Release protocols and release environment: what influences reintroduction success for the brushtail possum?

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CONTENTS

PUBLICATIONS

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ABSTRACT

This thesis examines the relative influence of release protocols and the release environment on short-term establishment and long-term persistence in reintroduction programs, using a brushtail possum reintroduction in semi-arid South Australia as a case study.

I present a comparison of three release treatments, as release methods are known to influence post-release parameters but vary greatly by species and other factors such as source and release environment. The survival, post-release dispersal, change in body mass and reproductive condition of possums in each treatment are compared and results highlight a mismatch between release protocols that may benefit a species and being able to deliver them effectively.

I investigated whether exposure to predators was likely to influence the antipredator behaviour of possums, and whether this translated to a difference in post-release survival between predator-exposed and predator-naïve possums. Antipredator behaviour was assessed using a variety of methods. Predator-exposed possums exhibited heightened antipredator behaviour compared to predator-naïve possums in all tests. However, post-release survival of both source populations was high, suggesting that successful fox control may negate the need to source predator-exposed animals for release.

With predation the leading cause of reintroduction failure in Australia, the successful control of foxes at the reintroduction site provided an opportunity to investigate the impact of habitat quality. Habitat quality was assessed via the availability and recruitment of hollow bearing trees, mid storey vegetation cover and known preferred food plants in arid systems. Effects of habitat quality were measured post-release. Body condition and mass was maintained or increased over the study period following an initial post-release drop, and reproduction was constant. Most mortalities were due to predation by feral cats. Results suggest that habitat quality varies according to the factors tested but that despite a history of degradation at the site, short term reintroduction success was achieved. However, longer term persistence may be compromised unless further habitat restoration occurs.

I investigated the interaction between diet and time since release to understand acclimatisation patterns and likelihood of long–term persistence. Next-generation DNA sequencing was used to identify plant genera within possum scats. Vegetation surveys were conducted to measure plant availability. Diet changed significantly over time and suggested that acclimatisation periods revealed by diet may be longer than indicated by other commonly used measures. Results have implications for reintroductions and restoration.

Finally, I documented the survival, movement and growth of juvenile possums, as an indicator of the feasibility of population growth and persistence. I found sex effects for movement and growth, which interacted with maternal effects. Dispersal involved multiple movement phases and was male-biased. Most mortalities were attributed to predation by feral cats, but were not high enough to arrest population growth. Dispersal behaviour is interpreted in light of other studies of mammalian dispersal, and the influence of sex, maternal behaviour and environmental conditions are discussed.

Release environment was found to be more important for short-term reintroduction success for brushtail possums than release protocols, but its influence on long-term

persistence should be carefully monitored over time and, particularly, through drought.

This thesis includes three chapters that have been published (chapters 2, 3 & 6) and two chapters that have been submitted to journals (chapters 4 & 5). Formatting styles may thus vary slightly between chapters. A single reference list is provided at the end of the thesis.

THESIS OBJECTIVE

Investigate the importance of release protocols and the release environment on reintroduction success, using the brushtail possum as a case study.

THESIS AIMS

The aims of this study were to:

1. Identify factors influencing the short-term reintroduction success of brushtail possums, by investigating:
    a. the effect of alternative release methods on post-release survival, dispersal, body mass and reproduction, and;
    b. the influence of previous predator exposure on antipredator behaviour, habitat use and survival.
2. Identify factors that may influence the long-term persistence of a reintroduced population of brushtail possums in the Ikara-Flinders Ranges National Park, by studying:
    a. whether sub-optimal habitat influences post-release parameters such as habitat use, reproduction and body condition, and whether habitat quality is a limitation to reintroduction success;
    b. the diet of the semi-arid brushtail possums, whether it changes with time since release and whether diet is likely to limit population persistence, and;
    c. the survival, growth and movement of juvenile possums within the population.

1. INTRODUCTION

1.1 DECLINES AND EXTINCTIONS

Biodiversity is declining as native species contract their distribution, become locally extinct or, ultimately, become globally extinct (Butchart *et al.* 2010). Australia holds the worst rate of mammal extinctions worldwide, losing more than 10% of endemic terrestrial mammals to extinction in the past 200 years, with a further 21% assessed as threatened (Woinarski *et al.* 2015). Losses are usually a result of a combination of predation by introduced predators (feral cats *Felis catus* and foxes *Vulpes vulpes*), altered fire regimes, habitat loss and alteration, competition with domestic stock and feral herbivores (rabbits *Oryctolagus cuniculus* and goats *Capra hircus* among others), or persecution (Morton 1990; Woinarski *et al.* 2015). Most native species extant at the time of European arrival in Australia were able to co-exist with the dingo (*Canis lupus dingo*), a eutherian predator introduced to Australia more than 4000 years ago (Corbett 1985). The introduction of feral cats and foxes in the 1800s (Abbott 2002; Abbott 2011) led to widespread species declines, particularly in mammals falling within the 'critical weight range' (35–5500 g) and living in the arid zone (Burbidge and McKenzie 1989; Chisholm and Taylor 2007; McKenzie *et al.* 2007). Almost 90% of native mammals within the Australian arid zone had either become locally extinct or had declined by 1989 (Burbidge and McKenzie 1989).

There is a synergistic effect between many threatening processes (Doherty *et al.* 2015b; McGregor *et al.* 2015). The impacts of introduced predators may be exacerbated by habitat use (ground dwelling versus arboreal species), body size, fecundity and habitat degradation (Burbidge and McKenzie 1989; Cardillo 2003; Johnson and Isaac 2009; McGregor *et al.* 2015). The successful introduction of the European rabbit in the early 1800s and its subsequent domination of most open habitat types across the southern half of Australia (reviewed by Peacock and Abbott 2013) led to widespread habitat destruction and alteration, depleting the food and shelter resources available to many native species. Rabbits form a major component of the diet of introduced predators, namely feral cats and foxes (Catling 1988; Davis *et al.* 2015; Woinarski *et al.* 2017). Thus, fluctuations in rabbit numbers in response to resource depletion or disease can lead to fluctuations in the populations of introduced predators (Read and Bowen 2001; Pedler *et al.* 2016; Mutze 2017). Habitat alteration, including (but not limited to) altered fire regimes, can influence both the susceptibility and exposure of prey to introduced predators (McGregor *et al.* 2015; Hohnen *et al.* 2016). Threat mitigation, therefore, often requires several threats to be addressed simultaneously to have a net benefit for threatened species.

In order to reverse the decline of a threatened species, one or more of the original significant threatening processes must be reduced (Brambell 1977; IUCN 1987). This implicitly requires an understanding of the species' ecology, which, for threatened species, is often lacking. Synergistic threats often provide a better hypothesis for species decline than single threatening processes, despite the former providing a more palatable and simplistic answer (Armstrong *et al.* 1995). While identifying key threats is essential, reducing or eliminating such threats is even more problematic. Broadscale control of introduced mammals, particularly foxes, feral cats and rabbits, is challenging and often unsuccessful (Algar and Burrows 2004; Saunders *et al.* 2010), and a combination of control methods are usually required, with complete eradication unlikely in the near future. Aerially applying poison baits can be effective for locally eradicating foxes when applied at landscape scales (Moseby and Hill 2009; DEWNR 2012; Marlow *et al.* 2015b), but this is not feasible at a continental scale. Feral cats prefer live prey and are thus more difficult to control using poison baits and baited traps (Algar and Burrows 2004; Moseby and Hill 2009). Shooting, leg-hold and cage trapping and automated poison applicators (grooming traps) are alternative methods used for both species and can be variably effective at small scales, but are expensive to scale up to effective levels. The development of innovative control techniques continues to be a research priority (Read *et al.* 2014; Read *et al.* 2016; Kinnear *et al.* 2017; Moro *et al.* 2018). Despite such problems, introduced predators and/or rabbits have been successfully controlled or eradicated on some islands (Priddel *et al.* 2000; Algar *et al.* 2011; Raymond *et al.* 2011; Glen *et al.* 2013), inside fenced reserves (Moseby and Read 2006; Miller *et al.* 2010; Manning *et al.* 2011; Short and Hide 2014) and, in a few cases, on mainland areas (Kinnear *et al.* 1988; Short and Turner 2000; DEWNR 2012; Marlow *et al.* 2015b).

While controlling predators on a local scale is achievable, reinvasion can occur relatively quickly when control is irregular or too infrequent (Moseby and Hill 2011). Sustained funding and commitment is essential for control programs to continue long enough to have a positive, lasting impact on native species; some landscape scale predator control projects have achieved conservation success: the Western Shield project in Western Australia involves landscape fox control and has led to the recovery of several native mammals including the black-flanked rock wallaby (*Petrogale lateralis lateralis*) (Kinnear *et al.* 2010; DBCA 2018). The Bounceback Project in South Australia began controlling foxes (among other pest species) in the early 1990s across three range systems, which led to the recovery of the yellow-footed rock wallaby (*Petrogale xanthopus*) in those areas (DEWNR 2012; Brandle *et al.* 2018). Some fox baiting programs have led to the recovery of a suite of small mammal species such as bandicoots, possums and potoroos (Burrows and Christensen 2002; Dexter and Murray 2009; Robley *et al.* 2014). To remain successful, these projects are dependent on ongoing predator control. Importantly, the effects of the removal of one invasive species on another need to be carefully considered—they can be positive, such as a decline in introduced predators following a decline in rabbits (Read and Bowen 2001; Pedler *et al.* 2016; Mutze 2017), or negative, such as the release of or dietary shift by feral cats following fox control (Marlow *et al.* 2015a; Molsher *et al.* 2017). When the control of introduced predators does not take place early enough or is ineffective, localised (or global) extinction can take place. In the case of localised extinctions, if predator control is later successfully implemented, then reintroductions of locally extinct species may be feasible.

1.2 REINTRODUCTIONS

The International Union for the Conservation of Nature defines a reintroduction as "the intentional movement and release of an organism inside its indigenous range from which it has disappeared" (IUCN/SSC 2013). Reintroductions are a form of translocation—"the human-mediated movement of living organisms from one area, with release in another" (IUCN/SSC 2013). In an effort to prevent the ongoing loss of species to extinction, reintroductions are increasingly being used to increase the distribution and global population size of threatened species. Reintroductions are expensive and logistically difficult, therefore identifying ways to improve the outcomes of reintroductions is a key conservation concern (Kleiman 1989; Seddon *et al.* 2007). The reduction or elimination of threatening processes is considered essential for a reintroduction to succeed (Brambell 1977; IUCN 1987; Armstrong *et al.* 2019). Importantly, reintroductions should not replace other forms of conservation, but should complement them (Kleiman 1989). To improve reintroduction success, reintroductions should be conducted as experiments (Serena and Williams 1995; Soderquist 1995; Seddon *et al.* 2007), noting though that the practicality of this is sometimes limited. Failed reintroductions pose an ethical issue, as animals have died in the process (Bekoff 2002). Unfortunately, the reasons for many failed reintroductions remain unclear (Armstrong *et al.* 1995; Fischer and Lindenmayer 2000; Armstrong *et al.* 2019), which does little to advance reintroduction biology. In Australia, predation is usually the main cause of reintroduction failure, and reintroduction success is generally higher when introduced predators are absent (Fischer and Lindenmayer 2000; Short 2009; Moseby *et al.* 2011). Conducting reintroductions as experiments enables the development of best practice standards, reduces the risk of failure for future reintroductions and can lower the risks and costs for future projects if the results are made publicly available. Factors common to successful reintroductions include:

- Original threatening processes have been addressed (Brambell 1977; IUCN 1987; Seddon *et al.* 2007)
- Predators are excluded or effectively controlled at the release site (Short *et al.* 1992; Moseby *et al.* 2011)
- A large founding population (MacArthur and Wilson 1967; Wolf *et al.* 1996; Seddon *et al.* 2007)
- A high rate of increase (MacArthur and Wilson 1967)
- Low competition (MacArthur and Wilson 1967)
- Good habitat quality (Griffith *et al.* 1989; Wolf *et al.* 1996) and the presence of refugia (Goodman 1987)
- Herbivorous (Griffith *et al.* 1989) or omnivorous (Wolf *et al.* 1996) diet
- Translocations into the core historical range, rather than the periphery (Griffith *et al.* 1989; Wolf *et al.* 1996)
- Wild-sourced animals rather than captive-bred (Griffith *et al.* 1989; Fischer and Lindenmayer 2000)

1.2.1 Problems with fences

While reintroductions to predator-free areas have higher reintroduction success than reintroductions to areas where predators remain present (Short 2009; Moseby *et al.* 2011), these ‘solutions’ contain their own problems. Fences are costly to build and maintain, and can disrupt the natural movement of animals both inside and outside the fenced area (Hayward and Kerley 2009). In turn, this can limit gene flow. For fenced areas where predators have been removed, native and reintroduced species can become overpopulated. For example, at the Arid Recovery Reserve in South Australia, burrowing bettongs (*Bettongia lesueur*) have become overpopulated inside the fenced reserve, and so despite providing initial ecosystem benefits following their reintroduction (James and Eldridge 2007; Read *et al.* 2008), they are now causing considerable vegetation damage inside the reserve (Linley *et al.* 2017; Moseby *et al.* 2018). At Yookamurra Sanctuary, a fenced reserve owned by the Australian Wildlife Conservancy, brushtail possums are abundant inside the fenced, predator-free area, but are rarely seen outside the fenced area (pers. obs.), despite being able to disperse over the fence because of their arboreal nature. Presumably, many possums that leave the fenced area fall victim to predation by introduced predators.

