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Behavioural ecology of the black-flanked rock-wallaby (Petrogale lateralis lateralis): Refuge importance in a variable environment

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Behavioural ecology of the black-flanked rock-wallaby (*Petrogale lateralis lateralis*); refuge importance in a variable environment

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USE OF THESIS

Acknowledgement

DECLARATION

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Craig Pentland

Dated; 20/07/2014

Abstract

The black-flanked rock-wallaby (*Petrogale lateralis lateralis*) has suffered a significant decline in its distribution in Western Australia. This has been attributed to introduced predators (predominantly the red fox) and herbivores, fire, and habitat destruction due to clearing. Although since 2001 the Department of Environment and Conservation (DEC) had begun to reintroduce this species back into its former range, little was known of the behavioural ecology of this species. Fox control in the 1980s and 1990s resulted in population increases of rock-wallabies on several reserves in the central wheatbelt of WA. However, recently these populations have rapidly declined despite continuing fox control. All too often, management and conservation programs are based on little understanding on the natural history and ecology of animals, which can ultimately result in poor management. One of the major problems with our understanding of the ecology of *P. l. lateralis* was that there was little information on their behavioural, foraging and feeding patterns, and how these affect the population dynamics of the species. Although this species appears to be substrate bound, requiring complex rock structures that are believed to protect them from both predators and adverse climatic conditions, there was still little understanding of how these animals utilise this important resource, particularly in highly variable environments. There is a long-standing premise in behavioural ecology that highly variable environments can significantly affect the behaviour and demography of animal populations. Although this has been well documented in birds, and primates, behavioural elements are rarely incorporated into marsupial studies. For the success of any current and future reintroductions of rock- wallaby populations into new areas, we needed to understand the relationships between the landscape and climatic elements and the behavioural patterns and population dynamics of the species'.

This study describes the behavioural ecology of the rock-wallaby subspecies *P. l. lateralis* in the central wheatbelt region of Western Australia. It focuses on environmental variables that have rarely been studied simultaneously, those of climate, fear of predation and conspecifics, and habitat structure. The Nangeen Hill Reserve population was chosen because it is one of seven small fragmented reserves, within a landscape, with strong seasonal climatic patterns. A methodological approach was developed that enabled identification of the key ecological determinants of the foraging and feeding behaviours of *P. l. lateralis* in this highly variable environment. The study included a comprehensive examination of all the behavioural characteristics and

abilities of *P. l. lateralis*, compiling a detailed behavioural repertoire (ethogram), a first for this species, and included both nocturnal and diurnal observations.

P. l. lateralis uses a complex arrangement of non-agonistic and agonistic behavioural acts that determines its social organisation, and indicates a linear dominance hierarchy. There is little vocal communication, and instead the rock-wallabies appear to rely on both ritualised behaviour acts and chemical cues to exchange information about the physiological or behavioural state of the individual, thus evolving very diverse and complex social behaviours. Nangeen Hill rock-wallabies occupy a permanent central rock refuge, with strong signs of site fidelity. Their foraging patterns reflect those of a central place forager, but distances travelled are restricted in open habitats, with stronger preferences for areas of rock structural complexity. Their foraging behaviour is not strictly nocturnal nor can it be considered crepuscular, exhibiting significantly different seasonal patterns. Time allocation for foraging is strongly affected by fear of predators and to a lesser extent conspecifics, and certain climatic conditions.

Although rock-wallabies use multiple behavioural strategies to reduce predation risk, energy costs, and intraspecific agonistic interactions, they can only can survive in their present environment if they have access to complex rock refuge. This rock resource not only enables them to avoid extreme ambient temperatures, but also gives them protection against predators particularly when environmental conditions are unfavourable. In addition, their cave refuge also gives them protection from precipitation, reducing heat loss, and provides a safe environment for both rearing young and for courtship without the cost of predation. Rock refuge is the most important resource that defines this species and is central to all aspects of its life history.

Although this reserve has been under a fox-baiting program since 1982, and subsequently resulted in a rock-wallaby population increase and habitat expansion, within the rocky outcrop (Kinnear et al., 1998), it was clear from my research that the ecological situation was more complex. There is a strong predation influence on the behaviour indicating that the population is now predominantly fear-driven. It is the fear of predators and dominant conspecifics that restricts both the foraging range and time spent feeding. This results in animals being tightly restricted to their rock refuge, resulting in overgrazing and habitat degradation. These concerns led me to believe that if the current situation was not alleviated, then a population crash was imminent.

A population crash subsequently happened in 2010, and the cause of this decline is a result of a complex ecological relationship, that includes direct and indirect predatory effects, weed invasion, and drought. The results of this research and the subsequent recent population decline, show the importance of including behaviour into an ecological study to have a better understanding. It provides a better understanding of a species as well as providing important insights into its evolutionary past, and how this has shaped their social and demographic patterns. This research also demonstrates how the use of a permanent central rock refuge both contributes to the animal's continued survival, and restricts its future distribution, particularly in ecologically altered landscapes.

Although this study was not designed primarily to resolve conservation and management problems, its findings are already being used to design an active management plan for the central wheatbelt rock-wallaby populations. The complex relationships between how an animal obtains and uses its resources, the availability of different vegetation patches, and population demographics creates significant problems for the management of a species. This emphasises the need for future research on all animal groups, to understand the relationships between the habitat and landscape elements, and that of behaviour and population dynamics. Understanding how animals perceive their environment and how they adjust to its changes will be paramount for the future management and survival of many species.

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Introduction and Literature Review

1.1   Introduction

This research examined the behavioural ecology of the rock-wallaby sub-species *Petrogale lateralis lateralis*, commonly known as the black-flanked rock-wallaby. The study focused on environmental and biological variables of marsupial foraging patterns, including climate, fear of predators, fear of conspecifics, and habitat structure; aspects that have rarely been studied. As there were very few published detailed rock-wallaby behavioural studies, and no published ethogram on the *P. l. lateralis* a comprehensive behaviour repertoire of this species was developed during this study. The Nangeen Hill *P. l. lateralis* population was chosen because it is located within highly altered ecological landscapes and is closely associated with seasonal climatic conditions. This population is one of seven isolated populations of *P l. lateralis* found on a cluster of granite outcrops in the central wheatbelt of Western Australia.

Over the last twenty years there has been an increased focus on foraging research, partly because feeding behaviour is now considered central to our understanding of the ecological and evolutionary connection between animals and their environment (Ydenberg et al., 2007). Behavioural ecology investigates the evolutionary mechanisms of animal behaviour and its relationship with the biotic and abiotic environments. It is now regarded as an important ecological sub-discipline for not only understanding important complex ecological relationships between an organism and its environment, but also for the conservation and management of animal populations. Whilst foraging theory has commonly been linked to the impact of food resource availability and distribution, other environmental factors such as climate, predation, and habitat structure have more recently been found to influence foraging strategies and population dynamics of animals (Brown & Kotler, 2007; Erkert & Kappeler, 2004; Hill, 2005; Holt & Kimbrell, 2007). Many aspects of behavioural ecology, including foraging strategies, are becoming recognised for their importance to improved animal management and conservation (Festa-Bianchet & Apollonio, 2003); yet they have rarely been incorporated into Australian research studies.

A methodological approach was developed for this research to enable identification of the key ecological determinants of the foraging and feeding behaviours of *P. l. lateralis*

in a highly variable climate. Genetically rock-wallabies are a highly diverse group, with discontinuous and fragmented distribution across a wide range of climatic conditions and landscapes (Tyndale-Biscoe, 2005). They display strong site fidelity and forage away from a central refuge (Jarman & Bayne, 1997; Laws & Goldizen, 2003; Sharp, 2009), making rock-wallabies excellent subjects for examining the effects of climate, predation fear/risk, and habitat structure on behavioural patterns and population dynamics.

This chapter reviews the evolutionary record of the marsupial family Macropodidae, specifically the historical distribution of the rock-wallaby genus *Petrogale.* A brief description of the biology and ecology of modern-day rock-wallabies has been provided, followed by a review of animal behavioural ecology, with a focus on past and current foraging theories and adaptability to ecosystem changes – new directions within highly debated ecological paradigms. Finally, the importance of behavioural ecology for the conservation and management of animal species is discussed in the context of this behavioural ecological study on *P. l. lateralis* in Western Australia.

1.2 Rock-wallaby evolution, biology, ecology and historical record

1.2.1 Evolution and distribution of rock-wallabies

The family Macropodidae is the largest of the Diprotodontia marsupial families and comprises 62 species (Van Dyck & Strahan, 2008) including the kangaroos, wallaroos, wallabies, hare-wallabies, nail-tail wallabies, pademelons, quokka, tree-kangaroos, swamp wallabies and rock-wallabies. The macropod classification used throughout this thesis, and the taxonomy of the genus *Petrogale* (Figure 1.1), are based on reviews by Tyndale-Biscoe (2005) and Van Dyck and Strahan (2008). Like other Diprotodontia, Macropodidae dentition is adapted to an herbivorous diet, and although the group includes some browsing species, most have evolved morphological and physiological adaptations of grazers (Van Dyck & Strahan, 2008). It is believed that the macropods formed the major radiation of terrestrial herbivores in Australia and New Guinea during the late Miocene period, where they may have crossed an adaptive threshold from their unique incisor occlusal cycle and stomach morphology, opening up new adaptive niches (Flannery, 1989). However, the Macropodidae has also suffered the biggest loss of species and geographical range since European settlement (Johnson et al., 1989).
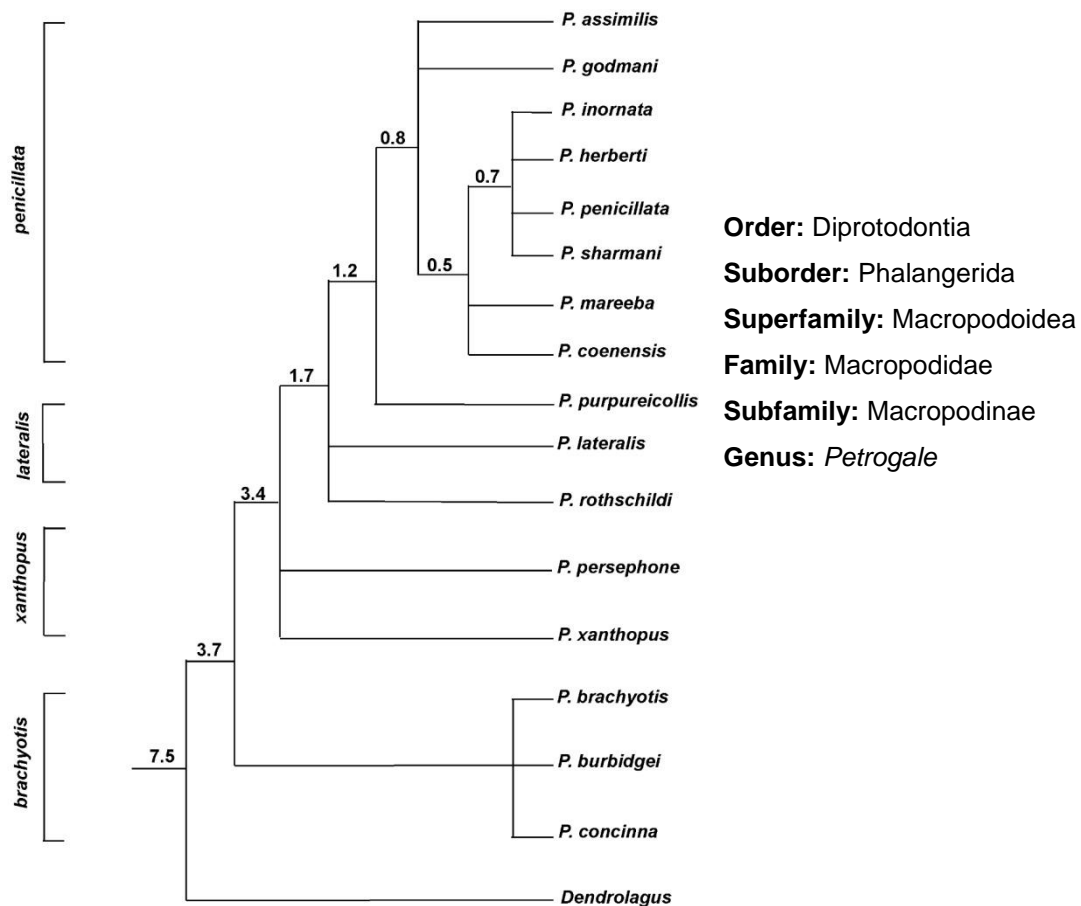
Figure 1.1 The taxonomic relationship between rock-wallabies, genus *Petrogale* (tree kangaroo branch, *Dendrolagus,* arising from the same pademelon ancestral stock), and the classification of the genus *Petrogale* (rock-wallabies), based on Tyndale-Biscoe (2005) and Van Dyck and Jarman (2008). Numbers indicate estimated time of branch in million years before present (from Tyndale-Biscoe, 2005).

It is necessary to examine the geological and climatic changes that have influenced a species' evolution in order to understand its morphology, physiology and behaviour. In the case of macropod marsupials, the major radiation in the early Tertiary coincided with the opening up of forests (Flannery, 1989, Tyndale-Biscoe, 2005). This radiation led to the development of the modern-day arid-adapted fauna (Hope, 1982).

During the early Miocene the climate was wet and warm, and closed *Nothofagus* forests dominated most of the Australian continent (Galloway & Kemp, 1981; Tyndale-Biscoe, 2005). By the mid-Miocene the hard-leafed (xerophilous) plant species had appeared, and except for some fragments on the eastern side of the Australian continent, had largely replaced the *Nothofagus* forests (Tyndale-Biscoe, 2005). Concurrently grasses began to appear (Tyndale-Biscoe, 2005) and there is strong palaeontologic and geomorphic evidence of a major faunal assemblage switch-over

that coincided with the emergence of Australian vegetation (Flannery, 1989). During the Pliocene period seasonality increased in Australia, and warm, wet summers alternated with dry winters (Hope, 1982). This resulted in populations undergoing numerous fragmentations, bottle-necks, and intense directional selection, all conducive to speciation (Baverstock, 1982). Such major environmental changes resulted in a wide range of morphological, physiological and behavioural adaptations in Australian macropod fauna. Whilst the morphological and physiological adaptations have been studied across most macropod groups, research on behavioural adaptations has been limited to the larger species that occupy more open habitats, such as free-ranging kangaroo species.

As the forests receded, macropods either took refuge on rocky outcrops or adapted to the drier open woodlands and plains. For rock-inhabiting animals the rocky outcrops provided a number of advantages, including increased availability and predictability of food, shelter from predators, amelioration of climatic variables, and the possibility of defensible food and refuge resources (Mares, 1997; Maynes, 1989). For rock-wallabies, the move to a rocky refuge was either an adaptation to avoid predators as the surrounding habitat became more open, or a need for shelter from unfavourable climatic conditions.

Rock-wallabies are only found on mainland Australia. There is no historical record of them ever occurring in New Guinea or Tasmania, but some smaller islands close to the Australian continent contain populations of these mainland species. It is believed these islands became separated as sea levels rose during the past 9000 to 15000 years (Tyndale-Biscoe, 2005). Past studies of the taxonomic relationships of rock-wallabies across the continent appear contradictory. However, with the advancement of genetic techniques, more recent studies have identified 16 species and 21 distinct chromosomal races distributed among four main species complexes (Tyndale-Biscoe, 2005).

The rock-wallaby genus, *Petrogale,* has the highest species diversity in the family Macropodidae. It is believed that rock-wallaby divergence from its closest ancestor, the pademelon, occurred about 4-million years ago in the eastern Australian forests, about the same time that tree kangaroos appeared in New Guinea (Tyndale-Biscoe, 2005). The evolution of this new macropod, *Petrogale,* may have opened up a new niche for this group on the rocky cliffs and gorges (Maynes, 1989). The ancestral stock of rock-wallabies subsequently spread westwards across the continent (Figure 1.2) and from

the south-west, where the *P. lateralis* species complex arose 3.4 million years ago eastwards across the southern and central regions. The *P. xanthopus* species complex, thought to be the closest genetically to the ancestral stock, arose about 3.7 million years ago and moved in a south-western direction (Tyndale-Biscoe, 2005). Two offshoots of the original eastern stock *P. Brachyotis evolved* in the north about 2.2 million years ago, and around 1.7 million years ago the *P. penicillata* species complex evolved from the eastern branch (Tyndale-Biscoe, 2005).
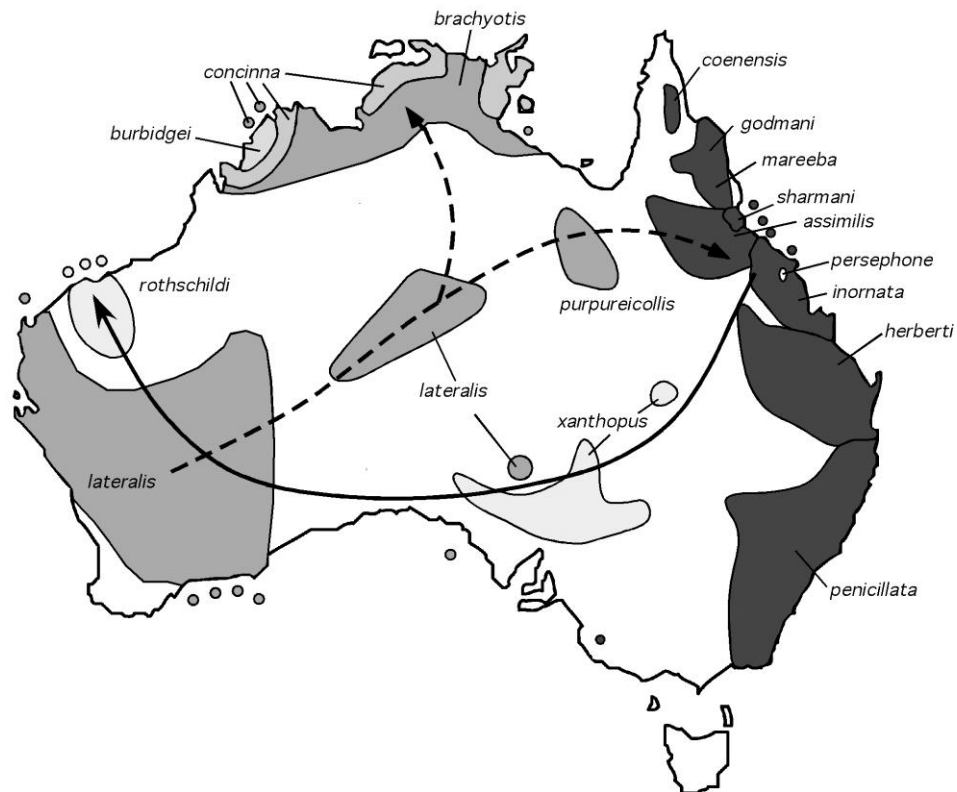
Figure 1.2 Distribution of all 16 species of rock-wallabies, genus *Petrogale* (Tyndale-Biscoe, 2005), after Eldridge and Close (1992, 1997) and Eldridge et al. (1999).

Some rock-wallaby species occupy a wide geographical range and are characterised by discontinuous, widely separated populations. Merrilees (1979) suggested two possible hypotheses for their spatial distribution:

- The species has a high ability to colonise and spread across unfavourable environments until it reaches favourable ones; and
- The present isolated populations are relics from an originally more continuous distribution.

Climatic and vegetation changes during the early evolution and distribution of rock wallabies across the continent may have constrained their movement patterns, particularly when a drier and more open habitat dominated the continent in the late Pliocene. This is consistent with the theory that behaviour patterns evolve to restrict a species' distribution because of negative factors associated with other habitats in their evolutionary past (Drickamer & Vessey, 1992). In addition, since European settlement, changes in landform and the introduction of exotic predators and herbivores would have further isolated these populations.

As discussed earlier, rock-wallaby species are believed to have arisen from a forest-dwelling wallaby, a common ancestor of the pademelon. Evidence exists of significant changes in vegetation across the Australian continent during the rock-wallabies' evolutionary history. Within a forest environment their movements were relatively unrestricted, allowing animals to spread across the entire continent, but over time, vast sections of the continent began to dry out, forcing species to either adapt to a drier open environment or to seek refuge. The adaptation of rock-wallaby ancestors to a drier open environment would have brought about similar physiological adaptations to those of other desert-adapted species, such as the red kangaroo (*Macropus rufus*) and spectacled hare wallaby (*Lagorchestes conspicillatus*). Without these physiological adaptations, rock-wallabies would have to rely heavily on behavioural adaptations around a refuge, which would have significantly constrained their movement patterns, especially during extreme environmental conditions.

1.2.2   Biology and ecology of rock-wallabies

Rock-wallabies range in weight from 1 to 7 kg and like other macropods, have larger hind feet and more powerful hind limbs, which give the animals their characteristic, fast-hopping gait. They have large, well-developed ears, no canines, and adult males are considerably larger than females. Unlike most other macropods, rock wallabies' fur is often distinctively decorative – this acts as a camouflage in the shade and shadows of the rocks they inhabit. Their feet have unusually large pads and short nails (Plate 1.1) enabling them to move easily over smooth rocks (Tyndale-Biscoe, 2005). In addition, their hairy, robust, non-prehensile tail serves as a balancing pole as they move through rocky outcrops, their speed and agility making them ideally suited to life on the rocks.

The main sensory attributes of rock-wallabies are vision and hearing. The eyes are positioned high in the skull, giving them a wide field of vision. The ears are large and move independently through ± 180 degrees, allowing them to detect sounds of varying intensity and frequency from all directions. Although many rock-wallabies occupy sites within dry zones, they do not display the same water conservation physiology as other arid-zone macropods, such as highly concentrated urine. Instead they rely on behavioural (occupying caves and exhibiting nocturnal foraging activity) rather than physiological responses for survival during adverse conditions (Bradshaw et al., 2001; King & Bradshaw, 2008).

a)   b)

Plate 1.1   a) *P. l. lateralis* pes and b) *P. l. lateralis* paw. Photos provided by Hayden Cannon (2012)**.**

Rock-wallabies' feeding strategies limit their distribution to refuge sites that contain both good rock refuge and the necessary food sources. Unlike pademelons, their diet includes more grasses and their molars are crowned higher, reflecting this greater dependence on grass (Tyndale-Biscoe, 2005). Despite this dentition, rock wallabies switch their seasonal diet from predominantly herbaceous plants (grasses and forbes) during the wetter months, to browsing plants during the drier months (Dawson & Ellis, 1979; Copley & Robinson, 1983; Horsup & Marsh, 1992). As in other macropods, the large fore-stomach is adapted for microbial fermentation of cellulose, which together with their dentition, allow rock-wallabies to feed on and digest plant material with a high content of fibre and silica (Tyndale-Biscoe, 2005). Although rock-wallabies obtain most of their water from their food sources, they have been observed drinking (Lim & Giles, 1987; Sharp, 1999).

Rock-wallabies are primarily nocturnal, however all populations studied showed some daytime resting and social activity during the early morning and late afternoon. In some studies researchers observed diurnal feeding during the cooler months (Barker, 1990; Jarman & Bayne, 1997; Telfer & Griffiths, 2006; Sharp, 2009). Generally rock-wallabies shelter inside rock caves and crevices during the day and move out to surrounding feeding areas at night (Jarman & Bayne,1997; Carter & Goldizen, 2003), and could therefore be considered central-place foragers (Sharp, 2009), selecting foraging locations on the basis of forage quality and the ability to see predators (Carter & Goldizen, 2003). However, rock-wallabies do not fit the classical definition of a central place forager, where animals move out from a central location and return to that location to consume their food. Few studies have been conducted on the nocturnal foraging behaviour of rock-wallabies, and none have compared their nocturnal activity patterns on a seasonal basis or compared their diurnal and nocturnal activity patterns.

Rock wallabies have several predators, including the red fox (*Vulpes vulpes*), wedge-tailed eagle (*Aquila audax*), dingo (*Canis familiaris dingo*), cat (*Felis catus*), and carpet python (*Morelia spilota*), (Hornsby, 1997), however only the red fox has been shown to significantly affect population sizes (Kinnear et al., 1988; Hornsby, 1997; Jarman & Bayne, 1997; Kinnear et al., 1998; Lapidge & Henshall, 2001). Kinnear et al., (1988) believed that extant rock-wallaby populations in the central wheatbelt only persisted without fox control if they had access to high-quality rock refuges. If cave occupancy was primarily to avoid predation, then we would expect a refuge expansion once predator pressure is reduced. This was demonstrated when a fox-baiting program was implemented on some of the central wheatbelt reserves and rock-wallabies expanded their range of rock shelter sites within the main rocky outcrops (Kinnear et al., 1998).

 Individuals use more than one cave and more exposed resting sites, and although caves are often shared by individuals, there appears to be male to male intolerance (Telfer & Griffiths, 2006). Females may group together in a cluster of caves, with one adult male defending access to them and their refuges (Jarman & Bayne, 1997). Group size appears to be linked to both the number and size of caves (Barker, 1990; Jarman & Bayne, 1997). Individuals have been shown to continue living in their diurnal refuge sites even after a fire event (Telfer & Griffiths, 2006). Studies have also revealed a refuge-site preference for rocks exposed to the morning and afternoon sun, especially during the cooler months when animals are regularly observed basking (Short, 1982; Nolan, 1997). It is believed that these caves provide protection from both temperature extremes and predation (Short, 1982; Sharp, 1997a), while foraging is limited to

habitats near rock shelter sites (Jarman & Bayne, 1997). The behavioural use of caves and other refuge sites may act as special adaptations for conserving and retaining water, including nocturnal activity. Thus, suitable sites need to have both a number of suitable shelter sites and high food quality and/or abundance in close proximity throughout the year (Telfer & Griffiths, 2006; Sharp, 2009).

Home range sizes appear to vary significantly, from just a few hectares up to 160 hectares, however the majority of studies have suggested that rock-wallabies forage within 400 m of their diurnal refuge (Lim, 1988; Jarman & Bayne, 1997; Telfer & Griffiths, 2006; Sharp, 2009). Variability may be due to weight, sexual, and food availability differences (Telfer & Griffiths, 2006; Sharp 2009).

Although rock-wallabies are found in groups within their diurnal refuges, there is little information on the effects of group size on foraging activity. Blumstein et al. (2001) found group size affected the behavioural patterns of yellow-footed rock wallabies' (*Petrogale xanthopus*), while rock-wallabies foraged more and scanned less as group size increased. Although these authors looked at various mean distances for determining group size, the variance was best explained by the number of conspecifics within a 10 m area, less than that normally used to quantify group size in macropods. It is important to note however, that this study was done in an enclosed environment with supplemental food and water.

In general, macropod dispersal appears to be undertaken predominantly by sub-adult males (Johnson, 1989). However, few studies have examined dispersal patterns of rock-wallabies and existing information is conflicting. Previous trapping and observational rock-wallaby studies did not show any significant dispersal between populations except for some rare single events (Sharp, 1997b; Eldridge et al., 2001). While there is no strong evidence of frequent long-distance dispersal patterns, there are strong signs of inter-group dispersal patterns within populations (Hazlitt et al., 2004; Hazlitt et al., 2006; Piggott et al., 2006). There also appears to be a strong relationship between the timing of inter-group dispersal and the availability of positions within social hierarchies of adjacent groups (Sharp, 1997b). More recently, genetic studies on rock-wallaby populations suggest that they either have poor inter-population dispersal patterns or that the surrounding vegetation in altered landscapes is not conducive to their dispersal (Sharp, 1997b; Piggott et al., 2006). In general, rock-wallabies show high site fidelity with some movement between groups within a population (Sharp, 1997b).

Despite the limited data on rock-wallaby movement patterns, there is general consensus that individuals are unlikely to establish new colonies, especially when the source population is in decline (Sharp, 1997b). A recent genetic study conducted on brush-tailed rock-wallaby (*Petrogale pencillata*) colonies found evidence of four individuals (three males and one female) moving from one colony to a new one (Piggott et al., 2006). There have also been two recorded instances of long-distance movement in *P.l. lateralis* with the establishment of a new colony in the WA wheatbelt (Eldridge et al., 2001) despite the presence of foxes in the surrounding areas reducing their probability of survival. These findings of rock-wallaby dispersal could be a reflection of environmental changes or simply a limited view due to a lack of long-term studies. All rock-wallaby populations studied so far show them to be opportunistic breeders with reproduction success linked to rainfall, but there are signs of continuous breeding when conditions are favourable (Delaney, 1993; Tyndale-Biscoe, 2005). A seasonal effect on survival of pouch young has been found on *P. penicillata*, where offspring born during autumn or winter have a substantially higher probability of survival through to pouch emergence than those born in other seasons (Wynd et al., 2006). Similar results have been found for *P. assimilis* (Delaney, 1993). Sexual maturity is reached between one and two years, and like other macropods, a feature of their reproduction is embryonic diapause, where the developing embryo becomes dormant until more favourable conditions allow it to develop (Poole et al., 1985; Delaney, 1993). Only adults with established good refuges appear to breed, and although one male may have more than one female occupying the refuge, the dominant female appears to produce more young than subordinate females (Jarman & Bayne, 1997).

This limited information on the social structure of rock-wallaby species suggests a linear dominance hierarchical system (Barker, 1990) which is to be expected, since animals with small home ranges regularly encounter one another and would there-fore recognise neighbouring individuals, or at least their status (Sutherland, 1996). Individuals form bonds through regular social grooming and sharing of resting sites and other parts of the home range (Barker, 1990). It is believed that passive displacement behaviour indicates well-stablished dominance relationships (Kaufmann, 1974), so should be common in rock-wallaby species.

These studies highlight the lack for detailed rock-wallaby qualitative behavioural descriptions. In general there were very few studies on macropod behaviour until Kaufmann's (1974) detailed study on the whiptail wallaby (*Macropus parryi*).

Kaufmann's (1974) study strongly influenced the development of macropod ethograms, however these types of studies have been largely restricted to the larger macropod species, and none have been done on *P. l. lateralis*. Clear definitions are needed in any scientific study. Without clear definitions, researchers would not be able to repeat the observations and experiments of others or to interpret the validity of published work, because it would not be clear exactly what behaviour was observed and measured. Therefore it is important to classify, and describe all of the behavioural patterns that are measured in a study (Ploger & Yasukawa, 2003). This review illustrates that there are still many gaps in our understanding of rock wallabies' behavioural ecology and population dynamics.

1.2.3   Historical record of rock-wallabies in Western Australia

In Western Australia, five species of rock-wallabies are distributed over a large geographical range (Figure 1.3). *Petrogale brachyotis*, *Petrogale burbidgei* and *Petrogale concinna* are found only in the northern tropical habitat. *Petrogale rothschildi* is found in the Hamersley and Chichester ranges of the Pilbara region and extends to some offshore islands (Pearson & Kinnear, 1997). The black-footed rock-wallaby, *Petrogale lateralis,* is a genetically diverse species, consisting of three named sub-species (*P. lateralis lateralis, P. lateralis haketti,* and *P. lateralis pearsoni*) and two chromosome races (Eldridge & Pearson, 2008). *P. lateralis* has the greatest recorded distributional range of all rock-wallabies in Australia, from the southern offshore islands and mainland to the central wheatbelt, Western Cape Range and the West Kimberley.

The nominated sub-species, *Petrogale lateralis lateralis,* known commonly as the black-flanked rock-wallaby, was first collected by John Gilbert in the Avon Valley near Toodyay (where it became extinct). Adults range in size from 2.3 to 7.1 kg. Sexual maturity is reached between one and two years, when breeding can be continuous but varies according to seasonal rainfall (Pearson & Kinnear 1997; Van Dyck & Strahan, 2008). Its current conservation status is listed as "vulnerable" by the IUCN and "threatened" under the Western Australian Wildlife Conservation Act. Distribution of this species was formerly widespread (Figure 1.3). It was found in sustainable habitats in the Western Pilbara (WA), on the eastern side of the MacDonnell Ranges (WA, NT and SA), in the central wheatbelt (WA), Darling Range (WA), and southern coastline (WA); as well as on the Recherche Archipelago (WA) and Pearson Island (SA), but its current distribution has significantly declined (Pearson & Kinnear, 1997). This has been attributed to the introduction of predators (primarily the red fox *Vulpes vulpes*) and

herbivores, fire and habitat destruction due to clearing (Pearson & Kinnear, 1997; Kinnear et al., 1998; Gibson, 2000).

P l. lateralis has suffered the largest decline in all WA rock-wallabies (Pearson & Kinnear 1997), with local and regional extinctions occurring most recently on Depuch Island, Querekin Rock in the wheatbelt, and the Murchison River Gorge in Kalbarri National Park. However, translocations were made in 1986 to Querekin Rock and wallabies are still present at this site today. In Western Australia they are now found only in the Cape Range, Calvert Range, Barrow and Salisbury Islands, and seven isolated wheatbelt reserves of granite outcrops (Nangeen Hill, Mt Caroline, Mt Stirling, Sales Rock, Kokerbin Rock, Gundaring and Querekin Rock).

Five of the isolated wheatbelt populations of *P l. lateralis* found on a cluster of granite outcrops in the central wheatbelt, south of Kellerberrin (210 km east of Perth), have been the focus of a long-term experiment designed to assess the impact of fox predation on population dynamics (Kinnear et al., 1988; Kinnear et al., 1998). The region (approximately 150 km²) has granite outcrops ranging from 1 to 3 km² in area, each surrounded by a thin veneer of fringing vegetation consisting of acacia thickets and open low eucalypt woodlands with an understorey of grasses and low shrubs.
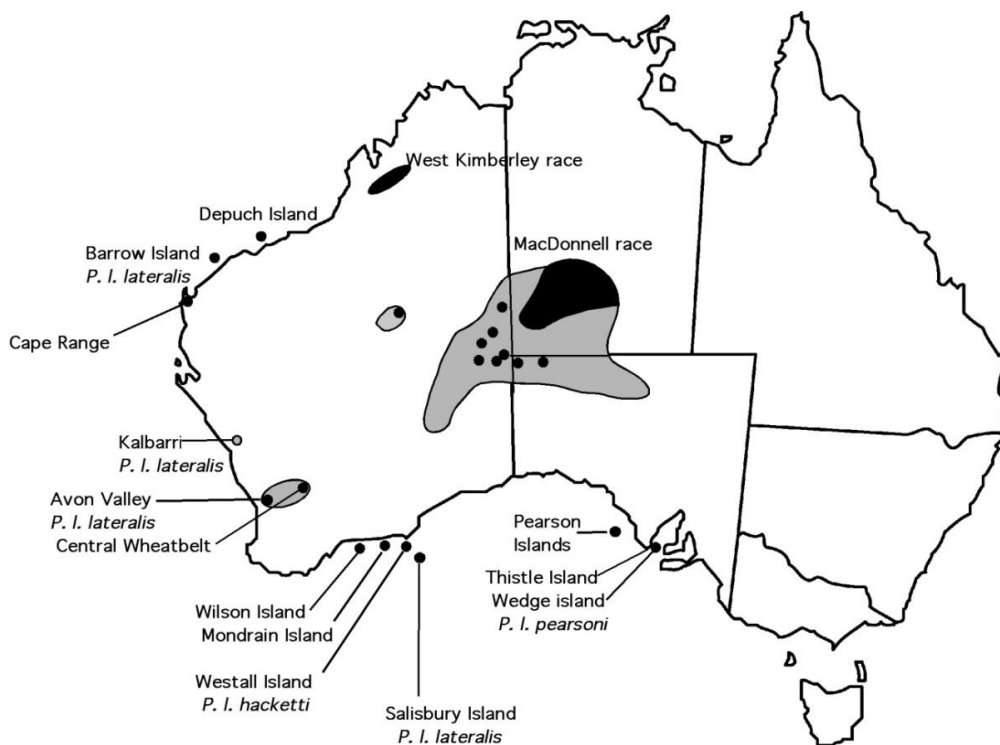
Figure 1.3 Distribution of *Petrogale lateralis*. The dark grey shading represents current distribution, and mid-grey shading, former distribution (modified from Eldridge & Pearson, 2008).

Outcrops and fringing vegetation are surrounded by a matrix of agricultural land primarily used for sheep and cereal crops. Researchers concluded that fox predation was the principal factor limiting the size and distribution of *P l. lateralis* populations and that survival was dependent on the availability of refugia. Removal of predator pressure (fox baiting) produced significant expansion in habitat utilisation and foraging range (Kinnear et al., 1988). Similar conclusions have since been made for other rock-wallaby species (Hornsby 1997; Jarman & Bayne 1997; Lapidge & Henshall, 2001). The persistence of these isolated populations prior to predation control could be attributed to their refuge habitat, which although perceived to be effective, was not the only one utilised once predation pressure was reduced. The refuge habitat was also necessary for shelter from climatic conditions.

Continued predator control has seen rock-wallaby numbers increase on the wheatbelt sites to such an extent that one population (Mt Caroline Nature Reserve) has reached pest proportions, causing damage to adjacent commercial cereal crops (CALM 2001, now DEC). Consequently, boundary fences have been upgraded and a number of animals have been translocated to the Avon Valley National Park (located ± 190 km from Mt Caroline).

There is a long-standing view in behavioural ecology that highly variable environments can significantly affect the behaviour and demography of animal populations. Although this is well documented in birds, primates, and some macropod groups, it has rarely been documented in rock-wallabies. For the success of any current and future re-introductions of rock- wallaby populations into new areas, we need to understand the relationships between the landscape and climatic elements, as well as the behavioural patterns and population dynamics of the species. In addition, although a long-term fox-baiting program has resulted in population increases for this species in the central wheatbelt, fox presence was regularly observed throughout the study. Little is known about the effects of this continual presence on the behavioural patterns of rock-wallabies.

1.3   Behavioural ecology

1.3.1   Foraging and spatial patterns

Animal distribution and foraging patterns have been at the centre of many animal ecological studies for more than forty years, yet they still generate heated debate within scientific circles. Understanding animal distribution and foraging patterns have become important themes for many ecological sub-disciplines; including population, behaviour, landscape, and conservation ecology. Why have these patterns been so important to researchers in the past and why are they still important today? From the perspective of a behavioural ecologist, an individual animal's ability to identify patches in the environment with the highest food density, the highest protection from predation, optimal microclimate for thermoregulation, and food items with the greatest nutritional value is evidence of their ability to solve complex problems (Krebs & Inman, 1994). Studying the ability of animals to track spatial and temporal changes in their environment has thus become an important theme for behavioural ecologists.

Studies of animal foraging patterns have not only contributed to studies of animal learning, they have also led to the highly debated optimal foraging theory. Many ecologists believe that empirically, animals either cannot or do not optimise their foraging behaviour, particularly in ecologically complex situations (Stephens & Krebs, 1987; Johnson et al., 2001). It was thought that the term "optimality" emphasised the wrong aspect of the problem in some instances, and may have done more to obscure than illuminate the scientific questions (Ydenberg et al., 2007). As foraging and distribution theories continued to develop, the importance of habitat/landscape structure emerged. Defining an organism's habitat has also been a contentious issue, mainly due to an earlier human definition of vegetative groups and boundaries. Unfortunately this led to habitat availability being largely determined by the researcher's perception, which is not necessarily the same as that of the animal (White & Garrott, 1991). More recently an organism-centred approach has shown how other factors such as predation and climate also have significant effects on animal foraging and spatial patterns. This chapter discusses the theories developed to understand animal foraging and spatial patterns, as well as their limitations and potential for further development.

The pioneering theoretical paper of MacArthur and Pianka (1966) highlighted the importance of spatial distribution of animals and their interactions with the environment for determining optimal foraging patterns in a heterogeneous environment.

This approach of observing how animals interact with their environment to answer key questions in population ecology was a radical departure from the way ecologists initially viewed foraging behaviour, namely that animals eat what they find and stop when they are satisfied or when the food is gone (Giraldeau, 2005). Several optimal foraging theories and models have been developed, but all predict the behaviour of an animal while it searches for resources, such as food, water, nesting sites, refuge site, or other key niche components.

Although terminology initially differed, the basic components of the models have remained the same over the last two decades (Ydenberg, et al., 2007). Stephens and Krebs (1987) divided these basic components as follows:

- Decision assumptions - which of the forager's problems (or choices) are to be analysed;
- Currency assumptions - how various choices are evaluated; and
- Constraint assumptions - what limits the animals' feasible choices and pay-offs (currency) that could be obtained?

The purpose of these basic optimising foraging models is to predict foraging strategy under specified conditions, where it is assumed that optimal use of energy and time is based on whether the resulting gain in time spent per unit of food exceeds any loss. The currency in early simplistic foraging models referred predominantly to net energy. They assumed that the fitness of a foraging animal was a function of the efficiency of foraging measured in terms of the above currency, and that natural selection had resulted in animals approximating an optimal strategy, providing greater fitness and chance of survival for those individuals (Schoener, 1971).

These simple optimality models have been particularly successful in addressing two main foraging decisions for some animal groups (Pyke et al., 1977; Stephens & Krebs, 1987):

- For predators: whether to attack/consume an encountered prey (prey models); and
- For non-predators: whether to persist in exploiting a patch (patch models).

The processes underlying these decisions may differ between these two main feeding (carnivores or herbivores/granivores) groups.

1.3.2   Prey model

The initial prey model was developed primarily from a predator perspective and required food items to be ranked according to some measure of profit to the feeder, usually expressed as net energy per unit feeding time (Schoener, 1971). The experiment of Krebs et al. (1977) on great tits (*Parus major*) is an excellent example of the prey model. Captured wild great tits were placed in an experimental apparatus where they had the option of collecting one of two prey types - profitable and unprofitable meal worms - by perching above a small window with access to a conveyor belt upon which each type of prey appeared at experimentally set rates. They found that the birds selectively ignored the less profitable prey type, irrespective of encounter rates. Those findings provided the first experimental evidence that relative prey abundance did not determine an animal's choice of prey (Giraldeau, 2005).

The prey model assumes that predators instantly recognise their prey. Erichsen et al. (1980) examined the effects of introducing cryptic prey into the model, again using great tits. Their findings suggested that when predators eat cryptic prey they are highly discriminatory, and even stop looking for profitable prey when they become sufficiently cryptic, thereby excluding it from its optimal diet. The prey model makes a number of assumptions (Sinclair et al., 2006):

- Foragers rank food types in terms of their energetic profitability;
- Foragers always catch the most profitable prey first, then expand their diet to include less profitable prey when the expected rate of gain from specialising in more profitable prey, matches the profitability of poorer prey;
- The decision to specialise or generalise depends on the abundance of more profitable prey but not on the abundance of less profitable prey; and
- An optimal forager has an all-or-nothing response, where the perfect forager will either always or never accept alternative prey, depending on whether the rate of energy gain is below or exceeds the upper limit.

However, this model performs badly with predators of mobile prey and for herbivores in general, as they require a balanced intake of nutrients rather than just energy gain. Although this model predicts that animals will favour the most profitable food items, it does not consider the variation in the quality of food items within the patch. Food sources for both predators and herbivores are rarely uniformly distributed.

1.3.3   Patch model

An individual's choice about when, where, and how long to stop for a feeding bout is an important decision when the resources are widely distributed within a heterogeneous habitat/landscape. This information was disregarded in early simple prey models, and an alternative model was developed called the Patch model. One of the simplest patch model theories in foraging ecology is the Marginal Value Theorem. First introduced by Charnov (1976), this theorem considers the "giving up time" as the time after which an individual should leave the patch it is exploiting. It predicts how long an animal should remain in a given patch until the rate of energy gain from the patch falls below the expected rate of energy gain from all remaining patches. However, the model assumes that all prey items are randomly distributed within identifiable patches, and that the forager has no control over its rate of encounter with patches and prey within a patch, or the amount of time it takes to move from one patch to the next (Gialdeau, 2005).

One special case of the marginal value theorem involves the concept of a central-place forager, which initially referred to animals that forage out from a central location (e.g., burrows, nests, or caves), collect food items and return back to that central location to consume within a safe environment (Orians & Pearson, 1979). This model has attracted a great deal of attention in recent years and now also includes animals that forage more-or-less from a central location and consume prey at their encountered location (Kotler et al., 1999). It makes two fundamental assumptions about central-place foragers (Orians & Pearson, 1979):

- The greater energetic cost of travelling to distant food requires selectivity of food use; and

- The foraging distance travelled should correlate with energetically higher-profit food types consumed away from or brought back to the central location.

The model works well for predators that use a central location for their foraging bouts and for some seed gatherers like rodents, chipmunks and squirrels. The importance of the "giving up time" in the Marginal Value Theorem has been used by Brown (1988) as an indicator of predation risk for granivorous rodents now referred to as "Giving up Densities" (GUD) with higher rates of GUD with increasing rates of predator encounter rates.

There are also many small to medium-sized herbivores that live in burrows and other permanent refuges, such as caves and crevices, and consume food items at their encountered location. These central forms of permanent refuge provide shelter from predators and weather, as well as a safe place for their offspring. Living in permanent refuges affects the interaction between animals and their environment, and strongly affects spatial and foraging patterns. Many herbivores are exposed to predation while foraging and are at greatest risk when distracted by looking for and consuming food. As these animals consume their food at the site of location they are strongly influenced by the threat of predation, so the cost of energetic return must outweigh the risk of predation.

This model also does not take into consideration animals faced with two or more patches of unknown food resource density. An individual that chooses just one patch to forage in without checking others may be in the least profitable patch. It would therefore be prudent to first sample from each patch before selecting the one with the highest return. This has been shown to occur in some species. Krebs et al. (1978) set up such an experiment with birds, where each individual had a choice of two different prey type density feeders. Initially the birds fed from both feeders, but gradually shifted to the one with the highest profitability, lending support to the theory that benefits and costs associated with a foraging bout determine where (Roach et al., 2001) and when (Bakker et al., 2005; Druce et al., 2006) animals forage.

Animals must weigh up the benefits and costs associated with a potential foraging bout. The benefits are food quantity and quality, while the costs are travelling time, handling time, predation risk, thermoregulatory and energy consumption. Habitat structure as well as distance from centrally located refugia could also be expected to influence foraging patterns, since concentrating their foraging in areas that reduce predator efficiency may lower the risk of predation. The resulting spatial variation in foraging intensity can have important implications for distribution and abundance of food sources.

The predictive power of these basic models is limited because they do not include the effects of other individuals' behaviour (Stephens & Krebs, 1987) or social group effects (Giraldeau & Livoriel, 2000), and a new approach was needed to include individual behaviour variability in the model. Two initial approaches comprised the Ideal Free and Ideal Despotic distribution models.

Although these models dominated much of the theory up to the early nineties (Tregenza, 1995), they were first introduced by Fretwell and Lucas (1970), who looked at territorial behaviour and other factors influencing habitat distribution of birds in order to predict the distribution of a single species among several patches.

1.3.4   Ideal Free and Ideal Despotic distribution models

The Ideal Free distribution model refers to an animal that move between patches where rewards are highest without constraint (Fretwell, 1972). Under such conditions animals distribute themselves in the patch where gains will be highest. An individual that first moves into a high-quality patch must then decide the optimal time to move into another patch once more competitors begin to move in. If too many competitors move into the patch, the net energy return would be improved if some moved into the patch of the next highest quality. In this way the model predicts that animals will continually move to new patches until their sampling efforts provide the highest energy-rate gain (Sutherland, 1996). However, as the number of competitors affects the quality of the patch, it may not be beneficial to move among patches, so the average reward should be the same for all individuals in the different occupied patches (Sutherland, 1996).

The Ideal Free distribution model has proved useful in ecological studies, but the two main assumptions of "ideal" and "free" are rarely met in most natural situations, since the model does not account for territorial or dominant animals (Sutherland, 1996). It also assumes that animals have full knowledge of the relative quality of all available patches (Boulinier et al., 2008). Fretwell (1972) developed an alternative model, the Ideal Despotic (or dominant) distribution model to address these concerns. In this model dominant individuals monopolise the best resource patches (Fretwell, 1972). This inter-individual difference in competitive ability imposes constraints on individual movement between patches, thus the assumption of "free" individuals is no longer accurate (Boulinier et al., 2008). The model predicts that there will be disparities in food intake, mortality risk, and reproductive success among individuals (Sutherland, 1996; Sinclare et al., 2006). This negative impact on other individuals' foraging success has also been referred to as "interference", and results in a short-term decline in feeding rates due to fighting, stealing food, or making prey inaccessible by disturbance (Sutherland, 1996).

For species that have clear dominance hierarchies and low-ranking individuals occupying poorer patches, there is a greater risk of mortality due to higher rates of predation as well as lower quality food sources, so an understanding of the relationship between dominance and intake should facilitate a prediction of the number of individuals a site can sustain (Sutherland, 1996).

From a social structure perspective, studies of rock-wallaby populations suggest that they form linear dominance hierarchies (Barker, 1990). If this was common amongst all rock-wallaby species and populations it will have a significant effect on the evolution of foraging strategies due to interference factors and forms of disturbance discussed above. Disturbance in a particular habitat type can also come from threat of predation and is often referred to as risk-sensitive habitat use. One way of reducing this risk is to forage in groups.

1.3.5   Group foraging

The advantages of foraging in groups include learning about local food abundances through introductions to sites where others are already foraging, and learning new foraging techniques (Krebs & Inman, 1994). It also increases the likelihood of detecting predators (Caro, 2005), finding mates, and defending the resource (Schoener, 1971).

However, grouping can also hinder feeding efficiency (Menard, 2004). As competition for food sources is determined by food source distribution and abundance (Menard, 2004) we would expect foraging competition within groups to be high when resources are patchily distributed, and low when they are evenly distributed or wide enough for large groups to feed together, especially where food items are too small to share (Menard, 2004). Individuals that forage in groups must be experiencing a higher payoff than foraging alone, and a simple lowering of the animals' perception of risk will change its behaviour in ways that increase its foraging efficiency.

1.3.6   Predation and climatic effects on foraging decisions

One way to look at group effects on animals' perceptions of risk during foraging bouts is to measure the vigilance and feeding rates, as well as distance from cover of individuals within different group sizes. Vigilance is usually defined as raising the head above a certain level off the ground, a behavioural act that is referred to as scanning. For predators time spent scanning can preclude other important activities such as

foraging. One way to recoup this lost opportunity for foraging in a group is to rely on other members to take on some of the burden of scanning for predators (Barbosa, 2002; Caro, 2005). Vigilance rates have been found to decrease with increasing group size in many animals, including primates (Teichroeb & Sicotte 2012) and some macropods (Blumstein et al., 1999; Blumstein et al., 2001; Wahungu et al., 2001). For some species, distance to cover has been found to be important for determining vigilance rates (Burger et al., 2000; Hochman & Kotler, 2007). Similarly, the distance to the nearest neighbour has been more important to others for determining vigilance rates than group size. There are also individual differences associated with size/age, sex, and the reproductive condition of individuals (Marino & Baldi, 2008).

Climatic conditions play an important role in an individual's decision to not only forage in a group, but also which patch to forage in, and not all patches necessarily have the same perceived risk for each individual or group under different climatic conditions. For example, open habitats may be perceived by animals as a higher risk under specific climatic conditions. A number of animal groups have been found to restrict foraging behaviour to specific patch types when predation risk is perceived to be high, and in situations where they use indirect indicators such as increased moon illumination (Brown et al., 1988; Carter & Goldizen, 2003; Orrock et al., 2004) and high wind velocity (Carter & Goldizen, 2003) to assess predatory risk. However these indicators may not be universal as their effectiveness may be indirectly impacted by anthropo-genic activities such as farming (Shapira et al., 2008). These authors found that gerbils close to farms shifted their foraging habitat during high-illumination nights when fox density was higher. The wheatbelt *P.l. lateralis* populations are contained within an agricultural landscape, with both populations and social groups occupying refuges at different distances from farming patches. A similar foraging habitat shift could therefore be expected. The outcrop on Nangeen Hill Reserve (the focus of this research) contains a large open meadow running along the western side of the rock, and shrub-enclosed habitat along the other sides of the rock. It is therefore possible for rock-wallabies on Nangeen Hill Reserve to exhibit a foraging habitat shift under different climatic conditions.

Fernandez-Duque (2003) found temporal effects of moon illumination on the activity patterns of owl monkeys, *Aotus azarai azarai*. During full-moon nights, nocturnal activity levels were high and the following diurnal period showed very low activity levels; whereas nocturnal activity levels were low in the absence of moon illumination, followed by high activity levels in the following diurnal period. This suggests that

animals were able to satisfy their foraging and social needs during full-moon nights, so there was less need to be active in the following diurnal period (Fernandez-Duque, 2003). Predation risk has also been found to be temporally scale dependent within both the diel period and seasonally in other mammal groups including a rock-inhabiting central-place forager, the hyrax (Bakker et al., 2005; Druce et al., 2006). Thus it is important that studies record activity and behaviour at different times of the day/night and on a seasonal basis under different climatic conditions. While it is clear that predation affects the behaviour of prey, such as increased vigilance in the form of higher scanning rates, vigilant behaviour may also be a response to disturbances by other conspecifics (Hirsch, 2002; Lung & Childress, 2007; Marino & Baldi, 2008).

Another behavioural strategy for reducing predation effects is hiding behaviour. Many animals seek refuge as an avoidance strategy from predators (Sih, 1987; Bakker et al., 2005; Rhoades & Blumstein, 2007). This has significant implications for central-place foragers, where individuals tend to graze less at further distances from their refuge thereby creating a gradient of increasing vegetation (Bakker et al., 2005), and suggests there are important indirect effects from predation and direct mortality effects.

Although the direct effects of predation, such as changes to survival rates and population dynamics are well documented, the indirect cost of predation caused by changes to prey behaviour, is more subtle but nonetheless costly for foraging animals (Searle et al., 2008). Some behavioural ecologists now believe it is important to develop models that incorporate these indirect effects (Brown & Kotler, 2007). Traditional mammalian predator-prey models treat individuals as virtually unresponsive, and focus on predators killing prey. Predator-prey systems are sophisticated games of stealth and fear, so models need to consider the prey's behavioural responses to the presence of predators (Brown et al., 1999). Brown and Kotler (2007) outlined two different predator-driven systems: a) mortality-driven (N-driven) and b) fear-driven (μ - driven). In the former, predators influence the dynamics and abundance of their prey primarily through direct mortality. In a fear-driven system however, predators are no longer controlling their prey's population through mortality, but are strongly influencing prey behaviour through increased vigilance levels (Caro, 2005) and reduced foraging range, predominantly in high-risk patch/habitat types. For a central-place forager this reduction of foraging range places feeding pressure on the resources close to the central refuge (Huntly, 1987; Holmes, 1991; Roach et al., 2001; Bakker et al., 2005). In the wheatbelt rock-wallaby populations, high fox density has been shown to have a severe and direct effect on rock-wallaby dynamics and abundance through mortality

(N-driven system). In the past, a reduction in fox numbers, but not the total eradication, has been accompanied by an increase in rock-wallaby abundance and some range expansion (Kinnear et al., 1998). However, we need to know if the populations alter their foraging behaviour in response to predatory fear (μ -driven system) by increasing their vigilance levels, reducing their movement away from good refuges, and accepting the disruption of foraging bouts when the presence of predators has been detected. It has been shown that the foraging behaviour of macropods is significantly affected by predation risk, including increased vigilance levels, and they remain close to cover when feeding in risky habitats (Wahungu et al., 2001). However the effect of this modified behaviour on macropods is unknown.

Other factors such as thermoregulation also play an important role in foraging strategy (Brown & Downs, 2005; Hill, 2005). How does the animal control its metabolic expenditure to meet seasonal changes in thermal conditions? Some use strategies such as daily torpor, hibernation and diapause to reduce high-energy consumption during unfavourable periods (Schoener, 1971). Others utilise their refuges, assigning higher-energy activities to specific times of the day when conditions are most favourable (Brown & Downs, 2005), or restrict these activities to habitats with more favourable microclimates (Belovsky & Slade, 1986). The cost of sub-optimal thermoregulation can be expressed as an energy deficit and should therefore be viewed as a feeding cost (Schoener, 1971).

Rock-wallabies must assess the cost and benefits of refuge emergence. Benefits include greater foraging opportunities and more social interaction (increasing the probability of finding a mate and therefore the reproductive output of the population). However, refuge emergence must be seen in the context of a specific refuge area, i.e. the enclosed central refuge (caves and crevices) and the foraging refuge (rock and shrub cover). Animals first choose when to emerge from their enclosed refuge and whether to engage in active behaviour (forage and social interaction) or non-active behaviour (rest, groom, and scan) either within or away from the protective refuge situated within or away from the enclosed refuge. Individuals also choose to engage in an activity in the same patch or different patch from other conspecifics. If any of the environmental conditions change, individuals must decide whether to change their activity accordingly, change the location of the activity, or return to the enclosed refuge.

Predation has been shown to be the primary cause of mortality in many declining rock-wallaby populations (Kinnear et al., 1988; Hornsby, 1997; Jarman & Bayne, 1997; Kinnear et al., 1998; Lapidge & Henshall, 2001). In the wheatbelt, Kinnear et al., (1988) believed that prior to fox-baiting, individuals in these populations restricted their movements to the close vicinity of good rock refuge. After a fox-baiting regime was put in place there was an initial expansion in both the permanent enclosed refuge they inhabited and their foraging ranges (Kinnear et al., 1998). Although good rock shelter is important for rock-wallabies to reduce predation risk, it is also believed that the refuge may ameliorate climatic conditions. Thus, hiding time is an important option for rock-wallabies, not only for predatory avoidance, but also to escape from unfavourable climatic conditions. If rock-wallabies stay inside an enclosed refuge too long they will have difficulty meeting their energy needs and may not reach an optimal weight during the winter/spring periods of higher resource availability, to improve survival during the summer/autumn period of low resource availability. Rock-wallabies are expected to balance both the cost of predation and unfavourable climatic conditions with their daily nutritional requirements, resulting in both temporal and spatial changes to seasonal and daily foraging patterns, and possibly even within diel periods. This results in highly variable activity levels over time, reflecting both climate and habitat effects on rock-wallabies' foraging and spatial patterns, as these environmental factors drive the evolution and adaptability of their foraging behaviours.

1.3.7   Habitat effects on foraging and spatial patterns

Patch and habitat choices have been at the centre of the foraging debate, and have been investigated within various spatial model frameworks such as source-sink metapopulations (Pulliam, 1988). For species with geographically discontinuous and fragmented sub-populations, the source-sink metapopulation model has worked well. In this model, habitat patches vary in quality. Source populations are found on high-quality patches where reproduction exceeds mortality and sink populations are found on low-quality patches where mortality exceeds reproductive output.
However, as discussed previously, defining an organism's habitat and patch has caused much debate, the main problem being that the definitions of vegetative groups and boundaries are viewed from a human perspective. The term "habitat" generally refers to a set of environmental conditions under which an individual, species, or community exists (Morrison et al., 2006). A similar definition of an organism's habitat is described by the Grinnellian niche, as the range of environmental factors necessary

and sufficient to allow a species to carry out its life history (James et al., 1984). The Grinnellian niche is now synonymous with the term "habitat" (Shugart, 1998).

The presence of a given species in a particular habitat may not necessarily indicate that the habitat is optimal or even adequate for that species (Van Horne, 1983), since the occupation of a particular habitat may only be due to a preference for that habitat in a specific set of environmental, behavioural, and demographic conditions (such as a refuge for predator avoidance). If one of these conditions changes, habitat preference may also alter. An environment and/or population not in a static state creates significant management problems and landscapes that are significantly modified and controlled, such as the central wheatbelt in Western Australia, are not static because climatic conditions alone are continually changing.

Habitat selection and habitat utilisation are therefore not necessarily synonymous. The active choice of an area by an individual represents habitat selection, whereas habitat utilisation means that an individual occupies a given area, not necessarily by choice (Bell, 1991). An animal may be constrained to a particular patch type due to increased predation pressure, human activity, and inter- or intra-competition.

As with habitat, describing a patch is also problematic, since a vegetation patch may be defined as an area differing in appearance from its surroundings, and a resource patch may be defined by the availability of that resource, its boundaries and its distribution. The problem of a patch definition can be approached in a similar way to the niche concept which defines the total set of resources an organism can utilise in the absence of competition and other biotic interactions as its fundamental niche. However, where there are constraints the actual uptake of those resources by an animal may be very different to its fundamental niche, and is referred to as its realised niche (Hutchinson, 1957). The rock-wallaby population may not have access to all the habitat found within Nangeen Hill Reserve due psychological barriers resulting from strong predator presence or conspecific competition, thus restricting them to a discreet boundary around their rock refuge. So the totality of potential food resource patches and its boundaries could be defined as the "fundamental resource patch". The resource patch actually used by an individual, group or population could be referred to as the "realised resource patch". In this organism-centred perspective on resource, habitat patch and landscape size will differ among organisms because the size depends on the habitat mosaic and resource patches meaningful to that particular organism (McGarigal & Marks, 1995).

The smallest and coarsest scale of heterogeneity from an organism-centred perspective is "grain" and "extent" respectively. Patches can be defined hierarchically in scales, ranging between the grain and extent for the individual, group, population and total range of each species (Kotliar & Wiens, 1990; With, 1994). From a human perspective, patch boundaries are artificially imposed; boundaries, sizes and types of patches are only meaningful if they reflect an organism-centred perspective. This organism-centred approach is now being adopted into ecological research design (With, 1994; Kerthoff et al., 2000).

A resource can be defined as a food source, water, cover, shelter, or potential mate. Resources are generally patchy, so the search behaviour of animals is designed to locate a patch and search within a patch (Bell, 1991).The amount of time spent moving to acquire resources and the movement patterns employed are specific to a particular type of resource and vegetation patch type, to the individual's sex, age, reproductive state and its hierarchical position, and to particular seasons and climatic conditions (Bell, 1991). Researchers studying resource usage will investigate the acceptable range of a given resource type, which may include grasses and browse, and more acceptable food types than others. The same criteria can be applied to shelter so for example, shelter could include caves, crevices, dense understorey, or even tall herbaceous plants (e.g. agricultural plants such as wheat). Each type of shelter must meet specific (or individual) requirements.

Resource use by an animal is restricted by the landscape structure, the behaviour of conspecifics, the population structure, size and dynamics, and inter-specific competition and predation pressure. These constraints ultimately determine the niche of an animal at a given point in time and in a given unit of space. One or more of these constraints may confine an individual or population to a narrower resource range. For example, only the outer edge of a food resource patch (such as open grassland) close to cover may be utilised by a group of animals, especially if predation pressure is high.

