Establishment, behaviour and ecology of the SA mainland tammar wallaby (*Macropus eugenii eugenii*) following an experimental reintroduction.

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Abstract

The South Australian mainland tammar wallaby (*Macropus eugenii eugenii*) was presumed extinct in the wild from the early 1930's, until a feral population was re-discovered in New Zealand. Eighty-five animals were returned to Australia as part of a repatriation program into their former range. The establishment phase after a reintroduction is a critical time as animals may fail to survive if they cannot find resources and avoid predators in an unfamiliar habitat. To maximise reintroduction and establishment success, reintroductions need to be planned with a good understanding of the animals' ecology and anti-predator strategies. To improve this understanding requires experimental reintroductions and detailed monitoring. This thesis investigates the experimental reintroduction of 46 wallabies into Innes National Park in South Australia and examines the influence of release group familiarity on establishment. Part of this was an investigation of home range, habitat requirements and social behaviours during establishment and seasonally post-establishment. The thesis includes three data chapters which focus on (1) home range and core area, home range stability and degree of overlap with conspecifics; (2) habitat selection at the landscape scale and for day and night use within home range; and (3) factors influencing fine scale habitat use and social grouping behaviours in light of predation risk. In this study, the animals' perceived risk of predation is assumed to be reflected by surrogate measures of risk, such as distance to cover, likelihood of using cover, group size, and distance to nearest neighbour.

Release group familiarity was established by housing animals together in captivity for at least one month prior to release ("familiar" groups), whereas "unfamiliar" release groups comprised animals housed separately but released together. After each reintroduction the first month was considered to be a time of "establishment" in the environment. During the establishment month, home ranges were not randomly located within the landscape, as indicated by the biased occupancy of particular habitat types. Habitat types selected at the landscape scale were similar for familiar and unfamiliar release groups. However, animals released in unfamiliar groups showed a stronger preference for denser high cover habitat during their nocturnal activities within their home range. As tammars use cover to conceal themselves from predators, this result suggests that animals released in unfamiliar groups were more cautious than those released in familiar groups. Indeed at the fine scale, it was also found that animals released in unfamiliar groups were more likely to be found in high cover habitat, and forage closer to cover at night than did those released in pre-established familiar

groups. Using habitat with more caution and capitalising on communal vigilance in an unfamiliar habitat may ultimately improve the likelihood of survivorship and overall reintroduction success.

Comparing habitat decisions and social behaviours during the establishment period to similar times of year post-establishment suggested that animals' naivety about their new environment influenced some decisions they made. While habitat selection at the landscape scale was similar during establishment and at an equivalent time of year post establishment, analyses showed that they preferred to use melaleuca (a high cover habitat) during their nocturnal activities during establishment much more strongly than they did once they had established. Home range and core areas were also significantly smaller during the establishment month than at an equivalent time of year post establishment. This result supports the idea that animals will restrict their movements when they are unfamiliar with the habitat and predation risks. It also suggests that some habitat choices improved once they were familiar with their new environment and presumably predation risks. Their habitat choices reflected better anti-predator behaviour than those made during the establishment period: they were more likely to use high cover habitat, they remained significantly closer to cover while foraging, and group sizes were larger than during establishment.

Seasonal habitat selection at the landscape and home range scales suggested that the five habitat types within the study area provided different fundamental resources for the animals, as they were preferred at different times of year. Some differences in habitat selection were observed between the sexes, and the females were more selective in their diurnal and nocturnal activities. These differences most likely reflected, in part, differences in predator avoidance and reproductive strategies of the sexes, where females' preference at the landscape scale shifted towards high cover habitat during spring, the time of year when pouch young vacate the pouch and start to become independent. While no such selection at the landscape scale was observed for the males, it was also observed that within their daily activities both sexes were more likely to be found in high cover habitat during spring than any other time of the year, perhaps suggesting that as males were following the females. Overall, females generally selected *Eucalyptus diversifolia*, *Acacia anceps* and grassland at the landscape scale, and used *E.diversifolia* for refuge during the day and the other two habitats for foraging at night, whereas males generally preferred *Melaleuca halmaturorum* instead of *E.diversifolia* for diurnal refuge. *Eucalyptus rugosa* was mostly avoided by both sexes.

From month to month, both sexes expanded rather than shifted their home ranges to incorporate new areas, and these new areas were explored with conspecifics (when the amount of new area increased the amount of sharing also increased), highlighting their reliance on communal vigilance when in unfamiliar habitat. More new areas were incorporated into home ranges from July to December than from January to May. Time since release was not influential, which also supported the conclusion that perhaps home ranges moved to follow resources or overlap conspecifics more. Indeed, in one circumstance when neighbouring animals had died, a male wallaby was observed to move four kilometres through unfamiliar habitat and completely shift his home range in search of other residence.

Compositional analysis of habitat use versus availability indicated that monthly home ranges were selectively positioned in the landscape and were always larger than 4ha. Males' home ranges were larger than females', and males shared more of their home ranges than females did, supporting the usual sex bias observed for polygamous species. Core areas were proportional to the size of the home range, with similar sizes held by males and females and throughout the year. Core size was not influenced by the degree of overlap with conspecifics, with similar amount of core area shared by both sexes year round. The time of year influenced home range size, the smallest were held in winter when food resources were likely to be most abundant, but also when inclement weather was likely to restrict movements, as the animals' ability to detect predators may be hindered due to wet and windy conditions. Living with conspecifics is known to assist predator detection by group vigilance. Indeed, this study found the amount of home range overlap and the time two individuals spend together was positively correlated, and the size of home ranges decreased when more of it was shared with conspecifics, which suggested that sharing of home range was important. The degree which home ranges were shared was observed to be a fairly stable requirement for both sexes and did not change with season or time since release.

Despite previous isolation from predators, the wallabies displayed anti-predator behaviours which incorporated interrelated benefits obtained from group vigilance and using protective cover. Additionally, these behaviours were adjusted according to their familiarity with the habitat. Post-establishment, animals were observed to go further from cover when they were a greater distance from their nearest neighbour but surrounded by larger numbers of conspecifics. Whereas during the establishment period, animals ventured further from cover when they were closer to a nearest neighbour, but group size was not influential. It is known that larger groups of animals have more false alarms to predators, and false alarms result in the animals' wasting energy in fleeing. If false alarms are more prevalent while occupying unfamiliar habitat with unfamiliar risks, then relying on large numbers of conspecifics while establishing may have been more of a liability than a benefit during the establishment period. However, some anti-predator strategies were commonly used, regardless of familiarity with their habitat. During the establishment month and post-establishment, animals were always more likely to be found in high cover habitat when they were further from their nearest neighbour, or were surrounded by fewer conspecifics. Some strategies and habitat decisions may have reflected differences in reproductive needs. While females, with and without pouch young did not differ in how far they would forage from protective cover, females with pouch young remained closer to their nearest neighbour than those without. This finding perhaps reflected the importance of relying on communal vigilance when their flight time from a predator may be hindered due to increased weight and bulk of a pouch young. These findings supported the theory that group vigilance anti-predator strategies are somewhat innate in the tammars, as having previously been completely isolated from predators their responses could have been lost, and once released there was no opportunity to socially learn the appropriate responses off an established population.

Some habitat and social grouping behaviours were occasionally unexpected but may have been balanced out by other behaviours. This study observed that animals foraged further into the open during winter than at any other time of year, which contradicts findings by other authors where tammars foraged further into the open when the weather was fine. However, I also found that animals remained closer to their nearest neighbour during autumn and winter than at any other time of year. Perhaps foraging further into the open in inclement weather is actually safer if it provides a greater chance to detect and react to an approaching predator. For example, a fox approaching from the scrub edge would not give the wallaby enough time to respond. An additional benefit of foraging further away from cover in larger group sizes, is that animals can flee in different directions confusing the fox, as it would have to make a quick decision and chose one animal to pursue. Animals were furthest from their nearest neighbours in spring which was also somewhat surprising as this is when pouch young vacate the pouch and it was observed that females with pouch young remain closer to their nearest neighbour suggesting they gain some anti-predator benefit from doing so. However, during spring the animals were also more likely to be found in high cover habitat than at any other time of year, so this may have somewhat balanced out the need for a close neighbour.

Overall, this study confirmed that tammars retain anti-predator behaviours despite previous isolation from predators. However, their habitat and social decisions improved with time since release. In this experimental study, animals released in groups with unfamiliar conspecifics appeared to be at an advantage as they displayed habitat use and social groupings which suggested they were using their new habitat with more caution. Therefore, this study recommends releasing groups of unfamiliar conspecifics. Releasing animals at different times of year also had an influence on how they used their habitat. Animals released in spring displayed behaviours suggesting that they were more cautious in avoiding predators: they were more likely to be found in cover, foraged closer to cover, and were in larger group sizes than those animals released in winter. Therefore, it is recommended that animals are released at a time of year where conditions are fine and resources are abundant. Releasing females with pouch young did not appear to hinder the animals after their release (compared to females without pouch young) and could be recommended as young permanently evacuating the pouch in the wild are at a greater advantage than juveniles released from captivity. Results from this experimental study were used to assist ongoing management decisions and were imperative in the planning of subsequent reintroduction events for this species, and can be applied more generally to other species with similar anti-predator strategies.

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Names of my volunteers, and the number of days each of them worked. (DEH) = Department for Environment and Heritage employee, (GreenCorp) = Green Corps trainee, (CVA) = Conservation Volunteers Australia volunteer. * = volunteered on more than one field trip.

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1 Chapter 1: Overall introduction: reintroduction biology

1.1 History of extinctions

The extinction of animals is not a new phenomenon. Fifty thousand years ago, continents were populated with more than 150 genera of megafauna (animals larger than 44kg). However, by ten thousand years ago at least 97 of these genera were extinct (Barnosky *et al.* 2004; Koch and Barnosky 2006). Extinctions began in the places first reached by colonizing humans, followed by remote islands apparently not colonized until recent centuries (Burney and Flannery 2005). This trend sparked the hypothesis of a strong human influence on animal extinctions. Human influences such as “blitzkrieg” (rapid overkill), “sitzkrieg” (fire, habitat fragmentation and the introduction of exotic species and diseases), and the introduction of predators were considered primarily responsible (Barnosky *et al.* 2004). However, while humans may have been considered the primary influence and precipitated these late Pleistocene extinctions (especially in Australia, North America and South America), late Pleistocene climatic change is considered instrumental in controlling the timing, geographic details and perhaps magnitude of the extinctions (Barnosky *et al.* 2004). This was especially the case in Eurasia and Africa where, for example, it is unlikely that species such as horses in Alaska and mammoths and giant Irish deer in central Eurasia would have survived beyond the late Pleistocene climatic change regardless of the presence of humans (Barnosky *et al.* 2004). Climate change is known to affect animals by triggering vegetation changes (Barnosky *et al.* 2004; Koch and Barnosky 2006) which essentially affect the habitat resources necessary for their survival. Records reveal that climatic change has contributed to extinctions by driving range adjustments in large mammals (Barnosky *et al.* 2004).

Debate as to the cause of the worldwide Pleistocene megafauna collapse, whether it resulted from climate change or human colonisation, has given way to the idea of interaction of the two, whereby the influence of human impacts on fauna extinction may have been exacerbated by climate change (Barnosky *et al.* 2004; Burney and Flannery 2005; Koch and Barnosky 2006). Furthermore, the less direct forms of human influence (such as disease, habitat transformation, and biological invasions) are now considered in theoretical models (Burney and Flannery 2005), as there is growing evidence that many threats can act synergistically, where each ecological response reinforces the other driving ecosystem change (Brook *et al.* 2008; Myers 1993; Stork 2010). Johnson (2002) suggested that the disappearance of so many and varied mammal groups from such a range of environmental situations indicate that different combinations of factors may have applied in each case, and generalising a cause of extinction across all cases is unrealistic.

Climatic change and direct human impacts on fauna are occurring today at unprecedented rates (Barnosky *et al.* 2004), and there is a widespread belief that we are currently experiencing a mass extinction event, referred to as the ‘sixth mass extinction event’ (Myers 1993; Stork 2010). This is thought to be as extensive and rapid as the five previous mass extinction events in the last 600 million years, where 65-95% of the marine animals (known from the fossil record) disappeared (Stork 2010). Extinction of animals such as herbivores, carnivores and scavengers, is of significant importance as it implicates the stability of global ecosystems (Barnosky *et al.* 2004). The International Union for Conservation of Nature (IUCN) has listed 766 fauna species as ‘extinct’ (where no living individual has been seen for 50 years) since the 1600’s (IUCN 2010). This number may very well be a vast underestimate for a number of reasons: there is potentially a 50 year time lag on animals going extinct and being listed as extinct, especially if within this time many changes have occurred in the global environment causing sudden extinctions; it is hard to determine when the last animal has been sighted, especially those that are cryptic and hard to monitor; and many species may have become extinct before they were even discovered and described (Stork 2010).

1.1.1 Decline of Australian native mammals

Currently, about one-quarter of all mammals worldwide are in danger of extinction, and more than half of all mammals populations are in decline (Davidson *et al.* 2009). Exacerbating the risk of extinction are certain ecological traits such as small geographic range, low population density, slow life history, and large body size, all known to correlate strongly with extinction risk in mammals (Davidson *et al.* 2009).

The Australian terrestrial mammal fauna has proved to be particularly susceptible to extinctions and declines in abundance and range (Burbidge and Manly 2002). Indeed worldwide, fifty percent of all the mammal species that have become extinct in the last two hundred years have been from Australia. This is the worst record for mammal conservation for any country or continent (Short and Smith 1994). Seventeen of the known mammal extinctions in Australia have occurred since European settlement, and the area occupied by another 27 species has been reduced to less than 10% of their former range (Short and Smith

1994) (Short 1999 cited in Short and Turner 2000). Of those, most have been medium-sized terrestrial species in the “critical weight range” of 0.35-5.5kg (Short and Smith 1994). These declines are most likely a result of human activities since European settlement: hunting, habitat clearing, grazing by feral and domestic stock, altered fire regimes and predation by foxes and cats (Short and Smith 1994). The cat (*Felis catus*) was thought to have been introduced to Australia 210 years ago, and the red fox (*Vulpes vulpes*) has been present for 140 years (Short *et al.* 2002). Colonisation by foxes and cats has been particularly detrimental to the survival of our non-flying mammals (Burbidge and Manly 2002; Burbidge and McKenzie 1989; Hobbs and Mooney 1998). In particular, animals in the body weight range of 35-5500g were heavily preyed upon after the introduction of the fox, while smaller species likely succumbed to the introduction of the cats before the foxes were introduced (Johnson *et al.* 1989). The susceptibility of Australian native mammals to predation reflects their ineffective anti-predator defences when they encountered a novel predator, to which they had no evolutionary exposure (Short *et al.* 2002). Their susceptibility to predation by introduced predators was a function of their stage of life, morphology, and the availability of refuge habitat (Short *et al.* 2002). In light of the correlation between the presence of foxes and cats and native mammal extinctions (Burbidge and Manly 2002), controlling fox numbers may allow remnant populations of animals in the critical weight range to recover, while also facilitating successful reintroductions for conservation (Short *et al.* 2002; Short and Turner 2000).

1.2 Reintroductions

The management of threatened or endangered species by translocating animals to re-establish populations is now considered an important strategy for conservation (Griffith *et al.* 1989; Moro 2003), and is becoming increasingly common (Seddon 1999a). Scientists may also reintroduce animals into an area to expand their current range, increase population sizes to avoid genetic problems, or introduce a species in another area to reduce the likelihood of losing it via a local environmental catastrophe (Abbott 2000).

A reintroduction is defined as “an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct” (IUCN 1995), due to human activities or natural catastrophe (IUCN 1987). Reintroductions are particularly useful for restoring a species to an original habitat when the original causes of extinction have been controlled or removed, and where the habitat requirements of the species are satisfied (IUCN 1987). The aim of any reintroduction should be to establish viable, free ranging populations in the wild, of a species which had become globally or locally extinct in that area. Ideally these reintroductions should require minimal long-term management (IUCN 1995).

Reintroductions have been carried out on many taxa including invertebrates, fish, amphibians, reptiles, birds, mammals and plants (Soorae 2008). Indeed, according to the IUCN Reintroduction Specialist Group (RSG) database, at least 489 animal species are the focus of recent, current or planned reintroductions for conservation (Seddon *et al.* 2005). Griffith *et al.* (1989) reviewed the success of intentional releases of native birds and mammals between 1973-1986 in Australia, Canada, Hawaii, New Zealand, and the United States. They showed that species classed as threatened, endangered or sensitive had a reintroduction success rate of 44%. More recently, Fischer and Lindenmayer (2000) conducted a comprehensive review of 180 case studies on animal translocations published in 12 major international journals over the previous 20 years. Most of the translocation studies were of mammals (49%) and birds (44%), with the remainder on amphibians, reptiles and invertebrates. Reintroductions were the most common type of translocation (116 of the 180 cases reviewed), with 75% stating they were undertaken for conservation purposes. Most reintroductions were conducted in Australia & New Zealand, North America, and Europe, followed by Asia, Africa, and Central & South America. For the purpose of Fischer and Lindenmayer’s (2000) review reintroduction success was defined by the achievement of a ‘self sustaining population’ (Griffith *et al.* 1989). However they acknowledge that this could not easily be determined as it was dependant on the objectives of specific translocations, which at times were not clearly stated. Using the data available only 26% of the reintroductions were considered successful, while 27% were failures (the outcome of the other 47% was unknown at the time the studies were published, party due to the lack of generally accepted criteria to assess success). Of importance, reintroductions conducted within Australia and New Zealand were noted to have a particularly high rate of failure (53%: see section 1.3.1 for discussion on criteria for success).

There has been limited success with past reintroductions worldwide (Fischer and Lindenmayer 2000; Griffith *et al.* 1989), where predation is often the factor responsible for failure (Griffin *et al.* 2000; McCallum *et al.* 1995; Short and Smith 1994). The poor success rate of previous reintroductions suggests that use of reintroductions as a conservation tool needs to be further investigated and improved upon in order to ensure that they are viable options and not just a waste of money (Jule *et al.* 2008). Indeed, continual review of failed reintroduction attempts has provided information to suggest ways and means of increasing the chances of getting successfully sustainable reintroduced populations. For example, Short *et al*. (1992) reviewed six attempts to reintroduce various species of wallaby, all of which ended in failure. From this they drew conclusions as to the necessary means to plan and undertake a reintroduction for maximum likelihood of success. Any translocation should be based on careful research, planning, assessment, implementation, monitoring and reassessment (Copley 1994).

1.3 Reintroduction guidelines and recommendations

Following the poor success of many early translocations, various guidelines have been put forward to improve the likelihood of reintroduction success, such as those outlined in 1987 by the Species Survival Commission (SSC) of the International Union for the Conservation of Nature and Natural Resources (IUCN) in collaboration with the Commission of Ecology, and the Commission on Environmental Policy, Law and Administration (see IUCN 1987). Additionally, in 1988 the Reintroduction Specialist Group (RSG) of the IUCN Species Survival Commission (SSC) was created to bring together expert knowledge on matters pertaining to reintroducing species into their natural habitats. In 1995 the RSG produced the now widely-used IUCN Guidelines for Reintroduction and taxon-specific guidelines for a number of species (Dublin, cited in Soorae 2008 p.4). Closer to home, the Australian Nature Conservation Agency has developed a more specific draft policy for translocating vertebrate animals in Australia (Federal Endangered Species Advisory Committee (former) 1994). Since the publication of the IUCN/SSC Reintroduction guidelines, the numbers of reintroduction projects for animals and plants have steadily increased to cover virtually all taxa and habitats (Launay, cited in Soorae 2008 p.6).

The basic program for reintroductions should consist of a feasibility study, a preparation phase, the release and a follow-up phase (IUCN 1987). For animal reintroductions specifically, there should be an initial ecological study assessing the biological needs and habitat requirements of the animal and the suitability of the habitat where the reintroduction is proposed, to ensure the animals’ needs would be met (IUCN 1987; 1995). The initial studies should detail the animals’ social behaviour, group composition, home range size, shelter and food requirements, foraging and feeding behaviour, predators and diseases (IUCN 1995).

Prior to release, previous causes of decline need to be indentified and eliminated or reduced to a sufficiently low level. Such causes have included disease, over-hunting, over-collection, pollution, poisoning, competition with or predation by introduced species, habitat loss, adverse effects of earlier research or management programs, and competition with domestic livestock (IUCN 1995). Furthermore, animals should be screened for disease/parasites, and various factors need to be considered such as the ideal age, sex ratio and group size for reintroducing individuals, as well as the most appropriate season (IUCN 1987). Additionally, capture techniques and a suitable mode of transport need to be decided. If animals are re-introduced from captive-bred stock, researchers need to assess whether any adaptations to captivity will affect the animals' ability to re-adapt to the wild (IUCN 1987; 1995). Furthermore, the attitudes of the local community need to be taken into account, and sufficient funds secured to ensure the completion of the project through to the follow up phase (IUCN 1987). Following the release, long term monitoring and research should be carried out to determine the animals' rate of adaptation and dispersal, the species impact on the habitat, whether there is a need for further releases, and ultimately identify the reasons for the success of failure of the program (IUCN 1987). Clear criteria for success or failure should be defined a priori.

1.3.1 Measuring success of reintroduction

There is no general agreement on what constitutes a successful reintroduction (Seddon 1999a). Although a variety of definitions of success have been proposed by various authors, due to differing life history traits of various target species any one criteria can not be applied across the board (Seddon 1999a). Furthermore, while the goal of a reintroduction may be to establish a self-sustaining population, and this is commonly used as the benchmark of measuring success, this can not be defined as the "criterion" of success, as it is assessed at one moment in time and does not necessarily equate to long-term persistence (Seddon 1999a). Alternatively, Seddon (1999a) proposed that a reintroduction has three objectives: the survival of the release generation, breeding by the release generation and their offspring, and persistence of the re-established population (perhaps assessed through extinction probability modelling). Additionally, through a sustained period of detailed monitoring, information about the animals' behaviour, including aspects of the animals' interactions with other animals, use of the vegetation, and sustainability of the environment needs to be obtained (Chivers 1991; IUCN 1995). There should also be a collection and investigation of mortalities, studies into the process of long-term adaptation by the animals, and continuing public relations activities (IUCN 1995). All of this information will help determine whether the reintroduction has been successful (Kleiman 1989).

Determining whether a reintroduction has been successful or not requires a set of guidelines or criteria outlining what makes a reintroduction successful (Moro 2003). Furthermore, these need to be species specific, reflecting the various goals and reasons why the reintroduction was undertaken, and relating directly to the animals' biology and what outcomes can be reasonably expected. Success should be gauged using these clear objectives for the reintroduction (Short *et al.* 1992). For example, in a study of a reintroduction of the western barred bandicoot (*Perameles bougainville*), criteria for success were given as all of the following: greater than or equal to 50% survival of translocated bandicoots after one month, greater than or equal to 10% survival of translocated animals after 6 months, reproduction in the wild within 6 months of translocation, wild-bred bandicoots reproducing in the wild within two years, population persistence and increase over the subsequent two years after successful reproduction in the wild, with no requirement for additional translocations (Richards and Short 2003). Moro (2003) outlined the criteria for a successful reintroduction of dibblers (*Parantechinus apicalis*) to be if individuals within the free-ranging population produced second-generation young that survived to breed and produce viable dispersing offspring. Similarly, the success of a reintroduced population of burrowing bettong (*Bettongia lesueur*) was defined as the population persisting for greater than five years, with likely ongoing persistence under continued regular management, and that the numbers of bettongs were greater than 265 within five years of first release (Short and Turner 2000). This number was chosen as in theory (using simple logistic modelling), a population of 265 bettongs should be able to sustain predation of 99 animals per year, and therefore be sustainable (Short and Turner 2000). These reintroductions employed clear objectives as well as experimental design and sufficient monitoring (both of which are further discussed in section 1.5). Animals were radio tracked for a period of time (intensively straight after release), predator control was in place, the animals were released in appropriate habitat, the researchers had a good understanding of the animals' ecology and requirements, release group size and sex ratio was considered (particularly in the bettong and bandicoot studies), and the bettongs and bandicoots were wild-caught. All of these studies defined a set of criteria to determine the success of the reintroduction.

1.4 Factors affecting establishment success

In a review by Fischer and Lindenmayer (2000) of 180 reintroduction case studies, reintroduction success (defined by a self-sustaining population) was not found to have changed over the last two decades, but reintroductions appeared to be more successful when the source population was wild, a large number of animals was released (*n*>100), and the cause of original decline was removed. Griffith *et al.* (1989) suggested several additional factors: the need for high genetic diversity (in the founder stock), a high rate of population increase, low competition, a suitable abundance of high quality protected habitat (for refugia and food), reduced environmental variation, and suitable, proper care and training of naïve captive reared stock about predators. This highlights the importance of considering and accommodating factors which may improve the likelihood of reintroduction success.

Prior to choosing a release site and releasing the animal there needs to be an understanding of the animals' ecology and requirements (Short *et al.* 1992). Specific aspects that are relevant include: habitat preferences, social behaviour, group composition, home range size, shelter and food requirements, foraging and feeding behaviour, predators, diseases, dispersal mechanisms, reproductive biology, and relationships with other species (IUCN 1995). An understanding of the critical needs of the animal will help determine what habitat will be most suitable for the animal. The following section outlines several factors that are known to limit the success of reintroductions.

1.4.1 Predation

The control of predators is often a key factor influencing the success of a reintroduction (McCallum *et al.* 1995; Moro 2003; Moseby and O'Donnell 2003; Richards and Short 2003; Short *et al.* 1992; Short and Turner 2000). A review by Short *et al.* (1992) on reintroductions of macropods in Australia included nine attempts to restore them to the mainland in the presence of predators. Of these, only one was successful, namely that of the brush-tailed bettong (*Bettongia penicillata*), which was shifted within a nature reserve where fox control was implemented during establishment. However, reintroductions to islands (free of mainland predators) have resulted in a far greater (60%) success rate. Similarly, Fischer & Lindenmayer (2000) reviewed previous reintroductions, and they noted that 16 of 32 reintroductions in Australia involved animals being reintroduced into areas with predators. Of these 16, only two reintroductions were deemed successful, 69% failed, and the success of the remainder was unknown. These findings highlight the importance of implementing ongoing predator control when undertaking reintroductions in areas which have introduced predators (Short *et al.* 1992).. For example, unlike previous attempts to reintroduce the burrowing bettong (*Bettongia lesueur*), it was successfully reintroduced to the Australian mainland in 1992 after a 50 year absence (Short and Turner 2000). The western barred bandicoot (*Perameles bougainville*) was reintroduced to the Australian mainland in 1995 after a 60 year absence (Richards and Short 2003). Likewise, the greater bilby (*Macrotis lagotis*) was reintroduced in 2000 and was able to successfully recolonise parts of their former range in arid South Australia (Moseby and O'Donnell 2003). The success of each of these reintroductions was in part due to the intensive control/eradication/exclusion of cat and fox predators.

The success of reintroductions into areas where there is still a risk of predation (which may or may not be the original cause of decline) will be largely dependant on the animal’s ability to detect and evade predators. McLean *et al.* (1994) identified two key processes for responding to predators: recognition and coping. Predator recognition may be innate or acquired through experience, where coping skills are likely to be entirely learnt and will improve with experience (McLean *et al.* 1994). Most species of mammals and birds rely heavily on individual experience and learning as juveniles for their survival (IUCN 1995; McLean *et al.* 1994). However, animals raised in captivity or originating from predator-free islands will be naive about predators, they have no prior opportunity to learn about the predators they may encounter at a release site or the appropriate responses they should implement (McLean *et al.* 1994; van Heezik *et al.* 1999). Therefore, animals raised in captivity are more susceptible to predation within several months after release (Short *et al.* 1992). For example, one third of the post release mortality of a reintroduced threatened waterfowl, the crested coot (*Fulica cristata*) born and reared in captivity took place within the first month after their release (Tavecchia *et al.* 2009). Habituation to humans while in captivity may also compromise reintroduction success. For example, the degree of human interference prior to release was found to significantly influence the survival of reintroduced fallow deer (Zidon *et al.* 2009). Two-hundred days post-release, 80% of the fallow deer originating from captivity with reduced human presence had survived, whereas all animals originating from captivity with high human activity (resulting in human habituation) had died. Of the mortalities, 87% were caused by collisions with trains, and the remainder had been preyed upon. The immediate susceptibility to predation of released animals following their release seems to be a common feature of reintroduction projects and is likely due to the inexperience of captive born individuals to face the new environment (Griffith *et al.* 1989; Tavecchia *et al.* 2009). Zidon *et al.* (2009) stated that wild animals entering new areas are timid and invest much time and effort in anti-predator behaviour, while animals reared in predator-free conditions (and in close proximity to humans in their study) may initially lack this tendency.

Thus, animals reintroduced from captive breed situations or those translocated from predator-free sites are more likely to fail than those using wild-caught animals (Mathews *et al.* 2005). A review by Beck *et al.* (1994 cited in Jule *et al.* 2008) estimated that only 16 out of 145 reintroduction projects using captive-born animals were successful. Similarly, Fischer and Lindenmayer's (2000) review of 116 reintroduction case studies found the success rate of the reintroduction was higher (31%) when animals were sourced from a wild population, whereas animals relocated from captive populations had very low reintroduction success rate (13%). Likewise the Griffith *et al.* (1989) review of reintroductions of native birds (134 reintroductions) and mammals (67 reintroductions) in Australia, Canada, Hawaii, New Zealand and the United States between 1973-1986, found that translocation of wild-caught animals were more likely to succeed (75% successful) than were those of captive-reared animals (38% successful). Not surprisingly, the IUCN (1995) recommended that wild stock be reintroduced over captive bred stock.

1.4.2 Training to increase awareness about predators

In some situations only captive animals may be available for translocation. However, the animals' adaptations to captivity may seriously compromise the success of reintroduction programs (Gilligan and Frankham 2003; McPhee 2004). Therefore, in instances where captive stock is released the IUCN recommend that they should be given the opportunity to acquire the necessary skills to enable survival in the wild through means of training in their captive environment (IUCN 1995). Likewise, following a review of macropod reintroductions in Australia, Short *et al.* (1992) recommended the use of predator-avoidance training for captive-bred stock or those coming from predator-free islands. Predator training is suggested to increase reintroduction success (Beck *et al*. 1994 cited Gilligan and Frankham 2003).

To ascertain "risk", prey need to be able to discriminate between predator types, which may require previous interaction with them, social learning or training (Botham *et al.* 2008). Deciphering the appropriate training will be assisted by an understanding of the animals' natural anti-predator behaviour (Anthony and Blumstein 2000; Blumstein 2000), and care should be taken to ensure that pre-release training is done in ways that avoid increasing predation risk in the wild. For example, researchers need to be careful not to condition animals into thinking that running 10m and hiding is an appropriate strategy (if that's all the animal could do in captivity) (McLean *et al.* 1994). There is also the consideration of whether using live or model predators are preferable. A study on captive-reared houbara bustards showed improved post-release survival through exposure to a live predator before release, whereas training with a model predator had no effect on post-release survival (van Heezik *et al.* 1999). Similarly, Griffin *et al.* (2001) acknowledged that while they observed significant fear response by tammar wallabies to a model fox, they questioned whether similar results would be obtained using a live model and if this would be sufficient to enhance survival in the wild. Training in the presence of an experienced conspecific (social learning) may also assist naïve animals to develop appropriate responses to predators. For example, predator training of naïve juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) in the presence of the experienced adult prior to release increased the survival compared to animals trained without the experienced adult (Shier and Owings 2007). Social learning by captive animals in this situation was a sufficient training technique, as their survival rate was not significantly different to wild born juveniles (Shier and Owings 2007) who had the advantage of learning about predators as they develop.

While it may not be feasible to train the animals about all the predators they may encounter, Frair *et al.* (2007) suggested that releasing animals which are at least partly familiar with predation risk could be sufficient to establish local populations without further management intervention. Their study on reintroduced elk found that animals which were familiar with wolves or hunters prior to their reintroduction (familiarity achieved by natural prior experience in their source habitat) had two times greater survival rates than animals' naïve to both predation risks (Frair *et al.* 2007). Furthermore, the intensity of a previous experience may affect the level of response in the animal. For example, the Trinidadian guppy from high risk populations had heightened response to predators compared to those from low risk populations (Botham *et al.* 2008).

Despite authors recommending training animals to recognise predators, the feasibility of training requires the animals to have retained the "behavioural precursors" to make training possible (Griffin *et al.* 2000). Additionally, once animals have learnt to recognise the predators, the animals still need to learn to cope in those situations. Both their recognition and coping skills will improve with experience with predators or predation risk (McLean *et al.* 1994), and with this experience the animals' responses will become rapid and appropriate (McLean and Rhodes 1991, cited in McLean *et al.* 1994) .

Even animals reared in predator-free conditions and which have not received training prior to release can reacquire some anti-predator behaviour over time (Banks *et al.* 2002). This notion is supported by Blumstein *et al*. (2000) and Blumstein and Daniel (2002) who hypothesised that some anti-predator behaviour will persist for many thousands of years after isolation from predators. However, the concern remains, that the speed at which they reacquire the behaviours is critical as animals have an increased susceptibility to predation immediately following their release (Zidon *et al.* 2009).

1.4.3 Population dynamics

The number of animals released into an area is another important component to the success of reintroductions. Fischer & Lindermayer's (2000) review of 116 reintroductions from around the world over the last 20 years revealed that a higher proportion of reintroductions were successful when greater than 100 animals were reintroduced. Griffith's *et al.* (1989) review of intentional releases of native birds and mammals between 1973-1986 in Australia, Canada, Hawaii, New Zealand, and the United States found an asymptotic relationship between number of animals released and probability of success, where they recommended release groups of 80-120 for game birds, and 20-40 for large mammals. Conversely, they found little evidence that larger release groups increase probability of success for macropods, and suggested that successful reintroductions have often resulted from releases of smaller numbers. However, McCallum *et al.* (1995), modelled the impact of predation on reintroduced bridled nailtail wallabies (*Onychogalea fraenata*) and suggested that even small rates of predation (2-4 individuals per six months) can be sufficient to cause reintroductions of up to 50 animals to fail.

Animals may be reintroduced over one or multiple release events. Griffith's *et al.* (1989) review showed that between 1973 and 1986 a typical translocation consisted of six releases over the course of 3 years. However, the appropriate strategy may depend on the threat to the animals' survival. If constant-quota predation is the prime threat, McCallum *et al.* (1995) recommend a single large reintroduction event with the objective of swamping the predators. Alternatively, if the prime threat is a catastrophe which could eliminate an entire population, they suggested a 'bet-hedging' strategy of releasing multiple groups in a number of areas. Acknowledging that the optimal strategy is less obvious in light of environmental stochasticity and aggregated predation, McCallum *et al.* (1995) suggested overall that a single reintroduction of a given size is preferable to multiple reintroductions of the same total number of animals. Irrespective of the release protocol, the number of founder animals released needs to be sufficient to avoid creating genetic bottlenecks in the population (Miller *et al.* 2009). Larger founder groups will help to maximise genetic diversity, reduce inbreeding, and maintain genetic diversity across generations (Miller *et al.* 2009). While genetic diversity may be restored by adding further animals to the population (Swanson and Kyle 2007), consideration needs to be made about where to release supplemental animals if the resident population has established territories, as newly released animals may be forced to disperse if released within the resident population territory (Bertolero *et al.* 2007; Stoen *et al.* 2009).

In addition to the overall number of animals reintroduced, the success of the reintroductions may be affected by release group size and compositions of released animals. Chivers (1991) recommended that when capturing wild animals one objective should be to capture the entire social group to minimise stress to individuals. Similarly, Blumstein (2002a) suggested that familiarity between release group members may reduce misinterpreted alarm warning calls between conspecifics, which is advantageous as “false alarms” result in wasted energy expenditure in fleeing and reduced time spend foraging. Importantly, consideration of the social ecology (group dynamics) of the species needs to be included when deciding appropriate release group size and sex ratios for a particular species. Species that socially aggregate for predator avoidance will be susceptible to attack if reintroduced alone, whereas species that do not have an anti-predator advantage from aggregating may be vulnerable to be killed if released as a clumped group. Blumstein *et al*. (1999) suggested that scientists should pay particular attention to group size when reintroducing endangered macropods. In the past, managers have reintroduced macropod marsupials solitarily with individuals dispersing throughout their new habitat (Blumstein and Daniel 2003). However, small macropods in the critical weight-range seemingly benefit from social aggregation (Blumstein *et al.* 2003), and captive studies on the tammar wallaby in particular suggest they would benefit from being reintroduced socially (Blumstein *et al.* 1999).

1.4.4 Habitat use

The ability of animals to establish and survive depends on many factors including the availability of suitable habitat which meets food resource and shelter requirements (Hardman and Moro 2006a; Kleiman 1989). In particular, releasing animals into the core of the species’ historical ranges are noted to be more successful than those on the periphery or outside historical ranges (Griffith *et al.* 1989). Previously animals have often been released into areas that were not known to be their former range, or in areas that were too small to sufficiently support the animals without significantly impacting the vegetation. Indeed in a review of native vertebrates translocations in South Australia from 1907-1993, 62% (67 of 108) of all translocations were outside the species' former known range (Copley 1994). This was to provide a potential food source for ship-wrecked mariners, or to establish populations of rapidly disappearing species of mainland fauna on islands.

Griffith *et al.* (1989) highlighted the importance of releasing animals into good quality habitat. Their review of 193 bird and mammal translocations showed the success rate was 84% when reintroduced in excellent habitat, 69% in good habitat, and 38% in fair or poor habitat. It is also important to consider the ways in which animals will use the available habitat before deciding upon a release site. Not only are dietary requirements and refuge sites a consideration but also the particular predator avoidance tactics of the released species relative to the types of predators that will co-occupy the area. For example, if an animal relies on visibility to detect the approach of a fox, it may not be wise to reintroduce the animal into dense vegetation. This is a tactic of the western grey kangaroo. When alarmed, western grey kangaroos will leave cover quickly and occupy the centre of an open grassy area, from here they can presumably identify and monitor distant predators (Blumstein and Daniel 2002). In contrast, tammar wallabies forage closer to cover and tend to retreat into the cover when alarmed (Blumstein and Daniel 2002). From this it can be inferred that kangaroos perceive safety in the centre of open areas, whereas wallabies perceive safety in cover (Blumstein *et al.* 2003).

Predation risk is considered an extremely important factor in determining habitat selection by herbivores (Frair *et al.* 2007). Predation risk will increase when in less familiar areas as the animals need longer to find cover and escape routes from predators (Janmaat *et al.* 2009). Bright and Morris (1994) suggested that animals released into an unfamiliar area will not move very far after release, presumably because they are unfamiliar with safe sources of food and escape routes from predators. Spatial ignorance (unfamiliarity with the surroundings) in reintroduction programs is suggested to be associated with an initial 'cost of release' where there is lower survival during a habituation period following a reintroduction (Bar-David *et al.* 2005; Sarrazin and Legendre 2000). The cost of spatial ignorance has been shown in birds, fish and mammals. For example, wapiti (*Cervus elaphus*) translocated into a new area showed a high degree of variability in their initial habitat selection and site returns in response to predation risk. Wolf *et al.* (2009) suggested they possibly failed to recognise areas used by wolves because they were inexperienced with wolf predation altogether, or it took them a longer period of time to become familiar with predation risk in new area. However, increased familiarity with an area may reduce predation risk and increase foraging effectiveness (Janmaat *et al.* 2009; Wolf *et al.* 2009).

1.5 Importance of monitoring and experimentation

Fischer and Lindenmayer (2000) concluded in their review that better monitoring after a translocation is required, specifically gathering information on key parameters which reflect the success of the translocation at previously specified time intervals. They suggest examining the number of animals, sex ratios, adult/juvenile ratios, population change and a constant reassessment of the threatening process. Monitoring is an essential component of reintroductions, the level and nature of which should change adaptively as the reintroduction proceeds. Long term monitoring of animals is required to regularly assess the degree of intervention necessary to assist population persistence (Seddon 1999a), particularly when releasing captive-bred animals, where it is unreasonable to expect survival and persistence without some degree of post-release care (Seddon 1999a). Without monitoring it would be impossible to say if or when a reintroduction has been successful, or what factors contributed to the success or failure (IUCN 1995; Seddon 1999b). For example, with no data available on the reintroduced mallee fowl on Kangaroo Island, or of bettongs on St Francis Island the causes of these failed translocations could not be determined (Copley 1994).

In light of a lack of detailed monitoring and many failed reintroduction attempts, many authors (including Armstrong and Seddon 2007; Hardman and Moro 2006a; Seddon *et al.* 2007) have suggested the importance of incorporating experimentation when undertaking reintroductions. However, very few reintroduction attempts detailed in the literature have been experimental in nature. A review by Seddon *et al.* (2007) of 291 reintroduction papers revealed that only 12% were experimental. Experimentation allows researchers to test theories (Seddon *et al.* 2007) and determine specifically how the animals are establishing and what is driving their habitat and social behaviours while establishing in unfamiliar territory.

The IUCN (1995) highlight the importance of pre- and post-release monitoring, so that each reintroduction is a carefully designed experiment, with the capability to test methodology with scientifically collected data. Importantly, the research questions should drive the monitoring, rather than the questions being driven by the data available (Armstrong and Seddon 2007). Armstrong & Seddon (2007) also suggested that a distinction be made between the establishment phase and post establishment (persistence), as reintroduced populations can fail to survive the establishment phase in conditions that would normally enable long-term persistence once established (Armstrong and Seddon 2007).

To ensure the future stability of a species, an approach that encompasses all of the above strategies should be implemented and undertaken (Short and Smith 1994), incorporating appropriate monitoring and experimental design (Short *et al.* 1992).

1.6 Thesis aims

For reintroductions to be appropriate and successful, and to assist management decisions, we need an understanding of both the animals' habitat and social requirements. Studies have been conducted on captive or established populations of tammar wallabies, however a detailed knowledge about the social structure and behaviour of the tammar wallaby in the field is currently lacking in the literature (Blumstein *et al.* 2002a). In particular, there are no detailed studies on the group dynamics, and habitat use of tammar wallabies reintroduced into an area, especially those reintroduced into areas where predators are still present. Reintroduction success is somewhat reliant on the animals' familiarity with predators and predation risk. However during this project there were two problems: released animals had been isolated from predators, and as a result it is somewhat unclear whether they would have retained appropriate anti-predator behaviors (Griffin *et al.* 2000). For this study I assumed that the perceived risk of predation would be reflected by surrogate measures of risk, namely: distance to cover, likelihood of using cover, number of animals within 100m, and distance to nearest neighbour. Using surrogate measures of risk has previously been used in a comparable study by Matson *et al.* (2005) on impalas (*Aepyceros melampus*).

The aims of this thesis were to:

1) use an experimental reintroduction design to determine whether pre-established release group familiarity influenced habitat and social behaviours during establishment.

While it has been suggested that the moderately social tammar should benefit from being reintroduced in groups (Blumstein *et al.* 2002b), experimental reintroductions are required to see if the benefits wallabies receive while aggregating with others actually increases survival when released into areas with predators (Blumstein *et al.* 1999). Here, I examined whether one aspect of release group composition, pre-established familiarity, influenced the animals' anti-predator behaviour. This was reflected by the surrogate measure of risk described above.

2) examine tammar habitat use and social grouping during the establishment period and post-establishment, relating it to the perceived risk of predation and likelihood of reintroduction success.

Reintroduced populations can fail to survive the establishment phase in conditions which would normally enable persistence for established populations (Armstrong and Seddon 2007). In part this may be due to spatial ignorance, which is suggested to be associated with an 'initial cost of release' while animals are establishing in an unfamiliar area (Bar-David *et al*. 2005; Sarrazin and Legendre 2000), and predation risk which is greater when in less familiar areas (Janmaat *et al*. 2009). Therefore, it would be expected that animals exhibit stronger anti-predator behaviours while establishing in a novel habitat. Here I distinguished the establishment phase from the post establishment phase (as suggested by Armstrong and Seddon 2007) to determine if differences in perceived risk existed, as reflected by the surrogate measure of risk described above.

3) describe aspects of the habitat and social ecology of a wild population of tammars in light of perceived predation risk.

As detailed knowledge on tammars in the wild is currently lacking (Blumstein 2002a), results from this work bring two main benefits: It furthers our understanding of reintroductions of native mammals, and greatly increase our understanding of the ecology of the tammar wallaby. Here particular attention was paid to home range size and location, group cohesion and social behaviours, habitat selection and detailed habitat use.

4) recommend appropriate reintroduction and management strategies for tammar wallabies and other macropods.

The knowledge gained here can be used to assist in the management of the species and shape further reintroductions, ensuring that decisions made about future reintroductions will provide animals the best chance of survival in the long term. Findings from this study may also be used to assist in reintroduction or management decisions for other species of similar social behaviour and requirements.

2 Chapter 2: SA mainland tammar wallaby reintroduction overview and general methods

2.1 Study animal

2.1.1 Overview of biology

The tammar wallaby (*Macropus eugenii*) is one of the smallest wallabies, weighing 4-10kg (Hinds 2008; Smith 1983), with males larger than the females (Figure 2.1). They are dark grey-brown above, becoming rufous on the sides of the body and limbs (especially in the males), and pale grey-buff below (Hinds 2008; Smith 1983). Male tammars (from Kangaroo Island) have been observed to live up to 11 years, while females live up to 14 years (Hinds 2008; Smith 1983).

Figure 2.1 Tammar wallaby (*Macropus eugenii eugenii*). (Photo: Tony Lewis).

Prior to European settlement, there were three recognised subspecies of tammar wallaby in Australia: one in Western Australia, one on Kangaroo Island in South Australia, and one on the mainland of South Australia (Figure 2.2). Populations of the Western Australia sub-species (*Macropus eugenii derbianus*) are currently small and scattered, with larger populations on Garden Island, East and West Wallabi Islands in the Abrolhos, North Twin Peaks Island and Middle Island in the Recherche Archipelago (Hinds 2008; Poole *et al.* 1991). In South Australia, *Macropus eugenii decres* thrives on Kangaroo Island & Greenly Island (Hinds 2008). The South Australian mainland sub-species (*Macropus eugenii eugenii*), once occurred on the mainland in Eyre Peninsula, Yorke Peninsula and the Adelaide Hills, and on Flinders, St Francis, St Peter and Thistle islands (Smith 1983). It was thought to suffer under the pressure of European settlement, habitat clearance and predation (McKenzie 1995; McKenzie *et al.* 2007; Poole *et al.* 1991), and was considered extinct in the wild by the early 1900s (Poole *et al.* 1991; Smith 1983; Van Oorschot *et al.* 1989).