Isolation from predators can facilitate the onset (or maintenance) of prey naivety (Blumstein *et al.* 2004; West *et al.* 2018), making the population unsuitable as a source for reintroductions to areas where predators have not been excluded, or reducing post-release survival as a result of predation. For animal movement, overpopulation, genetic, prey naivety, financial and logistic reasons, reintroduction biology should continue to aim for reintroductions 'beyond the fence', while still acknowledging the value that predator-free reserves do provide. Reintroductions to unfenced areas are risky, and for that reason it is often inadvisable to use critically endangered species, where a failed reintroduction could lead to species extinction, and would be politically sensitive (Serena and Williams 1995). Moderately threatened species provide good candidates for these types of reintroductions, enabling them to be conducted as experiments (Serena and Williams 1995; Soderquist 1995). This allows methods to be refined so that eventually critically endangered species may have an opportunity for reintroduction with a lower risk. In addition, successful reintroductions can be used to prevent moderately threatened species from joining the critically endangered species list (Serena and Williams 1995).

1.3 STUDY SPECIES

Brushtail possum

The common brushtail possum (*Trichosurus vulpecula*, hereafter 'possum' or 'brushtail possum') is a semi-arboreal marsupial belonging to the family Phalangeridae. Possums are nocturnal and during the day typically shelter in tree hollows, but also use hollow logs, burrows, sinkholes, rock crevices, caves and termite mounds (Kerle *et al.* 1992; Foulkes 2001; Wayne *et al.* 2005; Cruz *et al.* 2012a). Possums were historically distributed across most of Australia, across all climatic zones (Fig. 1.1). In the early 1900s possums were described as "an extremely abundant animal over wide areas and…one of the chief food species of the natives in some districts" (Finlayson 1961, cited by Kerle *et al.* 1992). Today, however, brushtail possums are common only by name and not by nature, having disappeared from more than 50% of their historic range, with declines most prominent in the arid and semi-arid zones (Fig. 1.1). Possums were historically not restricted to watercourses as many populations are now (Kerle *et al.* 1992). Declines have been attributed to a suite of factors including predation by introduced predators, habitat clearance, altered fire regimes, competition with and habitat alteration by domestic stock and introduced herbivores, hunting and persecution, and disease (Burbidge *et al.* 1988; Evans 1992; Kerle *et al.* 1992; Abbott and Whitford 2002). Some factors are likely to have a synergistic effect (Doherty *et al.* 2015b; McGregor *et al.* 2015). It has been hypothesised that arid zone possum populations contract to watercourses, where conditions are more moist, during drought, and are then slow to expand and recolonise as conditions improve (Morton 1990; Kerle *et al.* 1992). The introduction of domestic stock resulted in the degradation of areas surrounding natural waterbodies, impacting on optimal possum habitat and competing for some food plants. Other introduced herbivores, including rabbits, were also direct competitors for food resources. The fur trade was also likely significant enough to have contributed to the decline of the possum. In one example, over 100,000 possum skins were exported from South Australia in a four month period in 1920 (Wood Jones 1923, cited by Kerle *et al.* 1992). Significant land clearing for agriculture and development is a contributing factor to the decline of this hollow-dependent species (Abbott and Whitford 2002; Cruz *et al.* 2012a). Introduced predators, particularly foxes but also feral cats, further contributed to the possums' decline and remaining arid zone populations are now thought to be in a 'predator pit', whereby densities are so low that they are unable to expand with current levels of predation (Newsome 1990; Kerle *et al.* 1992). At such low possum densities, dingoes (*Canis lupus dingo*) can also have a negative impact on populations (Foulkes and Kerle 1991). In areas where fox control has been successfully implemented and possums are still present, numbers have increased (Burrows and Christensen 2002; Kinnear *et al.* 2002; Robley *et al.* 2014).

The biology of the possum varies across its range. Five subspecies are currently recognised: *T. v. arnhemensis* (north-west Australia), *T. v. fuliginosus* (Tasmania), *T. v. hypoleucus* (south-west Australia), *T. v. vulpecula* (central and eastern Australia), and *T. v. johnstoni* (north-east Australia). The status of populations in north-east Australia remains unresolved, with a sixth subspecies (*T. v. eubarensis*) sometimes referred to (e.g. Atlas of Living Australia, ala.org.au) (Kerle *et al.* 1991). Subspecies vary by body mass, fur colour, fur density, tail 'brushiness' and aggression, but genetic work suggests they remain a single species (Kerle *et al.* 1991). Possums weigh between 1 and 4 kg (Kerle 2001), with smaller subspecies found to the north and west and the largest subspecies found in Tasmania (Kerle *et al.* 1991). Possums are primarily a solitary species; home ranges partially overlap, with males overlapping with both males and females, while females tend to overlap to a lesser degree with other females (Wayne 2005; DeGabriel *et al.* 2014; Short and Hide 2014). In temperate areas, females give birth in autumn and occasionally spring (Pilton and Sharman 1962; Dunnet 1964; How and Hillcox 2000; Wayne *et al.* 2005), while in arid and tropical areas breeding occurs at any time of year (Kerle and Howe 1992; Foulkes 2001; Short and Hide 2014). Usually a single young is born, spending at least four months in its mother's pouch before advancing to back young (Pilton and Sharman 1962; Gemmell and Hendrikz 1993). Females begin breeding at an age of 1–2 years, (Dunnet 1956) varying considerably across their range (Crawley 1973; Kerle and Howe 1992).

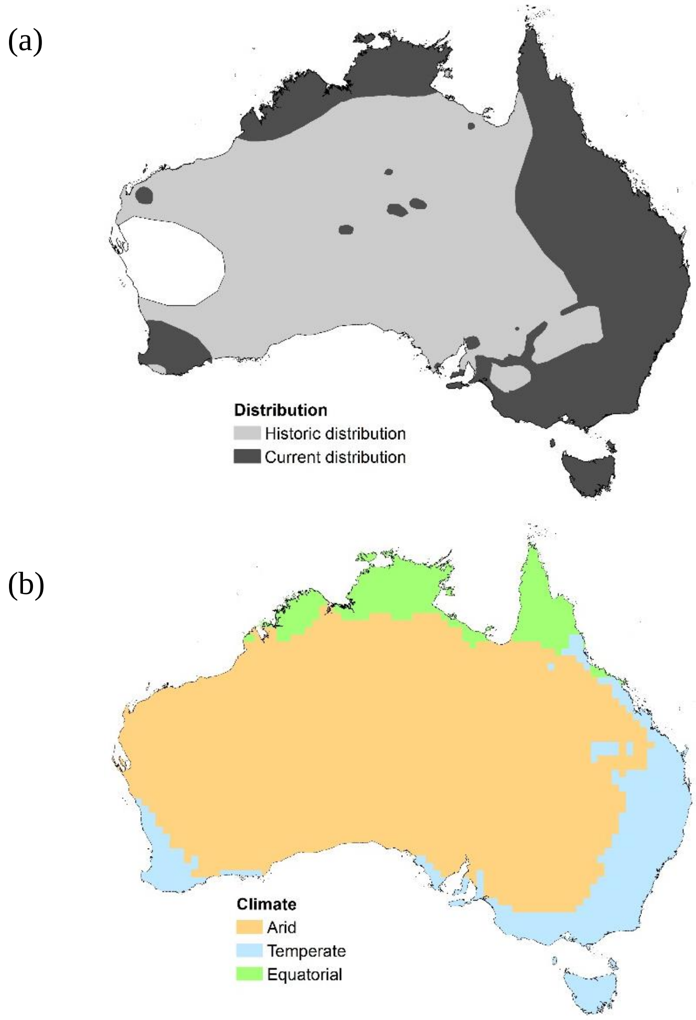

Figure 1.1: (a) The current and historical distribution of brushtail possums, based on IUCN distribution data (Morris *et al.* 2008) and sub-fossil and pre-European distribution data from Kerle (2001). (b) Australia's broad Köppen-Geiger climatic zones (Rubel and Kottek 2010).

1.3.1 Conservation status

The conservation status of brushtail possums varies by location, with the species listed as rare, vulnerable and endangered in SA, WA and NT respectively (Table 1.1). More than 20 years ago, the 1996 Action Plan for Australian Marsupials and Monotremes (published by the International Union for the Conservation of Nature), suggested a 10–50% decline in area of occurrence for *T. v. arnhemensis*, *T. v. fuliginosus* and *T. v. vulpecula*, and a 50–90% decline for *T. v. hypoleucus* (Maxwell *et al.* 1996). Despite the significant decline in area of occupancy for, *T. v. hypoleucus*, the subspecies does not have threatened species status in Western Australia. The International Union for the Conservation of Nature (IUCN) lists the species as least concern, but their trend as declining (Morris *et al.* 2008). Currently, management actions appear to concentrate on areas where the species is abundant (or overabundant), for example where destruction permits are issued (Tasmania, Kangaroo Island (S.A.) etc.), or where 'pest' removal takes place, in urban areas. Brushtail possums were introduced to New Zealand in the 1800s, where they are now considered a pest species, and are relatively well studied there because of the threat they pose to local agriculture and native fauna (Green 1984; Cowan 2005). The ecology of brushtail possums in areas where the species has declined or become locally extinct is poorly documented (Russell *et al.* 2013).

Table 1.1: The conservation status for brushtail possums in each Australian state/territory, as well as their national and international listing.

Location	Legislation	Status
Australian Capital Territory	Nature Conservation Act 2014	Not listed
Australia-wide	Environment Protection and Biodiversity Conservation Act 1999	Not listed
New South Wales	Biodiversity Conservation Act 2016	Not listed
Northern Territory	Territory Parks and Wildlife Conservation Act 2000	**Endangered** (*T. v. vulpecula*)
Queensland	Nature Conservation Act 1992	Least Concern
South Australia	National Parks and Wildlife Act 1972	**Rare** (*T. v. vulpecula)*
Tasmania	Threatened Species Protection Act 1995	Not listed
Victoria	Flora and Fauna Guarantee Act 1988	Not listed
Western Australia	Wildlife Conservation Act 1950	**Vulnerable** (*T. v. arnemhensis)*

1.3.2 Previous brushtail possum translocations

Moderately (but not critically) threatened or declining species are good candidates for reintroduction as there is less risk to the species' persistence if the reintroduction fails. The reintroduction can be designed as an experiment to identify ways to improve reintroduction success. The outcome is thus less politically-sensitive compared to the reintroduction of a critically threatened species, and there is an opportunity to prevent a species in decline from joining the endangered species list, by reversing the species' decline (Serena and Williams 1995). Because of their drastic decline across Australia, but widespread distribution and relatively high abundances in some areas, brushtail possums make ideal candidates for reintroductions to areas where they have become locally extinct and threatening processes have been addressed.