The total resources used, i.e. the way resources are exploited by an individual, group or population, can be measured and defined as the niche width. If niche width for a specific individual, group or population is constrained by the availability of different vegetation patches, and this availability increases, we need to examine whether the niche width increases. For example, in Western Australia, rock-wallabies translocated from significantly altered landscapes in the central wheatbelt (Mt Caroline Reserve and Querekin Rock) to more ecologically stable landscapes in the Avon Valley (Avon Valley

National Park and Paruna Sanctuary) significantly increased their niche width due to an increase in habitat diversity, and the availability and spatial scale of resources. It is therefore important to examine the behavioural patterns and population demographics that are affected by environmental changes in order to better understand the complex relationships between animals and the environment.

The correlation between resource availability in different vegetation patches and population demographics creates significant problems for the management of any species. This highlights the need for future research to understand the relationship between the landscape, and the behaviour and population dynamics of the species using that habitat. Understanding how animals perceive their environment and how they adjust to changes in their environment are paramount for the future management and survival of all species. To ensure the survival of *P. l. lateralis* populations, long-term, demographic and behavioural data are needed to identify factors that affect the population dynamics.

The focus of this study is to understand how the Nangeen Hill Reserve rock-wallaby population perceives its environment. This is an important step towards predicting the future spatial distribution of this subspecies, and reducing the risk of decline under different sets of environmental and population demographic conditions.

We have seen that the earlier foraging theories and subsequent models viewed the quality and distribution of food items and their abundance as the primary causes of variation in foraging behaviour. Although other environmental factors such as climate and predation have been touched on, they are still rarely considered. In seasonally changing environments foraging behaviour must be adapted so that animals can meet their nutritional needs (Owen-Smith, 2006). This adaptation is especially important, and possibly essential, for central-place foragers who rely on the refuge during times of environmental stress. No theory that includes optimal choice of feeding periods over an activity cycle has yet been fully developed even though there is considerable observational evidence to suggest that climate is extremely important in models of optimal feeding periods. This will become more important in the future as climatic conditions are expected to become more variable and unpredictable. Understanding how animals adjust to the changes in their environment is a key element in behavioural ecology to examine and measure their adaptability. Not only has it been important in understanding which foraging patterns a species, population or individual adopts, but also for further development of theories and our understanding of social systems,

population dynamics, and predator-prey dynamics. All of these are intrinsically linked to the evolution of the species.

1.3.8   Animal adaptability to ecosystem change

Understanding why a population or species lives in a particular habitat or landscape, including population, behavioural, landscape and conservation ecology is a central theme in a number of ecological disciplines. In behavioural ecology, researchers assess how an individual, population, or species has adapted to its environment. The populations of a widely distributed species may experience different climatic and/or landscape conditions, each resulting in a different set of selection forces and associated behavioural adaptations. Management regimes developed from data based on one population may not apply to other populations living under a different set of environmental conditions. Similarly, if the tested population is found in a highly variable environment and this is ignored by the researcher, management regimes developed from the data may also be inappropriate if any one of the environmental conditions changes over time. Understanding how animals react to these changes provides insights into their ability to make complex decisions. This has clearly been shown in some animal groups such as primates (Van Schaik & Brockman, 2005), but rarely in marsupials, due to the exclusion of behavioural elements as direct components of the monitoring and research framework.

Unlike marsupials, primates are predominantly diurnal, so once habituated, easy to observe. This has resulted in more highly descriptive profiles of their activity budgets, range use, and reproduction, than any other mammalian order (Van Schaik & Brookman, 2005). Studying the behavioural ecology of marsupials is difficult as they are predominantly nocturnal, often very cryptic, and inhabit harsh environments. This limited understanding of the behavioural mechanisms of our marsupial species could result in inappropriate management, such as poor success in translocations and inadequate long-term monitoring procedures. Like primates, rock-wallabies appear to be substrate-bound and unable to undertake lengthy seasonal migrations to escape from periods of unfavourable conditions (unlike other macropods such as the red kangaroo). Therefore, if some behavioural adaptations of our substrate-bound macropods are similar to eutherian counterparts such as primates, it may help us further understand the evolution of adaptations to highly variable environmental conditions and complex decision-making processes.

Distribution of a species is influenced by conditions in its abiotic environment, which include variable factors such as temperature and rainfall. The climatic limits that a species can acclimatise too are referred to as its tolerance limits. These can be offset by using a refuge to extend the range of conditions that a species can reside in. The downside for animals occupying a refuge is restricted movement, which can isolate populations if spatial distances are too great between refuge habitats, and may occur only at times when strong seasonal climatic changes prevail, such as increases in temperature. The potential for the thermal environment to constrain habitat choice may be exacerbated if protective cover, either in the form of rock or vegetation, is not equally distributed between habitat types (Hill, 2006). Changes in biotic conditions, such as changes to landform by agriculture and the introduction of feral animals, also impact on movement between sites. An understanding of how animals react to these changes is important for their conservation and management, since reserves are continually fragmented by human activity and affected by feral animals and weed invasion. Before any management practices are implemented a species' tolerance limits and behavioural adaptability to changes in both its biotic and abiotic environments must be determined, yet this is rarely done in marsupial studies, and could result in poor survival rates for reintroduced animals and increased extinctions of local populations in small fragmented reserves.

In general, the effect of the abiotic environment on the ecology of animals has received less attention than the biotic, even though both temperature and rainfall have been shown to have significant effects on the distribution of many species. Many use habitat structures for refuge, yet the physical habitat structure has received even less attention. These structures may take the form of rock caves, crevices, overhangs, sand dunes and dried river bank walls – physical structures that tend to have a discontinuous and fragmented spatial distribution and reflect the distribution of species reliant upon them. Rocky outcrops, their associated plants and microclimate, make it possible for many species to specialise in habitats on the rocks, or to live on the rocks when the surrounding habitat is marginal due to drought or other factors (Mares, 1997). As discussed earlier, these physical structures also aid in ameliorating climatic conditions by helping animals to reduce their energy and water expenditure.

When looking at energy storage and expenditure, and water retention, there are two main types of adaptations a species may have evolved:

- physiological adaptations; and
- behavioural adaptations.

1.3.9   Physiological adaptations

Animals have evolved a number of physiological adaptations to reduce energy expenditure and water loss. Body size is one, where the lower surface to body mass of larger animals leads to greater thermal efficiency needed for colder climates (Degen, 1997). In contrast, the higher surface to body mass in smaller animals offers greater relative area for heat dissipation, an advantage in warmer climates (Degen, 1997). An animal's extremities or appendages can also be used to reduce or increase heat loss. For example, large ears in desert animals compared to their non-desert counterparts are important sites for heat exchange with the environment (Degen, 1997). Animals that occupy arid habitats have evolved very efficient kidney and renal functions to produce highly concentrated urine as a physiological response and for survival during adverse conditions (Degen, 1997; Bradshaw et al,. 2001). This adaptation has been found in some of Australia's macropod species, including the spectacled hare-wallaby, *Lagorchestes conspicillatus* (Bradshaw et al., 2001; King & Bradshaw, 2008), the euro kangaroo, *Macropus robustus* (King & Bradshaw, 2008), and the red kangaroo, *Macropus rufus* (Denny & Dawson, 1977), but not in rock-wallabies (Bradshaw et al., 2001).

1.3.10   Behavioural adaptations

Behavioural adaptations provide alternative ways of increasing energy by reducing energy expenditure (Brodin & Clark, 2007). This also applies to reduced water loss and predation costs. Both metabolic and predation costs will vary under different climatic conditions. Since energy stores will last longer if an animal reduces its metabolic rate (Brodin & Clark, 2007), a number of behavioural strategies have evolved to minimise the metabolic costs during environmentally stressful periods. These strategies generally fall into one of the following categories: hibernation, torpor, or hypothermia.

Species that have not evolved any of these strategies can only reduce their activities during environmentally stressful periods by adopting more sedentary behaviours (Hill, 2005), by remaining inside a refuge until conditions become more favourable, or by conducting specific activities within habitats with more favourable microclimates (Hill, 2005).

All terrestrial animals that do not live on or near the equator experience seasonal changes in day length and associated climatic variables, and would therefore require behavioural flexibility in their diel activity patterns and time budgets (Van Schaik & Brookman, 2005; Hemingway & Bynum, 2005). The affects of seasonal changes on activity levels have been recorded in a number of animal populations (Fernandez-Duque, 2003; Hill et al., 2003; Mun Oz-Delgado et al., 2004; Hill, 2005). These changes have been linked to a number of abiotic environmental conditions and include day length (Erkert & Kappeler, 2004), temperature (Hill, 2006), and moon illumination (Brown et al., 1988). Many animal species reduce their daily activity as daily air temperature increases (Belovsky & Slade, 1986). However, little is known about how rock-wallabies react to these seasonal and meteorological changes.

There is a scarcity of research on how animals react to environmental changes within the diel period. Moon rising and setting times change daily, and wind velocity, cloud cover, precipitation and temperature change daily and within the diel period. How do animals compensate for these changes in their environments? Do they adjust their behaviour accordingly, or do they only adjust their activity levels on a seasonal basis but not on a daily basis? Change in animal activity budgets within the diel period is an indication of its ability to make complex decisions, by continually assessing its environment and deciding which activity to engage in and where. Animals that are subject to predation within highly fluctuating climatic conditions have to balance metabolic and predation costs, creating a strong selective pressure for the evolutionary development of complex decision-making processes. Without this ability for finely-tuned management of energy, crucial for survival and reproduction, these animals would not be able to survive in seasonally fluctuating environments (Brodin & Clark, 2007). However, few studies have investigated these effects.

Examining animals under differing climatic conditions provides an opportunity to assess climatic effects on habitat use relative to predation risk. Natural selection favours the development of either physiological or behavioural adaptations. Researchers who

ignore behavioural adaptability will fail to develop robust and predictable ecological models to manage populations, particularly during geological periods of highly accelerated climatic changes. It is therefore important to determine the level of variability and their effects on tolerance levels and adaptability, so that those individuals at higher risk to changes in their ecosystem can be identified. For example, if females show a greater sensitivity to increased predator presence or vegetation clearing, then a proportion of that population will be more restricted and isolated. Similarly, if males predominantly disperse away from source areas, the long-term establishment of new colonies will be severely restricted. Dispersal studies have frequently found males to be the predominant dispersers. However we don't know whether this is due to the evolution of their social structure and dynamics or to ecosystem changes that have had a greater selective effect on one group of individuals. Without understanding these effects, the social and foraging patterns, and population dynamics could be misinterpreted and poorly managed.

Rock refuges provide a thermally comfortable, mesic micro-environment within a harsh, xeric macro-environment for rock-wallabies. These refugia reduce the daily and seasonal fluctuations of temperature that occur throughout the range of *P.l. lateralis*. Small macropods cannot remain exposed to hot summer conditions for lengthy periods without resorting to evaporative water cooling for heat dissipation, as their relatively large ratio of surface area to body mass compared with larger animals will result in excessive loss of water and dehydration. They do not possess sweat glands, so cutaneous water loss occurs by diffusion through tissues. Emergency thermoregulation is achieved by salivating on the forearms. Access to free water is an important thermoregulatory strategy for many mammals (Hill, 2005), and plays an important role in rock-wallaby populations subjected to prolonged periods of drought. The absence of free water could impose significant thermoregulatory constraints on rock-wallaby populations.

It is clear that the thermal environment, as well as other climatic and meteorological conditions, can significantly constrain an animal's decision-making (Hill, 2006). However, the importance of these abiotic conditions as a constraint on behaviour, including activity scheduling and habitat choice, have received little attention in the literature compared to other ecological factors (Hill, 2006).

1.4 The relevance of behavioural and landscape ecology to conservation and management

In order to manage and conserve any population we need to understand its morphological, physiological and behavioural adaptations to the environment. Elements of behavioural ecology in regard to reproduction, use of habitat, dispersal, competition and predation have all been important to the development of modern ecological principals, including a number of foraging and social paradigms, predator-prey dynamics, and animal and habitat interactions. In addition, these behavioural characteristics impact on population size (Anthony & Blumstien, 2000) and are important determinants of the spatial dynamics and distribution of populations (Lima & Zollner, 1996), yet behaviour has rarely been incorporated into population ecology, landscape ecology, or conservation and management programs.

Over the last ten years the importance of understanding how individual and group behaviour affect ecological processes, thereby effectively integrating the various sub-disciplines, has received growing support (Fryxell & Lunderberg, 1998; Anthony & Blumstien, 2000; Caro, 2007). If the general aim is to understand the effects of landscape heterogeneity on higher-level processes, then it is important to investigate behavioural responses of individuals to landscape structures (Peles et al., 1999).

Combining behavioural ecology with conservation biology was deemed problematic at first, since conservation biology is largely aimed at preventing population extinction, while behavioural ecology attempts to understand the way in which behavioural and morphological traits contribute to the survival and reproduction of individual animals under different ecological conditions (Caro, 1998). However, behavioural biologists have much to contribute to conservation biology, and their exclusion from conservation and management plans may result in avoidable setbacks, waste of precious funds and the loss of animals, populations and ultimately species (Blumstein & Fernandez-Juricic, 2004).

Combining behavioural ecology with conservation biology has seen the evolution of a new discipline, "conservation behaviour," which investigates how proximate and ultimate aspects of an animal's behaviour can help to prevent the loss of biodiversity (Buchholz, 2007). Many researchers fail to recognise that behavioural biologists and conservationists can produce generalised and predictive models (Blumstein & Fernandez-Juricic, 2004). It seems impossible to understand the behavioural ecology of an individual, population or species outside the context of its physical environment,

and it is therefore not surprising that we have seen the emergence of the new scientific discipline of landscape ecology.

Like conservation biology, landscape ecology is a relatively recent branch of ecology, which emphasises the interactions between spatial pattern and ecological process. It covers many fields of ecology-related sciences, such as geography, botany, zoology and animal behaviour. All of these incorporate the problem of "space", which is widely recognised as the new frontier of ecology. Landscape is an important component of this space (Farina, 1998; McIntyre & Wiens, 1999). It is clear that regardless of spatial scale, nature is never uniform and patchiness prevails, so that the landscape appears to be comprised of a mosaic of habitat types (Hansson et al., 1995). In an ecological context, a heterogeneous landscape can be defined as an ecological system containing vegetation patches of more than one community-type (Forman & Godron, 1986; Lidicker Jr., 1995) occurring in both terrestrial and aquatic situations and varying greatly in absolute size (Lidicker Jr., 1995). Although ecologists have always known that nature is patchy and heterogeneous at virtually any scale, field ecologists have historically tended to focus on the patterns and dynamics of ecological systems within relatively homogeneous habitat types (Wiens, 1997).

This mosaic of habitat types may serve different functions, such as reproduction, foraging and/or dispersal (With et al., 1997). The composition, configuration and connectivity within a heterogeneous landscape may change in space and time due to natural and human disturbances such as fire, drought, weed invasion, and habitat loss from land clearing and/or introduced herbivores (Morrison et al., 2006; Gough & Rushton, 2000). Animals that are sensitive to their surroundings may make important decisions with regard to movement, dispersal and habitat selection which will determine their dynamics and spatial distribution, all of which are related to both landscape and behavioural ecology (Farina, 1998).

The patterns of movement in heterogeneous landscapes are interrelated with the concept of habitat use, where the ability of individuals to move among patches within the landscape varies depending on the quality of landscape elements that are utilised by individuals (Barrett & Peles, 1999). In a landscape with a matrix predominantly composed of agricultural land, the long-term survival of populations that are reaching carrying capacity could be significantly hindered if movement of these animals is restricted between populations. In the Western Australian wheatbelt populations of *P l. lateralis,* one type of movement, dispersal, believed to be a decisive factor in both the

persistence of colonies and the establishment or re-establishment of new colonies (Hansson et al, 1992), has been significantly restricted due to human activity.

Resource use by an animal may be restricted by the landscape structure and its dynamics, the behaviour of conspecifics, population structure, size and dynamics, as well as inter-specific competition and predation pressure. These constraints ultimately determine the niche of an animal at a particular time in a particular unit of space. One or more of these constraints may confine an individual or population to a narrower resource range. For example, only the outer edge of a food resource patch (open grassland) close to cover may be utilised by a group of animals, especially if predation pressure is high. The total resource use, i.e. the way resources are exploited by an individual, group or population can be measured, and is defined as its resource niche width. If niche width for a specific individual, group or population is constrained by the availability of different vegetation patches, and this availability increases, we should examine whether the measure of niche width increases. The complex relationship between resource use, availability of different vegetation patches and population demographics creates significant problems for the management of any species, and emphasises the need for future research to understand the relationships between the landscape elements and the behaviour and population dynamics of a species and its habitat use. Understanding how animals perceive their environment and how they adjust to changes in their environment are paramount for the future management and survival of all species. For the survival of *P l. lateralis* populations, long-term demographic and behavioural data are needed to identify features that determine the dynamics of these populations.

In this chapter, the reader has been introduced to the main themes underlying the research aims within the literature, and the gaps in current research on rock-wallaby behavioural ecology. In chapter 2 these issues are brought together within a theoretical framework that forms the setting for the major aims of the research study. The methodological approach is outlined and the study location described. Thereafter each chapter is constructed with its own specific aims, introduction, methods, results and discussion. The final chapter summarises the outcomes of the research in the context of the main aims.

Chapter 2

Theoretical framework, research aims, study site, and the importance of preliminary studies

2.1 Theoretical framework

This study investigated how animals adapt their foraging activity to seasonal environments, fear of predators and conspecifics and how their behavioural ecology, the landscape and habitat structure, social interactions, population size and structure influence niche parameters (resource states). This type of study involved the confluence of a number of ecological sub-disciplines, including behavioural ecology, landscape ecology and population ecology. All are important to enhance our understanding about population and species extinctions, so this study was designed to combine different aspects of these fields of research. The research questions were aimed at examining three factors**:**

- The behavioural characteristics and abilities of *P. l. lateralis;*
- External environmental and conspecific factors determining what resources are available, the risks of obtaining those resources and the potential barriers to accessing them; and
- Internal factors, such as the level of physiological need relative to a certain kind of resource (e.g. starvation or sexual maturity), determining what an animal requires at a particular time, and the manner in which that requirement is altered by age, sex, reproductive status and external environmental influences.

It is important to note that all species are dependent on a number of environmental resources, and at the same time, restricted by the specific environmental conditions in which they live. A species' environmental resources are confined to their habitat, which is not a static system since resource availability, abiotic (climatic conditions) and biotic conditions (resource distribution and abundance) change over time. Before we set out to understand how an animal population responds to disturbances and environmental changes, we need to determine the species' habitat requirements and how its structure and composition affect animal movement and habitat use. We also need to understand how the biotic and abiotic habitat conditions affect the animals' behaviour, their population structure and dynamics, their social interactions and ultimately their ecological niche.

Animal movement patterns in the environment reflect an organism-centered response to habitat structure and resource distribution. There are many different interpretations of the term "landscape." Since this study uses an organism-centred perspective, the size of the landscape varies depending on what constitutes a habitat mosaic or resource patches meaningful to that particular organism (Mcgarigal & Marks, 1995). On both an individual and population level, animals may respond to the above factors at different spatial and/or temporal scales. Investigation across scales allows us to track processes that are functioning along hierarchical systems and to determine whether patterns alter at different scales.

Since the abundance and structural complexity of shelters available to rock-wallabies depends on the prevailing geology, their distribution is largely determined by the landscape. The size and number of caves determine the local density of rock-wallabies; whereas the refuge distribution, the surrounding habitat and other environmental conditions shape their social structure, population structure and foraging patterns. These in turn are not static, as strong seasonal influences continuously change environmental conditions.

Optimal foraging theory predicts that as preferred food items become scarce, less preferred items will be included in the rock-wallaby's diet and patches of food will be more depleted before the forager moves on to the next patch. We know that rock-wallabies behave like central-place foragers, causing a grazing gradient radiating from the central refuge. Viewed from the perspective of an ideal despotic/interference distributional model, we would expect to see individual variation of patch occupancy, with dominant individuals occupying the more favourable resource patches. In populations under predation there would be a higher probability of animals occupying microhabitats that reduce predation, again with dominant individuals occupying the more favourable resource patches. Optimal foraging theory predicts that animals maximise their net energy and nutrient gains while minimising their metabolic and predation costs in extreme climatic conditions, either by scheduling their activities during more favourable conditions and/or shifting their activities to microhabitats with more favourable microclimates.

Rock-wallabies have a highly fragmented distribution over a large geographical range and are subject to significant environmental variation. They appear to be substrate-bound and show strong signs of site fidelity. These factors make rock-wallabies an excellent species for studying the effects of various environmental conditions at

different temporal and spatial scales on their behavioural ecology, and how this in turn affects their social structure and population dynamics. Central to this study is the importance of a diurnal central rock refuge (hereafter simply called "the refuge") and how this important resource shapes the ecological niche of this species.

If rock-wallabies lack the physiological adaptations to cope with extreme unfavourable conditions, then we would expect evolution to maximise the behavioural adaptations to allow these animals to successfully maximise their energy and nutrient gains while minimising their metabolic and predation costs. Where existing behavioural foraging patterns have not evolved to cope with present or future environmental conditions, such as the introduction of exotic carnivores and herbivores, and habitat loss or change, including weed invasion, we would not expect to see populations in equilibrium with their environment. This could result in significant losses in population abundances and distribution, and eventually, local extinctions.

This study enables a greater understanding of the various environmental conditions affecting behavioural patterns in rock-wallabies and how they can be used to assess the effects of climate change in the future. It also provides a greater understanding of the evolutionary processes that have shaped these behavioural adaptations, including the ability of animals to make complex decisions.

2.2   General research aims

The rock-wallaby population in the Nangeen Hill Nature Reserve in the central wheatbelt of Western Australia was the focus of this study. It was aimed at:

- Developing a comprehensive behavioural repertoire of this rock-wallaby population;
- Examining the effects of a number of selected environmental variables on the behavioural ecology, social structure and population dynamics of rock-wallabies. The factors investigated were:
    - climatic and meteorological conditions;
    - predation;
    - conspecific interactions; and
    - habitat structure

- Investigating the behavioural mechanisms that determine the realised niche width parameters (food and shelter states) of this rock-wallaby population;
- Investigating the foraging patterns employed by this species in the ecologically altered landscape;
- Investigating the behavioural adaptations that *P.l. lateralis* undergoes to find resources, while maximising net energy and minimising metabolic and predation costs;
- Investigating any modifying effects of sex and age on the behaviour of the rock-wallabies, and how this in turn affects the population's behavioural ecology under different day/night lengths, climate, habitat, and demographic conditions; and
- Investigating how the population size, density, and structure, influence the behavioural interactions and movement within the landscape.

From the literature review in chapter 1, it is clear that there are a number of biotic and abiotic factors that can influence the behavioural ecology of a species. The Nangeen Hill rock-wallaby population is found within an ecological altered landscape and a highly variable climatic environment, is under constant predation threat, inhabiting a discreet continuous rock refuge habitat, resulting in a possible high population density. Using this information and the preliminary result of this study the following predictions were made:

1. The Nangeen Hill rock-wallaby population will exhibit dominance hierarchical behaviours such as passive and non-passive supplanting (displacement);
2. The Nangeen Hill rock-wallaby population will exhibit strong seasonal foraging and non-foraging behavioural adaptations, reducing water and heat loss;
3. The Nangeen Hill rock-wallaby population will exhibit strong vigilance and avoidance (disturbance) behaviour, to offset risk from predators and conspecifics;
4. The Nangeen Hill rock-wallaby population will show strong signs of foraging constraint, restricted to close vicinity of rock refuge, less adverse climatic conditions and/or good habitat cover, due to fear of both predators and dominant conspecifics;
5. The Nangeen Hill rock-wallaby population will exhibit strong rock-refuge site fidelity reflected in a defined individual and group spatial distribution;
6. The Nangeen Hill rock-wallaby population will significantly decline if food resources are continually depleted.

The Nangeen Hill population appeared to have reached or was close to the carrying capacity of the reserve, and individuals appeared to be restricted in their movement patterns and habitat use, yet there was little understanding of the mechanisms that impacted this. As the ecological niche of a species includes both the animals' physical habitat and its adaptation to that habitat, this study combined elements of animal behaviour, landscape ecology and population ecology. For this reason the methodology for this study formed an integral part of the research aims, combining multiple approaches to develop a more comprehensive picture of the environmental variables that impact on the behavioural ecology, social structure and population dynamics of rock-wallabies. The advantages and disadvantages of each method are discussed for both biological and management implications.

2.3   Methodological design

2.3.1   Target population

The Nangeen Hill *P. l. lateralis* population is located in the central wheatbelt of Western Australia. It was chosen because of its location within a significantly altered ecological landscape and exposure to variable climatic conditions. In addition, the concentrated refuge spatial distribution located on one side of the rocky outcrop and adjacent open meadow allowed easy viewing and observation of a large population sample size at one time.

During stage 1 of the fieldwork, social conspecific groups in these populations and in the best rocky outcrop section, including largest surrounding meadow area, were identified for maximum visibility of the groups and their foraging movements. Within the selected groups animals were categorised into age classes, sex, and where possible, reproductive status.

2.3.2   Study and thesis design

In order to understand the environmental effects on the ecological niche and needs of the black-flanked rock-wallaby (*P. l. lateralis*), a fundamental understanding of their behaviour is imperative. A behavioural ecological field study of this kind needs to employ an array of methods that complement one another to achieve the major research aims. In addition, each method set out to accomplish a set of specific aims that contributed to the main research aims. A number of preliminary field studies were required to establish the feasibility of the methods chosen. Thus the research was organised in two stages.

Stage 1 was designed primarily to:

- Habituate rock-wallabies to the presence of the observer;
- Develop appropriate behavioural observation methods (including locating adequate observational viewing locations), scat distribution methods and trapping techniques to evaluate their feasibility in adequately answering the major research aims;
- Develop a comprehensive qualitative behavioural repertoire (ethogram) for the Nangeen Hill rock-wallaby population to further develop and finalise the observational methods;
- Identify and select a number of representative individuals and social groups at Nangeen Hill Reserve for observational research studies in stage 2; and
- To determine the central diurnal refuge locations.

Stage 2 comprised the main data collection (chapters 4, 5 and 6). The ethogram and a comprehensive qualitative description of this rock-wallaby population's behavioural patterns (chapter 3) was not finalised until the completion of stage 2. The result of such a methodological design, was that the study included major research objectives and a strong investigative component, including a critique of the methods themselves. Each of chapters 3 to 6 includes a short introduction, a set of specific aims, methods, results and a discussion. The final chapter summarises the outcomes of the research in the context of the main aims and provides a critique of the methods used, conservation and management outcomes, and a discussion about the contribution of behavioural ecology to future animal studies.

A population decline occurred (field studies requested by DEC and undertaken by the researcher between 2010 and 2012) during the writing phase of this thesis, and whilst unfortunate, it provided an opportunity to apply the research outcomes to important management strategies for this population. It also provided an excellent forum to discuss the importance of including behavioural ecology into ecological studies for enhanced understanding of the complex ecological relationships between animals and their environment.

Behavioural data was first analysed by JWatcher 1.0 and then transferred to SPPS version 16 for further analysis. Other raw data were transferred to Excel and then to SPPS version 16 for further analysis where required. Due to the nature of the

behavioural data, multivariate parametric methods were found not to be applicable, so non-parametric tests were conducted where possible, to compare seasons, times of day, sex and climatic conditions between the numbers of active animals observed, and the amount of observation time spent on each general behavioural activity.

2.4   Study area

2.4.1   The central wheatbelt (Kellerberrin) in Western Australia

The central wheatbelt *P.l. lateralis* populations are located in the south-western region of Western Australia, about 200 km from Perth. They are situated within the south-west Yilgarn Craton composite terrain (Figure 2.1), a large body of Archaean crust comprising predominantly gneiss, granite and greenstone rocks of 3.7 to 2.6 Ga in age (Myers, 1993).
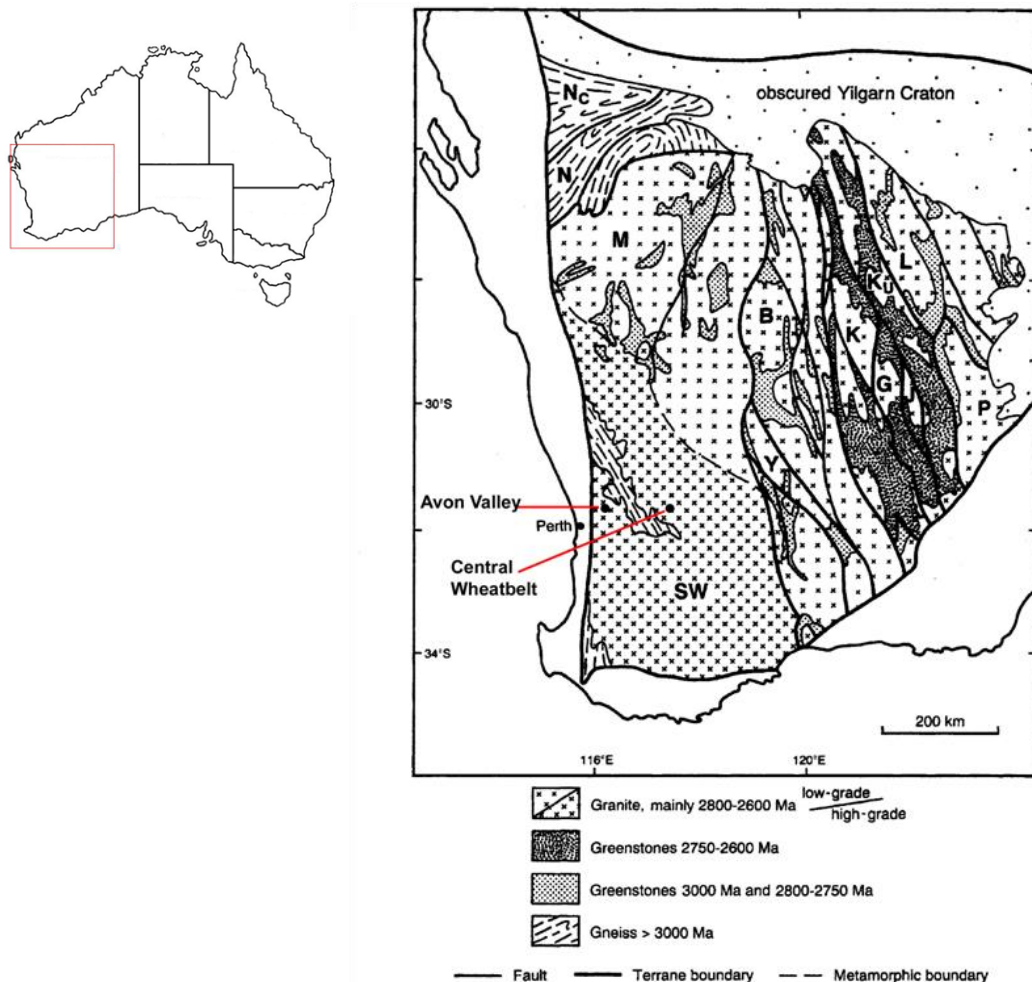
Figure 2.1   Study site location and the main tectono-stratigraphic terrains of the Yilgarn Craton: B – Barlee, G – Gindalbie, K – Kalgoorlie, Ku– Kurnalpi, L – Laverton, M – Murchison, N – Narryer, P – Pinjin, Y – Yellowdine, SW – South-west Yilgarn composite terrane, Nc– Narryer Terrane involved in the Capricorn Orogen (Modified from Myers, 1993).

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2.4.2   Landscape and habitat characteristics

In general the landscape is one of gentle topography with low-lying hills, except for prominent granite bornhardts (large rocky domes). Prior to clearing, the original vegetation consisted of a complex mosaic of plant communities, with distribution largely determined by rainfall, soil, and landform characteristics (Beard, 1980; Beard, 1990). The variations in soil and landforms (Figure 2.2) and their associated characteristic vegetation types have been described by Lantzke (1993) and McArthur (1993) as follows:

- **Ulva unit (kwongan)** – upland areas containing the laterite soils. Associated vegetation is typically heathland or shrubland *of Leptospermum erubescens, Eucalyptus burracoppinensis, Acacia assimilis, Allocasuarina acutivalvis, Allocasuarina huegeliana, Xylomelum angustifolium, Hakea coriacea*, various *Melaleuca* spp., and sedges;

- **Danberrin unit** – irregular low hills and gentle slopes, highly weathered and dominated by shallow soils of gritty sandy loam over granite. Associated vegetation is typically woodland with the main species *Eucalyptus loxophleba* and *Acacia acuminate*;

- **Booraan unit** – upper slopes of the lateritic sand plain formed from weathered granite material with sandy loam over clay. Vegetation is typically woodland, the main species being *Eucalyptus salmonophloia, Eucalyptus wandoo, Eucalyptus capillosa, callitris canescens Melaleuca* spp., *Allocasuarina campestris, Acacia hemiteles* and *Beaufortia bracteosa*;

- **Collgar unit** – very gentle slopes containing stratified sandy and clay soils with vegetation typically comprising mallee scrub; the main species being Eucalyptus transcontintalis, Eucalyptus cylindriflora, *Eucalyptus capillosa, Eucalyptus erythronmema, Eucalyptus hypochlamydea, Melaleuca uncinata, Acacia hemiteles, Westringia cephalantha* and *Olearia muelleri*;

- **Merriden and Belka units** – broad, flat, alluvial areas typically marked by many earlier shallow stream channels. Soils comprise sandy loam over clay, with the Belka having more sandy soils than the Merriden units. The vegetation is typically woodland: *Eucalyptus salmonophloia, Eucalyptus salubris, Eucalyptus capillos, Melaleuca* spp., and *Acacia hemiteles*;

- **Nangeenan unit** – found on the edges of the salt lakes with soils containing clay, gypsum, calcium carbonate and salts. The vegetation is woodland:

Eucalyptus salmonophloia, Eucalyptus salubris, and Eucalyptus longicornis, with a dense shrubland layer 0.5 m high of halophytes, including *Atriplex paludosa, Maireana carnosa* and *Maireana appressa*;

- **Baandee unit** – ancient drainage zones occupied by lakes, swamps and playas, dominated by salts from summer evaporation of the drainage water collected during winter. The soils are very saline, so the vegetation is halophytic and includes the *Atriplex* spp., *Maireana* spp., and Enchylaena spp;

- **Rocky outcrops** – normally associated with the Dunberrin unit and its associated vegetation, but may also contain dense *Allocasuarina huegeliana* fringing the outcrops. The rock surface has an almost complete cover of lichens, and mosses.
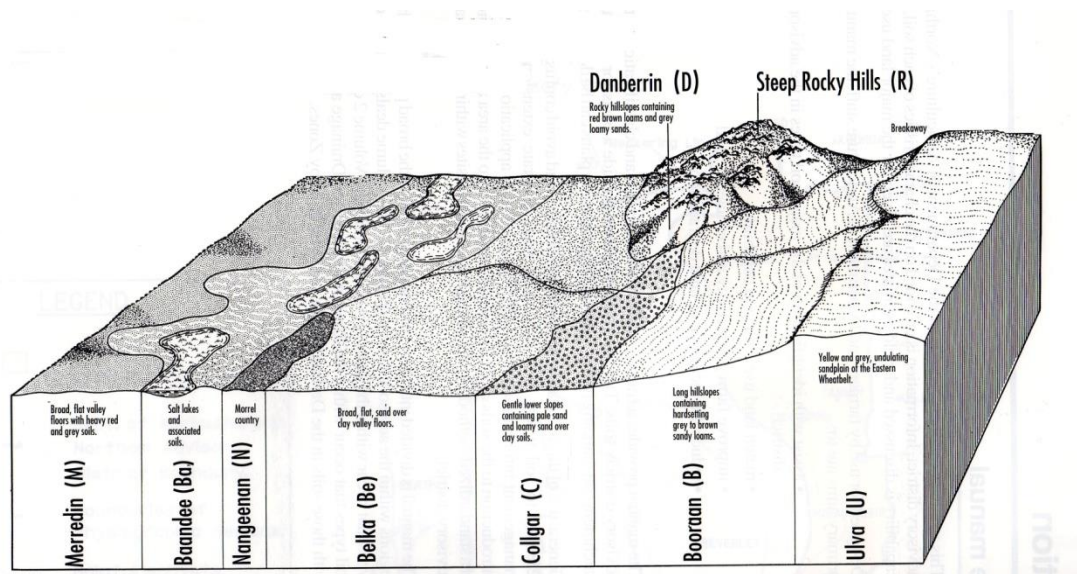
Figure 2.2 An idealised wheatbelt landscape showing the major soil landscape units (Lantzke, 1993).

Since European settlement, 93% of the native vegetation has been cleared, leaving only remnants of native bushland, predominantly on poor soil types or rock outcrops ranging in size from less than 1 ha up to 10000 ha (Hobbs, 1993; Saunders et al., 1993). This clearing and fragmentation of native bushland has led to changes in the physical and chemical fluxes across the landscape, including fluxes in radiation, wind, water, and nutrients (Hobbs, 1993). The naturally saline water table has risen over much of the wheatbelt (Landbeck, 1999), resulting in further habitat degradation and loss of native bushland (Department of Water, 2008). The number of animals in the region has significantly declined since European settlement, and only 26 of the original 43 mammal species recorded now remain (Friend, 1987), with many of these now endangered or threatened. Some of the existing mammal populations are dependent on remnants of natural vegetation (Friend, 1987), however physical and chemical changes coupled with the invasion of exotic predators, herbivores, and non-native plant species has resulted in this remnant bushland being under constant threat of further degradation (Jenkins, 1998; Pigott, 2000). Consequently many of the animal biota, including *P. l. lateralis,* face significant risk of extinction.

The *P l. lateralis* wheatbelt populations are found on a cluster of prominent bornhardts or dome-shaped granite hills which are scattered around a salt-river complex (Figure 2.3). These granite outcrops originated as bedrock projections from weathering of the lateritised land surface during the Cretaceous, and became fully exposed by the Miocene period (Twindale et al., 1999), a time when rapid macropod radiation began to occur (Flannery, 1989). Each of these large granite outcrops is contained within small remnant reserves, ranging in size from 64 to 351 ha in a greatly modified agricultural landscape. Although the reserves are regularly fox-baited, the surrounding agricultural matrix is not. The size of the area that contains all of the wheatbelt populations of *P. l. lateralis* (except Querekin Rock) is approximately 150 km² (Kinnear et al., 1988) with the reserves separated by 0.5 to 7 km. The study population was located on a boulder-strewn outcrop (Plate 2.1) standing 270 – 320 m above sea level and 40 m above the adjacent plain on Nangeen Hill Reserve (Twindale et al., 1999). Like all the outcrop reserves found around this salt-river complex, Nangeen Hill Reserve has a thin veneer of fringing vegetation.

Figure 2.3 Central wheatbelt rock-wallaby sites scattered around a salt-river complex surrounded by agriculture.

Plate 2.1 The Western side of Nangeen Hill (this side contains extensive caves systems along the majority of its length, not found on the eastern side). The dominant thicket of *Casuarina campestris* is in the foreground.

Few vegetative surveys have been undertaken on the reserves so information is limited. The outcrop on Nangeen Hill Reserve occupies 15% of the reserve area. There are no detailed published data on the soil types found in the reserve, although a provisional report by Williams (1980) suggested that the soils mostly consist of light-coloured to reddish sandy loams. This indicates that the reserve is likely to contain mainly the danberrin, booran and ulva soil landscape units.
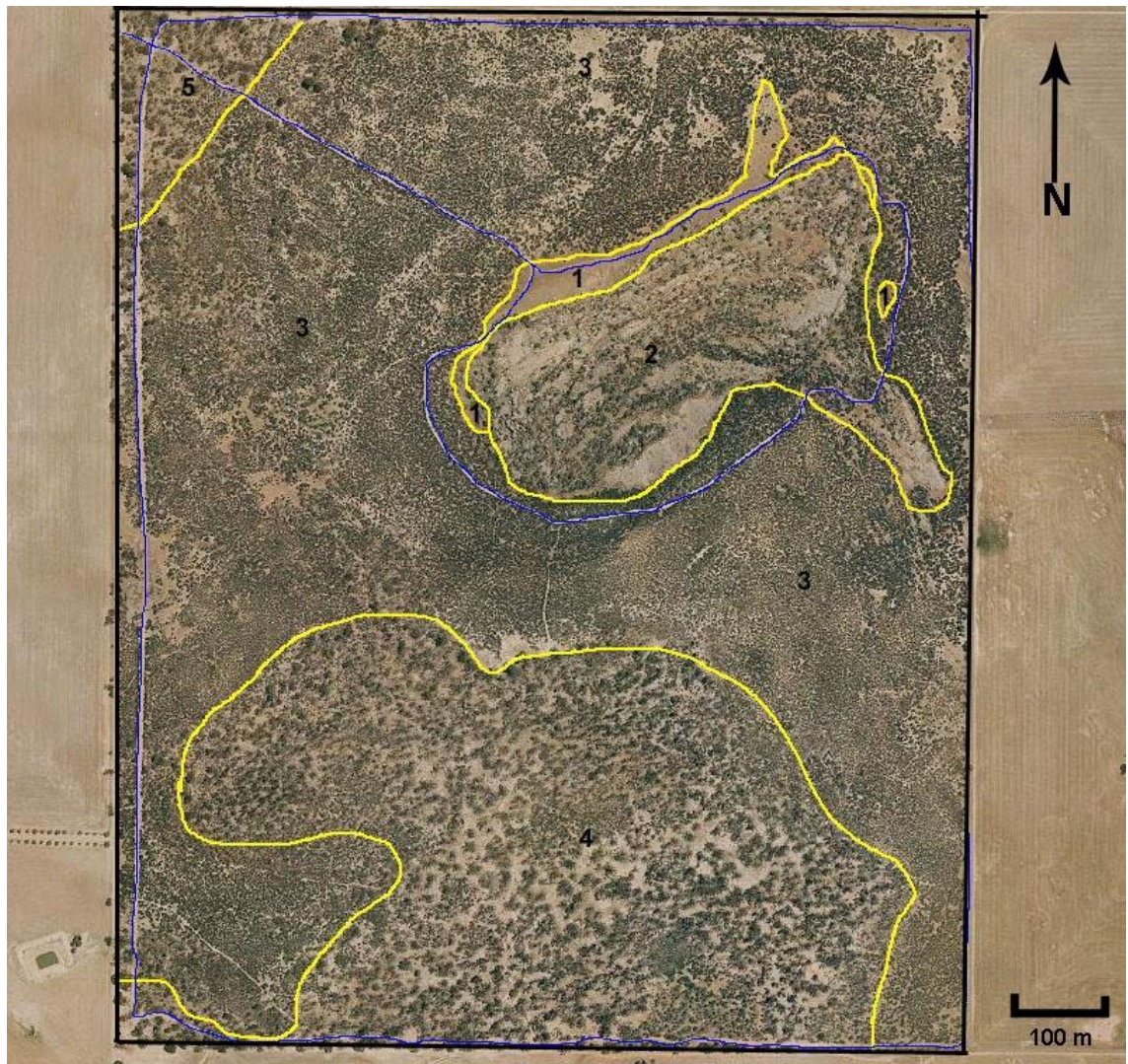
Figure 2.4 Nangeen Hill Reserve broad vegetation/habitat regions as described by Williams (1980). The yellow line represents vegetation boundaries and the blue line represents internal tracks.

The reserve area surrounding the base of the rocky outcrop supports four distinct vegetation types and a mosaic of vegetation groups on the rocky outcrop itself (Figure 2.4). These vegetation groups are:

- Open low grass including *Aristidia* spp., *Amphipogon strictus*, *Trifolium arvense, Bromus rubens, Bromus diandrus* and *Neurachne alopecuroides.* Weed invasion is apparent;

- Rocky outcrop with low woodland including *Acacia lasiocalyx* scrub (2 – 8 m tall) with *Rhinocarpus* spp., and *Diplolaena* spp., very low grasses, ferns and mosses;

- Thicket dominated by *Casuarina campestris* (1.5 – 3.0 m tall) over *Borya nitida,* with *Acacia lasiocalys*, Acacia spp., *Santalum acuminatum* and *Santalum spicatum* forming some smaller components of the association;

- Woodland including *Eucalyptus wandoo*, *E. Salmonophloia*, *E. Salubris* and E*. Loxophleba* (12 – 20 m tall) over open Mallee shrub with *Eucalyptus erythronema* and patches of *Melaleuca uncinata* shrub; and

- Low woodland dominated by *Eucalyptus loxophleba* (7 – 10 m) over mixed scrub of *Acacia* spp., *Melaleuca* spp. and *Santalum acuminatum*.

2.4.3 Climate

The central wheatbelt enjoys a Mediterranean climate with mild winters and hot summers. In the Kellerberrin region, the mean minimum winter temperature is around 6^0C and the mean summer maximum is around 33^0C (Figure 2.5). Around 75% of the annual rainfall occurs in the cooler months from April through to September (Figure 2.6) with a mean annual rainfall of 328 mm. The region is also subject to moderate to high winds, especially during the afternoons (Figure 2.7). Both frost and mist frequently occur in winter.
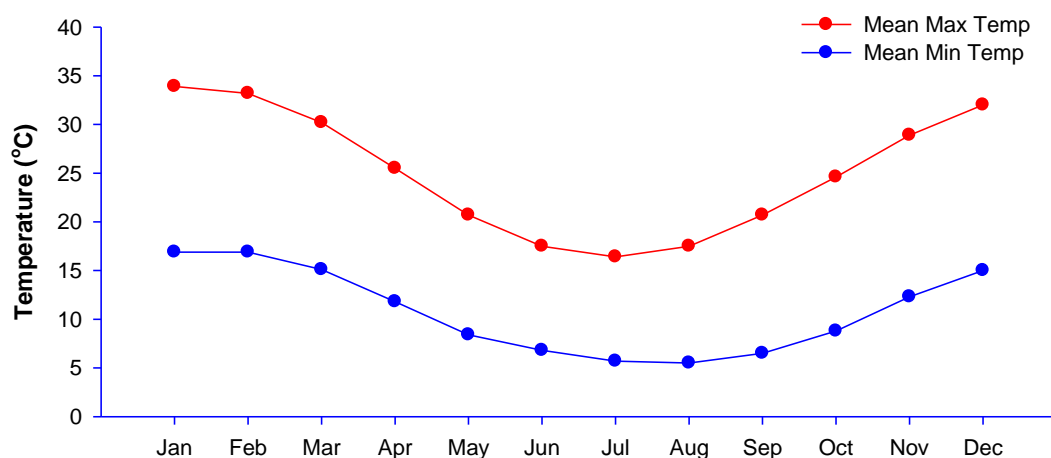
Figure 2.5 Monthly average mean maximum (red line) and minimum (blue line) temperature in the Kellerberrin region, modified from the Australian Bureau of Meteorology (2009).
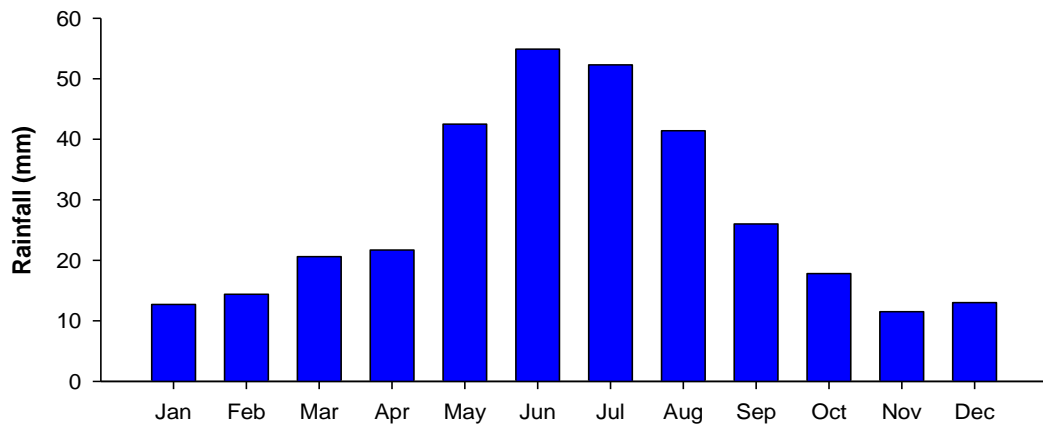
Figure 2.6 Monthly average rainfall (mm) in the Kellerberrin region, modified from the Australian Bureau of Meteorology (2009).
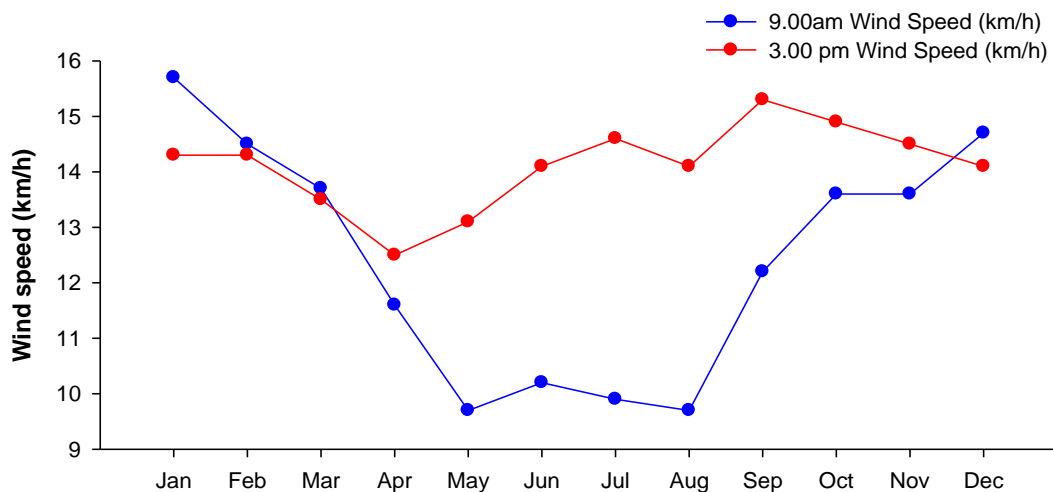
Figure 2.7 Monthly average mean 9:00 am (blue line) and 3:00 pm (red line) wind speed in the Kellerberrin region, modified from the Australian Bureau of Meteorology (2009).

2.4.4 Fauna (Nangeen Hill Reserve)

Nangeen Hill Reserve is inhabited by three macropod species, the target species black-flacked rock-wallaby (*Petrogale lateralis lateralis*), the western grey kangaroo (*Macropus fuliginosus*) and the euro (*Macropus robustus*). The western grey kangaroo predominantly inhabits the surrounding woodland and the *Allocasuarina huegeliana* shrubland, whereas the euro can often be seen foraging around the base and along the top of the outcrop, and sometimes feeding in close vicinity of the rock-wallabies within the open meadow areas. Echidnas (*Tachyglossus aculeatus*) can be found inhabiting both the rock outcrop and the surrounding habitat. Rabbits (*Oryctolagus cuniculus*) are found across most habitats within the reserve, but are never observed in large

numbers. Both foxes (*Vulpes vulpes*) and cats (*Felis catus*) have been observed within the reserve during this study. Wedge-tailed eagles (*Aquila audax*) are often observed searching above the rock outcrop.

2.5   Stage 1: Feasibility/preliminary studies

A number of preliminary studies were conducted between November 2003 and April 2005. Some of the information collected during the preliminary stage has been incorporated into the main analysis of stage 2. Rock-wallabies were observed at various locations in the Nangeen Hill Reserve and an artificial hide was trialled (Plate 2.2), covering the entire spatial distribution of the population. Observations were conducted at various diurnal times and all the behaviours exhibited were recorded. All field observation were undertaken by the candidate and observational notes were taken during the time of observations and at a later time from video recorded observations. Rock-wallabies initially appeared to be very cryptic; they were mostly observed at diurnal times, except during the middle of the day, when they were frequently observed for ten minutes or more before moving out of view. However, this only occurred on the western side of the rock, the site of their central diurnal rock refuge (Figure 2.8). The number of active individuals varied significantly between seasons and from day to day.

Night vision equipment (ATN Voyager night vision monocular generation 2+) was tested at the study sites. The main disadvantage of this equipment was that it was limited to open habitat types. In dense vegetation, individuals were both difficult to locate and observe for extensive periods. The night vision equipment made rock-wallabies easily distinguishable from other animals at distances less than 150 m, even during nights without moonlight. General rock-wallaby behaviours (foraging/ eating, scanning, moving and grooming) were easily identifiable at distances of less than 150 m. At night individual rock-wallabies could only be positively identified at distances less than 100 m with the aid of a spotlight and binoculars, but during the day they could be positively identified at distances up to 150 m.

Plate 2.2 An artificial temporary hide set up at Nangeen Hill Reserve.

Foraging activity occurred predominantly between 3 hours prior to sunset and throughout the night, except during the winter months when individuals were rarely seen after midnight.

Figure 2.8 The Nangeen Hill rock outcrop showing the boundary (in red) of the *P. l. lateralis* central diurnal rock refuge region.

Animals were rarely observed foraging at morning twilight during any season. Both the hide and a vehicle were used to observe animals within the meadow area directly opposite the western side of the outcrop without affecting movement patterns. Individuals were often observed feeding beside both the hide and the vehicle. Observations outside any enclosed structure appeared to affect the behaviour of rock-wallabies, often resulting in long periods of watchfulness in the direction of the researcher, and occasionally a change in movement once the researcher was detected. Some individuals appeared to ignore the researcher even when detected.

Both continuous and time-sampling were tested for the focal observations. Time-sampling cannot be used to adequately measure distances travelled, and this method frequently missed rare behavioural acts such as social interaction and self-grooming. Individuals were frequently observed for long periods (>5 minutes) while foraging, and repeatedly went out of sight when observations took place over more than 10 minutes. There also appeared to be significant variability in both the number of wallabies feeding each night and the time of cave emergence.

Rock-wallaby scats were easily distinguishable from those of other animals in the region, including other macropods and rabbits. A small trial belt of 3-belt transects were set up. These started 1 m from the rock edge and ran perpendicular from the outcrop within the meadow area until they reached the edge of the shrubland. A 1 m x 2 m quadrat was sampled every 5 m. The results suggest that rock-wallabies were predominantly active close to the rock (<15 m) and that other macropods were predominantly utilising areas close to the shrub edge where few rock-wallaby scats were found. However, fresh rock-wallaby scats were often encountered at greater distances outside the line of the belt transect, and within the line of belt transect but outside of the 1 m x 2 m quadrat. Scat numbers were very low at greater distances of 15 m, where just 1 - 3 scats were common.

Animals were trapped on the reserve between March 2005 and July 2005 in order to tag them individually so that they were identifiable (Plate 2.3) from distances greater than 100 m. A total of 36 individuals were captured and marked during this period. A further 20 individuals were captured and marked between January and March 2006 to increase the female sample size (see chapter 6 for a full description of the trapping methodology). This resulted in nearly half the population being individually marked. During the winter months (June - July) no animals were captured during the second

trap check (11:00 pm). The morphological and reproductive data collected are discussed in chapter 6.

Plate 2.3 Female *P. l. Lateralis* at Nangeen Hill Reserve with an individual identification tag attached to the left ear (green tag, red/silver tape).

The behavioural acts recorded during the preliminary studies are discussed in chapter 3. Observations showed that the southern half of the western side of the outcrop allowed the best recordable observations and provided the largest observable area. This section of the rock also appeared to carry a larger proportion of animals than the north-western half. Nocturnal observations on the top of the outcrop were limited. As foraging activity occurred predominantly during the first 3 hours prior to sunset and during most of the night, an observation regime needed to primarily encompass these periods. Focal data (individual) was best collected by continuous sampling, as time sampling missed important rare data and could not adequately record distances moved. However, a timed scan sample (group behaviour) was also included in the sampling method. This is discussed in more detail in chapter 4.

The results of the initial scat distribution trial suggested that a more vigorous sampling technique was needed to increase the number and size of the quadrats along each section of belt transect, especially at locations where rock-wallaby numbers were low.

The trial also suggested a possible competitive interaction between *P. l. lateralis* and the euro (*Macropus robustus*), which led to the design of a more vigorous scat dispersion sampling method using a high concentration of belt transects. This is discussed in chapter 5.

One major concern to emerge from these preliminary observations was the continued presence of foxes (*Vulpes vulpes*) and possibly wedge-tailed eagles (*Aquila audax*), which pointed to an indirect behavioural effect from predation on rock-wallaby foraging patterns, and so the final focal observational methods were designed to investigate vigilance rates.

The final methods developed from these preliminary results and observations are described in each relevant chapter. The researcher believed that by employing different methods to include direct observations (utilising both scan and focal sampling methods), scat distribution and trapping techniques, the major research aims would be appropriately investigated.

Chapter 3

The behavioural repertoire of *Petrogale lateralis lateralis*

3.1   Introduction and specific aims

It is widely accepted that for any effective animal behavioural research the investigator must familiarise with both the subject and the behaviour being measured. The behavioural acts and patterns in an animal's repertoire is called its ethogram, and this forms the fundamental backbone of behavioural research (Lehner 1996; Dawkins, 2007). The repertoire can be described at different levels of detail to determine the most appropriate measures and recording methods for a particular study. Before we can understand or interpret the evolution of behavioural traits we need to identify patterns between similar species (Langkilde et al., 2003). Although there are a few published behavioural repertoires on macropods there ae still significant gaps, particularly within the rock-wallaby species, and none have been composed on the *P. l. latralis* which makes comparisons difficult and limits our understanding of macropod behavioural patterns. As discussed in the literature review rock-wallabies may lack physiological adaptations compared to other macropod species that inhabit dry environments, but may offset this with behavioural adaptations that help minimise heat and water loss. Rock-wallabies appear to be very cryptic, and form dominant hierarchical social structures (Barker, 1990). In addition they are under constant threat from both exotic (*Vulpes vulpes* & *Felis catus*) and native predators (*Aquila audax*). So rock-wallabies would be expected to exhibit strong vigilant and disturbance behaviour, which would have significant effects on the foraging patterns of this population.

The major aims of this part of the study were to construct a full behavioural repertoire for *P. l. lateralis* and describe behavioural patterns strongly associated with the way rock-wallabies use their refuge, including behaviours that help form their social structures and reduce water and heat loss. The specific aims were:

- To compile a detailed list of all behavioural acts exhibited by *P. l. lateralis* and determine the best option for recording that behavioural act (event or state);
- To establish a letter code for each described behaviour, suitable for this and other future studies of this species;
- To determine the causes and effects of the behaviours recorded in this study;
- To determine if there were sex and age class differences in their behaviour;

- To determine if dominance hierarchies are adopted in this species;
- To investigate the causes and responses to observable disturbances in the Nangeen Hill population.

3.2   Methods

Individuals were either photographed, videoed and/or sketched, and identified by natural markings, colour and tags for future reference. Where tagging was required, rock-wallabies were trapped in suitable habitat areas (shallow topography). Trapping sessions were carried out over 2 to 4 consecutive days and nights. Traps were set in the afternoon and checked twice daily (11:00 pm and 6:00 am) and then closed on the second check. Captured individuals were then transferred into a hessian bag and examined by protruding the anterior or posterior of the animal from the bag as necessary. All wallabies were tagged on the ears with individually identifiable combinations of coloured tags (Plate 2.3). The full trapping methodology has been outlined in chapter 6.

Vantage points at Nangeen Hill Reserve were selected to allow the whole or most of the area to be observed with binoculars, a video recorder and night vision equipment. Each behavioural act was assigned to one of seven behavioural categories:

- Body postures
- Grooming
- Agonistic social behaviour
- Non-agonistic social behaviour
- Locomotion
- Feeding and foraging
- Other

A complete description has been provided for all behavioural acts, and where possible, a visual image (photograph or video still image) has been added to allow easy recognition for future studies. In addition, the observable sex and age classes (except postures) were recorded, as well as relationships between different behavioural acts (sequential) and any associated spatial features, like distance to other conspecifics or specific habitat types. For this study "behavioural patterns" refers to a sequence of behavioural acts, regularly observed, to fulfil a task, e.g. obtaining food, water, a mate, defend a resource, attack a conspecific or escape danger. To determine the most

appropriate measure for recording and analysing *P. l. lateralis* activity patterns, each behavioural act was labelled as either an event or a state or both (see chapter 4). *Events* were defined as behavioural acts of relatively short duration, like "bite conspecific," and were measured by the number of occurrences of the behavioural act per unit of time, commonly called the "frequency". *States* were behavioural acts of longer duration, like feeding or foraging, and were often measured as the mean or total proportion of time spent performing an activity, commonly known as "bouts". Some behavioural acts, like vigilance, could be measured as either an event or state, because they can occur over either a very short duration (a few seconds) or over a prolonged period (a few minutes). The information obtained was used to determine the most appropriate behavioural acts to be measured, as well as the most appropriate statistical analyses for investigating the behavioural activity patterns. In addition, a detailed qualitative description of several important and/or unusual behavioural patterns, specifically those influenced by their refuge habitat, has been provided. The information was collected over approximately 2500 hours of direct observations over a three-year period.

3.3   Results

3.3.1   Ethogram

Behavioural acts were assigned to one of seven broad behavioural groupings and each act or posture was assigned its own unique code. "Postures" and "grooming acts" were given lower-case codes and the remaining acts were assigned upper-case codes. The codes were comprised of the first letter of each act, area of body utilised or posture, with a different or additional letter if the same code already existed. "Postures" was given an additional vigilance code in cases where the animal was in an active vigilant (V) state. Where possible, additional information such as "age," "sex class," and their recordable options (event or state), has been provided.

3.3.2   Body postures (including vigilant and non-vigilant)

Rock-wallabies adopted a number of distinct standing, sitting and lying postures when stationary in either an active alert state (head up, eyes open) or complete rest (head down with eyes either downcast or closed). An individual's posture and associated

alertness (vigilance) may be dictated by fear (vigilant) or confidence (non-vigilant), so it was necessary to recognise these signs in order to understand and interpret them accurately.