Under the 2010 IUCN Red List of Threatened Species (version 3.1) tammar wallabies are listed as Least Concern (Morris *et al.* 2008). Similarly, under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act), two of the three subspecies (*M.e.derbianus* in Western Australia and *M.e.decres* on Kangaroo Island SA) are classified as Not Listed. However, the third subspecies, *M.e.eugenii* on the South Australia mainland, is listed as Extinct

NOTE:
This figure is included on page 38 of the print copy of
the thesis held in the University of Adelaide Library.

Figure 2.2 Distribution of tammar wallabies in Australia prior to European settlement (dark blue colour denotes their current distribution, red colour signifies reintroduced populations in South Australia, Hinds 2008).

Tammar wallabies inhabit coastal scrub, heath, dry sclerophyll forest and thickets in mallee and woodland (Hinds 2008). They sleep in low dense vegetation during the day, begin to move at dusk, and emerge from the scrub after dark. They are reported to use established runways to move to open grassy feeding sites up to 1km away for foraging at night, and return to cover before dawn (Cronin 1991; Smith 1983). While described as primarily nocturnal, Cronin (1991) and Blumstein *et al.* (2002b) both suggest that they are additionally active for a few hours before sunset and after sunrise.

Tammars are both “grazers” and “browsers”, although grasses are apparently preferred to browse (Lentle *et al.* 1998). Despite grasses being of lower nutritional value than browse (due to a higher fibre content in grass), they are more readily available and require less chewing (Williamson 1986 cited in Lentle *et al.* 1999a). Overall however, tammar wallabies’ food selection is driven by the need to optimise foraging in terms of nutrient and energy acquisition while also avoiding predators (Lentle *et al.* 2003). Tammars’ feeding rate has been estimated to be 115g of dry matter per day (Nagy *et al.* 1990), and they do not need to drink water when eating relatively succulent vegetable material (Lentle *et al.* 1999b; Nagy *et al.* 1990). However they are able to drink seawater when required (Cronin 1991; Smith 1983). Indeed other authors report that they are able to maintain body mass and fluid balance while consuming only low-protein food and seawater for at least 30 days (Bakker *et al.* 1982; Purohit 1971).

Habitat use and foraging location of the species may be somewhat influenced by environmental conditions. Tammar wallabies reportedly prefer grazing in open pasture in fine weather (Lentle *et al.* 1998), as it may be more conducive to detecting predators. Likewise, predator detection may be easier on moonlit nights. Indeed, it has been suggested that tammars associate safety with increased illumination, and exercise more caution in the dark (Biebouw and Blumstein 2003). A higher risk of predation has been suggested when animals are dispersing through or using novel environments, as it is harder to find refuge from predators, shelter and resources (Anthony and Blumstein 2000). This supports the suggestion that remaining in familiar areas is advantageous when resources are not limited (Janmaat *et al.* 2009). Indeed, Lentle *et al.* (1998) observed tammars to have a high degree of site fidelity, returning to within 50m of the same midday shelter area after nocturnal foraging excursions (based on three females, one male).

Tammars are described as having defined home ranges of ~30ha, which overlap that of others (Cronin 1991; Smith 1983). However, tammars are also reported as being solitary (Cronin 1991; Smith 1983), yet aggregate in open grassy clearings at night (Taylor *et al.* 1999). While Inns (1980) and Smith (1983) observed no particular social grouping amongst tammars, except between female and their young at foot, Blumstein *et al.* (2002a) reported that female tammars are likely to aggregate with kin and suggest they gain some fitness benefit from doing so (such as reduced aggression towards vulnerable young).

The reproductive cycle of tammar wallabies is well understood from both captive and field studies, predominantly on the Kangaroo Island sub-species. Tammars exhibit regularity in the annual onset of breeding, weaning only one young per year (Sunnucks and Taylor 1997). More than 90% of females have carried a pouch young by the end of the breeding season (Hinds 2008), although in some years pouch young are lost, especially by one year old females (Inns 1980). Females generally give birth around late January, with very few being born outside of January, February and March. They then mate again within a few hours of the birth and the embryo remains quiescent during the 8-9 months of lactation of the current pouch young (which emerge in September-October; Smith 1983). The embryo is reactivated within a few days after December 22 (the summer solstice) and the young is born ~25 days later (12 months after it was conceived) (Smith 1983). Interestingly it has been reported that the maternal weight of tammars strongly predicts the sex of offspring, where offspring are more likely to be male with increasing maternal weight (Sunnucks and Taylor 1997). There is a high rate of mortality of juveniles during their first summer (as high as 40 percent; Inns 1980). Females become mature at around nine months old while they are still suckling, and males do not reach sexual maturity until nearly two years old (Smith 1983). The species appears to have a promiscuous mating system, where there is a clear dominance hierarchy between adult males (Hynes *et al.* 2005). The dominant male usually mates first and then guards the female to prevent access to her by other males (Hynes *et al.* 2005). However, captive studies suggest this does not prevent further mating nor secure parentage, as Hynes *et al.* (2005) found females usually mated with more than one male. Additionally, while the dominant male sired 50% of the offspring, the subdominant males still contributed significantly to the population (Hynes *et al.* 2005).

Current predators of the tammar are both aerial and ground dwelling, specifically feral cats (*Felis catus*), foxes (*Vulpes vulpes*) and wedge tailed eagles (*Aquila audax*) (Blumstein *et al.* 2002a; Inns 1980). To combat these predators, the tammars' anti-predator strategies involve using protective cover and remaining cryptic when they are relatively solitary, and associating with conspecifics for group vigilance while foraging (Blumstein and Daniel 2002; Blumstein *et al.* 2002c). The tammars may also utilise multiple anti-predator strategies depending on the level of risk. For example, when foraging in open, high predation risk sites, animals may forage closer to cover (as observed in a field study on Kangaroo Island, South Australia; Blumstein and Daniel 2002) and aggregate in groups (as observed in captive studies at the Macquarie University fauna park, New South Wales; Blumstein *et al.* 1999; Blumstein *et al.* 2002b). Group aggregation both increases communal vigilance without reducing an individuals time spent on foraging (Blumstein *et al.* 1999; Lima and Dill 1990), and decreases the per capita risk of predation (Blumstein *et al.* 2002b). Tammars will alert conspecifics of a predatory threat by using foot-thumps as warning signals (Blumstein *et al.* 2002a; Blumstein *et al.* 2002c). Indeed Blumstein *et al.* (2002c) suggested that tammars relied somewhat on conspecifics to assess and manage risk.

Some anti-predator behaviour/responses are suggested to be innate in the tammar and may persist despite isolation from some (but not all) predators. For example, tammar wallabies living on Kangaroo Island which are isolated from foxes but remained susceptible to aerial predators were observed to exhibit group size effects (Blumstein and Daniel 2002). However, no group size effects were observed in tammars living in New Zealand, possibly a result of the complete relaxation of predation pressure, or low population densities in the study area (Blumstein 2002b). Indeed some anti-predator behaviour/responses are experience-dependant such as flight distance from predators, where tammars from predator-free islands were observed to be less wary than those from areas with predators (Blumstein 2002b). While tammar wallabies are able to learn general space use and wariness when released into a new environment (Blumstein and Daniel 2002), or learn from other experienced tammars (Griffin and Evans 2003b), predator training prior to release is likely to assist their anti-predator behaviour when released into the wild, and has been shown to be effective on captive tammars (Griffin *et al.* 2000; Griffin and Evans 2003a; Griffin *et al.* 2001; 2002). However, populations that have not experienced predators for many generations may have lost the required ‘behavioural precursors’ to make training possible (Griffin *et al.* 2000).

2.1.2 Re-discovery

In 1870 tammar wallabies were introduced to Kawau island in the Huraki Gulf of New Zealand by the former Governor of South Australia, Sir George Grey (Taylor *et al.* 1999; Van Oorschot *et al.* 1989). In the absence of predators, the tammars became over abundant and were consequently considered to be a “pest”, triggering a decision by the New Zealand Department of Conservation to commence an eradication program for tammars and other non-native species on Kawau Island in May 2004 (DEH 2004). With the exact origin of the Kawau Island tammars unknown they were subjected to genetic screening by Taylor and Cooper (1999). Fortuitously, it was discovered that the Kawau Island tammars originated from the SA mainland stock which had since suffered under the pressures of European settlement, habitat clearance and predation (McKenzie 1995; Poole *et al.* 1991) resulting in their extinction on the mainland. A recommendation was proposed to establish a colony of these animals back at their native location in South Australia (Taylor and Cooper 1999).

A SA mainland Tammar Wallaby Recovery Team was formed to establish and implement a recovery plan for the subspecies. Stakeholders in the recovery team were from the South Australian Department for Environment and Natural Resources (DENR, former Department for Environment and Heritage, DEH), Monarto and Adelaide Zoological Parks, the University of Adelaide and Innes National Park. Following consultation between the SA DEH, Royal Zoological Society of South Australia, Biosecurity Australia (BA), Australian Quarantine Inspection Service (AQIS), Environment Australia (now the Commonwealth Department for Environment and Heritage), the New Zealand Department of Conservation and the Auckland Regional Council, 85 tammar wallabies were captured from Kawau Island, screened for diseases, given a health check by a veterinarian, and returned to South Australia. The animals were held in quarantine for six months at Monarto Zoological Park in South Australia, and a captive colony and breeding population was established, with the view to reintroduce a number of these animals back into parts of their former range (DEH 2004).

The recovery team proposed a trial release of wallabies, followed by subsequent releases. The timing of the subsequent releases would be determined by the results of the trial release and environmental conditions at the time. The number and composition of animals released would be dependant upon the genetic diversity, number and composition of wallabies held at Monarto Zoological Park in the captive breeding colony (DEH 2004).

2.2 Reintroduction site: Innes National Park

2.2.1 Study site

A number of potential tammar wallaby reintroduction sites were considered within South Australia. Large-scale habitat clearance across much of the tammar wallabies’ former range limited the number of suitable release sites. Suitable release sites needed to be of sufficient size (>3,500ha), able to support a self-sustaining population of at least 500 wallabies, where appropriate predator control programs could be undertaken, and be located where the effects of grazing pressure on biodiversity values and agricultural production could be monitored and managed (justification outlined in DEH 2004).

Following a comprehensive site selection process, Innes National Park was chosen as the release site. Innes is located at the extremity of Yorke Peninsula in South Australia (Figure 2.3). It is part of the tammars' historic range, and was thought to be of sufficient size (9,322ha) to sustain a population of tammars (DEH 2004). Innes National Park contains a small abandoned gypsum mining town consisting of five cottages, which are now used for transient tourist accommodation. The area contains some 333 native plant species, with a diverse range of vegetation associations including dunes, coastal heath, mallee woodlands and salinas. Coastal heath dominates the coastline and merges further inland with extensive mallee and grasslands, considered to provide suitable habitat to meet diurnal and nocturnal needs of tammar wallabies (DEH 2004). The large areas of mallee and dense coastal heath are likely to be suitable for tammars to shelter in during the day, and open grassland areas resulting from prior habitat removal (approximately 10 percent of the park) considered suitable for animals to forage in at night (DEH 2004) (see Figure 2.4).

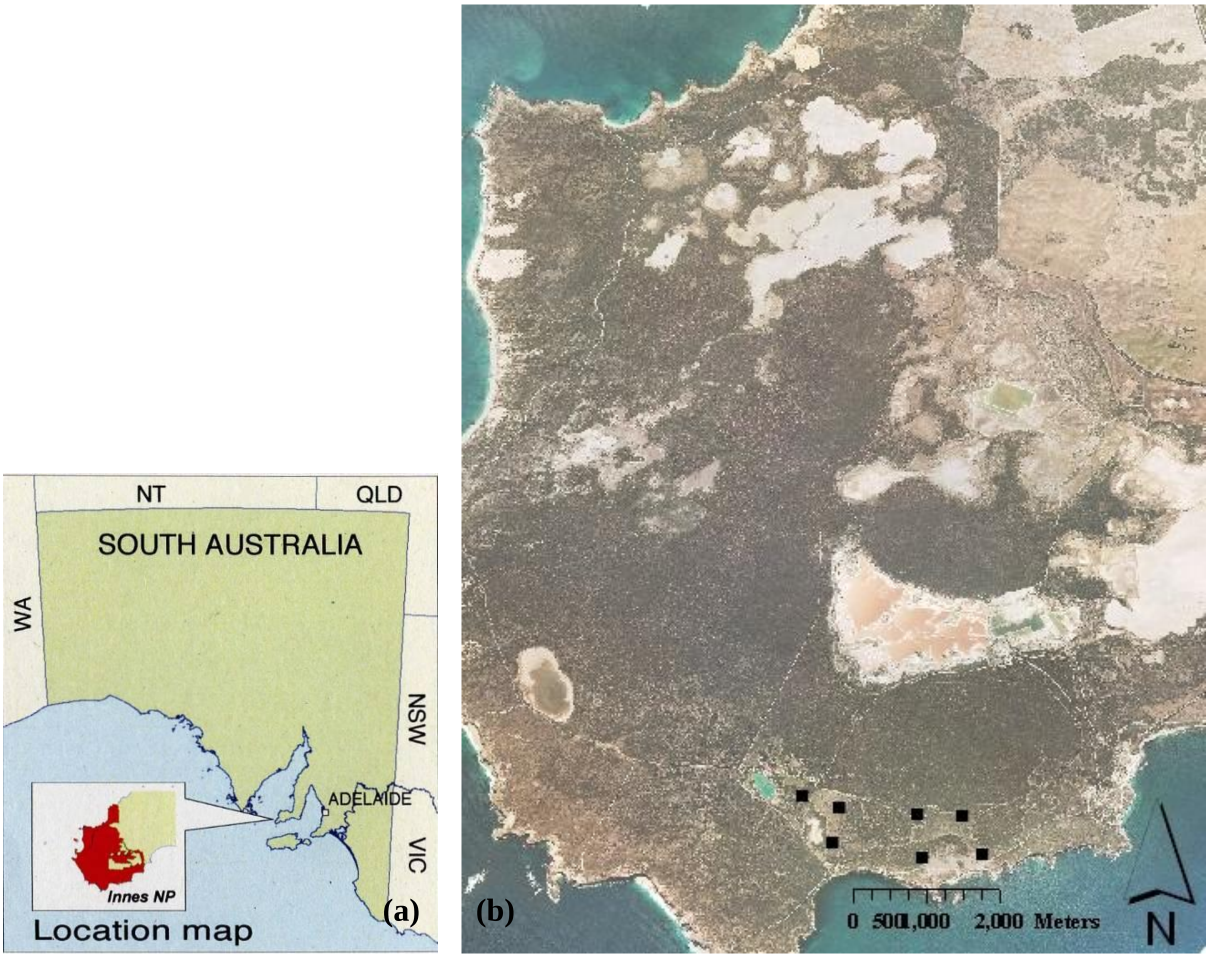

Figure 2.3 a) Location of Innes National Park in South Australia, and b) Release sites within the park (indicated by black squares).

Figure 2.4 Images of tammar wallaby release site habitat in the southern region of Innes National Park, South Australia.

Coastal heath communities in the area contain a range of species including coastal white mallee (*Eucalyptus diversifolia*), dune wattle (*Acacia ligulata*), Coast velvet-bush (*Lasiopetalum discolor*) and various bush pea species (*Pultenaea* sp). mallee woodlands are composed of species such as coastal white mallee, kingscote mallee (*Eucalyptus rugosa*), red mallee (*Eucalyptus oleosa*) and narrow-leaved red mallee (*E leptophylla*), with stands of she-oak (*Allocasuarina verticillata*) and scrub pine (*Callitris canescens*) throughout. Understorey species include dryland tea-tree (*Melaleuca lanceolata*), cockies tongue (*Templetonia retusa*) and other heath plants. Salinas vegetation communities consist of samphire (*Salicornia* spp) and bindyi (*Arthrocnemum* spp), with increasing thickets of paperbark tea-tree (*Melaleuca halmaturorum*) as salinity declines. Dominant groundcover species in areas of low salinity include cutting grass (*Gahnia trifida*), leafless ballart (*Exocarpos aphyllus*) and black-anther flax lily (*Dianella revoluta*). Dune systems contain: spinifex (*Spinifex hirsutus*), club rush (*Isolepis nodosus*), coast daisy-bush (*Olearia axillaris*), coastal wattle (*Acacia longifolia* var. *sopharae*), coast beard-heath (*Leucopogon parviflorus*), and sword rush *Lepidosperma gladiatum*).

The park is also inhabited by 111 species of native birds, 10 species of native mammals and 17 species of native reptiles (DEH 2003). The average summer temperature is 28ºC inland and cooler toward the coast. Winter temperatures do not usually fall below 10ºC. Maximum rainfall occurs during winter, with July recording the highest average monthly fall of 150mm. Total annual rainfall can vary considerably, but on average, the park receives approximately 500mm annually. Due to the coastal location, the area receives strong winds, predominantly from the south-west during winter and the south-east during summer (DEH 2003).

Prior to the first reintroduction of tammar wallabies, the existing fox control program was intensified in October 2003 to try and limit the threat of predation on wallabies. Poison (1080) baits were laid fortnightly at 0.5km intervals along internal and boundary tracks (DEH 2004). Two sand pad transects were also established (on the park boundary and along the main internal thoroughfare) and monitored over four consecutive mornings during July, October, January, and April each year to ascertain fox activity as an indication of fox abundance (DEH 2004). Analysis of bait take and sand pad results were mapped regularly to identity hot spots in fox activity. Increased baiting occurred around the release sites and hotspots one month prior to the reintroduction (DEH 2004). This work was done by SA DEH staff.

During the reintroduction proposal phase, local farmers had expressed strong concerns regarding the potential population expansion into their farming properties. Therefore all efforts were made to alleviate their concerns. All releases were undertaken in the southern section of the park (Figure 2.3b) within 4km of transient tourist accommodation. This area provided adequate habitat for the animals and sufficient accessibility for monitoring. Additionally, it was 6.5km from the park boundary adjoining farming properties, which reduced the chances of wallabies reaching the park boundary (DEH 2004).

The study area was centred on the release sites, with the boundary defined by the distances wallabies moved from the release sites throughout the study period. The study area boundary was delineated by a 500m buffer extended beyond all wallabies' monthly 100% MCP areas (Figure 2.5, and see Figure 4.1 in Chapter 4). A 500m buffer was chosen as it was the approximate radius of an average monthly MCP area and a distance they could potentially travel in any direction beyond the home range they occupied. This study area encompassed approximately 1440ha.

Five different vegetation communities were apparent in the study area, defined using floristic layer GIS (Geographical Information Systems) shape files and a digital aerial photograph obtained from DEH (Department for Environment and Heritage) surveys. The dominant species in each of the five main habitat types were: *Eucalyptus diversifolia*; *E.rugosa*; *Melaleuca halmaturorum*; *Acacia anceps;* and grassland (Figure 2.5). Three additional habitat types were present on the extremity of the study area, but these were such a small proportion of the total area they were not considered in the habitat analysis.

Minor adjustment of the original habitat GIS shape file was made prior to analysis. Inspection of the shape files and aerial map in ArcGIS 9.2 indicated that roads neatly matched the aerial map, however the boarders of the different floristic layers were inaccurate by up to 60m. Because this level of error was considered unacceptable the floristic layer shape file boundaries were edited in ArcGIS 9.2, using editor, snapping and clipping features. In addition a grassland shape file was created as this was not included in the original floristic layers but was apparent on the ground and in the aerial photograph.

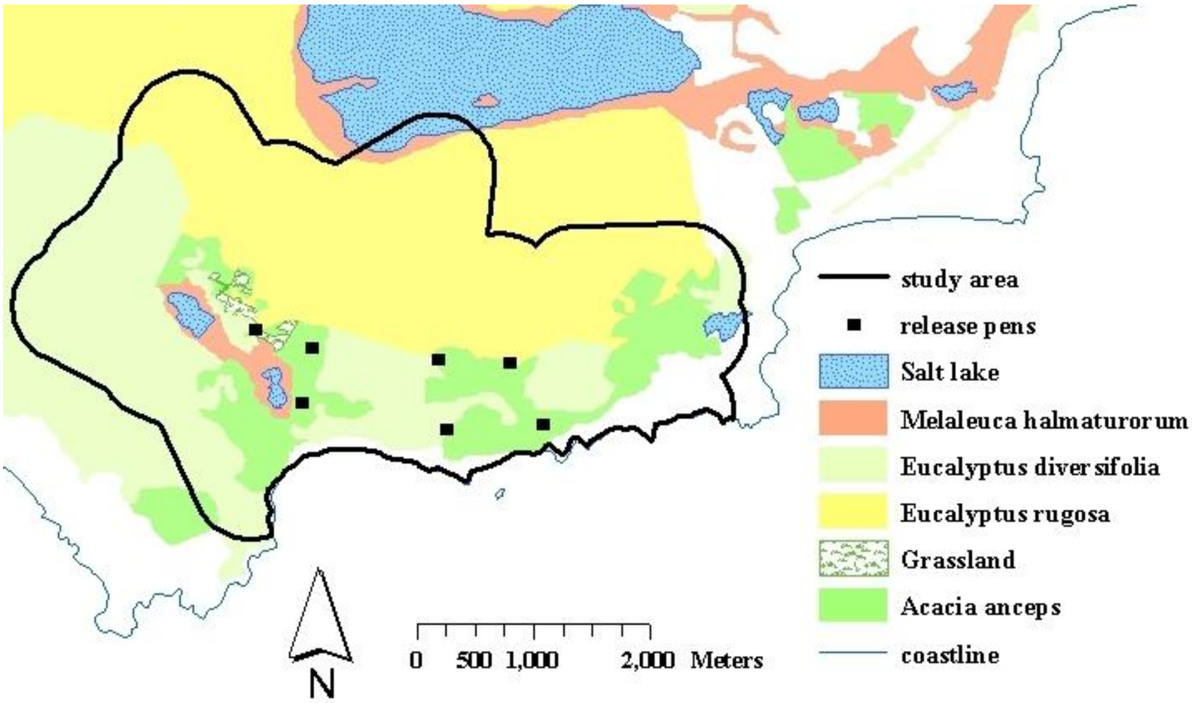

Figure 2.5 Habitat types of the study area within Innes National Park (map created in ArcGIS using vegetation layers supplied by DEH).

2.2.1.1 Habitat assessment of the five vegetation communities within the study area

To be able to infer the value each of the five habitat communities provided to the tammars, I further assessed their properties of habitat structural cover, species diversity, and plant and seasonal grass biomass available. This more specific information about the five vegetation communities could then be used to infer why the tammars may have used each habitat type in the following data chapters.

A total of 95, 4m² quadrats were randomly located across the study area encompassing each habitat type (Figure 2.6). Allocations were made using a random numbers table on a grid map of the area, so that relative proportions of habitat types had an equivalent number of quadrats assigned. Thirty-five quadrats were located in *E.diversifolia* and *E.rugosa* habitat types, 15 quadrats in *A.anceps*, six in *M.halmaturorum*, and four in grassland habitat.

At each location the 4m² quadrat was established in a north east direction of the GPS quadrat coordinates to eliminate human bias. Within each quadrat the habitat structure, species diversity, and biomass were assessed once in spring 2006, and the grass biomass was estimated four times, once in each season in 2006.

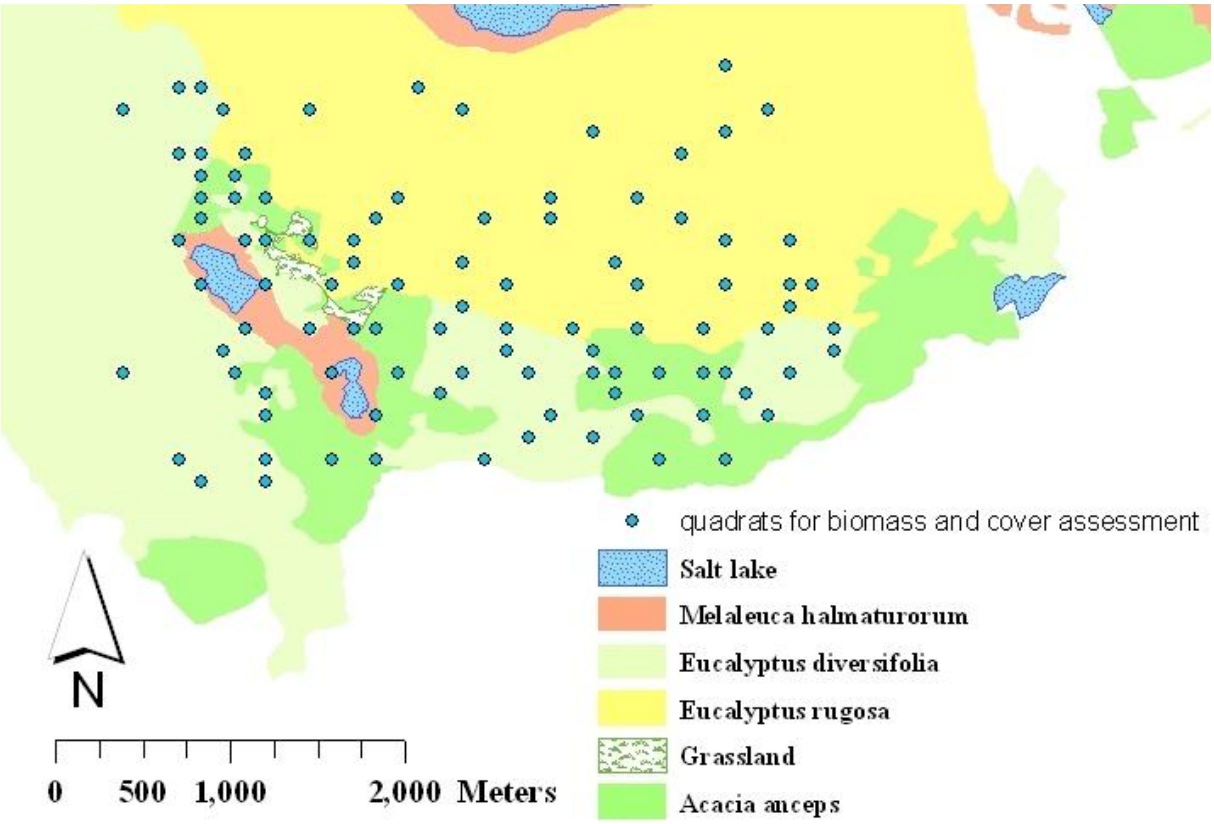

Figure 2.6 Locations of random quadrats in each habitat type within the study area. At each of the 95 4m² locations, the habitat structural cover, species diversity, and plant and seasonal grass biomass were assessed.

At each quadrat the percentage of habitat cover within four structural layers of cover was recorded. The height intervals were: 0-0.5m, 0.5-1m, 1-1.5m, and >1.5m. The percentage cover was a visual estimate of the density of foliage in that height category. Visual estimates put into categorical variables of: 0%, 1-25%, 26-50%, 51-75%, 75-100% cover. This assessment showed that of all the five habitat types, *E.rugosa* provided the least cover within 0-0.5m of the ground, but provided the greatest cover above 1.5m (Figure 2.7). *E.diversifolia* provided the second greatest amount of cover above 1.5m but also offered substantially more cover below 1m than did *E.rugosa* (Figure 2.7). The habitat communities offering the most cover below 0.5m were *A.anceps* and grassland habitats (Figure 2.7). While it appeared the grassland and *M.halmaturorum* habitat offered substantial cover below 1m, assessment of these communities were based on fewer quadrats than the other habitat types, and show a high degree of variability in the results.

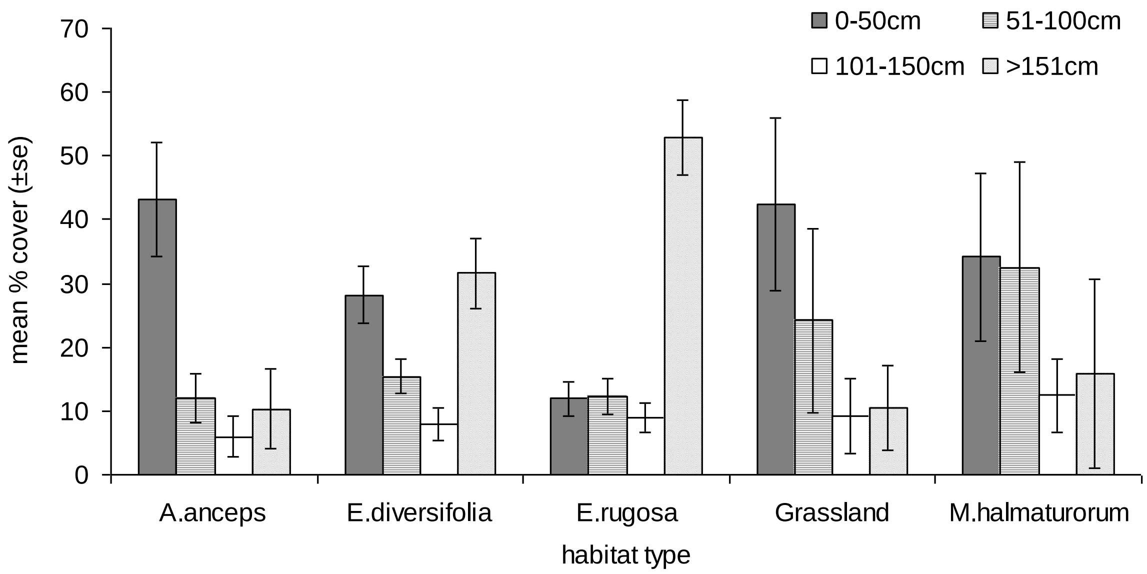

Figure 2.7 Mean percentage canopy cover for each height category (±se), in each habitat type, measured in 95 random $4m^2$ quadrats.

The species diversity and available forage biomass of each plant species in each habitat type was estimated using methods outlined by Tuft (2005). Within each quadrat every plant species present (browse and forb) was listed and ranked in order from dominant to least abundant with regards to the amount of foliage contributed by each species. Each plants relative foliage contribution to the quadrat was also expressed as a percentage, so that the combined percentages for each species in that quadrat added up to 100%. To work out the actual biomass in each quadrat a “hand held unit” (HHU) was used (Andrew *et al.* 1979). A HHU was a small piece of branch, the same species as the dominant species in that quadrat. The number of HHUs which represented the amount of foliage of the dominant species in that quadrat was estimated. The HHU foliage was later stripped, dried (at 70ºC for 24h) and weighed. The dry weight of the HHU was then used to calculate the biomass of all plant species in each quadrat, following the formula in Table 2.1.

Quad#	Habitat type	Plant species	Within category		# HHUs	Unit weight (gDM)	Multiplier	Biomass (gDM)
			rank	%				
				c	d	e	f =d x e / c	= c x f

Table 2.1 Calculations used for determining the available biomass of each plant species within each quadrat, after drying and weighing the hand held unit (HHU).

The seasonal availability of grass in the study area was determined in each of the habitat types by harvesting grass at the same 95 sites as discussed above. At each site three 0.25m² grass plots were harvested. The first of the three plots was placed on the GPS coordinates for that site, the next two were spaced at 20m and 40m to the east of the first location. Grass was harvested in summer, autumn, winter and spring (of 2006). All grass harvested was then dried (at 70ºC for 24h) and weighed.

General findings from the biomass assessment showed that of the two eucalyptus habitats, *E.rugosa* habitat contained lower species diversity than *E.diversifolia* habiat (Figure 2.8, and also see Appendix A for the frequency of occurrence of plant species observed in each habitat type). Of all the five habitat types, *E.rugosa* contained the lowest amount of available ground layer biomass (0-0.5m) of any habitat type (Figure 2.9).

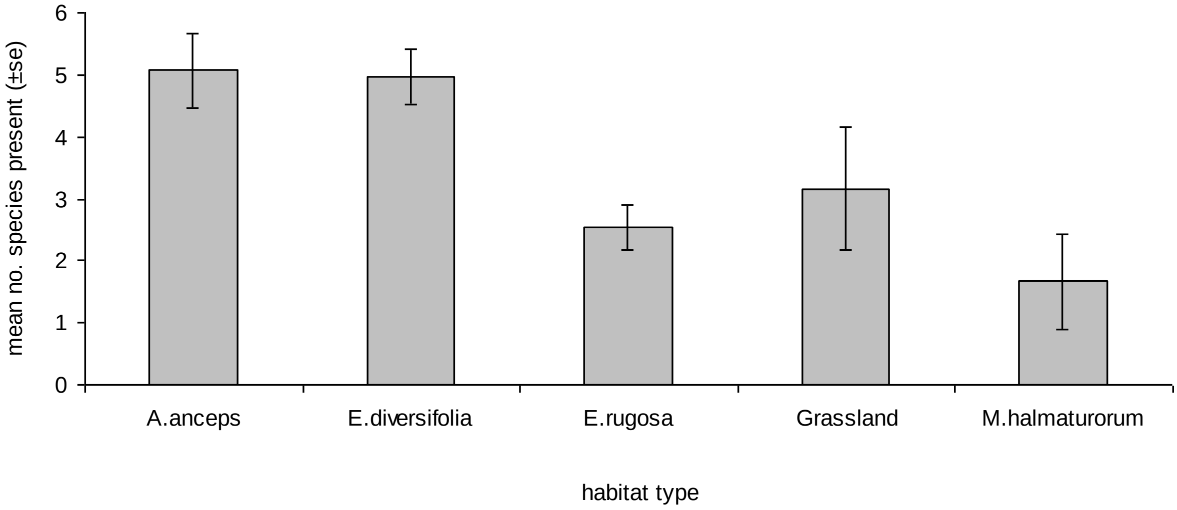

Figure 2.8 Mean plant species diversity found within each 4m² quadrat (±se) surveyed in each habitat type in the study area.

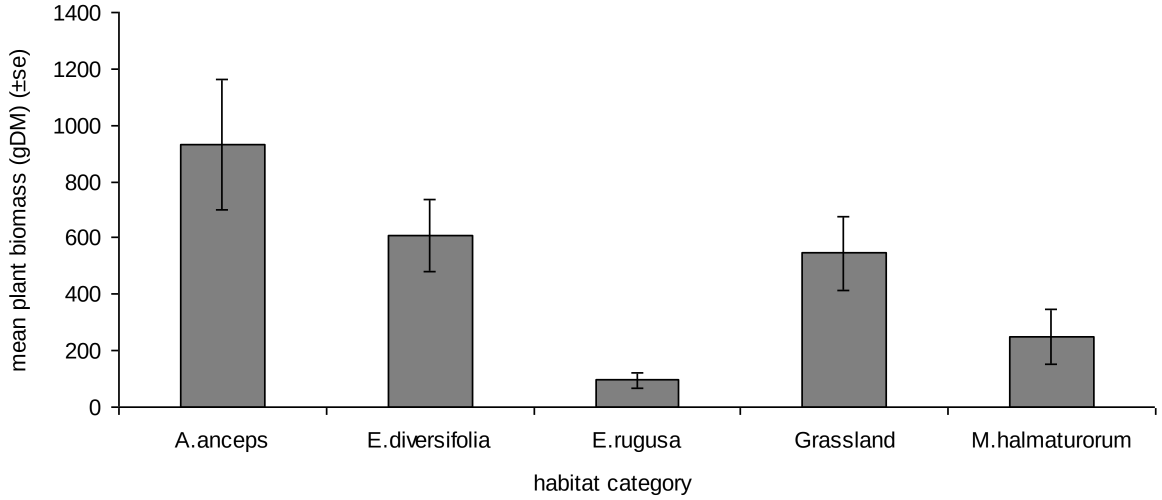

Figure 2.9 Mean total plant biomass available in 4m² (±se) quadrats within each habitat type. All foliage from 0-0.5m above the ground was included, as this was considered to be "available" forage for tammar wallabies.

Assessment of the seasonal availability of grass showed that grass biomass was predominantly available within the grassland habitat type, with the *A.anceps* habiat type also providing forage (Figure 2.10). Overall, the availability of grass was at it is lowest in autumn (Figure 2.10). Combining available plant and grass biomass showed the productivity is lowest in autumn (Figure 2.11), and the habitat types *E.rugosa*, followed by *M.halmaturorum* and *E.diversifolia* contributed the least to the available biomass under 50cm (Figure 2.11).

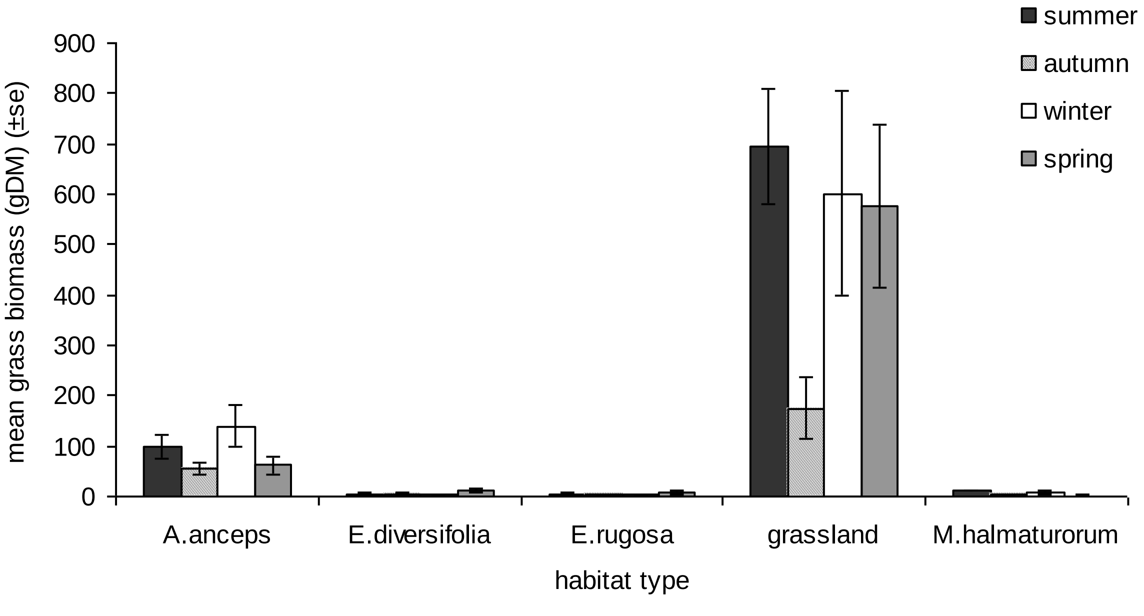

Figure 2.10 Seasonal mean grass biomass per 4m² (±se) quadrat within the each habitat type.

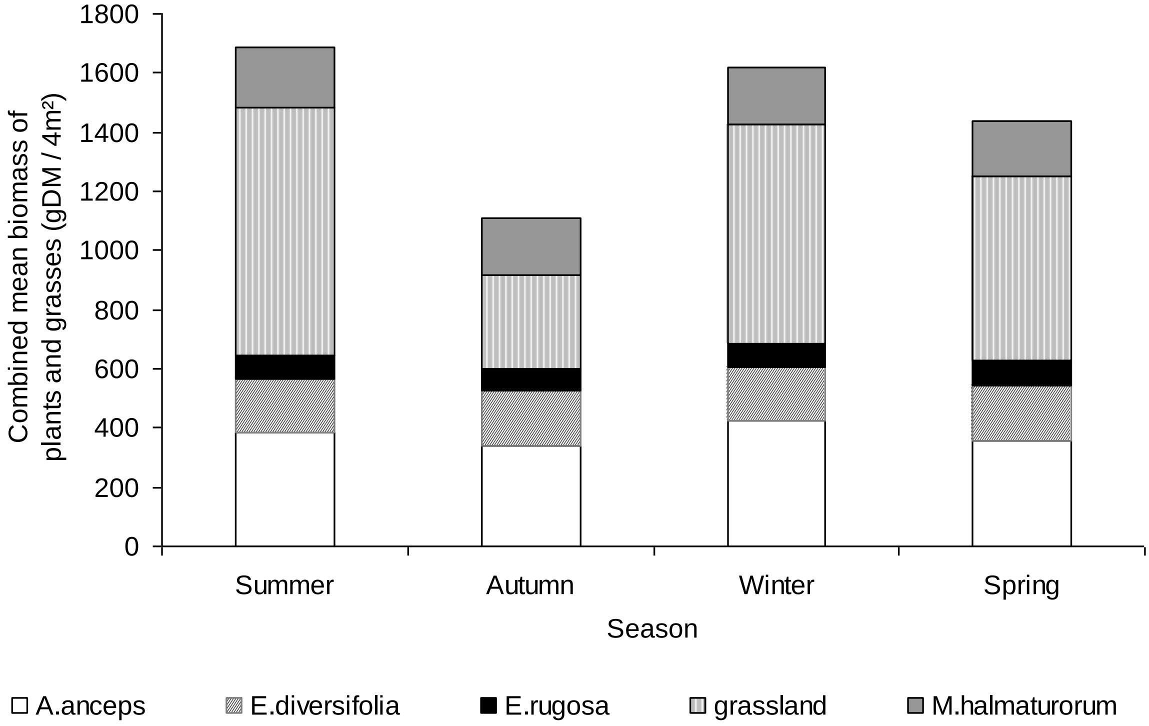

Figure 2.11 Overall seasonal productivity of habitat types: combined mean plant and grass biomass (gDM) per 4m² quadrat.

2.3 Reintroduction

2.3.1 Release group preparation and composition

As previously mentioned, many previous reintroduction attempts within Australia have failed, resulting in poor success/survival rate of the founder population (McCallum *et al.* 1995; Short *et al.* 1992). In order to improve the likelihood of reintroduction success for the SA Mainland Tammar Wallaby reintroduction, we attempted to implement a well thought out translocation plan (see DEH 2004), that considered the genetic composition of available animals, release group configuration, predator wariness, and incorporated extensive post-release monitoring. An initial trial release of 10 wallabies was followed by a more substantial release of 36 wallabies. Specific individuals selected for release were largely controlled by Monarto Zoo, which was in relation to initial pen allocation, and the availability of different sexes and ages surplus to the captive breeding program. These two releases comprised the foundation of this study. Subsequent reintroductions were also envisaged, pending information on the survivorship and reproductive success of animals from the first two releases and continued viability of the release site.

Prior to the reintroduction, genetic analysis was undertaken in collaboration with Andrea Taylor (Monash University) to assess genetic variability in the population and relatedness of the captive wallaby population. The aim was to retain a broad spectrum of genetic diversity within the animals to be released and in the captive breeding program at Monarto Zoological Park (DEH 2004). The captive population was established to provide a secure population of animals which could supplement the reintroduced population, or source future reintroduction events at different sites within South Australia (DEH 2004).

As already mentioned, tammars use communal vigilance for predator detection, and thus Blumstein *et al.* (2002b) suggested that tammars would benefit by being reintroduced in groups. Blumstein *et al.* (1999) further recommended release group sizes of six animals as captive studies revealed the anti-predator benefits of group living reached an the inflection point at a group size of two to four animals and an asymptote at six. Therefore, we applied Blumstein *et al* (1999) findings to the reintroductions conducted here. The first release comprised two groups of five animals (each with four females and one male), while the second release comprised six groups of six animals (each with four females and two males). Release groups had a strong female bias for several reasons: to approximate what was known of social structure in the wild, to facilitate maximum breeding potential, and to reduce male competition and need to disperse in search of mates soon after release (DEH 2004).

To facilitate understanding of animals’ establishment and ecology in a new environment, it is important to add an experimental element to a reintroduction (Armstrong and Seddon 2007; Hardman and Moro 2006b; Seddon *et al.* 2007). Here, I aimed to find out whether familiarity of group members (to each other) might influence their behaviour (assessed by habitat use and social configurations) while establishing in a new environment. Thus for each release, the animals which made up release groups were either housed together in captivity as a group for at least one month prior to release (categorised as “familiar” groups), or housed separately but were released together as a group (“unfamiliar”).

Animals raised in captivity or on predator-free islands have no opportunity to learn about predators they may encounter at a potential release site (McLean *et al.* 1994; McLean *et al.* 2000). Being aware of predators is of critical importance as predation has been the primary cause of the many failed previous macropod reintroductions within Australia (Short *et al.* 1992). The two processes required for animals to respond to predators are first to recognise and then to cope (McLean *et al.* 1994), where recognition is genetically acquired or through experience, while coping skills are likely to be entirely learnt and will improve with experience. Griffin *et al.* (2001) have previously shown that tammar wallabies' responses to a predator can be enhanced through training in captivity. Likewise, McLean *et al*. (2000) found that using a live predator (a trained dog) to train captive reared wallabies generated improved predator recognition skills after a minimum of one or two predator experiences lasting five to ten minutes. Here, to heighten animal wariness and response to potential predators prior to release, all 36 animals for the second release were subjected to four "predator training" events on consecutive days in the week prior to their reintroduction. On each occasion a domestic dog (red heeler breed) was muzzled and led (using an extendable lead) through the tammars' enclosure for five minutes by a human (foreign to the wallabies and wearing a beige coloured National Parks uniform). The dog was allowed to lunge toward the wallabies, but no contact was made (DEH 2006).

Early on the morning of each release, animals to be released were captured by hand in their pens, given a health check and a selenium and vitamin E injection to help reduce stress. Measurements of leg, foot and head length, weight and a body condition score out of five (developed by the Veterinarian based on their rump fat condition, pers comm. Smith 2004) were taken, along with the presence and sex of pouch young. All animals released were micro-chipped between their shoulder blades, and fitted with radio-tracking collars (as detailed below). Each animal was held in a hessian bag, and animals were transported to the release site in an air-conditioned van (Figure 2.12), taking approximately four hours.

Figure 2.12 Animals being transported to the release site at Innes National Park. (Photo: Trudie Jaques).

2.3.2 Release events & location

The first trial reintroduction occurred in the austral spring, November 2004, and comprised ten animals in two groups, each with four females and one male. One group was “familiar” and the other “unfamiliar” (as explained above). The second release took place in winter, June 2005, and comprised 36 animals in six groups, each with four females and two males, where three groups were “familiar”, and three groups were “unfamiliar”.

Once transported to the site, each group of wallabies was temporarily released into 10m x 10m pens with 1.2m high shade cloth walls (Figure 2.13), where animals were held for several hours. Temporarily holding the animals was to eliminate the likelihood of immediate dispersal due to stress or fear of human presence. The pens were opened at dusk, allowing the animals to make their own way out. Pens were approximately 500m apart (Figure 2.14). Supplemental feed (“Kangaroo pellets”) and water were provided in pens while the animals were being held. Following the second release, supplemental feed and water was supplied near the release sites every two to three days to help the animals survive through the winter months (DEH 2006).

