in this micronutrient (B Rich, personal communication). However, since captive warru had the lowest average AA value of all sampled sites, this suggests that less AA is available at Monarto. As such, after establishing any seasonal variation, AA could be used to monitor how well captive warru that are reintroduced to the APY Lands adapt to their new environment.

The second indicators of nutritional health are superoxide dismutases (SOD). These are a class of enzymes that are instrumental in detoxifying free radicals, with higher values representing better free-radical quenching ability (Misra and Fridovich 1972). Low SOD values may be due to animals having a zinc or manganese deficiency, or may be an indication of competitive inhibition within a site (Burtis and Ashwood 1994). Substantially lower SOD values occurred at each of the wild sites when compared to that in captivity, as well as in New Well and Kalka animals compared to those at Alalka. However, since SOD can be highly variable on a daily basis, zinc and magnesium assays should be conducted to validate these results.

Retinol, total carotenoids and alpha-tocopherol (a-toc) are also useful indicators. Retinol is biosynthesised from an essential nutrient, beta-carotene, and has a function in vision, immunology and reproduction. Beta-carotene availability is measured within the parameter „total carotenoids", which is positively correlated to quality and quantity of browse (Burtis and Ashwood 1994). Consequently, the lower levels of both retinol and total carotenoids in New Well warru indicate that animals here had poorer levels of nutrition than those at Kalka and Alalka. Possible causes of this may have been decreased food quality or quantity in 2009, and/or increased competition, potentially with euros. This is supported by New Well animals also having lower levels of a-toc, or vitamin E. An essential nutrient, a-toc protects cells against oxidative damage caused during cellular metabolism (Vogelnest and Woods 2008). Lower a-toc levels at a site or in a year are indicative of animals having lower available nutrition (Burtis and Ashwood 1994). Interestingly, the lower plane of nutrition at New Well was not reflected in reproductive output, with all sexually mature females caught in 2009 carrying a pouch young. It could, however, have played a part in the lower than average (albeit higher than 2007 and 2008) juvenile survival seen in 2009 (Chapter 5).

The result for urea also suggests that APY Lands warru may be experiencing some level of nutritional and/or water stress. Circulating levels of urea increase during periods of dehydration and starvation because urea is passively reabsorbed by the renal tubules at the same time that water is being reabsorbed (Jacobs 1993). As such, the higher average urea concentrations for New Well and Alalka are likely to be a reflection of these animals having a different plane of nutrition and/or possibly reduced water intake compared to Kalka warru, which have a perennial spring available to them.

Kalka warru also had the lowest cholinesterase (ChE) values of the wild colonies. The average was not low enough to be indicative of acute infection, chronic malnutrition or liver damage (Burtis and Ashwood 1994). However, since ChE is an enzyme involved in neurotransmission, the decreased levels may explain the higher anaesthetic-related mortality seen at Kalka compared to that at Alalka and New Well (two warru vs. none). Such population-wide, depressed ChE values may be due to a plant containing cholinesterase inhibitors being present at Kalka. To validate this hypothesis, the plants eaten by warru at Kalka should be investigated for the presence of such inhibitors.

The final measure of animals‟ nutrition is FRAP, which is absorbed from vegetation and measures the antioxidant capacity of plasma (Benzie and Strain 1996). Preliminary studies in *P. xanthopus* indicate that levels around 1 mM/L are optimal and that a drop below 0.5 mM/L is symptomatic of oxidative stress (B Rich, personal communication). Since Alalka and New Well had average FRAP values around one, each site‟s levels are adequate. This is supported by preliminary biochemical analyses undertaken at Adelaide Zoo of plants from the two sites that are known to be eaten by warru (Geelen 1999). Results indicated that some species have high FRAP values, including an average of 303 mM.kg^{-1} for *Cheilanthes lasiophylla.* This suggests that FRAPs are not limited in the eastern Musgrave Ranges environment. In contrast, Kalka warru had an average FRAP value of 0.6 mM/L, which should be monitored. Future research should also involve assessing the FRAP values of plants found at this site.