The Nangeen Hill population of *P. l. lateralis* exhibited the following body postures:

- **Standing bipedally, upright and vigilant (Vsu)** – head up, back straight, forepaws and rump off the ground, vigilant. Observed in all sex and age classes (state);
- **Standing bipedally, semi-upright and vigilant (Vss)** – head up, body slightly bent forward, head up, forepaws and rump off the ground, vigilant. Observed in all sex and age classes (state) (Plate 3.1c);
- **Crouched quadrupedally and vigilant (Vc)** – head up, body bent forward, forepaws on the ground, vigilant. Observed in all sex and age classes (state) (Plate 3.1d);
- **Crouched quadrupedally and not vigilant (c)** – bent forward, forepaws on the ground, not vigilant, eyes usually closed or looking downwards. Observed in all sex and age classes (state);
- **Sitting with tail forward and vigilant (Vr)** – head up, sitting on rump with tail in front and back legs outstretched resting on substrate, vigilant. Observed in all sex and age classes (state) (lPlate 3.1f);
- **Sitting with tail forward and not vigilant (r)** – head down, sitting on rump with tail in front and back legs outstretched resting on substrate, not vigilant. Observed in all sex and age classes (state) (lPlate 3.1e);
- **Sitting in upright mode and vigilant (Vru)** – head up, sitting on tail, back straight in upright mode, vigilant. Observed in all sex and age classes (state) (lPlate 3.1a);
- **Sitting in upright mode and not vigilant (ru)** – head down, sitting on tail backwards, back straight in upright mode, not vigilant. Observed in all sex and age classes (state);
- **Lying down on side and not vigilant (l)** – lying down on side with head resting on the ground, not vigilant. Observed in both sex classes in adults but not in sub-adults and juveniles (state) (lPlate 3.1h);
- **Lying down on side and vigilant (Vl)** – lying down on side with head up, vigilant. Observed in both sex classes in adults, but not in sub-adults and juveniles (state) (lPlate 3.1b).

Plate 3.1 Body postures: a) Sitting in upright mode and vigilant b) Lying down on side and vigilant c) Standing bipedally, semi-upright and vigilant d) Crouched quadrupedally and vigilant e) Sitting with tail forward and not vigilant (juvenile) f) Sitting with tail forward and vigilant g) Lying down on side and not vigilant h) Lying down on side and vigilant.

3.3.3 Grooming acts

Grooming acts predominantly occurred within the refuge areas, either at or relatively close to their cave or crevice openings. All possible appendages were utilised. Sometimes different appendages were used together, such as grabbing the tail to lift and scratch with their forepaws, followed by licking and biting with the mouthparts. Like all macropods, the second and third toes of the hind feet are syndactylous (see Plate 1.1) but retain separate claws. As these toes are very small and do not assist with support or propulsion, it is believed they are used primarily for grooming (Hume et al., 1989). Individuals at Nangeen Hill often used their hind limbs for grooming, usually in a sitting or a crouched position.

Three auto-grooming behavioural acts were recorded in all age and sex classes, with a fourth recorded in females only. Grooming acts were recorded in a number of different body postures, predominantly when individuals were within or near the rock refuge. *P. l. lateralis* utilised all appendages and mouthparts for auto-grooming. The grooming acts observed are stereotypical of most marsupials (Kaufmann, 1974; Russell et al., 1989), however, unlike the more free-roaming macropods, *P. l. lateralis* were rarely observed grooming while foraging away from their permanent refuge area, either at night or during the day. Furthermore, grooming the tail was never observed at these foraging locations. Differences between marsupial groups or species may be due to their habitats or the main activity states in which grooming acts are performed.

Mutual grooming (allogrooming) was rare in *P. l. lateralis,* and was only encountered between adult males and females using forepaw claws, and between females and juveniles using tongue, teeth and forepaw claws. Although adult males were observed grooming adult females, this type of grooming primarily appeared during courtship. There was no observable mutual response from the females. Mutual grooming in all macropods appears to be rare, even in the more gregarious species (Hume et al., 1989). *P. l. lateralis* do not engage in grooming merely for cleaning, but also as a ritualised agonistic interaction between males. Males have been observed moving towards each other and then performing an exaggerated form of grooming while facing one another in an upright position, utilising only their forepaws. Generally individuals remain 3-5 m away from each while in a resting/grooming state, suggesting a sense of personal space.

Grooming behaviour states and frequencies in relation to habitat and climate are further discussed in chapter 4. For the purpose of individual coding, the body region being groomed made up the first part of the code, followed by the grooming code (G) and then the appendage used, in lower case. For example, body grooming with forepaws has been coded (BGf). The Nangeen Hill population of *P. l. lateralis* exhibited the following grooming behavioural acts:

- **Body groom (BG)** – using all grooming appendages and mouth parts, (event or state). Includes the grooming of back leg and forearm appendages (Plate 3.2c, d and f);
- **Pouch groom (PG)** – using only the mouthparts (event or state), cleaning both inside the pouch and around the outside of the pouch opening (Plate 3.2a);
- **Face groom (FG)** – using only the forepaws (event or state)(Plate 3.2b and e);
- **Tail grooming (TG)** – using the forepaws and mouth parts. Individuals often adopted the sitting position with the tail forward (event or state);
- **Tongue and teeth (t)** – using the mouth parts only, individuals groom all of the body area except for the back, neck and head regions, while in most body postures (event or state);
- **Forepaw claws (f)** – using only the forepaw claws to reach all of the body regions except for some areas of the back (event or state);
- **Hind foot (h)** – using the hind foot to reach the sides of the body and head regions. Only used when sitting or crouched quadrupedally (event or state).
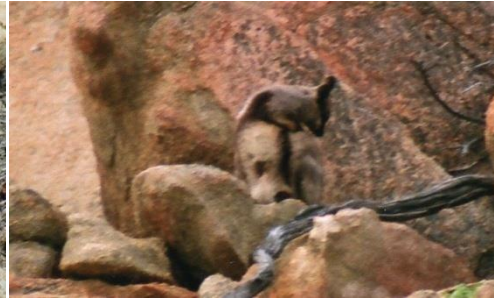
Plate 3.2 Grooming: a) Pouch groom b) Face groom utilising forepaws c) Body groom utilising mouth parts d) Body groom utilising mouth parts e) Face groom utilising hind feet f) Body groom utilising mouth parts and forepaws.

3.3.4   Agonistic social behaviour

Agonistic behaviour refers to all behavioural patterns that involve either aggressive or submissive social interaction. Although physical interaction does occur between rock-wallaby individuals, it appears that most agonistic interactions result in no physical interaction. One unusual posture related to agonistic aggression that has not previously been recorded in other rock-wallaby species, is an aggressive overt threat. It is possible that this behaviour is more widespread in rock-wallaby species and may be a ritualised warning behaviour to reduce the chance of physical interaction by displayinga readiness to engage in physical attack if the intruder does not desist from approaching.

This behaviour is initiated by an approaching conspecific or other intruder (such as the researcher). The animal reacts by dipping its head and leaning forward in a pouncing posture while staring in the direction of the intruder. This is very different from the crouched and alert posture, standing bipedally, or the semi-upright and alert posture. There is an exaggerated forward thrust of the head and shoulders, with the body at a more downward angle than the standing-bipedally semi-upright mode. Unlike the crouched mode, the forepaws are not touching the substrate. The Nangeen Hill population of *P. l. lateralis* exhibited the following agonistic behavioural acts:

- **Aggressive stare (AS)** – one wallaby stares in the direction of a conspecific without any change in body movement. Observed in all sex classes but only adult and sub-adult age classes (event or state);
- **Aggressive overt threat (AOT)** – dips head and leans forward in a pouncing posture while staring in the direction of a conspecific. Initiated by an approaching conspecific. Observed in all sex classes but only adult and sub-adult age classes (event or state)(Plate 3.3a);
- **Submissive head turn (SHT)** – one animal looks down or away from the aggressive stare of a conspecific. Observed in all sex and age classes (event);
- **Substrate foot-thumping or kicking ground (KG)** – thumps hind feet on the ground, usually on rock, producing a drumming sound effect. Follows a stationary overt threat initiated when conspecific continues to approach. Observed in all sex classes but only adult and sub-adult age classes (event);
- **Exaggerated self-grooming (EG)** – one or both wallabies stand in an upright body position, exaggerated self-grooming of the upper body while facing one another. Initiated by an approaching conspecific that has then shown a stationary overt threat, or after a passive nose-to-nose sniffing act. Observed in all sex classes but only adult and sub-adult age classes (event or state);
- **Grimace (GR)** – a facial threat where one individual looks at another with its mouth open and teeth bared. Has only been observed in females in female-to-male interactions. Initiated by grabbing or scratching by the male (event);
- **Bite conspecific (BC)** – a single short, sharp bite at a conspecific. Observed in all sexes including sub-adults and adults (event);
- **Strike/cuff conspecific (SC)** – one wallaby uses forepaw to strike/scratch at another. Has been observed in male-to-male, male-to-female, and female-to-female interactions, in both adults and sub-adults. In adults and sub-adults the strike or cuff is always initiated by the adult (event);

- **Stationary kick conspecific (SK)** – a frontal or lateral attack where one wallaby stands in a crouched body position, places its forepaws on the ground and kicks the body region of a conspecific with one or both back legs. This attacking behaviour is more common than the upright kick, and has only been seen between adult males or adult females (event);

- **Upright kick conspecific (UK)** – a frontal attack where one wallaby stands almost or fully erect on its hind legs and tail, using its forepaws to grab hold of a conspecific, and kicks with its hind legs. This attacking behaviour is rare and has only been seen between adult males or adult females. Has not been observed between male and female adults (event);

- **Moving kick: conspecific (MK)** – while moving, a wallaby attacks from the front, lateral or behind position, places its forepaws on the ground and kicks the body region of a conspecific with one or both back legs. This attacking behaviour has only been observed between adult males, adult and sub-adult males or adult females (event);

- **Tail grasping (TG)** – one wallaby grasps the tail of a conspecific with one or both forepaws. Observed between both adult and sub-adult males, and often between adult males and females (event);

- **Grab conspecific (GC)** – a wallaby reaches out with one or both forepaws and grabs hold of another animal. Predominantly observed in male-to-female interactions. In male-to-male interaction this can result in one male clinging to the other, pulling and twisting in a wrestling manner (event);

- **Approach conspecific (AP)** – approaching another animal using either a quadrupedal or slow-hopping gait. The approaching conspecific is usually the larger individual. Has been observed between both the same and different sex and age classes (event);

- **Chase conspecific (CH)** – hopping, scrambling or running towards another animal, often continued as pursuit even when the animal commences to flee. The chasing conspecific is usually the larger individual. Has been observed between the same or different sex and age classes (event or state)(Plate 3.3b);

- **Avoid conspecific (AV)** – moving slowly away from another animal, using either a quadrupedal or slow short hopping gait. The avoiding individual is usually the smaller one. Can occur between the same and different sex and age classes (event or state);

- **Flee conspecific (FL)** – starting from a stationary position, suddenly and quickly moving away from another animal using a scrambling or bipedal running gait. The fleeing individual is usually the smaller of the two. Can occur between the same and different sex and age classes (event or state) (IPlate 3.3b);
- **Retreat from conspecific (RE)** – similar to "flee conspecific" above, but moving only one step or jump from an approaching conspecific, usually just one body length away. The retreating individual is usually the smaller of the two. Can occur between the same and different sex and age classes (event or state);
- **Supplanting (SU)** – similar to "flee conspecific" above, but an individual vacates a location when a new animal enters the area and then occupies the same location of a supplanted individual. This could involve the conspecific directly approaching the individual and actually taking the place of the supplanted animal by occupying the same spot, or just causing the other to leave merely by the entering the region and staring at the individual. Has been observed between all sex and age classes. The new individual entering the region is usually the larger (event).

a   b
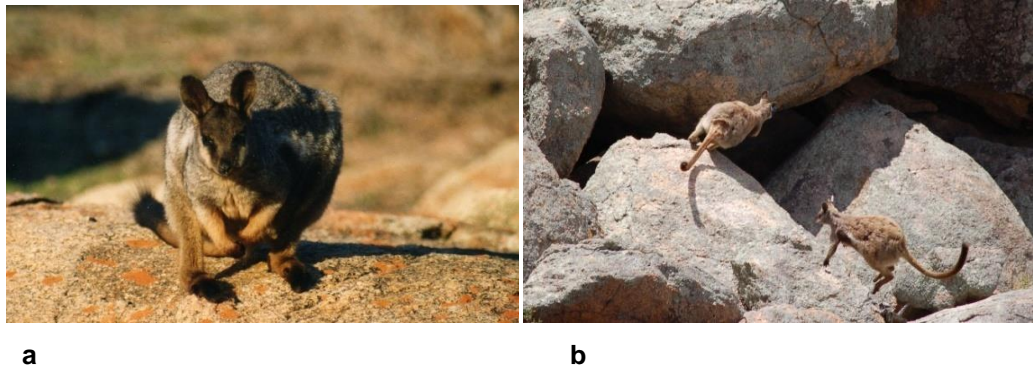
Plate 3.3   Agonistic acts: a) Aggressive overt threat b) Flee/chase conspecific.

3.3.5   Non-agonistic social behaviour

Non-agonistic social behaviour involves any social interaction that is not considered either aggressive or submissive, and includes maternal and sexual behaviour. Nose-to-nose sniffing was the most common non-agonistic social behaviour observed.

The Nangeen Hill population of *P. l. lateralis* exhibited the following non-agonistic social behavioural acts:

- **Allogrooming (AG)** – using teeth or foreclaws to groom conspecific. Only observed between female-to-juvenile and adult male-to-adult female (event or state);

- **Nose-nose sniffing (NN)** – approaches another, adopts a crouching posture, leans forward to sniff the nose of the conspecific (may not necessarily physically touch nose to nose). Observed in all sex classes but only adult and sub-adult age classes (event or state);

- **Nose-body sniffing (NB)** – lightly sniffing body region of conspecific where the individual normally comes from behind or from the side of the conspecific. Observed in all sex classes but only adult and sub-adult age classes (event or state)(Plate 3.4b);

- **Sexual checking (SC)** – a male investigates the anogenital region of a female conspecific (event or state) (Plate 3.4a);

- **Face rub conspecific (FR)** – a male approaches a female from the front, raises his forepaws and gently rubs the sides of the female face. This behaviour occurred both prior to and following sexual checking or nose-to-nose sniffing. Only observed between adult males and adult females (event or state);

- **Body rub/groom conspecific (BR)** – an individual male approaches a female from the side or from behind, raises his forepaws and gently rubs or scratches the body region of the female. Is usually performed before or after sexual checking. Only observed between adult males and adult females (event or state);

- **Mount (MT)** – an individual male climbs onto a female's back from behind, gripping her side or abdomen with his forepaws. This may or may not be followed by pelvic thrusting (event);

- **Push off/reject (PO)** – an individual female prevents a male from climbing onto her back or forces the individual off her body. This behavioural act often occurs

- after the female turns her head in the direction of the male and grimaces (event);

- **Mount acceptance (MA)** – an individual female accepts an individual male mounting (event); and

- **Huddle (HU)** – an individual approaches a conspecific and sits or crouches beside it with partial body contact. Observed between all sex and age classes, except for juveniles, where it was only observed between juvenile-adult female and not between juveniles and other sex or age classes (state).

a	b

Plate 3.4   Non-agonistic social behaviour: a) Sexual checking b) Nose-nose sniffing.

3.3.6   Locomotion

P. l. lateralis exhibited five main locomotion acts, distinguishable by the use of the hind limbs or both the hind and forelimbs, their travelling speed and the use of the tail. The quadrupedal gait is primarily used during foraging (head down actively searching for food sources) and across short distances on relatively flat rock. Hopping and running are primarily used for moving over longer distances on relatively flat surfaces, whereas scrambling and leaping are used to cross difficult rocky terrain. Their footpads and ability to use their tails for balancing are fully utilised when they adopt scrambling and leaping locomotion modes. Unlike the quadrupedal hopping and running modes of locomotion, scrambling and leaping seem to be confined to rock-wallaby macropods. Individuals at Nangeen Hill Reserve were observed on a number of occasions leaping at high speeds to heights of > 2 m and jumping across rock gaps >3 m wide. This ability to move quickly across difficult terrain provides an advantage for escaping from predators.

The Nangeen Hill population of *P. l. Lateralis* exhibited the following locomotion behaviour:

- **Quadrupedal gait (QU)** – involves the support of the forelimbs while the hind-limbs are brought forward. One pair of feet remains on the ground at all times. Observed in all sex and age classes (state);
- **Hopping (H)** – in this bipedal gait the weight of the body is on the hind limbs and sometimes the down-turned tail, with both hind legs moving together. The body posture remains slightly crouched. This gait is used for slow to moderate speeds. Observed in all sex and age classes (state)(Plate 3.5c);

- **Running (R)** – similar to hopping but the body posture is virtually horizontal and the tail never touches the ground. This gait is used for faster speeds. Observed in all sex and age classes (state) (lPlate 3.5b);
- **Scrambling (SC)** – a mixture of hopping and running that occurs across uneven substrate, such as broken rocky landscape, with animals often utilising the forelimbs when hopping from boulder to boulder. Observed in all sex and age classes (state) (lPlate 3.5a);
- **Leaping (L)** – jumping upwards from one surface to another. This spring-like action occurs when individuals moves from one surface to another where the height difference between the two surfaces is a body length or more. Can occur from either a standing or moving position. The individual initiates the leap by bringing the forelimbs and hind limbs close together in a tightly crouched position, pushing with all limbs in a downward motion followed by an upward motion. Observed in all sex and age classes (state) (lPlate 3.5d);
- **Retreating (RE)** – animal moves away from apparent danger (event or state).

a   b
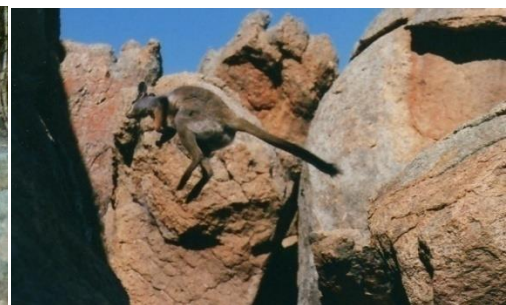
c   d

Plate 3.5 Locomotion and movement acts: a) Scrambling b) Running c) Hopping
d) Leaping.

3.3.7 Feeding and foraging

Rock-wallabies at Nangeen Hill Reserve were observed feeding on numerous plant species, eating roots, stems (soft and woody), leaves and flowers. They adopted various feeding strategies to accommodate both grazing and browsing.

The Nangeen Hill population of *P. l. lateralis* exhibited the following feeding and foraging behavioural acts:

- **Grazing (G)** – includes the direct acquisition and ingestion of herbaceous food, utilising the mouth parts only or with the forepaws first. Observed in all sex and age classes (state)(Plate 3.6b and d);
- **Browsing (B)** – includes the direct acquisition and ingestion of forbes (shrubs and trees), utilising the mouth parts only or manipulating with the forepaws first. Individuals often pulled tree branches downward, breaking a branch or pulling off individual leaves. Observed in all sex and age classes (state) (lPlate 3.6c, e and g);
- **Ground scratching/digging (GS)** – usually involves both forepaws, where the individual either scratches at the surface, forming shallow depressions to bite at roots, new shoots or highly grazed plant stem stubble. Observed in all sex classes but only adult and sub-adult age classes (event or state) (lPlate 3.6f);
- **Scavenging (SG)** – includes foraging for twigs and other dried material lying on the ground. Observed in all sex classes but only in adult and sub-adult age classes (event or state);
- **Foraging (FO)** – includes any form of searching for, or acquisition of food resources prior to ingestion. Observed in all sex and age classes (state);
- **Rock-wall feeding (RWF)** – scaling steep rock edges to graze on green herbaceous material growing in rock cracks. Adults and sub-adults of both sexes were observed engaging in this behaviour (state) (lPlate 3.6a);
- **Tree climbing (TC)** – climbing tall shrubs or small trees to browse on all vegetative parts (leaves, stems and bark). Only large adult males were observed in this behaviour (state);

- **Bark chewing/stripping (BC)** – individuals were observed biting sections of bark of various small shrubs and trees to consume. They were also observed biting into a section of bark while holding the branch in their forelimbs and pulling with their head and body, stripping long sections of bark on thinner branches (state);

- **Precipitation rock runoff drinking (PD)** – lapping up water that is running down on rock substrates. Shortly after a rain shower individuals often vacated their caves and started licking or drinking water directly from the rock runoff on the main rock outcrop. Observed in all sex classes but only in adult and sub-adult age classes (event or state);

- **Free water pool drinking (FD)** – lapping up free water that has collected in substrate. Individuals were observed drinking free water that had collected in a small seep adjacent to the main outcrop. They often congregated in dense groups (<1m apart) of up to five. This high-density grouping is not seen in any other behavioural situations. Observed in all sex classes but only in adult and sub-adult age classes (event or state); and

- **Suckling (SU)** – juvenile places head inside pouch to suckle on female teat (event or state)(Plate 3.6h).

3.3.8   Other behavioural acts

Rock-wallabies were observed engaging in a number of behaviours that did not fall into any of the other six behavioural groups. Basking behaviour was only ever observed during the cooler months, whereas shading behaviour was only observed during the warmer months. Substrate sniffing was a common behaviour and may have many purposes, such as detecting conspecifics, female sexual condition, and possibly predator presence.

Plate 3.6 Feeding and foraging acts: a) Rock-wall feeding b) Grazing on grass sp.
c) Browsing while standing bipedally upright on acacia spp. d) Grazing on cape weed
e) Browsing on rhinocarpus spp. f) Digging/scratching g) Adult female and juvenile
browsing on acacia spp. h) Suckling.

On hot days, individual rock-wallabies were often observed licking their forearms excessively, smearing saliva on their fur. This may act as a form of thermoregulation. Individuals were regularly observed in a vigilant state regardless of their behaviour or body posture. Stretching only occurred when individuals were within their central diurnal rock refuge, and took place predominantly near a cave or crevice entrance. Juvenile play was only observed in the close vicinity of a cave and an adult. Some of these behaviours are reviewed in more detail in the Discussion section.

The Nangeen Hill population of *P. l. lateralis* exhibited the following behavioural acts:

- **Urinating (U)** – eliminating urine from the body (event);
- **Defecating (D)** – eliminating faeces from the body (event);
- **Excessive smearing of saliva on the forearms (FL)** – repeated licking up the inside of the forearms producing a very damp external surface. Observed in all sex classes but only in adult and sub-adult age classes. This repeated licking appears different from grooming and only occurs on hot days (event or state) (Plate 3.7a);
- **Substrate sniff/ explore (SS)** – nose to substrate. This common behavioural act is often performed on rock and wood substrates and may have several purposes. Observed in all sex classes but only adult and sub-adult age classes (event);
- **Stretching (ST)** – extension of forearms, back legs, or neck in an upward or outward motion (event);
- **Basking (BSK)** – resting, usually on a rock, exposing body to the sun (state), (Plate 3.7d);
- **Shading (SHD)** – resting in the shade of either rock or vegetative cover, but still visible to the outside environment (state) (IPlate 3.7c);
- **Refuge concealment (RC)** – individuals are totally concealed within a cave so are not visible to the outside environment. This is different to shading behaviour (state);
- **Juvenile solitary play (PS)** – hopping either rapidly around the mother or close to a cave entrance. Sometimes exhibiting signs of foraging, such as picking up objects (e.g. twigs) to play with, or sniffing and exploring the environment (state) (Plate 3.7b);
- **Group play (PG)** – juvenile individuals chase each other sometimes exhibiting behaviour similar to adult agonistic and non-agonistic social behaviour (state);

- **Vigilant (V)** – individual raises its head, eyes open. Can be in any of the body postures described above and may also be in active mode, such as feeding (chewing food). Observed in all age and sex classes (event or state);
- **Resting (RS)** – any form of non-active mode, except vigilant, where the animal can be in either alert or non-alert mode (state).

a

b

c

d
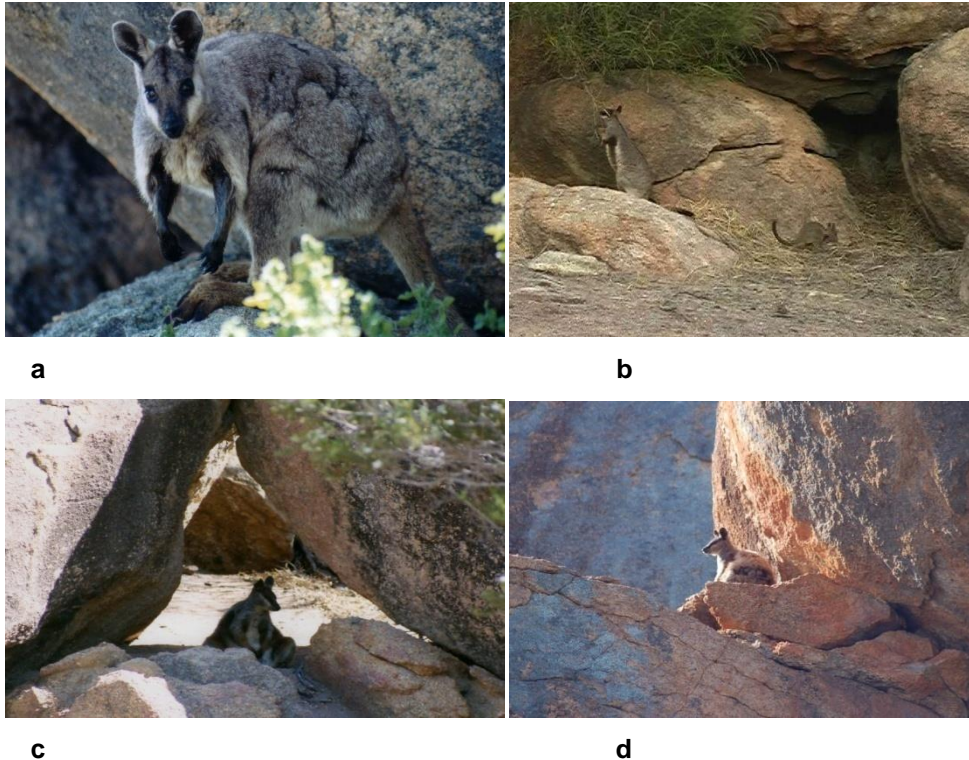
Plate 3.7   Other behavioural acts: a) Forearm licking b) Juvenile solitary play (running back and forth from mother to cave) c) Shading from the afternoon summer sun d) Basking and vigilant in the morning spring sun.

3.4   Discussion

Previous studies on the general behaviour of macropods are limited to a few species, mostly in captivity (Johnson, 1980; Bourke, 1989), and except for the *Macropus parryi* (Kaufmann, 1974), field studies have been conducted primarily on the larger free-ranging kangaroo species (Ealey, 1967; Croft, 1980). Although some ecological studies have included specific aspects of rock-wallaby behaviour, most have been confined to diurnal observations (Horsup, 1986; Barker, 1990; Bulinski et al., 1997). This has been partly due to the cryptic and predominantly nocturnal behaviour of these animals, making direct observation difficult. However, since the introduction of commercial night-vision devices there has been an increase in behavioural studies of nocturnal

macropods. These studies have generally focused on various activity patterns, particularly vigilance behaviour, across a number of macropod groups (Ord et al., 1999; Carter and Goldizen, 2003; Pays et al., 2009). Although night-vision devices have opened up new possibilities for advances in marsupial research, few ecological studies have included behavioural aspects, particularly on rock-wallabies, and no macropod studies have published full behavioural repertoires. The detailed behavioural repertoire (ethogram) compiled in this study is the first for this species and includes both nocturnal and diurnal observations. It has enabled analyses of the causes and effects of specific behavioural acts, and the construction of a comprehensive behavioural framework to investigate a range of behavioural patterns, including disturbance responses, social interactions, refuge use, and foraging. It has also aided the development of quantitative studies (discussed in chapter 4) on activity patterns.

In general, the behaviours exhibited by *P. l. lateralis* are not dissimilar to those observed in other macropods (Croft, 1980; Coulson, 1989) and other rock-wallaby species (Horsup, 1986, Barker, 1990; Bulinski et al., 1997). As few studies have examined the behavioural repertoires of macropods, particularly rock-wallabies, it is difficult to make comparisons. However, some similarities and differences were found in this species compared to other macropod species. It is important to identify the behavioural acts that may be influenced by the refuge habitat for future comparisons between other populations or similar species

3.4.1   Vigilance states and body postures within and outside the refuge

Rock-wallabies in the Nangeen Hill Reserve population of *P. l. lateralis* adopted ten different postures. They were rarely observed in a non-vigilant state within their refuge and never outside their refuge. Although many of these postures have been found in another rock-wallaby species (Horsup, 1986) and other macropod groups (Kaufmann, 1974), differences between the levels of alertness have not been described in detail. Such differences may be important to determine the level of fear in a particular environment. Behavioural distinctions have been made in other macropod groups (Croft, 1980) suggesting that vigilance activity may play an important part in the animals' daily activity levels. Rock-wallabies occupy a permanent central rock refuge which is an important resource to defend, so monitoring their environment for intruders, including other conspecifics, is necessary to determine their impact on daily activity patterns. Age and sex class, social hierarchy, spatial and temporal differences were also revealed. In this study it was found that when animals were resting, most postures

had an alert and non-alert form. Away from their caves, rock wallabies rarely adopted non-alert body postures. Once outside their permanent rock caves they were predominantly in alert mode and constantly scanned their environment. Adults were observed in non-alert resting modes within the rock refuge away from the cave entrance, but sub-adults and juveniles always remained alert in these areas, suggesting they felt vulnerable without the protection of good rock cover in the form of caves and crevices. Heightened alertness in the form of high vigilance rates away from caves may be due to fear of predators or other conspecifics.

3.4.2 Disturbance response

Rock-wallabies were regularly observed shifting from vigilance mode back into the refuge area. This is referred to as disturbance behaviour, and is characterised by a behavioural change of one or more individuals to a visual, acoustic or olfactory sign of perceived danger. When alerted, rock-wallabies chose one of four responses using a combination of behaviours. Behavioural reactions to disturbances were ordered and increased alarm as follows:

1. Remaining in the same body posture and location they were in prior to the disturbance, but looking up and staring in the direction of the perceived disturbance;
2. Rising up on their hind legs and tail and staring in the direction of the perceived disturbance but remaining in the same location;
3. Moving towards the refuge area, stopping to stare in the direction of the perceived disturbance; and
4. Moving towards the refuge area and entering a cave or crevice, not stopping to look back in the direction of the perceived disturbance.

Although escape behaviour is common in many animal groups (Carol 2005), and has been observed in macropods (Kaufmann, 1974), the ordered scale of the disturbance responses developed in this study has not been observed in any other published macropod study. As the severity of the disturbance increases individuals may escalate the scale of their disturbance response. Within a group, individuals may also differ in the scale of their disturbance response. Large adults tended not to react immediately with the highest scale response, particularly if the alarm had been raised by a sub-adult or small adult exhibiting response 3 or 4. Instead they exhibited responses 1 or 2 and increased the alarm if they detect the disturbance and perceived it as dangerous, or if

another large adult upgraded its response to that disturbance. Disturbance responses may be modified by large adults due to previous experiences of false alarms triggered by younger individuals. Every response to an alarm at the highest scale costs valuable energy and foraging time, so it is likely to be more favourable for individuals to grade their responses according to the class of conspecific that triggered the alarm. This would minimise false alarms and therefore also time and energy loss due to perceived disturbances.

What intruders do rock-wallabies perceive as dangerous? Are other macropods, including other conspecifics, perceived as competitors? Throughout this study foxes (*Vulpes vulpes*) were present in the reserve despite regular fox-baiting, and when detected by rock-wallabies while foraging away from the refuge, there was an immediate disturbance response, measurable at a scale of 3 or 4. If the detected fox did not desist from moving towards the refuge the rock-wallabies had retreated into, then some individuals did not retreat, but remained vigilant for an extended period of five minutes or more. If however the detected fox continued to move towards the rock refuge, then all rock-wallabies retreated back into their caves and remained there for durations of 5 to 30 minutes, gradually moving away with intensified vigilance before commencing foraging. Once commenced, they remained within the rock refuge area or within close proximity to rock cover (<5m). This high-disturbance response to foxes moving into their foraging areas clearly suggests a high level of predation fear. It also results in substantial energy costs and lost feeding time, as animals are continually moving to and from the refuge area. In addition, since individuals either remained within the rock refuge or within a 5-metre range after a fox disturbance, there is greater grazing pressure on these areas. The consequences of this behaviour are fully discussed in chapters 4 and 5.

Wedge-tailed eagles (*Aquila audax*) were also regularly present at Nangeen Reserve, and were often seen searching the rock refuge area during daylight hours. Despite this, no significant disturbance response was detected. Large adults appeared to rest or engage in foraging activity in the presence of wedge-tailed eagles. In contrast, sub-adults, juveniles and females carrying large pouch young were never present when eagles were in the area. These sex and age classes did not move far from a cave or crevice entrance even when there were no eagles present, and were only observed within very sheltered rock sites (Plate 3.8). Individuals of all classes rarely left the rock refuge during the daytime, and where this was observed, they remained within 5 m of the central diurnal rock refuge.

A single direct predatory kill by a wedge-tailed eagle of a sub-adult rock-wallaby inside the refuge area was observed (Plate 3.9), so although there wasn't a strong disturbance response from adult rock-wallabies to the presence of eagles, smaller individuals were at risk.

Plate 3.8   Two juvenile *P. l. lateralis* inside a large protected cave system on Nangeen Hill. Such a habitat provides a safe environment for diurnal play and interaction. This complex rock habitat contained many caves and cave entrances, with steep rock walls surrounding the entire open space (approximately 15 m²).

Plate 3.9   A wedge-tailed eagle (*Aquila audax*) capturing a sub-adult *P. l. lateralis* on Nangeen Hill.

Smaller individuals and females carrying large pouch young were rarely observed far from their caves, and displayed higher perceived predation fear than large adult males or females not carrying large pouch young. Although large males did not appear to monitor for the presence of eagles, they were nevertheless reluctant to forage in the open grassland during the diurnal hours, which may be due to a higher perceived predation fear of foxes during the day. Wedge-tailed eagles may therefore be perceived as a danger, but age and reproductive condition appear to strongly influence that perception.

Owls (*Ninox novaeseelandiae and Tyto alba*) were regularly observed at night in the Nangeen Reserve. Some rock-wallabies exhibited a low disturbance response to the vocal shrieks of owls. One owl was observed diving repeatedly at an adult rock-wallaby although this did not look like a predation attack. Young juvenile rock-wallabies would be vulnerable to adult owls, so they would in all likelihood be considered a predatory threat to juveniles at heel when exiting the pouch.

Only one other macropod species was observed in the same foraging habitat as rock-wallabies on Nangeen Reserve, the locally known euro (*Macropus robustus*). This significantly larger species did not appear to be perceived as a danger. The only time rock-wallabies were observed exhibiting a disturbance response to euros greater than 2 was when they were moving quickly through the rock-wallabies' foraging area. If there was no other intruder, rock-wallabies immediately returned to their previous location and activity even when the euros remained in the same patch. The fast movement of euros may simply be a response to another disturbance, and could be viewed as co-operative behaviour between the two species to increase detection of perceived sources of danger. This was also seen to occur in reverse, with some rock-wallaby individuals being the first to exhibit a disturbance response, followed by a similar disturbance response from the euros. When the euros moved slowly towards the rock-wallabies, there was either no response or they briefly exhibited a level-1 response and continued with their previous activity. On many occasions rock-wallaby individuals were observed feeding within 1 metre from euros. In one case an adult submissive male was observed moving closer to a euro each time a dominant male rock-wallaby moved closer to him. Even when the submissive male was feeding alongside the euro, the dominant male continued to approach and eventually chased the submissive male away. The euro completely ignored both rock-wallabies while all this was going on.

These disturbance responses suggest that females with large pouch young are at the greatest risk of predation during both diurnal and nocturnal periods, followed by sub-adult males and females. Large adult males and females without large pouch young were at the lowest predation risk and therefore displayed the lowest disturbance responses. These observations also suggest that this *P. l. lateralis* population was in a state of heightened vigilance to predation, shown to be a primary cause of mortality in many rock-wallaby populations (Kinnear et al., 1988, Hornsby, 1997; Jarman & Bayne, 1997; Lapridge & Henshall, 2001). Although Nangeen Hill Reserve is regularly fox-baited, foxes are still present.

3.4.3   Adapting locomotion to a difficult terrain

P. l. lateralis use five main modes of locomotion, distinguished by their travelling speed, the angle of the body, and the manner in which the tail and limbs are used. Unlike the quadrupedal, hopping and running modes of locomotion are found within all macropods (Kaufmann, 1974; Hume et al., 1989), but scrambling and leaping are confined to the rock-wallaby species (Barker, 1990; Horsup, 1986). Individuals at Nangeen Hill Reserve were observed leaping at high speed to heights of > 2 m and jumping across rock gaps >3 m wide on a number of occasions. This ability to move quickly over difficult terrain is an advantage for escaping predators, and their specific morphological adaptations (large pads, short nails and a robust non-prehensile tail) facilitate their agility across smooth rocks without slipping (Tyndale-Biscoe, 2005). It is believed that by the mid-Miocene, the Macropodidae had already evolved a bipedal morphology (Archer et al., 1999) and this may be because it provided an improved means of escape from predators (Baudinette, 1991).The utilisation of all limbs and the tail gives the rock-wallaby a scrambling gait that is unique to this species.

3.4.4   Social organisation

P. l. lateralis use a complex arrangement of non-agonistic and agonistic behaviours to determine their social organisation. These findings are similar to those observed in other rock-wallaby species, and are believed to reflect a linear dominance hierarchy (Horsup, 1986; Barker, 1990; Blumstein et al., 2001). However, the assumption that the Nangeen Hill population social structure reflects a dominance hierarchy would need quantitative studies to be conclusive. There is little vocal communication. Instead, rock-wallabies appear to rely on ritualised behavioural acts and chemical cues to exchange information about the physiological or behavioural state of an individual, and have evolved very diverse and complex social behaviours. Although vocal communication is

poor, *P. l. lateralis* make significant use of their olfactory senses – individuals were frequently observed sniffing the substrate (SS) and conspecifics. The importance of chemical communication for all marsupial groups (Croft, 1980) is borne out by their extensive olfactory sensory organs. At the conclusion of aggressive agonistic interactions on Nangeen Hill, *P.l. lateralis* individuals moved toward the area where the interaction occurred, stopped and sniffed the substrate excitedly, displaying heightened olfactory sensitivity. It is possible that individuals release chemical pheromones during these highly aggressive interactions, some of which is left on the substrate surface and exude a strong odour.

P. l. lateralis exhibit a greater repertoire of agonistic acts (19) than non-agonistic acts (10), and although the agonistic acts generally do not result in injury, they play a more significant role in determining the individual relationships and overall social organisation than non-agonistic behavioural acts. Victors of agonistic encounters in this population were predominantly the larger individuals of both sexes, reflecting a size-based dominance hierarchy. Although agonistic behaviour in other macropods normally occurs during competition for limited resources (Blumstein & Daniel, 2003), it is not always clear which resource is being defended. For rock-wallabies the refuge is an important resource, since it not only offers immediate protection from predators and adverse climatic conditions, but also provides a safe environment for rearing young. Further-more, good food resources both within and immediately adjacent to the refuge provide a safe environment for additional diurnal foraging. Rock-wallabies were never observed moving more than 10 m away from their permanent rock refuge area during daytime.

One important agonistic behavioural act, the aggressive overt threat (AOT), appeared to be a signal to the opponent that the individual is both able and ready to attack.The ensuing substrate foot-thumping (KG) also appeared to be an indication of the individual's strength and readiness to attack (a louder thump indicating strength), and may allow the opponent to weigh up the cost of attacking in terms of physical injury. This behaviour has not been observed in other macropods, but may be common in other rock-wallaby species. Such attacks can be very dangerous, especially within the rocky terrain, and could potentially result in damaged limbs, thereby reducing the individual's capacity to acquire food and escape danger. It is therefore not surprising that these animals have evolved ritualised displays and supplanting behaviours to reduce the likelihood of physical agonistic interactions. Evidence of substrate foot-thumping has been found in many macropods. In all cases it is believed to act as an

alarm signal (Croft, 1980; Coulson, 1989; Barker, 1990; Rose et al., 2006), however, it is less clear whether rock-wallaby alarm signals are directed towards predators or conspecifics, or both, and more importantly, whether this behaviour has evolved due to past predation pressure (Rose et al., 2006). Like the *P. l. lateralis* in this study, Barker (1990) found that *P. assimilis* stamped their feet in response to both external disturbances and conspecifics during agonistic encounters, suggesting a dual role for this behavioural act. Some researchers believe that when this alarm signal is directed towards a predator it acts as a warning for other conspecifics in the vicinity that there is an intruder present (Croft, 1980; Horsup, 1986) as a form of altruistic behaviour. Other dramatic postures used as ritualised threatening acts have been observed in the larger macropods. For example, adult male red kangaroos (*Macropus rufus)* stand on their hind legs with their heads thrown well back, one forearm outstretched and the other scratching or touching the sternum region (Croft, 1980). For rock-wallabies the stationary overt threat act is an alternative to the one adopted by larger macropods, providing posture stability in a rocky habitat. This stance also reflects the direct fighting behavioural acts these animals adopt, as they rarely use either the upright kick conspecific (UK) or the boxing-like fighting stance adopted by the larger macropods. The only instance where a boxing-like stance and sparring was observed in this study was between two adult males in the flat meadow area close to the rock edge.

Two common examples of an ordered mixed agonistic and non-agonistic behavioural sequence are described below.

Sequence A:

1. Stands and stares in the direction of another individual conspecific.

2. Head and body leans forward exaggeratedly towards conspecific.

3. Substrate foot-thumping.

4. Retreat or chase/attack.

Sequence B:

1. Stands and stares in the direction of another individual conspecific.

2. Approach one another.

3. Nose-to-nose sniff.

4. Retreat or chase/attack.

These types of agonistic interactions occurred predominantly between males, with the larger individual, where there was an observable size difference, being both the instigator and the victor. Such agonistic behaviours are common in macropods where size relationships usually determine supplanting success (Croft, 1980; Ganslosser, 1989). Female-to-female agonistic interactions always mirrored the second sequence; never the first. Although substrate foot-thumping was rarely observed between males during agonistic interactions, they often occurred when the researcher approached the focal male animal too closely (distances < 10m), and may therefore be more predominantly used as an alarm against predators or other non-conspecific intruders. This behaviour was never directed at other resident macropod species like the euro.

Many forms of direct physical agonistic behaviours occurred not only between pairs of wallabies but also within groups of 3 or more individuals. These group agonistic interactions were observed on a number of occasions amongst adult males, with one intruder versus two or more refuge occupants. Sub-adults also became involved in group interactions, but less aggressively, both within their own age class and with adults, but only between occupants and not intruders. Although agonistic behaviours predominated among adult males and females, they also occurred between different sexes and age classes, including juveniles. When juveniles were in close proximity to one another, their play often resembled a form of agonistic behaviour and included chasing. Juvenile group social play was only ever observed adjacent to one of the main cave systems, and only when adults were present. This type of play behaviour provides these juveniles with the social skills needed as they mature, and allows them to fit into the dominance hierarchy of their social group. Individuals appear to learn these social displays at a very young age, further reinforcing the role of ritualised displays in the establishment of group and social structure.

Females also appear to exhibit a linear dominance hierarchal behaviours, and agonistic encounters were observed within the same and different age classes. In one group a female was observed initiating an interaction with an adult male and was chased away by the larger dominant female who occasionally attacked both the smaller female and the male. This behaviour not only identified her as the dominant female in the hierarchy, but also signalled her female dominance to the males in the group by asserted her breeding rights. Other studies conducted on rock-wallaby social behaviour have found high levels of aggression between adult females due to competition for rock space and consort males (Horsup, 1986; Bulinski et al., 1997). At Nangeen Hill,

foraging females were observed cuffing juveniles when disturbed by their active play. The juveniles responded by re-entering the pouch or retreating into a nearby cave.

Although physical contact was observed between rock-wallaby individuals, most agonistic interactions resulted in no physical interaction. Instead, they resulted in fleeing (FL) or supplanting (SU). Supplanting (displacement) is the most frequent agonistic interaction in most macropods, including other rock-wallaby species (Horsup, 1986; Ganslosser, 1989), and was commonly observed in this study. As with other macropods, there are both passive and aggressive supplants (Kaufmann, 1974; Ganslosser, 1989). Passive supplants occur either when one individual directly approaches another and the approached animal moves away, or when an individual simply moves away from another individual entering the same patch. Active supplanting includes an additional form of ritualised agonistic behaviour, an aggressive stare (AS), just prior to the resulting supplant. It is generally believed that active supplanting is performed more in macropod species with well-differentiated ritualised display patterns (Ganslosser, 1989).

The *P. l. lateralis* population in this study exhibited a greater repertoire of agonistic than non-agonistic social behaviour. Non-agonistic behaviour in macropods is widely regarded as signs of sexual readiness (females in oestrus) and for establishing social bonds (Croft, 1980). Nose-nose sniffing (NN) and nose-body sniffing (NB) were the most common social interactions found in *P. l. lateralis* in this study, as it is throughout the macropod groups (Croft, 1980; Barker, 1990). Unlike other macropod studies, allogrooming (AG) was rarely recorded in this study, and where observed, only occurred in mother-juvenile and adult male-female interactions. The use of the teeth for allogrooming was never observed in adults, but was frequently seen in mother-juvenile interactions. Adult males were observed using their forepaws in social contact with adult females for body- and face-rubbing and scratching, which could be a form of ritualised courtship behaviour.

Another rare social bonding act observed in this study was a form of huddling (HU), where one individual joined another and either sat adjacent to the conspecific or engaged in the same activity as the conspecific, like feeding. This behaviour predominantly involved adult male-female interactions and was seen less frequently in other sex and age classes, leading to the conclusion that these behavioural interactions are used to reinforce and determine social grouping and potential pairs

for mating. It is not clear if this behaviour is common throughout all rock-wallaby species. One would not expect to see such non-agonistic interactions occurring between individuals from different social groups without an initial sequence of agonistic interactions in the form of ritualised behaviours to establish a level of familiarity. Non-agonistic interactions were not observed among marked individuals occupying different rock refuge regions (different zones) in Nangeen Hill. The predominance of agonistic outcomes from inter-group interactions may have caused individuals to adopt a spatial distribution pattern that reduced the likelihood of coming into contact with outsiders. These patterns could be determined by territorial social groups, each occupying a discrete core space for its refuge and foraging, thereby reducing the potential for agonistic encounters with other social groups forced to cluster around rare resources, such as a large cave system.

A number of behavioural acts recorded during this study were directly related to courtship. Some of these behaviours were similar to those found in other rock-wallaby species (Horsup, 1986; Barker, 1990) and other macropod groups, including *Macropus parma* (Coulson, 1989; Heathcote, 1989; Ord et al., 1999). The male initially approached (AP) the female and sniffed her anogenital region – this is referred to as sexual checking (SCH). Sometimes the male would approach from the front and perform a non-agonistic social act with a nose-nose sniff (NN), and after sexual checking (SCH), begins a series of light scratching or rubbing with his forepaws on her body (BR) or facial (FR) region. The female responded by lowering her head submissively (SHT), moving away (RE), or performing an aggressive agonistic act in the form of a grimace (GR), strike/cuff (SC) or bite (BC). Light scratching or rubbing by the male could last up to 30 minutes before he tried to mount the female (MT). She responded by either rejecting the male (PO) or allowing him to mount her (MA). On many occasions these ritual acts resulted in the female rejecting the male, while on others, the same male returned later the same day and repeated the procedure with the same female, suggesting a need for males to continually build on social bonds for future mating even if the female is not ready for breeding (not in oestrus). Access to females may also be an important defensive resource and play an integral role in the social organisation of rock-wallabies. One ecological study conducted on rock-wallabies found a number of females sharing a set of refuges with one dominant male defending access to them. In each of these social groups, the dominant female produced more offspring than the subordinates (Jarman & Bayne, 1997).

The social behavioural repertoire of *P. l. lateralis* is dominated by agonistic behaviour characterised by a large number of ritualised displays. These ritualised displays have evolved to communicate information. According to Drickamer & Vessey (1992) an animal's submissiveness inhibits attack by another, and not only avoids severe injury, but also creates a dominant hierarchical social system. Rock-wallabies clearly exhibit such behaviours, and all studies conducted on their social behaviour to date have identified dominance hierarchical social systems (Horsup, 1986; Barker, 1990; Blumstein et al., 2001). Since dominance is defined as an agonistic relationship, it is not surprising that it usually results in preferential access to limited resources (Ganslossser, 1989) such as refuge, food, water and mates (Horsup, 1986). Dominance relationships also influence foraging behaviour. Blumstein et al. (2001) found that higher-ranking individuals spent more time foraging and less time being vigilant than lower-ranking individuals, and concluded that the difference was caused by intra-specific competition resulting in decreased benefits for some rock-wallabies through aggregation. The social behaviours observed in this study reflect a significant number of agonistic ritualised behaviours that could strongly impact their activity and spatial patterns, as well as their social structure and population dynamics. This is further discussed in the following chapters.

3.4.5 Opportunistic feeding

Rock-wallabies at Nangeen Hill Reserve were observed feeding on numerous plant species including grasses, forbes and browse groups and their various structural components, including roots, stems (soft and woody), leaves and flowers. They adopted various feeding strategies to accommodate both grazing and browsing. *P. l. lateralis* sometimes used their forepaws to either pick up or pull and hold the food while bringing it to its mouth during grazing (G), browsing (B), and scavenging (SG). They frequently adopted a vigilant posture while feeding. During dry periods, *P. l. lateralis* commonly adopted a ground-scratching/digging mode to feed on roots or the remaining stems of herbaceous material. This behaviour resulted in significant substrate surface disturbance, likely to encourage opportunistic weed or pioneering species after the ensuing rain.

Scavenging (SG), whereby individuals picked up thin woody sticks to feed on, was regularly observed during dry periods. The animals adopted some unusual feeding and browsing behaviours during the dry periods, including climbing trees to browse and eating bark (Plate 3.10). Tree climbing to browse on new leaves has been observed in

studies on the allied rock-wallaby (*Petrogale assimilis*) in the tropics (Horsup & Marsh, 1992), but no previous reference was found to rock-wallabies eating bark. On a number of occasions rock-wallabies at Nangeen Hill were observed climbing into small trees (*Acacia* spp. and *Rhinocarpus* spp.) to feed on new leaves at the tips of branches unreachable from the ground. It was also common to see them eating dry sticks during dry periods. It is important to note that dry periods can include both autumn and early spring when the seasonal rains have been later than normal. Tree climbing was observed in the dry June of 2006 after a dry autumn. Individuals were also observed scaling steep rock faces that contained fresh green herbaceous material in the rock cracks.

There were many signs of bark consumption on a variety of shrub and tree species throughout the entire study period (Plates 3.11 and 3.12). Such evidence was clear within or immediately surrounding the rock-wallabies' permanent rock refuge area. Initially rabbits were thought to be responsible, but some shrubs and trees showed signs of bark consumption at heights out of reach of rabbits. During the summer of 2006/2007 rock-wallabies were seen consuming bark. They gripped the smaller branches (1-3 cm wide) with their forepaws and bit into the bark, stripping sections with their teeth before chewing and consuming them. In some cases the damage was so extensive that the plants eventually died. Since the study commenced, older signs of bark consumption have been seen close to the rock-wallabies' central diurnal rock refuge area (Plate 3.11), suggesting that this feeding behaviour has been occurring over a long period of time. However, bark consumption has only been observed during the dry months, suggesting it may be due to a scarcity of more nutritional items during this period.

All studies on the diet of rock-wallaby species have reported large variability in food resources, including forbes and browse species (Dawson and Ellis, 1979; Copley and Robinson, 1983; Horsup and Marsh, 1992). Together with the rock-wallabies' ability to adopt different foraging techniques, this broad food choice allows these macropods to remain in close proximity to their rock refuge, even during periods of drought. By doing so they reduce the energy required for long foraging journeys away from the refuge, and the risk of predation. Some rock-wallaby studies show a significant increase in home range size during the dry period (Lim, 1988), which may be due to a combination of poor food source availability around the rock refuge and predation pressure. These individuals chose to forage close to the refuge on poorer resources rather than risk exposure to predators (a fear-driven system) even at the expense of their nutritional

health and compromised reproductive ability, pointing to a current population density in excess of its capacity. The feeding and foraging behaviours of the *P. l. lateralis* at Nangeen Hill also appear to be degrading the habitat in and around their central diurnal rock refuge and will eventually reduce the carrying capacity of the reserve. These consequences are further discussed in chapter 4.

Plate 3.10 *Acacia* spp. with signs of bark-stripping by *P.l. lateralis.*

a   b

Plate 3.11 a) New and b) old bark stripping on shrub species on top of the Nangeen Hill rock outcrop.

Plate 3.12 Signs of severe bark damage due to *P. l. lateralis* feeding at Nangeen Hill Reserve.

3.4.6   Thermo- regulatory behaviour

Basking is a common behaviour in many rock-dwelling mammals, including the rock-hyrax (*Procavia capensis*) (Mares & Lacher, 1987; Brown & Downs, 2005), and is considered essential for energy conservation (Brown & Downs, 2005). For rock-wallabies, basking and shading behaviours are essential for energy conservation. Basking behaviour involves resting, usually on a rock, with the animal exposing its body to the sun (Plate 3.7). The rock-wallabies in this study displayed basking behaviour during the cooler months from April to October, predominantly in the early mornings and late afternoons. However, during the coldest months (June-August) basking behaviour was observed throughout the day. During the warmer months (November to March) basking was replaced by shade-resting behaviour   (Plate 3.7). Individuals rarely basked alongside one another and where observed, it was predominantly male and female pairs. Only adults were seen basking in open rock areas; females with young or small sub-adults were only seen basking in more

enclosed rock areas in close vicinity of a cave entrance. Individuals used both rock and vegetative structures for shade-resting, including cave entrances, and as in basking, rarely rested in the shade beside one another. It is important to note that shading behaviour is different from refuge concealment. The latter refers to animals that are completely out of view, whereas in shading behaviour, animals are still visible while in a resting behavioural state. Individuals observed in an active behavioural state during the summer diurnal periods were also generally within the shade of a rock or under vegetative cover.

Macropods are believed to use three main physiological means of evaporative cooling: panting, sweating, and saliva spreading (Dawson et al., 1974). The *P. l. lateralis* at Nangeen Hill were observed repeatedly licking their forearms during hot periods. This form of behaviour has been observed in most macropods (Croft, 1980) and is believed to play a role in temperature regulation. The presence of extensive branching and anastomosing superficial veins in the forelimbs of at least one species (*Macropus rufus*) of the macropods (Needham et al., 1973) supports this theory. Although licking the forelimbs is considered to be thermoregulatory behaviour, it is widely accepted that panting and sweating are still the principal means of evaporative cooling in macropods (Wallis & Ealey, 1972). Panting behaviour was not observed in *P. l. lateralis* at Nangeen Hill, however may only occur after high activity levels, especially during high diurnal temperatures when rock-wallabies are not generally active. Individuals were often observed with their mouths slightly open during high diurnal temperatures, even though there were no obvious signs of panting.

There is no information available on rock-wallaby sweat glands. Apocrine sweat glands have been found in the hairy skin and eccrine glands of many macropods (Mykytowycz & Nay, 1964), nevertheless, it is believed that sweating only occurs during exercise followed by panting (Dawson et al., 1974). Prolific sweat glands in some of the larger macropod species could be an adaptation to semi-arid environments (Hume et al., 1989). It is unknown whether rock-wallabies have similarly equally prolific sweat glands. Panting requires a higher metabolic rate, resulting in higher energy costs and water loss. By restricting some behavioural activities to more favourable climatic conditions and taking refuge, rock wallabies have avoided high metabolic expenditure. They tend to be inactive during high temperatures and rely more heavily on basking, shading and possibly saliva spreading as their principal means of thermoregulation, in addition to restricting other activities to more favourable climatic conditions. Activity time allocations during various climatic conditions are discussed in chapter 4.

3.4.7   Conclusions

This chapter has provided a comprehensive description of the behavioural repertoire of *P. l. lateralis*. It addressed some of the causes and effects of these behaviours and offers a framework for quantitatively analysing the activity patterns of this species in future research.

P. l. Lateralis use a complex arrangement of non-agonistic and agonistic behaviours to determine their social organisation which appears to reflect a linear dominance hierarchy, and are strongly influenced by a defendable refuge. There appears to be a strong predation influence on the behaviour of this population. Individuals within the rock refuge were rarely observed adjacent to each other when undergoing an activity suggesting a sense of personal space. Rare but significant behavioural acts, such as bark eating, attacking intruders, group fighting, tree climbing, responses to predators and other herbivore competitors were only seen after many hours of observation. *P. l. Lateralis* exhibited strong disturbance behaviour that can be scaled to determine the severity of the response, and so can be quantified in future studies. These observations provided important insights into the causes of some of these behaviours and will contribute to their conservation and management. They also provide some important evidence for predictions 1, 2 and 3, exhibiting behavioural adaptations for conserving water and heat loss, (Basking and shading behaviour), exhibiting dominance hierarchical behaviours (supplanting), and strong vigilance and disturbance behaviours in relation to fear of both predators and conspecifics.

Only when more detailed behavioural repertoires have been compiled for all macropod species will we be able to formalise more generalised behavioural acts, states and patterns for the purpose   of comparing populations, species and macropod groups. It will also allow us to determine important ecological differences related to evolutionary and environmental history. By placing detailed behavioural studies in the too-hard basket, we risk mis-management of both existing and future translocated animal populations, and restrict our ecological understanding of the species.

Chapter 4

Ecological determinants of foraging behaviour in *Petrogale lateralis lateralis*

4.1   Introduction and specific aims

It is widely believed that macropods are either predominantly nocturnal or crepuscular (Pople, 1989), but little is known about whether rock-wallabies mainly adopt one of these two foraging strategies. Although rock-wallabies are found over a wide geographic area and occupy refuges within a wide range of habitats and climatic conditions (Tyndale-Biscoe, 2005), few studies have been conducted on their foraging patterns. No previous studies have been undertaken to determine how climatic conditions affect the foraging strategies of rock-wallabies to cope with living in variable environments. Although some rock-wallaby studies have recorded diurnal foraging activity, they are generally considered to be predominantly nocturnal (Barker, 1990; Jarman & Bayne, 1997; Sharp, 2009; Telfer & Griffiths, 2006)**.**

Within each 24-hour period an individual *P.l. lateralis* must decide when to rest, when to forage and when to socially engage with other individuals. As metabolic costs vary under different climatic conditions, *P.l. lateralis* individuals would be expected to conduct their higher energy-consuming activities, such as foraging, during most favourable conditions, i.e. at ambient temperatures within their thermal neutral zone. In addition, predation risks may vary over time, space, and under different climatic conditions, and would therefore be expected to influence the behaviour of these animals. One generally accepted method to determine an animal's perception of predation risk when foraging is to measure its level of vigilance (Caro, 2005). Brown (1999) discusses how anti-predator behaviour should vary with predation risk, including vigilance levels, quitting harvest rate and giving up densities (GUD), with all three behaviours increasing in encounter rate with predators. Although an animal may make a trade-off between energetic reward and the risk of predation (Kotler et al., 1994; Kotler et al., 2010), the perceived risk may be so great that it chooses to forage close to its refuge in poorer food resource patches, even if this results in severe degradation of the habitat and poorer health. Like all rock inhabitants that forage away from a permanent refuge, their utilisation of this refuge resource has significant consequences for the long-term survival of the population, and affects structure, dynamics and spatial distribution over time.

In other mammals, predation risk has also been found to be temporally scale dependent within both the diel period and seasonally, including the hyrax, another rock-inhabiting central-place forager (Bakker et al., 2005; Druce et al., 2006). Thus it is important that studies record activity at different times of the day and night, and on a seasonal basis under different climatic conditions. Although it is clear that predation affects the behaviour of prey, such as vigilance levels, vigilance behaviour may also be a response to disturbances by other conspecifics (Hirsch, 2002; Lung & Childress, 2007; Marino & Baldi, 2008).

Another behavioural strategy for reducing predation is hiding. Many animals seek refuge from predators using avoidance strategies (Sih, 1987; Bakker et al., 2005; Rhoades & Blumstein, 2007). This has significant implications for central-place foragers, where individuals tend to graze less at further distances from their refuge, thereby creating a gradient of increasing vegetation (Bakker et al., 2005). This vegetation gradient is an indirect effect of predation fear.

The main aim of this component of the research was to investigate the aspects of the environment that affect *P.l. lateralis* choices of specific behaviours.

Specifically the objectives were to determine whether:

- Time spent on different behaviours differs between seasons, sex, group size, distance to nearest neighbour, and distance to rock refuge;
- Climatic conditions affect behavioural patterns. The variables investigated were mean and maximum wind velocity, temperature, precipitation, cloud cover, and moon phase;
- The light phase affects behavioural patterns. The variables were nocturnal, dusk and diurnal; and
- The rock refuge acts as an important thermal refuge.

Finally, another important aspect of the research was to determine the foraging spatial distribution of the population.

4.2 Methods

It was not possible to conduct continuous 24-hour observations, so a time period was chosen to align with rock-wallabies' most active times. Preliminary observations

indicated that periods of least activity occurred during midday and around dawn. Rock-wallaby activity was observed during the morning when most animals were observed in a vigilant resting state; grooming, and engaging in occasional social activity. Feeding acts were rare during the early morning period, and only occurred during summer. Unlike the larger free-roaming macropods, *P.l. lateralis* at Nangeen Hill were rarely seen in an active state just prior to or at dawn, and feeding individuals were either within or adjacent to the permanent refuge. Rock-wallabies were considered active when they were outside their caves and inactive when inside.

As discussed in chapter 3, the periods of highest activity were from 1.00 pm to 12.00 am and from 8.00 - 10.00 am during the cooler months, and between 5.00 pm and 5.00 am and between 7.00 - 9.00 am during the warmer months. In all seasons the periods of least activity occurred from 11.00 am to 1.00 pm and from 5.00 - 7.00 am. From this information, a session onset time of 5 hours prior to sunset, and a completion   time of 7-9 hours after sunset were adopted. Each session lasted 12-14 hours (with a one-hour break) and allowed observation of changes in foraging behaviour caused by changes in the environmental conditions within a single foraging period. In addition, a number of observations of 1 to 3 hours in length were also conducted outside these time periods throughout the entire fieldwork**.** Field trips for the quantitative studies were divided into continuous   4-5 day sessions (4- 5 group sessions every season commencing in May 2006). This method allowed both nocturnal and diurnal behaviour patterns, encompassing the rock-wallabies' most active period within a relatively constant time frame (session onset always 5 hours prior to sunset), to be recorded. The sessions were then combined into seasonal periods, enabling the investigation of seasonal effects on nocturnal and diurnal activity patterns. Approximately 800 hours of quantitative data were included in the focal and scan sample collection.