Figure 2.13 Tammar wallaby release pen.

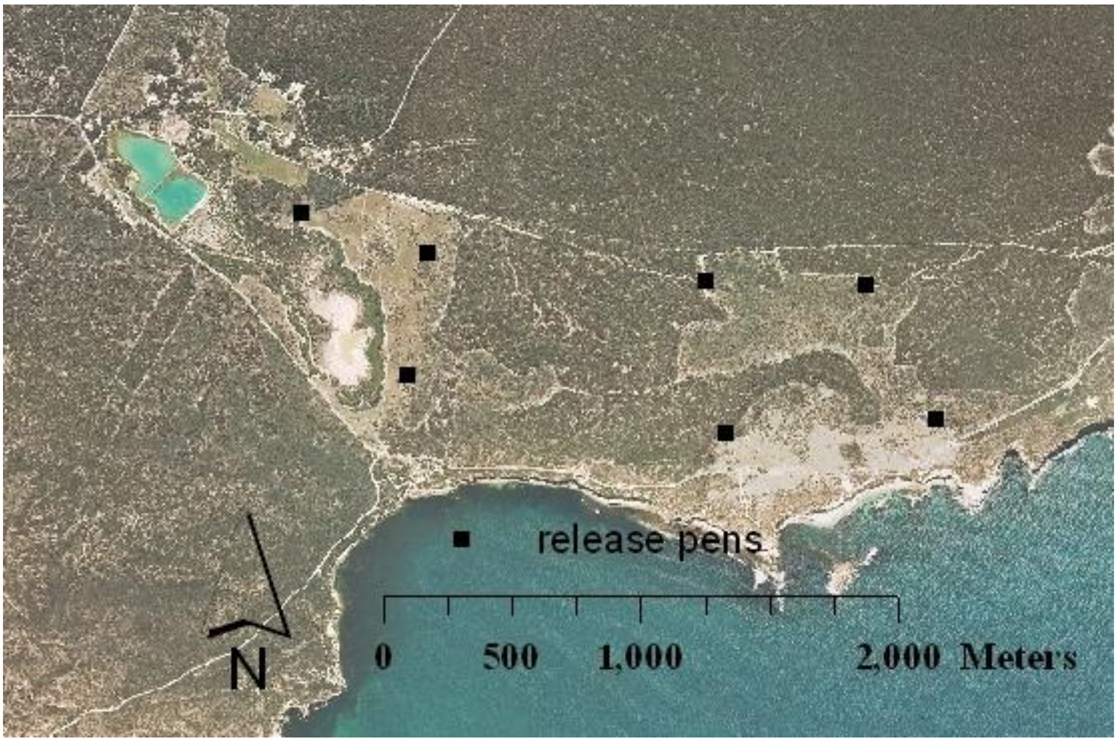

Figure 2.14 Spacing of pens at reintroduction site in Innes National Park.

2.3.3 Monitoring

All tammar wallabies released were micro-chipped and fitted with VHF radio collars (specifications given below). Animals were radio-tracked for twelve months following their release to determine survival, movement patterns, home range, habitat preferences, and group cohesion (see section 2.3.3.5 for details of monitoring frequency and timing). Bi-annual trapping also occurred in late summer (February) and late winter (August) for seven nights each time. This was done using cage traps covered by hessian, baited with carrots, rolled oats and peanut butter. To encourage animals into the traps, the traps were wired open at both ends and pre-baited for three nights prior to the scheduled trapping period. Traps were set late afternoon or overnight and checked at first light. Trapping allowed animals to be fitted with replacement radio collars, weighed, sexed, measured (leg, foot, and head length), and checked for breeding status and physical condition (body condition score, as mentioned previously). Newly captured individuals were micro-chipped and ear-notched to obtain DNA samples to contribute to the genetic analysis (DEH 2004).

2.3.3.1 Collar fitting:

Four weeks prior to the first reintroduction, animals were fitted with leather dog collars of similar dimensions to radio collars, to allow them to become accustomed to wearing a collar while they were still in captivity and to check any effects of collars on animals. One week before the first release, radio collars were switched on and fitted to the animals. For the second release, collars were fitted to the animals on release day. Collars were checked to ensure fit (where one or two fingers could fit under the collar), with dense self-adhesive foam used to adjust the size of the collar on smaller animals where necessary.

2.3.3.2 Collar specifications:

Radio collars obtained from Sirtrack Wildlife Tracking Systems Pty Ltd (Havelock North, New Zealand) were leather collars 250-300mm x 12mm x 12mm, with a buckle closure. They had high power boards (to maximize potential signal strength/coverage), and batteries inline around the collar. They had a pulse rate of 40ppm and latching mortality signal pulse rate of 80ppm. Antenna length was 220mm. Collars weighed less than 5% of the tammar wallabies' average body weight (5.5kg for females, 7.5kg for males; Hinds 2008).

For the first release, a mortality signal was set to activate after 24h inactivity, but in the second release this was decreased to 8h. With only an 8h delay I was aware of deaths more quickly than previously available on the collars from the first release.

Transmitters from the first release were powered by 3 x 2/3 AAA batteries, and had a life of 10.5months, while those from the second release had 3 x 1/2 AA batteries, and transmitter life of 9.8months. Unfortunately, the second release battery specifications or the batch of batteries were faulty, as the collars began failing after only four months.

Duty cycles were used in all collars to extend battery life. For the first release, the duty cycle was 19h on/5h off, and in the second release 21h on/3h off. The time period collars were "on" coincided with the animals' nocturnal periods of activity, early morning and late afternoon. The second release collars were "on" for more hours, as there were more nocturnal hours during winter.

To make identification of animals easier when sighted in the field, animals were given a unique combination of reflective colour tape on their collar (Figure 2.15). Following the second release, animals were given a single colour to signify which experimental release group they came from.

Figure 2.15 Wallaby and collar with reflective tape (Photo: Trudie Jaques).

2.3.3.3 Tower specifications and triangulation:

Towers for radio-tracking were constructed by Faunatech Pty Ltd (Bairnsdale, Vic), mounted onto 6’ x 4’ x 4’ trailers (Arrow Trailers), and the operational equipment was surrounded by a custom made tent for shelter (Figure 2.16). Towers consisted of a rotating mast seven meters high (excluding trailer height), with a pair of six element RhoTec Yagi antenna, aligned to “true north”. The antenna fed signals into an Australis 26K wildlife telemetry receiver (Titley Electronics) via a RhoTec Null/Peak switch box. “Null” signals were used preferentially to record the bearing of a signal. However, on occasion when signal strength was too weak to pinpoint the null, the range of the “peak” signal was recorded. These peak bearings were used during triangulation to strengthen and confirm the direction of null bearings obtained from the other towers. When angles obtained from the peak signal did not align closely with the other bearings they were discarded from the triangulation calculation.

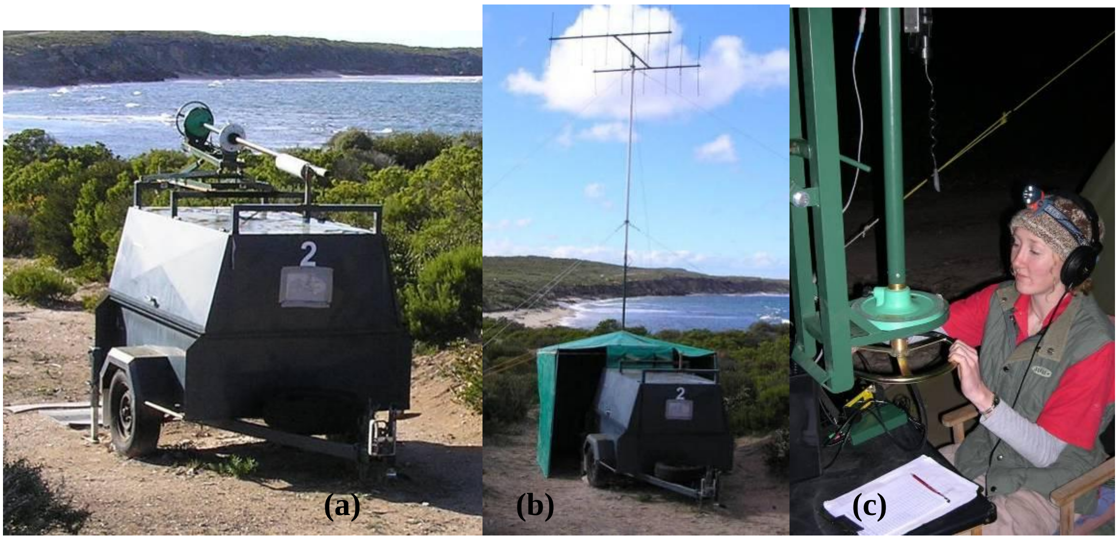

Figure 2.16 a) Radio-tracking tower dismantled and on top of trailer, b) Erected, and c) In use. (Photo a&b: Trudie Jaques, c: Leah Kemp).

Obtaining accurate location points for an animal relies on the accuracy of the equipment. Equipment accuracy was assessed nightly in every sampling period by obtaining bearings on two “fixed collars” of known location situated in the vicinity of the animals. The average error angle (tower bias) for each individual tower to these fixed collars was calculated nightly and for each month, and re-calculated for subsequent locations if cable or tower maintenance had occurred during the month. The bearings recorded from each individual tower to the animals were then adjusted according to their error margin to the fixed collars, and in particular, by the bias of the closest fixed collar to the animal.

The computer program Location Of A Signal (LOAS; Ecological Software Solutions 2007), was used to convert all tower bearing data obtained from the radio-tracking into triangulated GPS locations. The Maximum Likelihood Estimator was used when three or four towers gave a bearing, but when only two bearings were available the Best Biangulation Estimator was used. Of the 13,480 locations successfully triangulated from radio-tracking during the study, 13,058 locations were obtained with error ellipses <10ha. Only 12% of those records had error ellipses greater than 3ha. Locations with ellipses less than 10ha had an average maximum radius of 100m which was considered an acceptable margin of accuracy, as the ellipse size was smaller than the home range area (82% of all home ranges calculated were > 10ha, see Chapter 3).

2.3.3.4 Tower locations in the study area:

Preliminary studies were undertaken prior to the reintroduction of the wallabies to test the signal range of the collars and ideal tower locations. Using topographical maps and knowledge of accessibility, towers were erected at various elevated locations surrounding the proposed release pens. The range of the towers at each location was tested by locating trial collars (of similar specifications to the wallaby collars) at various positions throughout the study area, and encompassing varying topography (Figure 2.17). From this preliminary investigation, it was anticipated that towers would detect transmitters of our specifications for up to approximately 4000 metres.

Tower locations within the study area were altered during the study dependant upon the location of the animals so that the best signal strength and triangulation positions could be obtained.

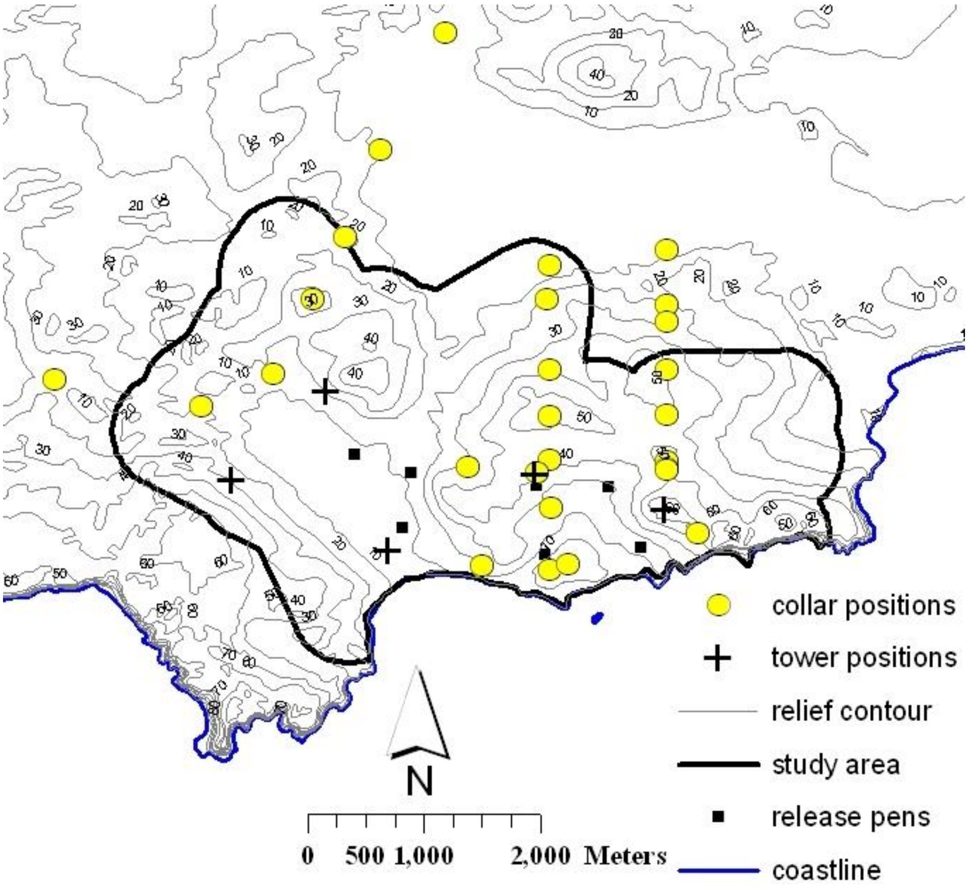

Figure 2.17 Preliminary investigation on the expected range of radio-tracking towers within the study area. Each trial collar position was detected by at least two towers.

2.3.3.5 Radio-tracking

Immediately following each release, all animals were radio-tracked for approximately 30 consecutive nights and days. Thereafter, animals were radio-tracked for approximately nine nights per month over the following twelve months after each reintroduction. Radio-tracking was conducted from three or four of the mobile radio-tracking towers simultaneously, where the towers were located strategically surrounding the animals in the study area. Radio-tracking the animals from remote towers permitted them to exhibit natural behaviours (uninhibited by human presence). Using mobile (as opposed to fixed) towers allowed animals to be followed if/when they moved out of range by moving the tower to a better position. As the animals are nocturnal, the majority of radio-tracking took place to coincide with their activity periods. Monitoring commenced at or soon after dusk, until one or two hours after dawn. A location for each animal was also obtained each afternoon. To avoid auto-correlation of the data for each individual (see Otis and White 1999; Swihart and Slade 1985; 1997) there was a minimum 60 minute break between obtaining locations for the same animal.

In order to assess possible social interactions between animals, animals needed to be located at approximately the same time so that distances between individuals could be estimated. Therefore, locations for all animal were obtained sequentially at three minute intervals within blocks of time termed “sampling periods”. The duration of sampling periods was dependant on the number of animals available to be radio-tracked, this fluctuated as a result of reintroduction events, deaths, and the battery life of the collars. The maximum duration of a sampling period was three hours (when the largest number of available animals was present).

The following chapters use radio-tracking data obtained as outlined here to detail home range, habitat selection, fine scale habitat use and social dynamics of the wallabies following their reintroduction.

3 Chapter 3: Home range & social dynamics

3.1 Introduction

To understand why animals live where they do, why they go certain places to do certain things, and how they share or divide the environment, researchers must grapple with the concept of “home range” (Powell 2000). The home range concept was first introduced by Burt in 1943 as “that area traversed by an individual in its normal activities of food gathering, mating and caring for young” (Burt 1943:351). It is commonly delineated as the smallest area which accounts for 95% of the animal’s space use, i.e. where you would find the animal with a 95% certainty (White and Garrott 1990). Animals generally use space disproportionately within a home range. The areas that receive concentrated use (“more than expected by random”, Powell 2000) by an animal are defined as “core area”. The concept of a core areas was first defined by Kaufmann in 1962 (cited in Samuel *et al.* 1985), and is considered to be the most important part of a home range (Burt 1943; Samuel *et al.* 1985), most likely containing home sites, refuges and the most dependable food sources (Burt 1943).

The size of a home range is thought to be a function of habitat quality, productivity, resource distribution, predation pressure, population size and individual energy requirements (Burt 1943; Morse *et al.* 2009; Thogmartin 2001). For example, for many mammal herbivores home range size has been observed to decrease as food availability or productivity increases (Stirrat 2003). This suggests that home range size may reflect an individual’s energy needs, whereby they only travel as far as necessary to obtain desired resources (Fisher and Owens 2000). Home range size may also vary as a function of the risk in moving. For example, female roe deer (*Capreolus capreolus*) with young reduced the size of their home range compared to females without young, as they did not want to roam too far from their fawns hiding in the denser habitat (Bongi *et al.* 2008). Home range size may also be a reflection of the location of conspecifics, either due to increased competition for resources so they need to expand or shift their area accordingly, or as a result of the breeding season if males need to expand or shift their range to search for mating opportunities (Lapidge 2001; Stirrat 2003). This sex bias in home range size is observed in most macropods (Croft 1989).

The amount of home range overlap between individuals can provide indirect information about the likelihood of social interactions (Shier and Randall 2004). However, considering home range overlap alone reflects the spatial dimensions of interaction and not the temporal dimension (Fieberg and Kochanny 2005), Doncaster (1990) proposed two types of overlap: static and dynamic, where static is the spatial overlap of two home ranges, while dynamic overlap involves the interdependent movements of the two animals. Powell (2000) suggested that static overlap should be studied in conjunction with dynamic interactions. The amount that animal home ranges or core areas overlap and the amount of time conspecifics utilise common area simultaneously may be influenced by a range of factors, such as the benefits or costs of group living, reproductive cycles/strategies of the animals, and the density and availability of resources.

If resources are plentiful, remaining faithful to an area has its benefits, as animals have spatial awareness of food resources and escape routes from predators. This site fidelity is seen in many taxa, including: insects, birds, mammals, reptiles, amphibians, and primates (Janmaat *et al.* 2009). However, as animals learn new things about their environment, or as new resources develop or are discovered and old ones disappear, the animal's cognitive map of the land changes over time (Powell 2000), and the locations they utilise may change. Furthermore, an animal's memory of high quality sites may influence future selection. For example, Wolf *et al.* (2009) reported that wapiti (*Cervus elaphus*) demonstrated a preference for familiar locations they had visited most recently, suggesting that memory of the high quality sites influenced the selection of those locations. Additionally, if the costs of remaining in an area begin to outweigh the costs of moving, the animals are likely to need to shift their home range and activities in search of suitable habitats in a landscape (which are generally not uniformly distributed). Shifting from a familiar site into new areas may be necessary if resource quality or quantity diminishes, if competition is high, or dispersal takes place (Janmaat *et al.* 2009). Shifting allows the animals to accommodate the changing seasons and their changing needs. For example, mangabey (*Lophocebus albigena*) home ranges were observed to drift within a year to follow resources (Janmaat *et al.* 2009), and iguanas (*Cyclura cychlura cychlura*) expanded their home range or used different areas between seasons (Knapp and Owens 2005). A notable disadvantage of moving is the lack of knowledge the animals will have about any new areas they encounter, and with this comes an increased likelihood of predation. For example Janmatt *et al.* (2009), found movement of mangabeys and vervets (*Cercopithecus aethiops*) into a new area increased the number of predation events.

Another reason animals may have to become familiar with a new area is if they have been reintroduced into an area. However, many deliberate releases of animals result in failure because the vast majority of animals frequently die soon after release (Teixeira *et al.* 2007).

To survive in a new environment an animal needs to be healthy, behaviourally competent (Mathews *et al.* 2005), have the capacity to learn and memorise the location of resources within its environment (Teixeira *et al.* 2007), and avoid predators (Box 1991 cited in Teixeira *et al.* 2007, also see Chapter 1). The first month following a reintroduction may be the most critical time. For example, Tavecchia *et al.* (2009) observed that one third of all mortalities for released crested coots (*Fulica cristata*) took place within the first month following their release due the animals' inexperience in a new environment. This supported the recommendation by Armstrong and Seddon (2007) to examine the establishment phase and post-establishment phase separately.

This thesis examines the reintroduction of the previously extinct South Australian mainland subspecies of tammar wallaby. This chapter looks at the influence of a range of variables on their home range and core area, home range stability and social overlap. These variables include: release group configuration, sex, number of conspecifics overlapped, amount of area shared, time of year, number of deaths in a previous month, and time since release.

In this chapter I aimed to determine any differences between the establishment and post-establishment phase. The establishment phase is a critical time following reintroductions as the population can fail to survive the establishment phase in conditions which would otherwise enable persistence for an established population (Armstrong and Seddon 2007); therefore, it is important to determine where those differences may occur.

To examine whether the release protocol may influence the tammars establishment an experimental element was incorporated in the reintroduction. This experiment aimed to test the hypothesis that animals released in pre-established groups (animals housed together for one month prior to the reintroduction to form a “familiar group”) would be more cohesive, and not disperse as far into novel habitat which may put them at a greater risk of predation compared to unfamiliar groups of animals (animals housed separately in captivity prior to the reintroduction and release together as an “unfamiliar group”).

The influence of seasonality on home range and core area, home range stability, and social overlap was also addressed in this chapter, as understanding the habitat requirements of a species is fundamental in assisting decisions about reintroductions and ongoing conservation management (Finlayson *et al.* 2008).

3.2 Methods

As outlined in the previous chapter, 46 tammar wallabies were reintroduced into their former range, Innes National Park (South Australia), over two reintroduction events using an experimental approach to assess the influence of group familiarity on home range and social behaviours while establishing in a new environment. The first release occurred in spring (November 2004), where 10 animals were released in two groups (one familiar and one unfamiliar), and the other in winter (June 2005), where 36 animals were released in six groups (3 familiar and 3 unfamiliar). Groups of animals were released approximately 500m apart (see Chapter 2). Reintroduced animals were intensively radio-tracked for approximately 30 nights in the month following their release, and then for approximately nine nights each month for the next twelve months. A total 13058 usable triangulated radio locations were obtained and used in these analyses (see Chapter 2).

3.2.1 Size of home range and core area

Various methods have been used to calculate home range area, the most common being Minimum Convex Polygon (MCP) and Kernel estimates. However, both estimators have their drawbacks and notably, even different software programs running the same method can compute different home range areas (see Gallerani Lawson and Rodgers 1997). While MCP's may overestimate an animal's area (Harris *et al.* 1990; Worton 1987), kernels are highly sensitive to the parameters used. In particular, various issues exist over appropriate bandwidth selection and smoothing for kernel estimates (Blundell *et al.* 2001; Fieberg 2007; Powell 2000; Seaman and Powell 1996).

In addition to selecting an appropriate home range estimate method, the number of locations obtained, the sampling interval between obtaining the locations, and duration of days in collecting the locations all need to be appropriately considered (Börger *et al.* 2006). The sampling frequency needs to be spaced so that location points obtained are independent (not autocorrelated; see Swihart and Slade 1985. See Appendix B for the mean distances tammars moved between consecutive sampling periods in this study). Sampling duration needs to be appropriate, as data collected over too short a time period may not sample an animal within all areas that might be considered part of its home range, while data collected over too long a time period may not reflect changes in an animal's home range during the time period (Powell

2000). Importantly, to be able to assess site fidelity over time and temporal/seasonal requirements, care needs to be taken when deciding at what temporal scale the home range area and location will be assessed. For example, the home range may be defined for a season, year, or a lifetime.

In these analyses home range areas were estimated using MCP methods as opposed to kernel. This decision was based on the fact that producing kernels requires the smoothing parameter (‘h’ value) to be adjusted appropriately for each kernel calculated, thus using kernels involves a level of subjectivity. As different ‘h’ values change the resulting size and area of a kernel, it was suggested that it was not statistically sound to use this technique when comparisons between animals within months and for individuals between different months would be done (Lethbridge *pers comm*. March 2009). Thus here, I use 95% MCP’s and 50% MCP’s for total home range and core areas respectively.

MCPs were created using the latitude/longitude location data derived from radio-tracking (as outlined in the Chapter 2). Locations were entered into ArcGIS 9.2 (ESRI Inc. 2006), and the home range tools (HRT) application (Rodgers *et al.* 2007) was used to create 95% and 50% MCP areas for each individual each month. The HRT software is an ArcGIS® version of the home range extension for ArcView GIS®. Monthly MCPs were created for the period November 2004 to July 2006. One trip was conducted at the end of February and beginning of March 2006, and was called FebMar06 in the analysis, with no trip conducted in June 2006. The first reintroduction occurred in November 2004, and the second in June 2005, both of these months were the longest in duration (spanning 30 days), while other months used data over an average nine day period. A minimum number of 35 location points were obtained for each animal in each month, with averages varying from 35 to 115 (Figure 3.1).

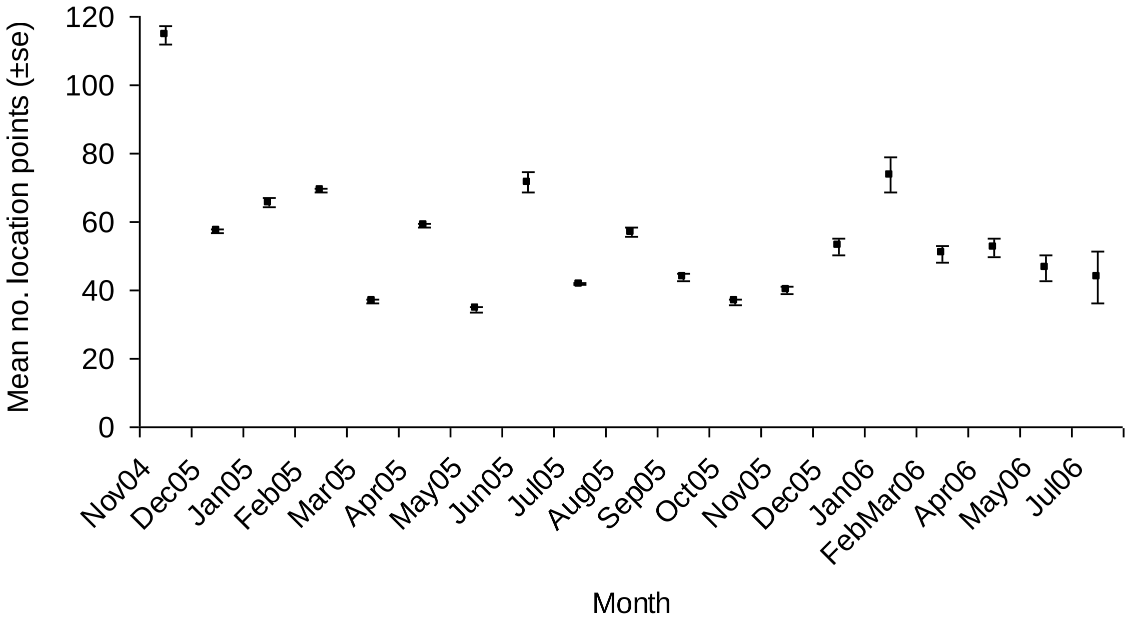

Figure 3.1 Mean number of location points (±se) obtained for each animal from radio-tracking (with error ellipses <10ha) for each month.

To define a home range it is generally recommended that animal location data is obtained over a sufficient number of days, encompassing all hours of the day in order to be representative of an animal's movements (White and Garrott 1990). A minimum of 30 location points (but preferably 50 or more) is recommended for an accurate home range size estimate (Millspaugh and Marzluff 2001). The applicability of this recommendation to my data was confirmed by assessing the minimum number of points required for a monthly home range size to reach a plateau using location points for six animals from varying months. Random points were selected in increasing increments of five (starting with 10, and ending with 60), using the sampling tools application in Hawths tools (Beyer 2006) for ArcGis 9.2. For each increment, a 95%MCP area was calculated using HRT tools. MCP areas were graphed against the incremental numbers of location points and the asymptote assessed. Preliminary tests reflected the recommended minimum requirement for accurate home range estimation. Therefore, all 95% MCP home ranges used in these analyses were estimated from a minimum of 30 location points. In actuality, an average of 56.55 location points (±1.36se) (ranging from 30 – 121) were used, with more than half of the estimates being derived from over 50 location points (Figure 3.2). Enforcing the minimum of 30 location points here meant that this could be ignored as a random effect during statistical modelling.

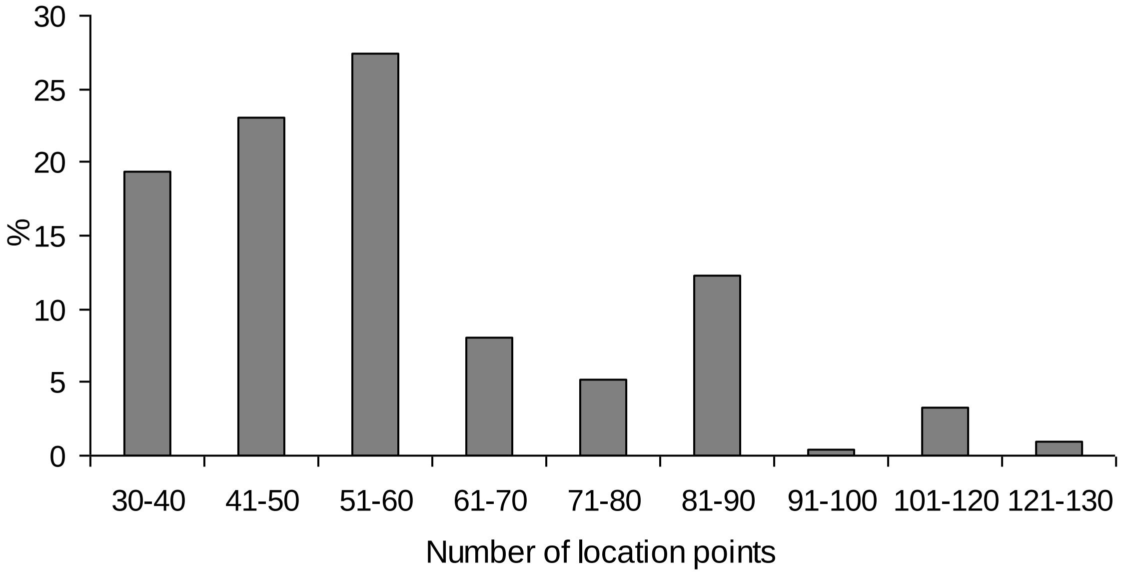

Figure 3.2 Percentage of 95%MCP areas derived from different numbers of location points obtained from animals (n=212).

The size of animal home range and core areas may be influenced by a variety of different factors. Using modelling I examined: the influence of the experimental group (familiar and unfamiliar); sex and pouch young status (males, females with pouch young, females without pouch young); the percentage of the area shared with one or more other animals; and the number of animals that overlapped (see section 3.2.3 for estimation methods) on home range and core area sizes of reintroduced tammar wallabies during their establishment month and for a year post-establishment. The time of year was an additional variable included in the post-establishment analysis. For analysis months were pooled into biologically meaningful categories: Jan-Mar, Apr-May, Jun-Aug, Sep-Oct, and Nov-Dec., which related to the climatic season and breeding periods (as outlined in Chapter 2). I also considered that immediately following a reintroduction, animals will be unfamiliar with their environment, and so their lack of knowledge of the environment may also be influential on home range and core area size. Nativity was therefore considered as a variable, with size of home range and core areas during the establishment month compared to the same time of year one year later when they were more familiar with the habitat. All analyses were carried out using SAS Version 9.2 (SAS Institute Inc. 2008).

Linear mixed effect models were used to model home range size and core area post-establishment (Bolker *et al.* 2009). A random animal ID effect was incorporated into the models to account for the dependence in the results from the same animal (Bolker *et al.*

2009). In the two models (home range size and core area), predictor variables were required to firstly satisfy a *P*-value criterion $p<0.10$ in a univariate model before they were entered into the multivariate model. When global *P*-values for predictor variables were statistically significant, *post hoc* tests were carried out to determine where the significant differences occurred.

In modelling the size of home range and core area during the establishment phase compared to an equivalent time of year post-establishment, data from the winter release (Jun05) was compared to the months of Jul-Aug more broadly. Univariate linear mixed effects models were used and a random animal ID effect also incorporated.

Linear regression models were used to assess the influence of predictor variables on home range and core areas during the establishment phase from the winter (Jun05) reintroduction only, as sample sizes for the spring release (Nov04) were insufficient. Significance of predictor variables was obtained at the univariate level only, as there was not enough data to warrant fitting multivariate models on the establishment phase data.

In all models for home range and core area the data was somewhat right skewed and thus log-transformed prior to modelling. For biological relevance these results are reported as the back-transformed value (with the 95% confidence intervals), which subsequently is a median value. Regression coefficients from log transformed data were not back-transformed in the text, however for biological relevance they were also reported as a percentage increase or decrease. All *P*-values associated with these home range and core area analyses are related to the modelled data on the log scale.

3.2.2 Range shifts and stability (home range location)

Following reintroduction, animals are required to establish their home range in a new environment. I sought to determine whether animals released in pre-established groups versus unfamiliar groups differed in they way they established. This was done under the hypothesis that familiar groups would be more cohesive and establish home ranges in closer proximity to each other than animals in unfamiliar groups. Following the winter (Jun05) release, I examined the distances between the mean centres of individuals' monthly home ranges and determined whether the two treatments (familiar and unfamiliar release groups) differed in the distance animals dispersed from their release group members for seven months following their reintroduction. Seven months was selected as beyond this there were not enough group members in each unit due to animal deaths and comparisons could no longer be made. In addition, the number of animals within each release group was also not constant during the seven months examined, therefore reducing available sample size of ‘within group’ comparisons across this time period (Table 3.1). I also compared the difference in home range proximity between group members and non-group members with time since release to identify how long after the reintroduction home range proximity of non-group members and release group members were not significantly different.

	Months post-release	Familiar Group			Unfamiliar Group		
		2	3	6	1	4	5
Jun05	0	6	6	6	6	6	6
Jul05	1	3	5	4	5	5	3
Aug05	2	3	4	3	5	4	(1)
Sep05	3	2	3	3	3	3	(1)
Oct05	4	2	3	3	3	3	(1)
Nov05	5	2	2	(1)	3	(0)	(1)
Dec05	6	2	2	(1)	3	(0)	(0)

Table 3.1 Number of surviving group members from each familiar and unfamiliar release group during the first seven months following the Jun05 reintroduction; each group started with six members. Bracketed numbers indicate that no comparisons ‘within group’ could be made as one or no group members remained alive.

Using the spatial statistics mean centre tool in ArcGIS 9.2 I obtained a latitude/longitude position for the centre of all monthly 95%MCP areas, and was then able to calculate the distance between these home ranges centres using ‘distance between points’ in Hawths tools (in ArcGIS 9.2). The average distance between the centres of group members’ monthly home ranges was calculated for the 6 release groups (3 familiar and 3 unfamiliar), as was each animals’ average distance to non-group members. The average distances between group members’ and non-group members’ monthly MCP mean centres was obtained for the establishment month, and for 6 months post-establishment, after which time the number of animals originating from each release group was insufficient to obtain a reliable ‘within group’ average (due to natural death or predation).

Three linear mixed effects models were constructed to examine: the average distance between animals within a group, comparing familiar and unfamiliar groups and over time; the average distance between non-group members, comparing familiar and unfamiliar groups and over time; and the difference in average distance to group members versus non-group members with time since release. In all models a random release group effect was added to the model to account for the dependence in results from the same release group. Type three tests of fixed effects were generated, and if an interaction was found to be not significant, the term was dropped from the linear mixed effects model. When significance was obtained, *post hoc* tests were carried out to determine where specific differences occurred.

In addition, for each individual I examined home range stability (common area used between months), and the amount of new area incorporated into their home range each month. A new area was defined as locations never previously encompassed by a monthly home range, as distinct from areas which may have been used previously and re-visited some time later. In particular, I was interested in finding if there was an effect of experimental group, sex and pouch young status, the time of year and time since release, the size of the home range, the amount of that area shared and by how many other animals, and additionally whether the number of deaths in a previous month caused a shift in home range of surviving individuals. The common area each individual used between months was determined by overlaying their successive monthly 95% MCP areas using “union”, and calculating the resulting area using Xtools (Data East LLC 2009) in ArcGIS 9.2. To calculate completely new areas explored and used each month, the most recent month was “erased” from the “merged” older months, and the area of the resulting unique polygon calculated by Xtools in ArcGIS 9.2.

Using linear mixed effects models, the degree to which a range of variables influenced both the amount of home range stability, and home range shift was assessed. The variables considered here were the same variables as used in the post-establishment assessment of home range size, namely: experimental group (familiar and unfamiliar); sex and pouch young status (males, females with pouch young, females without pouch young); the percentage of the area shared with other individual(s); the number of other animals’ area overlapped; and time of year. Additionally, these models also incorporated three more variables: the influence of home range size; the number of months since release; and the number of deaths which occurred in the previous month. Number of deaths was incorporated as a sudden removal of a wallaby(s) from the population (as a result of natural death, predation, or road kill) is likely to influence the remaining individuals. This aimed to examine if it had an effect on their space use.

All analyses were carried out using SAS Version 9.2 (SAS Institute Inc. 2008). To account for the dependence in the results from the same animal, a random animal ID effect was included into each model. Predictor variables which satisfied the *P*-value criterion $p<0.10$ in a univariate model were then entered into a multivariate model, and *post hoc* tests were carried out to determine where differences occurred if global *P*-values for predictor variables were statistically significant. As no transformation of the data was required for the home range stability and home range shift linear mixed effects models, results are presented as mean values, and regression coefficient values are presented as an area increase or decrease.

3.2.3 Sharing home ranges with conspecifics

It is expected that animals that are social or occupy areas with localised resources are likely to have overlapping home ranges. Here I examined the influence various variables had on the degree to which home ranges and core areas overlapped in the month following the reintroduction, and for the next 12 months. I also recognised that spatial overlap does not necessarily equate to temporal overlap, therefore I also assessed the relationship between the two.

The amount each animal’s 95% and 50% monthly MCP areas overlapped other individuals was determined in ArcGIS 9.2. All animals’ MCP areas for a month were overlayed using the union feature (with 95% and 50% areas done separately), and Xtools used to calculate the areas of the resulting polygons. From these, the area of shared use for each MCP was obtained, as well as the number of individuals it was shared with and size of the area shared with those specific other individuals.

During the establishment phase, I assessed the influence of three variables on the percentage of the home range and core area shared with other individuals. Because of the smaller sample size during the establishment period (compared to post-establishment), simple analytical techniques had to be employed as attempts to model this data resulted in unstable and unreliable models. Thus, the influence of sex and pouch young status and experimental groups were assessed using Kruskal Wallis tests, and the relationship between the percentage of area shared and the number of animals the home range overlapped was assessed using Spearmans rank correlation.

Post-establishment, the influence of sex and pouch young status and experimental groups on home range and core area shared with conspecifics were again assessed. In addition, the influence of the number of females and males overlapped by each animals’ MCP, the time of year, and month since release were all considered. Linear mixed effects models were used, where the outcome variable was area shared as opposed to percentage of area shared (attempted models with percentage values as the outcome variable were too unstable). Variables were firstly assessed in univariate models. However, there was a limitation with the univariate model, as attempting to control for the size of the home range (or core area) in the univariate model also resulted in instability of the model. Therefore, variables which did not reach the *P*-value criterion (and subsequently not factored into the multivariate model) were assessed at an individual level using Spearmans correlation to see whether a relationship between the variable and percentage of area shared existed. Where weak or no correlation existed, the exclusion of the variable from the multivariable was justified. Variables which did reach $p < 0.1$ in the univariate model were entered into a multivariate model. In the multivariate model a random animal ID effect was incorporated (to account for any dependence in the data from the same animal), and the analysis controlled for two things: the number of animals which could potentially overlap (as this fluctuated monthly), and the size of the home range and core area. Where global *P* values were significant, *post hoc* tests were undertaken to conclude where the differences occurred. As before, models were analysed using SAS Version 9.2 (SAS Institute Inc. 2008).

No data transformation was required for the linear mixed effects models of home range and core area shared post-establishment; therefore results are reported as mean values (and area increase or decrease for regression coefficients). However, median values are presented for the analysis of the establishment period, where Kruskal Wallis and Spearman correlation techniques were used.

Animals which have overlapping home ranges do not necessarily socialise together and use common area simultaneously (as distinguished by static and dynamic overlap, Doncaster 1990). The proximity between all individuals in each sampling period was determined using the Hawths tools application in ArcGIS 9.2. The proportion of time individuals spent as “nearest neighbours” was correlated to the degree of their home range overlap using Mantel Tests in the PopTools extension (Hood 2008) for Excel. Correlation analysis tools examine pairs of measurement variables to determine whether the two measurement variables tend to vary together, that is, whether large values of one variable tend to be associated with large values of the other (positive correlation), whether small values of one variable tend to be associated with large values of the other (negative correlation), or whether values of both variables tend to be unrelated (correlation near zero). Correlation coefficients are scaled to lie between -1 and +1 inclusive. For each month, matrices detailing the percentage of home range overlap for each individual by every other individual were correlated to matrices of the percentage of time each individual was a nearest neighbour with every other individual. The resulting output gave the true correlation coefficient, and an array of 998 correlation coefficients based on randomising the matrices. A significant correlation was indicated when the true correlation coefficient fell in a tail (above or below the percentiles) of the randomised correlation coefficient output. The *P* values were calculated by dividing the number of values exceeding or less than the true correlation coefficient by the number of randomisations (for when the true correlation coefficient was a positive or negative value respectively).

3.3 Results

3.3.1 Establishment month

3.3.1.1 Size of home range and core area, and amount shared

During the establishment month, home range sizes and amount of home range area shared did not differ significantly between the two experimental treatment groups (animals in groups with familiar or unfamiliar group members), nor were they influenced by the sex of the animal or presence of pouch young for females (Table 3.2). Home range size was not significantly influenced by the percentage of that area shared with other animals (Table 3.2). However, the number of animals with overlapping home ranges significantly influenced both their home range size and the area shared with other animals (Table 3.2). Specifically, as the number of overlapping animals increased, so did their home range size, and the area of their home range shared.

The size of the core area and amount of core area shared with conspecifics followed a similar trend to the total home range area. Neither experimental group nor sex of the animal had any influence (Table 3.2). Likewise, the size of the core area was not significantly influenced by the percentage of the area shared with other animals (Table 3.2). However, unlike total home range area and amount shared during establishment month, the number of animals that overlapped did not significantly affect the core area size or the amount of area shared (Table 3.2). Notably, none of the variables examined during the establishment month showed a significant impact on core area or amount of core shared with other animals (Table 3.2). These results will be outlined in detail below.

	Predictor variables			
	Group	Sex	% home range or core area shared	No. animals overlap with home range or core area
Home range size (ha)	0.5702	0.3861	0.3159	**0.0258**
Home range area shared (%)	0.9737	0.5634	-	**0.0151**
Core area (ha)	0.7371	0.3792	0.3830	0.2618
Core area shared (%)	0.9346	0.4748	-	0.2155

Table 3.2 Influence of predictor variables on home range and core area (determined by univariate linear mixed models) and percentage of those areas shared with other tammar wallabies (determined by Kruskal-Wallis tests for group and sex, and Spearman's Rho for no. animals overlapped) during the establishment period. Significance given as *P*-values, and highlighted in bold when significant. "-" = not tested.

The median home range area used during establishment month following the winter (Jun05) reintroduction was 11.1ha for familiar animals (95%CI 8.2 – 15.0) and 12.5ha (95%CI 9.2 – 17.0) for unfamiliar animals, and these were not significantly different (P=0.5702). Likewise, no significant difference between the sexes was observed (P=0.3861). Males used 14.2ha (95%CI 9.9 – 20.5), females with pouch young used 11.6ha (95%CI 7.4 – 18.1), and females without pouch young used 10.2ha (95%CI 7.3 – 14.1). The percentage of the home range area shared with other wallabies did not impact upon the size of the home range (regression coefficient: -0.00807, se: 0.007921, P=0.3159), but the number of animals that overlapped did, with a positive correlation between home range area and numbers of animal overlapping (regression coefficient: 0.1546, se: 0.06622, P=0.0258). Specifically, with every additional animal that overlapped, the size of the home range increased by 16.7%.

During the establishment month, the percentage of home range area shared by more than one animal was significantly positively correlated with the number of animals that overlapped: Spearman's Rho of 0.4076, P=0.0151. However, the percentage of the home range area shared did not differ between experimental treatment groups (familiar animals shared a median 96.78% (Inter-Quartile Range (IQR) for the 25th and 75th Percentiles: 86.27-99.29) of their home range, unfamiliar animals shared 95.74% (IQR 88.84-100.00), P=0.9737), or sexes (males shared 97.50% (IQR 89.65-100.00), females with pouch young shared 97.90%

(IQR 84.54-97.84), and females without pouch young shared 98.01% (IQR 80.07-100.00), *P*=0.5634).

The median core home range area used by animals during establishment month was not significantly influenced by any of the variables examined. There was no difference in core area between experimental groups (familiar animals 2.7ha, 95%CI 2.0 – 3.5; unfamiliar animals 2.5ha, 95%CI 1.8 – 3.3, *P*=0.7371), or sexes (males 3.1ha, 95%CI 2.2 – 4.4; females with pouch young 2.6ha, 95%CI 1.7 – 4.0; females without pouch young 2.2ha, 95%CI 1.6 – 3.0, *P*=0.3792), nor was it influenced by percentage of the area shared (regression coefficient: -0.00317, se: 0.00317, *P*=0.3830), or the number of animals overlapped (regression coefficient: 0.07947, se: 0.06961, *P*=0.2618). Similarly, I did not find any variables that significantly influenced the amount core areas were shared during establishment month. There was no difference between experimental groups (familiar animals shared 71.54% (IQR 53.79-88.51) of their core area, and unfamiliar animals shared 81.67% (IQR 38.93-93.96), *P*=0.9346), or sexes (males shared 83.14% (IQR 65.75-93.67), females with pouch young shared 64.17% (IQR 32.18-91.27), and female without pouch young shared 64.35% (IQR 38.93-87.11), *P*=0.4748). Additionally, no significant relationship was found between the percentage of core area shared and number of animals overlapped (Spearman’s Rho 0.2147, *P*=0.2155).