Several possum translocations have been undertaken previously, although relatively few have been undertaken for conservation purposes, with most occurring as ad hoc releases of a small number of animals or as relocations of 'problem' animals that have been residing in or near peoples' homes. The results from many possum translocations have not been published and the outcome of most translocations is unknown. For translocations where monitoring has taken place, translocation failure has usually been attributed to predation, particularly by foxes (Table 1.2). A reintroduction to Cape Range National Park in Western Australia reported that 74% of radio-collared possums were killed by foxes (DEC 2012), and a translocation to sclerophyll forest in the Dandenong Ranges of Victoria also found high post-release mortality, with most deaths attributed to predation by canids, probably foxes (Pietsch 1995). For reintroductions to fenced or partially fenced sites, predation remains a problem for possums that disperse outside of fenced areas or when predators are unsuccessfully controlled (Short and Hide 2014; May *et al.* 2016). Post-release weight loss and dispersal away from release sites have been identified as problems in previous translocations where monitoring was undertaken (Pietsch 1995; Miller *et al.* 2010; Table 1.2). Brushtail possums can be reintroduced to areas where they have become locally extinct and at least some of their key threatening processes have been reduced, providing an opportunity to prevent their threatened species status (which varies by state) from escalating. This also provides an opportunity to experimentally test reintroduction methods as well as determine which factors are key to achieving reintroduction success, and which may lead to failure.

Previous possum translocations have experienced poor survival as well as hyperdispersal away from release sites. Post-release monitoring has generally (with exceptions) been absent or poor, leaving the fate of released animals or cause(s) of reintroduction failure unknown (Table 1.2). Often, few animals were released and were unlikely to form a viable population. When monitoring has occurred, predation, particularly by foxes, has been identified as a key cause of failure (Pietsch 1995; DEC 2012). Most successful possum translocations involved the control of introduced predators, or the use of mammalian predator-free sanctuaries. Supplementary feeding and delayed releases have been used for some releases but without experimental controls (Table 1.2). To date, rigorous experimental testing of factors likely to influence reintroduction outcomes for possums have not been undertaken.

Table 1.2: The outcomes of previous brushtail possum translocations.

S = source population (W = wild, U = urban, R = rehabilitated, C = captive), DR = delayed release, SF = supplementary feeding reported, F = fenced release site free of mammalian predators, FC = fox control, M = post-release monitoring, H = hyperdispersal, n = total number of possums released, EP = existing population at the release site, MR = multiple releases reported. If multiple releases occurred, 'year' refers to the first reported release at that location. Blank spaces indicate unknown information. Y = yes, N = no. *N.B.* This table is also presented as supplementary material for chapter 2.

Location	Year	S	DR	SF	F	FC	M	H	*n*	EP	MR	Outcome	Comments	Reference
Arkaroola, SA	1968		N		N		N		14	N		Unsuccessful		Papenfus (1990)
Cape Range NP, WA	2010	W	N		N	Y	Y		104	N	Y	Unsuccessful	Failed due to fox predation, despite baiting	DEC (2012)
Ernabella, SA	1976	U	N		N		N		12	N		Unsuccessful		Papenfus (1990)
Gold Coast, Qld	1995	R	Y	Y	N		Y	Y	13	Y	Y	Successful?	No mortalities by introduced predators. Python predation. Some were humanised. Short term monitoring/success criteria.	Tribe *et al*. (2005)
Humbug Scrub, SA	1980s	U	N		N		N				Y			Papenfus (1990)
Karakamia, WA	1994	C(R)	N	N	Y	Y	Y		8	Y	Y	Successful	Orphaned (hand-reared) possums, supplemented existing population	Australian Wildlife Conservancy (unpub. data)
Katarapko Island, SA	1970s	W	N		N		N			Y				Papenfus (1990)
Lorna Glen, WA	2007	W	N	Y	Y	Y	Y		95	N	Y	Successful	Some deaths due to lack of resources and raptor predation.	Miller *et al*. (2010)
Mambray Creek, SA	1972	U,W	N		N		N		16	?	Y	Unsuccessful		Papenfus (1990)
Melbourne, Vic	1992	U(R)	N	N	N		Y	Y	64	Y	Y	Unsuccessful	Naivety, fox predation, stress.	Pietsch (1995)
Murray Bridge, SA	1980s	W	N		N		N							Papenfus (1990)
New Zealand	1993	W	N	N	N	-	Y	Y	43	Y	Y	-	Several were shot (pest status in NZ, introduced species)	Cowan (2001)
Oraparinna Mine, SA	1961	W(R)	N	Y	N		N		12	N	Y	Unsuccessful		Papenfus (1990)
Paruna, WA	2000	W	N	N	N	Y	Y	Y	118	Y	Y	Semi-successful	Numbers stable but not increasing. Predation by foxes/cats, pythons, raptors.	May *et al*. (2016), Australian Wildlife Conservancy (unpub. data)
Quorn, SA	1974	U	N		N		N		30+		Y	Successful		Papenfus (1990); SA DELM in Copley (1995)
Sandilands, SA	1970s	W	N		N		N				Y	Not reported	Translocation distance 30km	Papenfus (1990)
Stony Creek, SA	1974	U	N		N		N		>20		Y	Successful	Additional possums released at nearby Wilmington in the following years	Papenfus (1990); pers. obs.
Wadderin, WA	2008	W, U(R)	N	N	Y	Y	Y	Y	9	N		Successful	3 released in nest-boxes	Short and Hide (2014)
Wilmington, SA	1985		N		N		N		5			Successful		SA DELM in Copley (1995); pers. obs.
Wilpena, SA	1961	W(R)	N	Y	N		N		4	N	Y	Unsuccessful	Small release number	
Yookamurra, SA	1990s				Y	Y	Y			Y		Successful	Now at a high density	Australian Wildlife Conservancy (unpub. data)

1.4 STUDY AREA

Wilpena Pound, part of the Ikara-Flinders Ranges National Park

The Ikara-Flinders Ranges National Park (IFRNP, 31° 31’ 43” S, 138° 36’ 13” E) is a 934 km^2 semi-arid National Park situated in South Australia (Fig. 1.2). The focal area for the reintroduction in the southern section of the park receives an average annual rainfall of 437 mm (Bureau of Meteorology 2018). The average winter temperature is 3.2–13.9º and the average summer temperature is 15.2–30.5º (Bureau of Meteorology 2015). Dominant vegetation types within the park consist of river redgum (*Eucalyptus camaldulensis*) creeklines, river redgum floodouts, mixed eucalypt (*E. camaldulensis* and/or *E. intertexta*) and *Callitris glaucophylla* woodland, mallee (*Eucalyptus* spp.), *Acacia Allocasuarina* shrubland and rocky (shale) *C. glaucophylla* slopes. Tree hollows are predominantly found in the woodland, creekline and floodout habitats (Moseby *et al.* subm.).

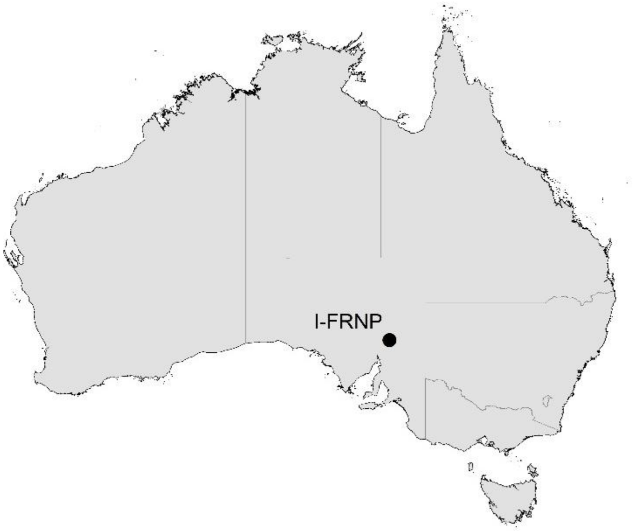

Figure 1.2: The location of the Ikara-Flinders Ranges National Park (IFRNP) within Australia, where brushtail possums were reintroduced in 2015.

In a similar story to much of southern Australia’s arid zone, the IFRNP suffered significant land degradation following European settlement, with the introduction of domestic stock and feral herbivores as well as some land clearing. Advantaged by habitat degradation and high rabbit densities, introduced predators (foxes and feral cats) had a significant impact on native species (Doherty *et al.* 2015b; McGregor *et al.* 2015). Eighteen mammal species (25 %) are considered Regionally Extinct in the wider South Australian Arid Lands region, with a further 25 % listed as Critically Endangered, Vulnerable or Rare (Gillam and Urban 2013). Brushtail possums are among those listed as Regionally Extinct (Gillam and Urban 2013). Native mammals most commonly found within the Park are kangaroos (red kangaroo *Macropus rufous*, euro *M. robustus* and western grey *M. fuliginosus*). Dingoes are present in low numbers, but are subject to mandatory control as the Park sits south of the dog fence (Downward and Bromell 1990). In the absence of a stable population of top-order predators (dingoes), kangaroo numbers have flourished to the point of negatively impacting native vegetation, in particular preventing the successful recruitment of native plant species and thus limiting habitat restoration (Brandle 2001). Very few critical weight range (35 - 5500 g; Burbidge and McKenzie 1989) native mammals were known to be extant within the park at the commencement of this study, with exceptions including the short-beaked echidna (*Tachyglossus aculeatus*) and the western quoll (*Dasyurus geoffroii*), the latter reintroduced to the Park one year earlier than possums (Natural Resources SA Arid Lands 2017). Similarly, smaller mammal species have also declined or become locally extinct, with few native mammal species now present including (but not limited to) dunnarts (*Sminthopsis* spp.) and several microbats (Order: Chiroptera). Introduced mammals found within the IFRNP today include rabbits, feral cats, goats (*Capra hircus*), house mice (*Mus domesticus*) and, occasionally, foxes and domestic sheep (*Ovis aries*).

The Department of Environment and Water (DEW, formerly DEH and DEWNR) initiated the Bounceback Project in the Park in the early 1990s (Bounceback 2012). The project involved the control of feral herbivores (goats and rabbits) and predators (foxes and feral cats), as well as some invasive weeds. Thousands of feral herbivores were removed, along with native Euros, but none were eradicated, and they continue to impact vegetation within the park. Annual culling of goats is ongoing. Foxes have been successfully controlled using aerial baiting, and this led to the local recovery of the yellow-footed rock wallaby (*Petrogale xanthopus*), a species listed as Vulnerable at both a state (National Parks and Wildlife Act 1972) and national (EPBC Act 1999) level. The apparent success encouraged a trial reintroduction of brush-tailed bettongs (*Bettongia penicillata*) in 1999, that ultimately failed (Bellchambers 2001). The introduction of aerial baiting that successfully controlled foxes combined with the reduction in browsing pressure from introduced herbivores led to a proposed trial reintroduction of the western quoll and brushtail possum in 2014 and 2015 respectively. The reintroduction of the brushtail possum to the park is the focus of this thesis.

The brushtail possum is known as the ‘virlda’ to the Adnyamathanha people of the Flinders Ranges (Tunbridge 1991). The species holds spiritual importance as well as being an important food source. Virlda also provided fur that could be used to make clothing, blankets, and string (Tunbridge 1991). Older Adnyamathanha people remember the virlda being abundant and on moonlit nights they would sing a possum hunting song to ensure a good catch (Tunbridge 1991). The reintroduction of possums to the IFRNP brings cultural and social benefits as well as the potential positive conservation outcomes; despite the importance of the virlda to the Adnyamathanha people, many living today have not seen a possum in the wild.