6.5.3 Protein electrophoresis

There were significant differences between sites in total protein, albumin and total globulins. However, since average results for these parameters were within the range found for *P. penicillata* (Barnes *et al.* 2008), it is unlikely that any of the study sites had a high proportion of animals suffering from chronic infections and/or immune-mediated diseases (Wilkins 1979). Nevertheless, the lower average values of Kalka warru for total protein do suggest that animals here had less accessible protein than did those in the other colonies. In contrast, warru at Monarto Zoo, where protein-supplemented food is provided *ad libitum*, had the highest albumin concentrations.

The suggestion that none of the study colonies were suffering from chronic levels of infection is also supported by results for fibrinogen, gamma globulins and the albumin/globulin (A/G) ratio. Fibrinogen is a protein produced in the liver that acts as a „marker" for inflammation (Clark 2004). Hawkey and Hart (1987) for example, found substantially increased concentrations of fibrinogen in red-necked wallabies (*Macropus rofogriseus*) with lumpy jaw. In the current study, none of the four study sites had averages high enough to suggest that their resident warru had chronic levels of inflammation (B Rich, personal communication). This is supported by the results for gamma globulins and the A/G ratio. Since the differences amongst sites in gamma globulins and the A/G ratio were not interpretable biologically (B Rich, personal communication), this suggests that from a disease perspective, warru at all sites were healthy.

6.5.4 Conservation implications

In general, warru in the APY Lands in 2009 were physiologically healthy, with no indication of chronic infections and/or immune-mediated diseases. More specifically, the haemoglobin, haematocrit and red blood cell values suggested that animals were not suffering from chronic anaemia, while the mean corpuscular haemoglobin values indicated that haemoglobin production was adequate. The lack of elevated white blood cell counts and the results for fibrinogen, gamma globulin and the A/G ratio also suggested that warru were not responding to infectious, inflammatory or detoxification challenges.

However, the lower SOD, retinol, total carotenoids and a-toc values of New Well warru indicated that animals here had a lower plane of nutrition than did animals at the other study sites. In support of this, the higher urea values potentially indicate some levels of water stress. Whether this is due to lower food quality, quantity or inter-species competition could not be established but should be investigated further, especially since the Musgrave Ranges experienced slightly above-average rainfall in 2009 (Chapter 5). The result suggests that it may be beneficial to provide supplementary food and water to New Well warru, especially during droughts. However, care must be taken that predator activity does not become focused at such sites. Alternatively, fire regimes that promote vegetational diversity should be established. To measure the success of such initiatives, warru could be monitored using the reference values provided. These are the first haematological, biochemical and protein electrophoresis reference values for *P. lateralis,* and only the second biochemical values for a species of *Petrogale* (Barnes *et al.* 2008). The values provided can also be used to investigate the physiological preparedness of captive warru to be released into, and their adaptation to, the wild. Future work involving repeated measures of the current parameters could help clarify if nutritional deficiencies and/or disease are limiting the recovery of warru.

Attaining an insight the health of populations of endangered species using their haematological values is arguably an under-utilised strategy, but one with substantial potential (Hanks 1981). Such work has the capacity to be used both to monitor populations and to clarify if physiological causes could be contributing to a species‟ decline. Consequently, it is a tool worthy of consideration in the management of other endangered species.

CHAPTER 7 – General discussion

‘As the [Davenport Ranges] rock wallabies showed, if we are not motivated into action we will continue to lose species and Australia will become a poorer place.’

John Read (2003). *Red sand, green heart* p. 294

Photo: View of sunrise from New Well, APY Lands. N. Staniford.