3.3.1.2 Establishment vs. an equivalent season post-establishment

To look at the influence of the establishment month on the size and amount of home range and core area shared between conspecifics, I compared the establishment month to a subsequent, but equivalent time of year. The size of home ranges and core areas were both significantly larger post-establishment than during the establishment month (Table 3.3). The amount of those areas shared with conspecifics between the establishment month and an equivalent time of year post-establishment could not be defined statistically. As there was more than one observation per animal, a non-parametric assessment of the percentage of home range and core area shared use was not valid (as non-parametric tests can not account for dependence). Despite this, descriptive statistics suggested that a larger percentage of the home range and core areas were shared with other individuals during the establishment month compared to a similar time of year post-establishment (Table 3.3).

	Establishment month	Equivalent season after establishment	*P* value
Home range size (ha)	11.8 (9.6-14.5)	15.9 (13.0-19.4)	**0.0020**
Core area (ha)	2.6 (2.0-3.2)	3.8 (3.1-4.7)	**0.0059**
home range area shared (%)	96.76 (86.27-99.82)	83.76 (70.57-98.75)	N/A
core area shared (%)	73.66 (46.09-93.37)	59.17 (25.52-84.01)	N/A

Table 3.3 The influence of establishment month on the size of home range and core area compared to an equivalent season post-establishment (determined by univariate linear mixed effects model). Percentage of area shared with one or more conspecifics is given as a median value from the descriptive statistics, with 95% confidence interval (for home range and core area size), and inter quartile range (for % area shared) in brackets.

3.3.2 Post Establishment

Following the first month after a reintroduction, animals have presumably sought out suitable habitat for their daily activities, adapted to their new environment, learnt about the local predators, and established themselves in a home range area. Following this establishment period, I examined the release group cohesion and three aspects of how the animals occupied the landscape over the following 12 months. These were, site fidelity and incorporation of new areas into home ranges, home range and core area size, and the degree those spaces were shared with conspecifics.

3.3.2.1 Group cohesion

Following the reintroduction, group cohesion of familiar and unfamiliar release groups was assessed within treatments, and between treatments for seven months post-release by examining the average distance between the mean centres of monthly home ranges. An interaction between treatment group and month after release was statistically significant (P= 0.0069) (Table 3.4). The home ranges of animals released in unfamiliar groups were in similar proximity of each other for the first seven consecutive months examined after release (Figure 3.3). Home ranges of familiar group members were significantly further apart four months after they were released than they were during the establishment month (P= 0.0142), and five months after their release they were significantly further apart than during any other month (*P* <0.0001 for all interactions) (Figure 3.3). Interestingly during the sixth and seventh month after release, the distance between familiar group member home ranges declined to be similar to that of the establishment month and first two months post establishment (Figure 3.3). Between treatments, no difference in proximity to group members was observed until the fourth month post-establishment, where familiar group members were significantly further from group members than what was observed for unfamiliar group members (*P*= 0.0003 Figure 3.3).

Effect	Num df	Den df	*F* value	*P* value
Treatment group	1	15	1.45	0.2468
Month after release	6	15	10.21	**0.0001**
Interaction group*month	6	15	4.71	**0.0069**

Table 3.4 Type III tests of fixed effects from linear mixed effects models: average distance between familiar and unfamiliar group members for seven months following reintroduction (distance calculated by mean centre of home ranges).

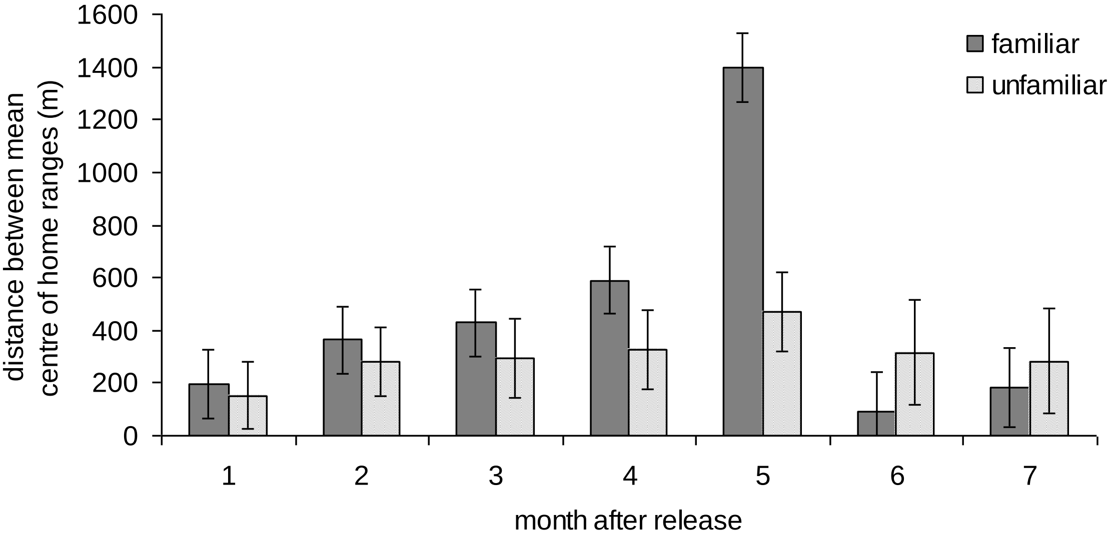

Figure 3.3 Mean distance between mean centre of home ranges (±se) for familiar and unfamiliar group members with time after release, as calculated by the distance between the mean centre of animals’ monthly home ranges.

To determine whether home range proximities of animals released in familiar or unfamiliar groups became closer to non-group members more rapidly after the reintroduction, linear mixed effects models were carried out. There was no evidence of an interaction between group and time after release (Table 3.5), suggesting that there was no significant difference in the rate at which familiar and unfamiliar groups merged with animals of other groups with time since release. Therefore, this variable was dropped from the model.

Independent of assignment to familiar or unfamiliar release groups, the average distance between non-group members' centre of home range was found to vary according to month after release ($P<0.0001$) (see the "non-group bars" in Figure 3.4). *Post hoc* tests revealed animals' home range centres were significantly closer to non-group members by the sixth month after their release than the previous months, and were even closer by the seventh month after release (Table 3.6).

Effect	Num df	Den df	*F* value	*P* value
Group	1	21	0.47	0.5026
Month after release	6	21	9.33	**<0.0001**
Interaction group*month	6	21	1.54	0.2140

Table 3.5 Type III tests of fixed effects from linear mixed effects models: average distance between familiar and unfamiliar animals to members of other release groups for seven months following reintroduction (distances calculated by mean centre of home ranges).

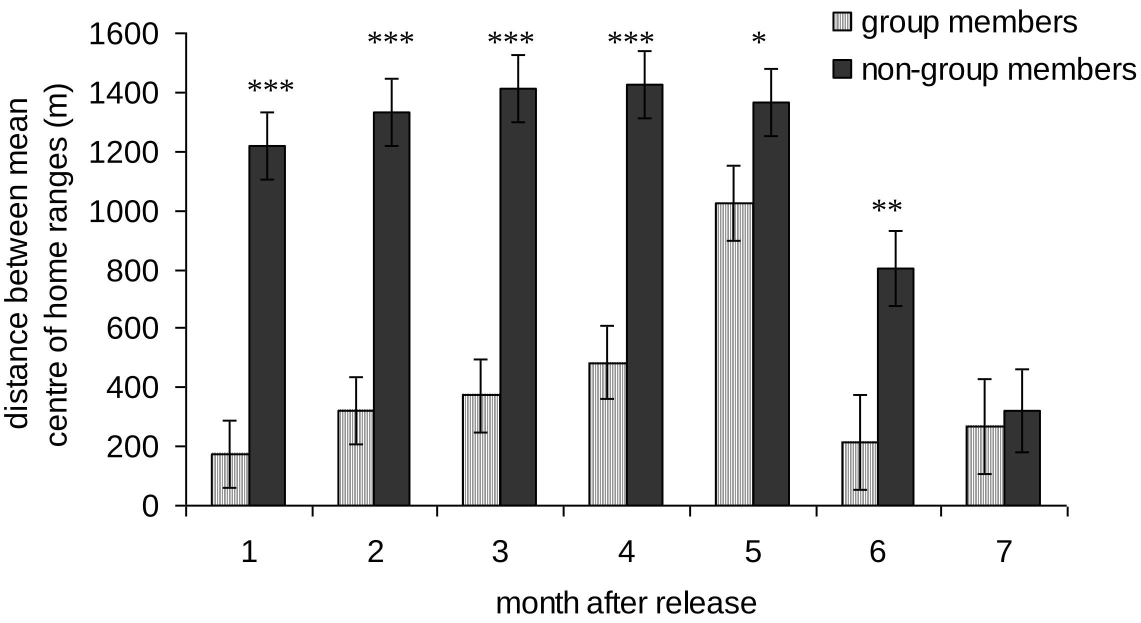

Figure 3.4 Mean distance ±se between mean centre of monthly home ranges for group members and non-group members with time after release. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively.

	Month after release	Month after release					
		1	2	3	4	5	6
Jun05	1						
Jul05	2	ns					
Aug05	3	ns	ns				
Sep05	4	ns	ns	ns			
Oct05	5	ns	ns	ns	ns		
Nov05	6	↓407.53m ±162.65 (**0.0186**)	↓517.49m ±162.65 (**0.0037**)	↓598.49m ±162.65 (**0.0010**)	↓612.21m ±162.65 (**0.0008**)	↓554.18m ±162.65 (**0.0021**)	
Dec05	7	↓882.46m ±174.50 (<**0.0001**)	↓992.43m ±174.50 (<**0.0001**)	↓1073.43m ±174.50 (<**0.0001**)	↓1087.15m ±174.50 (<**0.0001**)	↓1029.11m ±174.50 (<**0.0001**)	↓474.94m ±180.40 (**0.0138**)

Table 3.6 Difference in proximity between mean centre of home ranges of non-group members (± se) with each month since release, as determined by linear mixed effects model *post hoc* tests. Calculated independent of experimental treatment group, as no significant difference was detected between familiar and unfamiliar groups. ↓ indicates decrease in distance between mean centre of home ranges between the two months examined. Significant *P* values in brackets and highlighted in bold.

To assess when animals no longer preferentially resided with release group members, I examined when home range locations were no longer significantly closer to release group members, by calculating the difference between the home range proximity of group members versus non-group members with time since release (regardless of being familiar or unfamiliar assemblages).

A significant difference between distance to group members and non-group members was found, and their interaction with time since release was also significant (Table 3.7). During the first six months after release the distance between animals' home range centres were significantly closer for group members than non-group members. However, by the seventh month after release no significant difference in home range proximity between release groups and non-group members was apparent (Figure 3.4).

Effect	Num DF	Den DF	*F* value	*P* value
Month after release	6	53	10.00	**<0.0001**
Group member or non-group member	1	53	114.65	**<0.0001**
Interaction month*group or non-group	6	53	4.63	**0.0007**

Table 3.7 Type III tests of fixed effects from linear mixed effects model: average proximity to group members and non-group members for seven months following reintroduction (distances calculated by mean centre of home ranges).

3.3.2.2 Range shift and stability

Looking specifically at the location of the home ranges in the landscape, I examined the proportion of each animals' home range which utilised the same area in consecutive months, and the proportion of the home range which incorporated new area never previously encompassed by their home range. From this I was able to gauge the degree of site fidelity or home range shift and what the driving variables were.

Linear mixed effects modelling was used to examine the effects of a range of variables on the similarities in home range locations between months. Experimental group, sex, and number of animals with overlapping home ranges all failed to reach the required *P* value at the univariate level for subsequent consideration in the multivariate model (Table 3.8). All remaining variables showed significant influence on home range stability at the univariate level. Specifically, a smaller proportion of the home range area was the same as the previous month if more deaths had occurred during the previous month (regression coefficient -0.4752, *P* = 0.0045), or if it was Jul-Aug (significantly less home range stability than other months except for Nov-Dec, *P* = 0.0260). Home range stability was greater with time since release (regression coefficient 0.4462, *P* = 0.0471), with increasing amount of the home range shared with other individuals (regression coefficient 0.2790, *P* <0.0001), and with increasing home range size (regression coefficient = 0.3056, *P* <0.0001). However, once these variables were considered together in the multivariate model only one variable, home range size, continued to show a significant effect on the amount of home range stability (regression coefficient 0.3468, *P* <0.0001 Table 3.8). This showed that for every 1 hectare increase in home range size, the area retained by animals between consecutive months increased by 0.35 hectares.

	Predictor variable							
	Group	Sex	Home range size	Time of year	Month after release	Area shared	No.animals overlap	No.deaths in previous month
Home range stability	*(univariate)* 0.1803	*(univariate)* 0.1218	**<0.0001**	0.7071	0.6696	0.3660	*(univariate)* 0.4738	0.9015
New area in home range	0.5426	*(univariate)* 0.1664	**<0.0001**	**0.0033**	*(univariate)* 0.1751	**0.0337**	*(univariate)* 0.4997	*(univariate)* 0.5770

Table 3.8 Significance of predictor variables on home range stability (area of home range the same as previous month) and new area incorporated into monthly home ranges by tammar wallabies post-establishment after a reintroduction, as found by multivariate models, and given as *P*-values (significant values in bold). "*(univariate)*" did not meet the p>0.1 criteria in the univariate model for subsequent consideration in the multivariate model.

The amount of new area incorporated into an individual's home range each month was also examined. In the univariate models no significant effect on the amount of new area incorporated into home ranges was shown by four variables: sex and pouch young status of the animal (with males incorporating a new area of 13.5635±1.84ha, females with pouch young 7.82±1.98ha, and females without pouch young 8.94±1.69ha, *P* = 0.1664); number of animals with overlapping home ranges (regression coefficient 0.3065, *P* = 0.4997); the month after release (regression coefficient -0.3387, *P* = 0.1751); and the number of deaths occurring in a previous month (regression coefficient -0.1424, *P* = 0.5770) (Table 3.8). These four variables were therefore omitted from the multivariate model. The multivariate model revealed that familiar and unfamiliar animals showed no differences in the amount of new area incorporated into their home ranges (with familiar animals incorporating a new area of 9.59±1.09ha, and unfamiliar animals 10.56±1.08ha, *P* = 0.5426) (Table 3.8). However, significantly more new area was incorporated into home ranges when home range sizes increased. Specifically, when home range size increased by 1 hectare, the amount of new area incorporated increased by 0.41 hectares (regression coefficient 0.4075, *P* <0.0001). This was also significant when a greater area of the home range was shared with other animal(s). Again, specifically, when the amount of the home range shared increased by 1 hectare, the amount of new area incorporated increased by 0.19 hectares, regression coefficient 0.1980, *P* = 0.0337 (Table 3.8). Additionally, the amount of new area (area they had not previously occupied) included in a home range was significantly influenced by the time of year (*P* = 0.0033 Table 3.8), where significantly more new area was integrated into home ranges from July to December than there was from January to May (Table 3.9).

	Jan-Mar	Apr-May	Jun-Aug	Sep-Oct	Nov-Dec	New area±se
Jan-Mar		ns	↓ 5.86*	↓ 5.46*	↓ 4.66*	6.90±1.50
Apr-May			↓ 7.51*	↓ 7.11*	↓ 6.31*	5.25±1.78
Jun-Aug				Ns	ns	12.75±1.26
Sep-Oct					ns	12.36±1.87
Nov-Dec						11.55±1.67

Table 3.9 Amount of new area incorporated into home ranges at different times of year post-establishment, and differences between the times of year as determined by *post hoc* tests. ↓ indicates less new area included (compared to the corresponding period), ↑ indicates more new area incorporated. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= no significant difference between the two periods in the amount of new area incorporated into home ranges.

3.3.2.3 Size of home range and core area, and amount shared

3.3.2.3.1 Home range size

Monthly home range sizes were estimated for twelve months following the animals' reintroduction. No home range was smaller than 4ha, and more than half (52.36%) were between 11-30ha (Figure 3.5). Four of the five variables examined by multivariate modelling significantly influenced monthly home range sizes of animals following the establishment month (Table 3.10). Time of year had a significant influence on home range size, with home ranges being significantly smaller in winter (Jul-Aug) than any other time of year (Figure 3.6 & Table 3.11). The percentage of a home range area which was shared with one or more other animals significantly impacted upon the actual home range size, such that as the area shared increased by 1 hectare, the size of the home range decreased by 0.43% (regression coefficient -0.00433, se: 0.001950, $P = 0.0281$). Overall, the mean monthly home range size of male wallabies (31.2ha, 95% CI 24.7 – 39.5) was significantly larger than that of all females (males vs. females with pouch young, $P = 0.0353$, and males vs. females without pouch young, $P = 0.0180$), while females with or without young did not differ in the size of their home ranges (females with pouch young = 21.2ha (95% CI 16.5 – 27.3), females without pouch young = 20.4ha (95% CI 16.5 – 25.1), $P = 0.7435$). Interestingly, the experimental treatment group had an influence on home range size after the initial establishment period. Familiar animals had significantly larger home ranges than unfamiliar animals post-establishment (familiar animals = 28.1ha (95% CI 24.1 – 32.7), unfamiliar animals = 20.2ha (95% CI 17.3 – 23.5), $P = 0.0043$). The number of animals with overlapping home ranges had no influence on the home range size at the univariate level ($P = 0.1911$) and was not included in the multivariate model.

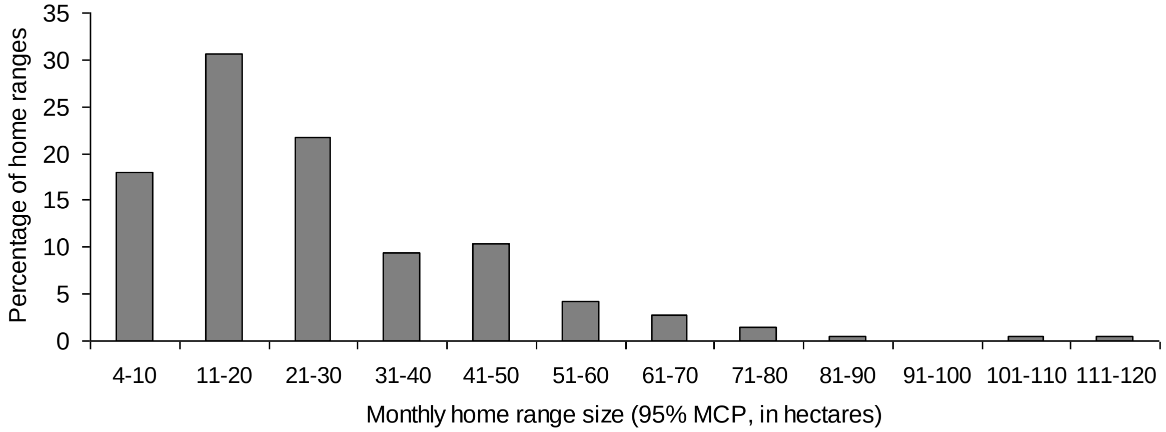

Figure 3.5 Percentage of monthly home range areas (n=212) of varying size estimated for tammar wallabies over twelve months following their reintroduction.

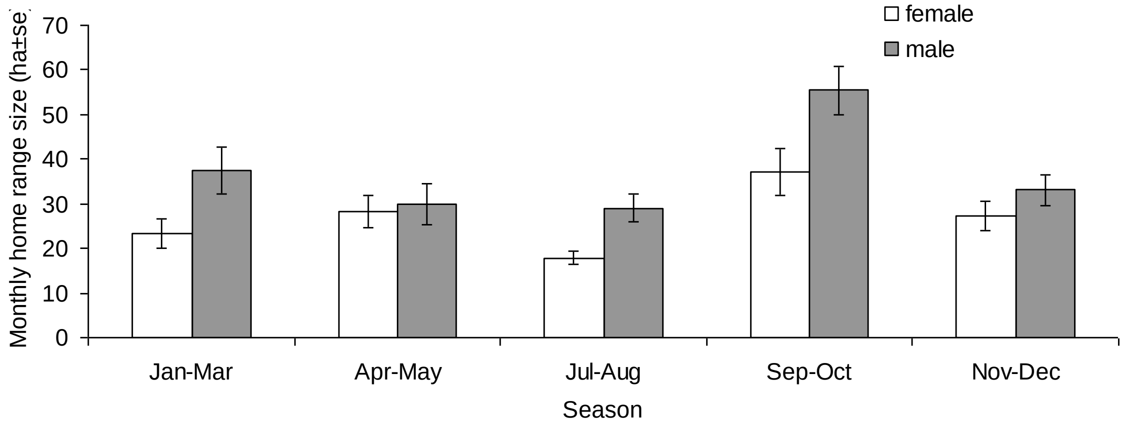

Figure 3.6 Mean monthly home range size (± se) for female and male tammar wallabies post-establishment following their reintroduction.

	Exp grp	Time of year	Sex	% or area shared	# animals overlap	# F overlap	# M overlap	HR size	# mth post-release	# deaths prev mth
HR size estab (only *univariate)*	*(univar)* 0.5702	-	*(univar)* 0.3861	*(univar)* 0.3159	**0.0258**	-	-	-	-	-
Core area estab (only *univariate)*	*(univar)* 0.7371	-	*(univar)* 0.3792	*(univar)* 0.3830	*(univar)* 0.2618	-	-	-	-	-
HR share estab *(Kruskal Wallis & Spearmans)*	0.9737	-	0.5634	-	**0.0151**	-	-	-	-	-
Core share estab *(Kruskal Wallis & Spearmans)*	0.9346	-	0.4748	-	0.2155	-	-	-	-	-
HR size estab vs. post-estab (only *univariate)*	-	**0.0020**	-	-	-	-	-	-	-	-
Core area estab vs. post-estab (only *univariate)*	-	**0.0059**	-	-	-	-	-	-	-	-
HR size	**0.0043**	**0.0010**	**0.0388**	**0.0281**	*(univar)* 0.1911	-	-	-	-	-
Core area	0.9424	*(univar)* 0.6526	0.3665	*(univar)* 0.1817	*(univar)* 0.1420	-	-	**<0.0001**	-	-
HR share	0.1913	0.2150	**0.0443**	-	-	0.6671	**0.0001**	-	*(univar)* 0.3991	-
Core area share	*(univar)* 0.7847	0.0658	0.7365	-	-	**<0.0001**	**<0.0001**	-	*(univar)* 0.9016	-
HR same area (stability)	*(univar)* 0.1803	0.7071	*(univar)* 0.1218	0.3660	*(univar)* 0.4738	-	-	**<0.0001**	0.6696	0.9015
HR new area	0.5426	**0.0033**	*(univar)* 0.1664	**0.0337**	*(univar)* 0.4997	-	-	**<0.0001**	*(univar)* 0.1751	*(univar)* 0.5770

Table 3.10 Significance of predictor variables on home range and core area size and amount shared during establishment month and post-establishment, including comparison between establishment month and an equivalent season post-establishment. Additionally, influence of predictor variables on home range stability and completely new area used. Significance highlighted in bold. “(*univar*)”=univariate model, “-”=untested.

	Jan-Mar	Apr-May	Jul-Aug	Sep-Oct	Nov-Dec	Home range size (ha)
Jan-Mar		ns	↑7.14*	ns	ns	25.29 (20.71-30.88)
Apr-May	ns		↑6.68*	ns	ns	24.83 (19.56-31.50)
Jul-Aug	↓7.14*	↓6.68*		↓13.06**	↓9.76*	18.14 (15.39-21.39)
Sep-Oct	ns	ns	↑13.06**		ns	31.21 (24.72-39.40)
Nov-Dec	ns	ns	↑9.76*	ns		27.91 (22.35-34.86)

Table 3.11 Home range size of tammar wallabies at different times of year post-establishment (median value and 95% CI in brackets) as determined by multivariate linear mixed effects models, and differences between the times of year as determined by *post hoc* tests. ↓ indicates reduction in home range size (compared to the corresponding period), ↑ indicates increase in home range size. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= no significant change in home range size between the two periods.

3.3.2.3.2 Core area size

Animals’ median core home area post-establishment was 4.5ha (Inter Quartile Range: 2.7-6.8) and was only influenced by one of the variables examined, that being home range size. As home range size increased by one hectare the core area increased by 2.3% (regression coefficient: 0.02244, se: 0.002765, *P* <0.0001). All other variables examined had no influence on core area. At the univariate level it was apparent that core area did not change with the time of year (*P* = 0.6526), and was not affected by the number of animals that overlapped each other (*P* = 0.1420) or the percentage of the core area shared (*P* = 0.1817). The multivariate model considered the influence of home range size, experimental group, and sex of the animal, however neither experimental group ((familiar animals = 4.2ha (95% CI 3.6 – 4.9), unfamiliar animals = 4.2ha (95% CI 3.6 – 4.9), *P*=0.94243)) nor sex of the animal (males = 4.6ha (95% CI 3.6 – 5.8), females with pouch young = 4.3ha (95% CI 3.4 – 5.6), females without pouch young = 3.8ha (95% CI 3.0 – 4.7), *P*=0.3665) proved to have a significant effect on the size of core area (Table 3.10).

3.3.2.3.3 Home range shared

Male and female wallabies shared different amounts of their home range with other animals (global *P* = 0.0443) (Table 3.10 & Figure 3.7). In particular, male wallabies shared significantly more of their home range with conspecifics than did female wallabies (males vs. females with pouch young, *P*= 0.0303, and males vs. females without pouch young, *P*= 0.0221), while females with and without pouch young did not differ (*P*= 0.9627). Additionally, shared home range area was also dependant on the sex and number of cohabitants, where the area shared significantly increased by 1.95 hectares with each additional male cohabitants (regression coefficient 1.9522, *P* = 0.0001), but was unaffected by increasing numbers of female cohabitants (regression coefficient 0.1500, *P* = 0.6671 Table 3.10). The multivariate model also revealed that neither experimental group (*P* = 0.1913), or the time of year (*P* = 0.2150) influenced the degree to which a home range was shared with other animals (Table 3.10 & Figure 3.7). It was found in the univariate model that time since release did not affect the degree to which a home range was shared with other animals (*P* = 0.3991 Table 3.10).

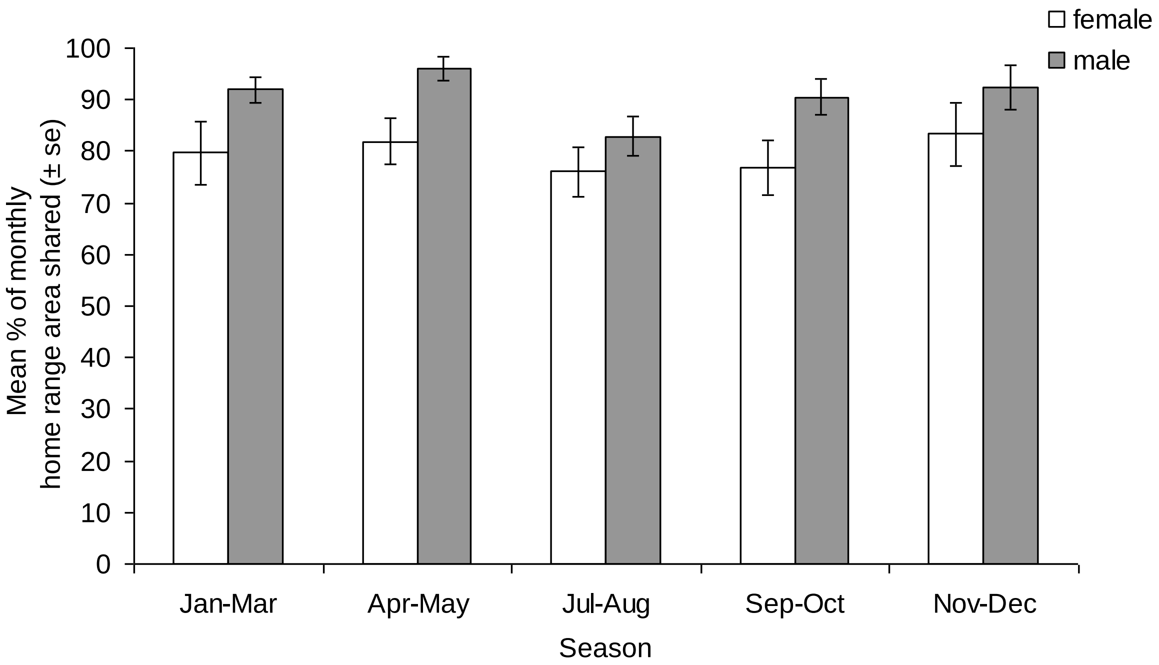

Figure 3.7 Mean percentage of monthly home range area shared (± se) for female and males tammar wallabies post-establishment following a reintroduction.

3.3.2.3.4 Core area shared

The degree to which animals shared their core area post-establishment was significantly influenced by two of the six variables examined. The amount of core area shared increased by 0.64 hectares with increasing numbers of male cohabitants (regression coefficient 0.6391, *P* <0.0001) and 0.52 hectares with increasing number of female cohabitants (regression coefficient 0.5292, *P* <0.0001). While descriptive statistics suggested an influence of sex and season on the percentage of the core areas shared (Figure 3.8), the multivariate linear mixed effects model revealed the degree to which core areas were shared did not differ between the sexes and pouch young status of the females (*P* = 0.7365), or with the different times of year (*P* = 0.0658). Additionally, it was found in the univariate model that sharing of core areas did not differ between animals from familiar and unfamiliar groups (*P* = 0.7847) and did not change with time since release (*P* = 0.9016) (Table 3.10).

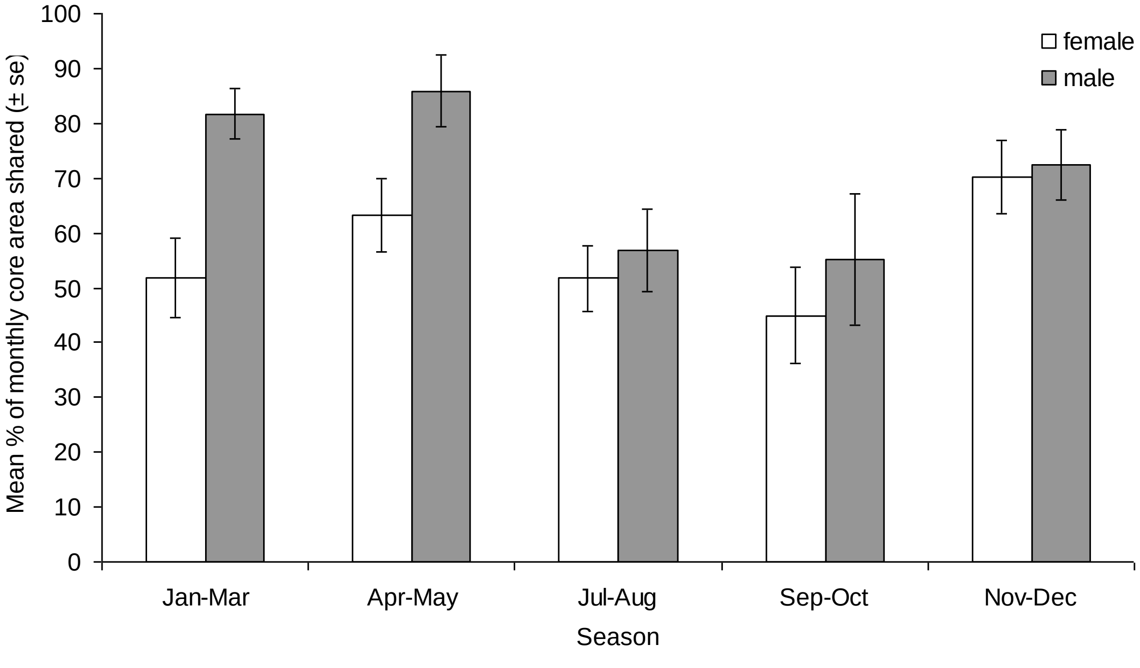

Figure 3.8 Mean percentage of monthly core area shared (± se) for female and males tammar wallabies post-establishment following a reintroduction.

3.3.2.3.5 Number of animals and percent of population overlapped

The number of animals that overlapped each tammar wallaby's home range varied from 2.8-7.0 animals (mean 4.6±0.35se) and did not appear to fluctuate with the population size (Figure 3.9). Despite this, a greater percentage of the population overlapped as population size decreased (due to natural deaths, fox predation and road kill, Figure 3.10). However, it is hard to distinguish if this was a function of the number of deaths (and subsequent number of animals available) or an artefact of time since release (as a greater percentage of the population was also overlapped with time since release, Figure 3.10), or both. For example, between Oct05 and Nov05 (months number five and six after the second reintroduction respectively) there was a large increase in the percentage of the population that overlapped (from 26.85 % to 62.5% respectively) despite only one death occurring between the months (Figure 3.10). As, it was also found that animals' home ranges shifted significantly closer to non-group members (by 554 metres) between Oct 05 and Nov05 (see Chapter 3 section 3.2.1 & Table 3.6). The increase in the percentage of the population overlapped here may be explained in part by animals' home ranges somewhat converging six months after their release, rather than by a substantial decrease in population size as only one death occurred. The time since release may indeed play a large part in the percentage of the population with overlapping home ranges. An incremental decrease in the percentage of the population overlapped was observed during the first three months following the first release (Nov04–Jan05), whereas compared to the same months one year later (Nov05-Jan06) there was an incremental increase in the percentage of the population overlapped (where there was also a similar population size. Figure3.10). More animals overlapping at this time of year is not surprising due the timing of the breeding season. In support of this, I previously observed that it took seven months for the distance between home ranges of group members and non-group members to be negligible (see Chapter 3 section 3.2.1).

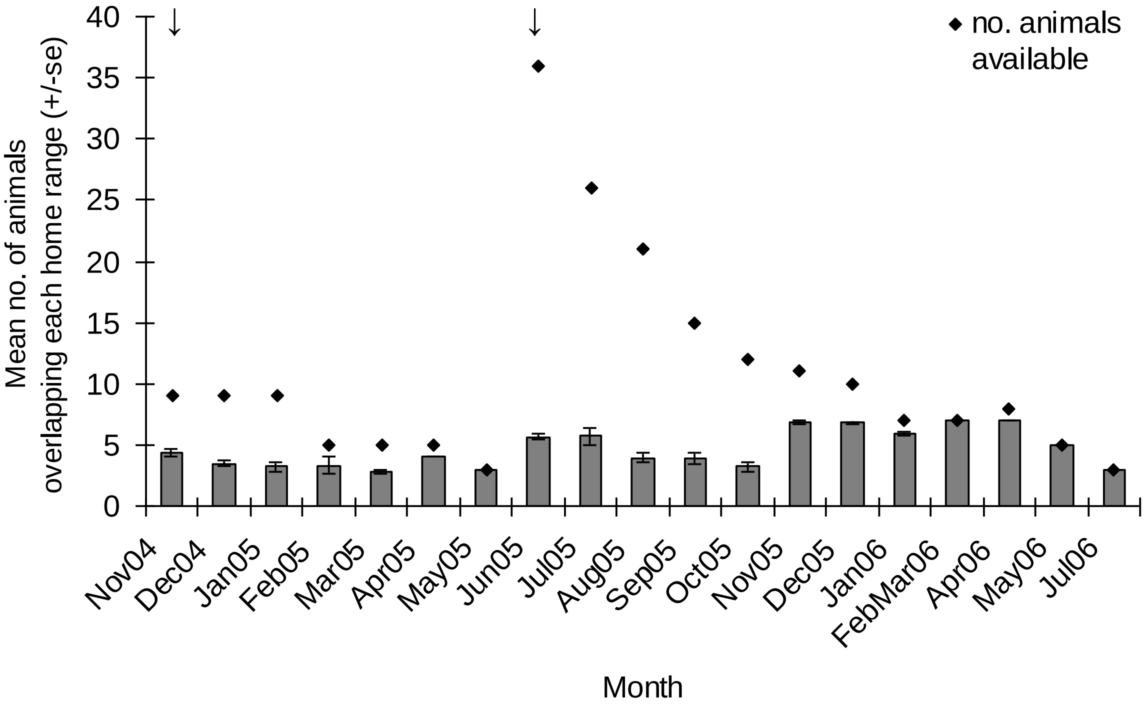

Figure 3.9 Mean number of animals overlapping each tammar wallabies' monthly home range (± se) following their reintroduction, relative to the number of animals available. ↓ indicates reintroduction event.

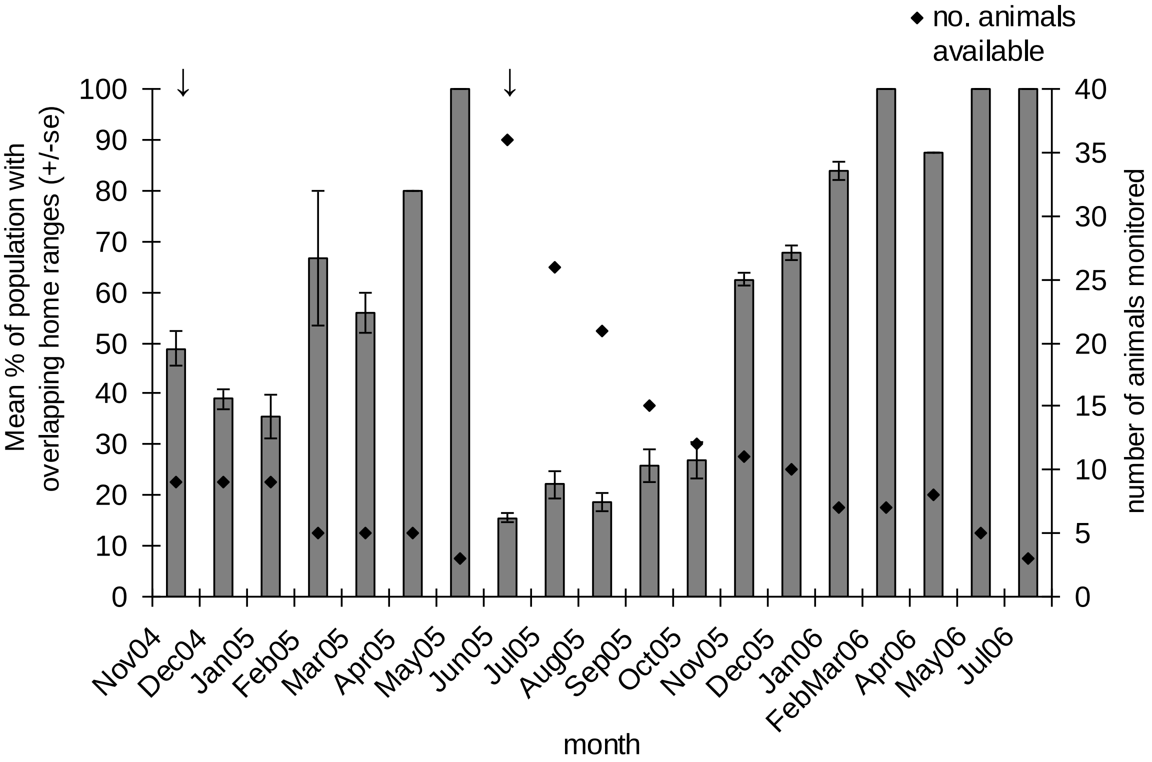

Figure 3.10 Mean percentage of the population overlapping each tammar wallabies' monthly home range (±se) following their reintroduction, relative to the number available. ↓ indicates reintroduction event.

3.3.2.3.6 Home range overlap & time spent as nearest neighbours

Animals that overlap their home ranges do not necessarily use those common areas simultaneously. I therefore examined whether there was a significant relationship between the degree of home range overlap and the proportion of time occupants spent together as nearest neighbours. Mantel's tests revealed that in most months (with three exceptions: Feb05, May05, and Jul06) the degree of home range overlap was significantly positively correlated with the proportion of time those animals spent together as nearest neighbours (Table 3.12), indicating that those animals with highly overlapping home ranges are aggregating in time and space.

		No. animals compared	No. animals excluded	Correlation coefficient	No. exceed test	No. less than test	*P* value
1st release	Nov04	10	0	0.72789	2	996	**0.002**
	Dec04	10	0	0.55140	7	991	**0.007**
	Jan05	10	0	0.66346	3	995	**0.003**
	Feb05	6	0	-0.06988	355	641	0.642
	Mar05	6	0	0.61892	25	971	**0.025**
	Apr05	6	0	0.91944	9	987	**0.009**
	May05	4	1	0.44449	166	785	0.166
2nd release	Jun05	37	3	0.17747	0	998	**<0.0001**
	Jul05	27	2	0.53446	0	998	**<0.0001**
	Aug05	22	2	0.61989	0	998	**<0.0001**
	Sep05	16	3	0.70466	0	998	**<0.0001**
	Oct05	13	5	0.60581	0	998	**<0.0001**
	Nov05	12	0	0.51480	0	998	**<0.0001**
	Dec05	11	0	0.52231	0	998	**<0.0001**
	Jan06	8	2	0.57257	0	998	**<0.0001**
	Feb-Mar06	8	1	0.69975	0	998	**<0.0001**
	Apr06	9	0	0.48066	2	996	**0.002**
	May06	6	1	0.46942	45	952	**0.045**
	Jul06	4	3	-0.16808	673	278	0.279

Table 3.12 Significance of relationship between percentage of monthly home range overlap and time spent as nearest neighbours for reintroduced tammar wallabies. Correlation calculated by two tailed mantel's tests where the number of randomisations in each matrix was 998. Numbers of randomisations falling above and below the true value are shown. Significance given as *P* values, and highlighted in bold when significant. Number of animals excluded from the analysis refers to those which could not be monitored during that month (due to radio collar failure).

3.4 Discussion

Newly reintroduced animals are required to establish home range areas, while familiarising themselves with the resources and avoiding the local predators. I examined factors that influenced tammar wallaby home range establishment and persistance following their reintroduction, and looked particularly at whether the grouping strategies implemented as part of the release program (familiar versus unfamiliar) impacted how the tammar wallabies settled into a new environment. To do this, I investigated the size of home range and core areas, degree to which they are shared with conspecifics, and the amount of home range stability or shift through the landscape for twelve months following the reintroduction.

3.4.1 Home range and core area: size and sharing during establishment

During establishment, all animals regardless of sex appeared to exercise a similar degree of caution when establishing in an unfamiliar environment. The sex of the animal and presence of pouch young did not impact upon exploratory range or the area shared, and all animals used a smaller amount of the landscape for their home range and core areas than they did at an equivalent time the following year. This was also found for reintroduced yellow-footed rock wallabies (*Petrogale xanthopus celeris*), where home range sizes were not equivalent to resident animals until 12 months post-release (Lapidge 2001). Using a restricted area when released into a novel environment is most likely due to unfamiliarity with the habitat, and animals being unwilling to explore too far too soon in light of the unknown risks involved. This finding is supported by Swihart *et al.* (1988) who suggested that perceived predation risk may force animals to rely on limited refuge habitat, whereby their movements and home range are constrained to a smaller area. Janmaat *et al.* (2009) similarly reported that predation risk is greater when in unfamiliar habitat as the animals need a longer time to find cover and escape routes from predators.

One way animals improve detection of potential predators and threats is by communal vigilance (Elgar 1989; Lima 1995; Pulliam 1973). This has been reported for the tammar wallaby (Blumstein *et al.* 1999; Blumstein and Daniel 2002; Blumstein *et al.* 2002b; Blumstein *et al.* 2002c). Therefore, not surprisingly, it was observed here that while establishing in an unfamiliar environment the tammars’ home range size and the amount shared with conspecifics both increased with the number of other individuals overlapped. However, whether overlapping more individuals facilitated the animals to increase their home range size, or whether home range expansion subsequently resulted in overlapping more individuals was not explicitly discernable. The small area each animal held during the first month post-release was likely in close enough proximity to a number of other individuals, such that a slight increase in home range size resulted in the range overlap with another individual. However, as the degree of home range overlap overall was positively correlated to the amount of time those animals spent together as ‘nearest neighbours’ (also seen in other species such as the tent-making bat (*Artibeus watsoni*); Chaverri *et al.* 2007), it does suggest the animals intentionally expanded their range into an area already occupied (as opposed to unoccupied territory). Similarly, individual adult male gray-cheeked mangabeys (*Lophocebus albigena*) were observed to occasionally move into areas which they had previously used or into unfamiliar areas occupied by another group (Janmaat *et al.* 2009). Moving into an area already occupied can overcome some of the cost of spatial ignorance, such as lack of ability to find resources and increased predation (Wolf *et al.* 2009; Yoder *et al.* 2004), as the benefit gained from remaining close to neighbours and occupying similar territory is the increased vigilance and predator detection achieved while associating with others (Blumstein *et al.* 1999). Understandably, this is especially important while in unfamiliar habitat with unfamiliar risks. Here, results combined suggest that the animals perceive benefit in sharing space with other individuals, particularly during establishment in an unfamiliar environment following their reintroduction.

3.4.2 Influence of experimental release protocol

Some studies have found that release protocol and prior experience had an influence on animals’ establishment and survival following their reintroduction. For example, a release of black-tailed prairie dogs (*Cynomys ludovicianu*) in groups of 10, 30 and 60 showed that one year after release only groups of 60 had more survivors and progeny than the original numbers released (Robinette *et al.* 1995). In another study, it was shown that dormouse (*Muscardinus avellanarius*) released during May-June, a period of food scarcity, had a greater rate of body mass loss than those released at a different time of year, August-September (Bright and Morris 1994). A different study revealed that elk (*Cervus elaphus*) with prior familiarity to wolves or hunters had survival rates 1.9-2.2 times higher following their reintroduction than animals’ naïve to both risks (Frair *et al.* 2007). Another study showed that of white rhinoceros (*Ceratotherium simum*) released into an area in four release events (32 individuals in total) over a two year period, animals in the last release were forced to disperse out of the area due to territories established by the animals released prior (Stoen *et al.* 2009). Lastly, modelling of the demographics and consequences of reintroduction of adult and juvenile griffon vultures (*Gyps fulvus*) showed that it was more efficient to release adults than juveniles (Sarrazin and Legendre 2000).

In an attempt to facilitate the animals' establishment in a novel environment, this study examined whether releasing animals in pre-established groups versus unfamiliar groups influenced their immediate habitat behaviours. Contrary to expected, releasing animals in pre-established groups made no immediate difference to the animals' home range establishment behaviour, as there was no difference observed between familiar and unfamiliar release groups in the size of the area they used or the amount they shared while establishing. Likewise, Armstrong's (1995a) study on a species of bird (saddlebacks, *Philesturnus carunculatus rufusater*) concluded that releasing familiar groups (compared to unfamiliar groups) of saddlebacks was unlikely to improve the outcome of the reintroduction, despite the fact that pair bonds formed more quickly among familiar birds.