Direct observations incorporated both scan sampling and focal sampling techniques. Diurnal observations were conducted from sheltered vantage points or a temporary hide using 10 x 50 binoculars and a digital video-recording device. Nocturnal observations were conducted with the aid of night-vision equipment (ATN Voyager night vision monocular generation 2+) and a digital voice recorder. The total observational viewing region was split into four vertically stratified locations (separated 60 m apart) starting at the top of the outcrop, running down the rock and across into the foraging area (Figure 4.1). Except for zone 3, each zone contained at least one large cave system, however, zone 3 contained numerous small caves and crevices. From the preliminary studies, rock-wallabies emerged predominantly from zones 1, 2 and 4,

and although individuals were often observed resting along the top edge of the outcrop, no individuals were encountered more than 5 m from the edge during the day. These observations were consistent throughout the study. The entire viewing region for the quantitative observations encompassed over 50 % of the rock-wallaby population, approximately 60 individuals, that occupied different regions of the rock refuge were included into the sample collection. This resulted in various sub-groups being sampled.
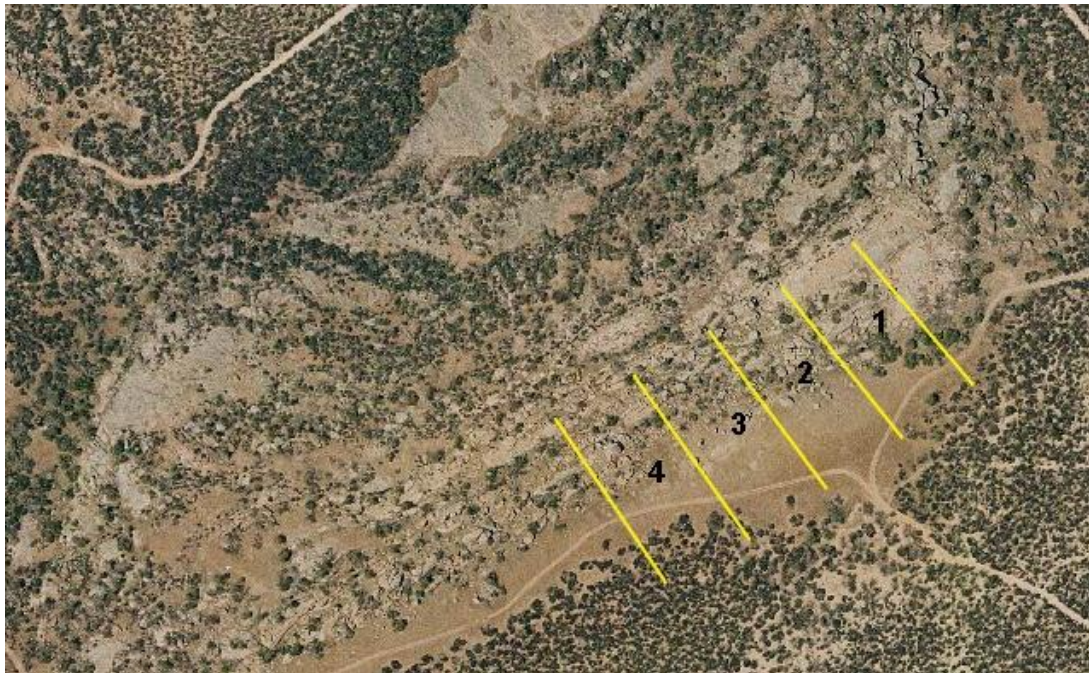
Figure 4.1 Nangeen Hill observational region showing the division into four zones.

4.2.1   Focal sampling

Continuous focal records were used to determine activity states (feeding, moving, grooming, scanning, resting and other activities), social interactions, space tolerance between conspecifics, and disturbance responses. Continuous focal nocturnal samples were recorded using a digital voice recorder and then played back on a computer at a later date to be analysed using the behavioural analytical program, JWatcher_V1.1. Diurnal samples were filmed using a digital video recorder and then played back on a computer and analysed using the behavioural analytical program, JWatcher_V1.1. At the start of and during observational periods climatic conditions were recorded, and particular individuals' orientation and distance (m) from the nearest cover and conspecific were estimated and group size using the criteria of the number conspecifics within 25 m from focal individual. For each focal observation time session, one individual was randomly selected from each age and sex class, and from a different zone location, reducing the likely hood of sampling from the same group each time.

Individuals were observed for a time period of 10 minutes, chosen because it was long enough to obtain sufficient data, including total distance moved and mean length of bouts of locomotion. Small focal time samples (less than 3 minutes) frequently resulted in no recorded movements and so were not included in the final analyses. During periods when individuals were active, approximately 3-4 focal samples were taken every hour (during active periods).

All individual behavioural acts recorded were derived from the ethogram developed in chapter 3. Raising the head and scanning the environment is widely accepted in the literature as anti-predator behaviour that increases under elevated risks of predation (Elgar, 1989; Lima & Dill, 1990). However, this behavioural trait is also used for detecting the location and behaviour of other conspecifics (Caro, 2005). For this study, rock-wallabies were considered active when outside their cave and inactive when inside. Resting behaviour just outside the cave was assigned to one of two categories:

   a) resting and vigilant (lying, sitting or crouching with head up, actively scanning the environment); or
   b) resting and non-vigilant (lying, sitting or crouching with head down).

All focal data were analysed using a behavioural analytical program, JWatcher_V1.1 to determine behavioural state frequencies, mean bout lengths and proportions, then transferred to an EXCEL database and finally into SPSS version 15.1 for further analysis. Krsukal-Wallis test and Spearman rank correlation were used where applicable to test for significant differences and strength of correlations.

4.2.2   Scan sampling

Scan sampling was conducted at 30-minute time intervals between focal sampling sessions, with approximately 1600 sampling points during the course of the quantitative data collection. For each scan sample the size of the group, the animals' orientation to one another, their activity, substrate occupied, the nearest shelter, and climatic conditions were recorded for all visible individuals. This method allowed the researcher to collect individual and group data simultaneously. All scan data were transferred to an Excel database and then into SPSS version 15.1 for further analysis. Krsukal-Wallis test was used where applicable to test for significant differences. In addition climatic and astronomical conditions were taken immediately after each scan sample, including temperature, wind velocity (mean and maximum), cloud cover, precipitation and moon phase.

4.2.3 Cave and external temperature recording

In order to determine the advantage, if any, of staying within a rock refuge during extreme climatic conditions, 5 caves (within the occupied rock-wallabies' refuge) and 3 external locations (within different habitats) were selected. For the temperature recordings Thermochron iButton® temperature loggers (DS1921G) were used. These are rugged, self-sufficient systems that measure temperature and record results in a protected memory section. Temperature is measured in 0.5^0C increments and readings are taken at equidistant intervals, ranging from 1 to 255 minutes.

The electronic iButton recorded the temperature at 20-minute intervals during two seasons: winter and summer. The data were transferred into Excel and pooled into single mean cave and external temperatures at 20-minute intervals over twenty-four hour periods. The ranges of cave and external temperatures were then compared to determine whether there were any significant differences between the two.

4.3 Results

4.3.1 Nocturnal foraging spatial distribution

The nocturnal focal data collection was also utilised to determine groups size and nearest neighbour distances, and included sampling from various sub-groups. *P.l. lateralis* had a relatively small mean group size of 3.2 (Table 4.1). Although the tested mean group size was significantly different between seasons (Kruskal-Wallis test: (3, N = 452) = 13.9, p <0.05) with group size smaller during autumn/winter than in spring/summer there was only marginal change. The mean distance to the nearest neighbour (individuals found in social groups of 2 or more, using the group definition in section 4.2), was relatively high (6.8 m), with a significant seasonal difference (Kruskal-Wallis test: (3, N = 336) = 11.4, p <0.05). During summer the mean distance decreased by nearly 2 m compared to the other seasons (Table 4.2). This decrease occurred in both sexes and during the driest period, when resources are expected to be less abundant. Sex class association between nearest neighbours showed significant differences, with male-male associations the highest (51%), followed by male-female (41%), and female-female the lowest at 8%.

Table 4.1 The group size of *P. l. lateralis* at Nangeen Hill Reserve, mean ± S.E.(N).

Sex	Autumn	Winter	Spring	Summer	Total
Male	2.9 ± 0.23(71)	2.7 ± 0.25(51)	3.5 ± 0.20(95)	2.9 ± 0.26(45)	3.1 ± 0.12(262)
Female	3.3 ± 0.36(31)	3.4 ± 0.39(22)	3.5 ± 0.26(49)	3.4 ± 0.28(36)	3.4 ± 0.15(138)
Total	2.7 ± 0.16(128)	2.8 ± 0.19(85)	3.4 ± 0.15(155)	3.1 ± 0.18(84)	3.2 ± 0.1(452)

Using the pooled data, 23.7% of rock-wallabies were foraging on their own and only 10% were foraging in groups of 6 or more in the open meadow area, so although rock-wallabies appear to forage in groups, a large proportion appear to feed alone or in pairs (Figure 4.2). Larger groups of 9 or more were only detected during spring, and a higher proportion of rock-wallabies foraged alone during autumn and winter.

Table 4.2 *P. l. lateralis* nearest neighbour distances (m) at Nangeen Hill Reserve, mean ± S.E.(N).

Sex	Autumn	Winter	Spring	Summer	Total
Male	7.7 ± 0.87(51)	6.5 ± 0.86(35)	7.5 ± 0.61(80)	4.9 ± 0.65(31)	7.0 ± 0.39(197)
Female	7.2 ± 1.11(22)	7.1 ± 1.54(18)	6.6 ± 0.67(43)	4.5 ± 0.57(30)	6.2 ± 0.44(113)
Total	7.5 ± 0.63 (85)	7.2 ± 0.75 (59)	7.1 ± 0.45(128)	4.7 ± 0.45(64)	6.8 ± 0.29(336)

There appeared to be some effect on the mean group size in the period after sunset. Group size initially increased and was followed by a downward trend during the night (Figure 4.3). The low mean group size close to daybreak is possibly due to the animals concluding their nocturnal foraging and returning to the rock refuge to rest inside their caves.
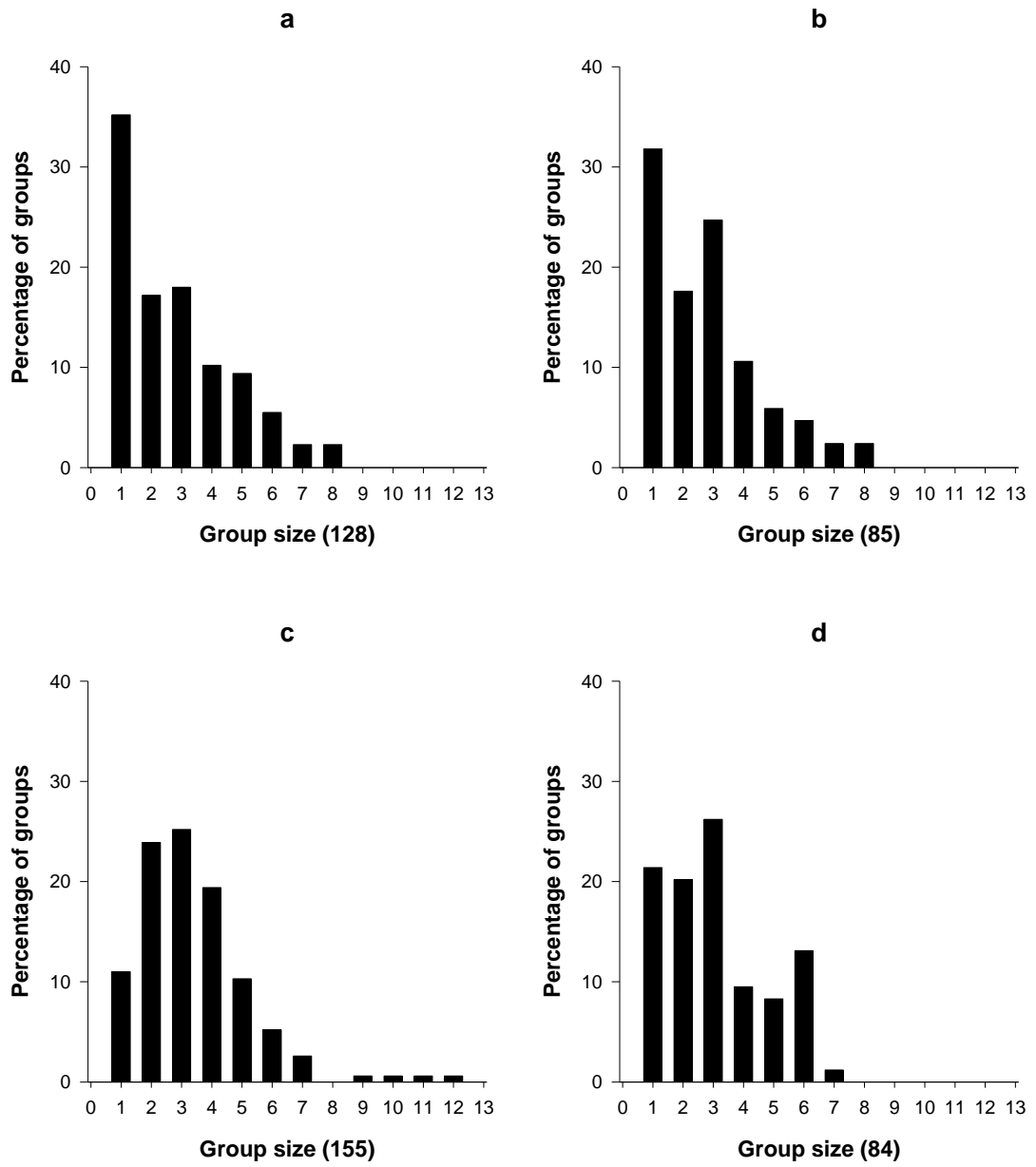
Figure 4.2 *P. l. lateralis* group size (N) distribution on Nangeen Hill Reserve in a) autumn b) winter c) spring and d) summer.
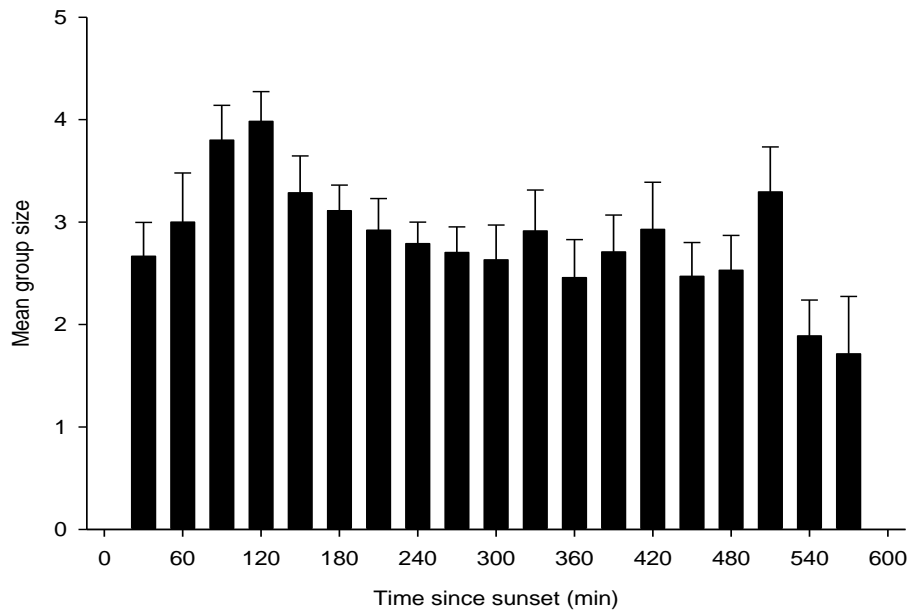
Figure 4.3 The *P. l. lateralis* mean ± S.E. group size distribution over time after sunset.

For foraging distances away from the rock refuge scan data was used as it encompassed larger samples sizes and included all sub-groups simultaneously. During summer rock-wallabies spent more time foraging at distances less than 5 m (40.7%) from their central diurnal rock refuge than any other season; while during autumn, they spent more time than any other season feeding at distances greater than 15 m (39.9%) (Figure 4.4). Rock-wallabies spent approximately 90% of their time foraging within the first 25 m from the rocky outcrop during all seasons, reflecting a high concentration of activity within a small proportion of available food resources within the meadow region.

P. l. lateralis individuals were reluctant to move away from the edge of the diurnal refuge (the edge of the rocky outcrop) until after twilight, when the sun had completely set. Approximately eight hours after sunset and before sunrise, individuals began to move back towards the rocky outcrop (Figure 4.5). Movement back to the diurnal rock refuge at the end of the night was reflected in the decreased group size as shown in Figure 4.3. The temporal difference was significant (Kruskal-Wallis test: (19, N = 8524) = 749.6, p <0.01).

The mean foraging distance from the central diurnal rock refuge recorded during nocturnal scan sampling was only 10.74 m, with significant differences between seasons (Kruskal-Wallis test: (3, N = 8524) = 49.5, p <0.01) and zones (Kruskal-Wallis test: (3, N = 8524) = 192.4, p <0.01).
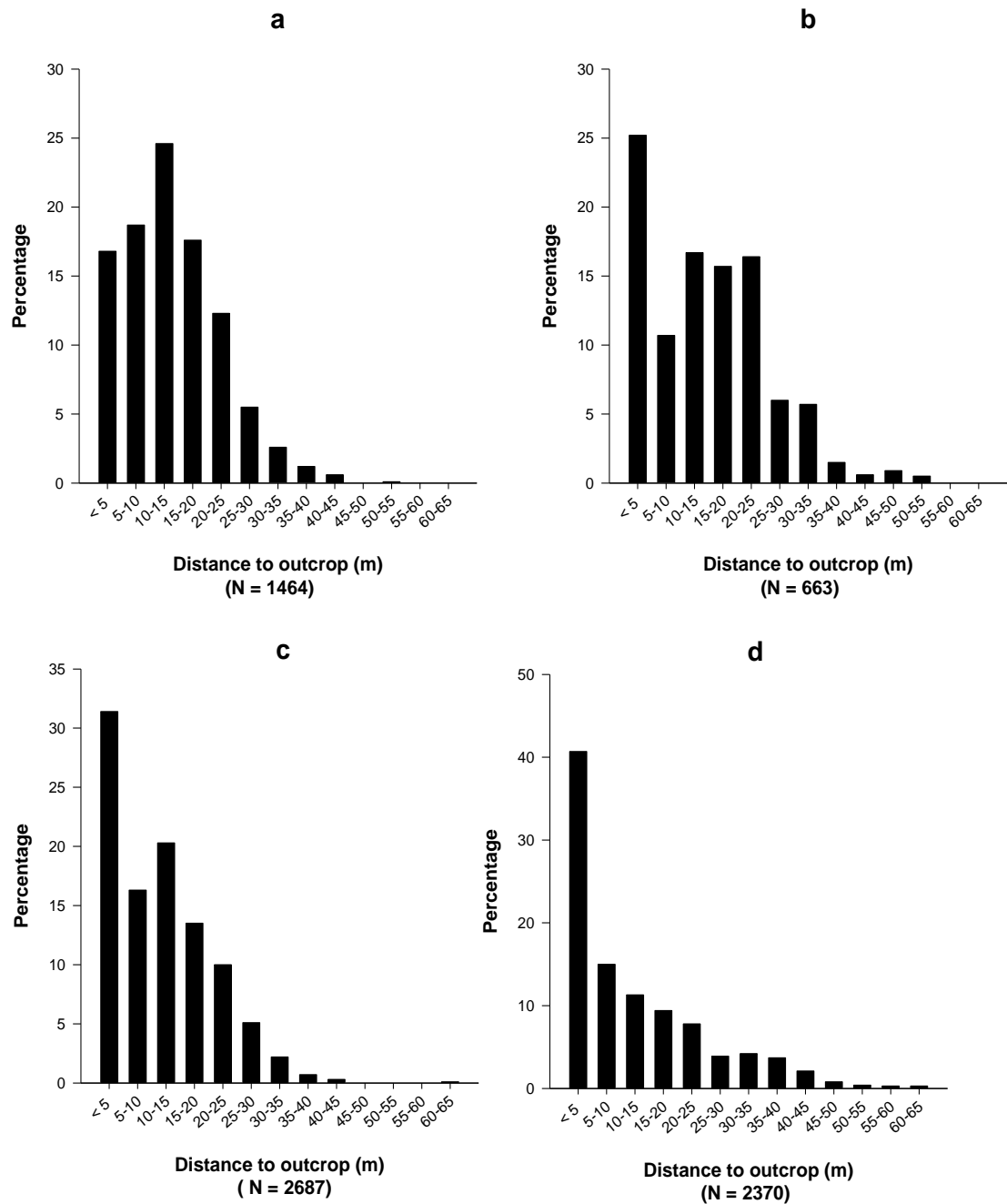
Figure 4.4 The percentage of *P. l. lateralis* individuals recorded at various distances from the permanent rocky outcrop using the pooled scan data set a) autumn b) winter c) spring and d) summer.

Individuals fed closer to the rock during spring and summer as compared with autumn and winter (Figure 4.6). The seasonal difference is also reflected in their distribution, shown in Figure 4.4. The greater distance in zone 4 (Figure 4.6) could be attributed to increased cover, as it was the only zone to contain some shrub cover adjacent to the rock edge and may therefore have affected the rock-wallabies' foraging pattern.
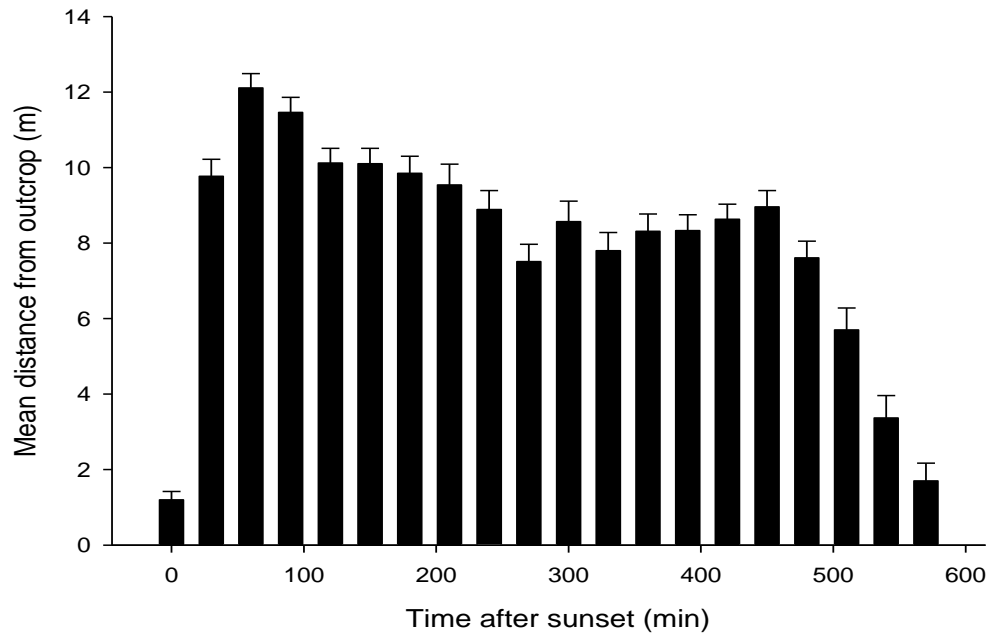
Figure 4.5 *P. l. lateralis* distance from the Nangeen rocky outcrop over time after sunset (mean ± S.E.).
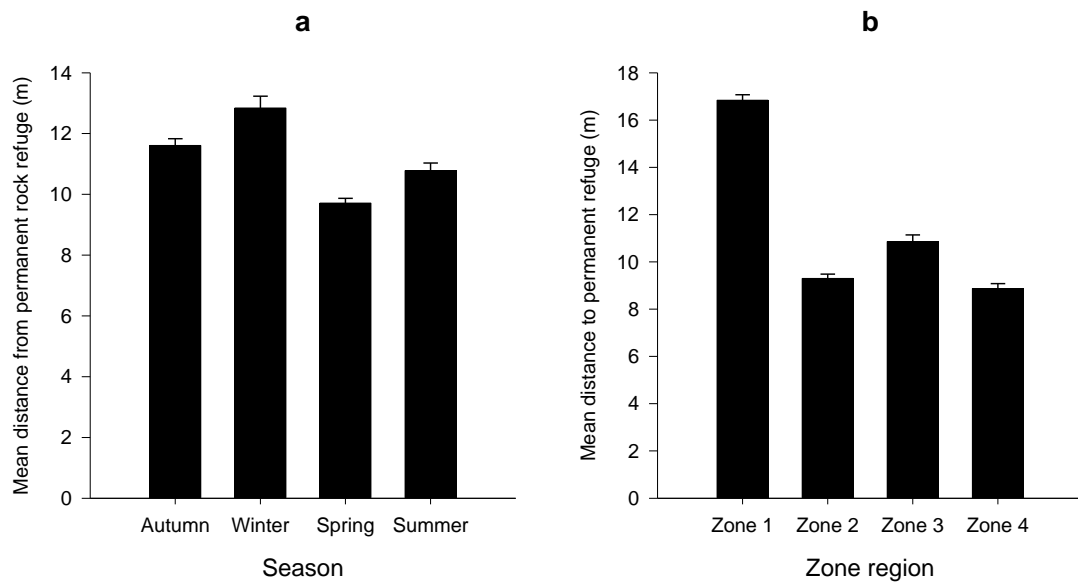
Figure 4.6 *P. l. lateralis* nocturnal foraging distances (mean ± S.E.) away from the bottom of their permanent rock refuge on Nangeen Hill rocky outcrop (scan data) by a) Season: Autumn (N = 1464), Winter (N = 663), Spring (N = 2687), Summer (N = 2370) and b) Zone: Zone 1 (N = 1149), Zone 2 (N = 3162), Zone 3 (N = 1447), and Zone 4 (N = 1426).

4.3.2 Behavioural activity levels (scan data)

There were significant seasonal differences (Kruskal-Wallis test: (3, N = 821) = 141.5, p <0.01) in nocturnal activity levels (Figure 4.7). In stark contrast to winter, and to a lesser degree autumn, summer and spring showed relatively consistent activity levels throughout the night. In winter there was a strong peak within the first two-and-a-half hours after sunset.
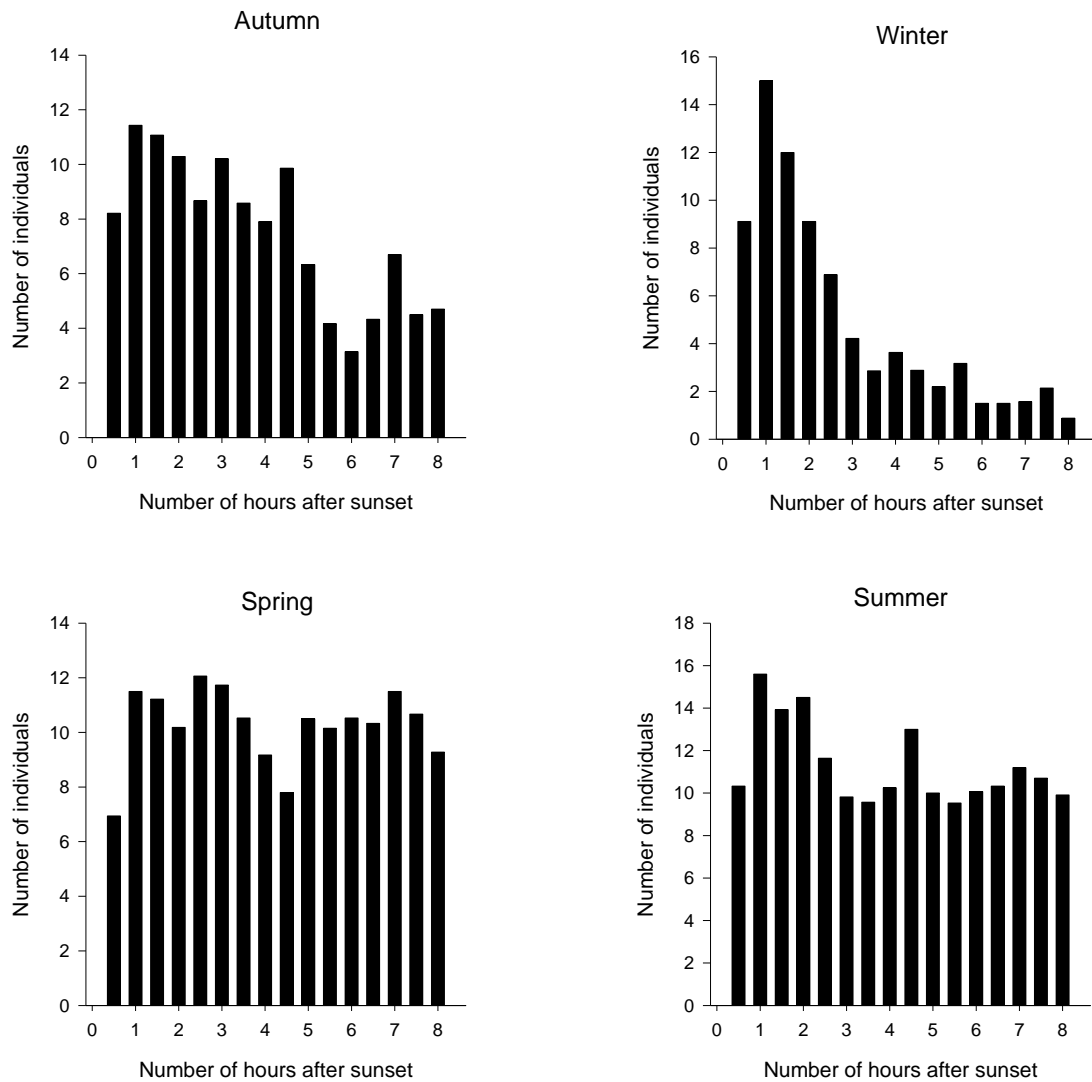
Figure 4.7 The number (mean) of *P. l. lateralis* individuals nocturnally active over time (h): autumn (N = 243), winter (N = 160), spring (N = 303) and summer (N = 236).

During summer, animals were strictly nocturnal, leaving their caves to engage in feeding activity only from the onset of dusk and throughout the night, but ceasing all activity at the onset of dawn. During winter, animals generally left their caves and engaged in feeding activity 3-4 hours prior to dusk, and reduced their activity levels 3 hours after sunset.
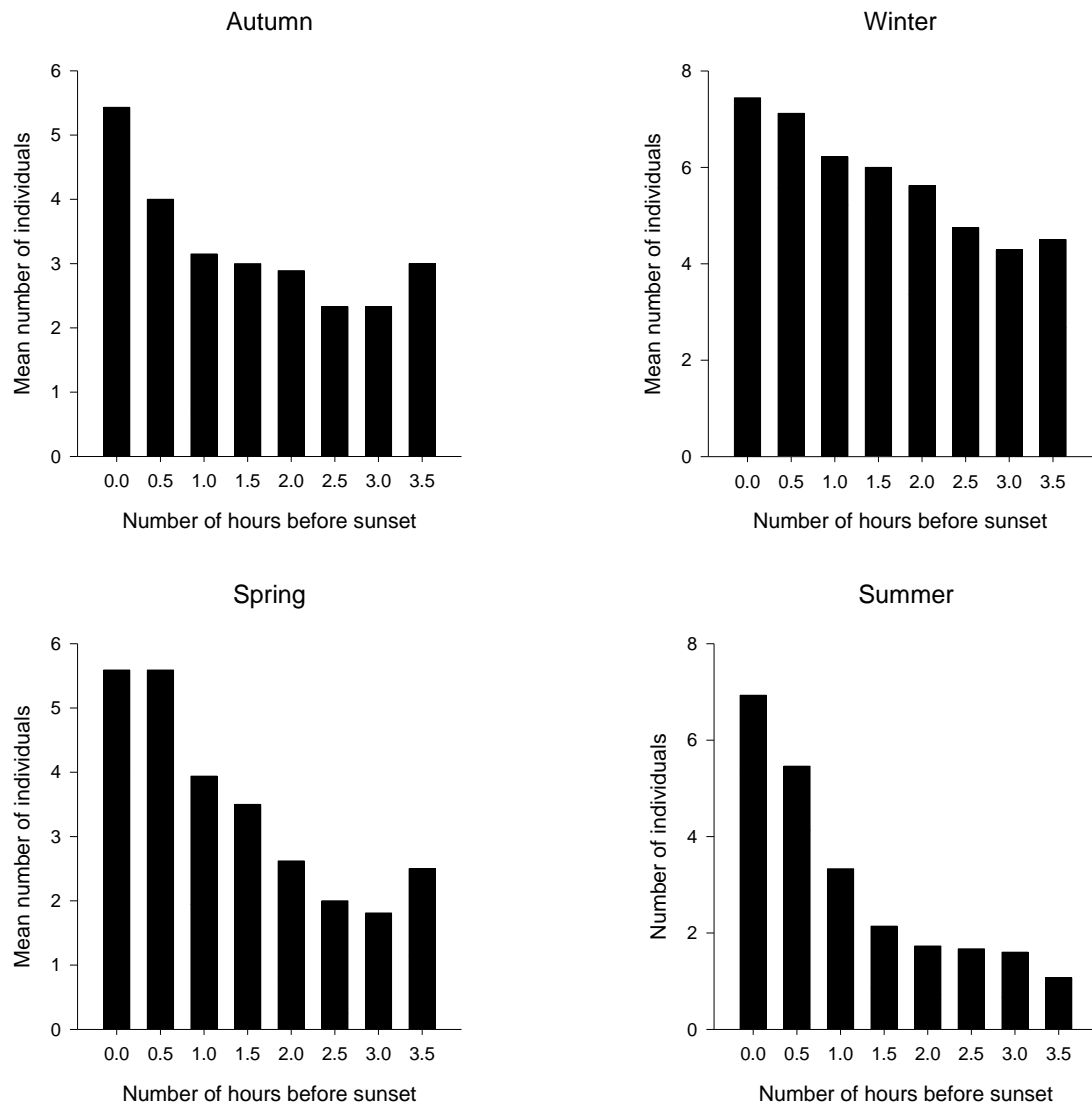
Figure 4.8 The number (mean) of *P. l. lateralis* individuals diurnally active over time (h): autumn (N = 93), winter (N = 71), spring (N = 123) and summer (N= 139).

There were significant seasonal differences (Kruskal-Wallis test: (3, N = 441) = 41.1, p <0.01) in diurnal activity levels (Figure 4.8). Diurnal temperatures appeared to drive sun avoidance in summer, while nocturnal temperatures (Figure 4.9) drove animals back to their refuge during winter. During the cooler months, individuals were often seen

basking throughout the day (see chapter 3), and on cooler overcast days during summer, animals became active prior to sunset but remained inside their refuge on hotter days. The number of animals actively feeding during winter also increased.

Diurnal Temperature

Nocturnal Temperature

Diurnal Mean Wind Velocity

Nocturnal Mean Wind Velocity
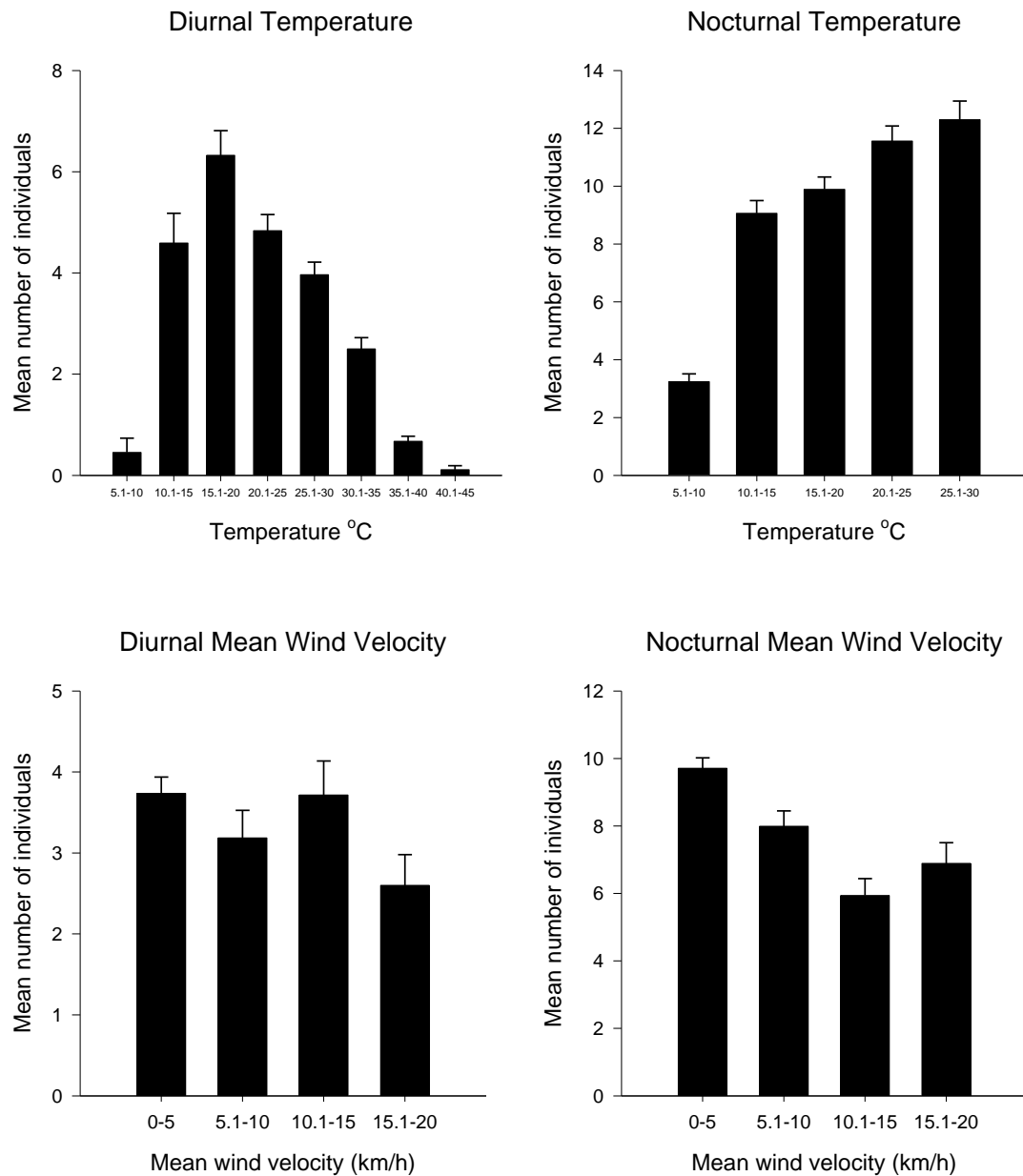
Figure 4.9 The number (mean ± S.E.) of *P. l. lateralis* individuals nocturnally and diurnally active during different temperatures: diurnal (N = 434) and nocturnal (N = 803), and mean wind velocity: diurnal (N= 438) and nocturnal (N = 819).

Significant differences were detected in activity levels by temperature, both diurnally (Kruskal-Wallis test: (8,N = 441) = 199.48, p <0.01) and nocturnally (Kruskal-Wallis test:(4, N = 803) = 198.1, p <0.05).The same was true for wind velocity, both diurnally

(Kruskal-Wallis test (3, N = 438) = 8.96, p <0.05) and nocturnally (Kruskal-Wallis test:(3, N = 801) = 34.23, p <0.01), with higher activity levels linked to lower wind velocity (Figure 4.9). Although there were significant nocturnal (Kruskal-Wallis test (3, N = 821) = 32.85, p <0.01) differences in activity levels according to cloud cover and moon illumination scales (Kruskal-Wallis test: (4, N = 718) = 32.01, p <0.01), there were no discernible patterns (Figure 4.10). There were no significant differences in activity levels with diurnal cloud cover (Kruskal-Wallis test: (3, N = 441) = 4.25, p >0.05) and between Precipitation during both nocturnal and diurnal periods had a negative effect on activity levels.
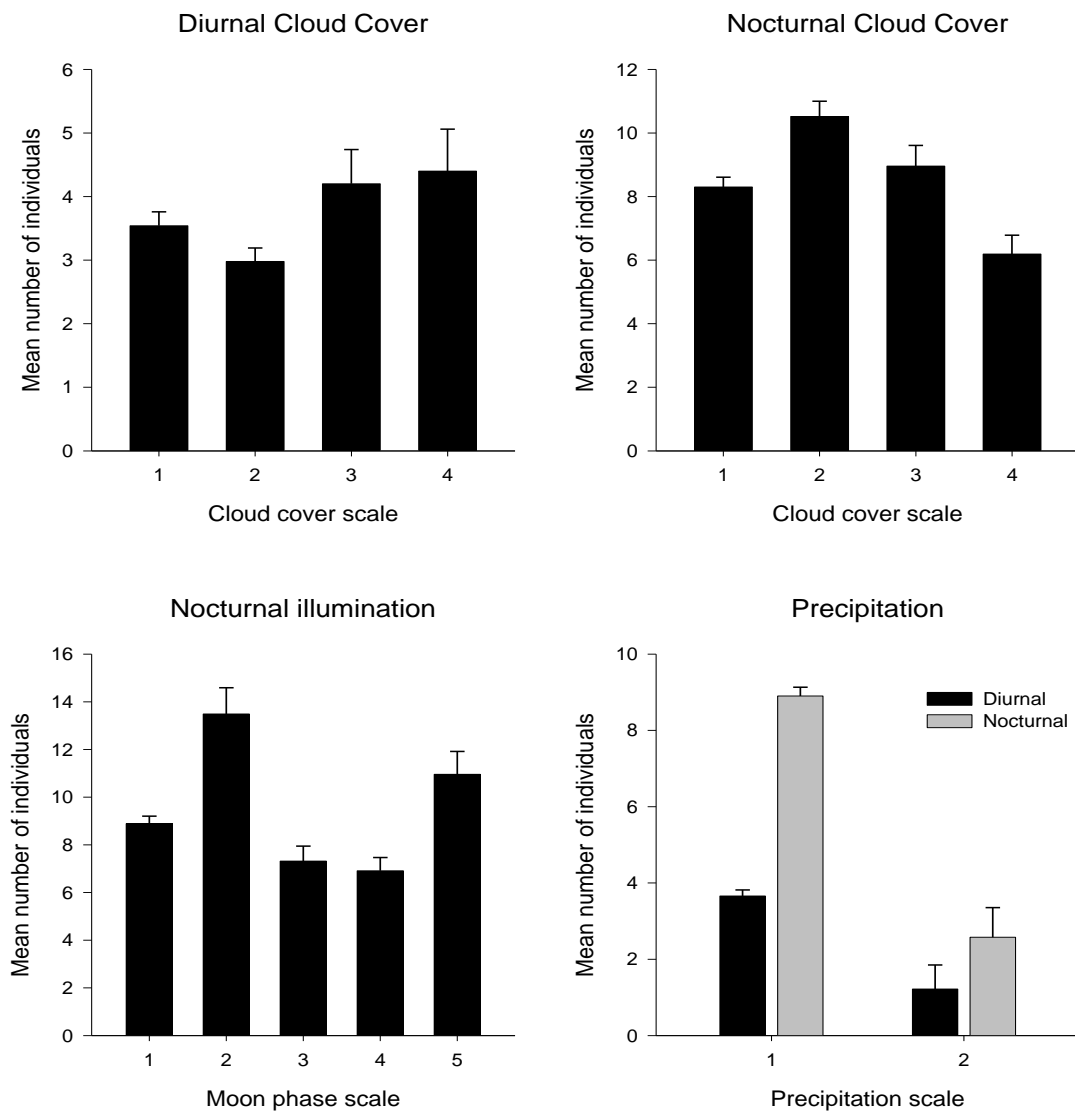
Figure 4.10 The number (mean ± S.E.) of *P. l. lateralis* individuals active during different cloud-cover scales (1 = no cloud, 5 = maximum cloud): diurnal (N = 441) and nocturnal (N = 821), moon phases (1 = no moon, 5 = full moon): Nocturnal (N = 718), and precipitation (1 = no precipitation, 2 = precipitation): nocturnal (N = 821) and diurnal (N = 427).

Rock-wallabies do not adopt a crepuscular foraging pattern, instead they adjust their foraging periods to best suit their environmental conditions. This behavioural adaptability is important for reducing energy loss and the risk of predation during unfavourable environmental conditions. Animals were most active within a temperature range of 15-30^{0}C and low wind velocity. A more detailed overview of ideal and tolerance times for various activities, based on the focal data, is provided in the next section.

4.3.3   The caves as a thermal refuge

There was a significant difference between the cave temperature and that of the immediate external environment. The cave temperature during winter (10.7 to 16.1^{0}C) and during summer (23.0 to 26.1^{0}C) had a smaller range to that of the corresponding external ambient temperatures, which varied from 5.4 to 20.7^{0}C in winter and from 17.5 to 37.8^{0}C in summer. There was a 10-12^{0}C difference between the highest and lowest daily external temperatures. These differences between the cave and external ambient temperatures are significant for rock-wallaby behaviour, because they remain within the cave refuge during extreme climatic conditions to reduce thermoregulatory costs by reducing metabolic levels and energy loss. The strong effects of both temperature and wind velocity on their activity levels (Figure 4.9) reflect the importance of access to an optimal rock refuge. The cave temperature is more likely to remain within the rock-wallabies' thermoneutral zone.
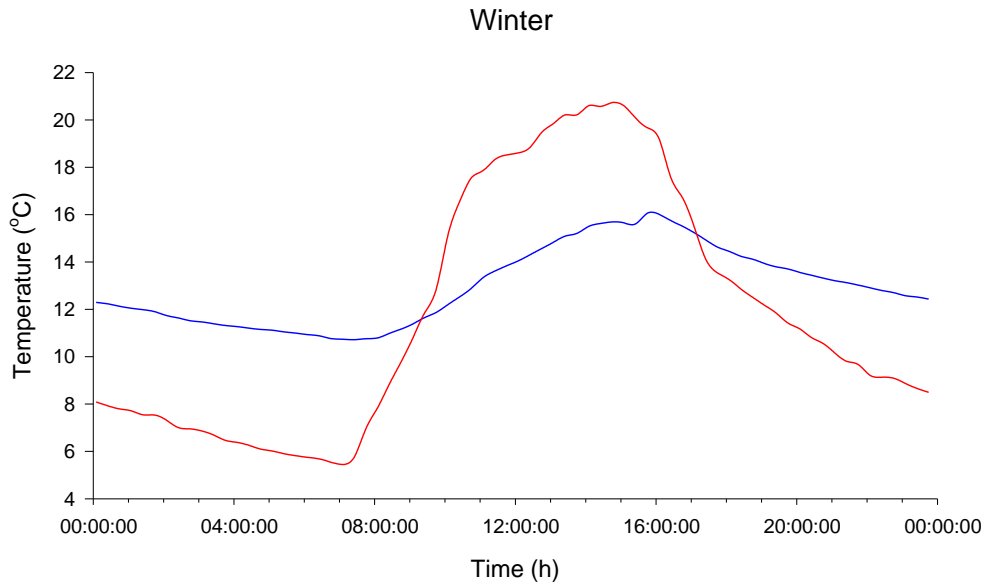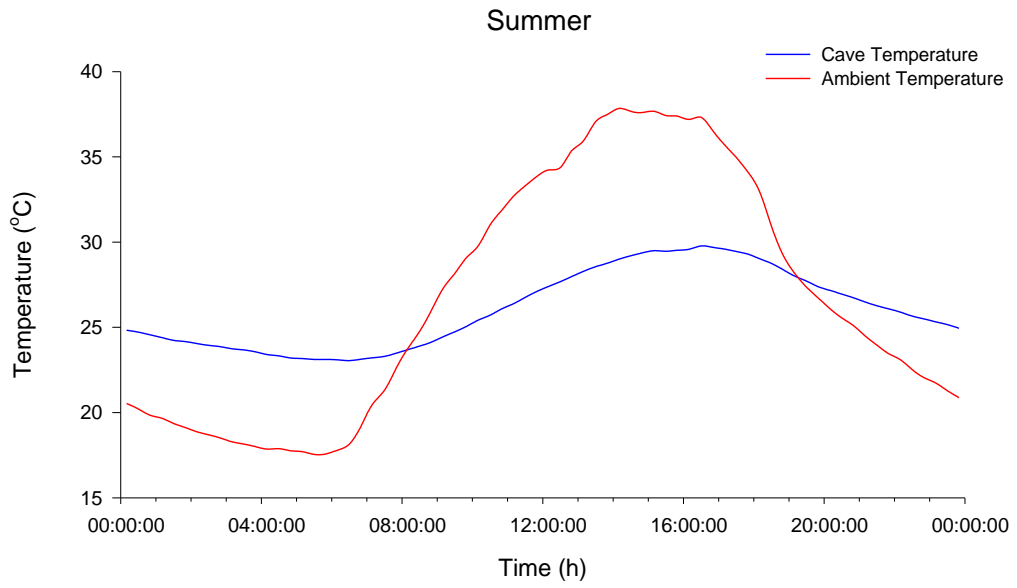
Figure 4.11 The mean cave and external ambient temperatures over a 24-hour period during the summer and winter months.

4.3.4 Focal data (foraging activity)

Six primary activities were examined after combining the nocturnal and diurnal focal data:

- Feeding (all food handling and processing);
- Vigilance (all forms of lifting head up and actively scanning the environment);
- Travel (all locomotion acts not directly related to agonistic behaviour);
- Grooming;
- Resting (stationary and inactive); and
- Social (all forms of agonistic and non-agonistic behaviour).

Grooming, resting and social activities were rarely recorded during the nocturnal focal data collection period, so for graphical representation resting and social activities were combined under "other" activities. Within the meadow region during the nocturnal period animals were never encountered in a non-vigilant, inactive state, and rarely engaged in grooming or social behaviour. Animals moved very short distances between bouts of behaviour. Movement over longer distances predominantly occurred in response to a disturbance, such as fear of predators and other conspecifics.

Concentrated foraging bouts close to the edge of the central diurnal rock refuge caused severe damage to the habitat and resulted not only in poor plant cover during the drier periods, but also soil erosion. Active individuals observed in the meadow area at night spent a significant amount of time feeding, followed by scanning (vigilant) and some movement. Few other behavioural activities were observed. Feeding accounted for the bulk of daily activity when not resting. Although aggressive interactions were rare within the meadow, displacement was common, with the larger adult always the displacer. Only animals engaged in foraging at the start of focal analyses were included in the results.

4.3.5   Effects of time of day

Although one of the primary aims of the research was to compare diurnal and nocturnal foraging behaviour, the dusk period was subsequently split from the diurnal period. Although no significant signs of crepuscular behaviour were found in this population, some changes in their behaviour were noticeable during the dusk period compared to the diurnal and nocturnal periods. Rock-wallaby behaviour varied with time of day (Figure 4.12). They fed more and were less vigilant at night than during the day or at dusk. Dusk appeared to be a transitional phase, with lower vigilance levels than during the diurnal period but higher than the nocturnal period. During the day, animals did not move away from the rock, choosing to either forage within their diurnal rock refuge, or occasionally, adjacent to the diurnal refuge and meadow patches. Animals only began to move away from the diurnal refuge at the onset of dusk, but remained within a short distance of their central diurnal rock refuge. Only after the sun had set did animals begin to move further away, one possible cause of this could be that rock-wallabies have a higher predation fear during higher light levels, when both aerial and boreal predators are active. Their movement back to the diurnal refuge before sunrise (Figure 4.5) also suggests this.
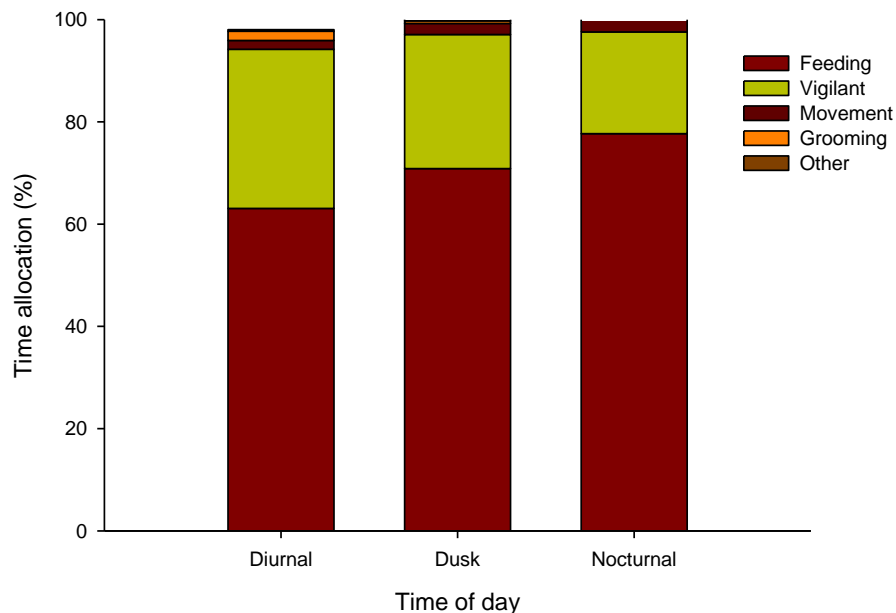
Figure 4.12   The percentage of time that rock-wallabies allocated to feeding, vigilance, movement, grooming, and all other activities at various times of day: Diurnal (N = 206), Dusk (N = 92), and Nocturnal (N =462)

4.3.6 Effects of seasonal and climatic factors

During spring and summer the rock-wallabies in this study spent less time feeding and more time being vigilant than during winter and autumn (Figure 4.13). This aligns with other aspects of their foraging behaviour: during spring and summer their mean foraging distance from the rocky outcrop decreased compared to the previous winter (see Figure 4.5). Animals appeared to perceive a higher predatory presence during seasonal periods when the quality and quantity of food resources were lower. This heightened fear also aligns with a decrease in mean foraging distance from the rocky outcrop during this time of year (Figure 4.6 a) and a decrease in the mean distance between neighbours during the summer (Table 4.2).
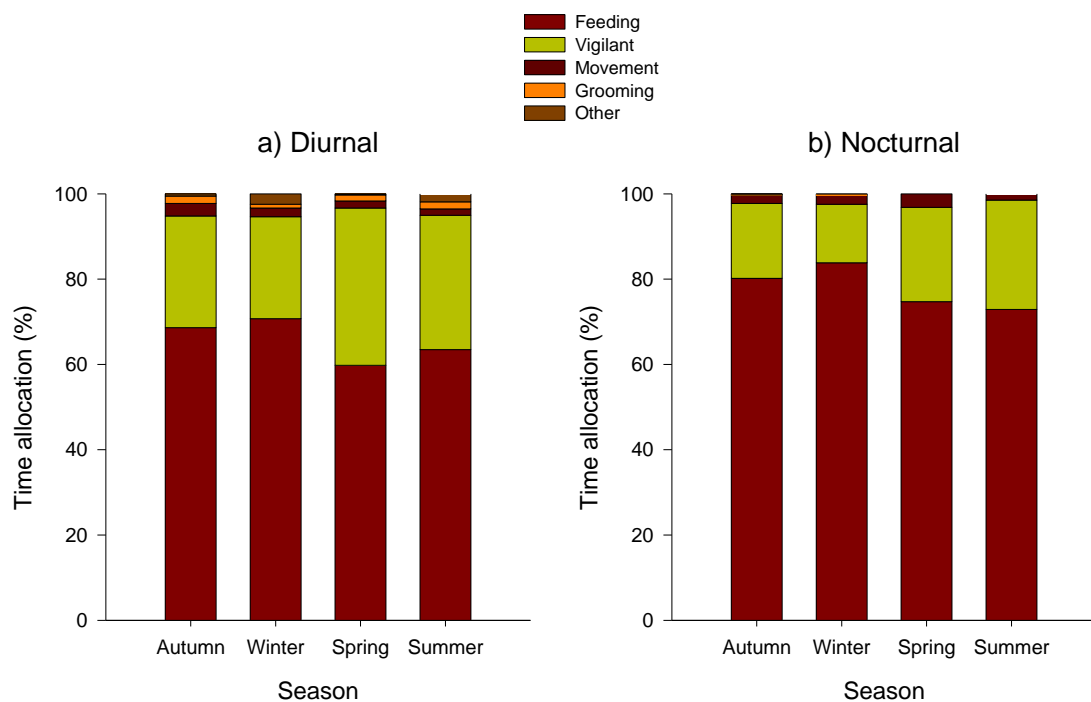
Figure 4.13 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming, and all other activities seasonally a) diurnal (N = 298) and b) nocturnal (N = 462).

Although ambient temperature was a good predictor of rock-wallaby activity (Figure 4.9), there was little variation of vigilance and feeding levels between different temperatures (Figure 4.14). At higher temperatures, there was a small increase in grooming and other behaviours like sitting down inactive. Resting behaviour never occurred away from the rock refuge.
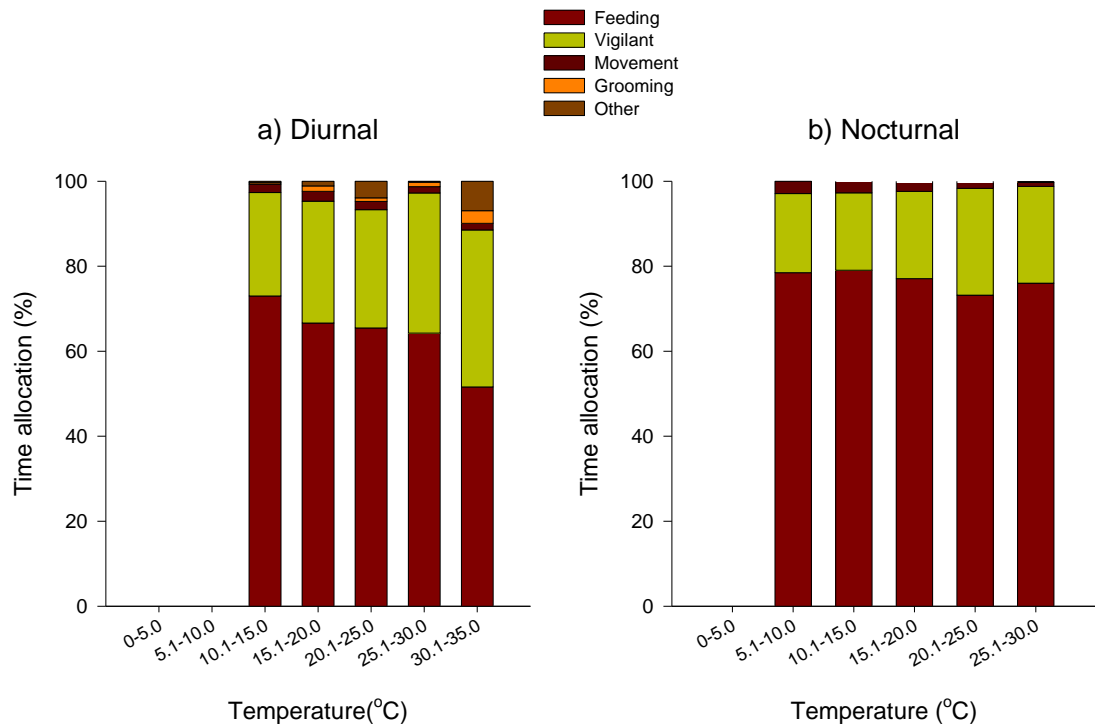
Figure 4.14 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming, and all other activities over different temperatures a) diurnal (N = 192) and b) nocturnal (N = 462).

These rock-wallabies fed less and were more vigilant with higher wind velocity (Figure 4.15). These trends were more obvious during the day when they allocated more time to looking (52.58%) than feeding (44.47%) when mean wind velocity was above 15 km.

4.3.7   Cloud cover and moonlight

There were no consistent trends between types of activities and degrees of cloud cover (Figure 4.16). Rock-wallabies spent more time feeding during highest periods of cloud cover in the daytime compared to all other times, suggesting they are sensitive to high temperatures during the day and reduce their activity levels in hot conditions. Individuals were occasionally observed foraging within the rock refuge on cooler summer days when there was a lot of cloud cover. Rock-wallabies exhibited only a small increase in vigilance levels with increased moon illumination.
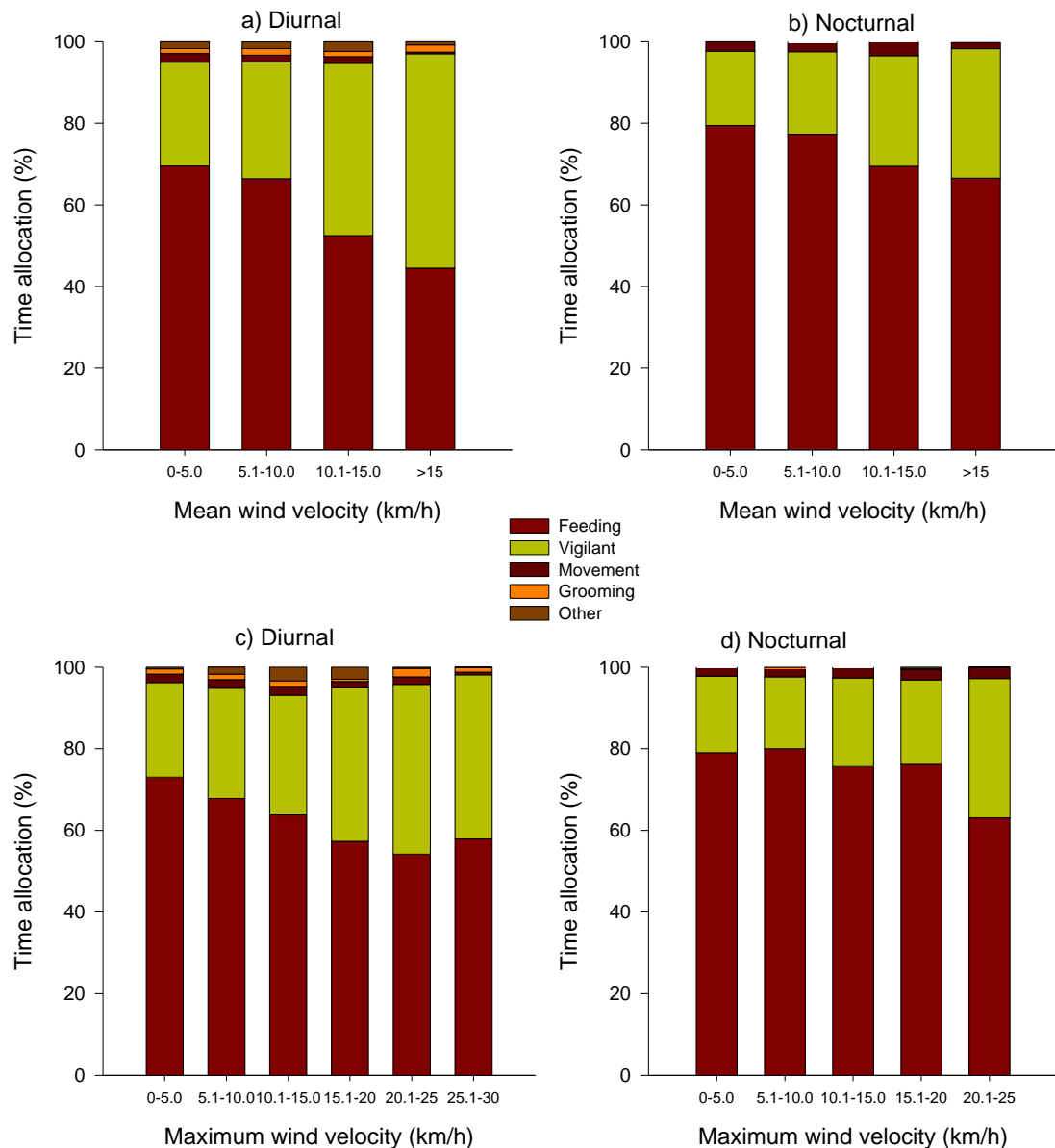
Figure 4.15 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming and all other activities over different mean wind velocity: diurnal (N = 205) and nocturnal (N = 462), and maximum wind velocity: diurnal (N = 206) and nocturnal (N = 457).