Chapter 7 – General discussion

Petrogale lateralis is of conservation concern in three of Australia"s states and territories. In Western and South Australia respectively, it may be seen as a symbol of threatened species management in the arid-zone. The current study used a process of elimination to determine the agent(s) that may have contributed to the decline of warru in northern South Australia, where animals are currently suffering the most precipitous declines. This strategy was effective and is potentially repeatable for other declining species. More specifically, the information presented is a significant contribution to our knowledge of warru ecology and is provided both as a means of facilitating better management, and as a platform for future research. In the following discussion, the key findings of the thesis are summarised and used to hypothesise on the feasibility of warru recovery. This is followed by a broad-scale analysis of implications for *P. lateralis* management and conservation. A discussion of shortcomings is then provided, complemented by suggestions for future research.

Key findings

Despite feral predator control being undertaken since 1996 (Geelen 1999) and an apparent decrease in the numbers of foxes observed around two warru colonies (Read and Ward 2011b), no substantial, population-wide response by warru has been evident on the APY Lands (Read and Ward 2011b). Until the current study was undertaken, the reason for this was inexplicable; however, potential factors included animals being limited by their habitat preferences, genetic diversity, population dynamics, disease and/or malnutrition.

Chapter 2 investigated the role that warru habitat preferences may have played. Previously, detailed studies on habitat use by *Petrogale* were limited to *P. xanthopus* (Lim and Giles 1987; Sharp 1997b) and *P. penicillata* (Short 1982; Waldegrave-Knight 2002). These concluded that rock-wallabies are habitat specialists with quite specific site preferences. However, whether this was also applicable to warru, and the details of such, were unknown. Chapter 2 clarified that, at the regional scale, warru have broad habitat preferences and that at this spatial scale, a lack of suitable habitat is unlikely to have facilitated the decline. However, specific abiotic and biotic parameters aid animals" long-term persistence at the site scale. Animals also select both for and against particular areas within inhabited hills and even frequent shelters with specific characteristics. Selection of „core" areas within inhabited hills and the choice of particular refuges would presumably be assisted by animals" high mobility because this would expose individuals to a wide range of potential sites.

Chapter 3 assessed the home range and movement patterns of warru within their preferred habitat. These aspects of *Petrogale* ecology had been investigated more thoroughly than had their habitat requirements, with the consensus being that rock-wallabies are generally sedentary and have low dispersal capacity (Sharp 1997a; Eldridge *et al.* 2001; Piggott *et al.* 2006b). Species in the semi-arid zone, however, appear to have larger home ranges than those in temperate environments (Sharp 2009), with the largest established being that of *P. xanthopus* in the Flinders Ranges of SA (Lim 1987). Set in the arid-zone, the current study‟s preliminary results for home range and movement patterns support this observation, with the Alalka female having a home range that represents the second-largest documented for a species of *Petrogale*. Furthermore, although the female showed high fidelity to the Alalka hill, her movement patterns were unprecedented - she ranged 50.8 km in 28 days, effected an off-hill movement and was active both nocturnally and diurnally. These results indicate that warru, although habitat specialists, are unlikely to be physiologically limited in their movement patterns and home range dynamics. They also suggest that, as with *P. penicillata* (Hazlitt *et al.* 2006a), warru are philopatric because of intrinsic factors such as social structure, rather than dispersal capability. Furthermore, a lack of mobility is unlikely to have facilitated the decline of warru in the APY Lands; conversely, this parameter is likely to assist with their recovery. This is because animals are likely to be capable of dispersing long distances and, when at suitable sites, selecting the most appropriate areas for fulfilling their resource and survival requirements.