Following the establishment month however, differences between the two experimental release groups became apparent with regard to home range size and release group cohesion. While experimental release groups held similar sized home ranges during the establishment month, during subsequent months the animals released in familiar groups held larger home ranges than those released in unfamiliar groups. However, these larger home ranges were not obtained at the cost of reduced group vigilance or spatial familiarity, as there was no overall difference between the experimental groups in the amount of new area incorporated into their monthly home ranges, degree that the home range was shared, or in their home range stability/site fidelity. This result suggests that the animals' experience prior to release influenced their confidence to expand their home range and utilise a greater area of habitat following their establishment in a new environment. Similarly, pre-release experience was observed to influence movements in dormouse (*Muscardinus avellanarius*), where captive-bred animals travelled significantly shorter distances overall, and nightly from nest sites, compared to those originating from the wild (Bright and Morris 1994). Bright and Morris (1994) further suggested that the limited movement of captive bred animals would have reduced their chances to locate adequate food, and were slower to establish in a novel environment. Similarly in the present study, animals released in familiar groupings held larger home ranges, which would presumably be advantageous if it also correlated to more opportunities to locate resources.

The confidence of animals released in familiar groups was also observed in the home range proximity of group members during spring. While a similar proximity of home range centroids (centre of home ranges) between unfamiliar group members was maintained for at least seven months following their release, the home range centroids of animals from familiar groupings were significantly further apart than unfamiliar groups during the fifth month after release (spring: October). However, during spring animals generally tended to have larger home ranges than at other times of year, and familiar animals had larger home ranges than unfamiliar animals. Therefore, this difference may not be a true indication of home range distance between group members. Despite this, the larger home ranges of familiar animals and greater distance between their centroids in spring still suggests that animals released in pre-established groups may have had greater confidence to search for resources at this time.

3.4.3 Merging of release groups

Preferentially associating with known conspecifics may have multiple benefits. For example, individuals may spend less time on social vigilance and more time foraging, such as observed in female eastern grey kangaroos (*Macropus giganteus*, Carter *et al.* 2009). Additionally, there may be more stable dominance hierarchies and less aggression between conspecifics (such as seen in sea trout, *Salmo trutta*, Hojesjo *et al.* 1998), especially when associating with kin, as observed for female tammar wallabies (Blumstein *et al.* 2002a). Associating with kin also may reduce the likelihood of inbreeding, as many species have been shown to recognise and avoid breeding with siblings (Pusey and Wolf 1996). Another advantage of living in stable social groups is that fewer false alarms to predators are exhibited, the animals may better understand contextual anti-predator warning calls of known individuals and can place more reliance on group vigilance anti-predator strategies (Blumstein 2002a). Additionally for some species, stable groups may also collectively protect and raise the young, such as seen in African elephants (*Loxodonta africana*, Riedman 1982).

In this study animals were released in groups of a recommended size of six animals (Blumstein *et al.* 1999). However release groups began to converge with each other six months after release (November), and by the seventh month (during summer: December) there was no significant difference in proximity between release group members and non-group members. This indicated that they were no longer preferentially associating with their release group mates. Despite the benefits of remaining with familiar group mates, the necessity for animals to converge with individuals from other release groups may have been a reflection of the population size at the time. A large number of predation events occurred within the first six months after release. Following the spring release four animals succumbed to fox predation three months post-release, while 10 of the 36 released in winter died during the first month. A large proportion of the winter deaths were attributed to cachexia (starvation) leading to easy predation (see DEH 2006; Sharp et al. 2010). These deaths left the surviving animals to seek conspecifics to associate with. For example, although the number of deaths did not statistically appear to be a driving force behind shifting of home ranges, on one occasion a male individual was left as the sole occupant of an area (resulting from death of surrounding conspecifics), and completely shifted its home range to join other individuals 4km away. Likewise, 50% of male swift foxes (*Vulpes velox*) were found to emigrate from their range when the female mate died or disappeared (Kitchen *et al.* 2005). Similarly, journeys by males have been observed in reintroduced yellow-footed rock-wallabies (*Petrogale xanthopus celeris*) where one dispersed 7.3km between two and four months post-release to join another reintroduced colony (Lapidge 2001). Despite the need for animals to converge with other release groups due to declining population numbers from death and predation, it may be that the animals would have naturally converged with time since release or with the time of year (where males make seek out breeding opportunities). With time since release animals would have gradually increased their habitat knowledge becoming more confident to move (Banks *et al.* 2002), and by summer, the males are likely to have wanted to locate potential mates for the mating period (Cooper and Randall 2007; Doerr and Doerr 2005). However, time after release was not found to influence home range shift (indicated by the amount of new area incorporated into home ranges), whereas the time of year did. Specifically, more new area was found to be incorporated into home ranges between July-December than January-May, suggesting that animals moved to incorporate more new area in their home ranges during winter and spring than during summer and autumn.

3.4.4 Seasonal influence

Seasonal home range sizes estimated here were comparable with that found by Inns (1980) for tammar wallabies' winter and summer ranges on Kangaroo Island in South Australia. However, Inns (1980) observed no difference in home range size between the sexes, while here male home ranges outsized those of females. This disparity in home range size has also been observed in other wallabies, such as the swamp wallaby (*Wallabia bicolor*, Di Stefano 2007), red-necked wallaby (*Macropus rufogriseus*, Johnson 1987; le Mar *et al.* 2003), and bridled nailtail wallaby (*Onychogalea fraenata*, Fisher 2000). The size of core areas however, were similar between the sexes and maintained throughout the year, as also observed for agile wallabies (*Macropus agilis*, Stirrat 2003).s

The tammar wallaby home range sizes estimated here were significantly smaller in winter (Jul-Aug) than at any other time of year. Smaller home ranges were also observed in winter for tammar wallabies living on Kangaroo Island in South Australia (Inns 1980). Similarly, jaguars (*Panthera onca*) have been observed to have a smaller home range during the wet season compared to the dry season (Cavalcanti and Gese 2009). Smaller home ranges are commonly observed when the abundance and quality of resources are at their highest. For example, home ranges of swamp wallabies (*Wallabia bicolor*) were observed to be smaller in areas with dense vegetation cover (Di Stefano 2007), likewise the home range size of bridled nailtail wallabies (*Onychogalea fraenata*) was inversely related to food availability and diurnal home range areas were larger on sites that had the lowest availability of cover (Fisher 2000). However here, smaller home ranges in winter may not only reflect habitat quality but also may result from poorer weather reducing the animals' inclination to move around and their ability to detect predators which may in turn limit their explorations due to the increased predation risk (Swihart *et al.* 1988). This was indeed reported for tammars by Lentle *et al.* (1998), where animals travelled a greater distance to good foraging ground when weather conditions were favourable. However, the smaller home ranges in winter reported here could also be an artefact of the timing of reintroductions and the data available for analysis. Most of the winter home range data contributing to the analysis was gathered in the year of the winter release, and the home ranges during the winter establishment month were significantly smaller than 12months later (also during winter). As the influence of month after release on home range size was not tested in the statistical model, it is possible that home range sizes increased with time after release. For example, the home range size of reintroduced yellow-footed rock-wallabies (*Petrogale xanthopus celeris*) was observed to increase and peak by 12 months post-release (Lapidge 2001). Therefore here, as a consequence of timing of data collection it is possible that home ranges reported during winter were smaller than what would normally occur at that time of year.

Here, tammar wallabies were observed to have overlapping home ranges, as also observed by Inns (1980) for tammars occurring on Kangaroo Island. Although the degree of home range overlap was not reported by Inns (1980), here I observed that males shared a greater percentage of their home ranges with other individuals than did females. This reflects typical behaviour observed by polygamous and sexually dimorphic macropod species, where larger animals hold larger home ranges, and males (particularly dominant males) seek to overlap as many females as possible for maximum breeding opportunity (Croft 1989). Interestingly however, the amount that the home range and core areas were shared was consistent throughout the year and did not increase during the breeding season. Additionally, although male home ranges were larger than females, they were not observed to expand their range significantly more during the summer breeding period (compared to the spring or autumn). This may not have occurred as increasing home range size was not found to increase the number of individuals overlapped, which suggested that the home ranges of a number of animals may have been almost entirely overlapping. When female home range overlap is high, males do not need not increase their home range size as much (Fisher and Owens 2000).

3.4.5 Site fidelity

Seasons are likely to influence animals' home range locations for two main reasons: location of resources, and location of conspecifics. In a heterogeneous landscape, such as this study site, forage biomass and habitat structural complexities are available to different degrees in different habitat communities (see Chapter 2 section 2.1.1 for study site description). As the animals' requirements are likely to change seasonally, they may need to shift their home range to utilise the resources they need (Frair *et al.* 2005). For example, female bridled nailtail wallabies (*Onychogalea fraenata*) with dependant young altered their behaviour to reduce the predation risk to their young, where they reduced their home range size and stayed closer to cover (Fisher and Goldizen 2001). Likewise the common wallaroo (*Macropus robustus erubescens*) used different parts of their home range at different times of year, instead of shifting their range entirely (Clancy and Croft 1989). Here, in a similar fashion the tammars' home range locations were generally quite stable throughout the year, suggesting that they had a strong preference to stay in a familiar environment. However, when incorporating new areas it appeared they would expand their home range to utilise new areas and habitat, rather than shifting altogether. Additionally, the amount of new area occupied was significantly greater when more of the home range was shared with conspecifics. This may reflect that either the animals required greater overlap when in new territories for better communal vigilance, or they incorporated new areas so they could join other animals if they had been isolated.

It is reasonable to presume that males would locate and move into closer proximity to females prior to (and during) the breeding season, as also occurs in other species such as the giant kangaroo rat (*Dipodomys ingens,* Cooper and Randall 2007). In late December the summer solstice triggers the activation of the female's embryo out of diapause, and it is born one month later, which is then followed immediately by mating (Smith 1983). After mating, male tammars are known to mate guard, while subdominant males are looking for opportunities to breed (Hynes *et al.* 2005). Interestingly in this study there was no significant difference between the sexes (including females with and without pouch young) in the degree of home range shift or stability through time, so it is possible that all wallabies moved into new territory at the same time, with either the males following the females and/or all wallabies moving in unison in pursuit of seasonal resources.

Site fidelity is advantageous and desirable when the risk in moving outweighs the risk in staying in a familiar location, where animals frequently need to weigh up the trade-off between such decisions (Brown and Kotler 2004; Cowlishaw 1997; Panzacchi *et al.* 2010). Here, the general stability of tammars' home range locations suggested that perhaps either the availability of resources was sufficient year round, or not bad enough to force them to take the risk to leave, and competition between conspecifics for the resources was not an issue. Indeed Wolf *et al.* (2009) suggest spatial familiarly is important for larger scale selection of home range location, whereby animals' previous use of habitat had strong positive relationship with subsequent use, and that they would select to use familiar sites, rather than avoid unfamiliar ones. Strong site fidelity has been observed in other species such as yellow footed rock wallaby (*Petrogale xanthopus celeris*, Sharp 2009), western grey kangaroo (*Macropus fuliginosus,* Arnold *et al.* 1992), Siberian chipmunks (*Tamias sibiricus,* Marmet *et al.* 2009), and fallow deer (*Dama dama L.*, Morse *et al.* 2009). Furthermore, a big advantage of remaining in familiar habitat is also knowing escape routes from predators (Yoder *et al.* 2004). This was evident for the tammars as the number of deaths in a previous month did not influence the location of tammars' home ranges in the landscape, which remained quite stable.

3.4.6 Conclusion

Unfamiliarity with the environment appeared to have a major influence on animals during the establishment period following a reintroduction. Home range size and core area were significantly smaller immediately following the release than what was observed at an equivalent time of year post-establishment, and were only influenced by the number of animals overlapped. This was most likely strategic behaviour, as being surrounded by a larger number of conspecifics would increase vigilance against predators (Blumstein *et al.* 1999; Elgar 1989; Lima 1995), and therefore presumably increase their likelihood of survival in an unfamiliar habitat. During establishment, all animals (males, female with and without pouch young) occupied home ranges of a similar size and shared a similar percentage of their home range area with conspecifics. Releasing familiar groups of animals did not seem to influence home range or core area size or the amount they were shared during the establishment month. Post-establishment however, familiar animals had larger home ranges and familiar group members' home ranges dispersed further apart sooner, as they were presumably more comfortable taking bigger risks. However, familiar and unfamiliar animals did not differ in their home range stability or amount of new area occupied.

Post-establishment, home range size was driven by the time of year and amount shared (but not number shared with), and core area was proportional to the home range size. Overall, tammars' home ranges were smaller in winter, when food resources are presumably most abundant, but also when inclement weather may have hindered predator detection and subsequently restricted movements. Home range size was related to the amount the area was shared, where animals shifted or expanded their home range to increase the area shared (such as when neighbours die). The amount of home range overlap between two individuals was positively correlated with the amount of time they spent together as nearest neighbours. Males had larger home ranges than females and shared more of their home range than females did, and this was consistent through the year. Core area size and amount shared were consistent between the sexes and through the year. Home range may only move to keep up with resources and to overlap conspecifics more. Most new areas were incorporated into home ranges from July-December than in January-May, with no difference between the sexes, so either they have similar requirements and move to follow resources, or the males just follow the females.

Home range size and location is also a function of habitat quality, productivity, and resource distribution (Burt 1943), and may reflect an individual's requirements at the time (Fisher and Owens 2000). The following chapter will look in detail at the resources selectively incorporated into home ranges from the landscape scale, and those preferentially used for diurnal and nocturnal activity within the home range areas.

4 Chapter 4: Habitat selection

4.1 Introduction

Animals’ habitat choices are primarily driven by their need to find food, associate with mates, use shelter, and avoid predators (Bolnick and Preisser 2005; Börger *et al.* 2008; Mangel and Clark 1986; Pople 1989; Pyke 1984). Habitat decisions are made at a number of different scales (Gordon and Wittenberger 1991; Johnson 1980a). Animals firstly select what habitat types they require and where to establish their home ranges. Secondly, they chose how they use those habitats for their daily activities. As there are multiple levels to habitat selection, most recent habitat selection studies examine habitat use and availability at two scales at least (Buskirk and Millspaugh 2006). Commonly, habitat selection is assessed at the landscape scale (“second order selection”: the habitat types encompassed within an animals’ home range from within the available landscape), and within the home range (“third order selection”: the habitat used within the home range for diurnal and nocturnal activity) as outlined by Johnston (1980a). Within third order selection, the habitats used during resting and foraging periods are normally differentiated as animals tend to have different requirements at different times of the day/night (Gordon and Wittenberger 1991).

Habitat selection will usually vary with stage of day, time of year, climate and breeding seasons, as conditions, resources and needs change (Blumstein *et al.* 2003; Bos and Carthew 2003; Ciuti *et al.* 2006). Additionally animals often have to compromise on their needs, as they may be restricted by intra and inter-specific competition for resources, such as food and shelter, and the risk of predation (Bolnick and Preisser 2005; Buskirk and Millspaugh 2006; Falkenberg and Clarke 1998; Lima and Dill 1990; Panzacchi *et al.* 2010). For example, fallow deer (*Dama dama*) with fawns selected poorer quality but safer habitat which compromises their energy intake but reduces predation risk to fawns (Ciuti *et al.* 2006). Predation pressure is reported to have a major effect on habitat utilization at finer scales (Johnson 1980b; Panzacchi *et al.* 2010; Pople 1989; Preisser *et al.* 2009). Additionally, a lack of knowledge of an area may restrict preferred activities, and put animals at a greater risk of predation (Janmaat *et al.* 2009; Wolf *et al.* 2009; Yoder *et al.* 2004). Animals most likely to have a lack of knowledge of an area are dispersing sub-adults, migratory animals, or animals newly reintroduced or translocated into an area.

Animals reintroduced into a new and unfamiliar environment, are at an immediate disadvantage as they lack knowledge on the location of optimal habitat, and are naïve to the local predation risks (Banks *et al.* 2002; McLean *et al.* 1994; Tavecchia *et al.* 2009). This is especially true of animals translocated from captive bred situations (Gilligan and Frankham 2003; McLean *et al.* 1994; McLean *et al.* 2000; McPhee 2004; Tavecchia *et al.* 2009; van Heezik *et al.* 1999; Zidon *et al.* 2009). Animals that have spent time in captivity have been shown to lose anti-predator vigilance as they are not exposed to predators (Griffin *et al.* 2000), and are likely to be at a greater risk of predation, and make poor habitat choices during an establishment period following their reintroduction (van Heezik *et al.* 1999).

To maximise reintroduction success, programs need to be tailored to assist the animals' likelihood of surviving the initial establishment period, such that animals should be released at an appropriate time of year (Bright and Morris 1994), in optimal habitat at local and landscape scales that meets their food resource and shelter requirements (Finlayson *et al.* 2008; Hardman and Moro 2006a), and in sensible release group configurations (Blumstein *et al.* 1999). Aggregation and group living may be of benefit in assisting vigilance and predator detection, as 'many eyes' are available to detect a predator (Lima 1995). However, from captive studies Blumstein *et al.* (1999) observed that when group size increased, tammar wallabies engaged in more aggressive behaviour, which may contribute to predation risk if the animals then pay less attention to their surroundings. Specifically, Blumstein *et al.* (1999) modelled the relationship between group size and vigilance for tammar wallabies and suggested that animals in groups of two to six would gain maximum anti-predator benefit, and further suggested that reintroduction programs should release animals in groups of four to six.

Further to group size, group familiarity may influence the establishment of reintroduced animals (Armstrong 1995a). Familiarity in birds is known to reduce aggression and improve reintroduction success (Armstrong & Craig 1994 cited in Armstrong 1995b). However, experimental translocations of familiar and unfamiliar pairs of saddlebacks (Philesturnus carunculatus rufusater; Armstrong 1995a) and New Zealand robins (*Petroica australis longipes*) (Petroica australis longipes; Armstrong 1995b) found no evidence that grouping familiar individuals would improve the outcome of bird translocations. Group familiarity may also reduce the frequency of misinterpreted alarm calls between conspecifics (Beauchamp and Ruxton 2007; Blumstein 2002a), if animals are able to learn each individual's contextual cues when a predator is approaching (Blumstein 2002a). Reducing the frequency of 'false alarms' will lower the amount of energy wasted in fleeing a non-existent predator and allow more time for foraging (Beauchamp and Ruxton 2007; Blumstein 2002a; b).

Understanding habitat preferences and patterns of habitat utilization by threatened fauna can be critical for informing management and conservation decisions (Finlayson *et al.* 2008). Here I used a reintroduction program established to repatriate the SA Mainland subspecies of tammar wallaby (*Macropus eugenii eugenii*) to examine habitat choices by animals as they became familiar with their new environment. By taking an experimental approach to the reintroduction, pre-established groups of animals ("familiar") and groups of unfamiliar animals were released to determine if release protocol made a difference to habitat choices. In addition, the ongoing monitoring enabled me to assess the wallabies' habitat requirements at different times of year, which may assist future timing and location of reintroduction events.

Specifically, I aimed to determine the importance of specific habitat types at two spatial and temporal scales (the landscape scale, and nocturnal and diurnal habitat selection within home ranges) during the first month after release, and for 12 months following release. As a part of this I assessed the influence of timing of release, experimental treatment group, and sex of the animal on habitat selection during the establishment month. I also examined seasonal influence on habitat choices by females and males post-establishment, and finally compared selection post-establishment to habitat selection during the release month.

4.2 Methods

Tammar wallabies were reintroduced into the coastal heath, mallee and grassland habitat of Innes National Park, in an area with five main habitat communities dominated by *Eucalyptus diversifolia, E.rugosa, Melaleuca halmaturorum, Acacia anceps* and grassland. These were designated by pre-defined floristic layer GIS shape files and an aerial photograph (refer to Chapter 2 section 2.2.1). Ten animals were reintroduced in November 2005, and 36 more were reintroduced in June 2005. All animals were radio-tracked intensively over twelve months following each reintroduction (see Chapter 2 section 2.3). Monthly 100%MCP home range areas created for each individual (using methods outlined in Chapter 3 section 3.2.1) were used to assess the degree of habitat selection which occurred at two scales.

4.2.1 Habitat selection: use v availability

At both landscape and home range scales I calculated use and availability of habitat at monthly intervals for each individual (study design three proposed by Thomas and Taylor 1990), and compared data using compositional analysis (Aebischer *et al.* 1993). Compositional analysis is a technique frequently used to assess proportional use of habitat for a variety of species (Aebischer *et al.* 1993; Thomas and Taylor 2006). Compositional analysis examines whether habitat use differs from random, and if so, habitats are ranked in order of preference with significance between rank differences identified. Here, Leban's (1999) resource selection software was used to run the compositional analysis. This software substitutes any zero values with 0.001 and adjusts the remaining components accordingly (to retain the unit sum), then details a matrix of t-tests and ranked habitat categories from most selected to least selected when selection occurs. Resource selection studies on radio-tracked animals assume that the monitored animals are a random sample of the population, that radio locations are independent in time, that each animals' resource selection is independent of other animals (commonly violated when animals are gregarious or territorial), that resource availability does not change for the specified period (i.e. monthly, seasonally etc.), and that used resources are classified correctly (Millspaugh and Marzluff 2001).

To assess use and availability of habitat, a precise estimate of the animals' location is required so they can be correctly assigned to a habitat type (White and Garrott 1990). However, a certain degree of error is associated with triangulated bearings, and this may be of subsequent concern when the error ellipse encompasses habitat boundaries and the estimated location is close to the boundary. The location may be misclassified in the wrong habitat type, therefore misleading the degree to which that habitat type was used. Therefore here, to reduce potential error I firstly only accepted estimated locations with error ellipses under 10ha (88% of the locations had error ellipses under 3ha), and secondly I assumed that if locations were misclassified into a habitat that this would be an equal likelihood amongst the different habitat types. This assumption may have somewhat balanced out the number of any misclassified locations in each habitat type. Ideally, I could have isolated the locations falling in a buffered boundary area between habitat types (with the width of the buffer based on the accepted ellipse size), or calculated the distance between the location and the habitat edge to determine a degree of confidence in assigning it to the habitat type. Defining what habitat is 'available' to the animals also has its problems, as what the researcher and the animal view as available may be two different things (White and Garrott 1990). For example, to the researcher an area of habitat may appear available but the animals' movements may be restricted by the presence of another animal (White and Garrott 1990).

At the landscape scale, I defined the boundary of available habitat by extending the perimeter of each animal's monthly home range (as estimated by 100% minimum convex polygon "MCP") by a buffer of 500m (using the Buffer Wizard in ArcGIS 9.2) (Figure 4.1). This figure was derived as home ranges were frequently ~1km in diameter (see Chapter 3 section 3.3.2.3.1), and animals could easily traverse this distance in a single night (similar distinctions of available habitat were made by Korte (2008) in defining available habitat for buffalo by a 1km buffer on merged home range areas). To calculate the proportional use and availability of the five habitat types each animal's monthly home range and buffered area were intersected with the habitat layer in ArcGIS 9.2. Table Operations in X tools (in ArcGIS 9.2) was then used to aggregate the habitat types in each MCP, and calculate the area of each habitat type in each MCP. Compositional analysis, using Lebans Resource Selection Analysis Software (Leban 1999) was used to determine whether habitat types were incorporated into home ranges in proportion to their availability in the landscape.

At the home range scale, the proportions of available habitat were defined by the boundaries of each animal's monthly home range (100%MCP) area (Figure 4.1). Proportional use of this habitat was calculated from the number of location points falling in each habitat type (by joining location point layers to the habitat layer and using X tools for calculation in ArcGIS 9.2). Animal locations were assigned to a stage of day or night using daily sunrise, sunset and twilight times available on the Australian Government Geoscience Australia website (Geoscience Australia). Notably, location points recorded in the morning (after sunrise) and afternoon (before dusk) were pooled to analyse diurnal activity and habitat selection while the animals were resting. Those recorded from the onset of dark until dawn were pooled to assess nocturnal activity and habitat selection while the animals were foraging and active. Compositional analysis was used to assess the proportional use of habitats for diurnal activity and nocturnal activity from within the animal's home range area. White and Garrott (1990) point out that using an animals' home range as the 'available' habitat does represent some prior selection, however they also suggest that this is tolerable when the objective is to determine habitat use during a particular portion of the day, when selection within the home range is expected.

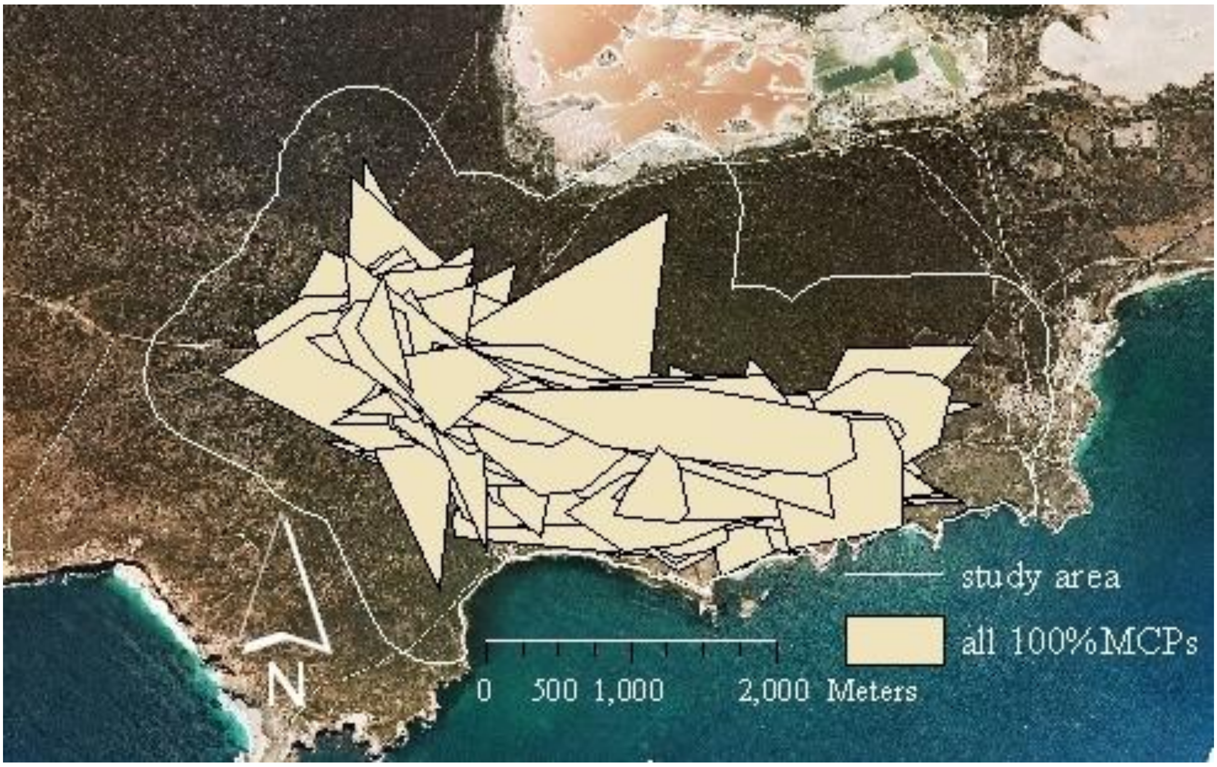

Figure 4.1 Study area (as defined by a 500m buffer on the perimeter of home ranges), and boundary of monthly home ranges (as calculated by 100%MCPs) of tammar wallabies radio-tracked for 12 months following their reintroduction.

During the establishment month, data was analysed to consider the influence of experimental groups (familiar and unfamiliar), sexes (male and female), and the timing of the reintroductions (spring Nov04 and winter Jun05) on habitat selection decisions at both landscape and home range scales. It should be noted that habitat selection for males during the spring (Nov04) establishment period could not be assessed as only two males were released and a minimum of five samples was required to process the data.

Post-establishment, the monthly data obtained were pooled into biologically and seasonally meaningful categories: Jan-Mar, Apr-May, Jul-Aug, Sep-Oct, and Nov-Dec. Animals are known to mate during late summer (Jan-Mar), females carry their pouch young through autumn (Apr-May) and winter (Jun-Aug), with young vacating the pouch during spring (Sep-Oct), leaving the adults and recently emerged pouch young independent around Nov-Dec (Hinds 2008; Smith 1983; Sunnucks and Taylor 1997). Habitat selection was analysed at the two scales for all animals together, and sexes separately as males and females have some unique requirements throughout the year which may influence their habitat selections.

4.3 Results

Following the two reintroductions, in spring (Nov04) and winter (Jun05), I assessed wallaby habitat selection at two spatial and temporal scales. I aimed to determine whether releasing animals in pre-established groups (as opposed to unfamiliar groups) altered the animals' habitat use in a new environment, and also distinguished whether males and females made different habitat choices following a reintroduction. In addition, I examined seasonal differences in habitat selection by males and females, and compared the wallabies' choices during the establishment month to those made at a similar time of year post-establishment. Comparing establishment decisions to those made post-establishment enabled an assessment of the influence unfamiliarity with the habitat has on habitat selection.

4.3.1 Habitat Selection during the establishment period

Habitat selection during the establishment period was evident at the landscape scale for both releases, but different habitat types were preferred by animals following each release (Table 4.1). The smaller number of animals released during spring 2004 primarily selected the grass habitat type in their first month, while those released in winter selected the *A.anceps* habitat followed by *E.diversifolia* for incorporation into their home ranges.

Animals released at the different times of year also made different habitat selections within their home range during the first month. In spring, selectivity was only evident during the day, with animals generally seeking *E.diversifolia* habitat for refuge. Conversely in winter, animals' habitat selectivity was only evident during nocturnal activities, with animals preferring *A.anceps* and *M.halmaturorum*. No habitat selection was detected during the daytime following the winter release, or nocturnal activity following the spring release, inferring that habitat was used in proportion to availability (Table 4.1).

		Rank							
		1	2	3	4	5	N	X^2	*P*
Landscape									
	Nov04	Gra	E.d^{a}	A.a^{a}	E.r^{a}	M.h^{a}	10	29.5061	<0.0001
	Jun05	A.a	E.d	M.h^{a}	Gra^{a}	E.r	36	50.4758	<0.0001
Home range									
day	Nov04	E.d	A.a^{a}	M.h^{a}	E.r^{a}	Gra^{a}	10	14.4311	< 0.05
	Jun05						36	4.0362	0.4011
night	Nov04						10	7.2990	0.1209
	Jun05	A.a^{a}	M.h^{a,b}	Gra^{b}	E.r^{a,b}	E.d	36	18.8542	< 0.001

Table 4.1 Habitat selection by tammar wallabies during the month following releases in November 2004 and June 2005, given as ranks at landscape and within home range scales obtained from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

Using just the animals from the larger winter (Jun05) reintroduction (n=36) I examined whether experimental group or sex of the animal made a difference to habitat selection decisions during the establishment period. At the landscape scale, both familiar and unfamiliar animals showed a preference for inhabiting *A.anceps* followed by *E.diversifolia*, while essentially avoiding areas of *E.rugosa* (Table 4.2). Grassland and *M.halmaturorum* were ranked in reverse orders by the two experimental groups, with grassland being more important for the unfamiliar animals. Conversely, within the home range, differences in diurnal and nocturnal habitat selection were apparent between the two experimental groups. Familiar animals selectively used habitat for diurnal refuge while unfamiliar did not (Table 4.2). Wallabies from familiar and unfamiliar treatment groups preferentially selected habitat for nocturnal foraging activities, however each ranked habitats differently. Familiar animals primarily foraged in *A.anceps* followed by grassland, while unfamiliar animals preferentially used *M.halmaturorum* and *A.anceps* (Table 4.2).

The selection of *A.anceps* at the landscape scale translated to selection within home range use (Table 4.2). Strangely however, the seemingly important inclusion of *E.diversifolia* in the home range from within the landscape did not equate to importance during diurnal or nocturnal activities, with *E.diversifolia* being ranked last when selection occurred (Table 4.2). Conversely, *E.rugosa* appeared least preferred at the landscape scale, but was used in equal ranking to the first or second preference for diurnal and nocturnal use when selection occurred within home range (Table 4.2).

		Rank							
		1	2	3	4	5	N	X^2	*P*
Landscape									
	Familiar	A.a^{a}	E.d^{b}	M.h^{a,b,c}	Gra^{c}	E.r	18	30.3052	<0.0001
	Unfamiliar	A.a^{a}	E.d^{b}	Gra^{a,b}	M.h^{b,c}	E.r^{c}	18	24.1902	<0.0001
Home range									
day	Familiar	Gra^{a}	A.a^{a}	M.h^{a}	E.r^{a}	E.d^{a}	18	14.8267	<0.05
	Unfamiliar						18	7.9393	0.0938
night	Familiar	A.a^{a}	Gra^{b}	M.h^{b}	E.r^{a,b,c}	E.d^{c}	18	11.6134	<0.05
	Unfamiliar	M.h^{a,b}	A.a^{a}	E.r^{a,b}	Gra^{b}	E.d	18	9.7950	<0.05

Table 4.2 Habitat selection by animals in experimental familiar and unfamiliar groups during the winter (Jun05) establishment period, given as ranks from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

Comparison of female and male habitat selection during the release month indicated identical preference ranking for habitats at the landscape scale during the winter (Jun05) establishment period (Table 4.3). Neither sex preferentially selected diurnal refuge habitats, although they did select habitat for nocturnal foraging. Both sexes incorporated a high cover habitat in their top two nocturnal preferences. Nocturnally, females preferred the protection of *M.halmaturorum*, followed by *A.anceps*, while males' first preference was *A.anceps* followed by *E.rugosa* (a high cover habitat) (Table 4.3).

		Rank							
		1	2	3	4	5	N	X^2	*P*
Landscape									
	Females	A.a ^{a}	E.d ^{a,b}	M.h ^{b,c}	Gra ^{c}	E.r	24	32.6778	< 0.0001
	Males	A.a ^{a}	E.d ^{b}	M.h ^{a,b}	Gra ^{a,b}	E.r	12	21.4151	< 0.05
Home range									
day	Females						24	3.3828	0.4959
	Males						12	3.4192	0.4903
night	Females	M.h ^{a,b}	A.a ^{a}	Gra ^{b}	E.r ^{a,b,c}	E.d ^{c}	24	13.3585	< 0.05
	Males	A.a ^{a}	E.r ^{a,b}	Gra ^{b}	M.h ^{b}	E.d ^{b}	12	12.0178	< 0.05

Table 4.3 Habitat selection by females & males during winter (Jun05) establishment period, given as ranks from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

4.3.2 Seasonal habitat selection

Seasonality of habitat selection by female and males after the establishment month was assessed at two spatial and temporal scales in light of climatic conditions and breeding status of the animals. Compositional analysis revealed that locations of home ranges within the landscape were generally not random. Selection at the landscape scale occurred year round for females and in all but spring for males (Table 4.4). Females selected habitats for diurnal and nocturnal activities during summer and autumn (Nov-Dec, Jan-Mar, Apr-May), with no selection detected during winter (Jul-Aug) or spring (Sep-Oct). Similarly, during winter males did not significantly select habitat for diurnal or nocturnal activities. Males were more inclined to selectively use diurnal habitats than nocturnal habitats. Males only selected nocturnal habitat during summer (Jan-Mar), whereas during autumn (Apr-May), spring (Sep-Oct) and early summer (Nov-Dec) they selectively used habitat for diurnal refuge (Table 4.4). The specific habitat types selected when selection occurred are outlined below.

	Jan-Mar	Apr-May	Jun-Aug	Sep-Oct	Nov-Dec
landscape					
females	<0.0001	<0.0001	<0.0001	<0.05	<0.0001
males	<0.0001	<0.001	<0.05	ns	<0.001
home range					
females	D** N*	D*** N*	ns	ns	D*** N*
males	D* N**	D*	ns	D*	D*

Table 4.4 Habitat selection at different times of year by females and males at two spatial and temporal scales: landscape scale and within home range, as analysed by compositional analysis (Leban 1999). Given as *P*-values where significant selection detected, temporal selection distinguished as diurnal (D) and nocturnal (N), ns = selection not detected. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. Data from the establishment month following the two reintroductions was excluded from these analyses.

4.3.2.1 Selection at landscape compared to selection within home range

Preference for a particular habitat type at the landscape scale translated somewhat to preferential use within the home range by both sexes (Tables 4.5 & 4.6). Females' top three preferences at the landscape scale were *E.diversifolia*, *A.anceps* and grassland (of varying rank order each season) with the inclusion of *M.halmaturorum* in winter instead of grassland. Of these habitats chosen at the landscape scale, *E.diversifolia* was strongly ranked for diurnal refuge, while *A.anceps* and grassland were always in the top three preferred foraging habitats (when selection occurred). *A.anceps* was also a preferred diurnal refuge during summer (Nov-Dec and Jan-Mar). Although *E.rugosa* was essentially avoided at the landscape scale, it was selected within the home range, especially in summer (Nov-Dec) where it ranked as second preference by females during resting and foraging. Males' habitat selection at the landscape scale differed slightly to the females. *M.halmaturorum* was amongst their top three preferred habitat types, in addition to grassland and *A.anceps* (in varying orders each season when selection occurred). However, *E.diversifolia* ranked above *M.halmaturorum* during winter (Jun-Aug). Nocturnal habitat selection by males was only detected during summer (Jan-Mar), grassland and *A.anceps* were the preferred foraging habitats, while *M.halmaturorum* was always in the top three diurnal refuge habitats when selection occurred. Also similar to the females, males used *A.anceps* diurnally for the duration of summer (Nov-Dec, Jan-Mar). Although *E.diversifolia* was not strongly preferred at the landscape scale, it was ranked as the first or second preferred diurnal habitat when selection occurred.

a)

	Jan-Mar			Apr-May			Jul-Aug			Sep-Oct			Nov-Dec		
rank	landscape	day	night	landscape	day	night	landscape	day	night	landscape	day	night	landscape	day	night
1	E.d ^{a}	E.d	Gra ^{a}	Gra	E.d ^{a}	A.a ^{a}	A.a			A.a ^{a}			A.a ^{a}	E.d ^{a}	A.a ^{a}
2	A.a ^{a}	M.h ^{a}	A.a ^{a,b}	A.a ^{a}	M.h ^{a,b}	Gra ^{a,b}	E.d ^{a}			E.d ^{a,b}			Gra ^{a}	E.r ^{a,b}	E.r ^{a,b}
3	Gra ^{a}	A.a ^{a,b}	E.r ^{b,c}	E.d ^{a}	E.r ^{b}	E.r ^{b}	M.h ^{a}			Gra ^{b}			E.d ^{a,b}	A.a ^{a,b}	Gra ^{b}
4	M.h ^{a,b}	E.r ^{a,b}	E.d ^{c,d}	E.r ^{a}	A.a ^{b}	E.d ^{c}	Gra ^{a}			E.r ^{b,c}			M.h ^{b}	M.h ^{b}	E.d ^{b}
5	E.r ^{b}	Gra ^{b}	M.h ^{d}	M.h ^{a}	Gra	M.h ^{c}	E.r			M.h ^{c}			E.r	Gra	M.h
N	27	27	27	18	18	18	34	34	34	20	20	20	23	23	23
X^2	44.1477	22.6087	18.2909	26.2506	43.9339	17.7668	37.0525	1.8766	8.1346	12.4357	3.8087	9.1572	25.5588	25.6025	17.8157
P	<0.0001	<0.001	<0.05	<0.0001	<0.0001	<0.05	<0.0001	0.7584	0.0868	<0.05	0.4325	0.0573	<0.0001	<0.0001	<0.05

b)

	Jan-Mar			Apr-May			Jul-Aug			Sep-Oct			Nov-Dec		
rank	landscape	day	night	landscape	day	night	landscape	day	night	landscape	day	night	landscape	day	night
1	Gra ^{a}	A.a ^{a}	Gra ^{a,b}	Gra	M.h ^{a}		A.a ^{a}				E.d ^{a}		Gra	E.d ^{a}	
2	M.h ^{a,b}	E.d ^{a}	A.a ^{a}	A.a ^{a}	E.d ^{a,b}		Gra ^{a,b}				M.h ^{a,b}		M.h ^{a,b}	A.a ^{a,b}	
3	A.a ^{a,b}	M.h ^{a}	E.d ^{b}	M.h ^{a}	A.a ^{a,b}		E.d ^{a,b,c}				E.r ^{a,b}		A.a ^{a}	M.h ^{a,b}	
4	E.d ^{b}	E.r ^{a,b}	E.r ^{b,c}	E.d ^{a}	E.r ^{b}		M.h ^{b,c}				Gra ^{a,b}		E.d ^{b}	E.r ^{b}	
5	E.r ^{b}	Gra ^{b}	M.h ^{c}	E.r ^{a}	Gra ^{b}		E.r ^{c}				A.a ^{b}		E.r ^{a,b}	Gra ^{b}	
N	11	11	11	7	7	7	19	19	19	11	11	11	10	10	10
X^2	39.3990	16.5507	20.4060	19.9411	13.1242	7.7743	18.1773	5.9509	5.7890	7.2297	11.2985	6.3028	18.5665	11.6059	9.4063
P	<0.0001	<0.05	<0.001	<0.001	<0.05	0.1002	<0.05	0.2028	0.2155	0.1242	<0.05	0.1776	<0.001	<0.05	0.0517

Table 4.5 Habitat selection by females (a) and males (b) at different times of year, at landscape level and during diurnal (day) and nocturnal (night) activities, given as ranks from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

4.3.2.2 Seasonal habitat choices by females and males

During January to March (the wallabies' mating season), females preferentially incorporated *E.diversifolia*, *A.anceps*, and grassland in their home ranges, while males selected grassland with *M.halmaturorum* and *A.anceps* (Table 4.5a&b). Both sexes seemingly avoided *E.rugosa* at the landscape scale. Nocturnal use of habitat within their home ranges was similar, with females and males both ranking grass and *A.anceps* habitat as their strongest selection. For diurnal refuge, *E.diversifolia* was the primary habitat selected for females, with males ranking *A.anceps* as their preferred habitat, although this did not differ significantly in rank from *M.halmaturorum* or either eucalypt species (Table 4.5a&b).

Over autumn (April to May) both sexes included more grassland into their home ranges than the other four habitat types, all of which did not differ in preference rank. Selection of nocturnal habitat was similar to the previous months for females, with the use of *A.anceps* and grassland. Males however did not selectively use habitat for nocturnal activities. Diurnally, both sexes preferred *M.halmaturorum* and *E.diversifolia*, with males also showing some preference for *A.anceps*. Indeed, both diurnal and nocturnal preferences followed that which occurred previously in late summer by both sexes (Table 4.5a&b).

For the period of winter (June to August) habitat selection was only evident at the landscape scale for both sexes. *A.anceps* was the primary selection by females, and was the strongest preference for males with the addition of grassland and *E.diversifolia*. *E.rugosa* was again essentially avoided by both sexes (Table 4.5a&b).

Interestingly, large differences in habitat selection were apparent between the sexes during spring (September and October), the time of year when pouch young were beginning to vacate the pouch and become independent. For the duration of spring, only females selected habitat at the landscape scale, and only males selected habitat within their home ranges, namely for diurnal refuge (targeting mostly *E.diversifolia*). Females targeted *A.anceps* and *E.diversifolia* for their home range locations, which also happened to be their preference ranking during winter, but did not select habitat for their diurnal and nocturnal activities. Diurnal refuge of the males was predominantly *E.diversifolia*, but with *M.halmaturorum*, *E.rugosa*, and grassland also similar in rank (Table 4.5a&b).

Throughout late spring and early summer (November and December) females selected similar habitat at the landscape scale as they did in early spring, with *A.anceps* their strongest preference, and grassland or *E.diversifolia* similar in rank to *A.anceps*. Male home range locations were driven primarily by the inclusion of grassland. Both sexes selected diurnal habitat, preferring *E.diversifolia*, with females also targeting *E.rugosa* and *A.anceps*, and males also selectively using *A.anceps* and *M.halmaturorum*. Only females selected their nocturnal habitat, using *A.anceps* and *E.rugosa* preferably, with grassland third in rank (Table 4.5 a&b).

4.3.3 Habitat selection during establishment month compared to an equivalent time of year

Habitat selected during the establishment month for newly reintroduced animals (irrespective of treatment group) was compared to an equivalent time of year post-establishment, to assess the influence a lack of knowledge of an environment might have on habitat decisions. Compositional analysis results from spring (Nov-Dec), and winter (Jul-Aug) were used for the post-establishment comparison of habitat selection.

During spring, grassland was highly selected within the landscape for both establishment and post-establishment times (Table 4.6). However, *A.anceps* was of greater importance for the post-establishment period, and ranked equally with grassland. Following the winter reintroduction, a similar trend occurred at the landscape scale, with the first and second habitat preference remaining unchanged between establishment and post-establishment periods. Although post-establishment, grassland and *M.halmaturorum* became of similar rank as *E.diversifolia* (Table 4.6).

		Rank					N	X^2	*P*
		1	2	3	4	5			
Landscape									
Spring	Release month	Gra	E.d ^{a}	A.a ^{a}	E.r ^{a}	M.h ^{a}	10	29.5061	<0.0001
	Post-establishment	Gra ^{a,b}	A.a ^{a}	E.d ^{b,c}	M.h ^{c}	E.r ^{c}	33	34.4310	<0.0001
Winter	Release month	A.a	E.d	M.h ^{a}	Gra ^{a}	E.r	36	50.4758	<0.0001
	Post-establishment	A.a	E.d ^{a}	Gra ^{a}	M.h ^{a}	E.r	54	48.3730	<0.0001

Table 4.6 Habitat selection at the landscape scale during the spring release month (Nov04) and post-establishment (Nov-Dec), and winter release month (Jun05) and post-establishment (Jul-Aug). Given as ranks from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

At the home range scale, similar habitats were used during establishment month and post-establishment throughout the day. During spring diurnal activities *E.diversifolia* was highly selected during the establishment phase, and was also the primary selection post-establishment. Likewise, both winter establishment and post-establishment were similar in that no habitat selection was detected for diurnal activities in either time period.

Nocturnal activities during establishment and post-establishment did show some differences. During spring establishment no selection of habitat was detected, whereas post-establishment the animals showed a preference for *A.anceps* and *E.rugosa* (Table 4.7). Interestingly, during the winter establishment month the primary nocturnal habitat selection was for “foraging” habitat and “protective” habitat, namely *A.anceps* and *M.halmaturorum*. Post-establishment however, *A.anceps* had become the clear favourite (as it was ranked significantly higher than the other four habitat types), and *M.halmaturorum* was ranked fifth and essentially avoided during nocturnal activities (Table 4.7).