4.3.8 Effects of rock-wallaby sex and spatial distribution

During daytime female rock-wallabies spent less time feeding and more time vigilant than males. Some seemingly conflicting results emerged from an examination of spatial distribution effects on rock-wallaby behaviour (Figure 4.18). During the day, when animals restricted themselves to foraging within the diurnal rock refuge, individuals spent more time feeding and less time vigilant with increasing group size (Figure 4.18 a). However, at night when individuals moved out into the adjacent meadow areas, there was no change in group size (Figure 4.18b).

Feeding
Vigilant
Movement
Grooming
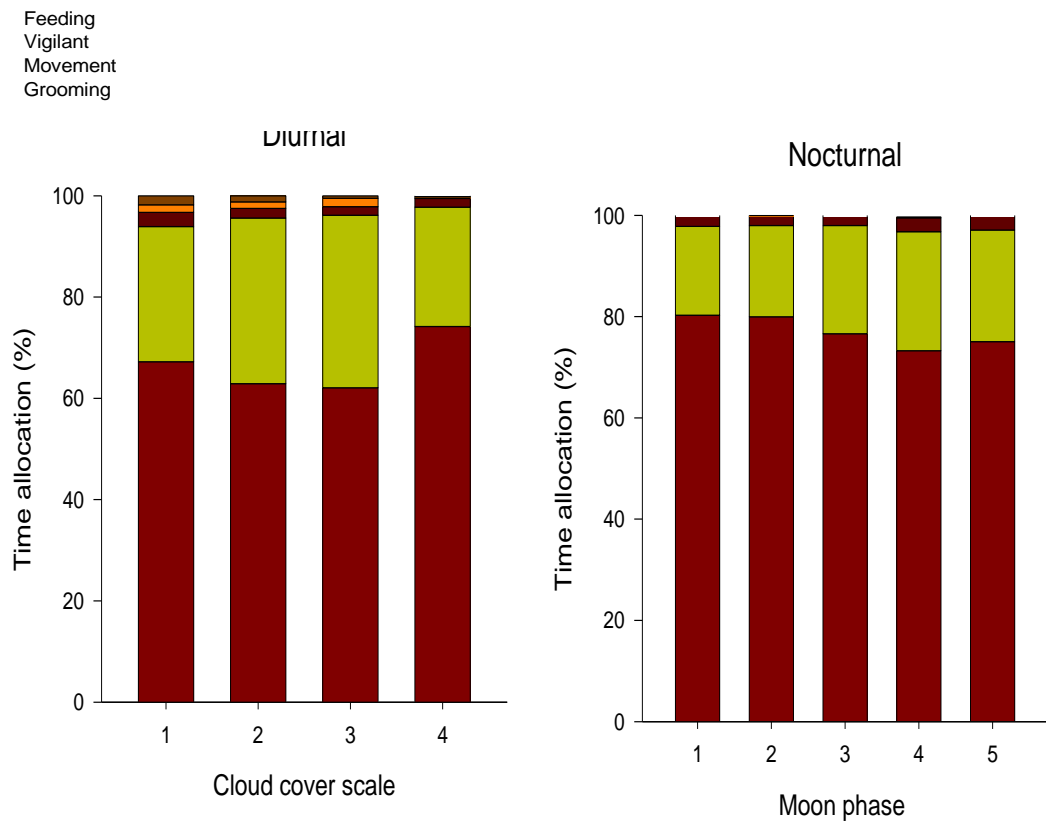
Figure 4.16 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming and all other activities over different diurnal cloud cover scales (N = 206) where 1 = no cloud, 4 = full cloud, and moon illumination (N = 462) where 1 = no moon, 5 = full moon.
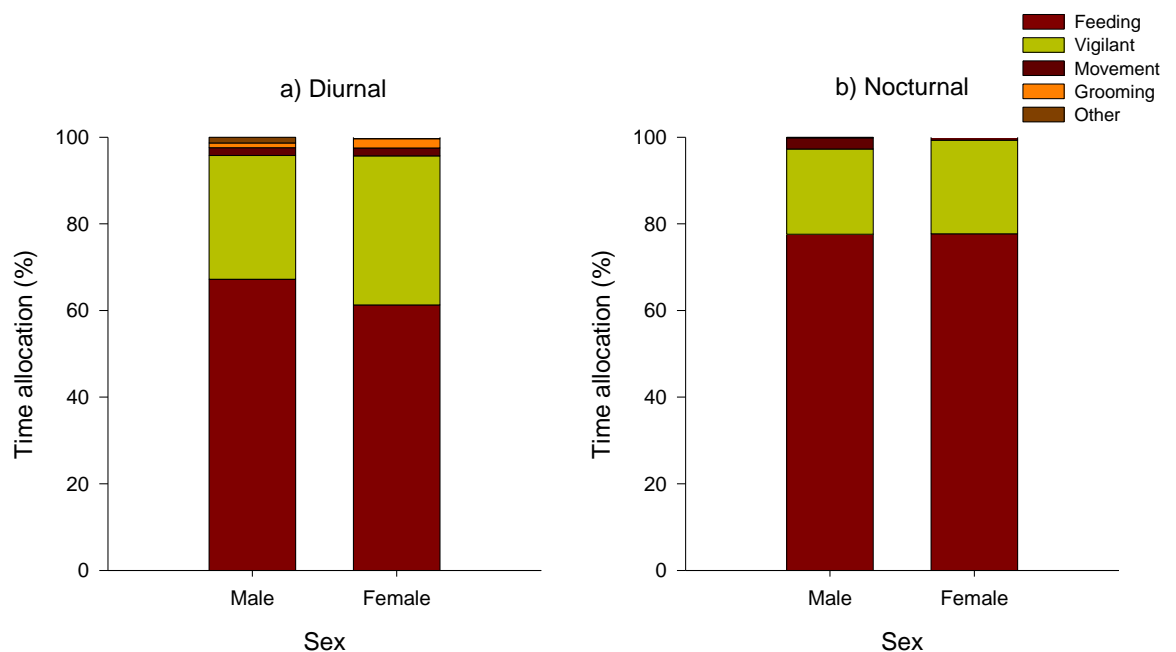
Figure 4.17 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming, and all other activities between sexes during diurnal periods: males (N = 129) and Females (N = 52), nocturnal periods: males (N = 269) and females (N = 139)

Despite the fact that individuals benefit from larger group sizes while foraging during the day within the diurnal refuge, the rock-wallabies in this study spent less time feeding and more time being vigilant when their nearest neighbour approached (Figure 4.18c). These different effects of group size and nearest neighbour may counteract any benefits of feeding in groups outside the diurnal rock refuge, since it would be reasonable to conclude that when animals feed within the rock refuge they are more likely to remain within their own social groups' refuge region to reduce the risk of encountering another group member.
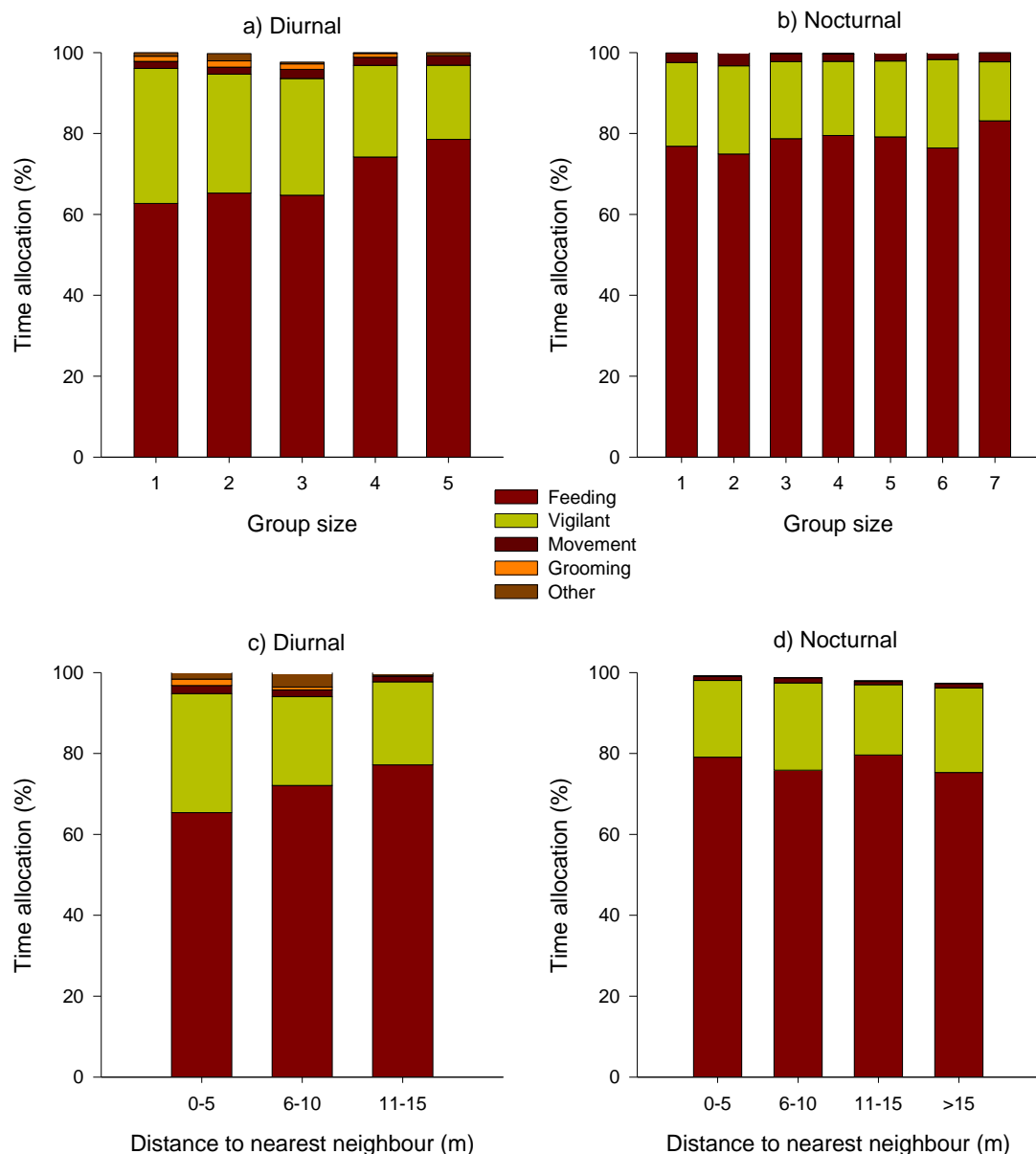
Figure 4.18 The percentage of time rock-wallabies allocated to feeding, vigilance, movement, grooming, and all other activities between group sizes a) diurnal (N = 235) and b) nocturnal (N = 365); and distance to nearest neighbour a) diurnal (N = 157) and b) nocturnal (N = 336).

Displacement of individuals from other conspecifics is very common in this population. Although animals may benefit from increasing group size, reducing the perception of predator fear, if individuals encroach too close, then this may also be perceived as a threat if it is a larger dominant individual that is approaching. This behaviour has a strong effect on the population spatial distribution. The mean distance between individuals (6.81m, table 4.2) is higher than the nearest neighbour distance that shows the highest vigilance levels. This clearly demonstrates that rock-wallabies have a minimum individual spatial size zone, that they feel comfortable to forage in. An individual that encroaches that zone, particularly if it is not part of their social group, may be seen as a threat to important food resources, thus choosing to either move away (be displaced) or approach (be the displacer). Rock-wallabies in this study were rarely seen foraging in large concentrated groups. When this did occur, it was during dusk and shortly after sunset, a time when individuals first started moving away from their refuge.

There were significant differences in the foraging distances from the diurnal rock refuge associated with mean (Kruskal-Wallis test: (3, N = 460) = 8.986, p <0.05), and maximum wind velocity (Kruskal-Wallis test: (4, N = 455) = 9.77, p <0.05) and moon phase (Kruskal-Wallis test: (4, N = 460) = 13.99, p <0.05), but not sex (z = -725 (N = 406), p < 0.01). Both mean and maximum wind velocities showed a decreased foraging distance from rock refuge with an increase in wind velocity (Table 4.3). Rock-wallabies foraged closer to their diurnal refuge when wind velocity was higher. These wind velocity effects are also reflected in Figures 4.15 and 4.9. There was no discernable pattern related to moon phase effects (Table 4.3).

Table 4.3 Distance (m) of *P. l. lateralis* to permanent rock cover during different climatic conditions and between sexes at Nangeen Hill Reserve (mean ± S.E.).

	Mean ± S.E. distance (m) to rock refuge (N)
Moon Phase (1 = no moon, 5 = full moon)	
1	12.9 ± 0.15 (207)
2	17.2 ± 0.49 (28)
3	12.3 ± 0.26 (60)
4	9.3 ± 0.20 (65)
5	13.8 ± 0.20 (100)
Mean wind velocity (km/h)	
0 – 5	13.4 ± 0.12 (277)
5.1 – 10	13.1 ± 0.20 (129)
10.1 – 15	9.1 ± 0.24 (47)
15.1 – 20	8.1 ± 0.44 (7)
Maximum wind velocity (km/h)	
0 – 5	13.2 ± 0.16 (152)
5.1 – 10	14.0 ± 0.19 (155)
10.1 – 15	12.8 ± 0.25 (77)
15.1 – 20	9.4 ± 0.24 (52)
20.1 – 25	9.7 ± 0.32 (19)
Sex	
Male	13.2 ± 0.13 (267)
Female	11.9 ± 0.15 (139)

4.4   Discussion

The Nangeen Hill black-flanked rock-wallabies (*P. l. lateralis)* are central-place foragers restricted to quality rock refuges (with available caves and crevices), and concentrate their foraging within close proximity to their permanent diurnal refuge, even when food resources are more abundant further away. The population does not exhibit a crepuscular foraging pattern. Neither can they be considered strictly nocturnal, since they are highly adaptable and adjust their foraging strategy to changing seasonal climatic conditions.

The benefits and costs associated with each foraging bout determine when and where animals forage (Roach et al., 2001). Although food quantity and quality are the most obvious benefits and have conclusively been shown to affect the foraging decisions of animals, the significance of predation cost and the impact of climate have only recently been acknowledged (Erkert & Kappeler, 2004; Hill, 2005; Brown & Kotler, 2007; Holt & Kimbrell, 2007).

Climatic conditions affect both predatory and metabolic costs, so their importance should not be overlooked when defining foraging patterns, particularly in animal groups that live in a variable environment.

The foraging behaviour of rock-wallabies at Nangeen Hill varied under different climatic conditions. There were also variances between time of day, group sizes, distance to rock cover and distance to nearest neighbour. These rock-wallabies were predominantly nocturnal during summer, but shifted their foraging activities to daytime in winter.

The heightened vigilance behaviour and the animals' reluctance to move further away from the rock refuge, suggest a possible heightened fear of predators. As discussed in chapter 3 rock-wallabies are often observed scratching or digging up the bare ground surface to possibly obtain roots, in a highly degraded patch close to their central diurnal rock refuge, rather than move further away where food resources were more abundant. During the day wedge tailed eagles are often observed searching the rocks, so may have an impact on the rock-wallabies foraging movements into open areas. However, during the night, wedge tailed eagles are not present, so another predator may be a factor. Foxes are often seen prowling both within the meadow and the rock-wallabies refuge. This predator presence (foxes and eagles), could be a detrimental factor, reducing access to more palatable food resources. However, this predator factor needs to be quantified to be conclusive. Predation was not the only factor to impact foraging behaviour. Two other factors that reduce foraging time and concentrate foraging area are unfavourable climatic conditions and the presence of conspecifics.

4.4.1   Rock-wallabies as central-place foragers

Many territorial animals forage from a central location (e.g. burrows, nests and caves) and adopt one of two foraging patterns (Orians & Pearson, 1979; Kotler et al., 1999):

a. Collect food items and return back to the central location to consume within a safer environment; and

b. Consume food items where encountered and then return to their central location.

Central permanent refuges act as shelters from predators and the weather, and provide safety for the rock-wallabies' offspring. Living in permanent refuges affects the interaction between animals and their environment, and strongly affects a population's spatial and foraging patterns. Many herbivores are subject to predation while foraging

and may be at greatest risk when distracted by acts of looking for and consuming food. As rock-wallabies consume food where it's located, they are likely to be strongly influenced by predation threat.

The cost of energetic return must outweigh the risk of predation for an individual, who in turn, has to weigh the benefits and cost associated with a foraging bout. Benefits take the form of food quantity and quality, less travel time, reduced handling time, reduced predation risk and decreased energy costs. Habitat structure, as well as distance from centrally located refugia, would therefore be expected to influence foraging patterns, since potential prey will lower their predation risk by foraging in areas that reduce predator efficiency. The resulting spatial variation in foraging intensity can have important implications for the distribution and abundance of food resources.

The rock-wallabies in this study adhered to pattern b) above, with individuals moving out of their cave refuge and slowly away in search of food when environmental conditions were favourable. Foraging bouts were predominantly short, and animals returned to their caves throughout the day and night. Despite the availability of better food resources at greater distances from the refuge, rock-wallabies concentrated their foraging close to the central diurnal rock refuge. If detected by a fox, their primary defence was to immediately run to a rock refuge (see chapter 3). Rock-wallabies are also vulnerable to avian predators and cats.

The distance at which rock-wallabies forage from their rock refuge provides a means of quantifying risk, since it is reasonable to assume that the risk increases as rock-wallabies move further away, particularly into patches where there is little cover. Rock-wallabies do not utter vocal signals (alarm calls) when predators are detected, instead the high behavioural disturbance response by one individual initiates a disturbance response by all conspecifics foraging in that patch.

Animals may also affect the favourability of their environment through over-exploitation. Usually they tend to move on as the environment deteriorates (Berryman, 1981), and for a central-place forager restricted to a refuge, over-exploitation of resources adjacent to or within the refuge should result in animals moving further away to exploit new patches. However, a psychological barrier caused by predation fear could restrict individuals to remain in a resource-depleted refuge to such an extent that they suffer

from malnutrition and higher mortality rates. In such an environment younger and less dominant individuals would be at highest risk, as dominant individuals will monopolise the remaining resources.

It is common for central-place foragers to create a gradient of increasing vegetation height and plant biomass, and an accompanying decrease in concentration of plant nutrients, at further distances from the central refuge location (Huntly, 1987; Bakker et al., 2005). This was also true of the rock-wallabies in this study and the change in composition of the vegetation at the rock/meadow ecotone had a significant effect on their behaviour and wellbeing. During the dry period the herbaceous layer began to disappear, the ground became bare, and any remaining woody stems or roots were eaten quickly. One would have expected this to lead to changes in foraging distances away from the rock edge, yet surprisingly, the mean foraging distance decreased during summer, even though there was a clearly visible vegetation zone 25 m beyond the rock. Although central-place foragers first deplete nearby patches before exploiting patches further away (Orians and Pearson, 1979), a heightened anti-predator fear appears to restrict foraging to poorer resource patches, eventually resulting in the animals' condition deteriorating. Animals trapped for this study in both 2006 and 2007 appeared to be in good condition, suggesting that their nutritional needs were being met, but heavy grazing was evident, as was heavy weed invasion, in both the patches adjacent to the rock and within the refuge area. Between 2008 and 2010 the researcher observed concerning signs of habitat degradation (Kinnear et al., 2010) and by 2011 there was a marked decline in rock-wallaby numbers (Pentland, 2011). This population decline is examined in the final discussion of this study (prediction 6) as it verified the importance of the research approach taken for this study.

4.4.2 How the fear of predation and conspecifics affect rock-wallabies' foraging patterns and spatial distribution

It was common to see animals look up and scan their environment while feeding. This alert behaviour is called vigilance, and serves one of three main functions: predator detection, searching for resources (prey), and detecting conspecifics (Bell, 1991). The level of vigilance in this study was used as an indicator of the rock-wallabies' perception of fear, since they look downward not upward when searching for resources. The detailed information collected on their qualitative behaviour outlined in chapter 3, showed that individuals used scanning for detecting both predators and other conspecifics that may encroach on their food patch.

Previous studies conducted on rock-wallaby anti-predator behaviour found conflicting results; with some such as *Petrogale xanthopus* (Bluemstien et al., 2001) and *Petrogale mareeba* (Blumstein & Daniel, 2003) showing group size benefits, and others, such as *Petrogale assimilis* and *Petrogale inornata* (Blumstein & Daniel, 2003), showing none.

The higher diurnal vigilance levels recorded during this study (Figure 4) reflect a higher perception of predation risk. Foraging during the day never occurred away from the permanent rock refuge. The rock-wallabies stayed close to cover, emphasising the importance of good food resources within the diurnal refuge to support diurnal foraging activities. If food resources were unavailable within this region, it is unlikely that rock-wallabies will forage further away since they will have less time to acquire food, particularly during winter when low night-time temperatures reduces the amount of foraging time. Although heightened daytime vigilance levels could be partly attributed to fear of conspecifics, the relationship to increasing group size (Figure 4.18) during the day suggests otherwise. As group sizes increased during the day, individuals spent less time looking around and more time feeding. They remained at longer distances from one another to reduce the likelihood of threat from dominating individuals. These distances between individuals influenced their foraging spatial distribution. The mean distance between foraging individuals in this study was 6.8 m. Vigilance levels were highest when individuals were less than 5 m apart and lowest when individuals were more than 10 m apart (Figure 4). These results suggest the need for a minimal distance between individuals for reducing aggression, and represent an intrinsic component of spatial distribution (Gromov et al., 2001).

Do rock-wallabies perceive a greater predation threat during the day due to increased visibility by predators and greater predator diversity or is there an increase in conspecific conflict due to the high density of individual residing within a confined space? Both foxes and avian predators are active during this period. Large wedge-tailed eagles were frequently observed searching the rock-wallabies' rocky outcrop during the day. It is therefore not clear whether the heightened vigilance was due to avian predators or foxes. It would however be interesting to know whether rock-wallabies will forage away from the rock refuge during daytime if there were no foxes present. The researcher rarely observed females with young at heel or small sub-adults foraging during the day, suggesting that these individuals had a higher perception of fear during this period, since they were more vulnerable to avian predators.

Females recorded higher vigilance rates (Figure 4.17) during the day, possibly due to carrying pouch young and being on high alert to predators. The only successful avian predation observed during this study occurred in a relatively open area of the rock region. The larger adult rock-wallabies appeared to be unconcerned by the wedge-tailed eagles searching above, as they often perched on the rock with no apparent intention of attacking. This could be due to prey size differences, with larger rock-wallabies considered too big to capture and beyond the capability of the wedge-tailed eagles.

It is possible that macropods have been preyed upon by terrestrial and aerial predators throughout their existence, and as a result, have developed highly evolved predator avoidance behaviours (Jarman & Coulson, 1989). It is also likely that foxes and cats were not perceived as threats when they were first introduced, so rock wallabies became easy prey for these predators. Like all other macropods, rock-wallabies have been subject to predation throughout their existence, and it is therefore reasonable to conclude that their anti-predatory behaviour would have heightened over time.

Predation is the primary cause of mortality in many declining rock-wallaby populations (Kinnear et al., 1988; Hornsby, 1997; Jarman & Bayne, 1997; Kinnear et al., 1998; Lapidge & Henshall, 2001). It has been suggested that individuals in the wheatbelt populations prior to fox-baiting were restricted to moving within close vicinity of good rock refuges (Kinnear et al., 1998). After a fox-baiting regime was put in place there was an initial habitat expansion in both their permanent refuge and their foraging range (Kinnear et al., 1998). Although direct predatory effects have clearly been shown to have a negative impact on rock-wallaby populations, very little is known about indirect predatory effects. For example, scanning for predators may preclude other important activities such as foraging. One way to mitigate these lost opportunities is to forage in a group, relying on other members of the group to bear some of the burden of scanning for predators (Barbosa, 2002; Caro, 2005). Vigilance rates have been found to decrease with increasing group size in many animal groups including macropods (Blumstein et al., 1999; Blumstein et al., 2001; Wahungu et al., 2001). For some species, distance to cover was found to be important for determining vigilance rates (Burger et al., 2000; Hochman & Kotler, 2007). In this study, distance to the nearest neighbour was more important than group size for determining vigilance rates. More detailed study is needed on predator behaviour and its effect on rock-wallabies to be more conclusive.

The proximity of conspecifics had a negative effect on the time rock-wallabies spent feeding. There were also individual differences associated with size/age, sex, and the reproductive condition of individuals (Marino & Baldi, 2008). When animals foraged under predation risk, individuals sacrificed feeding rate by allocating a different amount of time to foraging within safe and risky habitats, choosing to wait inside a refuge for more favourable conditions, or by being vigilant while active within a habitat. The timing of foraging activities are also related to the risk of predation, since predator activity varies with time of day, and darkness interferes with the ability of predators and prey to see one another (Clarke et al., 1995). If many predators hunt at night because of higher success rates, why do some prey adopt nocturnal foraging strategies? Is the perceived energy cost during unfavourable climatic conditions higher than the predation cost, or is the diurnal predation cost perceived to be higher than the nocturnal predation cost? Animals need to weigh up both energy and predatory costs, and timing their activities to minimise the risks would be a delicate balancing act. Forming aggregations may be one solution.

The problem with looking at group size effects is determining when a collection of animals is defined as a group and when it is defined as a large aggregation. How do we distinguish the members of each group? Where does one group finish and another begin? Previous studies on macropod group behaviour defined groups by an arbitrary maximal separation, by behavioural criteria or both (Jarman & Coulson, 1989; Blumstein et al., 2001). Animals can simply form aggregations around a spatially concentrated resource, so although they are brought into proximity, they do not interact cohesively with one another (Jarman & Coulson, 1989). However, if animals are brought into proximity due to a spatially limited resource and do react cohesively, then they can be defined as a group, not an aggregation (Jarman & Coulson, 1989).

In this study the boundaries of the meadow area could clearly be seen from all observational positions. It could therefore be expected that rock wallabies were also able to detect these boundaries and all the individuals within these boundaries. It was necessary to determine whether the rock wallabies who were feeding in this section of the meadow were behaving as an aggregation (multiple groups), a single group, or as individuals. The rock-wallaby study conducted by Laws and Goldizen (2003) found group members that emerged from the same region of rock refuge also foraged together in the same area of the colony. Similarly, the individuals in a particular region on Nangeen Hill were observed foraging together. However, on nights when rock-wallabies are moving out from different regions of the rock refuge into the large

meadow area, there was some merging with individuals from different locations, which may cause a disruption to the general group size, thereby negating any benefits. This group disruption out in the meadow area at night-time could also be attributed to visual alarm signals between group members impeded by darkness, making grouping a less effective anti-predator strategy at night than during the daytime (Clarke et al., 1995).

Studies on macropods have used a variety of distances between conspecifics for determining group sizes, ranging from 10 to 50 m (Jarman, 1987; Blumstein et al., 2001). A study conducted on group size effects on vigilance rates on the yellow-footed rock-wallaby (*Petrogale xanthopus*) determined their group size within a range of distances (5 to 20 m) and found variation in vigilance levels were best explained by the number of conspecifics within 10 m (Blumstein et al., 2001). In the Nangeen Hill population, such high concentrations resulted in increased vigilance due to fear of aggressive encounters and displacement. The researcher believes it is this fear of intra-conspecific competition that counteracts group size benefits, particularly during high concentrations and where increasing groups are feeding in close vicinity. Foraging competition has been found to influence other macropod groups, resulting in an increase in the number of aggressive encounters (Blumstein et al., 2002). In rock-wallabies it is believed to be an important factor in reducing the benefits of aggregation (Blumstein & Daniel, 2003).

Supplanting (displacement) was one of the most common agonistic behaviours found in the Nangeen Hill population (see chapter 3). Fear of other conspecifics had a strong impact on the foraging spatial distribution of this population, so although it is widely believed that animals reduce their risk of predation by forming groups (Caro, 2005) and that group size is likely to increase with increasing predator densities, the potential benefits may be counteracted by the cost of intra-specific competition within or between groups (Blumstein & Daniel, 2003). In addition, if vigilance increases considerably when a predator comes into view, then the predator's proximity and behaviour will override many of the factors known to influence vigilance under less precarious circumstances. For example, group size is likely to have little effect on individual vigilance if a predator is nearby (Caro, 2005). In this study, high vigilance levels in rock-wallabies combined with a reluctance to move further away from the rock even when resources were low, suggests strong predatory fear effects on their foraging behaviour.

Hughes et al. (1994) proposed that gerbil (*Gerbillurus tytonis*) populations in the Namib Desert were highly susceptible to predation results in a shared preference for the safest habitat, and led to competition for limited resources. This competition between animals can have strong negative effects on their behaviour and population structure in the form of increased aggression, leading to few dominant individuals controlling the remaining resources, and eventually to habitat degradation and high mortality rates. Therefore, although there are direct effects of predation, such as changes in survival rates and population dynamics, the indirect cost of predation caused by changes in prey behaviour is more subtle but nonetheless significant (Searle et al., 2008). Some behavioural ecologists believe it is important to develop models that incorporate these indirect effects (Brown & Kotler, 2007). Traditional mammalian predator-prey models treat individuals as virtually unresponsive and focus on predators killing prey. However, it has become increasingly clear that these systems are sophisticated games of stealth and fear, so models need to consider prey response behaviour to the presence of predators (Brown et al., 1999). Brown and Kotler (2007) outlined two different predator-driven systems: a) mortality-driven (N-driven) and b) fear-driven (μ-driven). In the former, predators influence the dynamics and abundance of prey primarily through direct mortality. In a fear-driven system, predators no longer control the prey population through mortality, but instead strongly influence prey behaviour by increasing their vigilance levels (Caro, 2005) and reducing their foraging range, predominantly in high-risk patches/habitat types. For a central-place forager, a reduced foraging range places more pressure on resources close to the central refuge (Huntly, 1987; Holmes, 1991; Roach et al., 2001; Bakker et al., 2005).

In the wheatbelt rock-wallaby populations, high fox density was shown to have an acute and direct effect on rock-wallaby dynamics and abundance through mortality (N-driven system). The reduction of fox numbers, but not the total eradication, led to an increase in rock-wallaby numbers and some range expansion (Kinnear et al., 1998). However, the current population on Nangeen Hill appeared to be altering its foraging behaviour in response to predatory fear by increasing their vigilance levels, reducing movement away from the refuge, and tolerating foraging disruptions by predators. It was now operating under a fear-driven system (μ -driven system).

Although the researcher believes that rock-wallaby vigilance rates are related to the combined fear effects of both predators and conspecifics, the refuge is central to these animals' decision making. Every decision to emerge from the refuge is made in relation to how rock-wallabies minimise predatory effects, and/or climatic effects (discussed in

following section). In this study, once an individual had emerged, it continually monitored its environment, keeping within a safe distance of the refuge in case of a disturbance, either in the form of predators or other conspecifics. Disturbance levels were high when rock-wallabies were out foraging in the open. For central-place foragers, early predator detection and access to refuge provide important advantages for increasing the likelihood of escape (Marino & Baldi, 2008).

Fox presence was shown to have a strong effect on rock-wallabies' disturbance responses. Animals immediately ran back to their caves and remained inside for long periods of time before re-emerging. This behaviour response has strong implications for time allocated to foraging. Although studies have been conducted on rock-wallaby anti-predator behaviour, seasonal differences have not been examined, and it is not known how, if at all, these influence behavioural patterns (Blumstein & Daniel, 2003).

Young foxes leaving their lairs during summer (Coman et al., 1991) may result in an increase in fox density and movement patterns. Foxes may then be more likely to encroach on rock-wallabies' foraging patches in the search for new territories, leading to increased fox-detection rates and heightened anti-predator responses. Higher rock-wallaby vigilance rates were recorded during this study during the summer period (Figure 4.13) and also exhibited shorter mean foraging distances from their rock cover (Figures 4.4 and 4.6a). This again further points for the need to have a greater understanding on exotic predator behaviour and how it may impact on the Australian faunal foraging behaviour. Group concentration also increased within the reduced resource patch as shown by the smaller mean distances between individuals (Table 4.2). Vigilance rates could have increased due to conspecific fear and increased competition for limited resources. Such impacts have been found in studies on other animal groups, including one on rodents, in which Hughes et al. (1994) proposed that high susceptibility to predation not only resulted in a shared preference for safer habitats, but also in increased competition for limited resources.

4.4.3 How seasonal and climatic factors affect the foraging patterns and spatial distribution of rock-wallabies

The central wheatbelt is a harsh environment characterised by low rainfall, cold winters and hot summers. Although good rock shelter is important for rock-wallabies to reduce predation risk (Kinnear et al., 2010; this study), it is also an important ameliorator of climatic conditions (Short, 1982; this study). In such a variable climate, the time spent

inside a refuge is an important behavioural response, not only to optimise predatory avoidance, but also to shelter from unfavourable climatic conditions. If rock-wallabies remain inside an enclosed refuge too long they will have difficulty meeting their energetic needs and may not reach an optimal weight during winter/spring periods of higher resource availability, needed for survival during summer/autumn periods of low resource availability. Rock-wallabies must assess the costs and benefits of refuge emergence, weighing up higher predation risks and higher metabolic costs during particular climatic conditions. The benefits may include greater foraging opportunities and potentially greater social interaction (increasing the probability of finding a mate and therefore the reproductive output for the population). The results of this study recorded highly variable activity levels over time, with both temporal and spatial effects on foraging patterns on a seasonal basis, daily basis, and within diel periods, suggesting high behavioural adaptability for this species.

An examination of refuge emergence in relation to rock-wallabies must make a distinction between two types of refuges: enclosed refuge (caves and crevices) and protective refuge (rock and shrub). Animals initially choose to emerge from their enclosed refuge and engage in either active behaviour (foraging and social interaction) or non-active behaviour (resting, grooming and scanning), either within or away from the protective refuge (rock or shrub habitat), located within or away from the permanent enclosed refuge. This is followed by another choice to engage in an activity in the same or different patch from other conspecifics. If any of the environmental conditions change, individuals must then decide whether to change their activity, change the location of the activity, or return to the enclosed refuge.

Time of year had a significant effect on rock-wallaby activity, with a high number of animals active throughout summer nights compared to other seasons (Figure 4.7). An increase in nocturnal activity would be expected in summer, as foraging and other activities have to be fitted into shorter nights. Higher summer night-time temperatures also impose lower thermoregulatory costs than in winter. Active animals observed during the hottest days in summer were predominantly accessing a seep on the edge of the outcrop adjacent to the meadow in zone 2. This was reflected in high activity levels around this region compared to other locations during the same time periods. Individuals were observed moving down the rock into the seep area which frequently contained 3 to 4 individuals in close proximity (1 - 4 m apart). This closeness to one another was rarely seen during other seasonal periods or in any other region. Although

distinct seasonal variations in behavioural parameters have been observed in many primate groups (Erkert & Kappeler; 2004), few studies have included both diurnal and nocturnal data. An examination of seasonal differences over both diurnal and nocturnal timeframes allowed the researcher to more deeply investigate temporal shifts in the animals' behavioural activities. Diurnal behaviour has been detected in other rock-wallaby populations (Telfer & Griffiths, 2006; Sharp, 2009) but the cause of their temporal shifts has not been investigated.

Although Nangeen Hill rock-wallabies generally foraged at night during summer, there was a shift towards a greater proportion of daytime foraging during winter. In addition, nocturnal foraging in winter peaked during the first 2 - 3 hours after sunset, with little activity evident throughout the rest of the night. Foraging outside of colder climatic conditions at night in winter and higher diurnal temperatures during summer are indications that rock-wallabies tend to conserve energy costs.

For mammals there is a thermo-regulatory cost in both energy expenditure and evaporative water loss, so a trade-off between foraging efficiency and the cost of thermoregulation is to be expected, particularly for species living in hot, dry environments (Brown & Downs, 2005). During extreme heat, individuals reduce their energy costs by becoming active at night and remaining within the refuge during the day. Similarly, extremely cold conditions can compel animals to be more active during the day and remain in their refuge at night. In such environments the selection of a thermal refuge plays an important role in reducing the energy cost of thermoregulation (Mares & Lacher, 1987; Brown & Downs, 2005). In this study, rock-wallabies were less active at temperatures below 10^0C and above 30^0C. The cave temperature range was smaller than the corresponding external temperature range, with cave temperatures up to 10^0C warmer and cooler than extreme low and high ambient temperatures respectively.

Rock-wallabies are smaller than most other macropods and have distinct dis-advantages with regard to thermoregulation due to a higher surface area to volume ratio. Smaller animals lose relatively more heat under cold conditions and may also suffer greater external heat loads at ambient temperatures above body temperature (Munn & Dawson, 2010). One way to offset this higher thermo-regulatory cost is to remain inside the refuge. Like rock-wallabies, wombats use a central refuge to rest in and forage from. Detailed studies conducted on their burrows (burrow refuge) have shown that there is a significant difference between the temperature ranges inside the

refuge as compared with the ambient temperature (Tyndale-Biscoe, 2005). Wombats timed their foraging activity to coincide with ambient temperatures within their thermo-neutral zone, and became severely distressed when air temperatures reached above 30^0C (Tyndale-Biscoe, 2005). Like wombats, the Nangeen Hill rock-wallabies adjusted their behaviours between various active and resting states, depending on the temperature and other environmental conditions outside their caves and at the cave entrance. They were often seen sitting at the cave entrance for periods of time before leaving and engaging in other activities. There were also differences between sex, age and reproductive class responses to environmental conditions, as larger adults were less susceptible to harsh climatic conditions and had a lower perception of predation fear in certain environmental conditions compared to smaller individuals or females carrying large pouch young.

After cold nights and during cool days, individuals reduced the cost of thermoregulation by adopting basking behaviour, thereby reducing the cost of endogenous heating (Brown & Downs, 2005). This is particularly important after extremely cold nights to help overcome nocturnal hypothermia. Individuals occupying lower quality refuges will be more vulnerable to extremely cold temperatures than those within good quality refuges, particularly smaller individuals with a greater surface area to body volume ratio, who may experience greater heat loss when ambient temperatures fall below their thermoneutral zone. It is therefore crucial for these individuals to use basking behaviour to increase their body temperature and reduce endogenous heating costs. However, smaller individuals are also more susceptible to aerial predators, so there may be a trade-off between thermoregulation and predation. This trade-off can only minimised by basking within steep protective cover, thereby reducing aerial predators' ability to detect them and attack. During this study, juveniles were rarely seen during the day and were never seen being active away from good protective cover. Small sub-adults were also rarely observed basking or foraging away from good steep cover, and tended to remain close to the cave entrance. During winter, individuals were never observed outside their enclosed refuges during the early mornings. Only once the sun's rays had reached the permanent refuge area did individuals begin to emerge. This is in stark contrast to summer, when individuals would often emerge from their enclosed refuge early in the mornings, but returned from mid-morning onwards.

Other climatic conditions such as high wind velocity and precipitation also impact thermoregulation cost. Blumstein and Daniel (2003) found that Bennett's wallabies

(*Macropus rufogriseus*) were sensitive to wind speed and were more vigilant when it was windy. Carter and Goldizen (2003) also concluded that *Petrogale penicillata* significantly increased their vigilance levels during high winds, but these authors did not look at diurnal and nocturnal differences. This researcher found high wind conditions had a greater effect on rock-wallabies' vigilance levels during the day than at night, but found similar results for both day and night for the number of active individuals. High wind velocity also affected their spatial distribution, with wallabies feeding closer to cover during windy periods. The high wind effects could be due to predation fear, as it may be more difficult to acoustically assess predation risk during windy conditions (Blumstein & Daniel, 2003). However, as wind affects both the number of individuals emerging from their cave as well as vigilance levels, rock-wallabies may perceive high wind as both a predatory and thermoregulatory cost. Precipitation also had a strong impact on the Nangeen Hill rock-wallaby populations by reducing activity levels. Although rainfall patterns are low in the central wheatbelt, precipitation rates are very high in many regions containing rock-wallaby populations around Australia, and could have a significant effect on time spent foraging.

Although Nangeen Hill rock-wallabies modified their activity patterns during different illumination periods, spending less time feeding and more time vigilant with increasing illumination, this increase was small, and may have been due to cloud cover and other climatic factors masking any effect. Carter and Goldizen (2003) found that *Petrogale penicillata* significantly increased their vigilance levels during moonlit nights. Climatic conditions may not only play an important role in an individual's decision to forage in a group, but also which patch to forage in. Not all patches have the same perceived risk for each individual or group under different climatic conditions. For example, open habitats may be perceived by animals as a higher risk under specific climatic conditions (Brown & Pinke, 2007). Restricting their foraging behaviour to specific patch types when predation risk is high has been found in a number of animal groups that use indirect indicators such as increased moon illumination (Brown et al., 1988; Carter & Goldizen, 2003; Orrock et al., 2004) and high wind velocity (Carter & Goldizen, 2003) to assess predatory risk. Moonlight may therefore have similar effects on rock-wallaby behaviour, resulting in habitat shifts and changes in distance from cover rather than vigilance levels. Unlike moon illumination which was not found to affect the spatial distribution of this population, high wind velocity caused the rock-wallabies to forage closer to rock cover. Like other climate-sensitive animals (Belovsky & Slade, 1986; Brown & Downs, 2005), Nangeen Hill rock-wallabies utilised their refuge effectively by

restricting higher-energy activities to specific times of the day when conditions were most favourable, and remaining inside their caves when conditions were unfavourable.

4.4.4 Conclusions

The rock-wallaby population at Nangeen Hill Reserve showed significant seasonal variation in both diurnal and nocturnal activity levels, adopting a strong diurnal foraging strategy during winter but remaining predominantly nocturnal during summer. The population did not exhibit a crepuscular foraging pattern, but neither can it be considered strictly nocturnal. The seasonal variability in activity levels appeared to reflect changes in ambient temperature, and the central rock refuge was a key component in the foraging strategy adopted by these rock-wallabies. Although their foraging behaviour varied significantly under different climatic conditions, the researcher believes that predation risk and aggressive defence against other conspecifics have greater impacts on rock-wallabies' foraging range than climatic conditions and food resource availability in this highly ecologically altered landscape. Climatic conditions affect rock wallabies' decisions about when and where to forage due to predatory and metabolic costs. However, it is more likely that the predatory fear cost and probability of aggressive encounters with other conspecifics restricts their foraging range, resulting in overgrazing and habitat degradation within close vicinity of their refuge. Adequate food resources were available at greater distances from the population's realised niche range, but predatory fear acted as a psychological barrier, suggesting that rock-wallabies do not fit either the Ideal Free distribution, or Ideal Despotic foraging models. Instead they reflect, in part, a special case of the marginal value theorem (patch model) which encompasses the concept of a central-place forager - animals that forage out from a central location such as burrows, nests, or caves (Orians & Pearson, 1979). However, as discussed previously, the heightened effect of predatory fear may have significantly restricted this population's realised food resource niche.

Rock-wallabies use multiple strategies to reduce predation risk, energy costs, and intra-specific agonistic interactions. They survive in their present environment only because of their cave refuge, which not only allows them to avoid extreme ambient temperatures, but also gives them protection from predators, particularly when environmental conditions are unfavourable, including increased light intensity (sun or moon) and increased wind velocity. In addition, their cave refuge provides protection from precipitation and a safe environment for courtship and rearing young without the

fear of predation. Even when foraging outside their cave systems, their rock refuge provides direct access to a safer environment when predators are detected. Rock refuge is the most important resource defining this species and is central to all aspects of its life history. These results provide evidence for prediction 2 exhibiting strong seasonal foraging behavioural adaptations, prediction 3 exhibiting strong vigilance behaviour, and prediction 4 showing strong signs of foraging constraint.

Although the observational results suggest rock-wallabies foraging movements are constrained to the rock refuge during the day and restricted in open areas during the night, observations were not undertaken on top of the rock-outcrop due to poor visibility for observational studies. After frequent surveys, no rock-wallabies have ever been seen active along the top of the rock during the day. However, during twilight and during the night rock-wallabies may be less restrictive in their foraging movement patterns along the spine rock-outcrop, due to an increase in cover. This is investigated in chapter 5 using scat distribution methods.

Chapter 5

Foraging spatial distribution and habitat preferences of *Petrogale lateralis lateralis:* scat distribution as a survey tool

5.1   Introduction and aims

Scat (faecal pellet) density has been used to measure dispersion and habitat utilisation in many herbivorous animals, including macropods (Jarman & Capararo, 1997), with varying degrees of success (Birks et al., 2004). During the observational studies rock-wallabies were often observed defecating while foraging and feeding. Although scat density dispersion has proven to be a successful research tool for macropod ecological studies (Telfer et al. 2006), the results are often limited by the methodology used. Rock-wallabies' cryptic behaviour and the physical environment they inhabit make them difficult to monitor for complex ecological studies. However, rock-wallaby scats are easy to distinguish from those of other macropod species, and rapid decay generally only occurs during periods of high rainfall (Telfer et al., 2006). In addition, rock-wallabies shelter inside rock caves and crevices during the day and move out from a permanent central diurnal rock refuge to surrounding feeding areas at night (Jarman et al., 1997; Carter & Goldizen, 2003; Telfer & Griffiths, 2006; this study 2013). These unique attributes make rock wallabies ideal ecological candidates for scat-density dispersion methods, provided a vigorous methodology is used.

As discussed above, direct behavioural observation studies can be used for determining foraging patterns in this rock-wallaby species, however, this method is limited to open habitats. Other methods were needed to look at both discrete home ranges and habitat preferences. Preliminary field studies found no evidence (no signs of recent scats or direct observations) of extended movements away from the outcrop, so it was appropriate to develop a scat-distribution design to investigate discrete rock-wallaby movement patterns and their habitat association within 200 m of the permanent rock refuge. The observational region used in chapter 4 was included in the scat dispersion study area to allow a direct comparison of the results from the two methodologies, and to evaluate the scat approach as an adequate reflection of the rock-wallabies' foraging patterns. An appropriate scat-density dispersion methodology allows inferences to be drawn about habitat preferences and movement patterns in habitats where direct observations are impossible.

The main aim of this component of the study was to use scat density and dispersion to examine the spatial foraging patterns of *P.l. lateralis,* and to investigate the effects of their spatial structure on their patch preferences.

The specific objectives were to determine whether:

- Rock-wallabies foraging spatial distribution differed between the habitat along the top of the rocky outcrop (rocky/vegetative mosaic) and the non-rocky habitat adjacent to the bottom of their rock refuge (open meadow and casuarina thicket);
- Rock-wallabies showed a preference for structurally more complex habitats (rock and vegetation);
- Distance to their diurnal refuge acted as a determinant of rock-wallaby activity and whether the spatial distribution reflected a central-place foraging pattern;
- Rock-wallabies show a preference for specific habitat types (vegetative and/or rock);
- The distribution of scats found within the observational zones in chapter 4, supported the data from the quantitative observations; and
- The methodology is appropriate for investigating foraging spatial patterns of rock-wallabies.

5.2   Methods

A sampling methodology was designed to investigate discrete movement patterns and habitat associations within 200 m of the refuge. As the refuge area at this site ran linearly along the north-western face of the rocky outcrop, belt transects were laid out at right angles to the rock refuge area, from both the ground and the top of the refuge area. A total of twenty-two belt transects, each 200 m long (Figure 5.1), were systematically marked out approximately 60 m apart; twelve along the base of the outcrop (1a -10a, 11 and 12) and ten along the top (1b - 10b). Scats were counted in every 5 x 2 m quadrat plot, placed continuously along each belt transect (22 x 40 = 880 plots).

5.2.1   Scat sampling

There were eight sampling periods throughout the year; two per season (commencing in May 2006). Scats in each quadrat plot were counted and cleared approximately every 5-6 weeks.
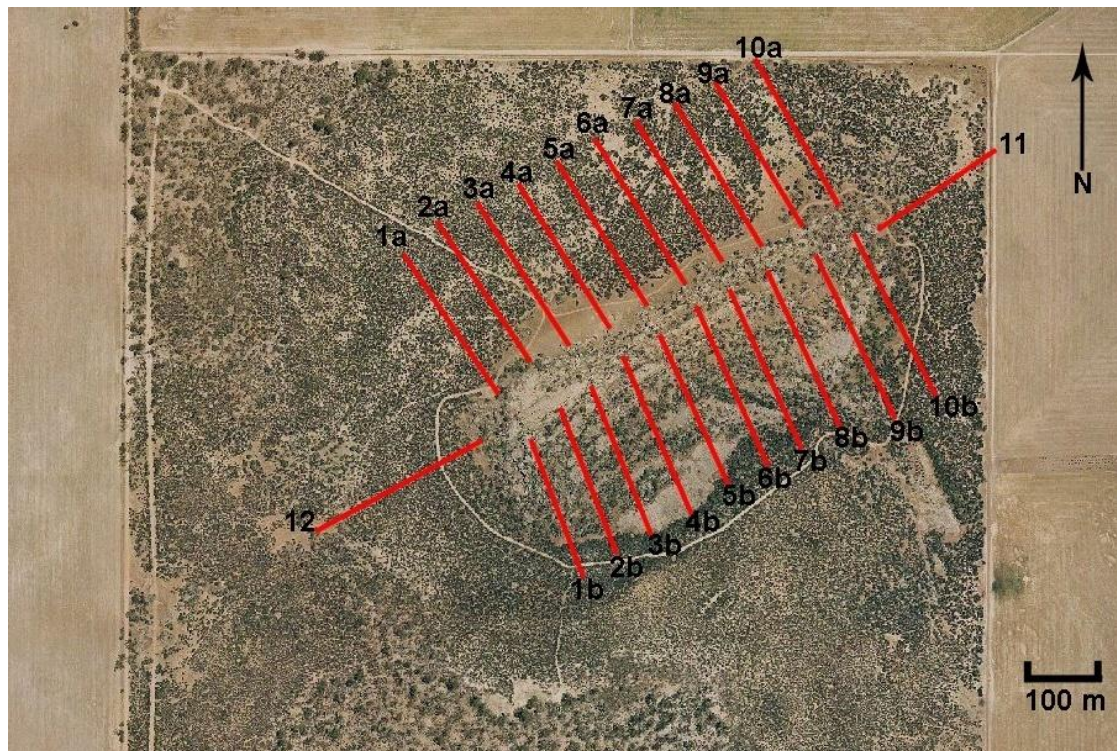
Figure 5.1 Transect locations at Nangeen Hill Reserve.

The time between each scat count was not consistent throughout the sampling period, and was subsequently standardised to a 42-day period so that comparisons could be made between periods. Standardised scat numbers in each plot were assigned an activity scale as follows: 0 scats = 1, 1-10 scats = 2, 11-20 scats = 3, 21-30 scats = 4, 31-40 scats = 5, 41-50 scats = 6, 51-60 scats = 7, and >60 scats = 8. In addition, for all eight periods sampled, a score was assigned to each quadrat plot in each belt transect to represent how often the plot was utilised (absence or presence of scats). Scats found in: 0 periods = 1, 1 period = 2, 2 periods = 3, 3 periods = 4, 4 periods = 5, 5 periods = 6, 6 periods = 7, >6 periods = 8. This methodology allowed for comparisons of scat density in each 5 x 2 m quadrat, including its rate of use throughout the year, and a particular number of habitat descriptive variables described below.

5.2.2   Habitat descriptions

Each 5 x 2 m quadrat plot was described by its vegetative structure and florisitics, and by its rock structural components under "habitat description". Individual plants were allocated to a height class on the basis of their highest live shoot as follows:

- Low = <0.3m
- Small = 0.3 - 1.0m
- Medium = 1.0 - 2.0m
- Tall = > 2.0m

For each vegetative stratum the total foliage cover (%) was calculated, and the dominant species identified, where possible. To determine the vegetation complexity in each quadrat plot, a score was calculated for each of the above vegetation strata (height classes) according to the percentage of estimated vegetation (foliage) in that area, using the following scale (in increasing complexity):

- Percentage cover   < 1 %   = 0
- Percentage cover   1-5 %   = 1
- Percentage cover   6-30 %   = 2
- Percentage cover   31-70 % = 3
- Percentage cover   > 70 %   = 4

The scores for each vegetation stratum were totalled to give a single complexity score for each quadrat, whereby the dominant vegetative species was determined by the highest percentage cover estimate.

When rock was encountered the following measures and classifications were used:

- Continuous unbroken bedrock;
- Discontinuous/broken bedrock or boulders;
- Block/boulder size;
- Spacing of blocks/boulders; and
- Caves or crevices present.

Where boulders were encountered, the average boulder size was allocated to one of the following height and spacing classes:

- Small   <300mm
- Large   >300mm
- Closely spaced   <300mm
- Widely spaced   >300mm

Boulder height and spacing classes were viewed from the perspective of average height of grazing rock-wallabies (head down) and adequate boulder distance to allow them to move rapidly between boulders. It was determined that less than 300 mm height would not provide sufficient cover, and less than 300 mm spacing between boulders would reduce rapid movement. To determine the rock complexity a score was allocated according to the following criteria:

- Continuous unbroken bedrock = 0
- Discontinuous/broken bedrock/boulders <300 spacing and <300mm height = 1
- Discontinuous/broken bedrock/boulders >300 spacing and <300mm height = 2
- Discontinuous/broken bedrock/boulders <300 spacing and >300mm height = 2
- Discontinuous/broken bedrock/boulders >300 spacing and >300mm height = 3

Vegetation and rock-complexity scores were combined to give a total habitat-complexity score. Log presence was also investigated and a score allocated according to the following criteria:

- No logs present = 0
- Logs present <0.3m = 1
- Logs present >0.3m = 2

Quadrat plots inside the transect belt were then split into 8 broad habitat groups based on the dominant vegetative and rock elements in each quadrat plot, as follows:

- Open meadow area, including *Aristidia* spp., *Amphipogon strictus*, *Trifolium arvense, Bromus rubens, Bromus diandrus* and *Neurachne alopecuroides,* with weed invasion including cape weed (*Artotheca calendula*) and ice plant (*Cleretum papulsum*);
- Rocky outcrop with low woodland including Acacia lasiocalyx (2 - 8 m tall), scrub including *Rutacea* spp., *Rhinocarpus* spp., and *Diplolaena* spp., very low grasses, ferns and mosses;
- Thicket, dominated by *Casuarina campestris* (1.5 – 3.0 m tall) over *Borya nitida,* with *Acacia spp.*, *Santalum acuminatum* and *Santalum spicatum* forming some smaller components of the association in some parts;
- Tall shrubland, including *Acacia* spp., *Myrtaceae* spp. over various grass species;
- Rocky low sedge species, with very low grasses, ferns and mosses;
- Discontinuous unbroken rock and boulders;

- Open flat continuous unbroken rock; and
- Open driving tracks, cleared within the reserve.

Six ecological variables were used to analyse the distribution of scats and their relationship to various habitat associations, as follows:

- Vegetative complexity score;
- Rock complexity score;
- Total habitat structural complexity score (combined vegetative and rock complexity scores);
- Presence/absence of logs;
- Distance to central diurnal rock refuge area; and
- 8 broad habitat groups.

Scat density data were tested for normality and homogeneity of variances prior to statistical analysis using SPSS 16. As normality and homogeneity of variance tests were rejected, parametric tests could not be applied to this data set, so non-parametric tests were used. The data were tested for mean differences (Krsuskal-Wallis test) between the various complexity scores, distance to diurnal refuge, and broad habitat groups. In addition, where associations between variables appeared linear in the scatter plots, the strength of the relationship was tested using Spearman's Rank Order Correlation. There were limitations to the analyses because the data set (including a high proportion of zero data points) did not conform to all the statistical requirements for more complex statistical analysis, such as multiple regression models.

5.3   Results

5.3.1   Spatial distribution

Very few scats were found at distances more than 35 m from the refuge area (Figures 5.2 and 5.3) and there were no signs of strong seasonal effects (Appendices 1-16). Within transects radiating out from the bottom of the refuge, scat densities were concentrated in a narrow range (0–50 m) within the meadow area (Figure 5.2). This contrasted with the transects at the top of the outcrop, where scats appeared to be more randomly distributed and presented in high densities at greater distances from the refuge area (Figure 5.3), reflecting greater heterogeneity and further foraging distance from the refuge at the top of the outcrop.

High concentrations of activity in the meadow area within the first 50 m from the refuge suggest that distance to diurnal refuge in this type of open habitat is a determinant of rock-wallaby foraging patterns. This effect can clearly be seen in Figure 5.4 which shows that pooled mean scat density dropped in each of the first two 25 m sections of transects radiating from the bottom of the refuge. Despite lower scat densities within the first 25 m of transects stretching outward along the top of the outcrop, densities were higher at further distances (Figure 5.6). The correlation between mean scat density and distance to diurnal rock refuge was significant at (r(120) = 0.647, p< 0.01). The results in transects 2a–5a showed that scat dispersion data reflected the same activity levels discussed in chapter 4, and suggested a strong association between the two.

While higher scat densities were a clear indication of higher use and activity, some habitats were more important throughout the year than simply on a seasonal basis, even when scat density numbers were low, because they provided food resources all year round and/or facilitated safe movement across the landscape. While the spatial distribution of the scat densities (Figures 5.2 and 5.3) was similar to the quadrat plot importance scale distribution (Figures 5.5 and 5.6) some relatively low-mean-density plots reflected a high-importance rating. As in the mean-density-scat-dispersion result, the importance rating reflected greater heterogeneity and further foraging distance on top of the outcrop than in the transects running outward from the bottom of the refuge.

These observed differences between the top and bottom transects are likely due to habitat type and heterogeneity. The habitat along the bottom of the outcrop on the north-western side of the refuge was dominated by large open meadows, surrounded by casuarina thicket which contained very little understorey. Rock-wallabies had never been observed browsing on the leaves of casuarinas. In contrast, the habitat on top of the outcrop was made up of a mosaic of vegetative and rocky patches, providing both cover and food resources, suggesting that rock-wallabies either had a greater preference for the habitats on top of the outcrop (food resources) or a lower perception of predator fear in those habitats (structural cover) or both.

Distance (m) from refuge
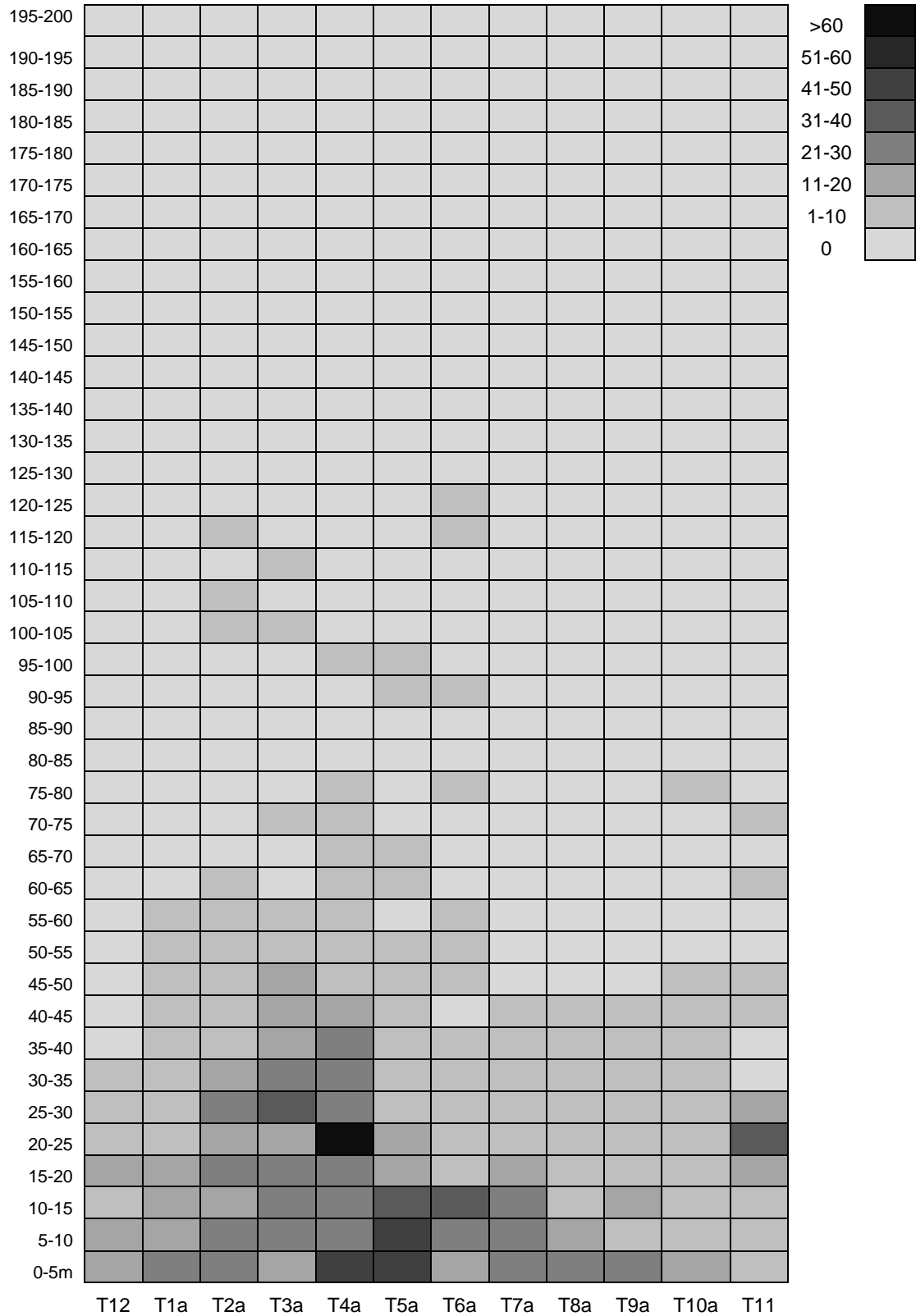
Figure 5.2 The mean scat density (legend shows scat density range) spatial distribution for transects running outward from the bottom of the diurnal rock refuge area of the rocky outcrop for the Nangeen Hill *P. l. lateralis* population (Transects 1a - 10a and 11 - 12).