The connectivity of habitat and animals‟‟ capacity to disperse through it has direct ramifications for the genetic diversity of their populations. In turn, genetic diversity allows species to evolve, adapt to environmental change and escape the effects of inbreeding depression, including depleted survivorship and litter size, decreases in juvenile development and low population improvement (Frankel and Soule 1981; Deckard *et al.* 1989; Mitton 1993). As indicated by a classic study on *P. lateralis* conducted by Eldridge *et al.* (1999), the genetic diversity of animals on islands is likely to be markedly lower than those on the mainland. Chapter 4 both supported and extended this conclusion. Specifically, using data from the APY Lands, the Northern Territory, SA‟s offshore islands (Jones 2001) and Western Australia (Eldridge *et al.* 1999), it established that the most secure and well-connected populations of *P. lateralis* also exhibit the highest genetic diversity. This is followed by populations that, excluding feral predators, are located in a relatively undisturbed landscape.

The lowest diversity occurs in animals that are geographically isolated, highly fragmented and/or were established via translocation.

The effect of isolation was also evident within the APY Lands. Specifically, the Kalka colony, which has the smallest population (Chapter 5) and showed no evidence of immigration (Chapter 4), exhibited the lowest genetic diversity. In contrast, the Alalka and New Well colonies, which are larger and better connected, had moderate to high genetic diversity. New Well warru, however, did show evidence of homozygote excess, potentially indicating inbreeding due to colony segregation. A key finding of this work was that although the Alalka and New Well colonies are genetically distinct, a low level of dispersal (5% of individuals with mixed ancestry) does occur between them. As such, they are likely to be part of a broader Musgrave Ranges metapopulation. This conclusion has implications for conservation and supports a previously-postulated hypothesis (Piggott *et al.* 2006b) that *Petrogale* perhaps undertake inter-colony dispersal more frequently than that which is generally inferred from trapping and telemetry studies. A similar scenario could also apply to other fauna which have specific habitat preferences and are presumed to be relatively sedentary (e.g. perhaps some bird species). The genetics results (Chapter 4) further suggest that inbreeding is unlikely to have been a factor in APY Lands population declines; instead, the genetic parameters of warru have positive implications for the race‟s recovery. In particular, they intimate that extant warru colonies are likely to be able to adapt to environmental change and unlikely to be suffering from the effects of inbreeding depression.

Warru are also not limited by their mating system (Chapter 4), as a polygamous strategy would allow animals to change partners to improve breeding success. Although it requires more investigation, such an action may have been in evidence with females that lost their pouch young to cross-fostering. This potential impact had not been previously investigated. Parentage analyses also suggested that, as with other species of *Petrogale* (Delaney 1997b; Eldridge *et al.* 1999), warru have high fecundity and that both males and females mate with multiple partners in one year. Given that, prior to the current study, data on genetic mating systems in the wild were previously only available for four of the approximately 70 species of macropodoids (Eldridge *et al.* 2010), this result represents an important contribution to our knowledge about this superfamily.

The results on population dynamics (Chapter 5) also provided insight into warru reproduction. Akin with *Petrogale* across Australia (Delaney 1997b; Eldridge *et al.* 1999), warru in the APY Lands are continuous breeders, with non-lactating females rarely found. However, as with *P. lateralis* on SA‟s offshore islands (Jones 2001) and in WA‟s Wheatbelt region (Willers *et al.* 2011), warru in the APY Lands exhibit a seasonal reproductive peak, in this case during autumn-winter. This timing would allow offspring to emerge during summer, when resources are likely to be more abundant. Importantly, the reproductive effort of APY Lands warru was high, averaging 88% across the three colonies and presumably bolstering colonies‟ capacity for population increases. The fact that this reproductive rate is higher than that of other *Petrogale* colonies which have demonstrated recovery (Kinnear *et al.* 1988; Sharp *et al.* 2006) both indicates that it is not reproductive output which is limiting APY Lands colonies, and bodes positively for warru recovery.

Warru recovery is also unlikely to be limited by disease or high parasitic loads, with the blood analyses (Chapter 6) indicating that in 2009, warru in the APY Lands were healthy, with no indication of chronic infections or malnutrition, and/or immune-mediated diseases. One of the key results of this chapter was the establishment of haematological, biochemical and protein electrophoresis reference values for warru. This is only the second set of comprehensive reference values for a species of *Petrogale* and can be used to monitor both the captive and wild colonies in the future.