			Rank							
			1	2	3	4	5	N	X^2	P
	Within home range									
Diurnal	Spring	Release month	E.d	A.a ^{a}	M.h ^{a}	E.r ^{a}	Gra ^{a}	10	14.4311	< 0.05
		Post-establishment	E.d	E.r ^{a}	A.a ^{a}	M.h ^{a}	Gra	33	33.5432	<0.0001
	Winter	Release month						36	4.0362	0.4011
		Post-establishment						54	3.2017	0.524
Nocturnal	Spring	Release month						10	7.2990	0.1209
		Post-establishment	A.a ^{a}	E.r ^{a,b}	Gra ^{b}	E.d ^{b}	M.h	33	25.120	< 0.0001
	Winter	Release month	A.a ^{a}	M.h^{a,b}	Gra ^{b}	E.r ^{a,b}	E.d	36	18.8542	< 0.001
		Post-establishment	A.a	E.r ^{a}	E.d ^{a}	Gra ^{a}	M.h ^{a}	54	13.5340	< 0.05

Table 4.7 Diurnal and nocturnal habitat selection within the home range during the spring release month (Nov04) and post-establishment (Nov-Dec), and winter release month (Jun05) and post-establishment (Jul-Aug). Given as ranks from Compositional Analysis, ranging from 1 (most preferred/selected) to 5 (least preferred). Habitat types were Grassland (Gra), *Eucalyptus diversifolia* (E.d), *Acacia anceps* (A.a), *Eucalyptus rugosa* (E.r), and *Melaleuca halmaturorum* (M.h). Habitats labelled with the same superscript (eg. ^{a}) do not differ significantly in rank. N= number of individuals analysed.

4.4 Discussion

Animals' knowledge of their habitat is important for both large scale selection of home range and small scale habitat selection and foraging (Pyke 1984; Wolf *et al.* 2009). However animals new to an area, including reintroduced individuals, will lack this crucial knowledge and need to assess the quality of their habitat and chose where to settle (Gordon and Wittenberger 1991). To establish and survive, it is paramount that animals find suitable habitat which meets their food resource and shelter requirements (Hardman and Moro 2006a), while also avoiding predators (Di Stefano *et al.* 2009; Frair *et al.* 2007; Lima and Dill 1990). This study examined whether releasing animals in pre-established groups assisted their adaptation to a new environment (compared to those in unfamiliar groups) by looking at their habitat selection, and examined the seasonal influence on habitat selection post-establishment.

4.4.1 Habitat selection at the landscape scale during establishment

While establishing in their new environment and presumably gaining knowledge on resource location and predation risk, the tammar wallabies selectively incorporated particular habitat types into their home range areas from the surrounding landscape. Furthermore, these selections following both reintroduction events reflected the typical selections they made during equivalent seasons post-establishment. Additionally, from examining the winter establishment month in detail, it was apparent that neither the experimental grouping treatment, nor sex of the animal influenced habitat selections at the landscape scale. Animals from familiar and unfamiliar groups selected very similar habitat types (with unfamiliar animals ranking habitats most similar to those post-establishment), and males and female displaying very similar habitat selection at the landscape scale, which were also equivalent to preferences post-establishment. This suggests that all animals were able to make appropriate habitat choices, find the resources they needed and orientate themselves quickly when in a foreign environment. This is particularly important as predation is a common cause of reintroduction failure (McCallum *et al.* 1995; Moro 2003; Moseby and O'Donnell 2003; Richards and Short 2003; Short *et al.* 2002; Short and Turner 2000), and is more likely when animals accustomed to captivity are released (Griffin *et al.* 2000; McPhee 2004; van Heezik *et al.* 1999; Zidon *et al.* 2009). Habitat decisions are known to reflect animals' anti-predator avoidance requirements at the time, whereby animals trade-off their habitat and safety requirements (Brown and Kotler 2004; Cowlishaw 1997; Panzacchi *et al.* 2010; Preisser *et al.* 2009). While animals in unfamiliar, and therefore high-risk, environments would be expected to exhibit their greatest anti-predator behaviours (Lima and Bednekoff 1999), here, all animals selected similar habitat at the landscape scale during the establishment and post-establishment periods. This suggests that they did not need to trade-off habitat and safety requirements in an unfamiliar environment at the landscape level, and the experimental protocol did not influence their habitat selection. However, some differences between experimental groups were apparent within home range selection, primarily during nocturnal activity.

4.4.2 Diurnal and nocturnal habitat selection during establishment

Generally, the reintroduced tammar wallabies selected habitats for diurnal refuge that they also preferred at the same time of year after they had established and become familiar with their environment. However, their nocturnal habitat selections during the establishment month suggest that they exercised a higher degree of caution while foraging than normally expected at that time of year post-establishment. In particular, female wallabies, and those released in unfamiliar groups tended to be more cautious while foraging at night.

Habitat selection by unfamiliar animals suggested that they were more cautious than familiar animals during nocturnal activities in the establishment month examined (winter). While unfamiliar animals showed a strong preference for the densest high cover habitat available (*M.halmaturorum*, with the addition of *A.anceps* and *E.rugosa*), familiar animals' strongest selection was primarily for low cover habitat types (*A.anceps* followed by grass and then *M.halmaturorum*) for their nocturnal activities, which would have offered them greater foraging opportunities. As animals released in unfamiliar groups were more inclined to utilise protective high cover habitat, and animals released in pre-established groups were more inclined to leave cover in search of good foraging ground, this finding suggests that the release protocol may have influenced the animals' immediate habitat use when in a novel environment. Differences in habitat use and confidence to explore unfamiliar territory have previously been observed between reintroduced captive-bred and wild-caught animals. For example, reintroduced captive-bred dormouse (*Muscardinus avellanarius*) travelled significantly less than the reintroduced wild-caught animals (Bright and Morris 1994). This restriction of movement reduced their chances to locate adequate food, and Bright and Morris (1994) concluded that captive-bred animals took longer to establish in a new environment.

Of the sexes, it was apparent that female wallabies in this study were more cautious than males while foraging during the winter establishment month. Females' strongest nocturnal preference was for the densest high cover habitat (*M.halmaturorum*), with males also selecting a high cover habitat in their top two preferences. *M.halmaturorum* habitat most likely provided the best concealment from aerial predators, with relatively clear ground to flee ground dwelling predators, and provided the good overhead protection from climatic conditions. Indeed, Barrett (2009) found that *M.halmaturorum* is typically used during diurnal resting by tammar wallabies. However here, during the winter establishment period *M.halmaturorum* was also selected while foraging, whereas post-establishment *M.halmaturorum* was the least preferred habitat at night. This result suggests that selecting *M.halmaturorum* for nocturnal activities was a response to being in an unfamiliar surrounding, and the animals traded-off safety and food acquisition while establishing in a new environment with unfamiliar risks (Brown and Kotler 2004; Cowlishaw 1997; Lima and Dill 1990). This preference for protection while foraging is also supported by the result that both sexes selected acacia more than grassland habitat while foraging, as acacia habitat still provided some degree of concealment from predators. Similarly, Moore *et al.* (2002) also noted the protection provided in clumps of acacia for eastern grey kangaroos (*Macropus giganteus*).

These finding support the idea that wild animals entering a new area are relatively timid and invest much time and effort in anti-predator behaviour (Banks *et al.* 2002; Zidon *et al.* 2009), especially while foraging at night. However, Zidon *et al.* (2009) commented that captive reared animals may initially lack this tendency, but that it can be reacquired over time. Whether our captive training program assisted the animals' reacquisition of this anti-predator tendency is unclear. However, these findings do seem to indicate that releasing animals in unfamiliar groups facilitated a greater degree of caution by the animals.

These results suggest that the animals' lack of knowledge of the habitat and predation risk primarily influenced habitat decisions (and ultimately survival) during the establishment period. Some of these risks associated with habitat and predator naivety can be counteracted by their social grouping decisions and will be explored in the following chapter.

4.4.3 Seasonal habitat selection at the landscape scale

Monthly home range locations were selectively located within the landscape at each time of year after establishment, as indicated by selection of habitat at the landscape level (with the exception of males in September). This has also been observed in a variety of animals including female wood ducks (*Aix sponsal*, Hartke and Hepp 2004), female forest buffalo (*Syncerus caffer nanus*, Korte 2008), and swamp wallaby *(Wallabia bicolour,* Di Stefano *et al.* 2009).

Differences between the female and male tammars' habitat selection at the landscape scale were apparent, with different habitat types selected at different times of year. Different habitat selection by each sex may reflect different reproductive strategies of males and females, as also hypothesised for swamp wallabies (*Wallabia bicolor*, Di Stefano *et al.* 2009). In this study it is likely that predator avoidance was more critical for females, particularly around the late stages of carrying pouch young and pouch young emerging and becoming independent during spring. This was evident by the shift in habitat selection at the landscape scale away from the dominant preference in winter for a low cover habitat type (*A.anceps*), towards incorporating an equal preference for high cover habitat (*E.diversifolia*) into their home ranges during spring. Furthermore, while grass (a good forage and low cover habitat type) was ranked top or equal top preference during summer and autumn by females at the landscape scale, their selection of grass during winter and spring (while carrying pouch young and the young vacating the pouch) was ranked third and significantly less than the amount of *A.anceps* and *E.diversifolia*. In contrast, grassland continued to rank equal top preference by males in winter, suggesting that males had a stronger preference for grass areas in their home range than females did at this time. Food acquisition and predator avoidance are principal but often conflicting components of survival strategies of most animals (Wahungu *et al.* 2001). This sacrifice by females to avoid the productive but more risky sites has similarly been found for other species, such as fallow deer (*Dama dama*) where the females selected safer habitat, at the cost of their own energy intake, to reduce predation risk to their fawns (Ciuti *et al.* 2006). In roe deer (*Capreolus capreolus*), female mothers avoided open areas and chose denser habitat for their fawn to shelter in (Bongi *et al.* 2008). While in Bridled nailtail wallabies (*Onychogalea fraenata*), females with juveniles stayed closer to cover to hide their young in denser habitat to avoid predation (Fisher and Goldizen 2001). These examples further support the notion that the habitat selection observed by female tammar wallabies here may reflect their need to target the use of protective cover around the time of pouch young emerging and becoming independent.

4.4.4 Seasonal diurnal and nocturnal habitat selection

Within a home range many animals selectively use certain habitat more than others (Horne *et al.* 2008). Generally habitat selections are likely to reflect animals balancing predation risk with energetic reward, as they need to maintain energy intake while avoiding predators and their ability to do this will vary depending on the type of habitat they occupy at the time (Bos and Carthew 2003; Lima 1987; Lima and Dill 1990).

In this study female wallabies were more selective than males in the habitat they used diurnally and nocturnally. This has also been seen in female swamp wallabies (*Wallabia bicolor*) which made more distinct choices than males within their home ranges (Di Stefano *et al.* 2009). However, female tammar wallabies did not select habitat diurnally or nocturnally during winter and spring (unlike during both periods at the other times of year). This is somewhat surprisingly as any females carrying pouch young during this time would likely be at greater risk of predation, as their flight response to a predator would be slower (Colagross and Cockburn 1993). Therefore, theoretically they should avoid open areas and use covered habitat more or remain closer to cover (Colagross and Cockburn 1993; Southwell 1987). This has been observed in species such as the bridled nailtail wallaby (*Onychogalea fraenata*, Fisher 2000) and red-necked pademelon (*Thylogale thetis*, Wahungu *et al.* 2001), where females with vulnerable young remained closer to cover due to their increased predation risk. Remaining close to cover allows them to remain inconspicuous to decrease the probability of attack, reduces the flight distance if a predator does attack (Wahungu *et al.* 2001). However, in this study as some degree of selection had already occurred at the landscape scale, that being toward avoiding open grassland areas, further selection within home range during winter and spring may not have been apparent or necessary. During late spring and early summer (Nov-Dec), while the young at foot were gaining independence, the females appeared reluctant to use grassland at night time although they had select grassland and *A.anceps* at the landscape scale. Rather, they preferred *A.anceps* and *E.rugosa*. Using *A.anceps* provided access to grass but retained a small degree of cover. Additionally as *A.anceps* bordered the eucalypt habitat, they were in close proximity to high cover habitat, which is ideal when young at foot are present. Similarly, Moore *et al.* (2002) found that eastern grey kangaroos preference for clearings also provided them with protection in acacia clumps, and suggested that this habitat type supplied complementary resources. Indeed Fisher (2000) also reported that bridled nailtail wallabies (*Onychogalea fraenata*) prefer to feed under cover when sufficient food is available.

Seasonal forage availability (outlined in Chapter 2.2.1.1), combined with the animals' different needs for shelter from climatic conditions, was reflected in the habitat choices made by the wallabies in the present study. During Jan-Mar both female and males based their nocturnal foraging in grassland and *A.anceps*. This choice of habitat at that time of year is also not surprising, as Lentle *et al.* (1998) also found the feeding activity of free ranging tammar wallabies was restricted by inclement weather, but when the weather was favourable they made considerable journeys to forage in abundant pasture grasses. Therefore here during summer (compared to winter), animals should be more inclined to use open areas as conditions would generally be dry and calm, facilitating predator detection when in the open.

Male wallabies were not selective during their nightly activities for the duration of the year except for Jan-Mar, when their habitat selections mirrored those of the females. However, as mating occurs at this time of year (Hinds 2008; Hynes *et al.* 2005), animals are likely to be in close proximity of one another, so similarities in habitat preference were expected. It appears from these results that males are not as cautious or selective as females, and it may be that habitat selection by males was potentially driven by the location of the females. Having observed male wallabies in very close proximity to young at foot while foraging, it is possible that their nocturnal habitat decisions revolved around where the females and young at foot were foraging. However, selecting refuge habitat during the day still appeared important for males each season (except during winter).

One limitation of these analyses was that the strength of preference for habitat types during diurnal or nocturnal activities may be somewhat confounded by the selection already made to some degree at the landscape level (Buskirk and Millspaugh 2006; White and Garrott 1990). Another issue was that an animals home range is not solely bound by habitat types needed, but also the whereabouts of conspecifics and their necessity to interact or avoid interaction (Buskirk and Millspaugh 2006; Carter *et al.* 2009). Therefore if an animal sacrificed using their preferred habitat type so that their home range may overlap that of another, some incorrect assumptions could have been made about their habitat preferences.

However, overall, the habitat types encompassed by the animals’ home ranges and used for diurnal and nocturnal activities differed during the year for both sexes. This result emphasised that the five different habitat types provided different fundamental resources for the animals at different times of year. Habitat selection decisions were likely to be strongly driven by acquisition of food, shelter from climatic conditions, predator avoidance, different reproductive strategies of the sexes, and proximity to conspecifics.

Following their reintroduction the animals instinctively chose appropriate habitat to use when reintroduced into a new environment, but they exercised more caution than expected at that time of year (particularly females and animals released in unfamiliar groupings). Therefore, it is likely that it is the animals’ familiarity with the habitat and how they use it, in conjunction with their social grouping decisions, which will most likely influence their survival during the establishment period and beyond. This will be explored in detail in the following chapter.

5 Chapter 5: habitat use & social behaviours

5.1 Introduction

Animals use their surrounding habitat to meet their primary needs of foraging, resting and reproducing. However, many animals are subjected to predation and so these activities are often done under the risk of predation thus influencing their behaviour (Bolnick and Preisser 2005; Brown and Kotler 2004; Cowlishaw 1997; Willems and Hill 2009). In evolutionary terms, successful animals must behave at all times as though there was a reasonable risk of being killed by a predator. Thus they should schedule activities, choose habitats and companions, and fine-tune their behaviour to either minimise the risk of being detected, or maximise the probability of detecting the predator before they are attacked, enabling them to be able to flee successfully (Bolnick and Preisser 2005; Jarman and Coulson 1989). Therefore animals need to weigh up the potential costs versus benefits of an action (Brown and Kotler 2004; Buskirk and Millspaugh 2006; Jarman and Coulson 1989), such that they use their environment strategically to optimise what they need, but have to consider what they will risk to get it (Lima and Bednekoff 1999). Theory predicts that animals' foraging effort will depend on an interaction between resource availability and predation risk, where animals will take fewer risks as resources become more abundant, and take more risks when the reward is higher (Bolnick and Preisser 2005; Brown and Kotler 2004).

An individual's perceived risk of predation will be dependent upon an amalgamation of a number of factors, such as the physical structure of the habitat they occupy, the stage of day or night, phase of moon, weather, climatic/seasonal conditions, their current breeding status, the surrounding group size and proximity to their nearest neighbour, and the current condition and needs of the animal (Buskirk and Millspaugh 2006). Perceived risk is therefore on a sliding scale, varying as conditions/situations change. Acceptable levels of risk may even vary for animals of the same species. For example, an animal in poor condition seeking breeding opportunities may be likely to accept greater predation risks, whereas a pregnant animal in good condition might tolerate little increase in predation risk (Houston & McNamara 1999, cited in Buskirk and Millspaugh 2006). In addition, different species may consider the same situation to have different degrees of risk, depending on their anti-predator strategies. For example, while western grey kangaroos have been found to view cover as obstructive and forage further from cover when in a high risk situation (Blumstein and Daniel 2002), small macropods (such as tammar wallabies) are thought to view cover as protective and forage close to cover when in a high risk situation (Blumstein and Daniel 2002).

For animals to ‘safely’ obtain their required resources, they should attempt to counteract the risk of predation by employing anti-predator strategies. The perceived risk and resulting anti-predator strategies will then be reflected in the animals’ habitat use and social behaviours at the time (Beauchamp 2010b; Blumstein *et al.* 1999; Pays *et al.* 2009), such as distance from cover (Lima 1987) and number of surrounding conspecifics (Blumstein *et al.* 1999; Jarman and Coulson 1989). For example, in the presence of predators chimpanzees were found to reduce their nearest neighbour distances as a communal defence tactic (Stanford 1995). For small macropods which rely on being cryptic to avoid predators, the habitat type they occupy is fundamental, as different habitat types provide different degrees of concealment and likelihood of being preyed upon while occupying them. Leaving cover to forage at night comes with increased predation risk. An animal’s foraging effort will depend on an interaction between resource availability and predation risk (Bolnick and Preisser 2005), and an animal’s proximity to cover will also be affected by the predation risk (Beauchamp 2010b; Fisher 2000; Pays *et al.* 2009). For example, female macropods with pouch young are more vulnerable to predation as their larger weight and bulk present difficulty in gaining speed during escape from a predator (Colagross and Cockburn 1993). Therefore, female bridled nailtail wallabies with vulnerable young were found to forage closer to cover than those without (Fisher 2000). Likewise female pademelons with young also foraged closer to cover than those that without (Wahungu *et al.* 2001).

Another way animals may minimise their risk of predation and increase predator detection is by living in groups. A group is defined by Jarman and Coulson (1989) as a number of animals observed in substantially closer proximity to one another than to other members of the population, and potentially able to communicate and interact cohesively with, and respond to the action of other members of the group. Group size is variously defined in macropods to include the number of conspecifics within 10-50m (Heathcote 1987; Johnson 1989), where the size of the group is a response to a complex set of selection pressures which include the acquisition of food and shelter, the need for social interactions, and minimisation of the predation risk (Jarman and Coulson 1989).

Communal awareness during group living may increase the collective predator vigilance and likelihood of detecting a predator (detection effect: more individuals able to detect predator), and decrease the per capita risk of predation (dilution effect: more alternative prey) (Blumstein *et al.* 2002b; Lima 1995; Lima and Dill 1990; Lima and Zollner 1996). Communal awareness allows individual group members to spend less time being vigilant and more time foraging (Lima 1995). However, this benefit may not be equal for all group members. Blanchard *et al.* (2008) and Matson *et al.* (2005) both noted that individual impalas' (*Aepyceros melampus*) foraging on the periphery of a group spent more time being vigilant than their central conspecifics. Theory predicts that individuals at the periphery of a group should be at higher risk than their more central conspecifics since they would be the first to be encountered by an approaching terrestrial predator (Hamilton 1971).

The familiarity or relatedness of group membership may also be of importance to increased fitness and survival. Grouping with familiar conspecifics may be more advantageous when the animals are able to learn each other's contextual cues when a predator is approaching (Blumstein 2002a). Reducing the frequency of fleeing due to 'false alarms' lowers the amount of energy wasted and lost foraging time (Beauchamp and Ruxton 2007; Blumstein 2002a) and retains their reliance on collective detection (Beauchamp and Ruxton 2007). For example, Ward and Hart (2003) report that fish are able to recognize kin and/or familiars, and that this ability potentially conveys significant benefits, including increased inclusive fitness, reduced inbreeding costs, reduced competition and enhanced anti-predator behaviour. Likewise, captive studies on tammar wallabies by Blumstein *et al.* (2002a) have suggested females are likely to aggregate with kin and imply that they gain some fitness benefit from doing so.

However, whether or not animals associate with kin or familiar conspecifics, larger groups will be more easily found by predators, and the potential cost of being found is only counteracted if the increasing group size improves the likelihood of detecting an approaching predator (Jarman and Coulson 1989). Furthermore, the benefits of being in a large group may be outweighed if an individual is unable to flee quickly, such as sick adults, females with pouch young, or juveniles. Jarman & Coulson (1989) suggests this to be one factor why females with young at foot may withdraw from being in groups and subsequently remain more cryptic.

Although different habitat types assist small macropods in remaining cryptic and group size helps to detect the presence of a predator, failing both of those, their ability to flee when being pursued is the only remaining option for survival and relies on their familiarity with the environment and knowledge of escape routes. The costs of spatial ignorance have been shown in birds, fish, mammals, where predation risk increases in less familiar areas as animals need longer time to find cover and escape routes (Janmaat *et al.* 2009). For example, an increase in predation was exhibited in vervets (*Cercopithecus aethiops*) when they moved into an unfamiliar area (Janmaat *et al.* 2009). Animals with reduced information and spatial awareness include those that have had to move due to depleting resources, competition for resources or mates, or those that have been reintroduced into an area.

Despite reintroductions being an increasingly important conservation tool, most have failed due to predation (Short *et al.* 1992). Anthony and Blumstein (2000), and Blumstein (2000) highlight the necessity of understanding an animal's natural anti-predator strategies and behaviour before releasing them to increase the likelihood of reintroduction success. Furthermore, Finlayson *et al.* (2008) noted that having an understanding of habitat preferences and patterns of habitat use by threatened fauna can be critical for informing management and conservation decisions. The disappointing survival rates from previous macropod reintroductions, coupled with a lack of detailed monitoring has meant that not much has been learnt about the way newly reintroduced animals establish in a new environment, much less the anti-predator strategies they draw on while familiarising themselves with their new surroundings. Fortuitously, we were in a unique position to repatriate the SA mainland tammar wallaby (a previously extinct species) back into its former range, from which we might answer some of these questions using an experimental approach to the reintroduction.

This species is preyed upon by foxes (*Vulpes vulpes*) and wedge tailed eagles (*Aquila audax*) (Blumstein *et al.* 2002a; Inns 1980). They rely on being cryptic to elude predators (Southwell 1987), and use social warning foot-thumps to alarm conspecifics when a predator is present (Blumstein *et al.* 2002a; Jarman and Coulson 1989). Tammars are known to perceive cover as safety, as when in high predation risk sites tammars have been found to forage closer to cover, and retreat to cover when alarmed (Blumstein and Daniel 2002). Under solitary conditions tammars' predator avoidance may take precedence over their optimal foraging behaviour (Lentle *et al.* 2003). Although tammars are able to utilise browse they rely mainly on grazing, and their feeding activity is somewhat constrained by inclement weather (Lentle *et al.* 1998). Lentle *et al.* (1998) found that when weather was favourable the animals would travel considerable journeys to graze on abundant pasture grasses in a high risk predation area. One way to counteract predation risk is foraging in groups, and although the benefit of group living for a number of small macropod species is unclear (Croft 1989), foraging, tammars are known to receive anti-predator benefit from aggregating with conspecifics (Blumstein *et al.* 2002b). Therefore, Blumstein suggested that tammars should benefit by being reintroduced in groups (Blumstein *et al.* 2002b). In particular, work on captive tammars has suggested the animals would receive the most anti-predator benefit from aggregation when released in groups of 6 animals (Blumstein *et al.* 1999), but added that this hypothesis needed testing in the wild (Blumstein *et al.* 2002b). Indeed, Blumstein *et al.* (2002a) further suggested that our understanding of many aspects of tammar social structure in nature would benefit from additional study, and more detailed knowledge about the behaviour of this nocturnal species in the field is presently lacking.

As the main limiting factor of many reintroductions has been predation (Griffin *et al.* 2000; McCallum *et al.* 1995), I was particularly interested in perceived risk of predation and how the tammars responded while establishing in a new environment following a reintroduction, and during seasonal habitat use after establishment. I aimed to assess these by investigating more detailed aspects of habitat use coupled with social grouping behaviour. Specifically, the likelihood that they would be using high cover habitat, the distance they would forage away cover at night, the number of animals within 100m of each other, and the distance between nearest neighbours were considered.

I aimed to assess how the habitat type occupied, and risks animals took when leaving protective cover were influenced by various factors, including the time of year, stage of day or night, their current breeding status, surrounding group size, and proximity to their nearest neighbour. Additionally, I examined how the number of surrounding conspecifics and proximity to their nearest may be influenced by the habitat type they occupy, or the proximity from cover, as well as the time of year, stage of day or night, their current breeding status. Furthermore, using an experimental element to the reintroduction, I aimed to test the hypothesis that reintroducing animals in pre-established groups (as compared to groups of unfamiliar animals) would influence their habitat and social grouping decisions, which may enable them to establish quicker and have a better chance of survival in a new habitat.

5.2 Methods

Forty-six tammar wallabies were reintroduced over two events into Innes National Park (South Australia). An experimental approach was undertaken to assess the influence of group familiarity on habitat use and social behaviours whilst establishing in a new environment. The first release occurred in spring (November 2004), where 10 animals were released in two groups (one familiar and one unfamiliar), and the other in winter (June 2005), where 36 animals were released in six groups (three familiar and three unfamiliar) (see Chapter 2). The study area was comprised of five main habitat types: *Eucalyptus diversifolia*; *Eucalyptus rugosa*; *Melaleuca halmaturorum*; *Acacia anceps;* and grassland (see Figure 2.4 in Chapter 2). Due to the sparseness and low canopy height of plants in the *A.anceps* area, I categorised *A.anceps* and grassland habitat as “low cover” and *Eucalyptus* and *Melaleuca* habitat as “high cover” for these analyses.

Reintroduced animals were intensively radio-tracked for approximately 30 nights in the month following their release, and then for approximately nine nights each month for the next twelve months. To analyse potential for social groupings animals needed to be located simultaneously within the same sampling period (see Chapter 2). Since on some occasions there was not enough time in a day to locate all animals in every sampling period, some sampling periods were missing animals and were excluded from the analysis of social grouping. Therefore, of the total 13058 usable triangulated radio locations, 11,969 locations were available for the analysis of social grouping and associated habitat use.

5.2.1 Analysis of habitat use and social grouping

Habitat use and social grouping decisions by animals may be interrelated, and influenced by their need to avoid predators, find food, shelter and mates. While traditional statistical modelling has generally assessed various elements (such as home range, resource selection, relationship among individuals) separately, Horne *et al.* (2008) suggested that greater benefit may come from modelling them simultaneously. Therefore, I examined the influence of a range of interacting behavioural and environmental predictor variables on four key aspects of habitat use and social decisions by reintroduced wallabies. The four key aspects assessed by modelling were likelihood of using high cover, distance to cover, distance to the nearest animal, and number of animals within 100 metres. As newly reintroduced animals will have limited knowledge of their habitat which may impact their fine scale habitat and social decisions while establishing in a new environment, the aspects were modelled for their establishment phase, at seasonally relevant intervals for following year, and to compare the establishment phase with 12 months after release.

Although some authors consider macropods within 10-50m to be in the same group (Heathcote 1987; Johnson 1989), and Blumstein *et al.* (2001) suggested tammars perceive conspecifics within 10m as group mates (the number of tammars within this distance explained the most variation in behaviour), here I used a radius of 100m to define density (group size) of animals for two reasons. Firstly, as the locations were based on radio-telemetry triangulation, this has a degree of error in estimating locations, therefore I could not interrogate the data at a much smaller scale than this error allowed for. Secondly, Wahunga *et al.* (2001) defined pademelons located in the same grassy clearing to be in the same group, where their grassy clearings were 1-3ha in size, similar in size to our field site.

For likelihood of using cover, locations were classified as being in low cover or high cover (see Chapter 2 section 2.2.1 & this Chapter section 5.2). This was achieved by defining what habitat type each GPS location occupied from joining the GPS locations layer to the habitat layer in ArcGIS 9.2. The distance animals were from cover while foraging in the open at night was determined by calculating how far each nocturnal location in low cover habitat was from the edge of cover (using ArcGIS 9.2). Distance to nearest and number of animals within 100m was determined using Hawths tools application in ArcGIS 9.2, by calculating the distances between all animals in each sampling period, and extrapolating the required information, including the sex and identity of the nearest neighbour.

5.2.1.1 Statistical analysis

During the establishment phase all four aspects (likelihood of using cover, distance to cover while foraging, number of animals within 100m, and distance to nearest neighbour) were modelled, using the data obtained during Nov04 and Jun05. For the 12 months post-establishment three aspects (likelihood of using cover, distance to cover while foraging, and distance to nearest neighbour) were modelled. The establishment phase was then compared to 12 months later by modelling all four aspects to univariate level (data from Nov04 and Jun05 were compared to Nov05 and May06).

Different models were used for the analysis of each aspect (Table 5.1). Likelihood of using cover was modelled using log binomial generalized estimated equation (GEE) regression models, distance to cover and distance to nearest were modelled with linear mixed effects models, and number of animals within 100m was modelled with a negative binomial GEE regression model (Bolker *et al.* 2009; Hanley *et al.* 2003).

	Predictor (independent) variables considered										
Dependant variable	establishment phase		establishment phase, & post-establishment				post-establishment			Estab v 12months later	
aspect	Group	Month	Stage of day	Habitat type	Distance to nearest	#animals within 100m	Time of year	Sex	Sex of nearest	Period	model
Likelihood of using cover	√	√	√		√	√	√	√		√	Log binomial GEE regression model
Distance to cover	√	√	√ (post-estab)		√	√	√	√		√	Linear mixed effects model
Distance to nearest	√	√	√	√			√	√	√	√	Linear mixed effects model
No. animals within 100m	√	√	√ (estab phase)	√ (estab phase)						√	Negative binomial GEE regression model

Table 5.1 Predictor variables considered in each model to assess their influence on the four aspects habitat and social grouping behaviours during establishment phase and post-establishment.

In modelling the number of animals within 100m, the number of animals available was included as an offset variable in the negative binomial GEE regression model to adjust for the differing numbers of animals available for measurement. To model distance to cover and distance to nearest neighbour, square root and logarithmic transformations were required (respectively) to meet the assumptions of the models. In addition, a random animal ID effect was included in both models so as to adjust for the dependence in results from the same animal.

For each aspect being modelled, it was determined whether a range of predictor variables had an independent influence on the aspect (Table 5.1 and 5.2). Predictor variables were first entered into a univariate model, and if they satisfied the criterion $p<0.10$, they were entered into a final multivariate model. When global *P*-values for predictor variables were statistically significant in univariate or multivariate models, *post hoc* tests were carried out to determine where the significant differences occurred. All analyses were carried out using SAS Version 9.2 (SAS Institute Inc. 2008).

Log binomial GEE regression models (used to model the likelihood of being in high cover) produce results in the form of a “relative risk”, while “rate ratio” results are obtained from negative binomial GEE regression models (used in modelling the number of animals within 100m). Relative risk determines the ratio of the probability of the “outcome (being in cover)” given the “predictor variable” is present divided by the probability of the “outcome (being in cover)” given the “predictor variable” is absent. Rate ratio is a ratio value that also compares the two probabilities by dividing a probability of interest conditioned on one group of subjects by the probability of interest conditioned on another group of subjects. Here for biological relevance, the relative risk and rate ratio results are expressed as a percentage and *P*-value in the text and *post hoc* tests. Relative risk and rate ratio values obtained from modelling will also be incorporated into the text (with their confidence intervals) where applicable.

Predictor variable	Categories	Comments
Group	Familiar, and unfamiliar	
Month of release	Nov04, and Jun05	
Period since release	Release month (Nov04, Jun05), and 12 months after release (Nov04, May06)	
Time of year	Jan/Feb/Mar, Apr/May, Jun/Jul/Aug, Sep/Oct, and Nov/Dec	Months grouped into meaningful seasonal and biological categories, based on the climatic seasons and reproductive stages of the tammars (see Chapter 2 section 2.1.1).
Sex and pouch young status	Male, female without pouch-young, and female with pouch-young	
Stage of day or night	Morning (after sunrise), afternoon (before dusk), 2h after dark (2h time period after dark), middle of night (from 2h after dark until 2h before dawn), 2h before dawn (2h time period before dawn)	Times marking the beginning and end of both dawn and dusk periods were obtained from the Australian Government Geoscience Australia website. Animal location data obtained within the dawn and dusk periods were removed from this analysis, as there were not enough locations for each animal each month for viable analysis.
Habitat type	*Eucalyptus diversifolia* (E.div), *Eucalyptus rugosa* (E.rug), *Melaleuca halmaturorum* (M.hal), *Acacia anceps* (A.anc), and grassland (grass)	
Number of animals within 100m	(continuous variable)	
Distance to nearest neighbour	(continuous variable)	
Sex of nearest neighbour	Male, and female	

Table 5.2 Specifications and categories of the predictor variables used for modelling various aspects of habitat use.

Median values were used to report results from the linear mixed effects models for distance to cover and distance to nearest neighbour. For both of these aspects the data required transformation prior to modelling due to right skewness. Distance to cover data was square root transformed, and distance to nearest neighbour data was logarithmic (natural) transformed. To report the results in more applicable units for ecological understanding, and assistance of management and future reintroduction decisions “back-transforming” was necessary. Only the logarithmic transformed data (for distance to nearest neighbour) could be back-transformed, whereby back-transforming an “adjusted mean” resulted in producing a median value. Therefore median values and 95% confidence intervals (CI) are given in the results, with adjusted mean and standard error also included where applicable. Square root transformed data (for distance to cover) could not be back-transformed, therefore in keeping with the same units, median values and inter-quartile range (IQR) from the descriptive statistics were only incorporated into the results to provide meaning to the adjusted mean and standard error obtained from modelling.

All findings presented, including the *post hoc* tests, are from multivariate modelling, unless explicitly stated to be from univariate modelling.

5.3 Results

5.3.1 Establishment phase:

Following the spring and winter reintroductions of tammar wallabies into the wild, four key aspects of their habitat use and social grouping behaviour were studied during the establishment month. Namely, the likelihood of using high cover, distance from cover while foraging at night, number of animals within 100m, and distance to nearest neighbour. These four aspects were significantly and independently influenced by many of the predictor variables considered (Table 5.3).

To summarise, the likelihood of animals using high cover and the distance they ventured from cover while foraging in the open at night were significantly different for familiar and unfamiliar animals in both releases. Animals were more likely to use high cover at particular stages of the day or night, and their use of cover was influenced by the number of animals within 100m as well as their proximity to a near neighbour. Proximity to a neighbour was more important than density of animals (number of animals within 100m) in how far the animals would venture away from cover while foraging. These aggregations were also highly influenced by the stage of day and habitat type. Familiar and unfamiliar animals maintained similar density and proximity to others, but the month of release did influence group size. Details about how each of the predictor variables influenced the wallabies' habitat and social grouping decisions are outlined below.

	Predictor variable					
	Group	Month	Stage of day	Habitat type	Distance to nearest	No. animals within 100m
Likelihood of using high cover	**0.0012**	**0.0002**	**<0.0001**	-	**0.0010**	**0.0002**
Distance to cover while foraging at night	0.0133	**0.0007**	-	-	**<0.0001**	0.5269
No. animals within 100m	*(univariate)* 0.3350	**<0.0001**	**<0.0001**	**<0.0001**	-	-
Distance to nearest neighbour	*(univariate)* 0.6444	0.0548	**0.0017**	**<0.0001**	-	-

Table 5.3 Significance of predictor variables as given by *P* values derived from multivariate models for four aspects of habitat use and social behaviour by tammar wallabies during the establishment period. Predictor variables which did not meet the p>0.1 criteria in the univariate model "*(univariate)*" were excluded from subsequent consideration in the multivariate model. Significant values are highlighted in bold, "-" = untested.

5.3.1.1 Likelihood of using high cover during establishment phase

Experimental group and month of release both had a significant influence on the probability of being in high cover (Table 5.3). Unfamiliar animals were 55% more likely to use high cover than the familiar animals (unfamiliar vs. familiar relative risk: 1.55, 95%CI 1.19 – 2.015, *P*=0.0012), and animals released in spring (Nov04) were 53% more likely to use high cover than animals released in winter (Jun05) (Nov04 vs. Jun05 relative risk: 1.533, 95%CI 1.223 – 1.922, *P*=0.0002).

Animals were more likely to be found in high cover during particular stages of the day or night (Table 5.3). In particular, the probability of animals being in high cover was significantly greater in the morning than any other stage of day or night during the establishment month (Table 5.4). In addition, the wallabies were more likely to be found in high cover during the two hours before dawn than they were during the preceding nocturnal hours, where likelihood of being in cover from the start of the night until two hours before dawn were equivalent.

	morning	afternoon	2h after dark	middle of night	2h before dawn
morning		↑ 20 *	↑ 68 ***	↑ 61 ***	↑ 35 ***
afternoon	↓ 17 *		↑ 40 **	↑ 34 ***	ns
2h after dark	↓ 40 ***	↓ 28 **		ns	↓ 19 *
middle of night	↓ 38 ***	↓ 25 ***	ns		↓ 16 **
2h before dawn	↓ 24 ***	ns	↑ 24 *	↑ 19 *	

Table 5.4 Percentage difference in the likelihood of using high cover for different stages of day or night during the establishment period, as determined by “relative risk” *post hoc* tests. ↓ indicates animals were less likely to be in high cover, ↑ indicates animals were more likely to be in high cover (read as: left column compared to top column). *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant.

The probability of animals using high cover was also significantly influenced by the numbers of animals within 100m of each other and distance of animals to their nearest neighbour (Table 5.3). For every extra animal within 100m, the probability of being in high cover decreased by 15% (relative risk: 0.84789, 95%CI 0.776 – 0.926, *P*=0.0002), and as the distance between nearest neighbours increased by 100 metres the probability of being in high cover increased by 6% (relative risk: 1.00060, 95%CI 1.000 – 1.001, *P*=0.0010).

5.3.1.2 Distance to cover during establishment phase

The distance animals foraged from cover at night during their establishment month was also influenced by both the experimental group and month they were released (Table 5.3). Familiar animals tended to be located further from cover (median 60.7m, IQR:33.1-88.5), than unfamiliar animals (median 48.7m, IQR:18.1-92.6) (familiar vs. unfamiliar mean square root of distance to cover: 7.60±0.27 vs. 6.61±0.27, *P*=0.0133), and animals released in winter (Jun05) foraged further from cover (median 62.8m, IQR:31.6-92.9), than those released in spring (Nov04) (median 32.1m, IQR:12.1-72.7) (Jun2005 vs. Nov2004 mean square root of distance to cover: 7.51±0.22 vs. 5.83±0.41, *P*=0.0007).

The distance animals foraged away from cover during the night was also influenced by the distance of nearest neighbours (Table 5.3). For every one metre increase in the distance to nearest neighbour, the square root of distance to cover was expected to decrease by 0.0052±0.0009 units (p<0.0001). Interestingly, the distance animals foraged from cover was not influenced by the number of surrounding animals within 100m (Table 5.3).

5.3.1.3 Number of animals within 100m during establishment phase

Baseline data showed that the number of animals within 100m of each other ranged from zero to six individuals during the establishment (and post-establishment) period. During the establishment period animals were within 100m of at least one other animal 58% of the time, while post-establishment this figure was reduced to 49%. During the establishment month, two animals were observed within 100m of each other 27% of the time, three animals were within 100m of each other 16% of the time, four animals were within 100m of each other 4% of the time, five animals were within 100m of each other 2% of the time, and six animals were within 100m of each other only 0.2% of the time. A similar decrease in numbers was also observed post establishment. Modelling was required to examine what factors influenced these trends.

In the univariate model the number of animals within 100m of each other was not significantly different for familiar or unfamiliar animals after adjusting for the total number of animals available (Table 5.3) (univariate model, familiar vs. unfamiliar rate ratio: 0.89110, 95%CI 0.705 – 1.127, *P*=0.3350). Therefore, experimental group was not incorporated into the multivariate model (as the *P*-value obtained in the univariate model did not reach the required criterion).

The timing of the reintroductions had a significant influence on the number of animals within 100m after adjusting for the total number of animals available for measurement (Table 5.3). Group sizes following the winter release (Jun05) were 49% lower than those during the spring establishment month (Nov04) (Jun05 vs. Nov04 rate ratio: 0.51326, 95%CI 0.403 – 0.654, p<0.0001).

The number of animals within 100m was significantly influenced by particular stages of day or night after adjusting for the total number of animals available (Table 5.3). However, contrary to expected for a nocturnally social species, *post hoc* tests revealed there were more animals within 100m of each other during the morning than at any other stage of day or night during the establishment month (Table 5.5).

	morning	afternoon	2h after dark	Middle of night	2h before dawn
morning		↑ 68	↑ 82	↑ 86	↑ 93
afternoon	↓ 41		ns	ns	ns
2h after dark	↓ 46	ns		ns	ns
Middle of night	↓ 47	ns	ns		ns
2h before dawn	↓ 49	ns	ns	ns	

Table 5.5 Percentage difference in group size (number of animals within 100m) for different stages of day or night during the establishment period, as determined by rate ratio *post hoc* tests. ↓ indicates smaller group size (compared to the corresponding stage), ↑ indicates larger group size. (P<0.0001 for all significant differences). “ns”= non significant.

Habitat type significantly influenced the number of animals within 100m (after adjusting for the total number of animals available) (Table 5.3). *Post hoc* tests indicated that there were expected to be more animals within 100m of each other when in the grass and *A.anceps* habitats (ie. the low cover habitats used for foraging) than the other three habitat types during the establishment month (Table 5.6).

	grass	A.anc	E.div	E.rug	M.hal
grass		ns	↑ 36 *	↑ 50 **	↑ 77 *
A.anc	ns		↑ 54 ***	↑ 70 **	↑ 200 ***
E.div	↓ 28 *	↓ 35 ***		ns	ns
E.rug	↓ 34 **	↓ 42 **	ns		ns
M.hal	↓ 44 *	↓ 50 ***	ns	ns	

Table 5.6 Percentage differences in group size (number of animals within 100m) while using different habitat types during the establishment period, as determined by rate ratio *post hoc* tests. ↓ indicates smaller group size (compared to the corresponding habitat type), ↑ indicates larger group size. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. "ns"= non significant difference.

5.3.1.4 Distance to nearest animal during establishment phase

Experimental group also appeared to have no significant influence on the distance to a nearest neighbour in the univariate model (Table 5.3), where the median distance to nearest for familiar animals was 76.3m (95%CI: 63.6–91.5) and unfamiliar animals was 71.9m (95%CI: 59.9–86.3). Therefore experimental group was not incorporated into the multivariate model.

The influence of month of release on the distance to nearest neighbour approached significance (Table 5.3), with the median distance to nearest in winter (Jun05) being 70.9m (95%CI: 62.3-81.0) while in spring (Nov04) it was 93.3m (95%CI: 73.0-119.3).

Proximity between nearest neighbours was significantly influenced by the particular stages of day or night (Table 5.3). *Post hoc* tests showed the animals tended to remain closer to their nearest neighbour in the middle of the night and morning, than they did in the two hour period before dawn and during the afternoon (Table 5.7, and also see Appendix B for the percentage of time animals spent within certain proximity of their nearest neighbour).

	morning	afternoon	2h after dark	middle of night	2h before dawn	Distance to nearest (median)	Adjusted mean±se
morning		↓ 21.12 *	ns	ns	↓ 14.90 *	71.06m	4.264 ±0.075
afternoon	↑ 21.12 *		ns	↑ 16.88 *	ns	92.18m	4.524 ±0.087
2h after dark	ns	ns		ns	ns	80.10m	4.394 ±0.080
middle of night	ns	↓ 16.88 *	ns		↓ 10.67 *	75.30m	4.321 ±0.061
2h before dawn	↑ 14.90 *	ns	ns	↑ 10.67 *		85.97m	4.454 ±0.072

Table 5.7 Distance between an animal and its nearest neighbour (median value) at the different stages of the day or night, and differences in proximity between the different stages of the day or night as determined by *post hoc* tests (in median metres) during establishment month. ↓ indicates animals were closer (compared to the corresponding stage), ↑ indicates animals were further apart. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. "ns"= no significant difference in distance to nearest neighbour between the two stages.

Distance between nearest neighbours during the establishment month was significantly influenced by habitat type occupied (Table 5.3). *Post hoc* tests revealed that animals remained significantly closer together when they were in the *A.anceps* habitat than in every other habitat type (Table 5.8), including grassland (the other low cover habitat type). There was no significant difference in distance to nearest neighbour when they occupied grassland, *E.diversifolia* or *M.halmaturorum* (Table 5.8).

	grass	A.anc	E.div	E.rug	M.hal	Distance to nearest (median)	Adjusted mean±se
grass		↑ 22.44 *	ns	↓ 26.08 *	ns	89.37m	4.493 ±0.115
A.anc	↓ 22.44 *		↓ 19.41 ***	↓ 48.53 ***	↓ 36.61 **	66.93m	4.204 ±0.062
E.div	ns	↑ 19.41 ***		↓ 29.12 ***	ns	86.33m	4.458 ±0.066
E.rug	↑ 26.08 *	↑ 48.53 ***	↑ 29.12 ***		ns	115.46m	4.749 ±0.081
M.hal	ns	↑ 36.61 **	ns	ns		103.53m	4.640 ±0.121

Table 5.8 Distances between nearest neighbours (median metres) during establishment while occupying different habitat types, and comparisons between neighbour proximities in the five different habitat types (in median metres), as determined by *post hoc* tests. ↓ indicates animals were closer (compared to the corresponding month), ↑ indicates animals were further apart. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

5.3.2 Post establishment:

Once a reintroduced population has established in a new environment, their continued survival is dependant upon acquiring adequate resources and avoiding predation in light of their perceived predation risks, breeding requirements and seasonal conditions. I examined the influence a number of predictor variables had on the wallabies’ behaviour and habitat use throughout the course of a year.