Distance (m) from refuge
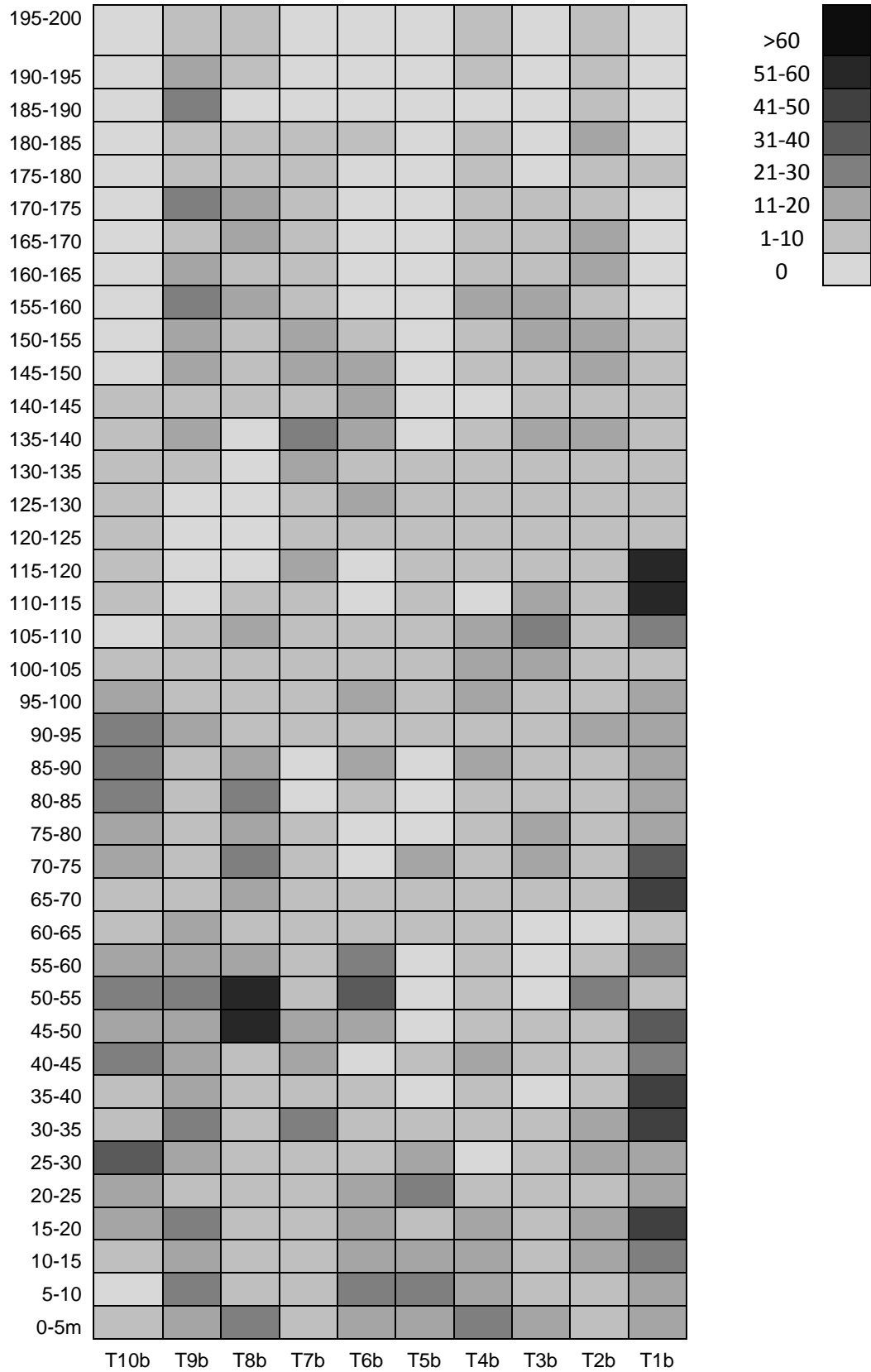
Figure 5.3 The mean scat density (legend represents scat density range) spatial distribution for transects running out from the top of the refuge area of the rocky outcrop for the Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).
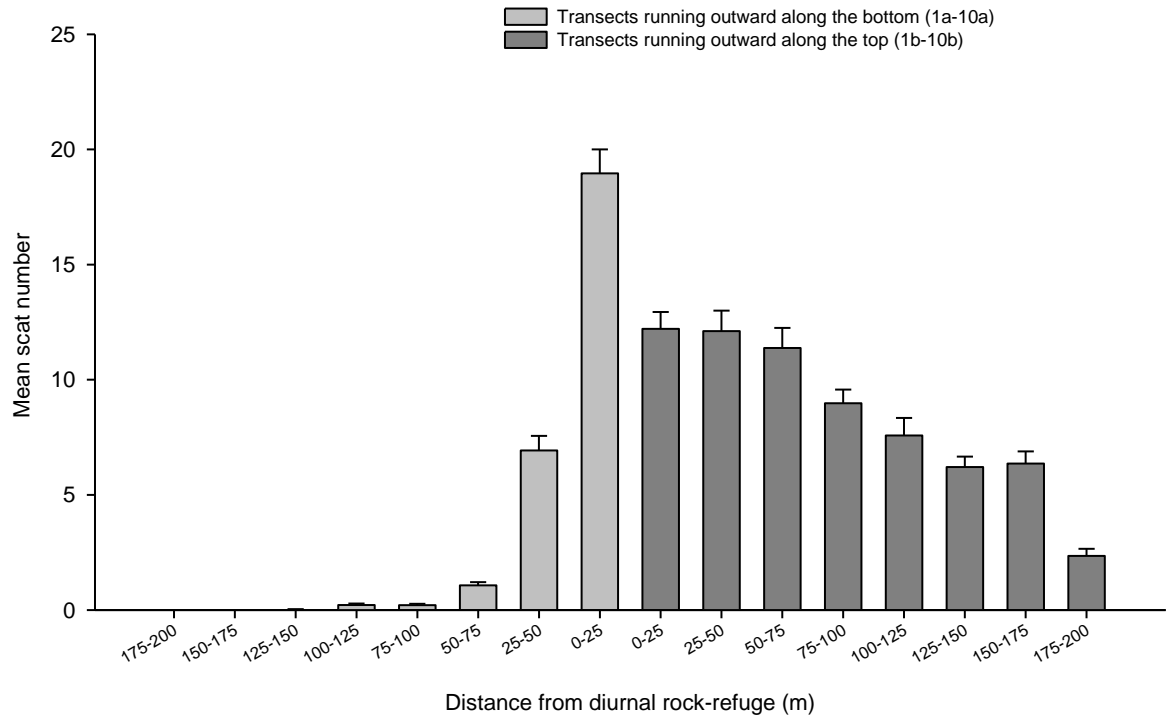
Figure 5.4 The total pooled scat numbers of Nangeen Hill *P. l. lateralis* population for the two main foraging regions (mean ± S.E.).

5.3.2 Scat density and habitat associations

Scat densities varied significantly across the different habitat structural complexities, Vegetation complex (Kruskal-Wallis Test: (6, N = 872) = 51.388, p< 0.01), rock complex (Kruskal-Wallis Test: (3, N = 872) = 280.07, p< 0.01), vegetation + rock complex (8, N = 872) = 187.78, p< 0.01), and logs (2, N = 872) = 19.47, p< 0.01). The highest scat densities were recorded in habitats with the highest complexity scores and vice versa, except for Logs (Table 5.1). The correlation between mean scat density and vegetation complexity was weak and not significant (r(872) = 0.066, p> 0.05). However, the correlation between mean scat density and rock (r(872) = 0.567, p< 0.01) and combined rock and vegetation complexity was significant (r(872) = 0.324, p<0.01). The linear relationship between mean scat density and rock structural complexity was stronger than that of vegetation and rock combined and vegetation complexity alone. This indicates greater significance for the rock structural component.

Distance (m) from refuge
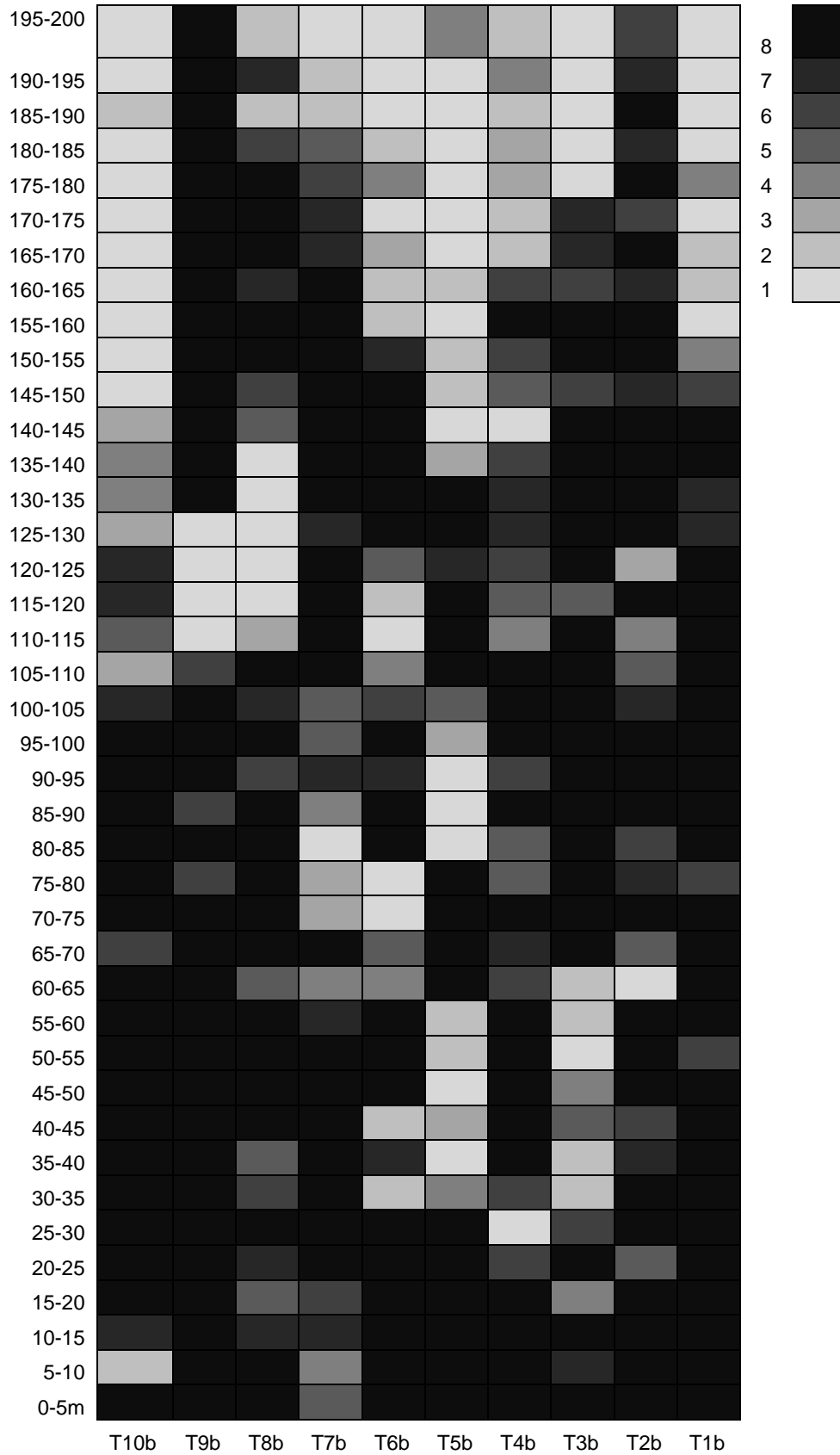
Figure 5.5 The importance scale (1 being the lowest) spatial distribution for transects running outward from the top of the diurnal rock refuge area of the rocky outcrop at Nangeen Hill. (Transects 1b-10b).

Distance (m) from refuge
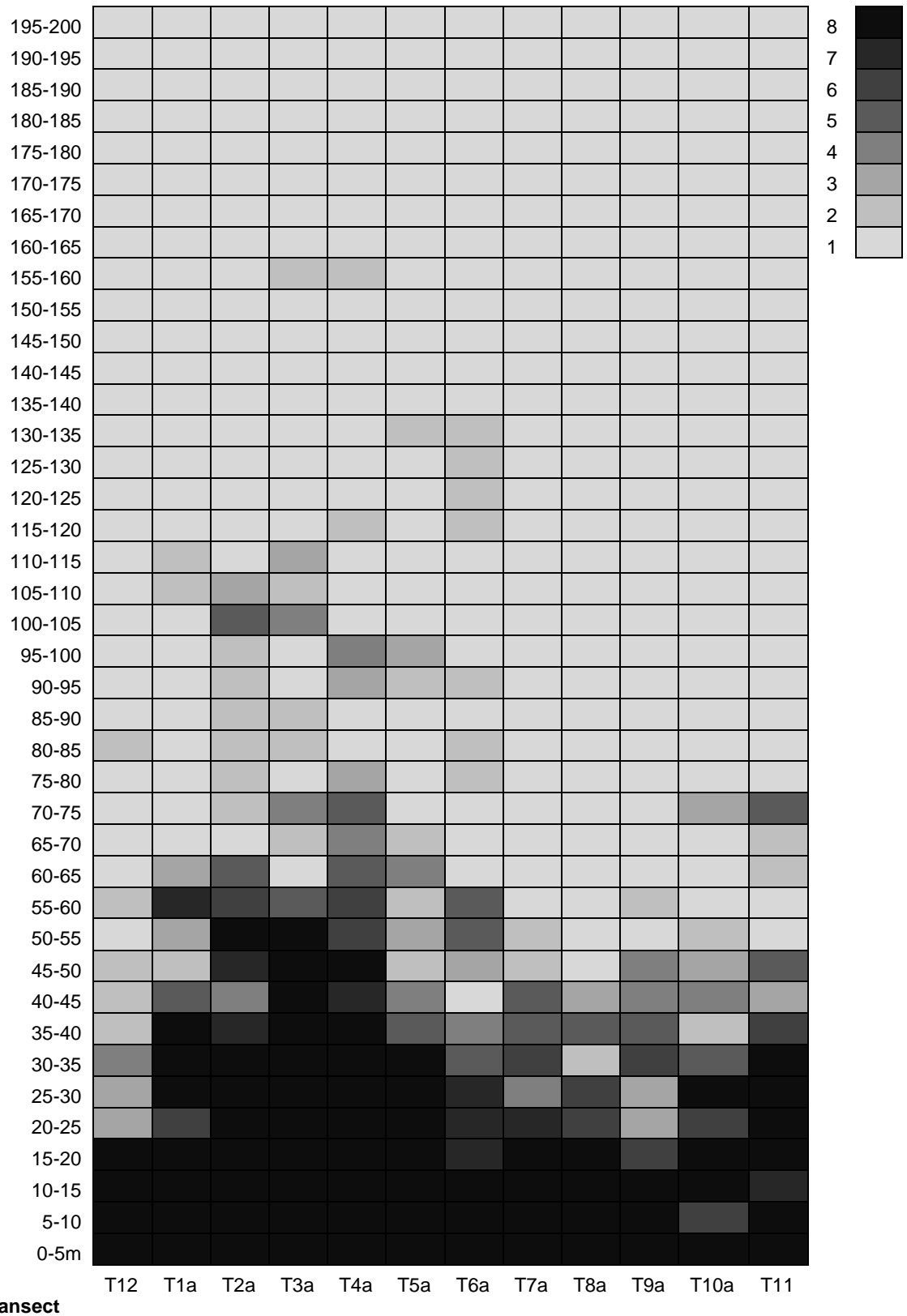
Figure 5.6 The importance scale (1 being the lowest) spatial distribution for transects running outward from the bottom of the diurnal rock refuge area of the rocky outcrop at Nangeen Hill (Transects 1a-10a and 11-12).

Table 5.1 *P.l. lateralis* scat densities for each habitat variable and associated complexity scores (mean ± S.E.).

Complexity score	Vegetation	Rock	Vegetation + rock	Logs
1	2.85 ± 1.06	3.3 ± 0.28	1.2 ± 0.75	5.8 ± 0.55
2	4.07 ± 0.76	9.0 ± 1.15	4.4 ± 1.84	4.5 ± 0.45
3	5.7 ± 0.67	12.8 ± 1.02	3.7 ± 0.61	7.1 ± 0.66
4	5.4 ± 0.56	16.3 ± 1.82	4.6 ± 0.55	NA
5	5.2 ± 0.64	NA	3.7 ± 0.52	NA
6	7.2 ± 0.89	NA	6.1 ± 0.63	NA
7	10.7 ± 1.84	NA	13.1 ± 1.84	NA
8	NA	NA	15.4 ± 1.79	NA
9	NA	NA	15.2 ± 2.47	NA

Although casuarina thickets were the most frequently recorded of all the broad habitat types within the belt transects, they contained the lowest scat densities (Table 5.2). Other habitats that were not used frequently by rock-wallabies were open continuous flat rock and human tracks. Whilst rock-wallabies showed a preference for sedge habitat, this habitat type recorded the lowest frequency in plots than any other habitat type. Other important habitat types were open meadow, rocky outcrop, low woodland, discontinuous rock/boulders, and tall shrubland.

Table 5.2 Mean rock-wallaby scat density ± S.E. and associated habitat groups

Habitat Group	Frequency of habitat groups (%)	Scat density (mean ± S.E.)
Open meadow	24.7	10.6 ± 0.75
Rocky outcrop low woodland	13.5	10.0 ± 0.99
Casuarina thicket	42.2	0.5 ± 0.1
Tall shrubland	1.9	7.3 ± 3.23
Low sedge	0.8	24.8 ± 5.28
Discontinuous rock/boulders	8.3	11.2 ±1.09
Open continuous flat rock	8.3	1.9 ± 0.43
Open track	0.3	4.10 ± 2.15

5.4   Discussion

The scat distribution findings support the conclusion that Nangeen Hill black-flanked rock-wallabies display a central-place foraging pattern, characterised by decreased scat densities at further distances from the central diurnal rock refuge. The rock-wallabies' foraging movements were restricted to open habitats, yet they remained in close vicinity of cover. They also showed a stronger preference for habitats with a high rock complexity than vegetation complexity.

This study showed that scat density can be used as an effective tool to investigate rock-wallaby foraging spatial patterns when the appropriate methodology is applied. The scat distribution results mirrored the observational results of spatial patterns discussed in chapter 4, confirming that the methodology developed for this study was appropriate for examining rock-wallabies' foraging spatial patterns. It also means that this methodology is appropriate for determining foraging patterns in other habitats.

In previous studies the interpretation of scat dispersion was often limited by the methodology used, particularly when used as a single research tool. Scat distribution methodologies have been used in previous rock-wallaby research, but were generally limited to answering questions associated with habitat only (Telfer et al., 2006; Tuft et al., 2011a), and not with both habitat and foraging distances. Until now, comparisons between scat distribution results and observational results have not been used to determine whether scat dispersion accurately reflects rock-wallabies' foraging patterns. An enhanced understanding of these animals' behaviour allowed the researcher to develop a more robust methodology. The results have shown that scat dispersion can be used as an effective tool for investigating not only habitat preferences, but also foraging spatial distribution and distances travelled, particularly in cryptic species that forage out from a central refuge.

Available vegetation patches and the biotic and abiotic components likely to be encountered are strongly influenced by the landscape conditions in which an animal settles (Orians & Wittenberger, 1991). Understanding how animals use their habitat is crucial if they are to be conserved and managed effectively (Pizzuto, et al., 2007). A major proportion of the Nangeen Hill rock-wallaby population's home range was located within a mosaic rocky habitat. This habitat had a greater degree of heterogeneity than areas radiating from the bottom of the outcrop on the eastern side. However, large expanses of meadow on the eastern side were more intensively used within the first 25 m of the outcrop and the refuge, reflecting very different distances

from the diurnal refuge areas in the two different habitats, and very different foraging spatial distributions. The distribution on top of the outcrop reflected the more heterogeneous habitat in the area, compared to the area adjacent to the bottom of the rock which was dominated by meadow and casuarina thickets. Faecal deposits are associated with feeding activity, therefore the observed differences in scat distribution should relate to an increase in food abundance and/or quality, or the amount of vegetative cover. Macropods are known to defecate predominantly while feeding (Ingleby et al, 1989) and in many other macropod species, foraging patterns have been found to reflect the partitioning of habitats, attributed to the different resource requirements they fulfil, including food and shelter states (Lundie-Jenkins, 1993). The researcher believes the extended scat distribution across the rocky mosaic habitat was caused by increased vegetative cover. However, the dilemma caused by different perceptions of habitat use and preference on the part of animals and researchers must be acknowledged (White & Garrott, 1991). Vegetation cover has always been viewed as an important resource for many animal groups (Brown & Morgan, 1995; Druce et al., 2006), including macropods (Lundie-Jenkins, 1993; While & Mcarthur, 2005). By incorporating different elements of structural complexity into the scat methodology, insights were gained about the different habitat uses, the effects of exotic predators, and rock-wallabies' perceptions of optimal cover.

This study found a stronger scat association with rock complexity compared to vegetation alone. Proximity to the refuge influenced rock-wallabies' foraging distances, particularly in open habitats, indicating a stronger association with open habitats compared to habitats with high rock complexity. These results suggest that habitat structural elements are essential to the Nangeen Hill population where foxes are present in the landscape. Studies on brush-tailed rock-wallabies (*Petrogale penicillata*) by Tuft et al., (2011a) found that distance to diurnal rock refuge was more important than canopy cover, but these authors did not include rock structural components in their study.

Rock cover is a good escape habitat for rock-wallabies since they have evolved in this landscape and would therefore have developed an advantage over their exotic terrestrial predators. It is also conducive to escaping from terrestrial predators because it provides cover to hide. However, it is important to recognise that these study results may have been influenced by the ecological constraints imposed on this population, like for example the presence of exotic predators. Rock-wallabies were never observed

away from their diurnal rock refuge during the day, and even when animals were foraging at night, they were reluctant to wander far out into the meadow area (as shown in chapter 4). Movement on top of the outcrop may also have been impacted by the high rock complexity, since it enabled them to forage in what they perceived as a safer habitat.

As conditions became drier and food resources were depleted, one would have expected to see an increase in distances moved by rock-wallabies, yet no strong seasonal shifts were detected (Appendices 1 - 16), even when food resources within 25 m of the meadow became severely degraded and large patches of bare ground were visible (Plate 5.1). This is a further indication of the significant effect of predator fear on the rock-wallabies' foraging patterns.

Plate 5.1   Nangeen Hill Reserve meadow area showing signs of severe over-grazing (March 2007).

The ability to recognise and respond to changes in the environment is an important adaptation to living in drier or seasonal regions where food availability is extremely variable (Lundie-Jenkins, 1993). Foraging behaviour must adapt to the seasonally changing environment if animals are to meet their nutritional needs (Owen-Smith, 2006). This adaptation is especially important, if not essential, to central-place foragers, who rely strongly on the refuge during times of environmental stress. The scat

distribution results support the results in chapters 3 and 4, indicating that a heightened fear of exotic terrestrial predators appears to mask the ability of rock-wallabies to adapt behaviourally to changes in their food resource environment. Instead of increasing their foraging distances to compensate for the scarcity and quality of food during adverse conditions, they remained in close vicinity of their diurnal rock refuge or complex rock habitat. This led to increased competition for depleted food resources in these areas.

Changes in rock-wallaby foraging patterns, in the form of less reliance on rocky cover, would be a predictable result of removing exotic terrestrial predators from the region. However, habitat preference could be due to a specific set of environmental, behavioural, and demographic conditions (such as refugia for predator avoidance). If just one of these conditions changes, habitat preference may also alter. For example, some habitats may provide good structural cover but lack consumable resources, so this may influence movement patterns. Casuarina thicket provides adequate cover for rock-wallabies but there is little understorey in this habitat, which may explain why they were never observed browsing on casuarina leaves. The scats found in the casuarina habitat were predominantly located in the meadow/casuarina thicket ecotone, which contained an understorey of various grass species.

Foraging direction favours more palatable food resources within particular habitats. However, even if exotic predators are removed from the equation, movement patterns may still be restricted to areas with large expanses of unpalatable food habitats, since travelling further distances and longer foraging bouts increase energy costs. Habitat structure as well as distance from centrally located refugia also influence foraging patterns by inducing a tendency to forage in areas that reduce predator efficiency and predation risk. This resulting spatial variation in foraging intensity has important implications for the distribution and abundance of food resources.

It is important to acknowledge that habitat selection and habitat utilisation are not necessarily synonymous. The active choice of an area by an individual represents habitat selection, whereas habitat utilisation refers to an individual occupying a given area, but not necessarily by choice (Bell, 1991). Rock-wallabies may be constrained to a particular patch type due to an increase in predation pressure, human activity, and/or inter-specific or intra-specific competition. Between 1982 and 1998 the removal of predator pressure (by fox baiting) appeared to stimulate significant expansion in habitat use and foraging range within the rocky habitat at Nangeen Hill, giving the impression that fox baiting was a success. However, the combined results of chapters 4 and 5

suggest that the situation was more complex. The rock-wallabies' reluctance to move further out into the meadow areas, even when food resources were depleted, and their strong reliance on rock cover, have significant implications for the health of the habitat and their population dynamics. These results provide further evidence for prediction 4 that the Nangeen Hill rock-wallaby population show strong signs of foraging constraint, restricted to close vicinity of rock refuge and habitat complexity.

Well-designed studies on scat distribution can provide important insights into habitat use and preferences. In particular, this study highlighted the importance of structurally complex, specialised habitats for rock-wallaby survival.

Chapter 6

Population Structure and Demographics

6.1   Introduction and aims

Chapter 3, described many aspects of *P. lateralis* behaviour that can have an impact on the social structure and the spatial structure of individuals, groups, and the population as a whole. Chapter 4 and 5 described how their foraging patterns are strongly affected by the prevailing climatic conditions and the availability and distribution of the structural complexity of the habitat, and may be constrained by fear of both predators and conspecifics. These behavioural patterns are likely to affect their population structure and dynamics.

To understand the dynamics of a population, both density and total population must be examined. Immigration and birth rate, as well as emigration and mortality rate affect population size. In turn, the sex ratio and age structure affect the potential reproductive rate, mortality rate, rate of generation replacement, and possibly social interactions (Caughley, 1977). The population dynamics of terrestrial vertebrates, including rock-wallabies, are often closely linked to fluctuating food resources, which in turn are strongly related to rainfall patterns (Lapidge, 2001). Rainfall patterns have been shown to have a significant affect on reproductive output, and the survival and mortality rates of some rock-wallaby populations (Delaney, 1993; Wynd et al., 2006; Willers et al., 2011). Although rock-wallaby species have an extensive geographical range, populations are often fragmented, partly due to the restriction of a specialised rocky habitat, and a strong preference for complex cave systems (Short, 1982; Waldegrave-Knight, 2002).

Ecologists have long recognised150 that habitats are heterogeneous at some spatial scale. It is also widely understood that the distribution of individuals within a population may be affected by the availability of a suitable habitat (Bowers & Dooley, 1999). The age and sex of individuals and their behaviour towards one another affect their movement patterns, including foraging and dispersal. Even mammals that do not establish territories may behave aggressively around a permanent resting space to prevent other individuals from occupying or breeding in that space, resulting in similar effects on population dynamics to territoriality (Murray, 1979). Structural resources have been found to have a greater effect on the behaviour and spatial distribution of individuals than food resources (Pulido & Diaz, 1997). Habitat and the relationship

between individuals also impact the spatial distribution of populations. Since individuals are rarely distributed uniformly throughout their habitat, the boundaries of a population are often vague and usually fixed arbitrarily by the investigator.

Populations may be divided into local sub-populations, also referred to as demes. These are collections of individuals, composed of two or more interbreeding and interacting social groups, clustered in a particular space at a particular time. The individuals within these sub-populations may be genetically more similar to one another than to other individuals outside the sub-population. The movement of individuals in response to one another and the characteristics of their environment cause them to assume patterns in space that are often characteristic of that particular species (Berryman, 1981). However, these movement patterns change in time as the environment changes or as the responses between individuals change. Within a sub-population or social group, individuals may differ in sex, age, size and genetic makeup, resulting in different group structures which significantly affect the overall population structure and dynamics.

As discussed in the literature review, the population size and range of many of Australia's rock-wallaby species have undergone rapid decline since European settlement (McCullum, 1997). Consequently, many rock-wallaby populations are now confined to small and isolated colonies (Lethbridge, 2001) and are therefore sensitive to variation in the survival and reproductive success of individuals (Caughley & Gunn, 1996). Although the wheatbelt *P. l. lateralis* population increased significantly when a strict fox-baiting regime was implemented in 1982, these populations still exist in a highly modified landscape with a continuous fox presence, both within the agricultural matrix and the reserve boundaries. In addition, the central wheatbelt region recently recorded a high number of consecutive drought years. These factors combine to place the wheatbelt *P. l. lateralis* population under increasing pressure, highlighting the importance of identifying the stochastic and deterministic factors of individual survival and reproduction, and their impact on population dynamics. Spatial distribution of individuals and social groups within rock-wallaby populations have previously been difficult to determine due to the animals' cryptic nature and low trap success. However Kinnear et al., (1988) developed a successful trapping regime for the wheatbelt population, which was further developed by the researcher to explore individual and group spatial distribution and structure within the Nangeen Hill Reserve population. Since this population was distributed on a discrete rocky outcrop within a defined refuge space, the boundaries of the population could be determined with confidence.

During the data collection phase of this thesis, a number of predictions were made in relation to the effects of overgrazing, weed infestation, and habitat degradation on the Nangeen Hill rock-wallaby population. One of these was based on the observations discussed in chapters 3, 4 and 5, where it became evident that prowling foxes significantly affected the foraging time and foraging range of this population. It was anticipated that this would lead to overgrazing of important foraging sites and subsequent population collapse. These predictions unfortunately became a reality in 2010, with the decline associated with behavioural changes in rock-wallabies due to predator fear, increasing drought periods, and poor food resource availability (Kinnear et al., 2010; Pentland, 2011).

Such population events have catastrophic consequences for endangered animals and illustrate the importance of understanding the behavioural ecology of a species for effective management and conservation. As the decline in this rock-wallaby population occurred prior to completion of this thesis, it is necessary to discuss the ramifications within the context of the study. It should also be noted that without the comprehensive behavioural data collected during this study, the ecological causes may not have been recognised. The nature of the decline is briefly outlined in the Discussion section of this chapter. Its causes and implications for management and conservation of this species are further discussed in the context of the research aims in chapter 7.

The aim of this chapter was to describe the Nangeen Hill rock-wallaby population size, density and structure, and to investigate how these influenced the behavioural inter-action and movement of individuals through the habitat. The impact of behavioural characteristics on population structure and dynamics, particularly in an ecologically altered landscape, are also described. The specific aims were:

- To describe the structure and dynamics of the Nangeen Hill rock-wallaby population during two significantly different sets of seasonal conditions, and to determine how this affects their behavioural patterns;
- To describe the individual and group spatial distribution of rock wallabies within the central diurnal refuge area, and investigate the extent to which site fidelity and variability in inter-group (deme) structure affect population dynamics and behavioural patterns; and
- To evaluate the trapping regime used, outlining the importance of its design for management and future monitoring of rock-wallaby populations.

6.3   Methods

6.3.1   Trap methodology

A mark and recapture program of the *P.l. lateralis* at Nangeen Hill was undertaken during November 2006 and March 2007. In addition, preliminary trapping was intermittently undertaken between March 2005 and May 2006 for the primary purpose of individually marking wallabies and continually monitoring their condition for the observational sections of the study. Rock-wallabies were trapped in Thomas traps (Figure 6.1), a design that minimises adverse physical impact on the animals. Traps were pre-baited prior to commencement of each trapping period.

Figure 6.1   Thomas trap

For the purpose of estimating the whole population structure and dynamics, two seasonal time periods were chosen. The spring trapping period (November 2006) was selected to maximise the probability of catching females with pouch young and to investigate reproduction condition. The November spring period followed the winter/spring rains when conditions are most favourable for breeding, and individual condition at its best due to availability of sufficient food resources. The following autumn (March) was chosen to investigate body condition and survival rates over the summer period when resources became depleted. Traps were located around the perimeter of the main permanent refuge area (Figure 6.2), spaced 30 m apart and secured to the ground with large steel tent pegs. Each trapping period consisted of 9 nights. Traps were baited with fresh apple and set twice daily (set at 5.00 pm, checked

and reset at 11.00 pm, checked and closed at 6.00 am). Where possible, traps were placed adjacent to a vegetative or rock shelter to minimise any adverse climatic effects on the animals and reduce the probability of premature trap release due to wind.

Traps were placed around the entire perimeter of the main refuge area to maximise success, to investigate the individual spatial distribution, and to determine whether the population was divided into discrete sub-populations. Observations indicated that rock wallabies emerged from their caves and predominantly moved either directly down to the grassed area or up onto the rocky platform directly above (see chapter 3). This methodology increased the probability of individuals coming into contact with a trap when they were either just emerging from or returning to their central refuge area.
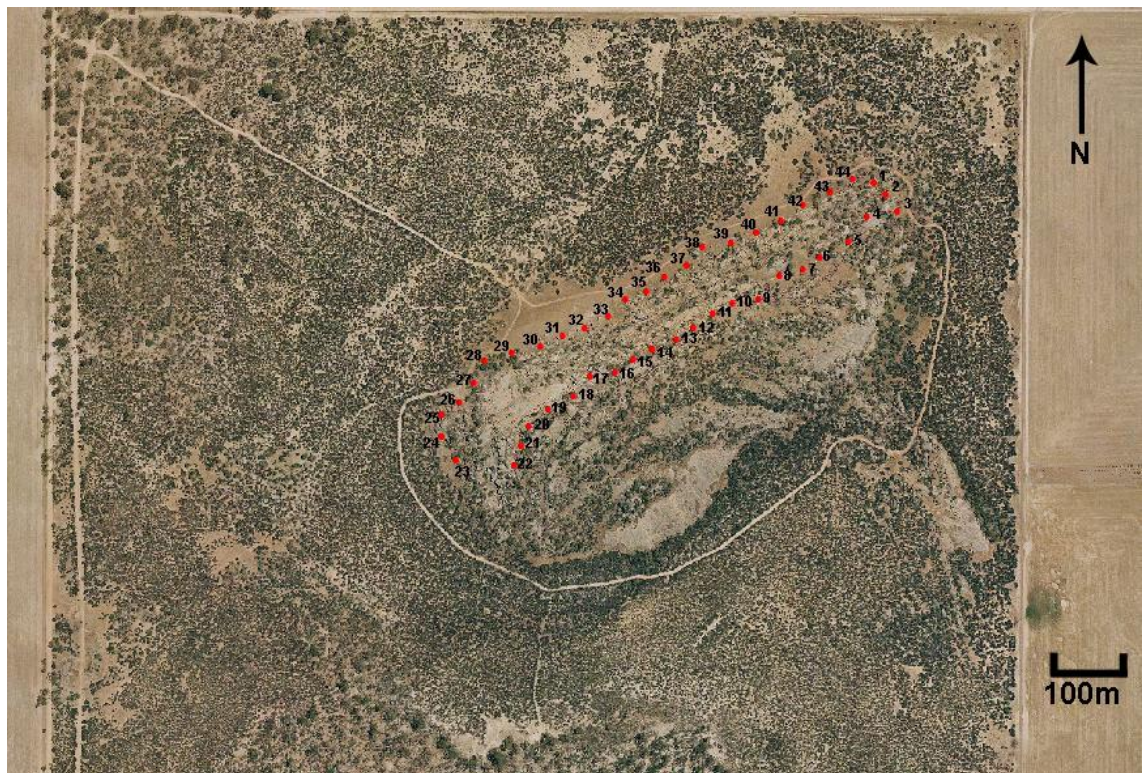
Figure 6.2 The distribution of trap station locations on Nangeen Hill Reserve (44 traps).

6.3.2   Animal measurements

Captured individuals were transferred from the trap into a hessian bag and examined by exposing the anterior or posterior of the animal as necessary. All wallabies were tagged on both ears with individually identifiable metal ear tags. The following measurements and morphological features were recorded at each trapping session:

- sex;
- age class (adult, sub-adult, or juvenile);
- reproductive status;
- weight;
- pes length;
- general body condition (including peculiar markings/injuries, and for females, pouch condition).

A pouch examination of females was undertaken to assess reproductive condition. "Non-lactating" described a developed pouch with small, turgid teats; while "lactating" described a developed pouch with distended, lactating teats. Where pouch young were present, weight, sex and general morphological features were measured only if they were ejected from pouch. In such cases pouch young were inserted back into the pouch with Fixomull tape (easily removable medical tape). Where they could not be re-inserted into the pouch, mother and young were left together in an unsealed hessian bag, placed into a cave with a single entry hole, and checked one or two hours later to ensure they had both vacated the bag and cave. Ear tags were applied to well-developed pouch young. Individuals were released at their trapped location immediately after processing.

The following demographic parameters were recorded for each trapping period:

- total density;
- percentage of males and females reproductively active;
- mean weight and weight class distribution of males and females;
- sex ratios (total and for each age class);
- natality rates (seasonally and annually);
- mortality rates (seasonally and annually);
- age distribution and structure.

All raw data were transferred to SPSS version 16 for analysis of the demographic parameters (grouped and analysed by population, and where possible, sub-population).

6.3.3 Population size and density

A wide variety of models have been developed for mark-recapture methods. They generally fall into one of two categories: those appropriate for closed populations and those appropriate for open populations. A closed model assumes that the population is of a constant size during the study - there are no permanent deletions (deaths and/or emigration) or additions (births and/or immigration). An open model on the other hand, allows for additions and deletions from the population during the study. All mark-recapture estimates require a number of essential conditions, as follows:

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

Variations in capture rates can cause bias in population size estimates. In rock-wallaby population studies, female adults and small sub-adults were considered trap shy (Sharp, 2000), and trap success has generally been low (Lim, 1988; Jarman & Bayne, 1997). It has been difficult to utilise traditional mark-recapture methods in rock-wallaby populations due to low capture probability and spurious estimates of population size (Lim, 1988; Sharp, 2000), however, past capture probability of the Nangeen Hill population has been high (Kinnear et al.,1998). Estimates were initially based on the Known to be Alive (KTBA) method, but were subsequently re-evaluated using closed population estimates (Kinnear, et al., 2010). The trapping method used in this study is similar to that employed by Kinnear et al. (1988) on Nangeen Hill, where trapping continued until no new animals were caught. Thus rock-wallaby population size in this study has been recorded as KTBA as well as using two closed-population estimating methods: the Schnable and Schumacher-Eschmeyer.

The differences between the methods employed during this study and that of Kinnear et al., (1998) were that in this study, traps were placed along the entire length of the top of the outcrop as well as along the bottom on the meadow/rock edge. In addition, trap station locations were recorded in order to determine individual rock-wallaby

distribution patterns. The Nangeen Hill population can be considered a closed population for one trapping period (9 trapping nights); trapping was done over a short period of time and the dispersal rate within the wheatbelt population was considered to be very low. However, mortality could also have occurred from predation during the trapping period.

Age determination, body size and condition

Age structure was divided into three main categories: juveniles (growing and developing <1.0 kg), sub-adults (not reproductive ≥ 1.0 – ≤ 3.0 kg), and adults (reproductive > 3.0 kg). In studies on *Petrogale xanthopus celeris* and *Petrogale xanthopus xanthopus* (Lapidge, 2001), animal weight and size strongly correlated with age. During this and previous studies conducted by Kinnear et al., (1998) on the wheatbelt population, the smallest females recorded carrying pouch young were 2.4 kg and 2.0 kg respectively. Animals were grouped into weight classes of 500 g intervals (500-6000g). Weight, scarring and other physical damage were used to determine the condition of the individuals.

6.4   Results

6.4.1   Population size and density

During the entire trapping phase from March 2005 to March 2007, a total of 152 individuals (86 males and 66 females) were captured and marked. Fifty of those were marked for behavioural observations. The three population estimates within each trapping period were similar, and the population size appeared stable between November 2006 and March 2007 (Table 6.1).

However in March 21% of the individuals trapped had not been caught previously; 83% of these individuals were adult size (weight 3100 – 5750 g) and 17% were sub-adult size (weight 2025 – 2400 g). Therefore, unless there were recent immigrants, which is unlikely, they would have been part of the population during the spring of November 2006. Twenty-three wallabies (14 females and 9 males) were trapped in November 2006 but not in the summer of March 2007. Of these, 13 weighed less than 3.0 kg. The confidence limits for the Schumacher population estimates are relatively narrow, but larger for the Schnabel estimates (Table 6.1). Using the total size of the permanent refuge area, the population density equalled 22 wallabies per hectare.

The precision of estimating population size using mark and recapture methods relies on trap success and equal catchability of sub-groups. Over the two trapping periods (November 2006 and March 2007) total trap success was 49.9% (Table 6.2).

Table 6.1 Nangeen Hill Rock-wallaby population estimates and their corresponding confidence limits.

Date	KTA	Schnabel population estimate	Schnabel 95 % Confidence Limits	Schumacher population estimate	Schumacher 95% Confidence Limits
Nov 2006	111	108	89-136	108	97-122
March 2007	112	112	93-142	110	96-127

There was a significant difference between the two seasonal periods, largely due to an increase in recapture rate in March 2007 rather than an increase in the number of new individuals trapped (first captures). There were no significant differences between sex and season for both first and repeat captures. Fewer than 7% of all individuals captured had lost one metal ear tag, and no individuals had lost two tags between captures. There was no difference in the initial trap response (first capture) between males and females during both seasons.

Table 6.2 Nangeen Hill rock-wallaby population trap success per capture status, sex and season.

Capture status		Nov 2006 % of captures (n)	March 2007 % of captures (n)	Mean total % of captures (n)
First capture	Male	8.8 (49)	10.8 (60)	9.8 (109)
	Female	10.3 (57)	9.0 (50)	9.6 (107)
	Total	19.1 (106)	19.8 (110)	19.4 (216)
Repeat capture	Male	11.7 (65)	20 (111)	15.8 (176)
	Female	10.6 (59)	18.7 (104)	14.7 (163)
	Total	22.3 (124)	38.7 (215)	30.5 (339)
Total capture	Male	20.5 (114)	30.8 (171)	25.6 (285)
	Female	20.9 (116)	27.7 (154)	24.3 (270)
	Total	41.4 (230)	58.5 (325)	49.9 (555)

6.4.2　Population sex ratios and age structure

The age structure of this population was dominated by sexually mature adults (Figure 6.3) with a higher number of juveniles recorded in November 2006 than in March 2007. Although the sub-adult population appeared stable between the two periods, 22% of those trapped in March 2007 were new individuals, and 28% of the sub-adult population trapped in November 2006 were not re-trapped in March 2007.

Sex ratios were defined for four groups: totals (adults & sub-adults); adults; sub-adults; and juveniles. Except for juveniles, sex ratios did not significantly differ from parity (Table 6.3). Due to the low sample size of pouch young and the low number of positively identified sex in March 2007, only November 2006 data were used. The juvenile sex ratio was significantly skewed towards males (3.4:1).

6.4.3　Body size and condition

The mean weight and pes length were both significantly different between sexes, with males larger than females. Both male and female weight classes were skewed towards large adults, with a significant loss of lower-weight classes in March 2007 (Figures 6.4 and 6.5).
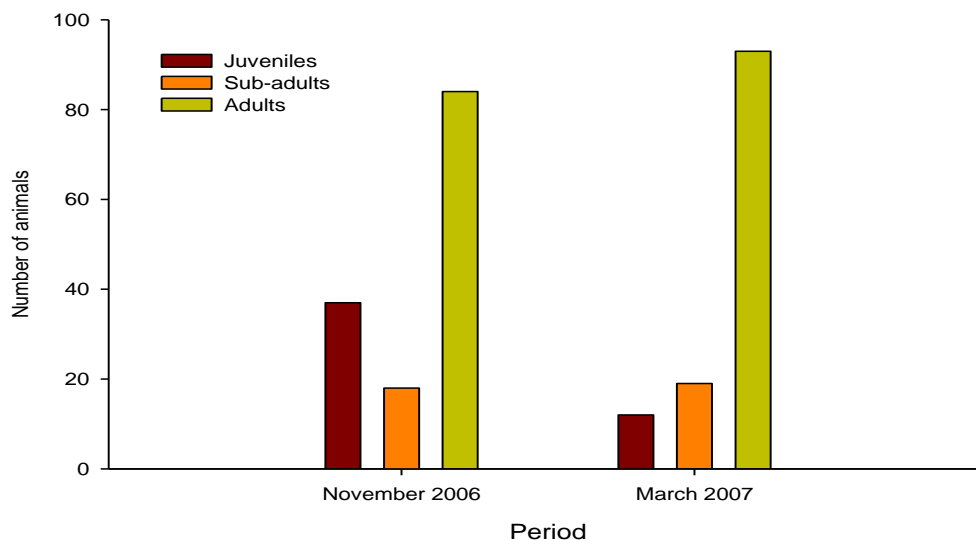
Figure 6.3　Age structure of Nangeen Hill *P.l. lateralis* (Juveniles: < 1.00 kg, sub-adults: 1.00 – 3.00 kg, adults: > 3.00 kg).

To determine the effect, if any, of drought and resource reduction on this population, the weight of individuals was compared between the two periods. In addition, scarring was recorded to determine whether the rate of aggressive interactions between conspecifics had increased. The weight difference of females between November 2006 and March 2007 was complicated by the addition of pouch young. As there was a significant difference between the number of females carrying pouch young in the two periods (a large proportion of females were carrying large pouch young during November 2006), only females that were weighed without pouch young were included in the analysis. Males were significantly larger and heavier than females (Table 6.5) so mean weights could only be used for totals.

Table 6.3 Nangeen Hill rock-wallaby population sex ratios

Period		*% of Males (N)*	*% of Females (N)*	*x^2*
Nov 2006	Totals	47.6 (50)	52.4 (53)	$x^2 = 0.087$, P > 0.10
	Adults	49.4 (42)	50.6 (43)	$x^2 = 0.012$, P > 0.10
	Sub-adults	44.4 (8)	45.6 (10)	$x^2 = 0.222$, P > 0.10
	Juveniles	77.3 (17)	32.7 (5)	$x^2 = 6.545$, P < 0.05*
March 2007	Totals	55.4 (62)	44.6 (50)	$x^2 = 1.08$, P > 0.10
	Adults	57.4 (54)	42.6 (40)	$x^2 = 2.085$, P > 0.10
	Sub-adults	38.8 (7)	61.1 (11)	$x^2 = 0.889$, P > 0.10

Table 6.4 Mean body dimensions (± S.D.) of male and female (animals >1.0 kg) *P.l. lateralis* on Nangeen Hill. * P<0.01

Measurement	Totals	Males	Females	t-value
Weight (g) ± SD	44021 ± 1026	4517.1± 960	3508.2 ± 826	6.266, P< 0.01*
Pes length (mm) ± SD	133.4 ± 8.6	139.6 ± 8.0	128.8 ± 5.7	7.572, P< 0.01*

A paired t-test was applied to individuals caught in both trapping periods. The mean weights were significantly different (paired t-test: t (57) = 5.368, P < 0.01) between seasons for all individuals (Table 6.5).

6.4.4   Scarring

There was a marked difference in the proportion of individuals showing signs of scarring between November 2006 and March 2007, with males showing higher percentages of scarring than females in both seasons (Figure 6.6).

Scarring (alopecia) results from intra-specific aggression which occurs predominantly between males (see chapter 3). The higher rates recorded during November 2006 compared with March 2007 (the end of the dry season) suggests that fighting incidences may have occurred due to acquisition of females in oestrous rather than acquisition of depleting food resources.

6.4.5   Reproduction

Seventy percent of all females showed signs of breeding in November 2006 compared to just 24% during March 2007 (Figure 6.7). During the entire trapping phase (March 2005 – March 2007) the presence of pouch young was recorded at each trapping period (all seasons).

Although the Nangeen Hill *P.l. lateralis* population appeared to breed continuously, there was a significant difference in the number of females breeding during November 2006 (spring), with a greater developmental range of pouch young (Figure 6.8) than that found in March 2007 (autumn). All individual pouch young found during March 2007 were within 0-75 mm in size and no females were found to have enlarged lactating teats without pouch young present. In addition, unlike in spring 2006, no large juveniles were trapped independently during autumn 2007. These results suggest that no females commenced breeding during summer 2006/2007 and that there was a high mortality rate of juveniles between spring 2006 and autumn 2007.
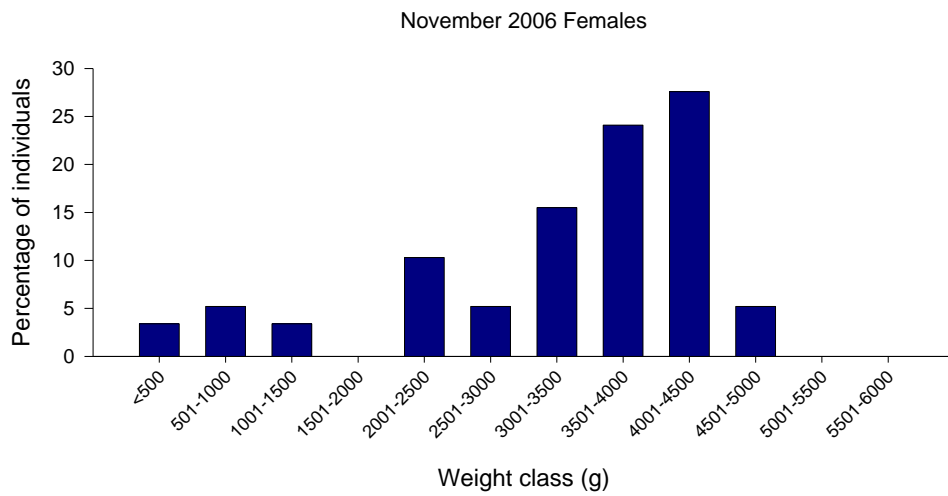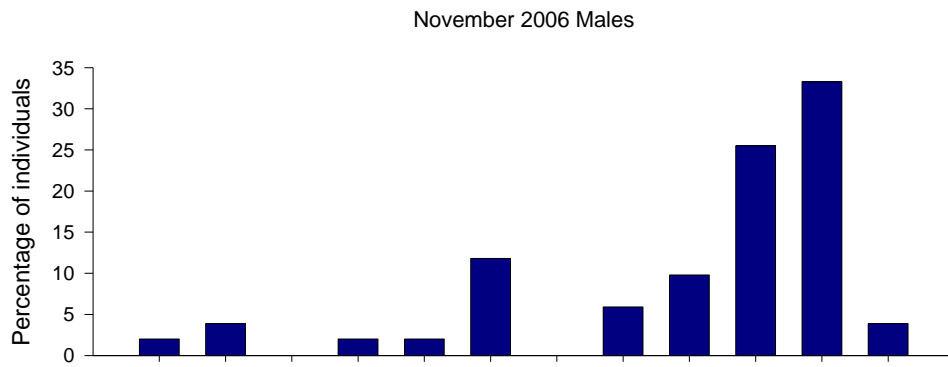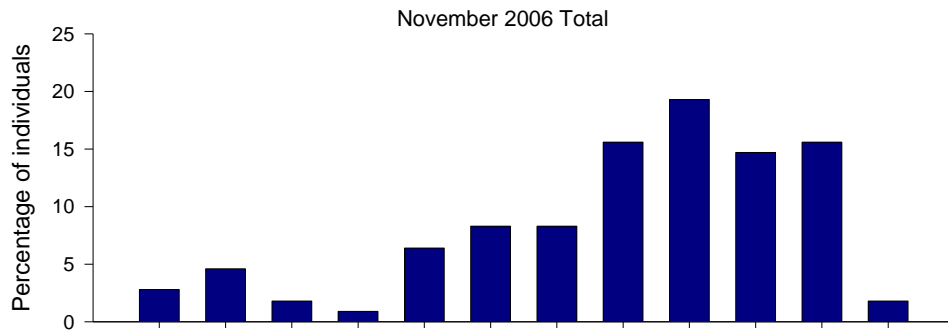
Figure 6.4 Nangeen Hill *P.l. lateralis* weight class distribution during November 2006.
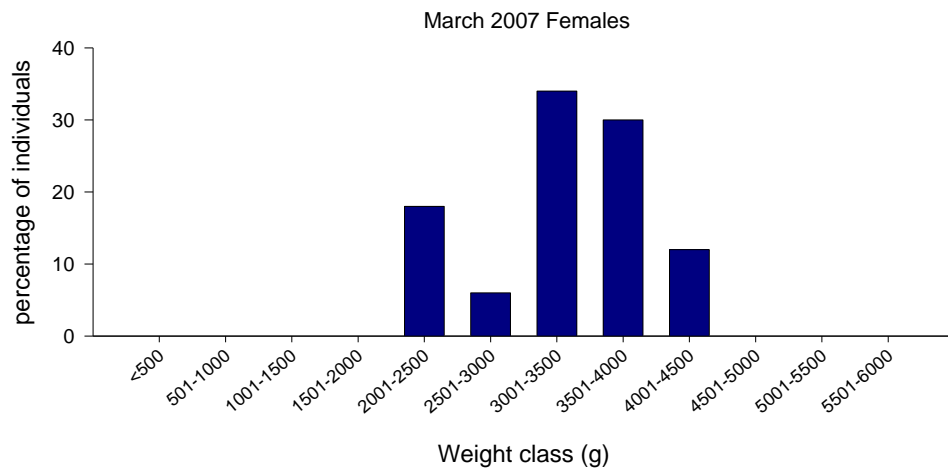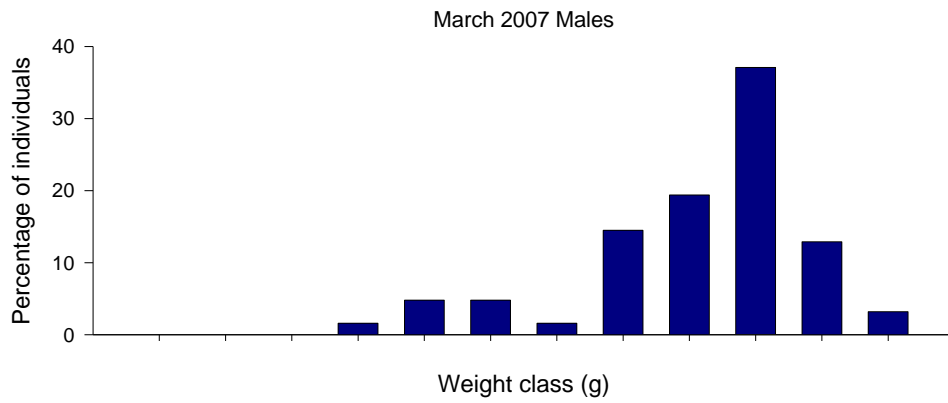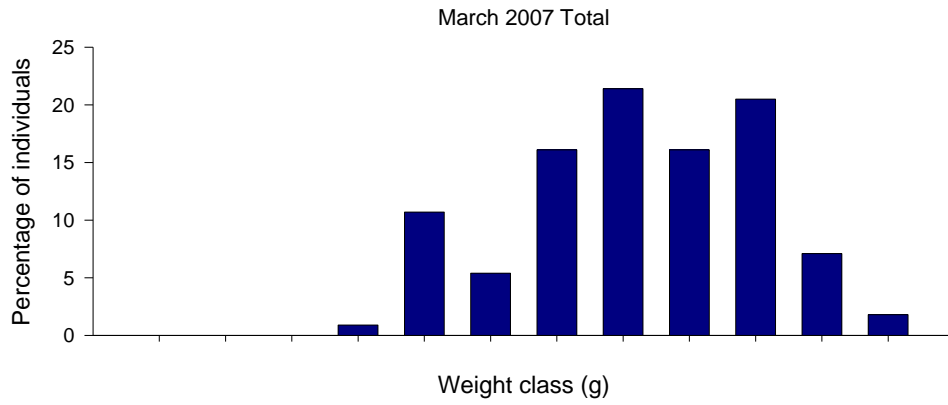
Figure 6.5 Nangeen Hill *P.l. lateralis* weight class distribution during March 2007.