Possums are thought to have gone extinct in the IFRNP between the 1920s and 1940s (Tunbridge 1991; Kerle *et al.* 1992), with unconfirmed sightings in 1963 (Wilpena), 1989 (Prelinna Ford) and 1990 (Wilpena) (Tunbridge 1991; Kerle *et al.* 1992). The nearest extant possum population to the IFRNP is found in the southern Flinders Ranges, around towns such as Quorn, Wilmington and Melrose. In farmland, populations appear somewhat restricted to creeklines, where hollows are plentiful and tree canopies are reasonably well connected (pers. obs), reducing the need for possums to come to ground regularly, where predators may be encountered. Possums can also be found in peppermint box (*Eucalyptus odorata*) grassy woodlands in the region (pers. obs.), a Threatened Ecological Community (EPBC Act 1999). Recent surveys suggest their distribution within the area is likely to be patchy (pers. obs.; Menadue 2014).

1.5 REINTRODUCTION OF POSSUMS TO IFRNP

A radio-collared brushtail possum, translocated to the IFRNP in 2016.

This thesis comprises of research conducted during the reintroduction of brushtail possums to the Ikara-Flinders Ranges National Park. The reintroduction was undertaken via a partnership between the Department for Environment and Water (DEW) and funding provider the Foundation for Australia's Most Endangered Species Inc. (FAME). The reintroduction provided an opportunity to experimentally test theories of reintroduction biology, restoration ecology and dispersal biology, and this thesis summarises these findings.

Four possum releases occurred over a period of four years—three of the releases are incorporated into this study (Table 1.3, Fig. 1.3). In 2015, possums were first reintroduced to the Park, and various release methods were experimentally trialled, with 48 animals radio-collared. Possums were sourced from Yookamurra Wildlife Sanctuary (Fig. 1.3), a fenced reserve owned by the Australian Wildlife Conservancy, in which mammalian predators are excluded (Australian Wildlife Conservancy 2018). The results from the first release in 2015 guided the release techniques used for subsequent releases. In 2016, the influence of previous exposure to predators on post-release survival was investigated, with 20 animals radio-collared. Possums were sourced from both Yookamurra Wildlife Sanctuary (predator-naïve) and the southern Flinders Ranges (predator-exposed, Fig. 1.3), where feral cats and foxes were present. Walking spotlight transects were conducted to facilitate population estimates for both source sites prior to the removal of any possums, indicating the number of possums that could be taken from each source (Ecological Horizons, unpub. data). In 2018, an additional 51 possums were translocated from Kangaroo Island (Fig. 1.3), where feral cats but not foxes are present; the final translocation involved no intensive post-release monitoring and does not form part of this thesis. In total, 199 possums were translocated to the IFRNP between 2015 and 2018 (Table 1.3).

Table 1.3: The source and predator treatment for brushtail possums translocated to the IFRNP. *translocation and results not part of this thesis.

Year	Source	Treatment	No. of possums
2015	Yookamurra Wildlife Sanctuary	Predator-naïve	79
2016	Southern Flinders Ranges	Predator-exposed	19
2016	Yookamurra Wildlife Sanctuary	Predator-naïve	50
2018	Kangaroo Island*	Predator-exposed	51

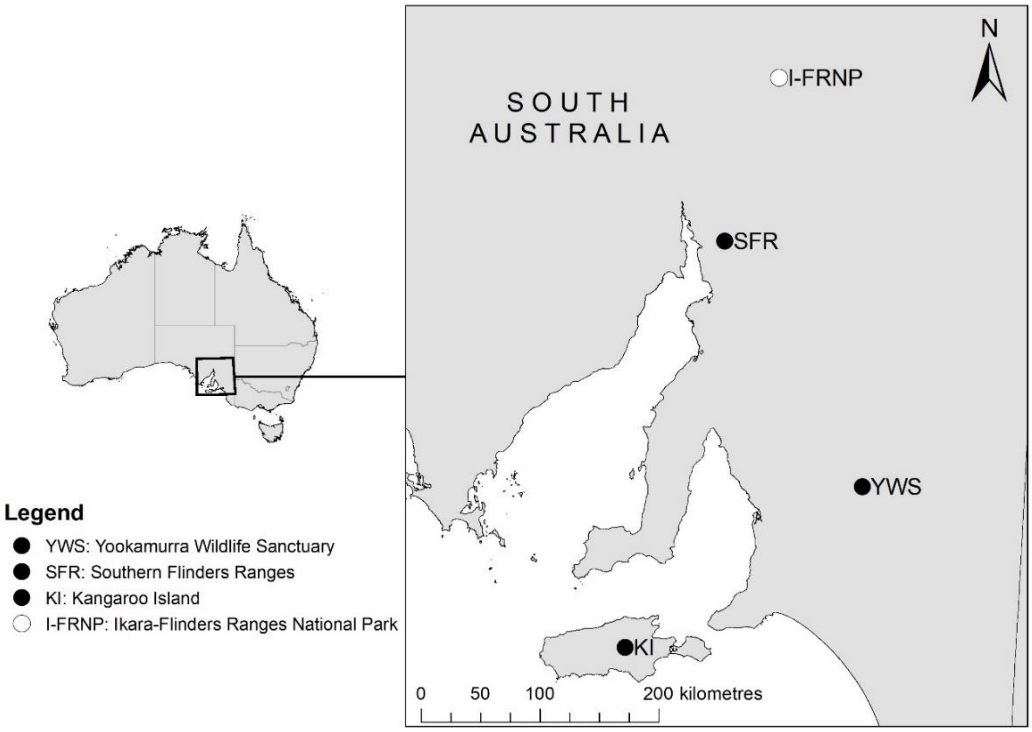

Figure 1.3: Three South Australian sites used as source populations for possums translocated to the IFRNP.

2. RELEASE METHODS

Supportive release techniques provide no reintroduction benefit when efficacy and uptake is low

Immediate release, nest-box release and delayed release methods

2.1 CONTEXTUAL STATEMENT

Few translocations or reintroductions of brushtail possums have been undertaken for conservation purposes, and experimental manipulations to investigate methods of improving translocation outcomes for the species have not been explored. Release methods are known to influence survival, dispersal, body mass and reproduction in some circumstances, but in others can have no effect or can even have the opposite effect to that desired (Bright and Morris 1994; Hardman and Moro 2006; Moseby *et al.* 2014). Previous possum releases have encountered poor post-release survival as well as hyperdispersal away from release sites (Copley 1995; Pietsch 1995; DEC 2012), therefore the identification of methods to improve post-release survival and limit dispersal are needed for future wild-to-wild translocations to succeed. Chapter two experimentally tested the influence of three release methods (immediate, delayed and nest-box) on the post-release dispersal, body mass, reproduction and survival of reintroduced brushtail possums in the Ikara-Flinders Ranges National Park. Results were obtained by monitoring 48 radio-collared possums (8M, 8F per treatment) using radio-tracking and regular trapping over a three month period. This chapter has been published in the journal *Oryx*.

2.2 STATEMENT OF AUTHORSHIP

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Author contributions

By signing the Statement of Authorship, each author certifies that the stated contributions to the publication are accurate, and that permission is granted for the candidate to include the publication in the thesis.

Primary author	Hannah Bannister		
Contribution to the paper	Designed the experiment, collected data, analysed the data and prepared the figures, wrote the manuscript and responded to reviewer comments.		
Overall percentage	75 %		
Signature		Date	24/12/2018

Co-author	Robert Brandle		
Contribution to the paper	Assisted with experimental design, assisted with data collection, reviewed the manuscript.		
Signature		Date	6/1/2019

Co-author	David Paton		
Contribution to the paper	Assisted with experimental design, reviewed the manuscript.		
Signature		Date	7/1/2019

Co-author	Steven Delean		
Contribution to the paper	Analysed data and assisted with the preparation of figures, reviewed the manuscript.		
Signature		Date	14/01/2019

Co-author	Katherine Moseby		
Contribution to the paper	Assisted with experimental design, data collection, advised on and reviewed the manuscript.		
Signature		Date	21/01/2019

2.3 ABSTRACT

Release methods can influence the outcome of reintroductions. We tested the effect of delayed, immediate and supplementary food/shelter release treatments on the reintroduction success of brushtail possums *Trichosurus vulpecula* in an environment where introduced predators, particularly foxes (*Vulpes vulpes*), were subject to control. Monitoring of 48 radio-collared possums over three months revealed that immediate release possums settled into a stable range significantly faster than other groups, but there were no differences in survival, dispersal distance, reproduction or body condition. Ten days after release possums from all treatment groups had lost body mass, but by day 60 most were heavier than at the time of translocation. After release, possums sometimes used shelter sites easily accessible to predators, but within three weeks they regularly selected safer shelter. Risky shelter selection and loss of condition immediately after release suggests that supplementary food and shelter could be beneficial, but supportive measures were rarely used or did not have the desired effect. In an environment with higher predator densities, risky shelter selection could lead to high post-release predation, and mass loss could encourage animals to forage in riskier ways, further increasing vulnerability. In these environments, effective uptake of supplementary food and shelter could reduce predation risk, but supplementary measures would need to be presented in a way that maximises uptake. In contrast, if post-release predation risk is low then supportive measures may not be required. Innovative methods for providing post-release support should continue to be developed for reintroductions to areas where supportive measures are needed.

Keywords: brushtail possum, reintroduction, release method, supplementary feeding, translocation, *Trichosurus vulpecula*

2.4 INTRODUCTION

Reintroductions are increasingly used as a tool to reverse the decline of threatened species. The method of release has the potential to influence a reintroduction outcome. Post-release supportive measures often include temporary confinement (delayed release), protection from predators or the provision of supplementary food or shelter. Delayed releases theoretically enable animals to acclimatise to a new environment before having to locate their own food and shelter (Scott and Carpenter 1987) and have been associated with smaller dispersal distances and higher survival compared to immediately released animals for some species (Bright and Morris 1994; Mitchell *et al.* 2011; Knox and Monks 2014). Small dispersal distances aid in retaining animals within an area where other factors, such as introduced predators, may be more effectively controlled (Rickett *et al.* 2013). Some studies, however, report no differences between the survival or dispersal of delayed and immediate release animals (Hardman and Moro 2006), or found lower reintroduction success with delayed releases than immediate releases (Thompson *et al.* 2001; Richardson *et al.* 2015). The source of animals for translocation (wild v captive-bred) may influence the effectiveness or necessity for alternative release methods (Fischer and Lindenmayer 2000; Moseby *et al.* 2014). Many studies reporting the outcome of delayed release methods have no control treatment (e.g. Pietsch 1995; Poole and Lawton 2009). Furthermore, the provision of supportive measures is often assumed to result in uptake, but is not often monitored. Delayed releases hold intuitive appeal but sometimes offer little benefit. Using reintroductions as experiments is essential to advance the science of reintroduction biology (Seddon *et al.* 2007; Swaisgood 2010).

Brushtail possums *Trichosurus vulpecula* (hereafter 'possums') are a medium-sized (1 - 4 kg, Kerle *et al.* 1991), predominantly arboreal mammal once widespread throughout most of Australia, but now present in less than 50% of their historic range (Kerle *et al.* 1992; Kerle 2001). Their decline is thought to be a result of a combination of factors including predation by introduced predators (red foxes *Vulpes vulpes*, feral cats *Felis catus* and dingoes *Canis lupus dingo*), habitat alteration, the impacts of introduced herbivores, hunting, disease and drought (Kerle *et al.* 1992). In locations where foxes have been successfully controlled, remnant possum populations have increased (How and Hillcox 2000; Burrows and Christensen 2002). We used a trial reintroduction of the species in southern Australia to test the effect of post-release support on reintroduction outcomes.

Several possum translocations have been undertaken previously, but they have rarely been used to advance reintroduction protocols for the species and the outcomes were often unknown or unsuccessful (Supplementary data S10.2.1). Furthermore, only nine of 21 (43%) reported possum translocations included post-release monitoring of any kind, and only six of those monitored post-release dispersal. Hyperdispersal (long distance movement away from release sites) was reported on all occasions for possums undergoing both immediate and delayed release, when dispersal was monitored. With predation a major contributor to failed possum translocations (Pietsch 1995; DEC 2012), retaining released animals at a predator-controlled release site may improve reintroduction success—an effective delayed release method could therefore be useful for translocated possums. The non-research driven approaches of most previous possum translocations are evident, and few attempts have been made to rigorously test methods to improve post-release survival or limit dispersal, despite both being problematic previously. In addition, no experimental comparisons have been made of delayed and immediate release methods for possums.