A number of the predictor variables were found to significantly influence the three key aspects of wallaby habitat use and social behaviour modelled (Table 5.9). The likelihood of using high cover was significantly influenced by time of year, stage of night and group size. However, likelihood of using high cover was not different for males, females or females with pouch young (Table 5.9). The sex or pouch young status of females also did not influence the distance animals ventured from cover while foraging in the open at night. Similarly, distance from cover did not significantly differ during the night, but was influenced by time of year, group size, and proximity to a nearest neighbour (Table 5.9). Distance to a nearest neighbour was influenced by many different variables: time of year; whether it was day or night; habitat type being used at the time; sex of the animal; and sex of the nearest animal (Table 5.9). Details about how each of the predictor variables influenced the likelihood of using high cover, distance to cover (while foraging at night), and distance to nearest neighbours is outlined below.

	Predictor variables						
	Time of year	Stage of day or night	Sex	Sex of nearest	Habitat type	Distance to nearest	No. animals within 100m
Likelihood of using high cover	**<0.0001**	**<0.0001**	*(univariate)* 0.1186	-	-	**0.0006**	**<0.0001**
Distance to cover (while foraging at night)	**<0.0001**	*(univariate)* 0.2906	*(univariate)* 0.6978	-	-	**<0.0001**	**<0.0001**
Distance to nearest neighbour	**<0.0001**	**<0.0001**	**0.0009**	**<0.0001**	**<0.0001**	-	-

Table 5.9 Significance of predictor variables on three aspects of habitat use and social behaviour by reintroduced tammar wallabies post-establishment, given as *P* values derived from multivariate models. Predictor variables which did not meet the p>0.1 criteria in the univariate model "*(univariate)*" were excluded from subsequent consideration in the multivariate model. Significant values are highlighted in bold, "-" = untested.

5.3.2.1 Likelihood of using high cover

There was no difference in the likelihood of males and females with or without pouch young using high cover versus low cover habitat. However, the likelihood of using high cover was significantly influenced by every other variable entered into the model (Table 5.9).

Animals' occupancy of high cover habitats (*E.diversifolia*, *E.rugosa*, and *M.halmaturorum*) was significantly related to the time of year (season) (Table 5.9). Specifically, during spring (September-October) animals were 31-59% more likely to be found in high cover habitat that during any other time of the year (Table 5.10). They were also 21% more likely to use high cover habitat in summer (November-December) than they were in winter (June-August).

	Jan-Mar	Apr-May	Jun-Aug	Sep-Oct	Nov-Dec
Jan-Mar		ns	ns	↓ 33 ***	ns
Apr-May	ns		ns	↓ 29 ***	ns
Jun-Aug	ns	ns		↓ 37 ***	↓ 18 *
Sep-Oct	↑ 50 ***	↑ 40 ***	↑ 59 ***		↑ 31 ***
Nov-Dec	ns	ns	↑ 21 *	↓ 24 ***	

Table 5.10 Differences in percentage likelihood of animals being found in high cover habitat at different times of year, as determined by relative risk *post hoc* tests. ↓ indicates animals were less likely to be in high cover (compared to the corresponding period), ↑ indicated animals were more likely to be in high cover. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

Habitats considered high cover were also used differently at different stages of day or night (Table 5.9). Not surprisingly, animals were more likely to be found in high cover during the day than at night, with significant differences between morning and all three night stages, and between afternoon and all three night stages (Table 5.11). Animals were 12% more likely to be in high cover in the two hour period before dawn than during the middle of the night, and once in cover by morning, their likelihood of still using cover by the afternoon was equivalent (Table 5.11).

	morning	afternoon	2h after dark	middle of night	2h before dawn
morning		ns	↑ 46 ***	↑ 53 ***	↑ 36 ***
afternoon	ns		↑ 45 ***	↑ 52 ***	↑ 36 ***
2h after dark	↓ 31 ***	↓ 31 ***		ns	ns
middle of night	↓ 35 ***	↓ 34 ***	ns		↓ 11 **
2h before dawn	↓ 27 ***	↓ 26 ***	ns	↑ 12 **	

Table 5.11 Differences in percentage likelihood of animals being found in high cover habitat during different stages of the day or night, as determined by relative risk *post hoc* tests. ↓ indicates animals were less likely to be in high cover (compared to the corresponding stage), ↑ indicated animals were more likely to be in high cover. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. "ns"= non significant difference.

The proximity of an animal to its nearest neighbour and number of animals within 100m were both highly significant factors influencing the likelihood of high cover habitat use (Table 5.9). In particular, as distance between neighbours increased by 100m, the likelihood of being in high cover significantly increased by 2% (relative risk: 1.0002, 95%CI 1.0001, 1.0003, *P*=0.0006), and for every additional animal within 100m, the likelihood of being in high cover decreased by 14% (relative risk: 0.85942, 95%CI 0.82193, 0.89862, p<0.0001).

5.3.2.2 Distance to cover

The distance animals ventured from cover while foraging at night was significantly influenced by only some of the variables: post-establishment time of year, group size (number of animals within 100m), and proximity to a nearest neighbour were important, while sex and pouch young status of the females, and stages of the night were not (Table 5.9).

During winter (Jun-Aug) animals foraged further into the open than any other time (Table 5.12). By spring (Sep-Oct) the animals foraged closer to cover than they did in winter, and closer again for the duration of the summer (Jan-Mar vs. Nov-Dec difference of adjusted means: -0.1449±0.1080, *P*=0.1854). However, during autumn (Apr-May) the animals remained significantly closer to cover while foraging than for any other time.

	Jan-Mar	Apr-May	Jun-Aug	Sep-Oct	Nov-Dec	Distance to cover (median)	Square root transformed mean ± se
Jan-Mar		↑ *	↓ ***	↓ ***	ns	15.9m	4.89±0.19
Apr-May	↓ *		↓ ***	↓ ***	↓ **	10.5m	4.53±0.20
Jun-Aug	↑ ***	↑ ***		↑ ***	↑ ***	48.9m	7.24±0.18
Sep-Oct	↑ ***	↑ ***	↓ ***		↑ **	19.8m	5.82±0.24
Nov-Dec	ns	↑ **	↓ ***	↓ **		20.0m	5.03±0.20

Table 5.12 Median distance to cover of foraging animals post-establishment, and differences between times of year, as determined by *post hoc* tests. ↓ indicates animals were closer to cover (compared to the corresponding period), ↑ indicated animals were further from cover. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

The distance animals ventured from cover while foraging at night was significantly influenced by both the number of animals within 100m and the distance between near neighbours. Animals foraged further from cover when the number of animals within 100m increased (regression coefficient 0.2455, p<0.0001). Surprisingly however, animals’ proximity to a neighbour increased the further away from cover they foraged (regression coefficient 0.001778, p<0.0001). This result is in contrast to that obtained for the establishment month, when neighbouring animals became closer the further away from cover they foraged.

5.3.2.3 Distance to nearest animal

The distance between nearest neighbours was significantly influenced by the time of year, stage of day or night, sex and pouch young status of the females, the habitat type being occupied, and sex of the neighbour (all variables entered into the model) (Table 5.9).

Neighbour proximities ranged from 77 median metres in autumn (Apr-May) to 134 median metres in spring (Sep-Oct) (Table 5.13). Interestingly during spring, animals were significantly further from a neighbour than any other time of year, coinciding with pouch young vacating the pouch. By summer, animals were closer to a neighbour than they were in spring, and remained within a similar proximity for the duration of summer (Nov-Dec & Jan-Mar). During autumn (Apr-May) and winter (Jun-Aug), animals were within their closest proximity to a neighbour compared with other times of year (Table 5.13).

	Jan-Mar	Apr-May	Jun-Aug	Sep-Oct	Nov-Dec	Distance to nearest (median)	Adjusted mean±se
Jan-Mar		↑ 21.03 ***	↑ 14.54 ***	↓ 35.97 ***	ns	98.4m	4.589 ±0.062
Apr-May	↓ 21.03 ***		ns	↓ 57.00 ***	↓ 15.65 ***	77.3m	4.348 ±0.065
Jun-Aug	↓ 14.54 ***	ns		↓ 50.51 ***	↓ 9.17 *	83.8m	4.429 ±0.056
Sep-Oct	↑ 35.97 ***	↑ 57.00 ***	↑ 50.51 ***		↑ 41.35 ***	134.3m	4.900 ±0.065
Nov-Dec	ns	↑ 15.65 ***	↑ 9.17 *	↓ 41.35 ***		93.0m	4.533 ±0.062

Table 5.13 Median distance between nearest neighbours post establishment, and differences between times of year, as determined by *post hoc* tests. ↓ indicates animals were closer (compared to the corresponding period), ↑ indicates animals were further apart. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

The distance between nearest neighbours was significantly influenced by the particular stage of day or night (Table 5.9). Specifically, neighbours were significantly closer together in the middle of the night than they were at any other stage of day or night, with similar distances between neighbours maintained during the day, two hours after dark and two hours before dawn (Table 5.14, and also see Appendix B for the percentage of time animals spent within a certain proximity of their nearest neighbour).

	morning	afternoon	2h after dark	middle of night	2h before dawn	Distance to nearest (median)	Adjusted mean±se
morning		ns	ns	↑ 5.87 *	ns	93.4m	4.537 ±0.062
afternoon	ns		ns	↑ 8.47 *	ns	96.0m	4.564 ±0.067
2h after dark	ns	ns		↑ 12.96 ***	ns	100.5m	4.610 ±0.063
middle of night	↓ 5.87 *	↓ 8.47 *	↓ 12.96 ***		↓ 13.21 ***	87.5m	4.472 ±0.056
2h before dawn	ns	ns	ns	↑ 13.21 ***		100.7m	4.612 ±0.061

Table 5.14 Distance between nearest neighbours, and differences in neighbour proximities for different stages of the day or night (median value) post establishment, as determined by *post hoc* tests. ↓ indicates animals were closer (compared to the corresponding stage), ↑ indicates animals were further apart. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

Sex of the animal and pouch young status of the females significantly influenced distance between nearest neighbour (Table 5.9). *Post hoc* tests revealed that females with pouch young and males remained within similar distances of their nearest neighbours (difference of median metres: 2.0, *P*=0.8399), but females with no pouch young were significantly further from their neighbour than those with pouch young (difference of median metres: 31.4, *P*=0.0004) and males (difference of median metres: 3.5, *P*=0.0304). Interestingly, the sex of the nearest neighbour also significantly influenced how far apart the animals were (Table 5.9), with animals being significantly closer together if the neighbour was a male (82.1m, 95%CI: 73.1, 92.1), than a female (97.6m, 95%CI: 87.1, 109.3).

The habitat type being occupied significantly influenced the distance between an animal and their nearest neighbour (Table 5.9). *Post hoc* tests revealed the distance between neighbours was significantly different in each of the five habitat types (Table 5.15). Not surprisingly, animals were significantly closer to their neighbour while using the two low cover habitats (*grassland* and *A.anceps*), than they were in high cover habitats. Of the high cover habitats, neighbouring animals were 45 and 31 median metres further apart while occupying *M.halmaturorum* than when using *E.diversifolia* and *E.rugosa* (respectively).

	grass	A.anc	E.div	E.rug	M.hal	Distance to nearest (median)	Adjusted mean±se
grass		↓ 9.81 *	↓ 25.57 ***	↓ 38.84 ***	↓ 70.71 ***	71.7m	4.273 ±0.065
A.anc	↑ 9.81 *		↓ 15.76 ***	↓ 29.03 ***	↓ 60.91 ***	81.6m	4.401 ±0.057
E.div	↑ 25.57 ***	↑ 15.76 ***		↓ 13.27 **	↓ 45.15 ***	97.3m	4.578 ±0.058
E.rug	↑ 38.84 ***	↑ 29.03 ***	↑ 13.27 **		↓ 31.88 ***	110.6m	4.706 ±0.060
M.hal	↑ 70.71 ***	↑ 60.91 ***	↑ 45.15 ***	↑ 31.88 ***		142.5m	4.959 ±0.074

Table 5.15 Distances between nearest neighbours post establishment while occupying different habitat types (median metres), and comparisons between neighbour proximities in the five different habitat types (in median metres), as determined by *post hoc* tests. ↓ indicates animals were closer (compared to the corresponding habitat type), ↑ indicates animals were further apart. *P* values of <0.05, <0.001, <0.0001 indicated by *, **, *** respectively. “ns”= non significant difference.

5.3.3 Release month vs. 12 months later:

To assess how apparent naivety of newly reintroduced animals influenced the wallabies during the establishment period we examined their habitat use and social decisions during the establishment period with those 12 months after their release. One year after release, reintroduced animals were 38% more likely to use high cover habitat than during the first month after release (Table 5.16), and when they did forage in the open at night they remained closer to cover by 47m (median) than they did in their release month (Table 5.16). Twelve months after release, group sizes (number of animals within 100m) were modelled as 3.2 times larger than during the release month (as a proportion of the total number of animals available) (Table 5.16). However, the distance animals were to their nearest neighbour did not differ significantly during or after establishment month (Table 5.16).

	Establishment month	**One year after establishment**	*P* value	
Likelihood of using high cover	25% less likely	38% more likely	**0.0333**	Relative risk 1.32441 (95%CI:1.022,1.715) (Estab. vs. 1 yr later)
Distance to cover while foraging	Further from cover (median 57.1m)	Closer to cover (median 9.5m)	**<0.0001**	Square root transformed mean 7.10±0.21, 3.768±0.33 (Estab. vs. 1 yr later)
No. animals within 100m	Group size 69% smaller	Group size 3.2 times larger	**<0.0001**	Rate ratio 3.17610 (95%CI:2.14,4.72) (Estab. vs.1 yr later)
Distance to nearest neighbour	ns (median 74.3m, 95%CI:64.4,85.6)	ns (median 63.7m, 95%CI:51.2,79.1)	0.0719	Logarithmic transformed mean 4.36±0.05, 4.08±0.09 (Estab. vs. 1 yr later)

Table 5.16 Differences between establishment month and in the month one year after establishment in the tammar wallabies' likelihood of using high cover, distance to cover while foraging at night, group size (number of animals within 100m), and distance between nearest neighbours. Results obtained from univariate models. "ns"= non significant difference.

5.4 Discussion

Animals should seek to use their habitat optimally while minimising their risk of predation. Perceived risk of predation will be situation specific, and dependant upon a number of interrelated factors, including the hunting techniques and type of predators (aerial or ground dwelling, diurnal or nocturnal), the health, sex, and breeding status of the individual (Bongi *et al.* 2008; Buskirk and Millspaugh 2006; Fisher 2000; Wahungu *et al.* 2001), as well as the time of year, stage of day, type of habitat occupied, resource availability (Bolnick and Preisser 2005; Fisher 2000; Lima 1998), weather and climatic conditions, proximity of conspecifics (Blumstein *et al.* 1999; Blumstein *et al.* 2002b; Carter *et al.* 2009; Lima and Dill 1990) and possibly relatedness or familiarity with conspecifics (Morrell *et al.* 2007; Ward and Hart 2003). To further complicate things for the prey species, in some situations they may need to avoid multiple predators simultaneously. Therefore, animals' daily use of habitat is strongly influenced by the risk of predation, which they need to mitigate to obtain sufficient resources. One main limiting factor in how well they do this may be an animal's prior experience with a predator (Botham *et al.* 2008), and knowledge of the habitat (Janmaat *et al.* 2009).

Animals reintroduced into a new environment are generally thought to be at an immediate disadvantage due to their lack of knowledge of the environment and predation risk (Banks *et al.* 2002; Wolf *et al.* 2009). Those reintroduced from captive breeding programs are especially naïve, and there has been limited success in establishing them in new environments following reintroductions (Banks *et al.* 2002; Gilligan and Frankham 2003; McLean *et al.* 1994). The establishment period is arguably the most critical time of a reintroduction when the animals are familiarising themselves with their new environment and seeking out the resources they need, while trying to avoid predators. Predation has been the major downfall of many previous reintroductions of small mammals (McCallum *et al.* 1995; Short *et al.* 1992).

Following a spring and winter reintroduction of tammar wallabies, the present study assessed habitat decisions and social grouping behaviours during the establishment period, and after establishment in light of perceived predation risk. An experimental element was also incorporated, whereby animals were released in pre-established groups (familiar) or unfamiliar groups, to assess whether this would alter their behaviour and establishment into a new environment which may ultimately increase their likelihood of survival.

5.4.1 Influence of experimental group (familiar and unfamiliar)

Results obtained here provided no support for the hypothesis that the familiarity of an animal to its group members would influence group size and proximity between nearest neighbours following a reintroduction. During the establishment period following a reintroduction, all wallabies maintained a certain population density within 100m and proximity to their closest neighbour, irrespective of familiarity with group members. Presumably this requirement is for the purpose of increased vigilance, suggesting that these social behaviours are fundamental and somewhat hard-wired in the animals, despite previous isolation from predators (Blumstein and Daniel 2002; Blumstein *et al.* 2002b; Blumstein *et al.* 2000). These findings support the notion that tammars rely heavily on conspecifics to assess and manage risks (Blumstein *et al.* 2002c). Interestingly, although group familiarity did not influence group size or proximity to neighbours, it did however significantly influence how they used their habitat.

Animals released in unfamiliar groups used their new habitat with more caution than animals released in pre-establishment groups. Unfamiliar animals were more likely to use high cover habitat, and stayed closer to cover while foraging than animals released in pre-established groups during the establishment period after the reintroduction. Both the likelihood of using cover and the distance they moved away from cover was a product of the experimental treatment alone, as there was no difference in group size or distance to neighbours (the other potential influencing factors) between the two treatment groups. Since wallabies rely on being cryptic to avoid predators (Southwell 1987), and perceive safety in high cover habitat (Blumstein and Daniel 2002), these results suggest that reintroducing animals in groups with unfamiliar conspecifics may be more advantageous than releasing pre-established groups as unfamiliar animals would exercise a higher level of caution (in their habitat usage) to perceived predation risk while in new surroundings.

On the other hand, groups of familiar animals may have exhibited more confidence to explore more habitat and range more widely following their release. This increased confidence may have been an artefact of associating with familiar group mates. Vigilance has been suggested to be more effective when associating with known conspecifics where animals learn each individual's contextual cues in their alarm calls, resulting in fewer 'miss-communication' and false alarms (Blumstein 2002a). With increased confidence (and hence reliance) in group mates' vigilance warning calls, perhaps the animals felt safer to take more risks (Beauchamp and Ruxton 2007; Blumstein 2002a).

5.4.2 Influence of timing of release

The timing of reintroductions can also be a very important influence on the likelihood of survival. For example, Tavecchia *et al.* (2009) found that a threatened waterfowl, the crested coot (*Fulica cristata*) released in late winter (February-March) had a higher chance of survival and reproduction compared to birds released later in the year, as they were released during better environmental conditions (optimal water level, food availability and the absence of hunting). Seasonal food shortages compromised the health of reintroduced dormouse (*Muscardinus avellanarius*), such that those released in May-June lost body mass at a significantly higher rate than those released in August-September (Bright and Morris 1994). As the two reintroductions I studied occurred in different seasons, the first in late spring (November), and the second (much larger) in winter (June), the timing of these reintroductions provided a good opportunity to observe any differences in how the animals behaved or established in their new environment as a product of seasonal differences. Although small numbers were released in spring, differences in habitat use, group size and distance to neighbours between the two reintroduction events were apparent, suggesting the timing of reintroduction events significantly influence how the animals use the habitat which they are released in.

Animals released in spring were more likely to use high cover habitat, and foraged significantly closer to cover than the animals released in winter. Both of these anti-predator strategies are typically expected of the tammars to improve their chances of survival, and both of these results reflected what naturally occurred at those times of year post-establishment. Different anti-predator strategies may be adopted at different times of year as animals' trade-off their resource and safety requirements to obtain what they need (Bongi *et al.* 2008; Brown and Kotler 2004; Cowlishaw 1997; Mao *et al.* 2005; Panzacchi *et al.* 2010; Preisser *et al.* 2009; Wolff and Van Horn 2003). Following the winter release the animals' anti-predator strategies seemed less than ideal, where animals were more likely to use low cover habitat and foraged further away from cover. However, this may reflect the different seasonal constraints. During winter, the poor weather conditions and lack of nutritious food were most likely to have caused a caused sudden reduction in the animals' body condition (as also confirmed by autopsies on deceased animals during the release month; see DEH 2006). Animals in poorer condition are known to take more risks when it comes to securing resources (Buskirk and Millspaugh 2006). Therefore here, the animals may have traded-off being inconspicuous to gain sufficient nutrition by foraging further away from cover. Additionally, in foraging further from cover the animals may have traded-off being inconspicuous to avoid predation in favour of waiting for an encounter before expending energy in fleeing (Mao *et al.* 2005). This was similarly observed for elk (*Cervus elaphus*), which showed different responses to the risk of wolf predation in two different seasons (Mao *et al.* 2005). During summer, forage was abundant and elk selected habitat which allowed them to spatially avoid predators. Conversely during winter, elk traded-off spatial avoidance of predators and selected more open habitats to secure their requirements, but then relied on other anti-predator strategies, such as grouping to avoid predators (Mao *et al.* 2005). Interestingly during the study here, tammar wallaby group sizes were smaller following the winter release than the spring release. This suggested that animals did not rely on either larger group sizes or the protective higher cover habitat anti-predator strategies following the winter release. However, as false alarms are more prevalent in larger groups (Beauchamp 2010a), and animals were in poorer condition following the winter release (DEH 2006), by foraging in smaller groups they would have reduced the likelihood of false alarms and only needed to expend energy in fleeing when absolutely necessary. Indeed, the proximity of nearest neighbours was similar following the reintroduction in each season, highlighting that this anti-predator strategy was not influenced by seasonal conditions.

It is possible that the timing of the reintroduction events, or the habitat choices made by the animals during the establishment month following each release may have contributed to their chances of survival. During the spring establishment period there were no deaths (from 10 released), whereas following the winter release, 28% of the released animals died during the establishment month (10 deaths of 36 released) (DEH 2006). However, other fundamental concerns (outside the animals’ anti-predator strategies) may have contributed to the poor survival rate following the winter release, including the weather and resource availability, a greater duration spent in captivity prior to release, more captive-born animals released, and the predator training given to the winter release animals (DEH 2006).

5.4.3 Habitat use and social proximity during establishment and post-establishment

Independent of when or how wallabies were reintroduced, their survival during the establishment period ultimately comes down to how well they cope in a new environment (Frair *et al.* 2007; McLean *et al.* 2000). In many reintroduction projects there is commonly an immediate 'cost of release' where many individuals fail to survive their first month, which is reportedly most likely due to the inexperience of captive-born individuals to adjust to their new environment (Tavecchia *et al.* 2009). Habitat decisions during an establishment period are undoubtedly harder as the animals are in unfamiliar habitat. Therefore, in these high-risk situations it is reasonable to presume that animals' habitat use and social grouping behaviours would reflect their strongest anti-predator precautions (Lima and Bednekoff 1999). For tammars and other small macropods which rely on being cryptic (in protective habitat) to avoid predators, and group vigilance to detect them (in particular, while foraging in the open), I anticipated that during the establishment period particularly, the animals would utilise high-cover habitat to a large degree, that they would forage within close proximity to cover, and do so in the presence of a large number of conspecifics or close neighbours to improve group vigilance.

Comparing habitat use and social behaviours from the release month to one year after release enabled me to distinguish whether or not the animals were more cautious during the establishment period, or if wise habitat decisions came with knowledge of the area. Surprisingly, the results suggested that the animals were less cautious during their initial establishment period than they were at a similar time of year post-establishment. While establishing in a new environment the animals were less likely to use high cover habitat, they were further from cover while foraging at night, group sizes were significantly smaller, and the animals were further from their nearest neighbour than they were 12 months post-establishment. These results, coupled with the mortality rate following the winter release (mentioned above), suggested that following the reintroduction it took time for the animals to use their habitat more effectively (with regard to avoiding predators), and that habitat use and social behaviours observed after the initial establishment period are more likely to reflect their ideal survival strategies. Likewise, Tavecchia *et al.* (2009) found a positive association between survival and time spent in the wild, with a third of all post-release mortality of crested coots taking place within the first month after their release. It is likely that animals will be able to use their habitat more efficiently and appropriately as they become more familiar with it and remember where the good resources are located (Haughland and Larsen 2004; Wolf *et al.* 2009).

Observing differences between the establishment and post-establishment periods, it was apparent that some habitat and social decisions may have improved with time spent in the wild, as the animals increased their experience and knowledge of their habitat. For example, the distance between nearest neighbours in different habitat types differed markedly between release month and after establishment. After establishment a more expected result was obtained with the animals significantly closer to their neighbour while occupying grassland, then acacia (the low cover habitat types used at night while foraging), followed by *E.diversifolia*, *E.rugosa*, and *M.halmaturorum*. However, during establishment animals were closer to their neighbour while they were occupying acacia habitat than they were in grassland. Furthermore, their distance to a neighbour while they were in grassland was no different to when they were in *E.diversifolia* or melaleuca, which was surprising as one would expect closer proximity between neighbours for better vigilance when in high risk sites such as low cover habitats. However, this apparent lack of need for a close neighbour while using grassland may have been somewhat counteracted as the number of animals within 100m during establishment was greater while they occupied grassland (and acacia) than when they used the eucalyptus and melaleuca habitats. This finding is in line with Kaufmann's (1974) proposal that macropods are under pressure to form groups when in increasingly open habitat areas as they are more exposed to cursorial predators. Associating in larger groups helps the animals to decrease their risk of predation, reduces the amount of time each individual spends on vigilance and allows for other activities such as foraging (Colagross and Cockburn 1993; Elgar 1989; Pulliam 1973). For example, Heathcote (1987) reported that eastern grey kangaroos (*Macropus giganteus*) in larger groups spent significantly less time vigilant and significantly more time feeding, than did those in small groups. Elgar (1989) reported that this negative correlation between group size and vigilance (scanning) has been observed in 52 species (32 bird species, 20 mammal species), including animals such as the European rabbit (*Oryctolagus cuniculus*), and red deer (*Cervus elaphus*).

Group size and nearest neighbours also had different influences on how far out from cover the animals would forage at night during establishment and post-establishment. During establishment, group size did not influence how far away from cover the animals would forage, but animals closer to their nearest neighbour would travel further from cover. After establishment the opposite was observed, where neighbouring animals were further apart with increasing distance to cover, but they were in larger groups. In this instance, perhaps any vigilance benefit lost from being a greater distance from their neighbour was counteracted by associating in a larger group. Similar anti-predator benefits from distance to cover and nearest neighbours have been observed for the red-necked pademelon (*Thylogale thetis*), where their individual vigilance duration decreased when they were closer to a neighbour, and the time between vigilance acts decreased when they were closer to cover (Pays *et al.* 2009).

Additionally, Wahunga *et al.* (2001) observed red-necked pademelons in smaller groups to forage closer to cover, where vigilance also decreased with increasing group size. Conversely, red-necked wallabies (*Macropus rufogriseus banksianus*) do not relax their individual alertness when with others because their groups are so unstable that no individual that joins a group can rely on the proximity of its companion for long (Johnson 1989).

The lack of group size effect on distance to cover observed during the establishment month may reflect a lack of reliance on conspecifics predator detection ability when newly reintroduced into an area. During the establishment period animals are in unfamiliar habitat and each individual is still learning to recognise and cope with potential predators (McLean *et al.* 1994), so is likely that false alarms may be more prevalent. False alarms result in wasted energy in fleeing and reduce the time spent on foraging, and are reportedly more likely to occur in large groups (Beauchamp and Ruxton 2007). Therefore, perhaps animals reduced their reliance on conspecifics while foraging during the establishment month, to reduce the likelihood of false alarms and wasted energy. Alternatively, as the animals had been isolated from predators prior to their reintroduction, perhaps they were still rediscovering the benefits of group living on communal vigilance (Blumstein and Daniel 2002; Griffin 2004). Post-establishment however, after the animals had settled and had re-learnt predator recognition and coping skills, it appeared the animals relied more on larger groups to detect predators, perhaps as false alarms may have been less likely with their increasing experience in the wild. Foraging in groups requires an energy risk trade-off, where the energy gained in foraging further from cover in larger groups must have been worth obtaining, as the downside is that larger groups travelled further from cover, which would mean more energy wasted in fleeing to cover in a false alarm. The differences in group size effects observed between the establishment and post-establishment periods may have reflected changes in perceived predation risk (Blumstein *et al.* 1999), as animals weigh the predation risks against the potential fitness gains of an action (Buskirk and Millspaugh 2006).

During establishment while the animals were resting in unfamiliar habitat during the morning they were surrounded by significantly larger numbers of animals than at any other time, and also had a close neighbour. As the animals were in unfamiliar habitat and are presumably less vigilant while resting, it is possible that their perceived risk of predation may have been quite large, and counteracted by resting in areas surrounded by larger numbers of animals than would normally occur. After establishment, animals were not significantly closer during the morning than other times. The importance of group vigilance during the day was not included in these analyses but presumably would be somewhat reduced as the animals would be more familiar and accustomed with their environment and better able to detect and flee predators. Post-establishment, the closest neighbours were observed during the middle of the night, while interestingly animals remained within a similar distance from cover for the duration of the night. Presuming that predation risk is similar for the duration of the night, and not the reason for the reduced distance to a neighbour, these results suggest the middle of the night is when the most social aggregation occurs.

While differences in habitat use and social behaviours were observed between the establishment month and post establishment, they still exhibited some expected habitat and social behaviours during establishment. During establishment, animals used the high cover habitat (eucalyptus and melaleuca) in the morning, while they were resting, emerged from cover in the 2h period after dark, and returned to cover during the 2h period before sunrise. Some of the habitat usage and social groupings observed during establishment also reflected good anti-predator strategies for animals which rely on group vigilance. Animals generally associated in larger groups and in closer proximity to their neighbour when they occupied the low cover habitats (acacia and grassland).

5.4.4 Influence of sex and season on habitat use and social proximity after successful establishment

Following a successful establishment, animals continually make habitat and social behaviour decisions. Understanding how the animals use their habitat and what influences their habitat use is vital to assist ongoing management decisions (Bos and Carthew 2003). In planning future reintroductions of threatened species, knowledge of their habitat requirements will be crucial in conservation and management decisions regarding habitat suitability or selection so that viable populations are maintained (Bos and Carthew 2003; Finlayson *et al.* 2008).

Time of year significantly predicted the type of habitat that would be used, most notably in spring, when there was a greater likelihood that the animals would use the high cover habitat of *Eucalyptus* and *Melaleuca*. During spring the animals were also significantly further from their nearest neighbour, and went further from cover while foraging than at other times of year except for winter (Jun-Aug) when they foraged the furthest from cover. This risk in going far from cover in winter (especially for females with young) was possibly somewhat counteracted by the fact that the animals remained very close to their nearest neighbour. The most cautious time of year for foraging may have been during autumn (Apr-May) with the animals not only significantly closer to their nearest neighbours, but also remained significantly closer to cover than at any other time of year.

The distance between an animal and their nearest neighbour was closer in autumn and winter, than summer, and at a maximum during spring. This result contrasts that found for eastern grey kangaroos which were found to be closer to each other in spring and summer than autumn and winter (Jaremovic 1984; Southwell 1981). This was put down to the seasonal availability of food being greater, allowing for increased tolerance of close neighbours while foraging (Jarman and Coulson 1989). Similarly, red-necked wallabies were observed to associate more closely in summer than in winter (Johnson 1985). The results obtained here however, may not reflect food abundance, but rather the effectiveness of group vigilance during poorer weather in the colder months. In wet and windy conditions there may have been a greater need to remain closer to conspecifics to be able to hear a neighbour’s warning calls (‘foot thumps’) about an approaching predator (Blumstein 2002a). Alternatively, this result may reflect the animals reduced necessity to have close neighbours when in high cover habitats. In spring when the animals were at their maximum distance from neighbours they were also more likely to be in high cover habitat, and it was found that the need for a close neighbour and large group size was significantly reduced while using high cover habitat. Coincidentally, using significantly more high cover habitat during spring than any other time of year coincides with the timing of pouch young vacating the pouch.

Surprisingly, the sex of the animals and of particular interest the pouch young status of the females did not influence the wallabies’ likelihood of using high cover habitat, nor their proximity to cover while foraging in the open at night. It was expected that females with pouch young would be more cautious and use more high cover habitat and forage closer to cover. For example, red-necked pademelons with pouch young were observed to forage closer to cover than other age/sex classes (Wahungu *et al.* 2001). Likewise, predation risk affected bridled nailtail wallabies’ (*Onychogalea fraenata*) proximity to cover at night, where females with vulnerable young foraged closer to cover (Fisher 2000). Admittedly, there may have potentially been three different stages of risks associated with producing offspring: when the female had small pouch young (low risk to female); large pouch young (high risk for the female and young);and young at foot (high risk to the young, low risk to the female). These stages were not distinguished in these analyses and may have influenced the results. However, overall the tammars with pouch young did still exercise some caution and remained significantly closer to their nearest neighbour than did the females without pouch young. This is contrary to anti-predator strategy of large macropods where the female isolates herself and her offspring from the other kangaroos when her pouch young is about to vacate the pouch or is a small young at foot (Jarman and Coulson 1989), where Croft (1981) suggests this is one means to avoid confusing the young which would occur in a group during alarm and flight, or reflects the poor locomotive ability of the young which would restrict the pairs movements.

Males were also significantly closer to a neighbour than females without pouch young. In actual fact animals were significantly closer together if the neighbour was a male. Likewise Jarman and Coulson (1989) reported that male eastern grey (*Macropus giganteus*) and western grey kangaroos (*Macropus fuliginosus*) aggregate with other males because they are attracted to a common resource (females) and a female red-necked wallaby (*Macropus rufogriseus banksianus*) or red-necked pademelon (*Thylogale thetis*) may be followed by a string of males in decreasing order of size. Additionally, males in close proximity to others may reflect mate guarding, and competition for females (Hynes *et al.* 2005).

5.5 Conclusions

An animal’s perceived risk of predation may be strongly influenced by their familiarity with their environment. Whilst establishing, the animals made some different habitat and social choices to those observed post-establishment. These may have reflected different perceptions of predation risks to naïve animals and their tactics to overcome them. It also could suggest that some habitat use and social behaviours may have simply improved with their increasing knowledge of the area.

These results also suggested that animals reintroduced in unfamiliar groups were more likely to use high cover habitat and remained closer to cover when foraging at night. These anti-predator strategies are beneficial when in unfamiliar habitat, and suggest that the unfamiliar groups of animals used their habitat with more caution than animals released in pre-established (familiar) groups. Therefore, it does not seem necessary to establish familiarity between release group members prior to release.

The time of year when animals are reintroduced may have contributed to their survival. Here, spring seemed to be a better time to reintroduce animals. During spring the animals naturally used more high cover habitat and foraged closer to cover. In addition, following the spring release, the animals associated in larger group sizes, not normally seen at that time of year. All of these habitat and social behaviours reflect good anti-predator strategies.

Perceived risk of predation influences the animals' daily decisions, and continually changes depending on their familiarity with the habitat, time of day, weather conditions, season, the habitat they occupied, and their social surroundings at the time. After the animals had established, their use of habitat and social proximities reflected the expected ideal survival strategies for tammars, those being, to incorporate high use of covered habitat, remaining close to cover while foraging, being close to a neighbour, and staying in areas with a dense number of wallabies. The animals' habitat use and social situations were inherently linked, and influenced each other. Animals were less likely to be in high cover habitat if they were closer to a neighbour, or in larger group sizes, and animals foraged further from cover when they were surrounded by a larger number of conspecifics. These results suggest that animals are able to manage and negate their risk of predation by altering their proximity to a neighbour, capitalise on group vigilance for predator detection, use protective high cover habitat or adjust their proximity to cover while foraging.

6 Chapter 6: overall discussion and conclusions

Reintroductions are frequently unsuccessful, especially those that involve releasing animals from captivity into areas where predators are still present (Gilligan and Frankham 2003; McCallum *et al.* 1995; McPhee 2004; Moro 2003; Moseby and O'Donnell 2003; Richards and Short 2003; Short *et al.* 1992; Short and Turner 2000). Much more work is needed to redress this issue, since reintroduction programs can help to restore biodiversity losses, but require significant resources. This experimental study on a population of animals reintroduced from captivity into an area still inhabited by low densities of introduced predators provides a solid foundation for future management and reintroduction decisions. The results of this study can be applied to species that exhibit similar anti-predator strategies, social organisation and habitat requirements.

Previous chapters have discussed results derived from locational (radio-tracking) data collected from 46 tammar wallabies for the 12 months following their reintroduction. Each chapter focused on a specific element of the tammars’ ecology. Chapter three examined the animals’ monthly home range and core area size and stability, and the importance of sharing area with conspecifics. Chapter four examined seasonal habitat selection at two spatial and temporal scales: the landscape scale and day and night use within home range. Chapter five examined factors which influenced their fine scale habitat use and social grouping behaviours in light of predation risk.

Here I will reiterate the key findings and synthesise the way in which they relate together, providing pivotal baseline ecological information on how tammar wallabies implement anti-predator strategies and utilise their environment.

6.1 Key findings during the release month

One key finding was that unfamiliarity with the environment appeared to impact on the animals’ use of habitat. All animals (irrespective of experimental release group or sex) constrained the size of their home ranges to approximately 11.8ha during the first month after release, which was significantly smaller than the 15.9ha observed at an equivalent time of year post-establishment. This apparent restriction of movement in newly reintroduced animals might be expected, as the animals are unfamiliar with the environment, the risks associated with it, and escape routes from predators. In the case of the ruffed goose (*Bonasa umbellus*), increased movement through or occupancy of unfamiliar habitat resulted in a higher risk of predation than activities in familiar habitat (Yoder *et al.* 2004). In that study, it was evident that residency in unfamiliar habitat posed a greater predation risk than moving through unfamiliar habitat, perhaps because residing in one area may attract predators to that area. For example, scent-hunting predators were suggested to be attracted to the waste accumulated in an area due to reduced mobility immediately following the reintroduction of captive-raised *Microtus* voles (Banks *et al.* 2002). In this study, high mortality of tammar wallabies occurred during the establishment month following the winter release. The high mortality rate was most likely a consequence of a number of factors including, poor weather conditions and low quality forage forcing the animals to trade-off anti-predator strategies to secure sufficient resources. This, coupled with their unfamiliarity with the area and predation risks, and occupancy of small home ranges, may have created a ‘sink’ effect for the population.

One way tammars appear to improve detection of potential risks is to rely on conspecifics (Blumstein *et al.* 2002c), under the “many eyes” hypothesis (Lima 1995). In the present study, sharing of space appeared to be very important for the tammars during the release month and overall. During the release month, all tammars (irrespective of experimental release group or sex) shared approximately 96.8% of their home range area and 73.7% of their core area with conspecifics. The importance of associating with conspecifics when in unfamiliar habitat was also later confirmed with the finding that as the amount of new area incorporated into monthly home ranges increased, so did the amount that the home range was shared with conspecifics. In addition, the amount of sharing was positively correlated to the percentage of time two individuals spent together as nearest neighbours. As an extension of this, detailed examination of habitat use revealed that animals relied on their nearest neighbours for increased vigilance during the establishment month. The further they foraged away from protective cover at night, the closer they stayed to their nearest neighbour, which suggests that they gain some anti-predator benefit from doing so. However unlike during post-establishment, their use of group vigilance was not apparent while foraging during the establishment period, as the number of animals within 100m did not influence the distance they would forage from protective cover. This may be due to the increased likelihood of false alarms with increasing group size (Beauchamp 2010a; Beauchamp and Ruxton 2007) as discussed in Chapter 5, where more false alarms may be likely to occur when the animals are familiarising themselves with their new habitat and potential predation risks. These false alarms may be costly as they will reduce time spent foraging and may waste energy in fleeing. Once familiar with the habitat and predation risks after establishment, the animals appeared to capitalise on the benefits of group vigilance and foraged further from cover when surrounded by a larger number of animals.

Use of protective cover is another anti-predator strategy used by tammars to conceal themselves, and the benefits of this may counteract any lack of group vigilance. During the release month and post-establishment the animals were more likely to be found in high cover habitat when they were further from their nearest neighbour, and less likely to be in cover when they were surrounded by a larger number of conspecifics. These results suggested that they gain benefit from communal vigilance when not in the protective cover of the habitat. Additionally, these results revealed that the animals did retain and display anti-predator behaviours despite complete isolation from predators, but that these behaviours improved with time in the wild. Furthermore, their responses to predation risk were dynamic and varied with situational grouping and activity requirements (Jarman and Coulson 1989).

Anti-predator behaviours were somewhat modified by their familiarity with the environment and appeared to improve with time spent in the wild. Twelve months after their release, animals were 38% more likely to be found in high cover habitat, foraged approximately 47.6m closer to cover at night (so were approximately 9.5m from cover on average), and aggregated in groups that were three times larger than they did during the establishment month. However the distance between nearest neighbours was the similar during the establishment and post-establishment periods, suggesting that this anti-predator strategy was innate, rather than learnt or improved with time. However, when foraging away from cover at night, distance between neighbours was influenced by their familiarity with the habitat. During the establishment period animals foraged closer together the further they ventured from cover, while post-establishment the animals were observed to forage further apart. In this instance, after establishing the animals may have relied on their surrounding group members for improved vigilance rather than one close neighbour (as discussed previously).

Generally animals were less likely to be in large groups when using cover, however during the mornings (resting time) of the establishment month they were more likely to be in cover and surrounded by more conspecifics than any other stage of day. Post-establishment they were still more likely to be in cover during the morning, but primarily aggregated with others during the middle of the night. Aggregation of tammars is known to occur during the night while foraging in open grassy clearings (Blumstein *et al.* 1999), and is of benefit to improve vigilance and detection of predators (Lima 1995). This correlation of more group mates while resting in high cover habitat during the mornings of the establishment month may perhaps reflect the animals' need to maintain sufficient vigilance when occupying unfamiliar habitat, especially while resting when each individual is presumably less alert.

6.2 Influence of release protocol: group familiarity and timing of release event

An experimental release was used in this study in an attempt to discover whether releasing pre-established groups would assist the animals' establishment in a new and unfamiliar environment. This has similarity been attempted in releasing groups of familiar and unfamiliar New Zealand robins (*Petroica australia longipes*), which concluded familiarity among founder groups was unlikely to have an effect following translocation (Armstrong 1995b). Here, reintroducing animals in groups with unfamiliar conspecifics affected some elements of how the animals used their new environment, but not necessarily in the way expected. Unfamiliar groups appeared to use slightly different anti-predator strategies, which may reflect their use of greater caution than familiar groups while establishing in their new environment. While both treatment groups made similar habitat selections at the landscape scale, they differed in their nocturnal habitat selection within the home range (see Chapter 4). Animals released in unfamiliar groups showed a stronger preference for the high cover habitat of *M.halmaturorum* while foraging at night. This was not typical of habitat utilised while foraging at an equivalent time of year post-establishment, suggesting that it was an active choice to increase concealment while in an unfamiliar environment. In addition, analysis of habitat use at the fine scale showed that unfamiliar animals were 55% more likely to be found in the high cover habitat and they foraged closer to cover than animals in pre-established groups during the first month following their reintroduction (see Chapter 5). Results from this experimental release suggested that animals released in groups with unfamiliar conspecifics conceal themselves from predators better than groups of familiar animals. When in a novel environment this strategy may ultimately lead to improved survival, meaning that releasing pre-established groups may not increase their likelihood of survival. Similarly, Armstrong (1995a) found no evidence that releasing saddleback birds (*Philesturnus carunculatus rufusater*) which were familiar with each other improved their translation success, as unfamiliar birds achieved a similar amount of pairing prior to the breeding season. Fortuitously this would also be easier for conservation managers as they would not need to specifically familiarise group members with each other prior to release.

The habitat use and social grouping observed following the spring release suggested animals were at greater risk of predation compared to animals released in winter. During the spring release animals were more likely to be found in cover, and foraged closer to cover at night. This finding is of significance as we know that tammars forage closer to cover in high predation risk situations and retreat to cover when alarmed (Blumstein and Daniel 2002). However, these trends were also observed between the seasons post-establishment, where animals were more likely to be found in high cover habitat during spring than any other season (perhaps to afford more protection to emerging pouch young), and foraged further in the open during winter (perhaps to give them more time to detect a predator approaching from the habitat edge in poor weather conditions). Therefore the differences in habitat use observed during the establishment months may not been an artefact of the timing of the release event but rather reflected normal occurrences which occur at those times of year, suggesting that the animals did quickly adapt to their new environment in some ways. Conversely, no difference was observed in the proximity of nearest neighbours between the spring and winter release events, whereas post-establishment animals were significantly closer to their neighbour during winter than spring. This difference and the importance of near neighbours further supports the idea that irrespective of release protocol (group familiarity or timing) animals rely more heavily on their neighbour for increased vigilance during establishment rather than the typical group vigilance observed post establishment. This also once again supports the idea that grouping in macropods will vary depending on their circumstances, where animals continually seek to minimise their risk of predation, and maximise their likelihood of detecting a predator (Jarman and Coulson 1989).

6.3 Release groups dispersing after release

The experimental release showed that release group familiarity did not influence core area or home range size, amount shared with conspecifics during the establishment month, or the rate at which group members merged with non-group members following the release. However, home ranges of animals in familiar groups were observed to spread further from group mates a few months after release than those of unfamiliar groups. This suggests that all animals similarly establish home range and core areas in the environment, and all maintained a certain degree of overlap with conspecifics, but that animals in familiar groups dispersed from their group mates before groups of unfamiliar animals. The original release groups were no longer coherently together seven months after their release, and had merged with non-group members, most likely due to deaths of release group members. Whether this would have still eventuated if deaths had not occurred is not clear. However, knowing the importance of social overlap, it is likely that death of conspecifics played a large part in animals’ moving through the landscape in search of others. This was probably especially the case for males, who generally shared more of their home ranges with conspecifics than females did, no doubt driven by their need to search for breeding opportunities (Croft 1989).