However, despite the positive connotations from the above results, as indicated by POPAN modelling (Chapter 5), the population sizes of the studied colonies remain small (New Well = 23, Alalka = 24, Kalka = 14). Given that even minor positive changes in juvenile survival can translate into substantial impacts on population size (Gaillard *et al.* 1998), this is likely to be due to the lower than expected survival of warru offspring. Mean annual survivorship of adults was 76%, as compared to 51% for juveniles (at New Well and Alalka only). This low juvenile survival may be due to a combination of youngsters being more susceptible to predation (including during any attempted dispersal events) and, as indicated by the POPAN modelling, more affected by fluctuations in rainfall. Given that predator abundance monitoring has suggested low abundances of foxes and dogs in the Musgrave Ranges (which can nevertheless wreak havoc due to animals being surplus killers), the predation effect may be due to the presence of cats, which are not currently targeted by the baiting strategy (Read and Ward 2011b). Cats have been speculated to focus predation on juvenile *Petrogale*

(Spencer 1991) and may be capable of suppressing rock-wallaby recovery even when foxes and/or dingos are controlled (Kendrick *et al.* 2010). Indeed, there is a growing body of work investigating the mesopredator release hypothesis (Crooks and Soule 1999; Hayward and Somers 2009; Richie and Johnson 2009), which postulates that when populations of apex predators (in the current study, foxes and dingos) are reduced or go extinct, previously suppressed mesopredator populations (cats) may substantially increase. As such, the current baiting program may have actually facilitated an increase in cat abundance, meaning that warru recovery may be underlined by effective cat management. To this end, in 2011, the Warru Recovery Team implemented a switch to Eradicat® baits, which are more attractive to cats than dried kangaroo meat baits injected with 1080 (Algar *et al.* 2007). The fox/dog control program may also have allowed for an increase in the abundance of euros, which may be competing with warru for both food and shelter resources (Chapter 2).

The result highlighting the role of rainfall, especially during winter, in increasing juvenile survival also supports a body of previous work that identifies the importance of rainfall for arid-zone fauna (Masters 1993; Dickman *et al.* 1999a; 1999b). For example, following high rainfall at Uluṟu National Park, Masters (1993) documented an increase in both the diversity and abundance (100-fold increase) of murid rodents in spinifex grassland.

Implications for management and conservation

The current results suggest that warru populations in the APY Lands are capable of expanding to other available habitat, are genetically diverse and that animals have high fecundity, adult survivorship and, in general, are not suffering from chronic infections or malnutrition and/or immune-mediated diseases. However, perhaps abetted by the implementation of apex predator baiting, warru populations may have failed to increase because of predation of juveniles by cats. Resource availability, especially during the winter period, may have accentuated this effect, especially given that the Musgrave Ranges experienced below average rainfall in four of the six study years (2005-2010, Fig. 5.1).

Managers of warru colonies should therefore develop a holistic approach towards managing predators and potentially, consider manipulating resource availability. More specifically, given the mesopredator release hypothesis, baiting strategies should attempt to suppress cat abundance around the extant colonies. This could be achieved by one of two techniques. The first would involve reinstating dingoes into the ecosystem using dingo-excluding baiting strategies. The second would involve managing cats using cat-specific baits such as Eradicat®, potentially supplemented with shooting. In order to improve juvenile warru survival, managers should also consider providing supplementary water to *in-situ* colonies during winter, bearing in mind that these may attract predators. Since New Well warru had poorer levels of nutrition than the other colonies in 2009, it would also be pertinent to monitor the haematology of animals in this colony and, if required, provide supplementary food during droughts.

Given the genetic diversity, high fecundity and high dispersal potential of warru, appropriate predator management should succeed in increasing warru abundances. If this occurs, it is proposed that captive warru and their offspring be used to establish a new colony in the APY Lands (reintroduction), rather than to supplement existing extant colonies. The exception to this is likely to be the Kalka colony, which, given its isolation, lower genetic diversity and low population size, would likely benefit from supplementation.