In the Ikara-Flinders Ranges National Park (IFRNP), foxes have been subject to intensive control since 1993 (DEWNR 2012), and because of this the reintroduction of possums was considered feasible. Expected low predation risk at our unfenced release site, combined with the relatively solitary, sedentary behaviour of possums suggests that an immediate release with supplementary food and shelter would be most effective (Moseby *et al.* 2014). Hyperdispersal has been identified as a problem previously, however (Supplementary data S10.2.1). Based on this, we tested the influence of various combinations of supplementary food, shelter and temporary containment on the post-release survival, movement, reproduction, and change in body mass of possums reintroduced to the IFRNP.

2.5 METHODS

2.5.1 Study area

Brushtail possums were sourced from the 11 km^2 fenced, introduced predator-free section of Yookamurra Wildlife Sanctuary (34° 32' 22" S, 139° 28' 33" E; Fig. 2.1), a conservation reserve run by the not-for-profit organisation Australian Wildlife Conservancy. The area receives 339 mm of rain annually (Station 24581, Bureau of Meteorology 2017) and the vegetation is predominantly old growth mallee (*Eucalyptus* spp). Possums were reintroduced to the 934 km^2 Ikara-Flinders Ranges National Park (IFRNP, 31° 31’43” S, 138° 36’ 13” E), approximately 400 km NNW of the source population (Fig. 2.1), where they became regionally extinct around the 1940s (Tunbridge 1991). Several habitat types are found in the park, including *Eucalyptus camaldulensis* dominated creeklines, open eucalypt (*E. camaldulensis* / *E. intertexta*) and/or *Callitris glaucophylla* woodlands, mallee (*Eucalyptus* spp) and mixed species (woodland / shrubland) rocky slopes or creeklines. Vegetation condition was good, with known favoured food plants available (*Eucalyptus* spp, *Acacia* spp, mistletoe (Loranthaceae family) and others (Kerle 1984)). Tree hollows are the most common form of diurnal shelter for possums (How and Hillcox 2000; Isaac *et al.* 2008), and release sites were limited to eucalypt dominated creekline and woodland habitats, where tree hollows were more abundant (H. Bannister and K. Moseby, pers. obs.). Average annual rainfall at the release area was 440 mm (Station 19070, Bureau of Meteorology 2017).

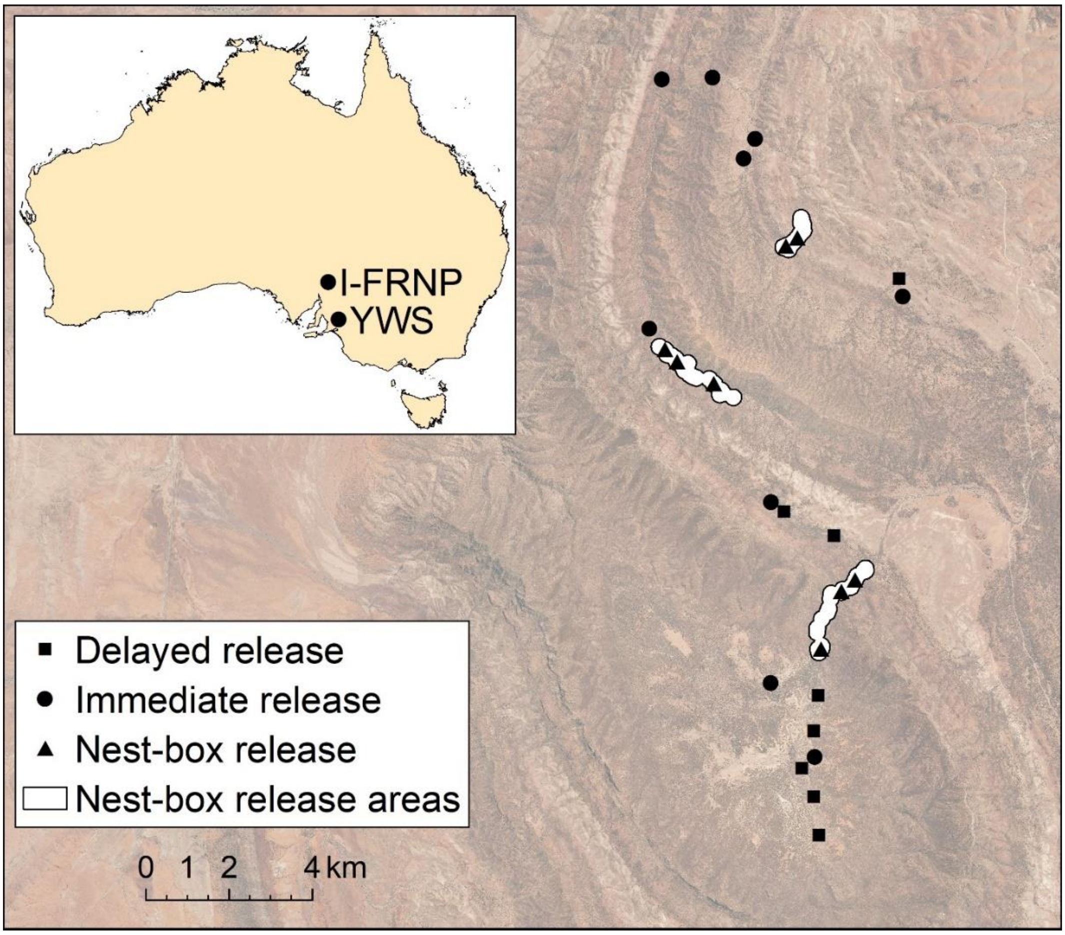

Figure 2.1: The source (YWS, Yookamurra Wildlife Sanctuary) and release locations (IFRNP, Ikara-Flinders Ranges National Park) for translocated radio-collared brushtail possums within Australia (inset), and the spatial arrangement of release sites within the IFRNP.

In the six months prior to the reintroduction, twenty-four remote cameras were deployed across an area of 47 km^2 within IFRNP, encompassing more than half of the release areas. Cameras were positioned at least 1 km apart, and detectios of the same species within a 10 min period were not counted unless it was obviously a different individual (based on markings/size etc.). Averaged camera trap detection levels were 0.02% for foxes (detected by one camera), 0.8% for feral cats (detected by 75% of cameras) and 4.2% for dingoes (detected by 58% of cameras) (DEWNR and Ecological Horizons, unpub. data). All three predators are known to influence possum populations (Kerle *et al.* 1992) and are subject to regular control within the park. Importantly, foxes are only detected a handful of times each year (DEWNR 2012).

2.5.2 The reintroduction

Seventy-nine brushtail possums were translocated from Yookamurra Wildlife Sanctuary to the IFRNP in June 2015. Possums were captured either in cage traps, nest-boxes or with nets (authors, unpub. data). Prior to their translocation, all possums underwent health checks under anaesthetic. Morphometric measurements (body mass and head, *pes* and testes length) and reproductive condition were assessed, and possums were given a unique microchip and ear tag. Forty-eight possums had VHF radio-collars fitted (V5C-161E, 35 g or V5C-162E, 41 g, Sirtrack, New Zealand), with mortality sensors that would activate after 10 h of inactivity. Female possums either had small pouch young or vacant pouches. Of the 48 collared possums (24 F, 24 M), two females and five males were subadults—the remainder were adults. Possums were transported inside soft bags inside wooden boxes, or loose inside nest-boxes. The vehicle journey took 6 h and possums were released less than 24 h after capture.

Sixteen radio-collared possums (eight male, eight female) were released in each of three release treatments. These involved either supplementary food (kangaroo pellets, apple, dates, peanut butter and rolled oats), shelter and containment within a fenced pen (“delayed release”), supplementary food and shelter without containment (“nest-box release”) or no post-release support (“immediate release”). All possums were released in randomly assigned pairs (one male and one female) and all releases occurred after dark. Releases of collared possums occurred over two nights.

2.5.3 Delayed release

Delayed release pens measured 10 x 10 m, with a fence height of 1.8 m. A 90 cm strip of thick plastic fixed to the inside of the fence on the upper half was designed to prevent possums from climbing out and a floppy top prevented other animals entering (Moseby and Read 2006). Each pen contained a large tree (some with natural hollows) and two nest-boxes hung approximately 3 m above the ground, as well as hollow logs and/or a wood pile. Supplementary food and water was provided *ad libitum*, presented in a planter box fixed to a tree, in a pet food dish on the ground (monitored via remote camera, Reconyx HC600 Hyperfire) and scattered throughout the pen; some natural food (*E. camaldulensis* and/or *C. glaucophylla*) was also available. Food was replaced late in the day. Pen gates were opened after 11 nights and remote cameras were positioned so that they recorded animals entering or exiting pens. Food continued to be provided inside pens daily for another ten days, then every 2–3 days for another week.

2.5.4 Nest-box release

Prior to the release, empty nest-boxes (28 x 28 cm base, 41 cm (front) to 46 cm (back) height, entrance diameter 11 cm) were hung 50–100 m apart in some creeklines and adjacent areas, creating three separate nest-box release areas of 850–2050 m in length, and nest-boxes containing possums were hung within these areas (Fig. 2.1). All nest-boxes were hung at a height of approximately 3 m. Two nest-boxes containing possums (one possum per box) were hung on adjacent trees at each release location. Possums released in nest-boxes were either animals that were already using nest-boxes at the source site (*n* = 7), where 50 nest-boxes had been installed seven months prior to the translocation, or were captured and placed in nest-boxes prior to translocation (*n* = 9) due to an insufficient number of possums using nest-boxes at the source location. Supplementary food was provided on top of all nest-boxes for the same duration of time that food was provided to delayed release possums. As many nest-box release possums dispersed outside nest-box release areas, they were left a small amount of food either at the base of their shelter tree or approximately 30 cm into the entrance of their shelter site, if accessible, when radio-tracked. This occurred around every four days, during the time when delayed release possums were receiving supplementary food daily. Remote cameras were used to monitor the use of five randomly selected nest-boxes for up to two months.

2.5.5 Immediate release

Immediate release possums were released in pairs at the base of two adjacent hollow-bearing eucalypts. They did not have access to supplementary food or shelter.

2.5.6 Monitoring

Radio-collar signals were checked every 1–3 days for the duration of the study and mortalities were investigated immediately upon discovery. Possums were radio-tracked to their diurnal shelter site weekly (at minimum), with few exceptions. Each shelter site was given a safety score of 1–3, where 1 was accessible to mammalian predators (at ground level and easily visible to the observer) and 3 was considered safe (a tree hollow well above the ground), similar to May *et al.* (2016). Moderately safe shelter sites given a safety score of 2 were typically hollow logs, rabbit warrens or rock crevices, where possums could have been accessed by a predator but with difficulty. Treadle-operated cage traps were set for radio-collared possums at their shelter sites approximately 10 (±1 day), 20 (±2), 32 (±3), 60 (±3) and 86 (±8) days post-translocation using standard cage trapping procedures (Petit and Waudby 2012). Body mass was measured using 2 kg (± 0.02) or 5 kg (± 0.025) spring scales and the reproductive status of females was assessed by recording the size of any pouch young, teat condition and pouch staining. Intensive monitoring and post-release comparisons are reported for a three-month period. We considered that differences after this initial period were unlikely to be related to release methods.

2.5.7 Data analysis

Distance from release site was compared over 12 consecutive weeks from release using a generalised additive mixed model (GAMM) with a temporal correlation structure and an identity link. For delayed release possums, release time was when pens were opened. Release treatment was a fixed effect and repeated measures on individual possums were accounted for as a random effect. Distances were log-transformed to meet the model assumptions of normality and constant variance, and we added one to each distance in order to retain data for individuals that were sheltering at their release site (distance = 0 metres). The final dispersal distance of possums once settled (week 6) was compared between treatment groups.