6.4 Home range and sharing

Overall, tammar wallaby home ranges were smaller in winter (18ha) than at any other time of year, with males having larger home ranges than females (31ha for males versus 20ha for females without pouch young, and 21ha for females with pouch young). Sharing space within the home range area appeared highly important to the animals. There was a positive correlation between the amount of area shared and the percentage of time those individuals spent together as nearest neighbours. Additionally, home range sizes were smaller when more of the area was shared, and animals explored and expanded their home range to include more new area when it was done so with a greater number of conspecifics (using more new area between Jul-Dec than Jan-May). Finding from this study support the idea that predation risk is greater when occupying new and unfamiliar territory (Banks *et al.* 2002; Yoder *et al.* 2004), but that is somewhat overcome by exploring those areas with greater numbers of conspecifics. This in turn also reinforces the importance of tammars' reliance on group vigilance for predator detection.

6.5 Importance of habitat types

Grassland and *A.anceps* habitat types were strongly preferred, with both sexes generally ranking them in their top three preferences both at the landscape scale, and during foraging (when selection occurred). *A.anceps* habitat was also preferred for refuge for the duration of summer by both sexes and into autumn by males. Similarly, eastern grey kangaroos (*Macropus giganteus*) have been observed to strongly select for clearings which were within close proximity to substantial cover; the clearings offered good forage and the acacia offered protective cover, thus providing complementary resources *(*Moore *et al. 2002).* The eastern grey kangaroos were also observed to utilise the protective benefit of these clumps of acacia for diurnal refuge.

In addition to grassland and *A.anceps* habitats, female tammar wallabies showed a strong preference for *E.diversifolia* habitat at the landscape scale, and it was their most strongly selected habitat for diurnal refuge (followed by seasonally changeable combinations of *M.halmaturorum, E.rugosa* and *A.anceps* habitat types). Conversely males preferred *M.halmaturorum* at the landscape level, and used this in conjunction with *E.diversifolia* and *A.anceps* for their diurnal refuge. Generally*, E.rugosa* was the least preferred habitat type at the landscape scale for both sexes. However, females did select *E.rugosa* within their home ranges for both diurnal and nocturnal activity during summer, while males showed some diurnal preference for it during spring. *Eucalyptus rugosa* was presumably least preferred as other habitat types provided more adequate resources. Of the five habitat types, *E.rugosa* had the least species diversity and the smallest available biomass, both of which may infer the least forage availability, and the lowest percentage cover under 150cm, which may infer less protection from predators.

Differences in habitat preference between the sexes were evident, with females generally showing greater selection than males within their home range year round. Females were selective in the habitat they used for diurnal and nocturnal and activities (except during winter and early spring), while males were predominantly only selective in the habitat they used for diurnal refuge. The preference differences observed by the sexes may reflect different reproductive strategies. Presumably the males are accustomed to accepting a greater risk as they need to search for females, while females can ultimately chose their preferred habitat to occupy. Selection observed by males diurnally suggests that they do select habitat to occupy when they are resting and less vigilant, and not searching for females. Similarly, female swamp wallabies (*Wallabia bicolor*) have been observed to be more selective than males, where differences in habitat selection were suggested to be driven by the need to find food and avoid predators but also reflect different reproductive strategies of the males and females (Di Stefano *et al.* 2009).

6.6 Fine scale habitat use and social behaviours

Animals' use of habitat and social behaviours changed seasonally and with time of day, implying that they use their habitat selectively as their requirements change. Additionally, the habitat use and social grouping behaviours examined during this study were generally found to be interdependent.

Proximity to a neighbour and the number of surrounding conspecifics were highly influential factors on the animals' habitat usage. Animals used high cover habitat for refuge and their use of high cover habitat was more likely if they were further from a neighbour or surrounded by fewer conspecifics. Conversely, tammars were more inclined to use low cover habitat when they were closer to a neighbour, and foraged further from cover when surrounded by a greater number of individuals. These results supported Blumstein's *et al.* (1999) conclusion that tammars' behaviour is sensitive to their perceived risk of predation, perceiving less risk of predation as their group size increases. Similarly, Pays *et al.* (2009) found red-necked pademelons (*Thylogale* *thetis*) were sensitive to the presence of conspecifics, and adjusted their behaviour relative to the distance separating them from their nearest neighbour.

Interestingly, the presence of a pouch young did not cause females to use their habitat with more caution. Unlike some other macropods such as red-necked pademelons (*Thylogale thetis*; Wahungu *et al.* 2001), and bridled nailtail wallabies (*Onychogalea fraenata*; Fisher and Goldizen 2001), female tammars did not stay closer to cover when they had pouch young in this study. Additionally, they were not more likely to use high cover habitat than those females without pouch young. However they did remain within closer proximity to a neighbour (31m closer). This suggested that they did exercise some caution and relied on neighbours for increased vigilance against predators. This finding is contrary to eastern grey kangaroos (*Macropus giganteus*), western grey kangaroos (*Macropus fuliginosus*), Common wallaroo (*Macropus robustus*), and antilopine wallaroo (*Macropus antilopinus*) where the females with emerging pouch young isolated themselves from conspecifics (Jarman and Coulson 1989). This may perhaps suggest that tammars with pouch young place greater importance and reliance on conspecifics detecting and alerting them to predators, than they do the necessity to alter their habitat choices to improve concealment from predators. This may allow them to forage as they normally would and continue to maximise their habitat use while still minimising their predation risk.

Results presented in this thesis suggest that the reintroduced tammars exhibited anti-predator behaviours despite isolation from predators. However, I also showed that some different anti-predator strategies were used during the establishment and post establishment periods. One year after the tammars were released they made seemingly more cautious habitat and social grouping decisions in an attempt to avoid predation, suggesting that anti-predator strategies may have improved with habitat familiarity and time spend in the wild.

6.7 Recommendations for reintroductions

While conservation managers need to decide the total number of animals available to be released overall, this study has shown that releasing animals in numerous small groups separated by a few hundred metres geographically is an appropriate release protocol. This supports suggestions from other researchers about typical tammar group sizes. Blumstein *et al.* (1999) suggested releasing animals in an average group size of 4-6 to be the optimal group size to benefit vigilance, while Jarman and Coulson (1989) calculated the mean group size for tammars to be 2.3 (using data from Vujcich's Masters thesis in 1979). Findings from my study support the suggestions that releasing tammars in small groups is appropriate, as during the establishment period released animals relied more on neighbouring animals than they did group size for predator vigilance. Additionally, even post-establishment when group size was found to influence foraging distance from cover, there was never observed to be more than six animals within 100m of each other. Furthermore, as the animals restricted their explorations immediately following their release (as also observed in *Microtus* voles by Banks *et al.* 2002), releasing fewer animals in one spot may reduce any odour accumulation which could attract predators to the area (Banks *et al.* 2002). Therefore, releasing a number of these small groups distributed within a couple of hundred metres of each other throughout the landscape (similar to the methods of this study) seems most appropriate, as over time the animals tended to move (maximum distance was approximately 4km by one individual in this study) to reside in one general area irrespective of their initial release location. This strategy for release may be the best compromise as too many animals in one area may accumulate odour and act as an attractant for predators (jeopardising the safety of the whole population), while too few animals may result in individuals needing to move through unfamiliar habitat to search for new mates (which is also known to increase predation risk (Yoder *et al.* 2004)) if release group members die soon after release.

Results from this study suggest that when the predominant predator is the fox reintroducing animals into habitat with sufficiently dense cover in close proximity to suitable grassy clearings and other grassy areas that provide some protective cover (such as acacia habitat) would be most beneficial. These locations need not be away from human activity, or far into the scrub. In this study, animals were not deterred by human activity. All animals were released within varying distances (up to 4km) of transient tourist accommodation, consisting of five cottages in a small abandoned gypsum mining town. Grassy clearings surrounded the cottages which the wallabies were most likely attracted to. Over time, all resident wallabies converged and utilised this inhabited area, seemingly irrespective of cottage occupancy.

Results from the release events over two different seasons during this study suggested that spring may be a more suitable time to release animals than winter. However, it is difficult to say conclusively whether releasing females with pouch young at this time is a good idea. On the positive side, post-establishment females with pouch young did not use their habitat differently to females without pouch young, suggesting that they still go about their normal activities while carrying a young, although they do remain in closer proximity to a nearest neighbour. If captive-fed adult females are released in spring just before pouch young emerge it may be that they are able to contribute a stronger pouch young to the population than their wild counterparts, which may be in poorer physical condition after foraging for themselves for the duration of winter in the wild. However this may only be the case if firstly, hand feeding in captivity results in better physical condition of the animals at sexual maturity, as is suggested for greater bilbies (Moseby and O'Donnell 2003); and secondly, and if stronger adults produce stronger young.. Pouch young that become independent in the wild may be at a greater advantage in learning survival skills. For example, juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) reared in the wild and translocated elsewhere were more likely to survive than captive-reared juveniles despite being predator-trained prior to their reintroduction (Shier and Owings 2007). Additionally wild born young may be further advantaged in learning how find adequate resources from day one. In a study by Moseby and O’Donnell (2003) the average daily weight gain of young wild-born greater bilbies (*Macrotis lagotis*) was found to exceed that of those born in captivity and reintroduced into the predator proof reserve and measured for the first month following their release. This suggested that wild born animals were better adapted to search for adequate food resources. However, if adults are released with large pouch young and social learning is required, those newly emerged pouch young do not have an adult familiar with the environment and risks to learn their survival skills from, but rather may be associating with a predator naïve adult unfamiliar with its environment. Shier and Owings (2007) highlighted the importance of social learning in black-tailed prairie dogs (*Cynomys ludovicianus*). They showed that 12 months after their reintroduction there was a higher survivorship of captive juveniles predator trained in the presence of an experienced adult than juveniles trained without an experienced adult. Additionally, releasing animals with large pouch young may disadvantage the adult and make them an easier target for a predator.

Females with young remained closer to their nearest neighbour than those without, suggesting they perhaps relied more heavily on conspecifics for predator detection as it is likely they would take longer to escape a predator due to their increased bulk and weight. Therefore if reintroductions occur during spring and females with large pouch young are available for release, consideration needs to be made as to whether there are existing adults in the population that may assist the social learning of released adults and newly emerged pouch young.

This study has concluded that establishing release group familiarity prior to a reintroduction is not necessary. Animals released in unfamiliar group configurations displayed more cautious habitat and social choices than animals released in familiar groups, which may ultimately improve their likelihood of survival.

Conclusions about the benefits of the pre-release predator training we conducted cannot be accurately drawn, as they were somewhat confounded. Pre-release training only occurred prior to the winter release, and was conducted on all individuals. Moreover, in hindsight the training probably occurred too near to the release event to be useful, and animals were perhaps under too much stress at the time of their reintroduction, which may have contributed to the large initial number of deaths. However it was apparent that a “hardening off” period should have been undertaken prior to release, as autopsies revealed a large proportion of the deaths were primarily due to cachexia (starvation) leading to easy predation (see DEH 2006; Sharp *et al.* (in press)). Cachexia was suggested to be the result of the animals not foraging on suitable food, but if they had been “hardened off” in captivity (whereby they were put in a larger enclosure, no longer given lucerne hay, and learnt to forage for themselves) the numbers of animals surviving the initial establishment period may have been greater.

6.8 Further research required

In this study it was presumed that an animal’s distance to cover, likelihood of being in cover, group size, and distance to nearest neighbour all reflected their perceived risk of predation. Perhaps further research should test this presumption by comparing these surrogate measures of predation risk with observed mortalities due to predation.

Utilising ArcGIS mapping and GPS transmitter technology (which can frequently record both location and proximity to conspecifics) could be of benefit here. The habitat type occupied and social situation at time of death could be established and examined to observe if, for example, more deaths occur when animals are further from cover, or in smaller group sizes. However, the transmitters would need to produce frequent locations, so that you could accurately back count a time of death from when mortality mode commenced, and be confident that there was not sufficient time for the carcase to be dragged into a different habitat type from where it was killed. The need to compare surrogate measures of risk to observed predation was similarly pointed out in Matson's *et al.* (2005) study who investigated the influence of various factors, including group size, position within the group, distance from cover, time of day, and time since a predator was nearby on the vigilance and flight distance of impalas (*Aepyceros melampus*).

Carter *et al.* (2009) highlighted that studies of the association patterns of marsupials are entirely lacking. Their study on eastern grey kangaroos (*Macropus giganteus*) found grazing behaviour was positively affected by strength of association, and they suggested that females may receive an energetic benefit from associating frequently with preferred individuals. They suggest that social organisation within eastern grey kangaroos may be more structured than previously thought. Similarly Blumstein *et al.* (2002a) suggested that female tammar wallabies associate with kin. Field observations during my research lead me to believe that tammars may preferentially associate with particular individuals, as I frequently saw the same animals' associating closely with each other. For questions such as these to be addressed, all animals within the population need to be monitored. This reintroduction was comprehensive in the fact that all animals in the released population were monitored, and all genetics and relatedness of animals in the population were known. This provides a unique opportunity to investigate further interactions at the population level, which is not normally achievable on entire wild populations of animals. Using data collected during my study, investigation of questions about preferential association and whether relatedness also plays a role could be addressed. Social network analysis (Whitehead 2009) could be used on the existing database of nightly locations collected from all animals in the released population over twelve months following their release. Due to time limitations these analyses could not be carried out as apart of this doctorate.

If animals do preferentially associate with particular individuals, further research could explore whether preferential association influences their habitat usage. Prospective prey will exhibit vigilance to protect themselves against predators (anti-predator vigilance) and to monitor other group members (social vigilance) (Favreau *et al.* 2010). Work by Carter *et al.* (2009) found that when female eastern grey kangaroos (*Macropus giganteus*) preferentially associated with specific individuals their foraging time increased because they dedicated less time to social vigilance, as they were more familiar with the behaviours of that female and therefore did not react to all of her "vigilance" acts (rather than sacrificing time spent on anti-predator vigilance). Similarly, Blumstein (2002a) suggested that when associating with kin or known conspecifics some species may place greater reliance on the other animals' warning calls as they are familiar with their contextual cues. This in turn may influence their habitat usage by allowing them to use habitat in more 'risky' situations than if they were relying on understanding the cues of conspecifics unknown to them. Using data from this study, analyses could be undertaken to determine if for example, animals foraged closer to cover or were more likely to be in cover when their nearest neighbour was not their preferred associate. Alternatively, like other studies that have used video surveillance and visual observation to identify individual animals and observe their vigilance acts (such as duration and number of times an individual raises its head while grazing), similar methods could be used here.

While it appeared from this study that the number of deaths of conspecifics did not influence aspects of the surviving animals' home range during the following month, I believe this deserves more investigation. The behaviour of surviving animals following the death of a conspecific could indeed jeopardise their own safely, as foxes are known to return to locations which have proved rewarding in the past, therefore animals which remain in those areas are at risk (Panzacchi *et al.* 2009). Indeed, I observed one tammar standing beside a wallaby that had recently died. I'm unaware of any literature documenting emotional bonds between individual wallabies, whereas other animals, such as elephants are known to understand death of conspecifics and grieving and mourning rituals are displayed as an integral part of the elephant culture

(Bradshaw 2004). If bonds form between individual wallabies, like it does in elephant and humans, they may be less inclined to leave deceased group members behind despite the risk of staying. Exploring preferential association and utilising computer programs developed to analysis social association, such as SOCPROG (Whitehead 2009) may help to answer these questions.

Further research could investigate the influence of predation events on immediate habitat use and social behaviours of the surviving wallabies, by examining how a successful escape from a predator may affect their immediate anti-predator behaviour, and how long this response lasts for. Similar investigation was done by Matson *et al.* (2005) on impala (*Aepyceros melampus*) where they analysed the extent to which recent exposure to a predator affected the impalas' anti-predator behaviour. Their results showed that female impala displayed greater vigilance when a predator had been nearby within the previous six hours. Likewise the grazing and social behaviour of the eastern grey kangaroo (*Macropus giganteus*) was observed to change as a result of a predation event (Carter *et al.* 2009). The strength of association with the nearest neighbour influenced grazing behaviour before the predation event, while group size was most influential after the predation event (Carter *et al.* 2009). This finding by Carter *et al*. (2009) may also somewhat explain the difference observed in this study, where during the establishment period predator naïve animals foraged further from cover when closer to their nearest neighbour, but post-establishment, when more aware of predation risks, animals foraged further from cover when in larger group sizes.

Blumstein *et al.* (1999) suggested that experimental introductions to areas with predators are required to see if the benefits wallabies receive while aggregating with others actually increases survival. Indeed, more work still needs to be done in this area to see whether aggregation influences survival. Retrospective analyses of the dataset obtained during this study could determine an approximate time of death (for animals which died during a field trip) and determine if the number of surrounding conspecifics at that time, deviates from the average number of surrounding conspecifics at an equivalent time of day (and in similar habitat and conditions) when no deaths occurred. Or more accurately, perhaps future work could use GPS collars which regularly determine locations and proximity to others to correlate exact time of death to the number of surrounding conspecifics, also factoring in habitat type, climatic conditions, and etcetera.

Many of the tammars released in this study seemed to naturally congregate and reside in the vicinity of an old township containing houses used as holiday and visitor accommodation. Tammars were frequently seen grazing in the yards of these houses. As many exotic and common garden plant species were planted and only occur this township, examining the scats collected during this study may help to conclude whether the animals were selecting those locations for specific forage availability or some other reason, such as habituation to human activity. The release populations had spent at least six months in captivity prior to release, so it could be interesting to investigate why the tammars chose to reside close to the Inneston township, and determine whether they had been somewhat habituated and human presence and activity afforded some kind of safety to the wallabies. Assessing how the occupancy or vacancy of the houses affected the tammars' relative locations and foraging decisions may give some indications into whether human presence influences habitat choices. Likewise, Onorato *et al*. (2003) found American black bears were more likely than random to be within 100m of anthropogenic features (such as roads and trails) but the effect was stronger when visitor numbers were low. They suggested that their data was useful in providing predictive capability for managers regarding the animals' recolonisation of other areas and facilitated the persistence of the current small population. Knowing if there is an effect of habituation on animals released from captive environments may be an important factor in future reintroduction programs conducted here. In Zidon's *et al.* (2009) study it was observed that the amounts of human activity Persian fallow deer (*Dama mesopotamica*) were exposed to in captivity affected their anti-predator behaviour, habitat use and likelihood of survival following their reintroduction into the wild. Two-hundred days after their release, 80% of the fallow deer originating from reduced human presence in captivity had survived, whereas none survived that had originated from lots of human activity in captivity.

One element of the tammars' ecology lacking from this study is analysis of their seasonal diet in relation to their habitat selection and home range location. Dietary analysis is required to assess if the tammars moved their home ranges for food resources or shelter resources, and to assess if they were being selective in their diet or just ate what was primarily available.

Overall, this study has served to significantly increase our understanding of the establishment, behaviour and ecology of tammar wallabies reintroduced into wild where predators are present. This thesis has examined the importance and relationship between habitat requirements and social grouping by an entire population of tammar wallabies for twelve months following an experimental reintroduction. Results from this study are fundamental to the planning of future reintroductions of this species, and can be applied to other mammals which adopt similar anti-predator strategies. Incorporating findings from this study into reintroduction planning should help to improve the likelihood of reintroduction success in the future.

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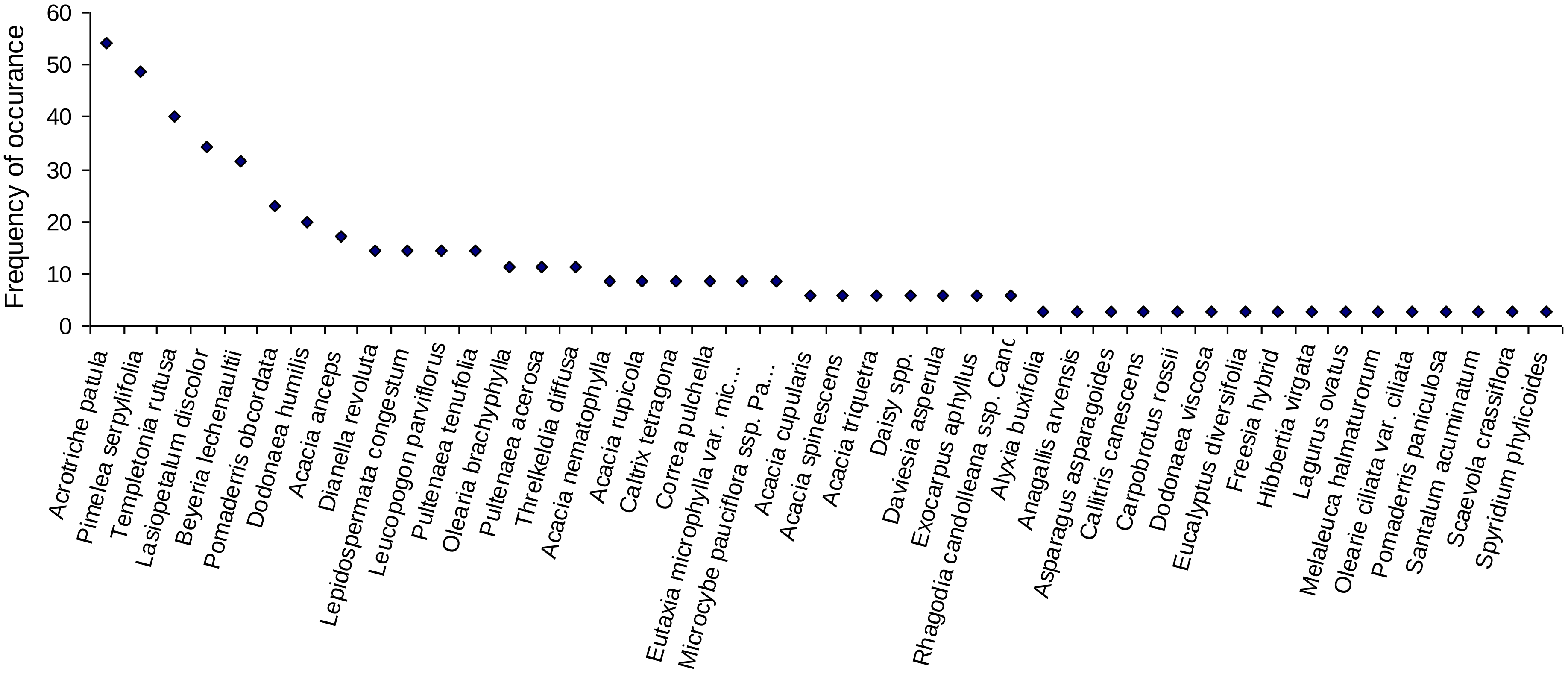
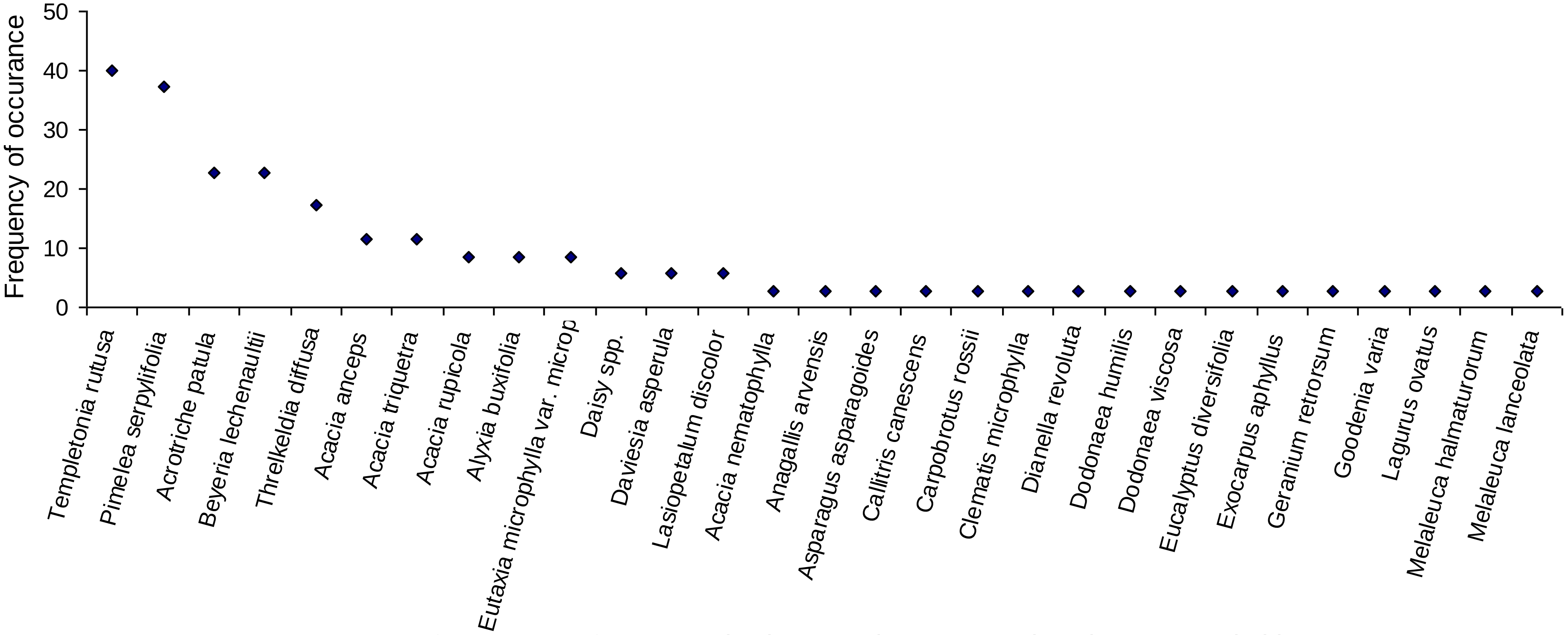
Appendix A: Frequency of occurrence of plant species observed in each habitat type



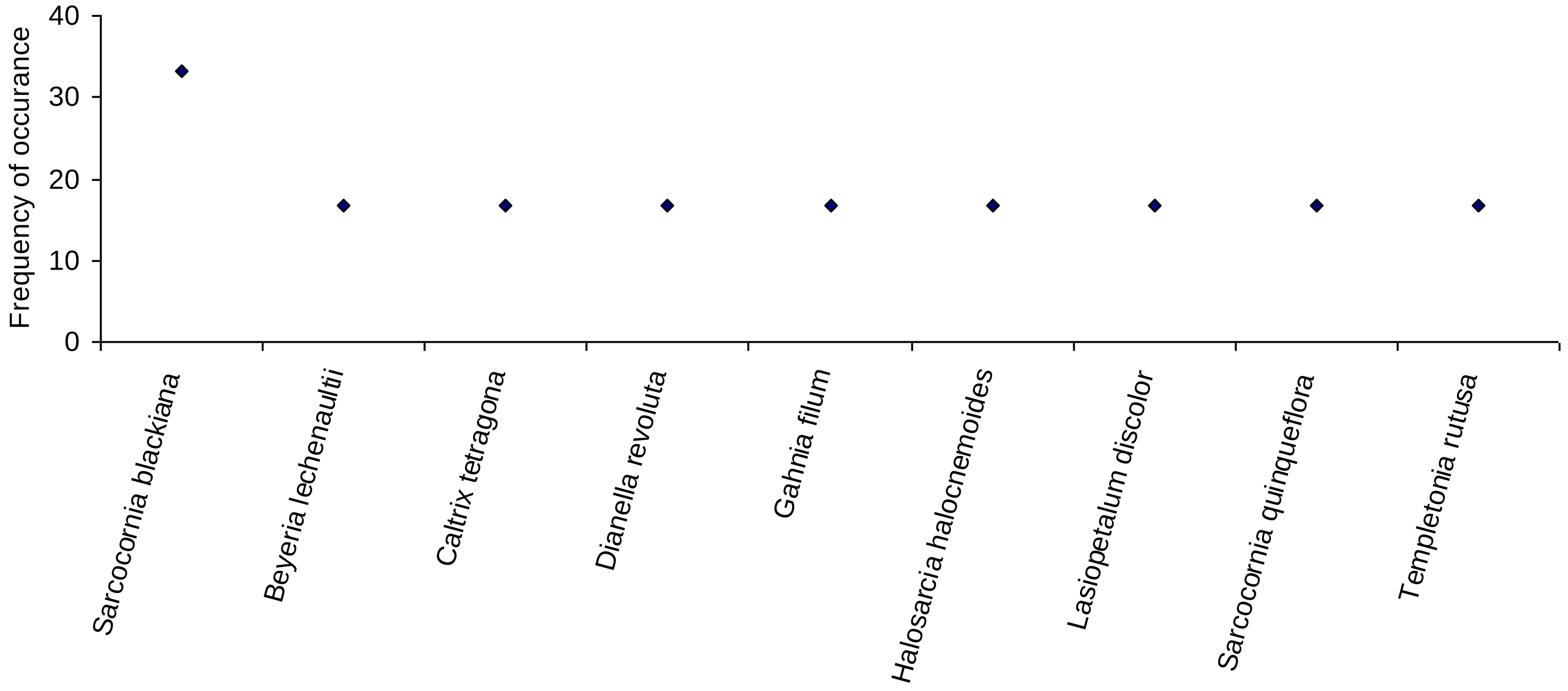
Frequency of occurance of plant species in 35 random 4m^2 quadrats in *E.diversfolia* habitat type
(most abundant to least abundant)

Appendix A: Frequency of occurrence of plant species observed in each habitat type



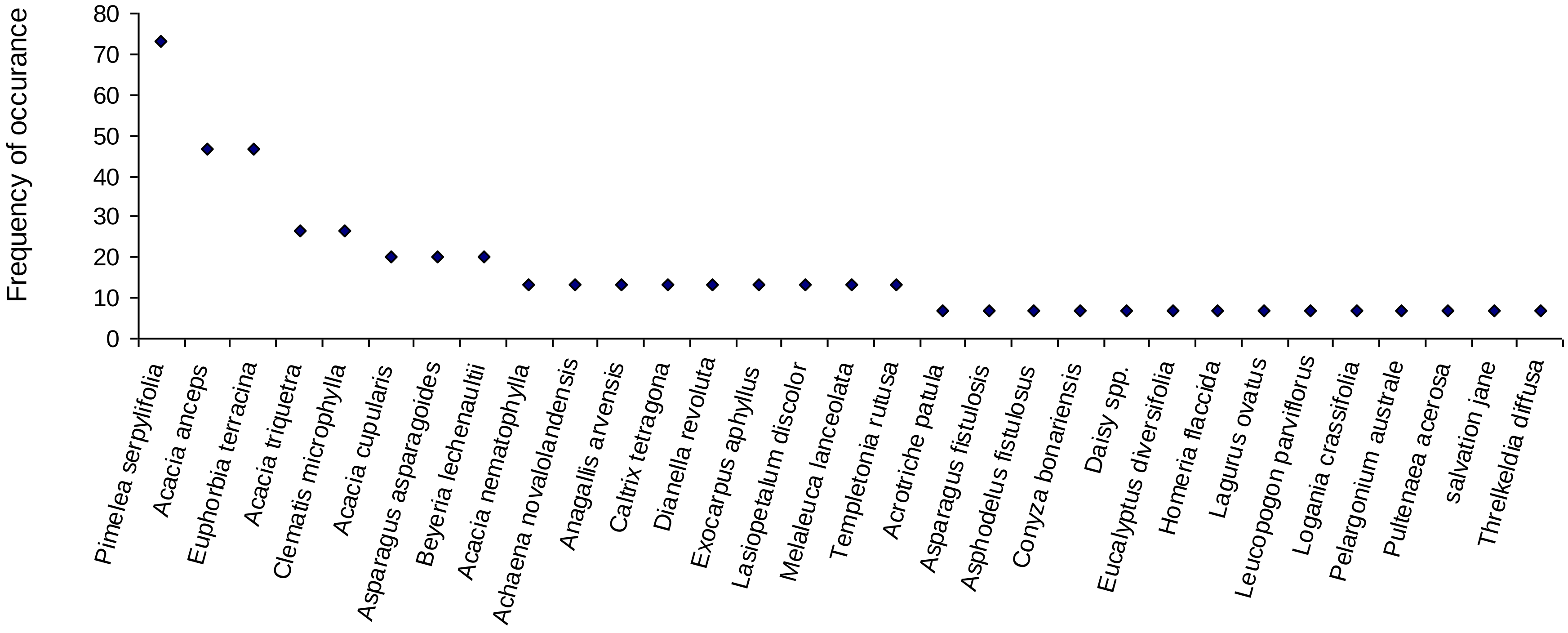
Frequency of occurance of plant species in 35 random 4m² quadrats in *E.rugosa* habitat type
(most abundant to least abundant)

Appendix A: Frequency of occurrence of plant species observed in each habitat type



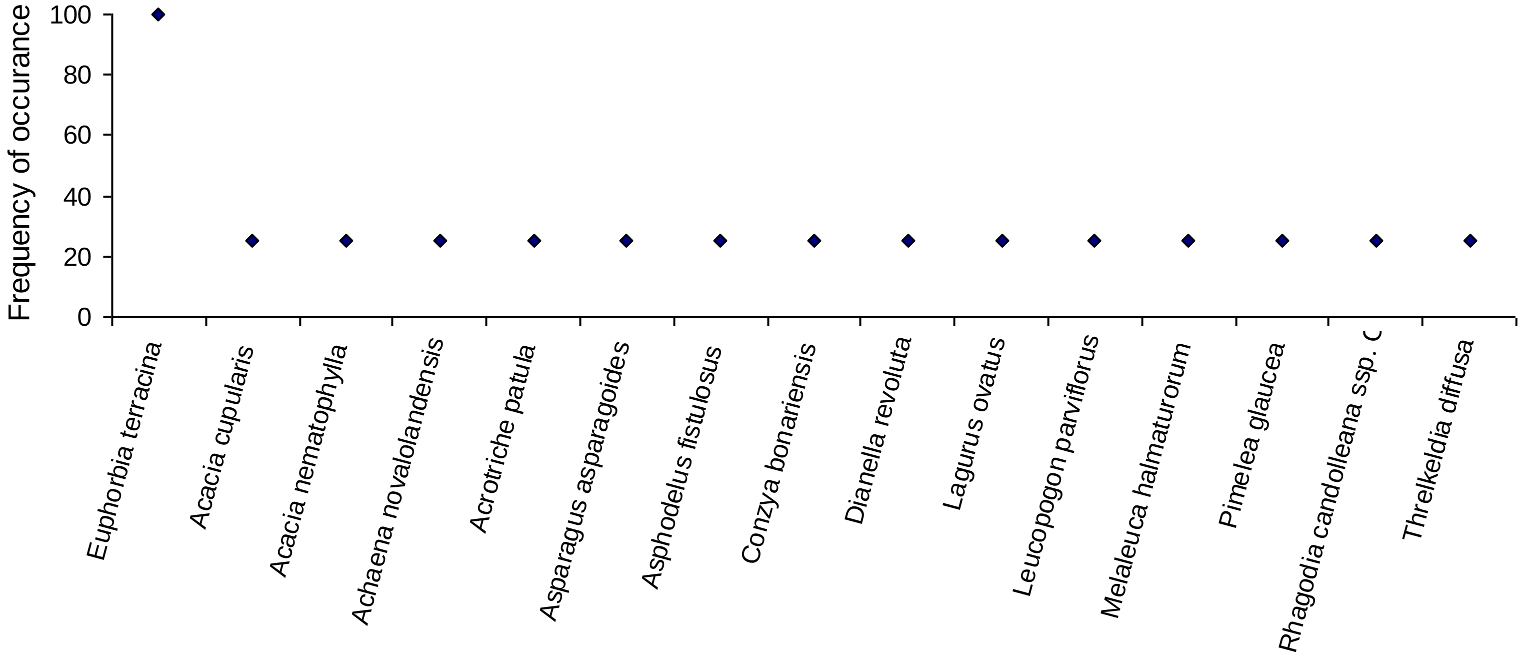
Frequency of occurance of plant species in 6 random 4m² quadrats in *M.halmaturorum* habitat type
(most abundant to least abundant)

Appendix A: Frequency of occurrence of plant species observed in each habitat type



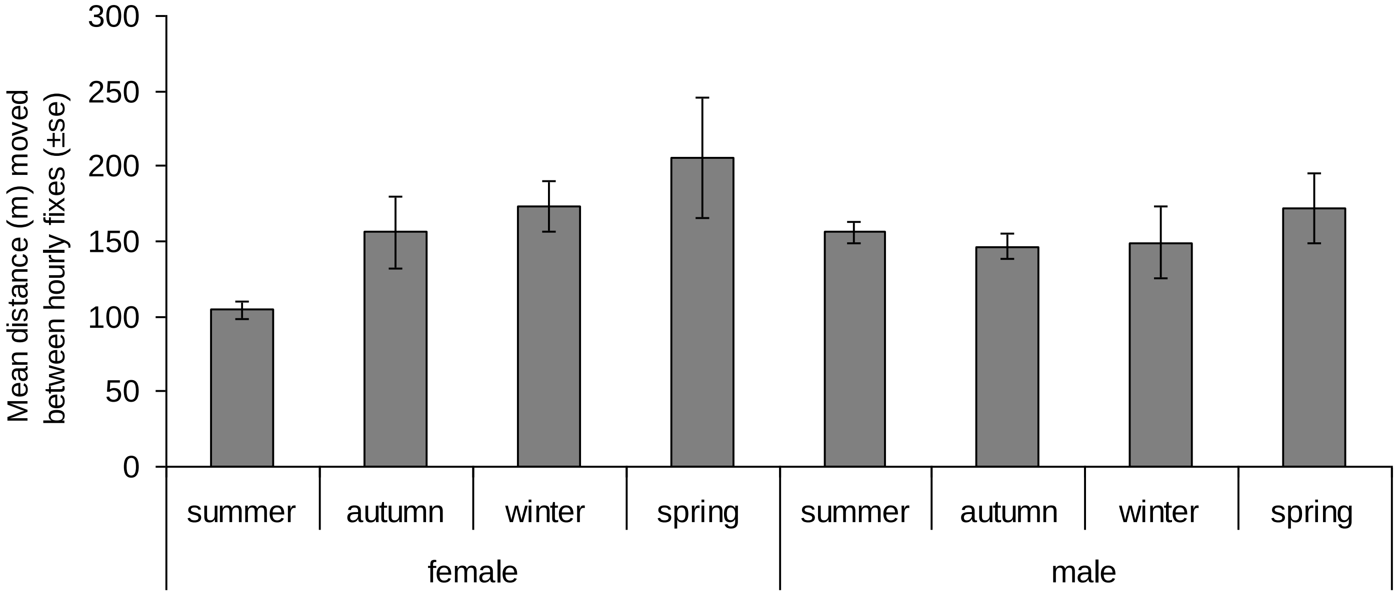
Frequency of occurance of plant species in 15 random 4m² quadrats in *A.anceps* habitat type
(most abundant to least abundant)

Appendix A: Frequency of occurrence of plant species observed in each habitat type



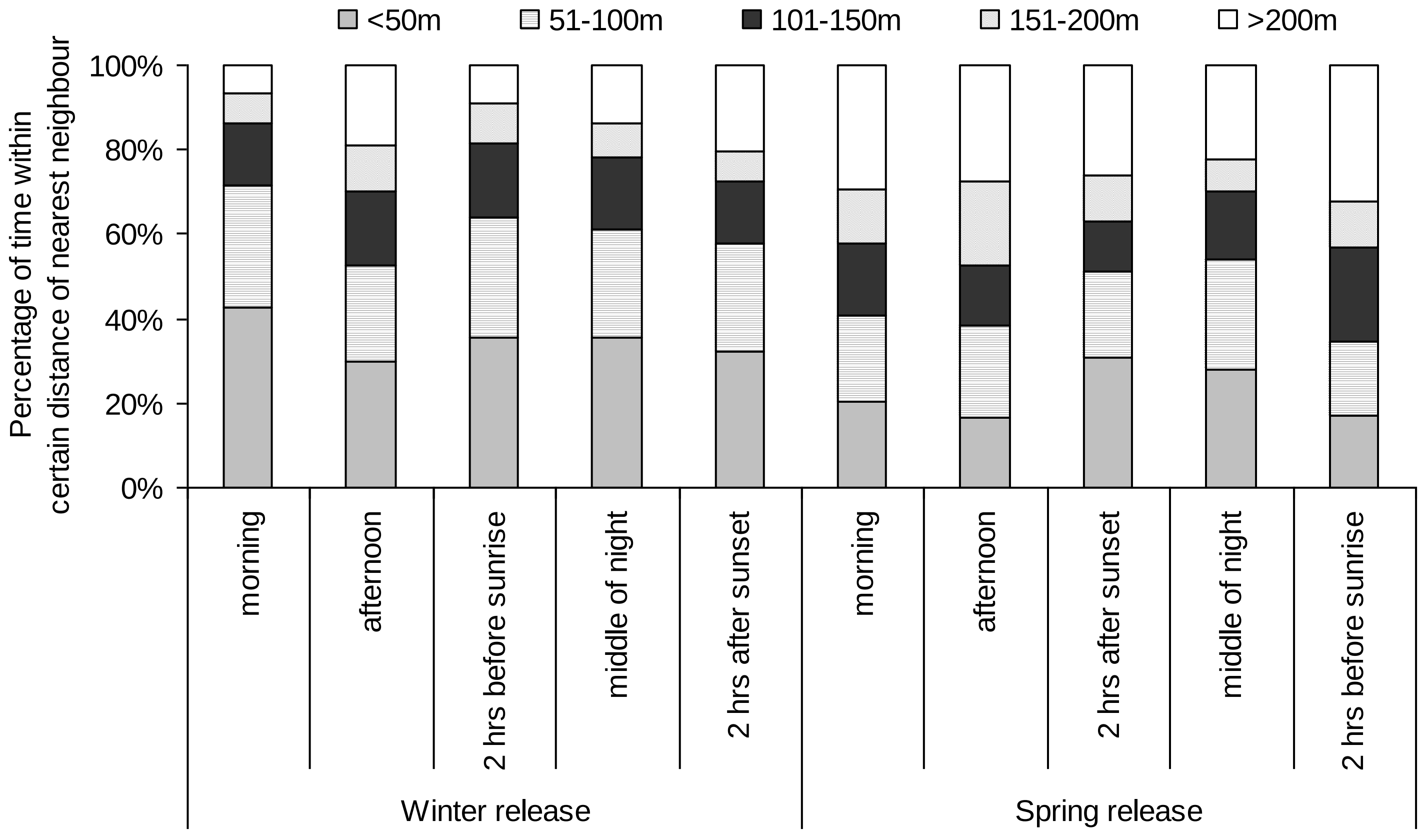
Frequency of occurance of plant species in 4 random 4m² quadrats in grassland habitat type (most abundant to least abundant)

Appendix B: Mean distance tammars moved between consecutive sampling periods



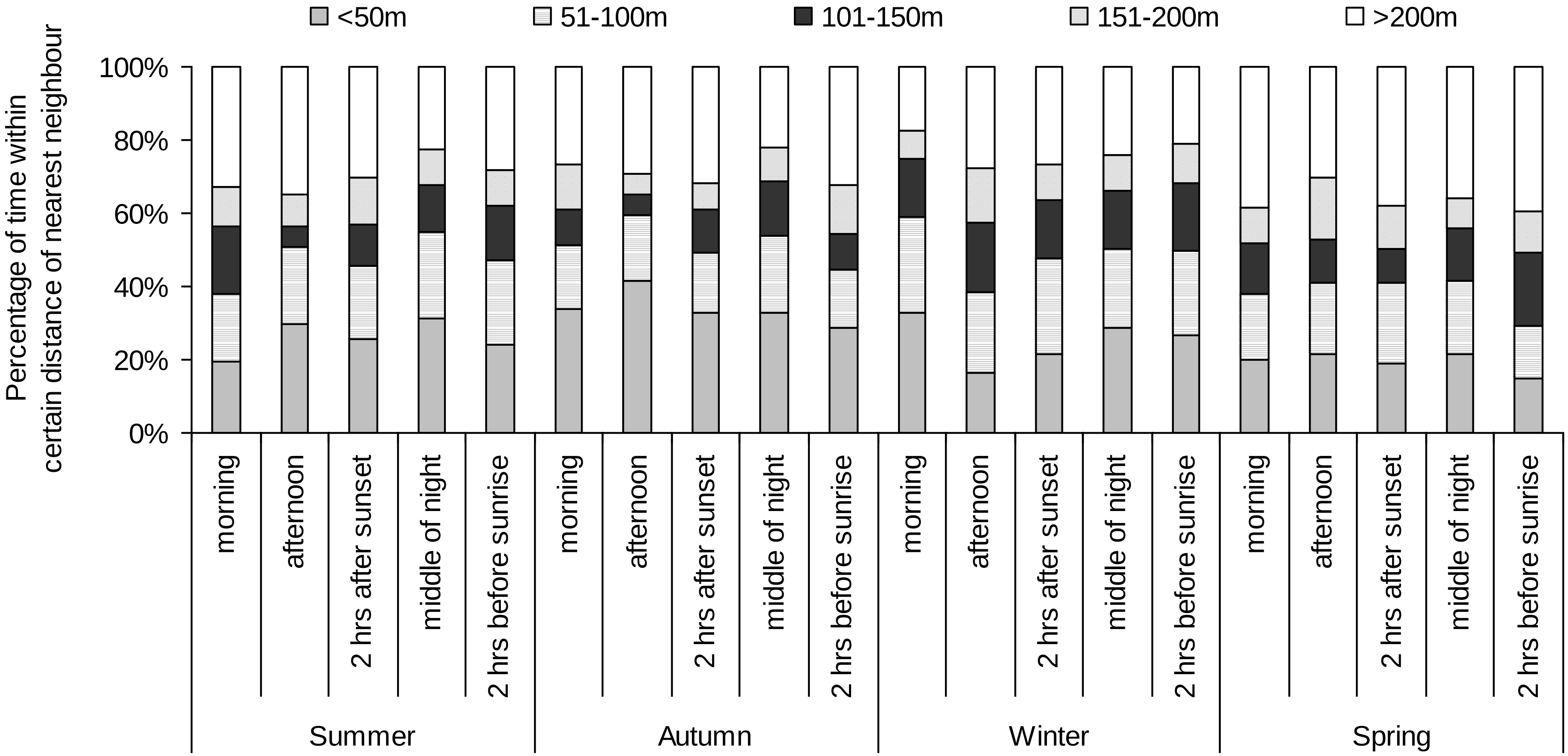
Mean distance tammars moved between consecutive sampling periods (m±se)

Appendix C: Percentage of time spent within certain proximity of nearest neighbour



Amount of time tammars spent within a certain proximity of their nearest neighbour
throughout the day during the month following the two reintroductions

Appendix C: Percentage of time spent within certain proximity of nearest neighbour



Amount of time tammars spent within a certain proximity of their nearest neighbour throughout the day during each season