Although focused on warru in the APY Lands, the current results may also be pertinent for the management of *P. lateralis* in the NT and WA. In particular, given the absence of comprehensive monitoring and contemporary surveys in the NT (Woinarski *et al.* 2007; Pearson 2009) and the threatened status of *P. lateralis* species in WA (Van Dyck and Strahan 2008), investigation and/or implementation management of cats and resources may be appropriate. The „process of elimination" technique used in this research may also be useful for other species, particularly those in the arid-zone, which have declined and/or are failing to respond to management strategies.

Shortcomings and future work

This thesis incorporates the research areas of ecology, reproductive biology, population genetics and health condition monitoring, all of which can be utilised by conservation biologists to better manage species of interest. However, there are a number of areas of research that would benefit from further study.

One of these is how the resource requirements of *P. lateralis* are influenced by abiotic factors. More specifically, although the current study investigated the link between resources and warru population dynamics (Chapter 5), and resources and warru health (Chapter 6), understanding how such resources themselves fluctuate was beyond the capacity of the project. For example, given that changed fire regimes are hypothesised to have contributed to the decline of many arid-zone fauna (Kimber 1983; Masters 1993; Burrows *et al.* 2006), managers need a better understanding of the influence of fire on arid-zone vegetational heterogeneity. Similarly, given the increasing scourge of buffel grass (*Cenchrus ciliaris*) in central Australia (CSIRO Centre for Arid Zone Research 2007; Greenfield 2007; Smyth *et al.* 2009), there needs to be investigation of the role of this pest plant in limiting native vegetation, and therefore the resources available to species such as warru. Buffel grass management also urgently needs to be conducted. Given the influence of rainfall on juvenile warru survival, there should also be an investigation of the effects of climate change on warru habitat preferences, resource requirements and animals‟ ability to survive *in-situ*.

Although there was a correlation between rainfall and juvenile warru survival, the exact nature of this interaction could not be established. That is, does warru survival improve because warru need drinking water, or because of the role of rainfall in rejuvenating vegetation? Furthermore, do juveniles benefit from rainfall by drinking it directly, or because of its effects on the lactation of dams? To answer these questions requires more survival modelling over a longer timeframe, as well as the direct manipulation of water resources. Future research should also investigate how the blood parameters of warru vary across seasons and years. An analysis of the biochemical properties of critical food plants from different sites could also be used to determine the plane of nutrition available at each colony. To assist with health monitoring of reintroduced animals, researchers could also establish the haematological „fingerprint‟ of rock-wallabies suffering from particular diseases, such as that of macropod herpesvirus.

Due to equipment failure, the preliminary investigation of warru home range and movement patterns described herein also needs to be supplemented with further research. However, traditional VHF radiotelemetry is likely to be hampered because of signal interference from the rocky terrain and because of the difficulties of moving at night in the environment (Telfer 2006). Consequently, further work should again attempt to use GPS and/or satellite transmitters, albeit hopefully with a higher success rate than that encountered during this project. An alternative technique would involve the development of species-specific microsatellites, which could then provide more detailed insight into the phylogeography, structure and dispersal of warru.

One of the key hypotheses arising from this project, that of the potential relationship between cat predation and lower juvenile survivorship (Chapter 5), also needs to be confirmed. This should involve using more comprehensive data, including, if possible, predator abundance data, and be conducted across a broader study area (for example, at least the incorporation of Kalka). The dynamics of predators and potential management options, including biocontrol agents, also obviously need to be investigated across Australia. Finally, it is recommended that both similar and more expansive research to that of the current study be conducted on both *P. lateralis* and other arid-zone fauna across their range. This would help to clarify the causes of such species‟ decline and the management strategies that are required for their long-term conservation.

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