To determine post-release changes in body mass, the difference between mass at release and at the time of recapture was calculated and divided by the release mass, then multiplied by -1, to give a proportional change in body mass. Negative values indicated mass loss and positive values indicated mass gain. Body mass was adjusted for radio-collars and pouch young mass, using approximate values from Gemmell and Hendrikz (1993). Delayed release possums were still in pens when captured and weighed at day 10. A linear mixed-effects model (LME) was used to test for differences in change in mass between treatment groups, with treatment, sex and time as fixed effects and individual as a random effect.

Shelter site safety scores were converted to binary values, where a score of 3 was safe and 1 or 2 was unsafe as possums were accessible to predators. Time period 1 (T1) was the first 10 days after release for immediate and nest-box release possums, and the first 10 days after pens were opened for delayed release possums. A binomial generalised linear mixed-effects model (GLMM) with a logit link was used to analyse the effect of treatment and time on the proportion of safe shelter sites used per time period (T1–T9), with individual included as a random effect.

All analyses were carried out using R (R Development Core Team 2018). GAMMs and LMEs were constructed within the package 'mgcv' (Wood 2011) and model selection statistics were calculated using 'MuMIn' (Barton 2016). GLMMs were constructed with the package 'lme4' (Bates *et al.* 2015). Statistical significance was assessed using Wald tests with the package 'car' (Fox *et al.* 2016). Contrasts were calculated using least-squares means with the package 'lsmeans' and summary statistics were calculated using 'doBy' (Højsgaard 2016).

2.6 RESULTS

2.6.1 Survival and shelter site safety

During the initial post-release period, many possums chose unsafe, exposed diurnal shelter sites (Fig. 2.2). Despite this, there was no significant difference in survival between treatment groups. One immediate release female died during the study period, 77 days after release. The cause of death remains unknown despite a post-mortem and testing for predator DNA. The deaths of two other possums during the study period was related to collar design (Moseby and Bannister 2016). The proportion of unsafe shelter sites used by possums changed significantly over time ($\chi^2 = 13.81$, $df = 4$, $p = 0.0079$; Fig. 2.2), but did not vary between release treatments ($\chi^2 = 0.14$, $df = 2$, $p = 0.93$) or with treatment over time ($\chi^2 = 6.69$, $df = 8$, $p = 0.57$). Of nine observation periods (T1–T9, 10 days each), four (T4, T6, T7 and T8) were removed from the analysis because a lack of variance within treatments prevented model convergence. Plotting these values suggested this would not significantly affect the results, as safety scores had almost stabilised by T3. Contrasts of least-squares means revealed no significant difference in safety scores between T1 and T2 ($z = 1.2$, $p = 0.55$), and a trend towards a difference between T1 and T3 ($z = 2.4$, $p = 0.056$), while T1 was significantly different to all subsequent time periods (T1:T5 $z = 3.1$, $p = 0.0074$, T1:T9 $z = 2.7$, $p = 0.028$). Possums were therefore significantly more likely to use unsafe shelter in the first twenty days after release compared to subsequent times. The use of unsafe shelters after T2 was mostly a small number of individuals that showed a preference for hollow logs rather than tree hollows.

2.6.2 Post-release dispersal

Immediate release possums settled quickly, within the first week after release (F = 1.30, edf = 1.0, p = 0.26), whereas delayed and nest-box release possums took significantly longer (nest-box release F = 5.18, edf = 2.38, p = 0.0026; delayed release F = 23.62, edf = 7.65, p = <0.0001, Fig. 2.3). However, there was no significant difference in the overall dispersal distance between treatment groups (Table 2.1). Six weeks after release, when possums in all treatments had settled, dispersal distances ranged from 0.08 km to 17.02 km, with a mean distance from release site of 1.03 km (range 0.09–4.09 km) for immediate release, 2.68 km (range 0.11–17.02 km) for nest-box release and 1.49 km (range 0.08–4.88 km) for delayed release possums. Seven out of 44 radio-collared possums in the study (16%) hyperdispersed, travelling more than three times the mean range length reported in previous arid/semi-arid studies (mean = 0.88 km, Foulkes 2001; Short and Hide 2014) before settling (Supplementary data S10.2.1). Release treatment had no influence on hyperdispersal (χ^2 = 1.19, df = 2, p = 0.55). Encouragingly, 61% of possums remained within 1 km of their release site six weeks after release.

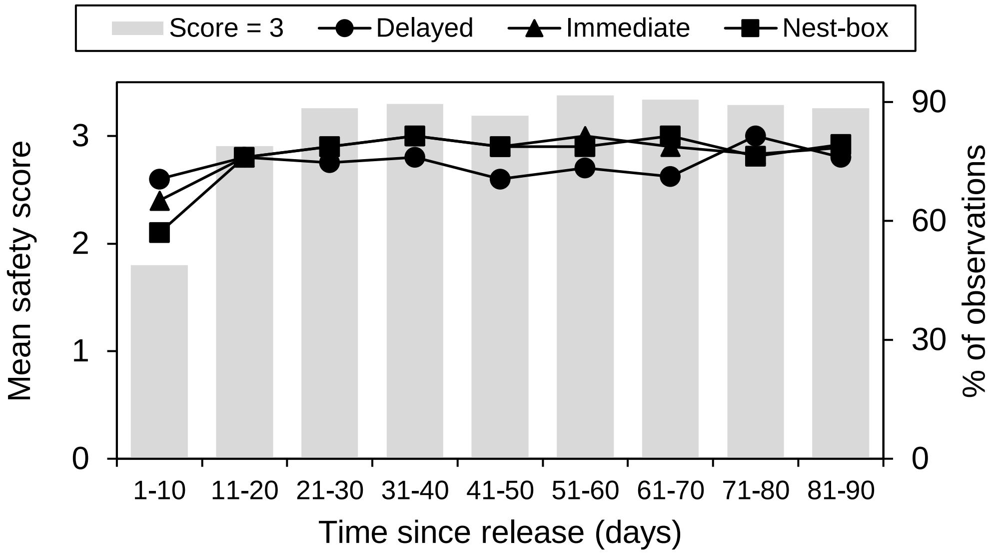

Figure 2.2: The proportion of possums using safe shelter sites at various times after release, with 95% confidence intervals. The interval between each time period was 10 days.

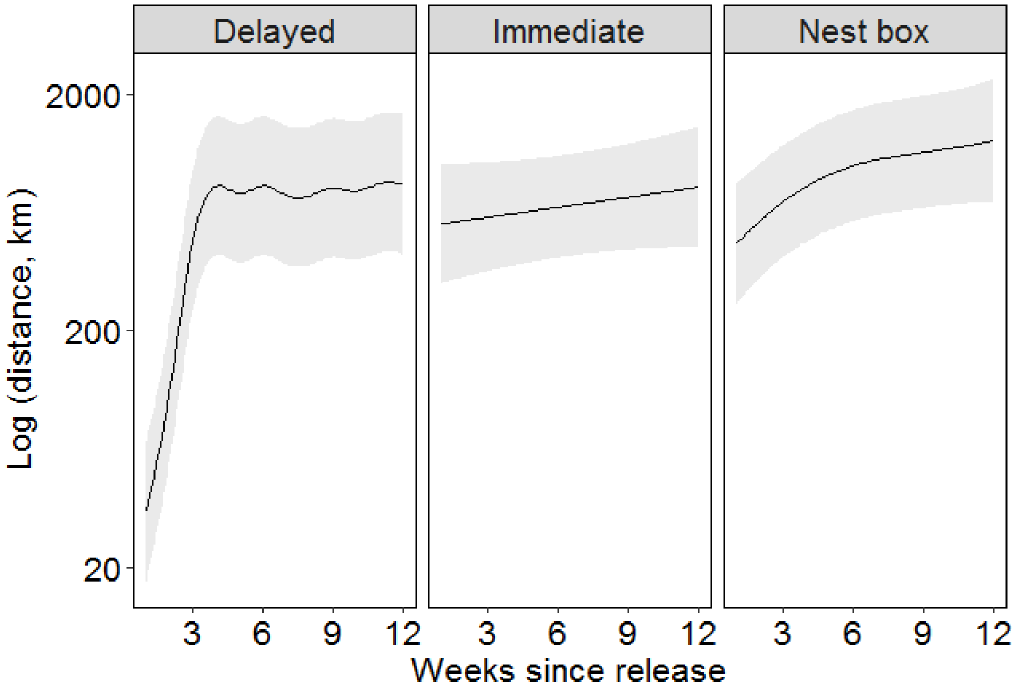

Figure 2.3. Estimated distance from release site for possums in three release treatments over time, with 95% confidence intervals. Delayed release time zero was when release pens were opened.

Table 2.1: Generalised additive mixed model coefficients contrasting the mean dispersal distance of possums by treatment group, six weeks after release.

Contrast	s.e.	*t*-value	*p*-value
Immediate v nest-box	0.36	0.83	0.41
Immediate v delayed	0.39	0.82	0.41
Nest-box v delayed	0.39	1.58	0.12

2.6.3 Body mass

At the time of translocation, the mean body mass of radio-collared possums was 1577 g (s.e. ± 38) and did not significantly differ between sexes (Wilcoxon rank sum test, $W = 292$, $p = 0.94$) or treatment groups (Kruskal-Wallis rank sum test, $\chi^2 = 5.06$, $df = 2$, $p = 0.08$). The mass of translocated possums changed significantly over the post-release monitoring period ($\chi^2 = 162.42$, $df = 1$, $p = <0.0001$), but there was no difference between treatment groups ($\chi^2 = 0.14$, $df = 2$, $p = 0.93$) and no significant interaction between treatment and time ($\chi^2 = 0.06$, $df = 2$, $p = 0.97$; Fig. 2.4). Most (83%) of the possums in delayed release pens lost mass after release. Around half of all possums (44%, 45% and 56% of nest-box, delayed and immediate release recaptures respectively) had lost more than 10% body mass 10 days after release, and 20 days after translocation 82% ($n = 39$) of recaptured possums had lost mass. However, 60 days after release, most possums (82%, $n = 17$) in all treatments were heavier than their translocation mass. Males gained mass at a faster rate than females ($\chi^2 = 11.67$, $df = 1$, $p = 0.00063$, Fig. 2.4). Owing to differences in trap success between individuals, not every possum was successfully captured for each sampling period.

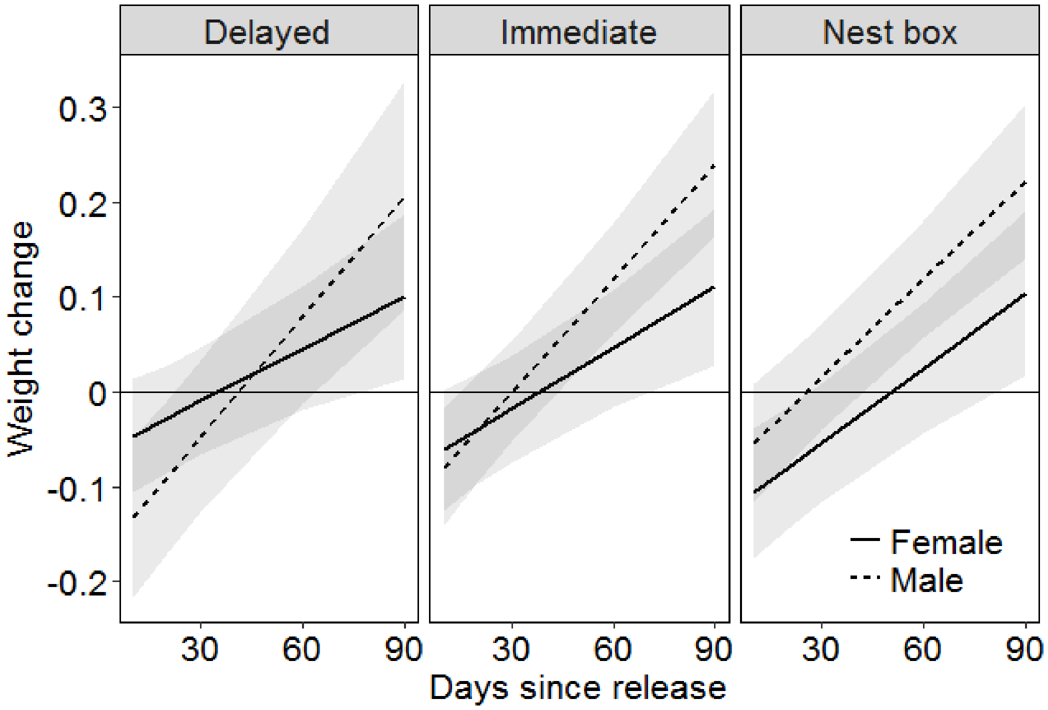

Figure 2.4: Estimated proportional change in body mass, with shaded 95% confidence intervals, over five sampling periods (day 10, 20, 32, 60 and 86) for translocated brushtail possums, starting at day 10, for three release treatment groups. Mass change at time 0 (translocation) was zero. Note—the first sampling period for delayed release possums (day 10) was when they were still contained in release pens.