Table 6.5 Mean weight loss (g) and mean percentage weight loss of male and female
P.l. lateralis on Nangeen Hill between November 2006 and March 2007. * p<0.01

Measurement	Males	Females	Males + females
Weight loss (g)	217.7	188.2	209.1
% Weight loss	4.1	5.8	4.6

Except for one animal, all breeding females were within a 3–5 kg weight range (Figures 6.9 and 6.10). The ratio of breeding to non-breeding females in these weight classes was significantly different (X^2 = 8.518, P<0.05), and indicated a relationship between the size of the individual and breeding status, with the 4.0-4.5 kg weight class (82.6%) recording the highest, and the 3.0-3.5 kg weight class (42.3%) recording the lowest percentage of breeding females.
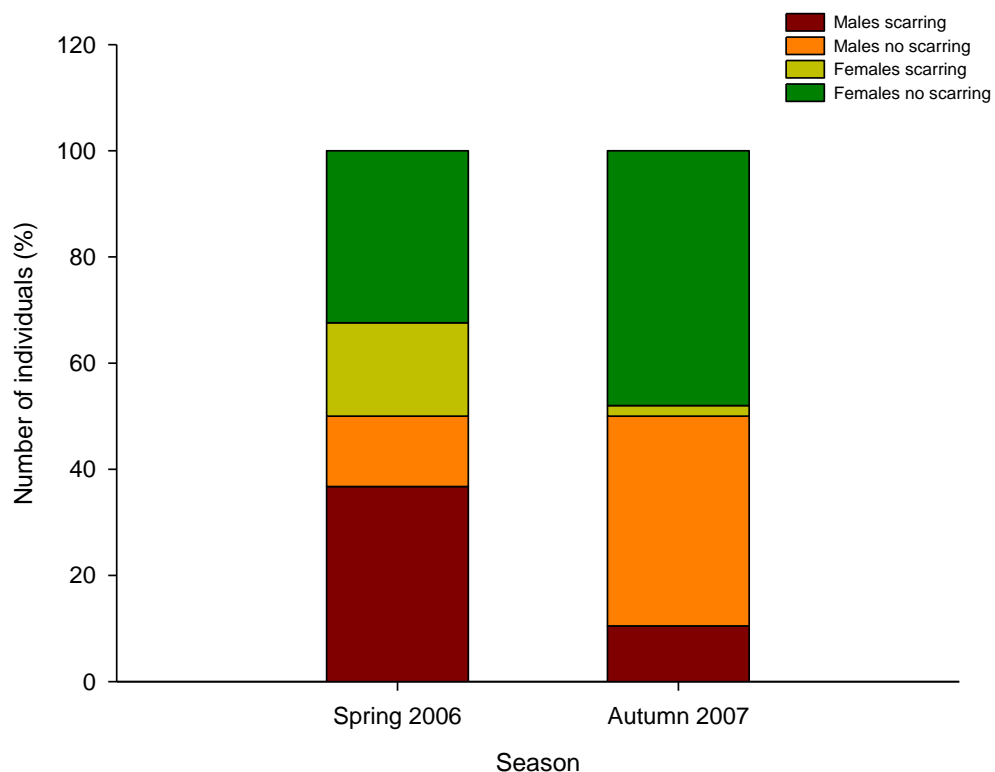
Figure 6.6 Relative proportions of *P.l. lateralis* individuals on Nangeen Hill showing presence and absence of scarring.
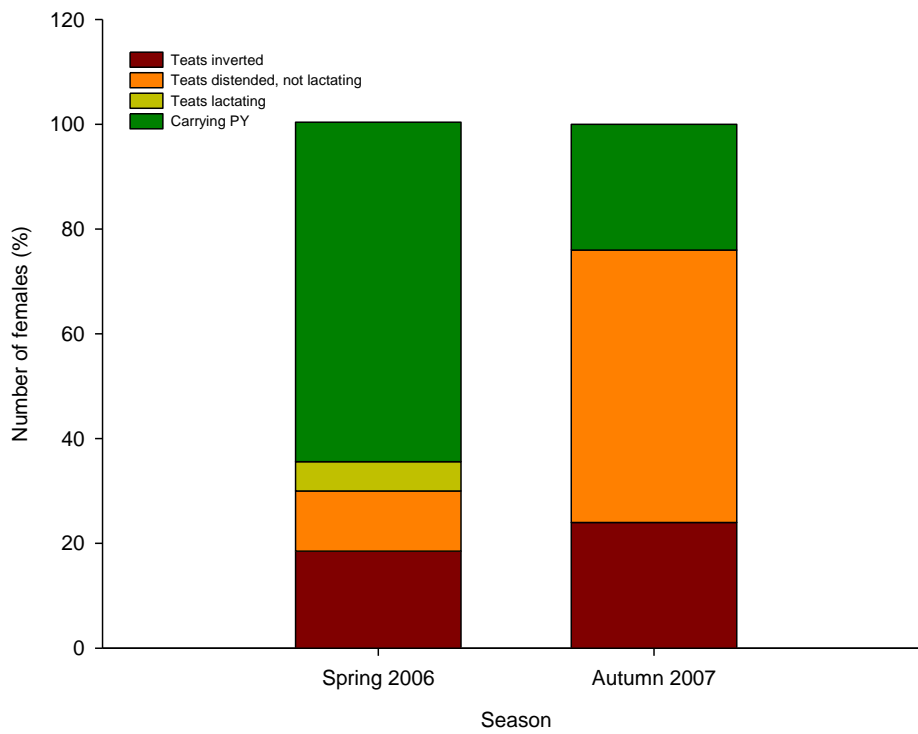
Figure 6.7 Relative proportions of breeding in *P.l. lateralis* females on Nangeen Hill.
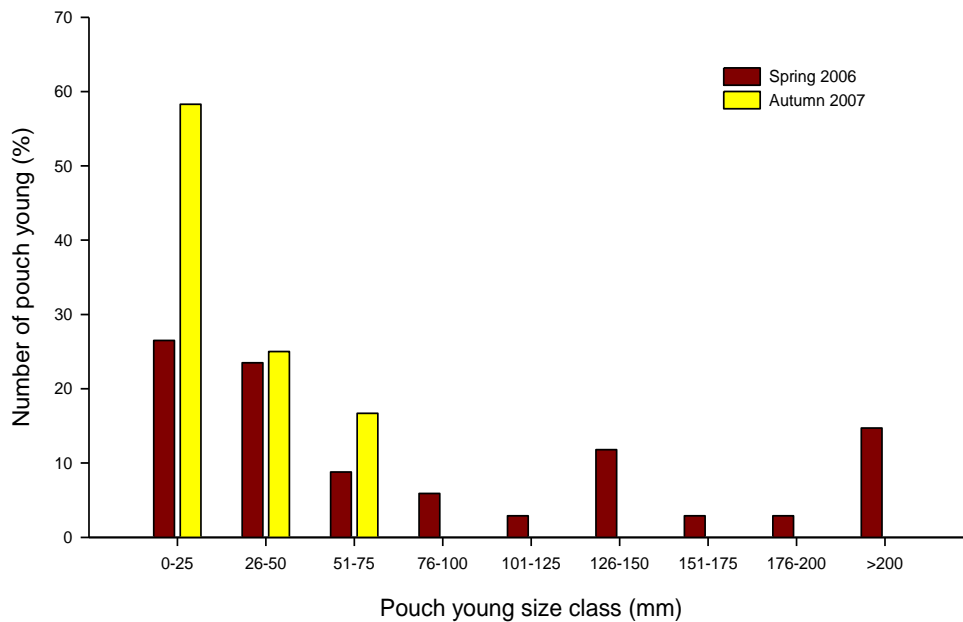
Figure 6.8 Population distribution of pouch young size class between seasons in Nangeen Hill *P.l. lateralis.*
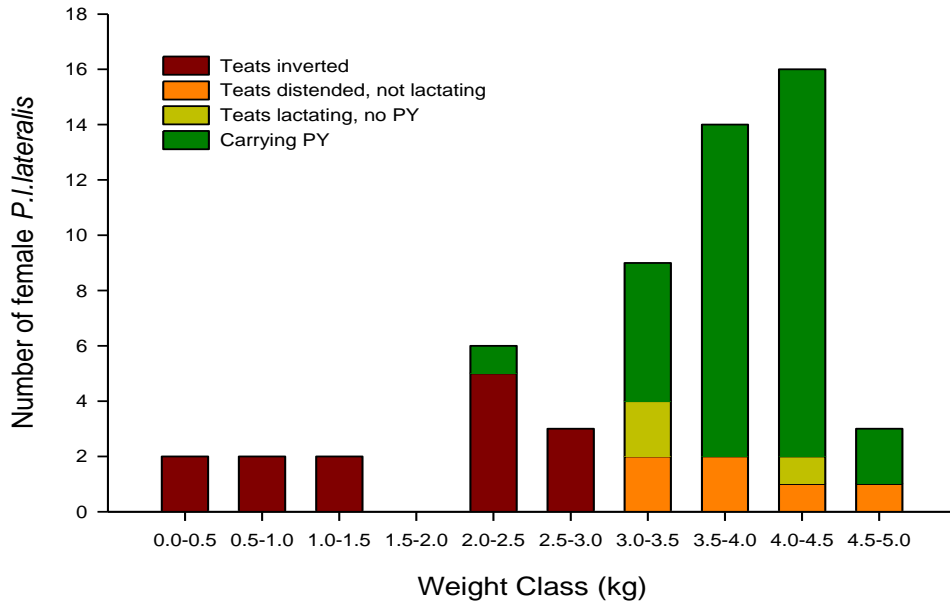
Figure 6.9 Reproductive condition between weight classes of female *P.l. lateralis* on Nangeen Hill Reserve. November 2006.
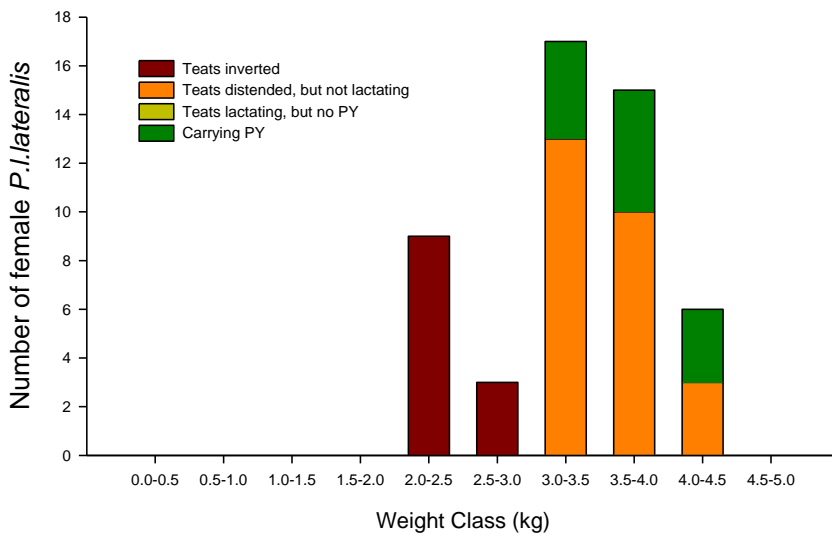
Figure 6.10 Reproductive condition between weight classes of female *P.l. lateralis* on Nangeen Hill Reserve. March 2007.
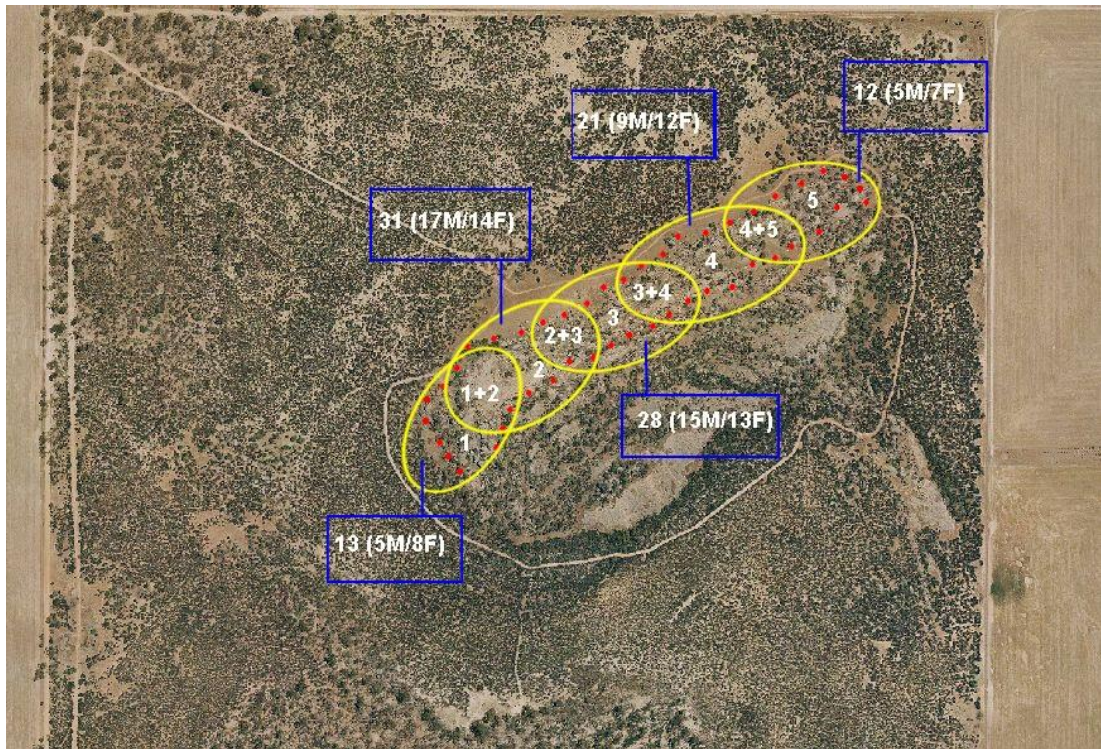
a) **Above:** November 2006   b) **Below**: March 2007
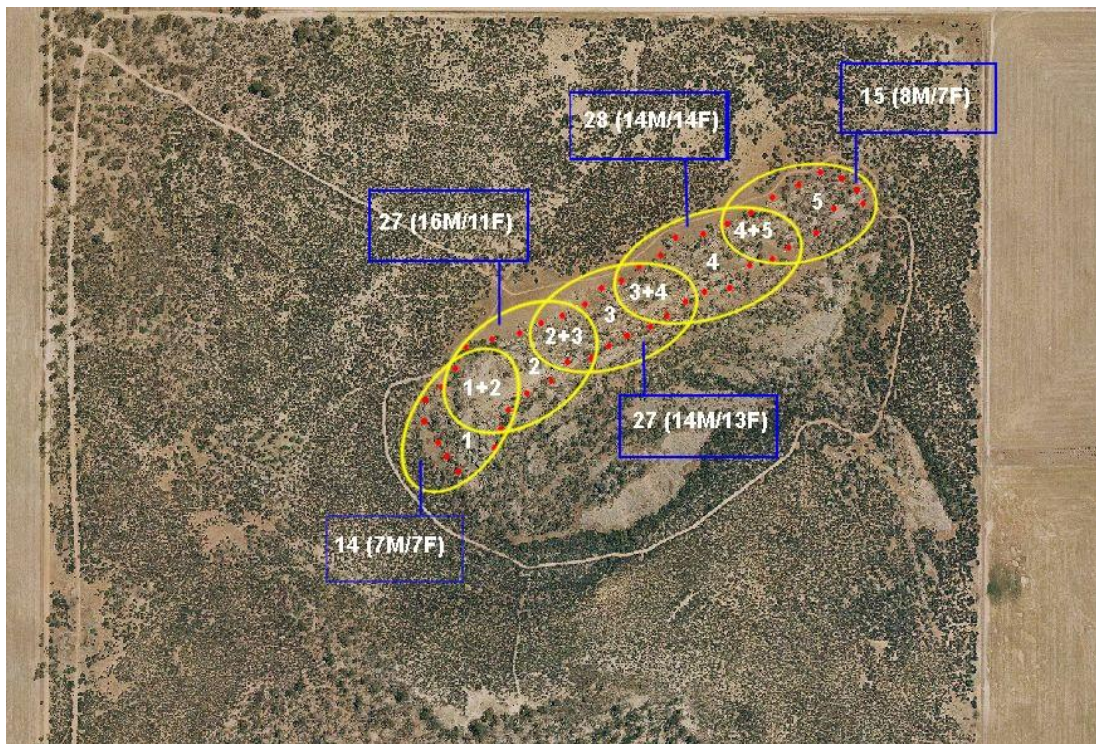
Figure 6.11   The spatial group distribution of *P. l. lateralis* individuals on Nangeen Hill during two trapping periods a) November 2006 and b) March 2007. The population is divided into five main groups as outlined in the yellow boundaries. The associated blue boxes contain the total number of individuals and sex ratios (M = Male and F = Female) found in each group. Where yellow boundary lines overlap, there was some mixing between those groups. The red dots represent the trap station locations.

6.4.6   Spatial Distribution

The spatial patterns for both individuals and groups were consistent between trapping periods (Figure 6.11). Using the trap locations and the individuals trapped at each station, the spatial distibution across the rock was divided into 5 main groups (sub-populations) as outlined in the yellow boundaries in Figure 6.11.

The boundaries and individuals in each group did not change between trapping periods. The marked individuals used for direct observations were also found to occupy discrete sections   of the central diurnal refuge throughout the study, suggesting strong site fidelity in the Nangeen Hill rock-wallaby population.

There were some signs of mixing between adjacent groups (1 and 2, 2 and 3, 3 and 4, 4 and 5), but not between non-adjacent groups. Although the population was spatially distributed along the entire north-western side of the outcrop, the highest concentration of individuals was found in the section of the refuge that contained groups 2 and 3, where the largest cave systems were located. Each group of individuals had similiar sex ratios (same as the population sex ratios) with a similiar proportion of females showing signs of breeding.

6.5   Discussion

6.5.1   Linking the behavioural ecology of *P. l. lateralis* with population structure and dynamics

Population structure is critical to demography because it encompasses both natality and mortality rates. The spatial distribution of individuals is important because it acts as an ethological regulatory mechanism. The density of a population will affect its spatial distribution, social structure, reproduction, movement patterns, and resource use; all topics of primary importance to behavioural ecologists (Sutherland, 1998; Anthony & Blumstein, 2000). The characteristics of a species' population structure are not static and continually evolve. For example, inbreeding depression favours increased dispersal away from natal groups, and local adaptation will increase the cost of dispersal (Davies et al., 2012). The structure of a population influences the precision of local adaptation, while gene flow determines the scale of variation in behaviour (Davies et al., 2012). The wheatbelt populations were highly fragmented and isolated, and there was little movement between populations. The results of this study show that rock-wallabies are significantly constrained in their movement patterns, and that both fear of

predators and conspecifcs may be the main contributors, reinforcing the value of understanding how behavioural ecology affects population structure and dynamics for developing current and future conservation management programs. Only then can we link behavioural ecological studies to the population ecology framework.

Despite the 2011 census of the Nangeen Hill population recording a significant decline (Pentland, 2011), it remained relatively stable from 1990 until 2007, suggesting that the population had reached carrying capacity. The population density equated to 22 wallabies per hectare (from 1990 until 2007) in the rock refuge area, a high concentration of individuals. The size, structure and distribution of sub-populations are dependent on the size of a suitable habitat (including refuge) to provide sufficient protection against predation and adverse climatic conditions. Aggregations (sub-populations) forced to occupy a discrete continuous refuge may be antagonistic towards one another and form territorial boundaries. The findings of this study suggest that rock-wallabies exhibit strong site fidelity and are spatially divided into large groups with little or no movement between groups. These findings provide evidence for prediction 5, that the Nangeen Hill rock-wallaby population would exhibit strong rock refuge site fidelity, reflected in a defined individual and group spatial distribution. Since these groups were in close proximity to one another, it was difficult to determine whether they should be classified as sub-populations (demes), i.e. made up of one or two or more interacting social groups. Therefore, for this study they have simply been referred to as a group, made up of a number of interacting individuals occupying a discrete section of the refuge area and collectively defending important refuge resources and mates (see chapter 3). In rock-wallabies, group size appears to be linked to both the number and size of caves (Barker, 1990; Jarman & Bayne, 1997), so for the Nangeen Hill population, group size was determined by the size and number of available cave systems found in each section of the refuge area. Higher concentrations of individuals were found in groups 2, 3 and 4, where there were larger cave systems than in groups 1 and 5.

This spatial distribution of caves and the strong agonistic behaviour described in chapter 3, caused strong territoriality with clusters of caves each containing a number of interacting individuals in social groups, resembling a dominance hierarchy social system. Individuals, particularly subordinates, cannot move across the entire rock-refuge without increasing the probability of agonistic interactions, so are more likely to remain within a discrete section of the rock. This creates and maintains a social spatial

structure without which higher rates of agonistic interactions would occur, particularly in refuge environments where all available cave systems are concentrated in one region.

The abundance and structural complexity of shelters depend on the prevailing geology, and their distribution is largely determined by the landscape. In this study the size and number of caves determine the population's local density and refuge distribution, while the surrounding habitat and other environmental conditions shaped their social structure, population structure and foraging patterns. However, if foraging ranges are restricted, particularly during adverse conditions (drought), then the available food resources will not be sufficient to support the carrying capacity of their available refuge. As population-carrying capacity is limited to the number and distribution of adequate refuges, individuals would be expected to use more than one cave or more exposed resting sites. However, male-male intolerance has been observed in *P. brachyotis* (Telfer & Griffiths, 2006), and females have been seen gathered together in a group of caves with one adult male defending access to them and their refuges (Jarman & Bayne, 1997). In this study, males were often observed foraging together within their rock refuge, and a number of different males and females were frequently seen occupying a specific cluster of caves. These differences between that of this study and other rock-wallaby studies may be due to the high concentration of caves within each section of the refuge area on Nangeen Hill.

Each group of rock-wallabies on Nangeen Hill appeared to contain a mixture of dominant and sub-dominant adults and sub-adults, including females exhibiting signs of breeding. The sex ratios in each group across the refuge were close to parity, and there were no signs of sections being utilised by sub-dominant adult males only. These demographic results were similar in each group. During 2006 to 2007 the population appeared stable, however, other signs of a possible future decline were starting to emerge, such as weight loss, and high juvenile and sub-adult mortality rates over the dry season.

Rock-wallabies are opportunistic herbivores and vary their diet according to plant availability (Dawson & Ellis, 1979; Copley & Robinson, 1983; Horsup & Marsh, 1992; Tuft et al., 2011b). They typically feed on both forbes and browse, but grasses are preferred (Horsup & Marsh, 1992; Tuft et al., 2011b). However, grasses are less abundant during the drier months, resulting in rock-wallabies switching to more browse species during this period (Copley & Robinson, 1983). By shifting their diet to available

plant groups during dry conditions and/or increasing their foraging range to access more abundant food resources, the Nangeen Hill rock-wallabies' weights would not be expected to decline significantly. However, there was a significant mean weight decrease over the dry period from November 2006 until March 2007. This weight loss may have been one of the earliest signs that the population had reached carrying capacity in its ecological environment (presence of foxes).

This study showed that rock-wallabies foraged within close vicinity of their refuge (chapters 3, 4 and 5), even during dry periods when food resources were very low, signalling dire consequences as food resource became more depleted in ensuing years, particularly when drought conditions worsened. Dry conditions also impact rock-wallabies' ability to access adequate water resources. Although rock-wallabies obtain most of their water needs from their food sources, they have been observed drinking (Lim & Giles, 1987; Sharp, 2000) when drinking rates increase as mean pasture moisture content falls below 20% (Sharp, 2011). Signs of water stress were observed in this study, with animals regularly accessing a seep at the edge of the refuge during dry conditions. As food and water resources become more depleted one would expect an increase in aggressive behaviour, and an increase in agonistic interactions between larger dominant individuals who monopolise remaining food and water resources resulting in greater stress and poorer body condition of smaller subordinate individuals. This study showed that displacement behaviour (chapter 3) was common in this population, with larger dominant individuals displacing smaller subordinate individuals.

Higher stress levels and poorer body condition in younger rock-wallabies would lead to higher mortality rates for this age class, which may account for a large proportion of sub-adults trapped in November 2006 not being re-trapped in March 2007. In addition, no large juveniles at heel or sub-adults in the 1.0 -1.5 kg weight class (that would have been at younger developmental stages in November 2006) were detected. Even though a large proportion of females were carrying pouch young during November 2006, there appeared to be no recruitment in March 2007. A poor recruitment rate was also detected in the wheatbelt rock-wallaby population at Mt Caroline for a number of years preceding the population collapse (Pentland, 2011; Willers et al., 2011). The scarcity of sub-adults may also have been the result of higher dispersal rates of new sub-adults into the surrounding landscape, after being chased out of the refuge by larger dominant individuals as resources became depleted.

Although there was no evidence of frequent mixing between the central wheatbelt

populations, the surrounding agricultural matrix was not fox-baited, so individuals dispersed throughout this landscape would have been subject to higher predation risks and may not have survived the journey between reserves. This higher mortality rate in younger individuals has resulted in an age structure for the Nangeen Hill rock-wallaby population that is dominated by sexually mature adults (March 2007). The researcher believes this age structure continually shifted towards older animals prior to the population collapse in 2010, with only the largest dominant adults remaining from each group (Pentland, 2011).

It is important to note that not all adult females have access to breeding rites. As the number of animals increases, space availability within the rock refuge decreases, resulting in more competition and increased agonistic behaviour. At the Nangeen Hill reserve, larger dominant females were observed chasing both smaller subordinate females and adult males away when they tried to interact, resulting in a smaller proportion of breeding females. This is reflected in the significantly higher breeding rates of larger adult females. Dominance hierarchies have also been found in other female rock-wallaby populations (Jarman & Bayne, 1997). Together with access to good refuges and food resources, breeding rites act as strong selective pressures on the social systems and spatial distribution of female rock-wallabies. These mechanisms may however be density-dependent, and selective pressure on the acquisition of all three important resources (food, refuge, and mates) may be reduced in lower-density populations, resulting in no significant differences between female weight classes and the ratio of breeding versus non-breeding individuals.

6.5.2 Trap Methodology

The trap methodology was designed to maximise trap success, to reduce variability in trap responses between sexes, and to reduce stress on the trapped individuals. Average trap success was high during this study (49.9%) with no detectable variability in trap responses between sexes. However, there were differences in male and female capture rates between the two clearance times (11.00 pm and 5.00 am). More males were trapped during the first session and more females during the second. This could be due to a behavioural phenomenon whereby males tended to emerge from the refuge prior to sunset and actively forage earlier than females, thereby increasing the probability of males entering the traps during the first trap-setting session, leaving fewer traps available for females.

The importance of employing two setting and clearing times should be noted. The narrow confidence limits for each population estimate using a closed model, suggest the trapping method was efficient for determining accurate population estimates in the reserve. In addition to a full population census carried out in November 2006 and March 2007, a number of trapping sessions were employed between March 2005 and May 2006 for the purpose of marking individuals for the observational studies. Trapping periods during winter 2005 returned a very low trap response (less than 10%) and no animals were trapped during the 5.00 am clearance times. The observational studies found rock-wallabies were sensitive to low ambient temperatures and started to return to their refuges once temperatures dropped below 10^0C. Temperatures on most nights during winter fell below 10^0C, so few animals foraged throughout the night, reducing trap response. During the winter periods there were also signs of new vegetative growth, so the low trap response may partly be due to an abundance of food, reducing the likelihood of animals entering the traps. This once again illustrates the importance of understanding how seasonal changes affect the behaviour of animals and reduce trapping success at specific times of the year.

6.5.3   Conclusion

The results of this study demonstrate the importance of including behavioural elements in ecological studies to improve our understanding of a species' population dynamics. They provide important insights into an animal's evolutionary history and how this has shaped their social and demographic patterns. The results also showed that food resource availability in close vicinity to the rock-wallabies' refuge was still sufficient to sustain the adult population during the period of data collection. However, the survival rate of sub-adults and juveniles between spring 2006 and autumn 2007 was low, and may have been caused by dominant adults restricting younger subordinate individuals from accessing remaining food resources during the drier months. As there was no significant change in population size and distribution from 1990 to 2007, the population appeared to have reached carrying capacity in the available rock refuges. As discussed in chapters 3 and 4, signs of heavy overgrazing were evident, and it was predicted that remaining food resources would not continue to support a high-density population unless individuals increased their foraging range (prediction 6). Without this, the likely result was a population crash which eventually occurred in 2010, not only on Nangeen Hill, but also at Mt Caroline, the largest wheatbelt population on the adjacent reserve (Pentland, 2011).

These declines were caused by a complex set of interacting ecological relationships, including direct and indirect predatory effects, weed invasion, and drought, and are further discussed in an historical context in chapter 7, together with implications for future management.

Chapter 7

General discussion

This research highlights the importance of using a behavioural ecological approach to understand the relationships between animals and their environment, including the effect of their environment on population structure and dynamics, spatial distribution and social structure. A review of past and current ecological studies on Australian mammals revealed that there is insufficient information on the effects of environmental variables; including climate, predation and conspecific fear, as well as habitat structure, on their behavioural ecology. By focussing on the combined effects of these environmental variables, this research clearly demonstrates that they are not only important for defining this species' ecological niche, but also for providing vital information to inform conservation and management programs. Detailed behavioural repertoires of species have been published all too rarely, and constrain the ability of researchers to compare studies between populations, species and different animal groups. By developing a methodology that combined a number of different ecological methods, this researcher was able to investigate different aspects of the species' behaviour; including spatial distribution, population structure and habitat use, to gain a better understanding of these animals' complex relationships with their environment.

In the context of the research aims, this concluding chapter discusses some of the important aspects of *P. l. lateralis* behaviour and how the combined factors of climate, predation fear, conspecific fear, and habitat structure play a significant role in defining the species' realised niche. Throughout the discussion, the importance of access to an optimal refuge is emphasised. The vital contribution of behavioural studies to ecological research is emphasised by an analysis of two recent declines in rock-wallaby populations in the central wheatbelt (Nangeen Hill and Mt Caroline). The detailed examination of the behavioural ecology of the Nangeen Hill rock-wallaby population undertaken in this study, facilitated an enhanced understanding of the complex ecological processes that contributed to these declines in an altered landscape. Without this understanding, the causes and solutions would be less clearly understood. The implications of these findings for the conservation and management of this species are also highlighted and finally, the importance of behavioural ecology for conservation and management of threatened species is discussed.

7.1 Behavioural ecology of the black-flanked rock-wallaby: refuge importance in a variable environment

The major aim of this research was to examine the behavioural ecology of the rock-wallaby sub-species *Petrogale lateralis lateralis* in Western Australia. It is widely accepted that food abundance and distribution significantly impact the foraging behaviour of all mammal groups; in this study the focus shifted to the combined effects of a number of environmental variables that have rarely been studied in macropods, including climate, fear of predators, fear of conspecifics and habitat structure. While rock-wallabies' preference for a specialised rock habitat is driven by protection from both temperature extremes and predation (Short, 1982; Sharp, 1997a), the way in which these animals use their refuge in differing climatic and exotic predatory conditions, was previously unknown.

This research showed that rock-wallabies occupy a permanent central rock refuge and display strong signs of site fidelity (prediction 5). Their foraging patterns reflect those of a central-place forager, but distances travelled were restricted in open habitats and there was a stronger preference for rock complexity than vegetation complexity (prediction 4). Their foraging behaviour is not strictly nocturnal, nor can it be considered crepuscular, exhibiting significantly different seasonal patterns (prediction 2). Time allocation for foraging was strongly affected by climatic conditions, fear of predators and conspecifics (prediction 3). An individual's survival and reproductive success critically depend on its behaviour, with selection favouring individuals that are efficient at foraging, avoiding predators and finding mates (Davies et al., 2012). Where resources are limited there will always be trade-offs, both within and between these various activities, so individuals are likely to compete with others (Davies et al., 2012).

Since the central diurnal rock refuge was an important resource for rock-wallabies in this study, one would expect to see the animals actively engaged in territorial behaviours (such as agonistic acts). In this study, *P. l. lateralis* exhibited a large number of agonistic behavioural acts, although aggressive interactions were rare. Instead, when two rock-wallabies encountered one another they generally used a series of subtle ritualised behaviours, which either resulted in one of the individuals retreating or in physical attack. These types of ritualised behaviours reduce the likelihood of severe injury, particularly within an elevated rocky habitat. The victor of agonistic encounters in this *P. l. lateralis* population was predominantly determined by

size in both sexes, reflecting a size-based dominance hierarchy (prediction 1). In most macropod species, including other rock-wallaby species, supplanting is the most frequent agonistic interaction (Croft, 1980: Horsup, 1986; Ganslosser, 1989). This also acts as a disturbance when carried out by nearby conspecifics. One strong disturbance observed in the Nangeen Hill population was the movement of predators inside the rock-wallabies' foraging areas. Fox intrusion resulted in the highest disturbance response and animals immediately retreated to their diurnal rock refuge, a clear indication that the high level of alertness was caused by the combined effects of heightened fear of conspecifics and predators (prediction 3). Levels of vigilance were used in this study as an indicator of the rock-wallabies' perception of fear. From the detailed information collected it was clear that individuals used scanning to detect both predators and other conspecifics. Even when resting within their refuges, individuals were predominantly alert, and only exhibited a non-alert state in the close vicinity of their caves. Individuals were never observed in a resting state once they moved away from their diurnal refuge, and rarely engaged in social non-agonistic behaviours.

Direct physical agonistic acts did not only occur between pairs of wallabies but also within groups of 3 or more individuals. This was one of the most unusual and significant findings related to the behavioural repertoire of this species. Group agonistic interaction was observed on a number of occasions between adult males, comprised of one intruding individual versus 2 or more individuals, who occupied the same refuge area. The outcome of these group interactions was always the same: the intruding individual fled, suggesting that individuals or mates in an area with good rock refuges (large caves systems) act as a single collective resembling a social group in defence of the resource.

Monitoring the environment for intruders forms part of rock-wallabies' daily activity patterns. If inter-individual behaviour between different social groups resulted in predominantly agonistic interactions, then it would be important for individuals to reduce their likelihood of coming into contact with individuals from outside their social group. This could result in a spatial behavioural pattern determined by territorial social groups, with each group predominantly occupying a discrete core space for both its refuge and foraging, thereby reducing the rate of agonistic interactions with other social groups forced to cluster around a scarce resource, such as a large cave system. Strong site fidelity and the frequent agonistic behaviours observed in this study support this hypothesis (prediction 5). Although individuals may occupy discrete diurnal refuge

areas and form social groups that interact and actively defend the refuge, foraging away from the diurnal refuge increases the probability of coming into contact with other individuals from different refuge regions. This conspecific fear and heightened vigilance reduces the benefits of group foraging behaviour. However, the fear of predators appears to have strong effect on the rock-wallabies' foraging patterns. This was clearly evident from the animals' strong preference for habitat cover (prediction 4), particularly with high rock complexity. Predation fear also restricts their movements in open habitats, even when food resources are depleted. Despite the eradication of foxes from the region, some structurally complex habitats will nevertheless not be used by rock-wallabies if they do not contain sufficient food resources (e.g. casuarina thicket).

The trade-off between the cost of thermoregulation, foraging efficiency, predator and conspecific avoidance, limits foraging time. The rock refuge acts as a facilitator and a constraint to foraging. This research has shown that climatic conditions, such as high wind velocity, intensify rock-wallabies' perception of fear. This not only affects their levels of vigilance but also foraging distances. Climatic conditions impact on an animal's ability to detect predators as well as their thermo-regulatory costs. In this study, rock-wallabies were less active at temperatures below 10^0C and above 30^0C and remained in their caves, which provided a thermal refuge, during adverse conditions (prediction 2).

The foraging patterns of the rock-wallabies at Nangeen Hill resembled those of central-place foragers; repeatedly moving from and back to their refuge area throughout the night. Although not in a classical sense of central place forager, that of returning back to a central place to consume their food resources. These individual foraging bouts were mainly short in both time and distance travelled; they did not move away from their refuge area for distant foraging bouts or long foraging time periods. Short foraging bouts out in the meadow areas were followed by a return to the rock refuge, seemingly due to a heightened fear of predators. The rock-wallabies were also sensitive to changes in climatic conditions, returning to the cover of the central rock refuge when conditions became unfavourable.

The findings of this study show that rock-wallabies rely heavily on a specialised rock habitat, which allows them to live in highly variable climatic regions. This reliance upon a specialised habitat, together with their physiology, limits the range of habitats these animals can survive in, which are further restricted by exotic predator density (foxes and cats), drought, and habitat loss and/or change. The need for rock-wallabies to

remain inside a refuge during adverse climatic conditions is an indication that they have not evolved physiological adaptations for the hot dry conditions that other macropods live in (Bradshaw et al., 2001; King & Bradshaw, 2008).

The ability to change their behavioural activities according to external factors, such as returning to the safety of the refuge when conditions are perceived to be unfavourable, can be seen as a behavioural adaptation to balance their food needs with their foraging and energy costs. However, predator-induced changes in foraging patterns also result in a significant loss of foraging time, and reduce the animals' ability to maximise fitness. This was observed during the summer by way of increased vigilance levels, decreases in mean distances travelled, and decreases in nearest-neighbour distances at a time when young foxes were leaving their dens (Coman et al., 1991).

Parsons and Blumstein (2010) found that dingo scents (*Canis lupus lupus*) elicited fear-based responses and deterred foraging in a number of macropod species (*Macropus fuliginosus*, *Macropus rufous* and *Macropus agilis*). In this study, fox scents may have been detectable, resulting in an avoidance of specific areas or a reduction in time spent foraging in a particular patch. This can only occur when populations inhabit an ecologically altered landscape, as different foraging patterns would have been followed before the landscape was altered (through land clearing and the introduction of exotic predators). Further behavioural ecological studies on rock-wallaby populations in different landscapes, will determine whether these foraging patterns are more widespread in all rock-wallaby species and other ecologically similar animal groups.

Although the impact of fox predation on rock-wallaby population size is well documented (Kinnear et al., 1988; Hornsby, 1997; Jarman & Bayne, 1997), little is known about the indirect effects on their behaviour. This research found that fox presence creates a state of fear in rock-wallabies, restricting time spent foraging as well as foraging range. Foraging distances were further investigated under different climatic conditions, such as high wind velocity.

The findings of this study reflected a predator fear-driven system (μ-driven) in the Nangeen Hill population. Prior to fox-baiting the wheatbelt rock-wallaby populations would have presented as a mortality-driven system (by foxes). Although a successful fox-baiting program was implemented, baiting only occurred within the rock-wallabies' reserves, not outside in the surrounding agricultural landscape, yet the continual movement of foxes would still have been perceived as a threat. For the Nangeen Hill

rock-wallaby population, the consequences of this fear-driven system (μ -driven) have been overgrazing and potential population collapse (Kinnear et al. 2010).

The reluctance of this population to forage at greater distances due to predatory fear imposes a troubling constraint during periods of drought and low food availability. Individuals and groups of animals differ in their ability to deal with such environmental conditions. Younger and smaller, less dominant individuals are forced to occupy less optimal rock refuges, and may therefore be exposed to higher thermoregulation and predation costs. They may also experience higher disturbance costs from dominant individuals who displace these animals from more abundant and safer food patches. These differences go unnoticed when environmental conditions are optimal, but become more apparent during extreme conditions, such as prolonged periods of drought.

In the past, all these constraints acted as a carrying-capacity regulator, forcing some animals to disperse and seek new locations. During favourable environmental conditions, the individuals that dispersed into less optimal refuge areas continue to have their energy needs met, with some rock refuge areas acting as sink populations. During less favourable environmental conditions, only those populations in optimal refuge locations adequately meet their energy needs, acting as source populations and reflecting a meta-population system. It is important to note that the study area was contained within a highly altered landscape, so the wheatbelt populations may no longer reflect a true meta-population system. The recent population decline in wheatbelt populations (prediction 6), including Nangeen Hill, (Pentland, 2011), led the researcher to believe that rock-wallaby populations in this region had undergone a meta-population collapse.

7.2   The cause of the rock-wallaby population decline in the central wheatbelt: A historical context

The findings and concerns discussed throughout this thesis relate to the recent drastic declines of two of the largest populations of rock-wallabies (Nangeen Hill and Mt Caroline) in the central wheatbelt region. Subsequent monitoring of all rock-wallaby-occupied reserves in the central wheatbelt revealed similar problems. The next section discusses these recent declines and explains how different ecological factors have contributed to the problem. Although recent rock-wallaby declines occurred over a short period (1-2 years), associated problems began to emerge when the surrounding

landscape was first altered by European settlement, eventually resulting in a rock-wallaby meta-population collapse.

In the earlier stages of this study, the researcher predicted that indirect predation effects would eventually lead to a population collapse in the Nangeen Hill population. By 2010 the two largest wheatbelt populations had significantly declined (Figure 7.1), likely due to a complex ecological dynamic involving the following interacting factors:

- **Predation fear** - restricts foraging distances away from cover resulting in overgrazing, soil degradation and resource depletion;
- **Drought** - resource depletion and no access to free water;
- **Weed invasion** - reducing plant diversity and causing a loss of important annual and perennial grasses;
- **Cat predation** - affects rock-wallaby recruitment (cats have been captured on camera traps in the same caves as females with large juveniles);
- **Fox predation** - although the reserves are currently fox-baited on a regular basis, the extensive surrounding agricultural landscape matrix is not, so foxes continue to pose a significant threat if baiting is not maintained, particularly when rock-wallaby population numbers are low, there is poor habitat cover, and alternative prey (e.g. rabbits) is at low density in the agricultural matrix.

One of the main possible causes of the decline is the effect of predator fear (primarily the fox), which restricts foraging distances away from cover and resulted in overgrazing and soil degradation of the habitat. This would be exacerbated by the invasion of weed species and the onset of drought conditions, resulting in food resource depletion. Heavy rainfall further eroded topsoil, particularly in strong rainfall run-off areas adjacent to the steep, flat, rocky sections. This was evident at both Nangeen Hill Reserve and Mt Caroline (Willers et al., 2011).

It is important to note that the current environmental conditions have evolved over many years. These changes can best be described in an historical context. From 1979 to1982, prior to fox control, the wheatbelt populations were low and animals were spatially restricted to optimal refuges (Kinnear et al., 1988). At that time, the Nangeen Hill population was restricted to a small core area of cave systems. There were no signs of overgrazing in the adjacent meadow or rock areas (Plate 7.1). Numbers were so low that individuals were able to obtain sufficient food without venturing far from

their caves. During that period, the wheatbelt populations presented strongly as a mortality-driven (N-driven) system, since there was a high density of foxes in the reserve. Only individuals with access to large complex cave systems survived.

Plate 7.1 Nangeen Hill habitat before fox control (November 1979). Photo provided by J. E. Kinnear.

After a comprehensive fox-baiting regime was implemented in 1982, the population increased in size and spatial distribution, eventually extending across the entire north-western side of the outcrop by the later 1980s. By 1983 signs of overgrazing had started to appear (Plate 7.2) and by 1990 the population had peaked. Weed invasion took hold (Plate 7.3) after 1990, primarily in the form of capeweed (*Arctotheca calendula*), and differences between intensively foraged and unforaged zones were clearly visible (Plate 7.4). The researcher believes that this period marked the shift from a predominantly mortality-driven (N-driven) system to a fear-driven (μ-driven) system.

The population remained relatively stable until 2007. However, by this time, significant signs of overgrazing and weed invasion were evident, with the first 25 m of the meadow region adjacent to the main outcrop dominated by weeds (Plate 7.5) particularly ice plant (*Cleretum papulosum*). In Plate 7.6 this plant can be seen growing over the entire rock refuge region.

The central wheatbelt region experienced a number of poor rainfall years (Willers et al., 2011) which worsened conditions and reduced the availability of water. The drought conditions were so severe that by 2010 there was even reduced weed growth in the disturbed areas. During the dry months, rock-wallabies actively sought seeps to drink

from, but even those dried up. They obtain most of their water needs from the plant material they consume and only need access to free water when conditions are driest.

Nangeen Hill Reserve
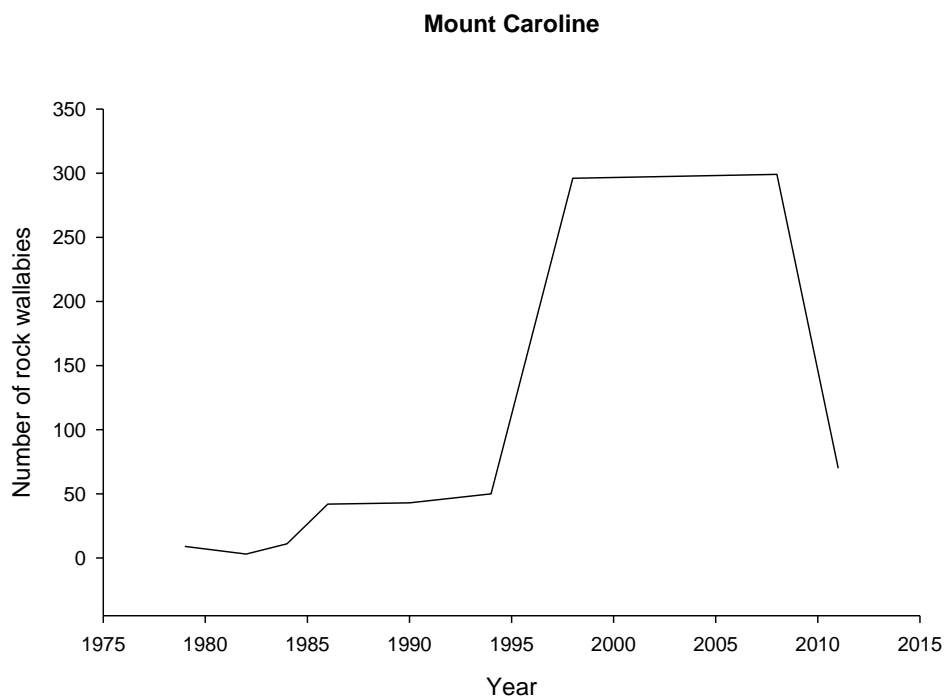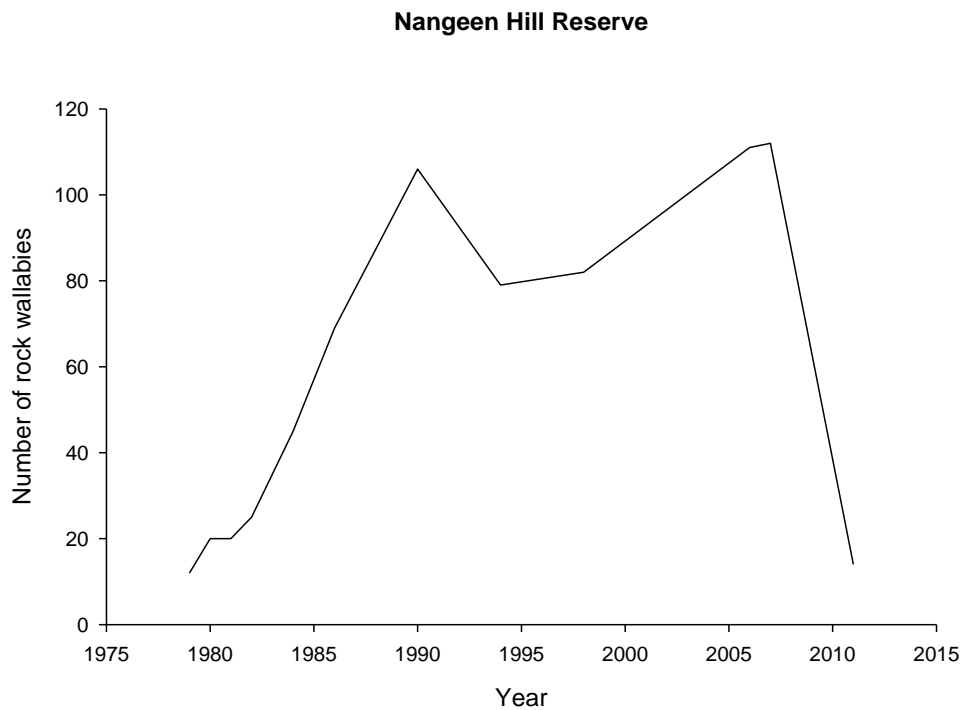
Mount Caroline

Figure 7.1 Changes in rock-wallaby population numbers at Nangeen Hill Reserve and Mount Caroline Reserve (Fox-baiting program began in 1982).

Plate 7.2 Nangeen Hill habitat (March 1983) under fox control. The first signs of grazing in the meadow region can be seen. Photo provided by J. E. Kinnear.

Plate 7.3 Nangeen Hill habitat (1990s) under fox control. Signs of over-grazing and weed invasion (cape weed) can be seen in both the meadow region and within the refuge. Photo provided by J. E. Kinnear.

Plate 7.4 Nangeen Hill habitat (1990s) under fox control. Signs of severe overgrazing close to the rock can clearly be seen. Photo provided by J. E. Kinnear.

Plate 7.5 Nangeen Hill habitat (August 2006) under fox control. The two contrasting shades of vegetation on the meadow area represent the green weed zone and the brown flower heads of the grass zone.

The high salt content of the dominant weed species, the ice plant (*Cleretum papulosum*) found within and adjacent to their rock refuge, coupled with a lack of available free water, could have further affected the condition of these animals. Prior to European settlement the wheatbelt rock-wallaby populations would have reduced resource pressure caused by drought by either expanding their foraging ranges or dispersing temporarily into new areas. Today continued fox presence restricts these behavioural patterns, further compounding the problem.

Plate 7.6   Nangeen Hill habitat (August 2006) under fox control. Ice plant can clearly be seen growing up into the rock refuge area.

Drought conditions also affect the behaviour of predators (foxes and cats) when the abundance of alternative prey in the agricultural matrix is significantly reduced. This leads to increased predator activity within the reserves, which either increases the mortality rate of rock-wallabies from direct predation, or places pressure on their foraging behaviour through indirect effects, further reducing access to adequate resources. One would expect an increase in direct predation from foxes to lead to a spatial reduction in rock-wallaby populations, similar to pre-fox baiting years, yet the 2010 census suggests otherwise – no spatial reduction in the rock-wallaby population was detected (Figure 7.2).

Between 2005 and 2010 habitat damage by the rock-wallabies themselves became more apparent. Not only were they impacting on the understorey, they were also having a significant impact on the shrub and tree layer (Plate 7.7). There was evidence of bark stripping; individuals were frequently observed stripping and eating the bark of various shrub species. Even when few resources remained, rock-wallabies continued to forage within close vicinity of their refuge, preferring to scratch at the surface and dig up dried ice plant roots rather than moving another 10 to 20 m away to forage on the remaining grass stems. Eventually this population reached a tipping point where the remaining resources in close proximity to their rock refuge could no longer support them. Similar environmental changes occurred in Mount Caroline Reserve, and more recently (2012 to 2013) in Querekin Reserve, where due to resource depletion, DEC has had to provide supplemental feed for the rock-wallabies.

Although a fox-baiting program was implemented in the Nangeen Hill Reserve in 1982, no cat-baiting program has ever been implemented. Cats do not generally take fox bait, so there is a concern that cat numbers may have increased inside the reserves. Cats have been recorded on camera traps within the same caves occupied by female rock-wallabies with large pouch young, raising concerns about their impact on the recruitment rate of these populations. Predation by feral cats, predominantly on juveniles, was documented in an isolated colony of *Petrogale assimilis* (Spencer, 1990). A significant population decline occurred in this colony between 1986 and 1990, believed to be due to a lack of adult recruitment (Spencer, 1990). Cat numbers in the central wheatbelt reserves are unknown, but may be another contributing factor to the decline of these rock-wallaby populations.

Despite habitat degradation, the 14 remaining individuals at Nangeen Hill were in reasonable condition when they were trapped in April 2010 in spatially distributed locations across the entire refuge area (Figure 7.2). This can be explained by their strong site fidelity and social dominant hierarchy. As food resources began to decline, the dominant adults in each group along each section of the refuge area would have defended the most abundant foraging patches, marginalising subordinate individuals to poorer resource patches. This resulted in higher mortality rates for subordinates unable to satisfy their nutritional needs, and as the population decreased, the remaining adults had increased access to sufficient resources to maintain their condition. This highlights the importance of an effective trapping design, since incorrect assumptions can otherwise be made about the condition of a population when a sub-sample only comprises larger dominant animals.
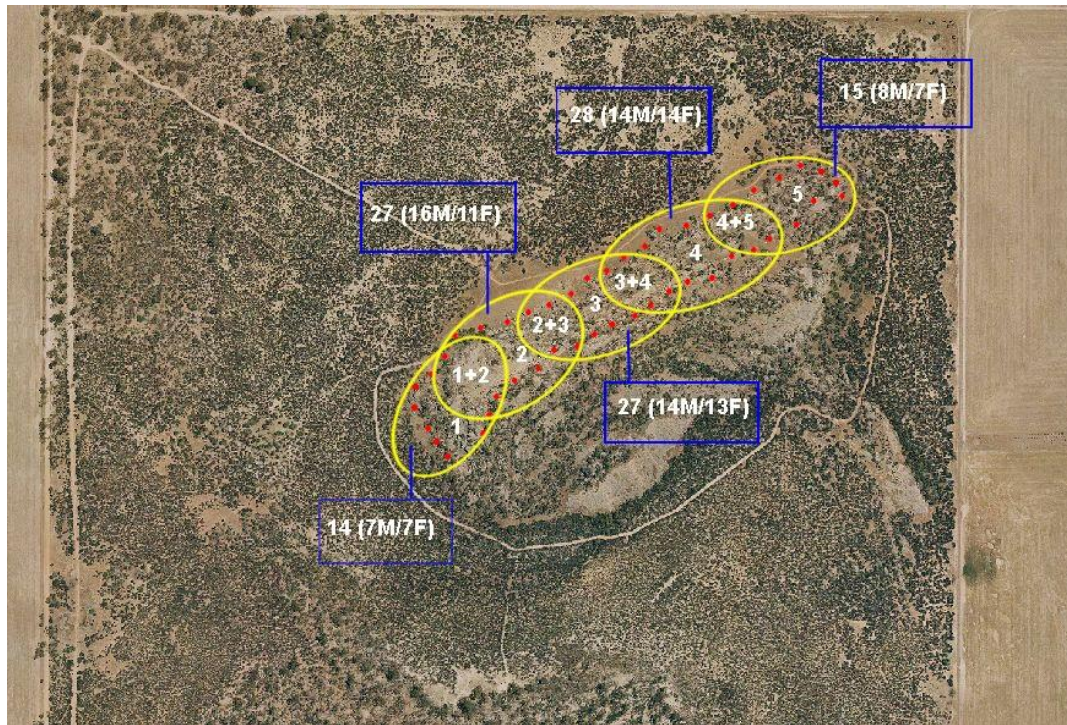
a) March 2007
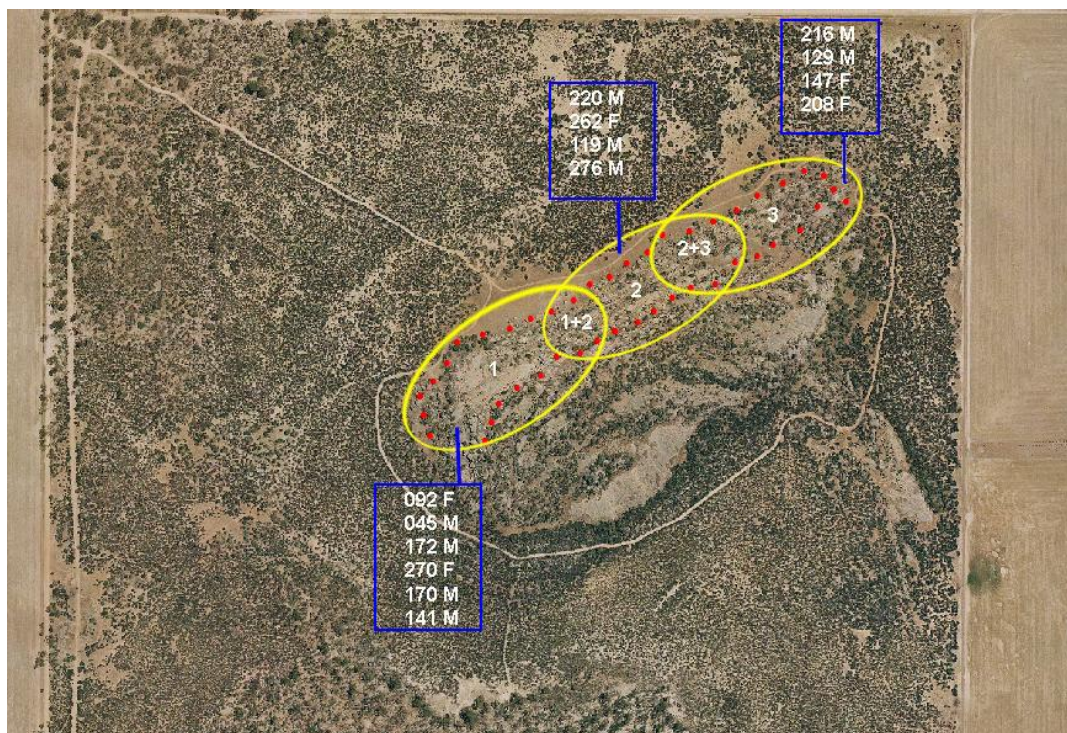
b) April 2010

Figure 7.2 The spatial group distribution of *P. l. lateralis* individuals on Nangeen Hill (April 2010). The population is divided into five main groups outlined in the yellow boundaries. The associated blue boxes contain the total number of individuals and sex ratios (M = Male and F = Female) found in each group. Where yellow boundary lines cross over there was some mixing between those groups. The red dots represent the trap station locations.

Plate 7.7 Signs of significant over-grazing and soil degradation can clearly be seen along the rock refuge (left), on the adjacent meadow (top right), and along the top of the outcrop (bottom right) in Nangeen Hill Reserve (April 2011).

A number of large juveniles and sub-adults trapped in 2006 were not re-trapped in 2007. In 2010 no sub-adults were recorded, suggesting that recruitment had ceased. A poor recruitment rate was also evident at Mt Caroline when population numbers were high but sub-adult recruitment had begun to decline between April 2007 and 2009, prior to the 2010 population crash (Pentland, 2011; Willers et al., 2011). A decline in recruitment may have been one of the triggers of the subsequent population decline. It is also possible that sub-dominant adults restricted to poorer food resource patches, may have dispersed out of the reserve in search of new rock sites. These individuals would have had to transmigrate across an agricultural landscape that was not fox-baited and may have succumbed to predation.

This complex ecological dynamic involving predator-prey relationships, spacing distribution, social systems, over-grazing, weed invasion, weed succession and drought, underscores the importance of understanding the behavioural ecology of

animal species and how they affect the environment in which they live. They also emphasise the need for more research on the behavioural patterns of our predators and how they affect the foraging patterns of our marsupial groups.

7.3   Implications for management of rock-wallabies

Recent population declines have emphasised the need for an adaptive management plan that incorporates the behavioural ecology of animals into conservation planning. One such plan is presented here. Important features of the methodological design for future monitoring are discussed. This is followed by a management strategy for the long-term survival and conservation of the central wheatbelt rock-wallaby populations.

This research showed that scat distribution can be used to monitor changes in foraging activity, including foraging distances and habitat preferences. The following design elements are essential:

- Clearly identifiable diurnal rock refuge areas;
- A high concentration of belt transects (split into quadrat plots) around the entire perimeter of the diurnal rock refuge; and
- Counting and clearing scats within a two-month period (to minimise climatic effects on scat degradation) using the same clearance times between periods. This eliminates the need for standardising the total number of scats found in each quadrat plot.

The study showed significant seasonal differences in activity levels and activity times. Variable daily climatic conditions also affected activity levels and foraging distances. The implications of these findings for monitoring programs which involve trapping, spot-lighting and direct observations are considered.

The optimal period for monitoring population dynamics through nocturnal trapping is during the drier months, when average minimum nightly temperatures are above 10^0C and food resources are low. The scarcity of food resources increases the probability of individuals entering a trap to access fresh bait. To assess body condition, monitoring should be conducted before the onset of autumn/winter rains. A significant proportion of the population should be assessed in order to avoid bias. Reproduction rate is best monitored after the winter rains and during spring when conditions are favourable for breeding.

Trap density and placement are also important. Like the scat monitoring program, identifying the rock refuge area was paramount to the success of the trapping program. Since prowling foxes in the region restricted foraging to the central diurnal refuge and/or the surrounding habitat comprising high rock complexity, placing traps around the entire perimeter not only resulted in a more successful catch rate, but also helped determine the spatial distribution of social groups and signs of site fidelity over time.

Using spot-lights at night and direct visual count observations during the day as monitoring techniques can result in highly variable results depending on the time of year, time of day, and prevailing climatic conditions. The best time to observe rock-wallabies in an active state (foraging or social) is at the onset of their foraging time. During this period, individuals are at their highest concentration within and around the perimeter of the rock refuge. Once animals begin to spread out detection is compromised.

The following optimal conditions for observing *P. l. lateralis* in the wheatbelt region may also be applied to other rock-wallaby populations in different geographical regions:

- Diurnal - within 15 - 25^{0}C with wind velocity below 5 km/h, no precipitation and within 1 - 2 hours prior to sunset;
- Nocturnal - within 10 - 30^{0}C with wind velocity below 5 km/h, no precipitation and within 1 - 2 hours after sunset.

Observing animals in resting states is possible throughout the day in the cooler months, but restricted to early mornings during the hotter periods.

7.3.1   An active management plan for the central wheatbelt populations

Stability can be achieved in rock-wallaby populations by controlling foxes and providing access to adequate food. However, action is needed to reverse over-grazing problems. The recommendations below apply to the Nangeen Hill population, where there is enough food available to support the population at carrying capacity, but the animals are too fearful of prowling foxes to access it. The fear factor needs to be suppressed by preventing foxes from entering the reserve. Two options are proposed:

- Fencing - exclusion of foxes/cats is absolute; and
- Baiting the surrounding farmland to create a buffer zone. Ongoing participation by land owners would be required, which may prove difficult to sustain and

administer, hence it may not be 100% effective and the fear factor may not be totally eliminated.

In addition, a revegetation (suitable grasses and browse species) for both degraded areas and those with low food resources should be implemented. These recommendations form part of a three-stage recovery program, with each stage requiring additional management steps. Elements of stage 1 have already been put in place at Nangeen Hill.

Stage 1

- Stabilise existing populations. This requires an intensive fox and cat-baiting program, and supplementary feeding when required;
- Full census of all existing wheatbelt populations. It is important to determine the population size, density, structure and condition of all remaining populations;
- Determine the genetic diversity of all populations. The significant decline of these populations may result in reduced genetic variability. This will have implications for management. New individuals will need to be introduced from other populations to increase genetic variability;
- Full census of translocated populations. If the genetic diversity of the wheatbelt rock-wallaby populations has significantly decreased due to recent declines and/or population recovery is slow, then there may be a need to translocate some individuals from recently translocated sites to increase the recovery rate. However, we would first need to determine if these translocated population numbers are sufficiently high to be used; and
- Implement a cat-baiting program. The presence of cats within the caves increases predation pressure on juvenile rock-wallabies, which in turn reduces the recruitment rate.

Stage 2

- Weed eradication - removal of weeds within and adjacent to the rock-wallaby refuge habitat, particularly the ice plant and cape weed at all sites;
- Habitat recovery - following weed eradication, re-seeding of native grasses should be undertaken and followed up with replanting important browse species that have not shown any recent regeneration;
- Population recovery (recruitment and translocations) - following habitat recovery, populations should be monitored for signs of recovery (i.e. recruitment

of sub-adults and newly-matured adults), and where needed, translocation of individuals from populations outside the wheatbelt or from recovered populations. In addition, sourcing new potential rock-wallaby sites within the wheatbelt for future translocations, reduce the risk of future declines and provide an opportunity to create greater genetic variability.

Stage 3

- Increase the foraging range of rock-wallabies – requires a strategy such as fencing, creation of a fox-baited buffer, and changing the vegetative structure to be more conducive to rock-wallaby foraging; and
- Establish genetically augmented populations comprised of individuals from all populations at other distant locations. Such "back-up" populations will be a vital insurance policy for rock-wallaby preservation in the event of a disaster.

It should be noted that a vigorous fox-baiting program is mandatory. Implementation of the management recommendations outlined above will ensure that this highly resilient rock-wallaby species continues to thrive in the wheatbelt, despite climatic changes in the region.

7.4   The relevance of behavioural ecology to conservation and management

Behavioural ecology is central to our understanding of the complex ecological processes within foraging patterns, wildlife-habitat relationships (habitat preference from an organism-centred perspective), predator-prey dynamics, and population dynamics (Sutherland, 1998; Caro, 2007). Although the above ecological processes are also important for conservation biology since they affect individual survival and population size (Sutherland, 1998; Berger-Tal et al., 2011), until more recently behavioural studies have rarely been included in conservation management. At first, combining behavioural ecology with conservation biology seemed awkward, since conservation biology is largely a theoretical and applied discipline aimed at preventing population extinction.   In contrast, behavioural ecology examines the ways in which behavioural and morphological traits contribute to the survival and reproduction of individual animals under different ecological conditions (Caro, 1998).There has been vigorous debate among behavioural scientists about the contribution of behavioural studies to conservation biology. Caro (2007) argued that although theoretical advances in our understanding of behaviour have made little practical contribution to

conservation over the past decade, descriptive behavioural studies (sophisticated natural history) have. The use of demographic models to assess the viability of populations is limited when there is insufficient data on the effects of environmental variables on demographic variance (Caro, 1998). Behavioural ecologists have an important role to play in conservation and management of animals, provided the information is accurately applied to the conservation framework.

At a time of significant development, Sutherland (1998) reviewed many areas of behavioural ecology relevant to modern conservation and active management practices. This included dispersal of fragmented populations, reducing predation, habitat requirements, trade-offs in habitat preferences, census techniques, small-population extinctions, mating systems, inbreeding depression, and the consequences of environmental change. Many of these were also investigated in this research, and examined in light of the recent decline in the central wheatbelt rock-wallaby populations.

The results of this research revealed a complex ecological relationship between rock-wallabies and exotic predators, the habitats they occupy, and the available food resources in close proximity to their rock refuge. When population densities are high, there is a risk of severe habitat degradation that can lead to a population crash due to a lack of food resources within the realised foraging range. It is important to distinguish between "realised niche" and "fundamental niche," since a researcher's perception of available food resources and/or cover may be very different from that of an animal's. For example, one would expect the open meadow areas in Nangeen Hill Reserve to have been a preferred foraging habitat (prior to weed invasion) for rock-wallabies, since these meadow areas were dominated by grasses, an important food resource for many rock-wallaby species (Dawson & Ellis, 1979; Horsup & Marsh, 1992; Tuft et al., 2011b). However, we now know that this habitat was not extensively used because of a heightened perception of predatory fear which changed the rock-wallabies' foraging behaviour. This phenomenon could only have emerged from a detailed behavioural ecological study.

Delaying the involvement of behavioural biologists in conservation and management programs has the potential to cause avoidable setbacks, waste precious funds and threaten animal species (Blumstein & Fernandez-Juricic, 2004). Behavioural ecologists have developed a new framework for integrating animal behaviour and conservation biology (Berger et al., 2011). It's called "conservation behaviour" and investigates how

proximate and ultimate aspects of animals' behaviour can help to prevent a loss of biodiversity (Buchholz, 2007).

In Australia there has been a recent upsurge in behavioural ecological research, yet it is rarely incorporated into conservation and management plans. As behavioural ecology is aimed at understanding behavioural evolution in relation to ecological conditions (Davies et al., 2012), the ways in which a species is affected by external environmental factors must surely be crucial to its conservation and management. In behavioural ecology, the ways in which individuals, populations or species adapt to their environment is assessed. A widely distributed species will have populations in different climatic and/or landscape conditions, each resulting in a different set of selective forces and associated behavioural adaptations. Where a population is in a highly variable environment and the researcher ignores that variability, the management regimes developed will be flawed if any one of the environmental conditions changes over time. By focusing on a number of environmental variables, including climate, predation fear, conspecific fear, and structural habitat, this study provides unique insights into how rock-wallabies adjust their behaviour to these variables, and provides an understanding of the effects on environmental variables on foraging patterns, spatial distribution and population dynamics in an ecologically altered landscape. A general hypothesis have been generated from this research:

- Fear of exotic predators will have significant impacts on the foraging patterns of our marsupial populations, particularly in ecologically altered ecosystems (habitat loss and weed invasion), and with increasing changes in our climatic conditions (increasing drought years).

Although this study was not primarily designed to resolve conservation and management problems, its findings have been used in the design of an active management plan for the central wheatbelt rock-wallaby populations. The complex relationships between animals and their resources, the availability of different vegetation patches, and animal population demographics, create significant problems for the management of any species. Future research on all animal groups is necessary to understand the relationships between elements of habitat and landscape, and between behaviour and population dynamics within the habitat. Understanding how animals perceive their environment and how they adjust to its changes are paramount to their future management and survival.

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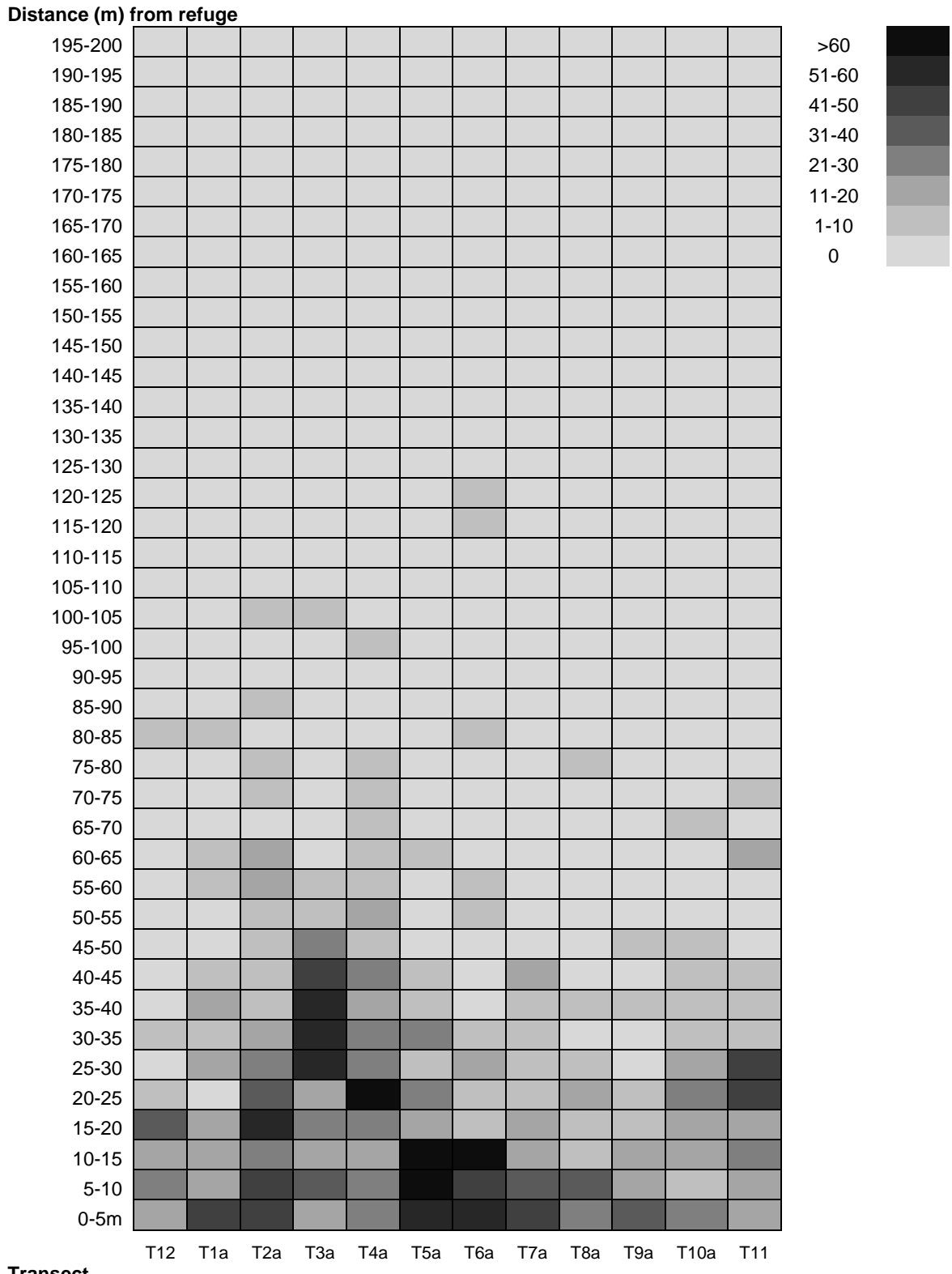
Appendix
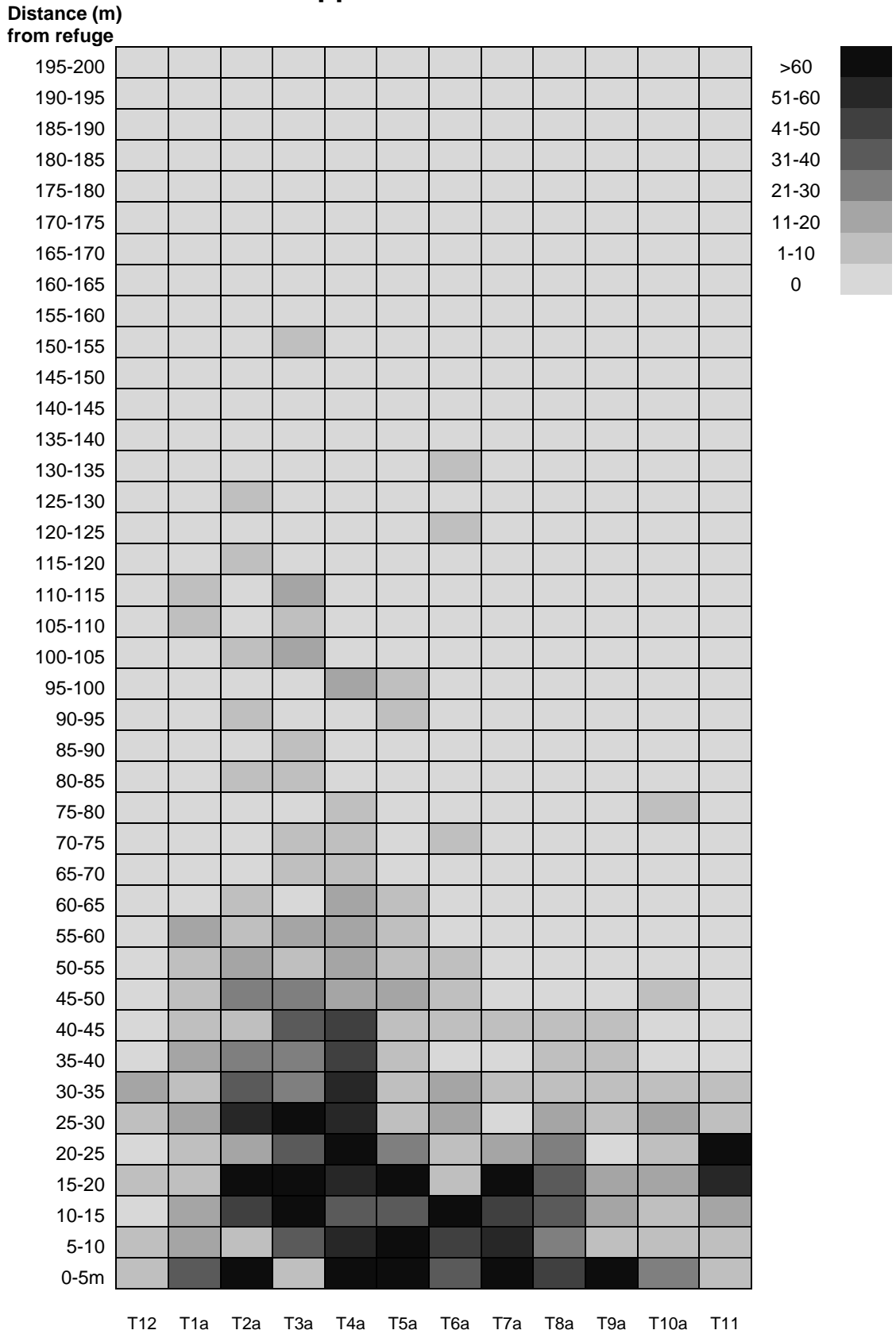
Appendix 1 Period 1 - the mean scat density spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
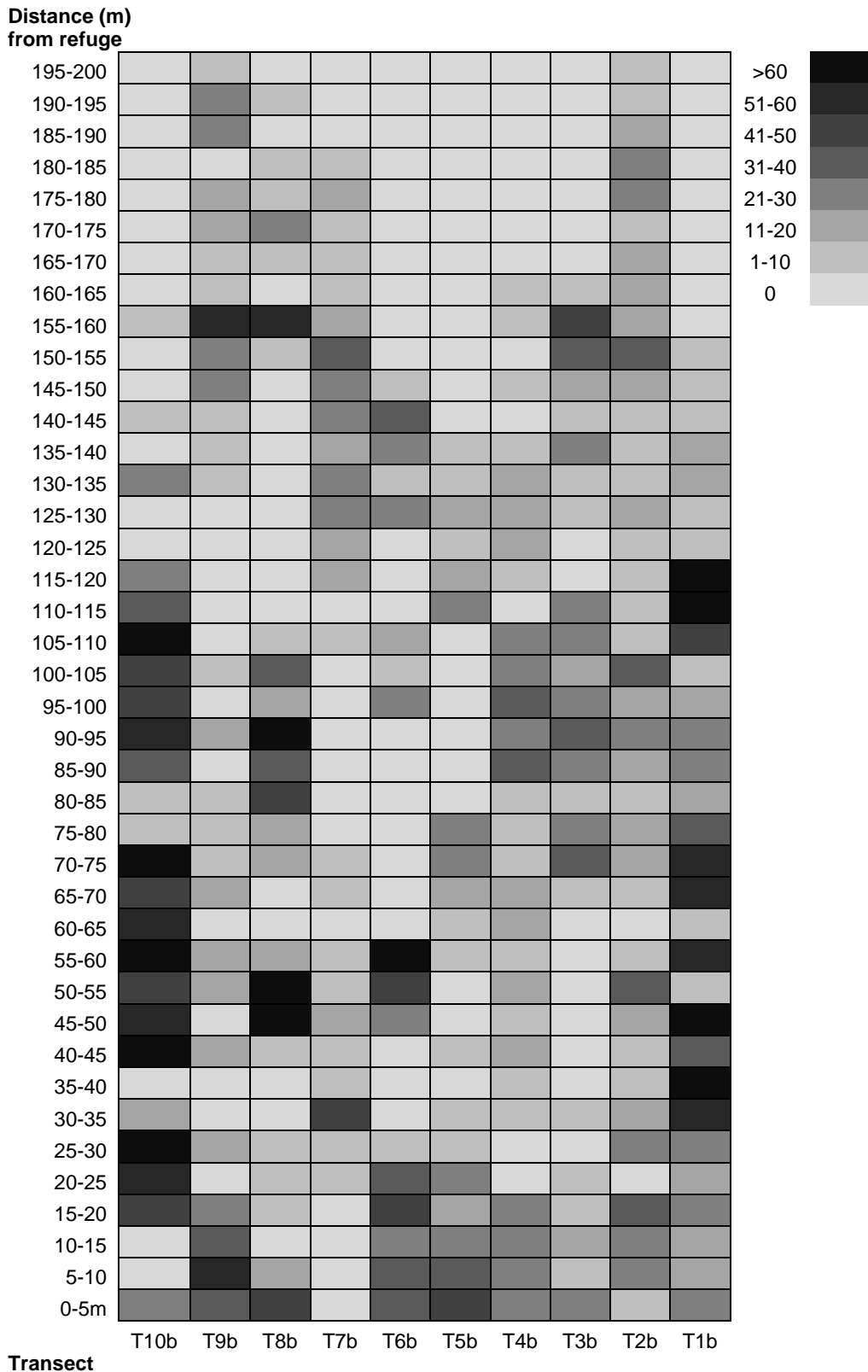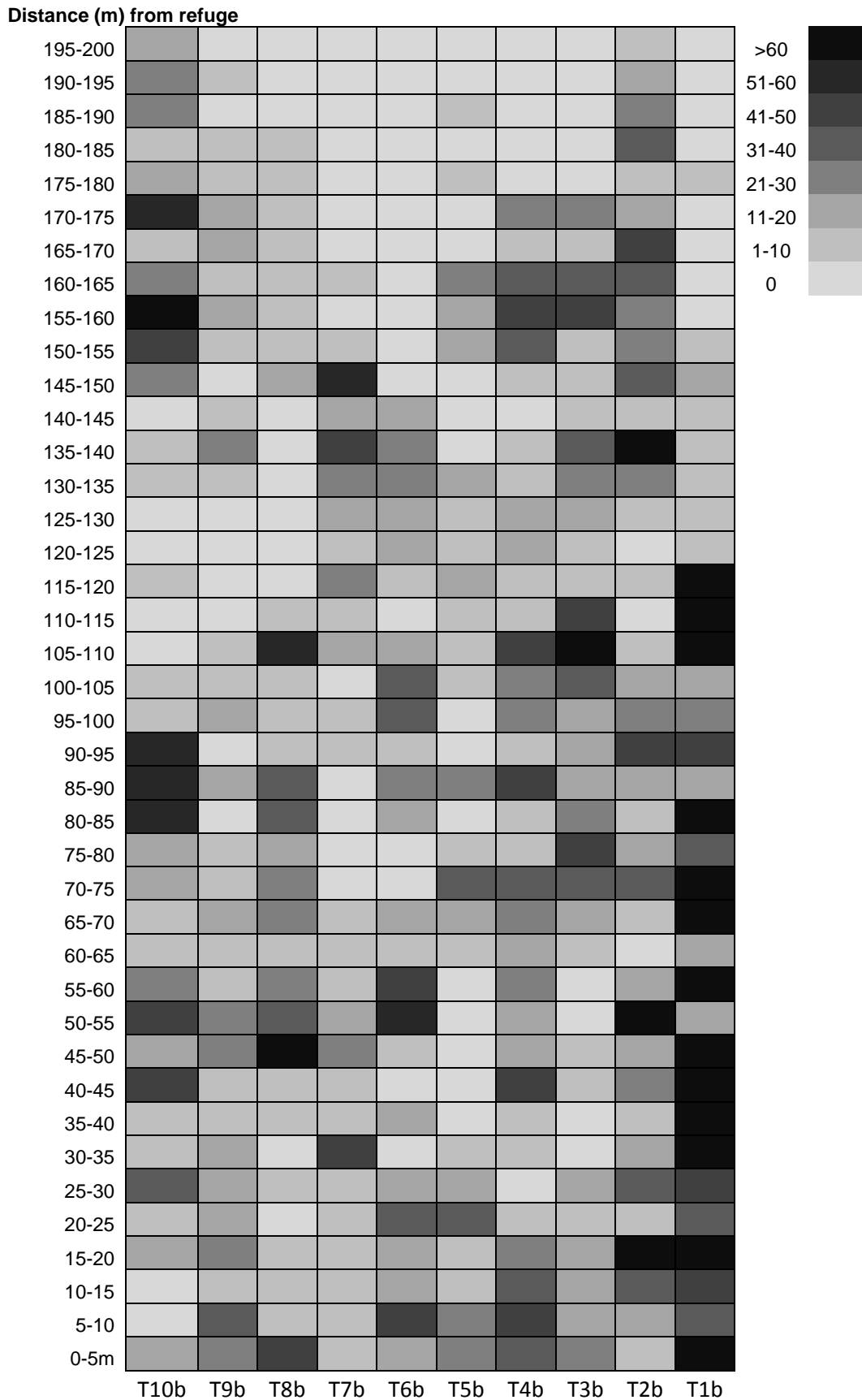
Appendix2 Period 1the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).
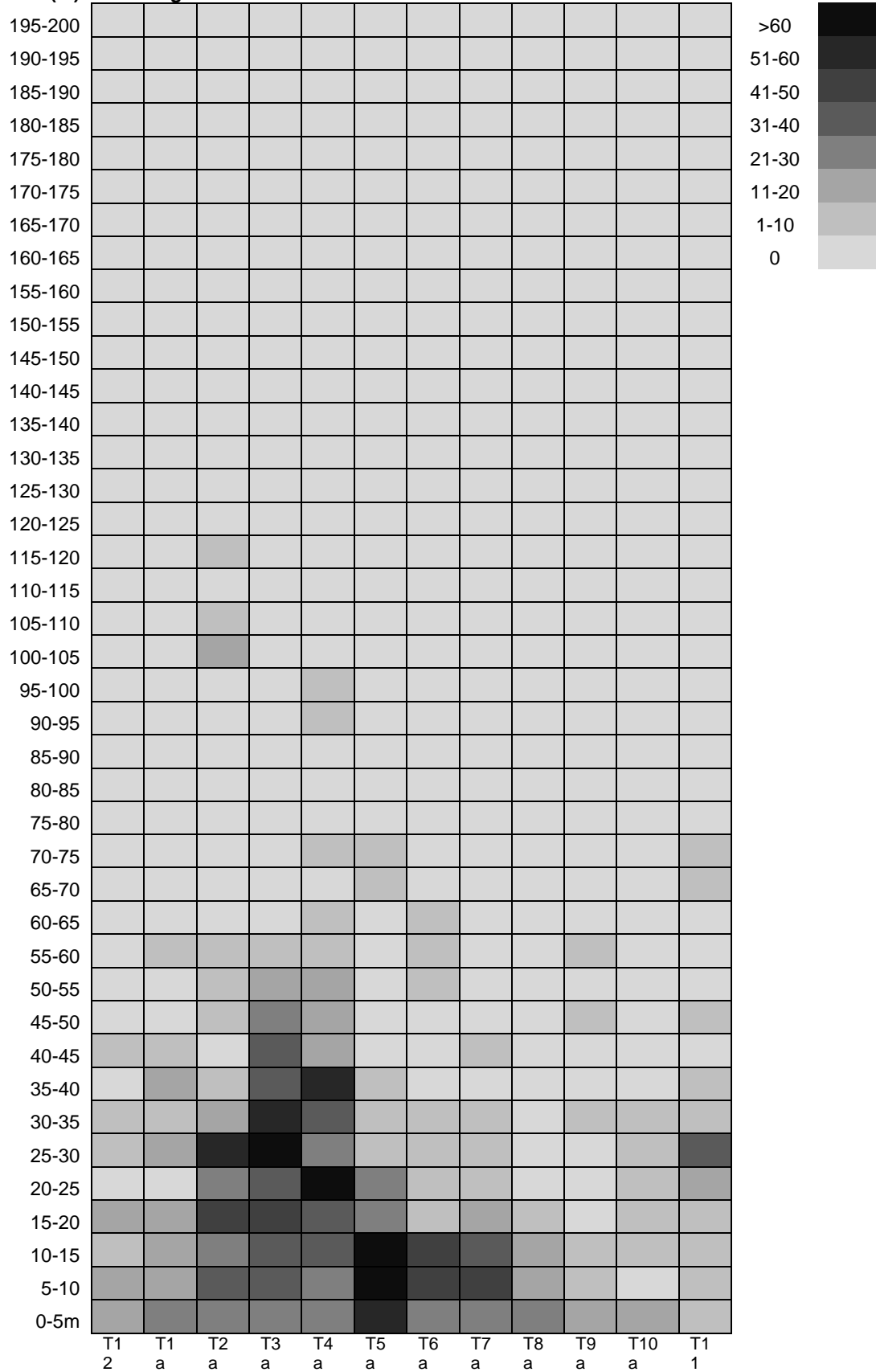
Distance (m) from refuge

Transect

Appendix 3 Period 2 the mean scat density spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
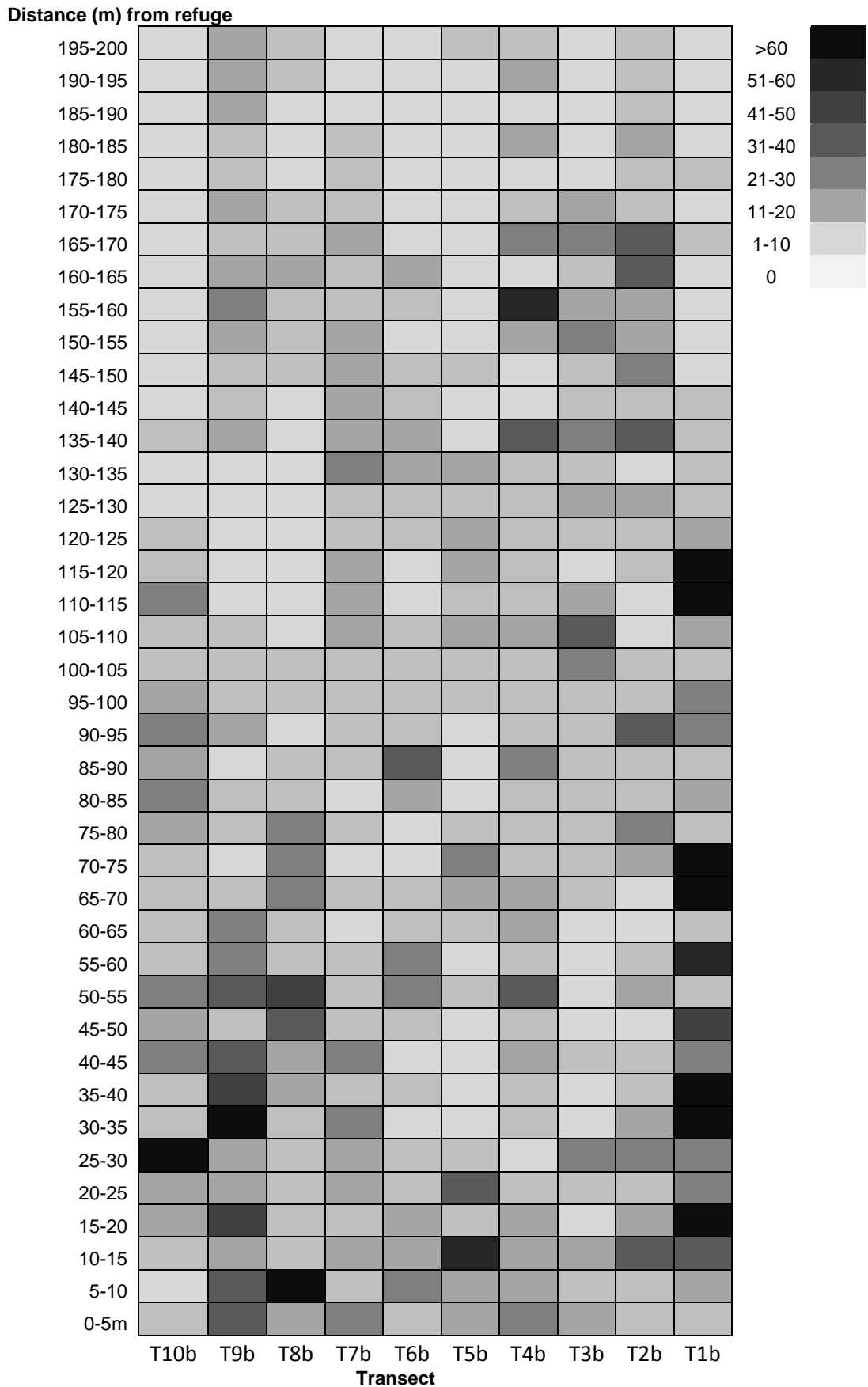
Distance (m) from refuge

Transect

Appendix 4 period 2 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).
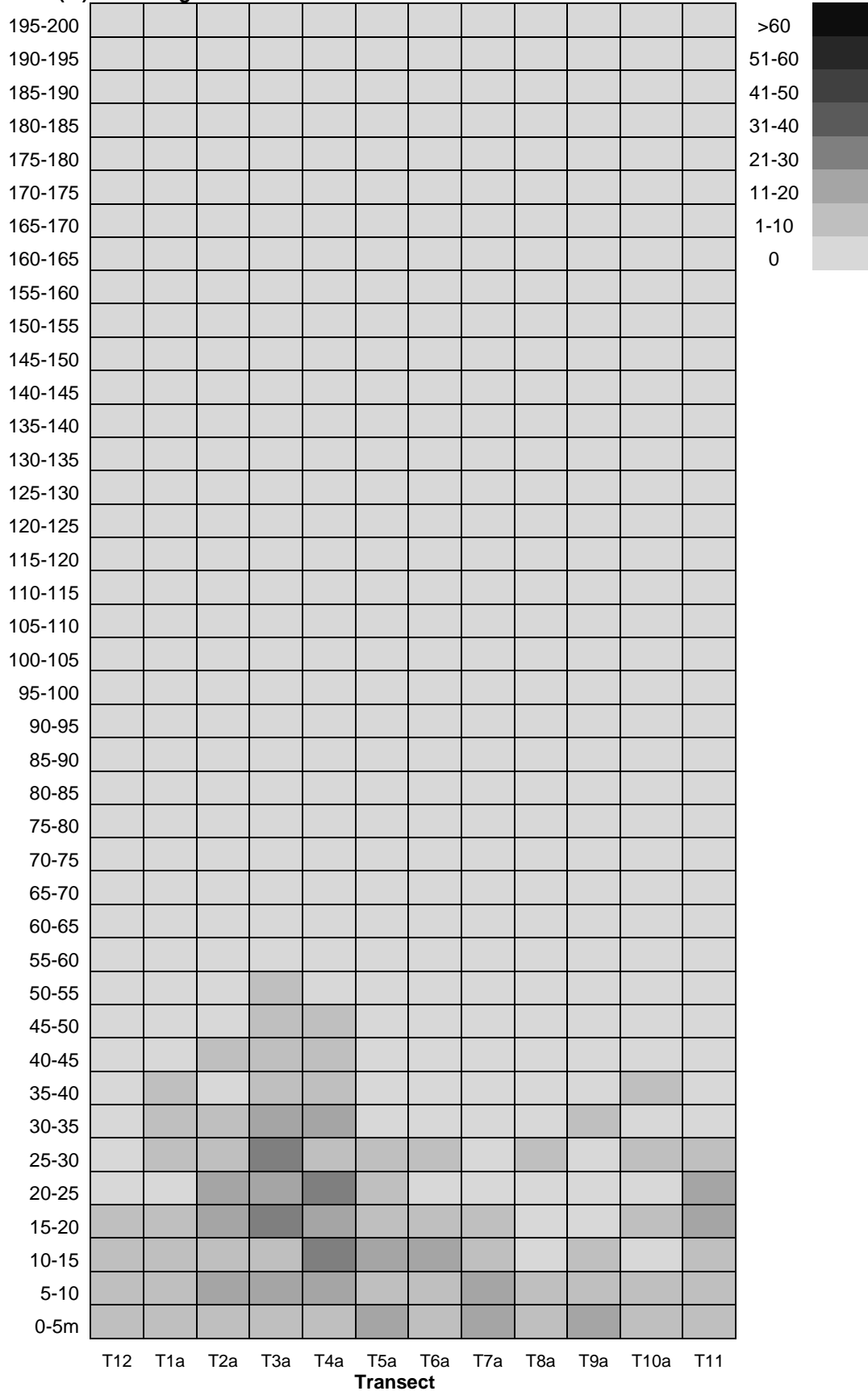
Distance (m) from refuge

Distance (m) from refuge	Legend
195-200	>60
190-195	51-60
185-190	41-50
180-185	31-40
175-180	21-30
170-175	11-20
165-170	1-10
160-165	0
155-160	
150-155	
145-150	
140-145	
135-140	
130-135	
125-130	
120-125	
115-120	
110-115	
105-110	
100-105	
95-100	
90-95	
85-90	
80-85	
75-80	
70-75	
65-70	
60-65	
55-60	
50-55	
45-50	
40-45	
35-40	
30-35	
25-30	
20-25	
15-20	
10-15	
5-10	
0-5m	

Transect: T12, T1a, T2a, T3a, T4a, T5a, T6a, T7a, T8a, T9a, T10a, T11

Transect

Appendix 5 Period 3 the mean scat density spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
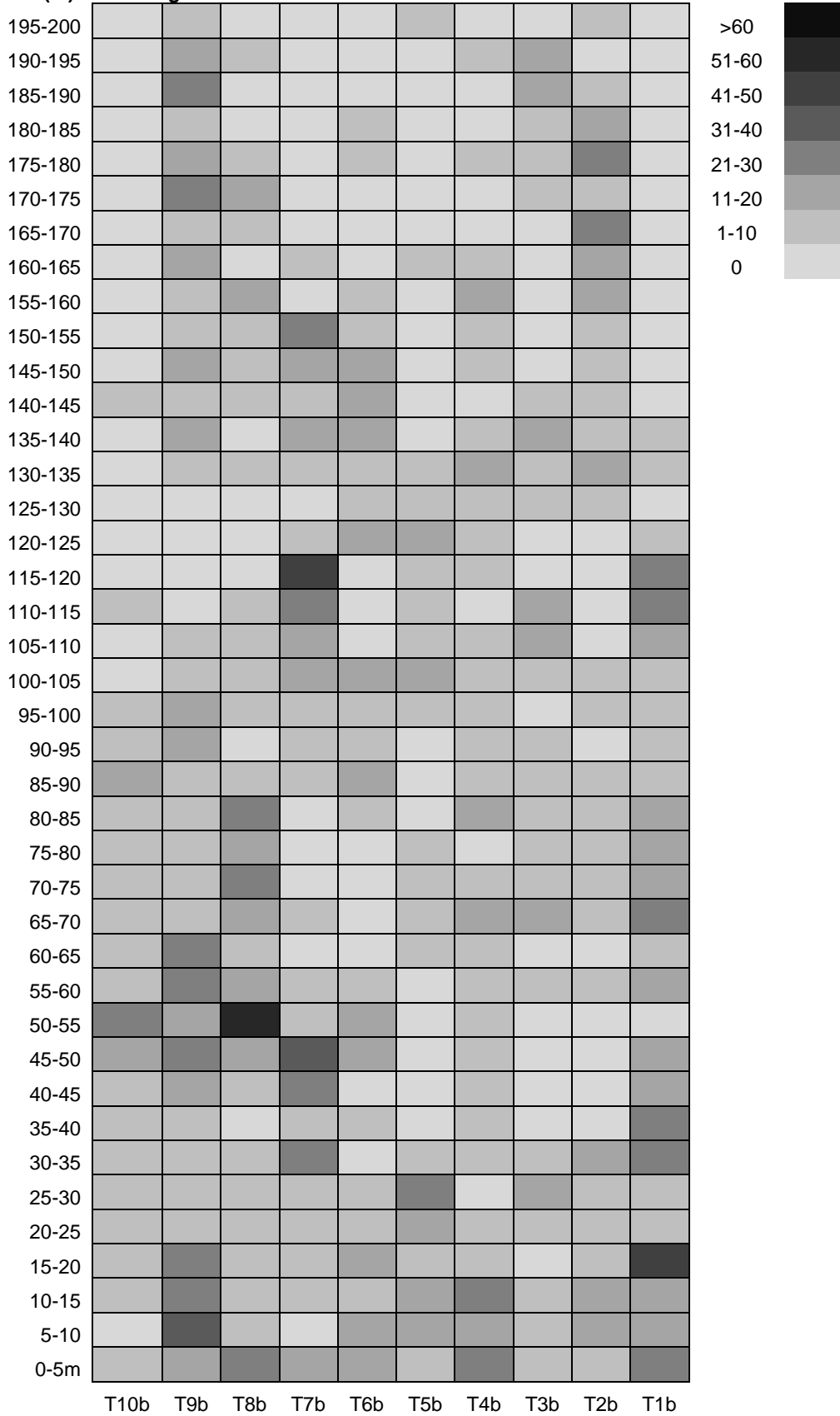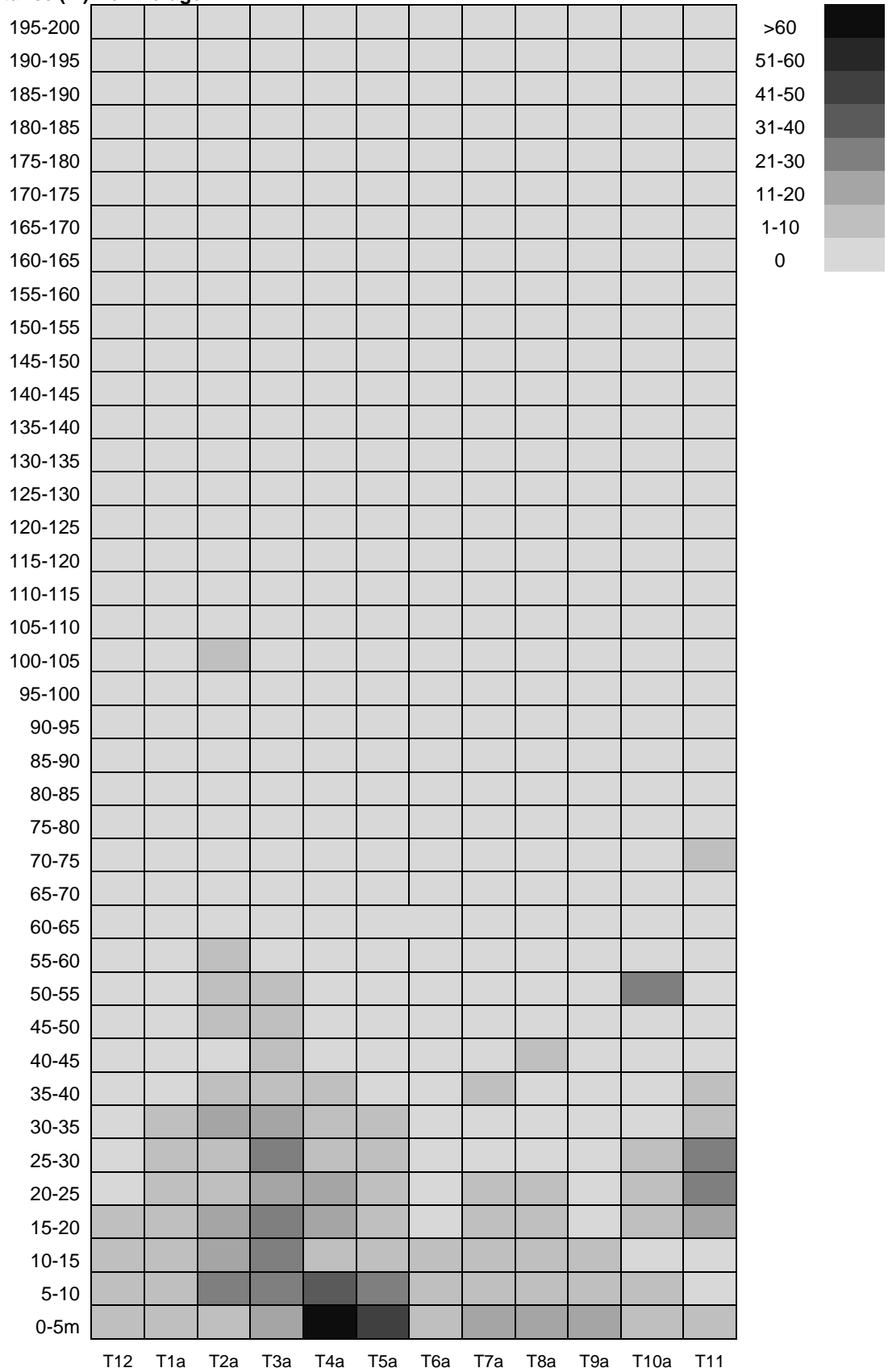
217

Appendix 6 Period 3 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).

Appendix 7 Period 4 the mean scat spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).

Distance (m) from refuge

Transect

Appendix 8 Period 4 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).
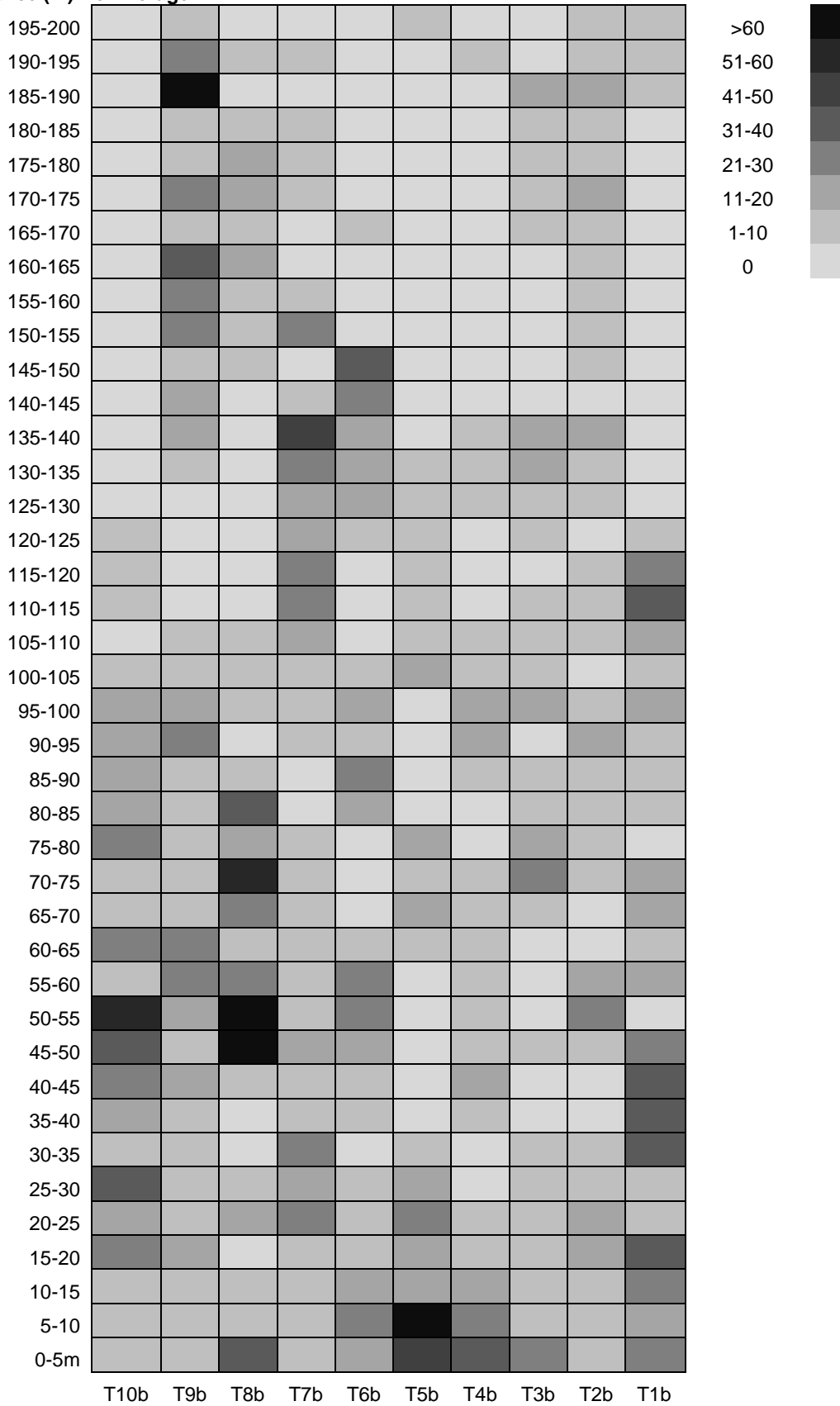
Distance (m) from refuge

Appendix 9 Period 5 the mean scat spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
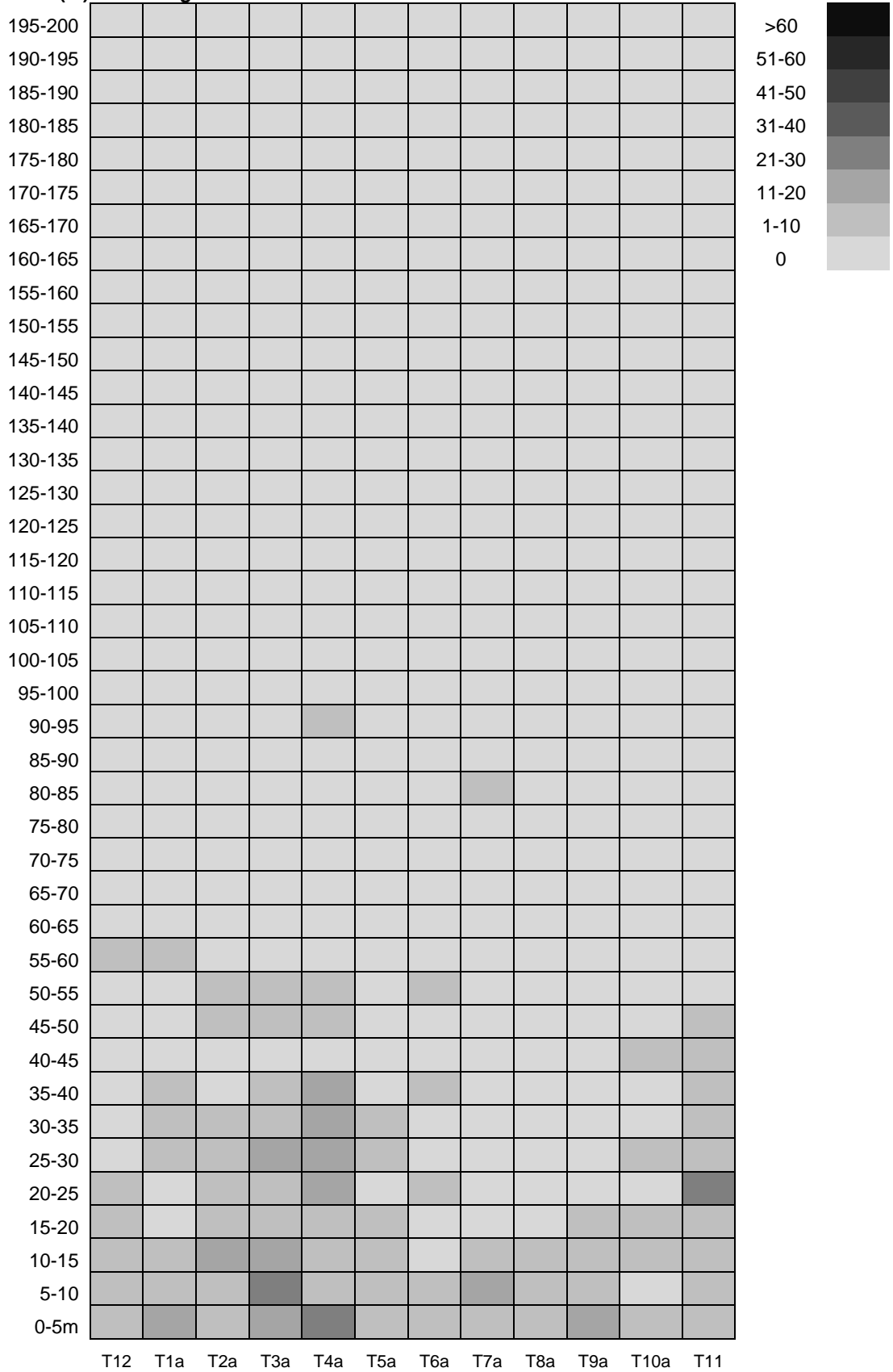
Distance (m) from refuge

Transect

Appendix 10 Period 5 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).
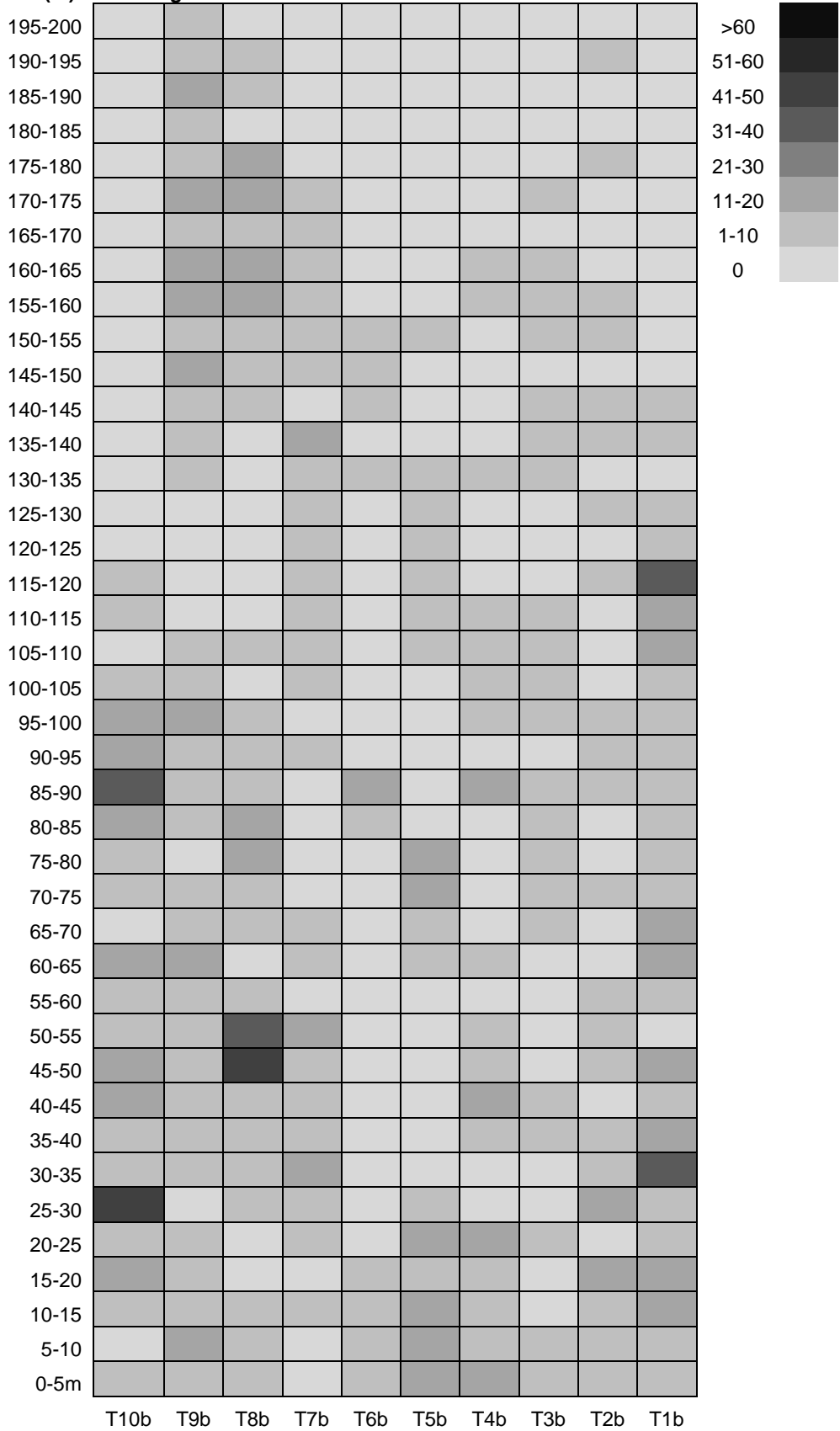
Distance (m) from refuge

Transect

Appendix 11 Period 6 the mean scat spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).

Distance (m) from refuge

Appendix 12 Period 6 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).

Appendix 13 Period 7 the mean scat spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
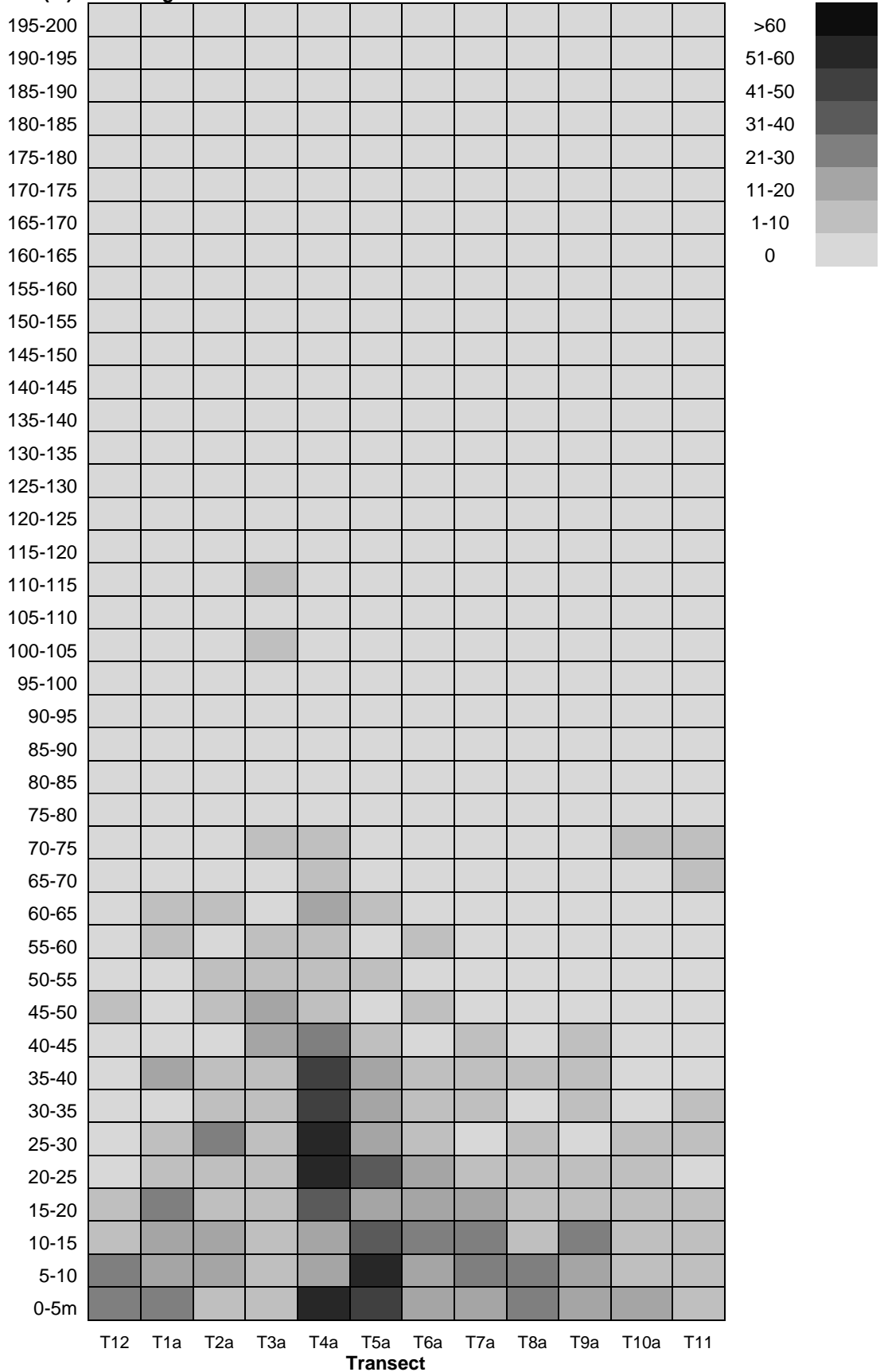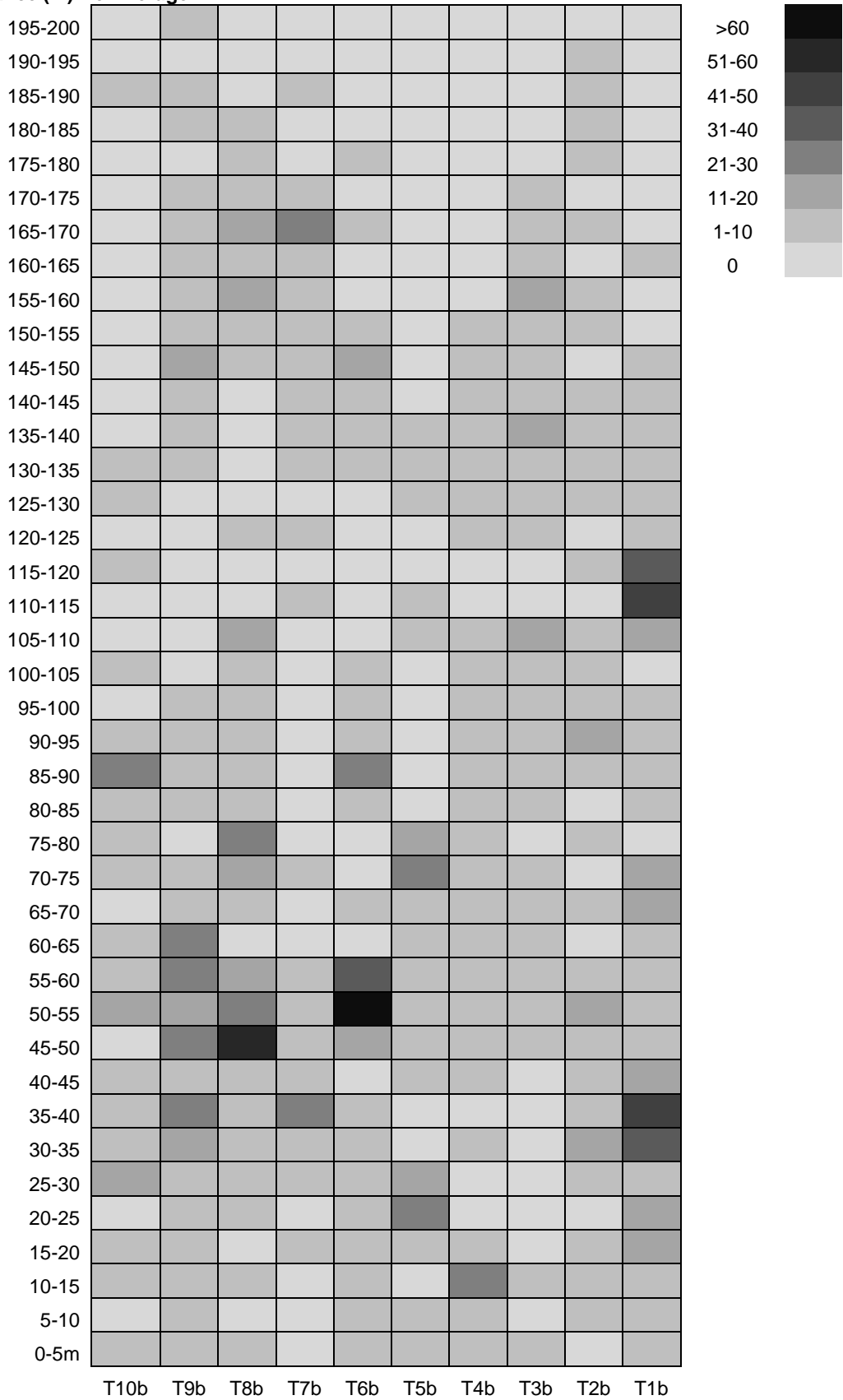
Distance (m) from refuge

	>60
	51-60
	41-50
	31-40
	21-30
	11-20
	1-10
	0

Transect

Appendix 14 Period 7 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).

Distance (m) from refuge

195-200													>60	
190-195													51-60	
185-190													41-50	
180-185													31-40	
175-180													21-30	
170-175													11-20	
165-170													1-10	
160-165													0	

Transect: T12, T1a, T2a, T3a, T4a, T5a, T6a, T7a, T8a, T9a, T10a, T11

Appendix 15 Period 8 the mean scat spatial distribution for transects running out from the bottom of the diurnal rock refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1a-10a and 11-12).
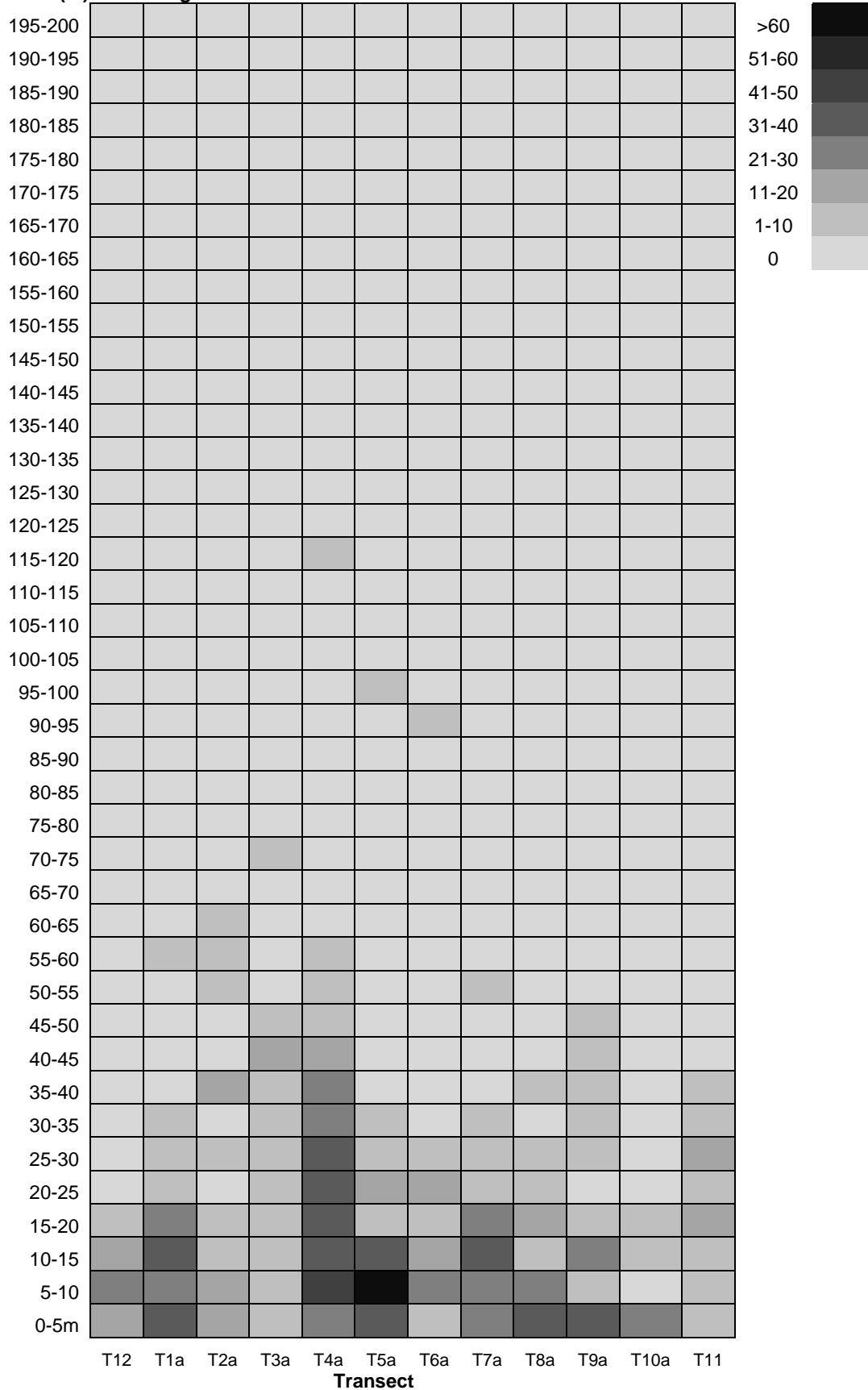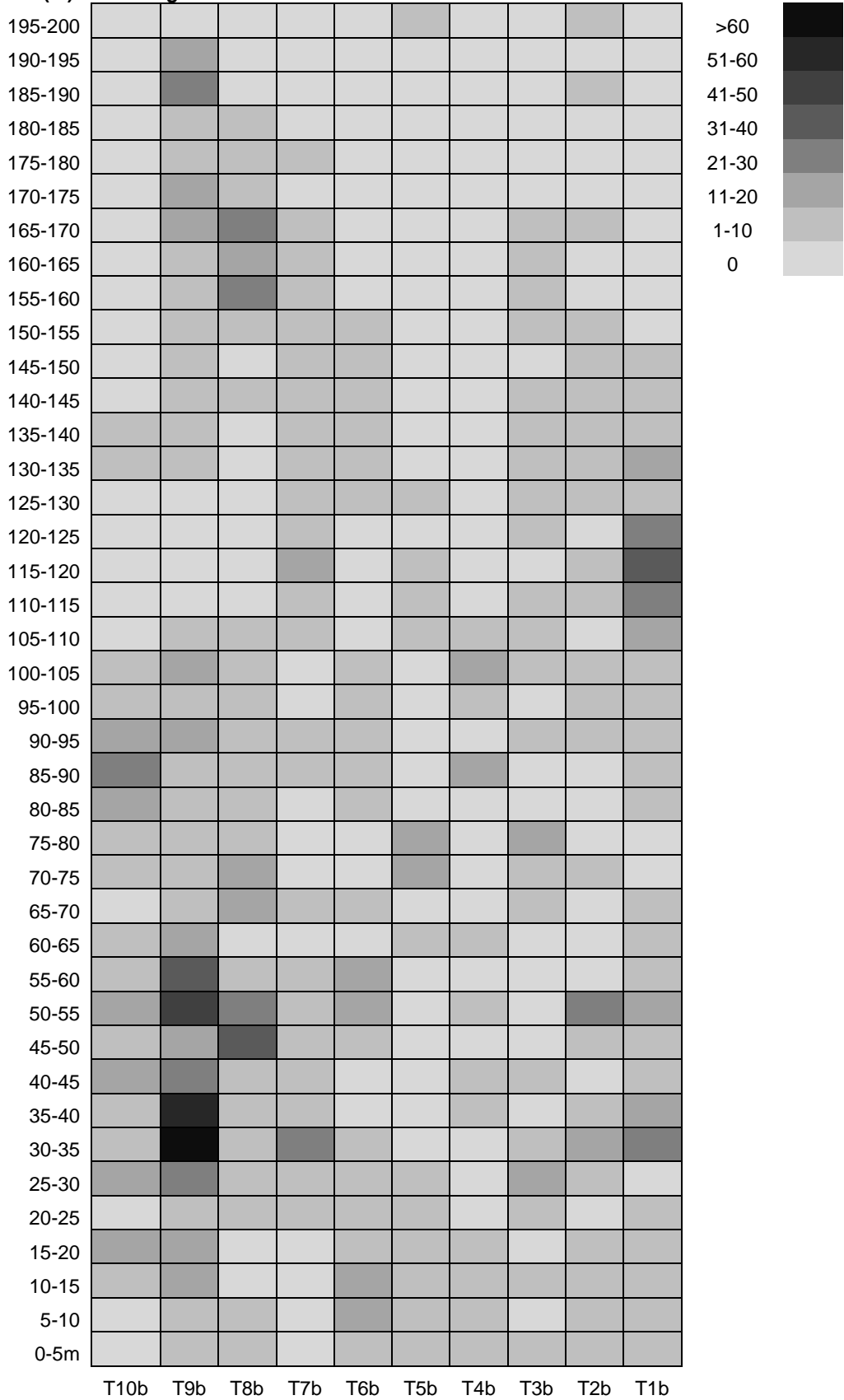
Distance (m) from refuge

Appendix 16 Period 8 the mean scat densityspatial distribution for transects running out the top of the refuge area of the rocky outcrop of Nangeen Hill *P. l. lateralis* population (Transects 1b-10b).