2.6.4 Reproduction

Release method did not influence female reproduction. Seventy-five percent, 100% and 63% of radio-collared females (immediate, nest-box and delayed release respectively) had pouch young prior to translocation and all were retained post-release. Additionally, females from each of the release treatments gave birth during the three-month study period (at least four delayed release females, one uncollared immediate release female and one nest-box release female). Only three radio-collared females (two immediate release and one delayed release) did not have pouch young at any time during the study.

2.6.5 Release techniques

Four males escaped delayed release pens (on nights one (*n* = 1), three (*n* = 2) and four (*n* = 1)) and were not included in subsequent analyses. The first day post-release, only one delayed release possum was sheltering in a safe location, in a nest-box. The remainder sheltered in more vulnerable locations—in hollow logs, under wood piles, in the open or at the top of a tree. In pens where natural hollows were present, possums took two (*n* = 5) or three (*n* = 3) nights to first use a tree hollow, with an eighth possum never using available tree hollows. Where nest-boxes were the only above ground shelter available, only one of three possums used one. Within pens, possums mostly sheltered in hollow logs/woodpiles (49%) or tree hollows (35%), occasionally using a nest-box (9%) or sheltering in the open (7%). Shelter sites were not dominated by larger animals or one particular sex, and possums were recorded sharing shelter on 47% of occasions where two animals remained in a pen. When contained in pens possums ate some of the supplementary food provided, but once pens were opened most used them for shelter rather than a food source, venturing outside the pen at night. Five of twelve possums left their pen on the first night it was open; the remainder took 2–9 nights (mean = 3 nights). Half of the possums used diurnal shelter sites inside the pen for up to 18 days (mean = 7 days) after the pens were opened, while two others sheltered outside the pen but returned for up to ten days after supplementary food ceased to be provided. In nest-box release areas, possums were detected a total of six times at three of the five nest-boxes that were monitored by remote camera over two months after release (256 camera trap nights, 2.3% trap success), eating supplementary food but not using the boxes as shelter. No radio-collared possums from any treatment were found using nest-boxes in nest-box release areas after the first night post-release.

2.7 DISCUSSION

Supportive release methods, including delayed release pens and nest-box release areas with supplementary food, did not provide tangible benefits to translocated brushtail possums at our study site. There was no significant difference in the survival, reproduction, change in mass, or dispersal distance of possums between release treatments, but immediate release possums settled fastest. The control of introduced predators, especially foxes, likely contributed to the high survival of possums; we recorded no predation within the first three months, in contrast to translocations at three other unfenced sites where 42%, 74% and 15% of released possums were killed by introduced predators (foxes/feral cats) shortly after release (Pietsch 1995; DEC 2012; May *et al.* 2016). The mitigation of threatening processes, particularly introduced predators, is considered a key factor in many successful reintroductions (Brambell 1977; Bellingham *et al.* 2010; Moseby *et al.* 2011), and our results support this.

While nest-boxes are readily used by brushtail possums in areas where natural hollows are limited (Harper *et al.* 2005; Lindenmayer *et al.* 2015), they were not used by possums in our study, suggesting natural shelter sites were plentiful. Further to the current study, no radio-collared possums were found to use nest-boxes as shelter in the 22 month period after release (unpub. data). Nest-box use may be influenced by nest-box height, orientation, dimensions, entrance size, temperature or low encounter rates, or simply a preference for natural hollows (Isaac *et al.* 2008; Goldingay 2015; Le Roux *et al.* 2016). The use of ground-level shelters such as hollow logs and woodpiles inside release pens instead of nest-boxes suggests that nest-box design, placement or accessibility may have influenced use. Despite the presence of natural hollows as well as nest-boxes (in some areas), many possums chose unsafe, exposed shelter during the initial post-release period, gradually improving shelter choice over time. Similar behaviour has been observed for other possum translocations (Pietsch, 1995; Short & Hide, 2014). We suggest that had predator numbers been higher or foxes been present we may have observed a high mortality rate during this acclimation phase. In that situation, easily accessible supplementary shelters may have been beneficial, yet possums in nest-box release areas did not use nest-boxes for shelter, and possums released in nest-boxes did not subsequently return to them.

Haylock (2008) found that possums captured from *in situ* nest-boxes made long distance movements upon release and did not return, even when the nest-box was known to be a preferred shelter site previously. Possums in our study may have responded similarly. Despite the availability of suitable shelter, some possums still required an acclimation period in their new environment before sheltering safely.

Because of this, predator management should be heavily concentrated around the time preceding and immediately following a possum translocation, and future translocations should consider the predation risks associated with this settlement phase.

Supplementary feeding did not influence body mass in possums, nor did it reduce dispersal distance. Similarly, supplementary feeding had no effect on the post-release mass of translocated mala *Lagorchestes hirsutus* or eastern bettongs *Bettongia gaimardi* (Hardman and Moro 2006; Batson *et al.* 2015). The combination of initial mass loss and poor shelter site choice by possums suggests that supplementary food and shelter might be beneficial immediately after release, particularly if predators are present, however neither were effective in our study—the available supplementary shelter was not used, supplementary food was rarely consumed when alternatives were available and it did not prevent loss of mass. The appeal or efficacy of these supportive measures must be improved for them to be of benefit to reintroduced animals in environments where post-release predation risk is high. In our study, temporary containment and supplementary food provided no discernible benefits for translocated possums, and immediate release possums settled the fastest. For this reason, combined with low post-release predation risk, an immediate release was the most suitable reintroduction method for possums in the IFRNP.

The absence of existing possum populations at release sites may have contributed to translocation success, as releasing possums into areas with an existing population has previously been linked to hyperdispersal and translocation failure (Pietsch 1995; Clinchy 1999). Immediate and nest-box release possums had an opportunity to disperse and settle earlier than delayed release possums (initially contained in pens), so it is possible that uncollared animals had dispersed to areas surrounding pens in this time. However, intensive, regular trapping combined with having a large proportion of the population radio-collared suggests this was unlikely. An absence of possums in the wider reintroduction area could, in contrast, have contributed to the delay in possums using suitable natural hollows. While possums are not highly social, they have overlapping home ranges and different possums sometimes use the same shelter site at the same or different times (Cruz *et al.* 2012a; H. Bannister, pers. obs.). The scent of conspecifics may encourage possums to use suitable shelters sooner, or to settle into a new area without feeling isolated, but this has not yet been explored. To date, the influence of resident possums on translocation success has not been experimentally tested.

Stress is an unavoidable component of translocations and although not monitored in our study, may have contributed to post-release mass loss or hyperdispersal (Moberg 2000; Dickens *et al.* 2010). Stress has been identified as a concern for captive possums (Presidente 1984; Baker and Gemmell 1999). However, immediate and nest-box release possums lost mass along with delayed release possums, suggesting that if stress was a factor then it affected the mass of all treatment groups equally. Radio-collars may have also initially caused possums to become stressed. Along with stress, mass loss probably resulted from possums having to locate new food and shelter sources or adapting their diet to their new environment. Because mass was relatively rapidly regained (and subsequently increased), mass loss and possibly stress ultimately did not affect the reintroduction outcome.

In environments where post-release predation risk is high, the use of risky shelters and post-release mass loss may necessitate the provision of supplementary food and shelter. Delayed release experiments typically follow similar formats and reintroduction biology has not yet explored novel ways of increasing the appeal and subsequent use of supplementary items. Future reintroductions should trial various ways of presenting post-release support, with the potential to improve reintroduction success for a suite of species. Encounter rates with nest-boxes and natural hollows shortly after release could be improved by conducting an experiment whereby a fence is erected around the base of a hollow-bearing tree prior to the release of a possum, removing it once it had climbed the tree, or after just one night, preventing possums from immediately moving off along the ground and sheltering in unsafe locations. This method would not involve containing the possums for several days as occurred with the delayed release, but would admittedly be labour intensive. Additionally, the influence of the scent or presence of conspecifics could be investigated. Nutritious, native supplementary food may have had a positive effect on mass compared to the non-native and sometimes processed supplementary food we provided. Improving the appeal and effectiveness of supplementary items should continue to be an aspect of research aimed at advancing reintroduction biology.

The relatively slow adaptability of possums to a new environment observed in the current study as well as previous translocations (Pietsch, 1995; Short & Hide, 2014) needs to be accounted for if future reintroductions are undertaken. An assessment of the adaptability of a species to new conditions as well as their post-release behaviour should be used to inform release methods for reintroductions of any species. Our results demonstrate that translocation projects should not assume post-release support is required or has a positive effect on translocation success, and we advocate only using such measures with an experimental approach. In our study, brushtail possums were most suited to an immediate release because natural food and shelter sites were plentiful and post-release predation risk was low. The challenge for future reintroductions will be to identify suitable methods to encourage released animals to use supportive measures effectively, in situations where they are required.

2.8 ACKNOWLEDGEMENTS

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3. PREVIOUS EXPOSURE TO PREDATORS

Antipredator behaviour of a native marsupial is relaxed when mammalian predators are excluded

Brushtail possum in the southern Flinders Ranges

3.1 CONTEXTUAL STATEMENT

Several studies have shown that populations isolated from mammalian predators show predator-naïve behaviour (Dickman 1992; McLean *et al.* 1996; McPhee 2003). Other studies have shown that reintroduction success is generally greater when wild-caught rather than captive bred (i.e. predator-naïve) source populations are used (Griffith *et al.* 1989; Fischer and Lindenmayer 2000; Moseby *et al.* 2014). This study aimed to link prior predator exposure with anti-predator behaviour of two source populations of brushtail possums and post-release survival (i.e. reintroduction success). Data were collected on the response of possums to a spotlight/observer, habitat use, trap success, predator scent aversion and feed tray use, prior to the translocation of animals. The survival of 10 radio-collared animals from each source was compared after translocation for up to 12 months. This chapter has been published in the journal *Wildlife Research*.

3.2 STATEMENT OF AUTHORSHIP

Title of paper	Antipredator behaviour of a native marsupial is relaxed when mammalian predators are excluded			
Publication status	☒ Published	☐ Accepted for publication	☐ Submitted for publication	☐ Publication style
Publication details	Published December 2018 in *Wildlife Research*. **45**:726-736. DOI 10.1071/WR18060			

Author contributions

By signing the Statement of Authorship, each author certifies that the stated contributions to the publication are accurate, and that permission is granted for the candidate to include the publication in the thesis.

Primary author	Hannah Bannister		
Contribution to the paper	Designed the experiment, collected data, analysed the data and prepared the figures, wrote the manuscript and responded to reviewer comments.		
Overall percentage	80 %		
Signature		Date	24/12/2018

Co-author	Robert Brandle		
Contribution to the paper	Assisted with experimental design, assisted with data collection, reviewed the manuscript.		
Signature		Date	15/01/2019

Co-author	Katherine Moseby		
Contribution to the paper	Assisted with experimental design, assisted with data collection, advised on and reviewed the manuscript.		
Signature		Date	24/12/2018

3.3 ABSTRACT

Context: Predator-controlled environments can lead to prey species losing costly antipredator behaviours as they exploit their low-risk environment, creating a 'predator-naïve' population. If individuals lacking suitable antipredator behaviours are used as source populations for reintroductions to environments where predators are present, their behaviour could result in high post-release predation. In contrast, animals sourced from environments with predators ('predator-exposed') may show effective antipredator behaviours and thus higher survival post-release.

Aims: The aim was to compare the antipredator behaviour of brushtail possums (*Trichosurus vulpecula*) at predator-exposed and predator-naïve source populations, and then compare post-release survival after their reintroduction to a low predator environment.

Methods: Data were collected from possums at two sites, one with and one without mammalian predators. The behavioural responses of possums to a spotlighter, their willingness to use supplementary feeders at 'safe' and 'risky' heights, whether they avoided predator odour at traps, and their general willingness to enter traps were recorded.

Key results: Predator-naïve possums showed weaker antipredator responses, were often found at ground level, engaged with novel objects, did not avoid predator scents and utilised different habitats regardless of associated predation risk. In contrast, predator-exposed possums had higher antipredator responses, chose connected trees, were rarely found at ground level and were generally difficult to capture. Post-translocation survival was high for both source populations. Predator-naïve sourced female possums began to avoid predator urine (feral cat, *Felis catus*) 12 months after translocation.

Conclusions: Our research demonstrates that environmental predation risk can predict prey naïvety in brushtail possums. Some aspects of prey naïvety behaviour appear to be able to change in response to altered predation risk.

Implications: With many threatened species now existing only in feral predator-free areas, these results have implications for future reintroductions into unbounded areas where feral predators are present, and for the management of fenced reserves. The addition of a small number of predators to fenced reserves may aid in retaining antipredator behaviours in fenced prey populations.

Keywords: brushtail possum, neophobia, predation, prey naïvety, reintroduction, translocation, *Trichosurus vulpecula*

Isolation from predators can lead to weakened antipredator behaviour. We found that predator-exposed brushtail possums (*Trichosurus vulpecula*) showed better antipredator behaviours than possums in a fenced, mammalian predator-free environment, which were considered predator-naïve. Managers should consider that if animals in predator-free sanctuaries are used as sources for reintroductions, then reduced antipredator behaviour could negatively influence reintroduction success.

3.2 INTRODUCTION

The decline of many animal species worldwide has led to an increase in the use of reintroductions as conservation tools. However, reintroduction success is typically low when key threats are still operating, and improving reintroduction outcomes is a conservation priority (Wolf *et al.* 1996). In Australia, predation by the introduced red fox (*Vulpes vulpes*) and/or feral cat (*Felis catus*) is often the primary cause of reintroduction failure (Short 2009; Moseby *et al.* 2011). When reintroductions are conducted in areas where introduced predators remain, the impacts of feral predators may be exacerbated by sourcing predator-naïve animals from sites where introduced predators are excluded (Moseby *et al.* 2016b). Unfortunately, for many threatened Australian mammals, feral predator-free areas are the only places where some species persist (Johnson 2006). Post-release predation of predator-naïve source animals is a problem mirrored worldwide (Grey-Ross *et al.* 2009; Biggins *et al.* 2011).

Historically, Australian mammals co-existed with mammalian predators such as the now extinct thylacine (*Thylacinus cynocephalus*) and the extant dingo (*Canis lupus dingo*), which was introduced more than 4,000 years ago (Corbett 1985); therefore antipredator behaviours towards mammalian predators should have evolved. However, in recent times the introduction of the red fox and feral cat have caused significant population declines and extinctions among small- to medium-sized native mammals (Burbidge and McKenzie 1989; Woinarski *et al.* 2015). The collapse of the Australian mammal fauna in the face of introduced predators may ultimately be attributed to an absence of co-evolution, expressed as a failure by native mammals to recognise or respond appropriately to these predators (Banks and Dickman 2007). A number of other factors may exacerbate the impact of introduced predators on native mammals, including habitat use (ground-dwelling versus arboreal species), body size, fecundity and habitat degradation (Burbidge and McKenzie 1989; Cardillo 2003; Johnson and Isaac 2009; McGregor *et al.* 2015).

With many threatened species now living as insurance populations behind predator-proof fences, these animals may become less wary of predators, thus making them suboptimal candidates for reintroductions to areas where predators remain present. Modified selection pressure can, in some cases, lead to rapid loss or gain of antipredator behaviours, and has been demonstrated for captive animals and animals on predator-free islands, where predator incursions can rapidly cause local extinction (McLean *et al.* 1996; Massaro *et al.* 2008). Some prey species quickly relax antipredator behaviours to exploit low-predator environments, or because the costs of maintaining such behaviours are high (Blumstein *et al.* 2004; Stokes *et al.* 2004). In contrast, some others retain the recognition of some or all predator cues despite isolation (Coss and Biardi 1997; Blumstein 2002). We suggest a species could also do both, retaining some antipredator behaviours but losing others, depending on selection pressures.

Using brushtail possums (*Trichosurus vulpecula*), we aimed to test whether a population isolated from mammalian predators for at least 15 years was more likely to exhibit relaxed antipredator behaviours compared to a population co-existing with introduced mammalian predators. The brushtail possum (hereafter ‘possum’) is a nocturnal marsupial weighing 1–4 kg (Kerle 2001). Once distributed across most of Australia, possums have significantly declined following European settlement, and the species is now present in less than 50% of its historic range (Kerle *et al.* 1992; Morris *et al.* 2008). Predation by foxes is cited as one of the key causes of the species’ continued decline (Kerle *et al.* 1992; Foulkes 2001), and where fox numbers have been successfully reduced, remnant possum populations have increased (How and Hillcox 2000; Burrows and Christensen 2002). Feral cats are also successful predators of possums (Cruz *et al.* 2013; authors, pers. obs.). Primarily arboreal, possums also forage and travel along the ground, where they are susceptible to mammalian predation. This risk may be enhanced in altered environments, where habitat loss reduces canopy connectivity. Although possums still co-exist in some areas with marsupial predators such as quolls (*Dasyurus* species), which are known to prey on them (Glen *et al.* 2010), they are more commonly exposed to introduced cats and foxes, which can inflict high predation rates (Kerle *et al.* 1992; Foulkes 2001; DEC 2012). Possum translocations to areas where introduced predators were present have either failed or been impacted as a result of predation by introduced predators (Pietsch 1995; DEC 2012; May *et al.* 2016). We hypothesise that the source population's previous exposure (or lack thereof) to predators may have influenced these outcomes.

We classified possum behaviour using spotlighting, habitat use, trapping, and feeder experiments and compared the survival of the two source populations after their reintroduction to an area with low numbers of introduced and native mammalian predators. As antipredator behaviours can sometimes be relatively quickly regained following exposure to predators, we repeated some experiments 12 months after release to test for altered behaviour in their low-predator environment.

3.3 METHODS

3.3.1 Study sites

Predator-exposed possums were sourced from the southern Flinders Ranges (32° 38' 49" S, 138° 05' 45" E, Fig. 1), in South Australia. The region has been subjected to significant land clearing for agriculture, but possums remain present in two habitat types—*Eucalyptus camaldulensis* dominated creeklines and peppermint box (*E. odorata*) grassy woodlands. Mean annual rainfall in the region varies from 440 to 580 mm (Station 19048 and Station 19024: Bureau of Meteorology 2017). Possums here co-exist with feral cats and foxes, and may also be exposed to domestic dogs from adjacent farmland. Wedge-tailed eagles (*Aquila audax*) are present in the region and would be capable of preying on possums active at dusk or dawn. Carpet pythons (*Morelia spilota*) are also present and capable of preying on possums. To confirm mammalian predators present at the site, four remote cameras (HCO Scoutguard SG560V, Scoutguard Australia, Molendinar, Australia) were deployed along access tracks throughout survey sites for a period of four weeks. Predator detections collected through continuous camera trapping (Reconyx Hyperfire HC600, Reconyx, Wisconsin, USA) at fixed locations on three transects at the reintroduction site during the same period also provided baseline information on the predator species present (the Department for Environment and Water (DEW) and Ecological Horizons, unpubl. data).

The mammalian predator-free ('predator-naïve') source population was located at Yookamurra Wildlife Sanctuary (34° 32' 22" S, 139° 28' 33" E, Fig. 1), a 5,026 ha private reserve in South Australia owned by the Australian Wildlife Conservancy, of which 1,100 ha is fenced. Two main habitat types are present: mallee (*Eucalyptus* species) and shrubland, where genera > 3 m include *Myoporum*, *Acacia*, *Exocarpus*, *Callitris* and *Eucalyptus*, among others. The sanctuary receives an average annual rainfall of 339 mm (Station 24581: Bureau of Meteorology 2017). Inside the fence, mammalian predators have been heavily suppressed from the early 1990s under the management of Earth Sanctuaries Limited, and completely excluded for the past 15 years under the management of the Australian Wildlife Conservancy (J. Kanowski, pers. comm.; Australian Wildlife Conservancy 2018). The fence has a floppy-top design (Moseby and Read 2006), and possums can climb out but cannot climb back in. Our original study design was to compare possum populations inside and outside the fence, but we were only able to locate two possums outside the fence during a pilot study and thus a comparison was not considered feasible. The apparently low possum density outside the fence may be testament to the effect of having predators present. Intermittent sand plot and remote camera monitoring is used to confirm the continued absence of introduced predators inside the fence (H. Crisp, pers. comm.). Similarly to the southern Flinders Ranges, wedge-tailed eagles and carpet pythons are present and potential predators of possums. Possums can live for up to 14 years in the wild (How and Kerle 1995; Clinchy *et al.* 2001). Therefore, the population within the exclosure during this study had not been exposed to mammalian predators.

An approximate possum density was calculated for both source sites to determine whether density effects may confound our results. We used the number of possums sighted on 7 nights of spotlighting at Yookamurra Wildlife Sanctuary and 6 nights at the southern Flinders Ranges, taking into account the distance and area covered each night and the visibility for each habitat type. Visibility was judged to be 60 m in mallee, shrubland and creekline habitats, and 50 m in the more densely vegetated woodland habitat. Detection was assumed to be 100 %. Densities were calculated for each night of sampling and compared between the two sites using a t-test.

In June 2015, 79 predator-naïve possums were translocated from the 1,100 ha exclosure at Yookamurra Wildlife Sanctuary to the reintroduction site at the Ikara-Flinders Ranges National Park (IFRNP, 31° 31’ 43” S, 138° 36’ 13” E, Fig. 1) (Bannister *et al.* 2018; DEW and Ecological Horizons, unpubl. data) in South Australia, where possums became locally extinct around the 1940s (Kerle *et al.* 1992). In May 2016, an additional 50 predator-naïve possums from Yookamurra Wildlife Sanctuary were translocated to the park, as well as 19 predator-exposed possums from the southern Flinders Ranges (Fig. 3.1).

The IFRNP reintroduction site consists of various habitats, including *E. camaldulensis* dominated creeklines, open woodland (*Eucalyptus* and/or *Callitris* spp.), mallee and mixed species rocky slopes dominated by *E. intertexta,* and *Callitris, Dodonaea, Olearia, Bursaria, Cassinia* and *Acacia* spp. The area receives an average annual rainfall of 437 mm (Station 19070: Bureau of Meteorology 2017). Feral cats and dingoes are present at the site but subject to sporadic control, while foxes are successfully controlled and rarely detected (DEW, unpubl. data). Wedge-tailed eagles and carpet pythons are both present. The western quoll (*Dasyurus geofroii*), a carnivorous marsupial weighing 1-2 kg, was reintroduced to the park in 2014 (Moseby *et al.* 2016a) and is capable of predating possums, although at least some of their possum consumption is considered to be scavenging (Glen *et al.* 2010). Western quolls were historically present at both source sites but became locally extinct around the 1930s (Morris *et al.* 2003).

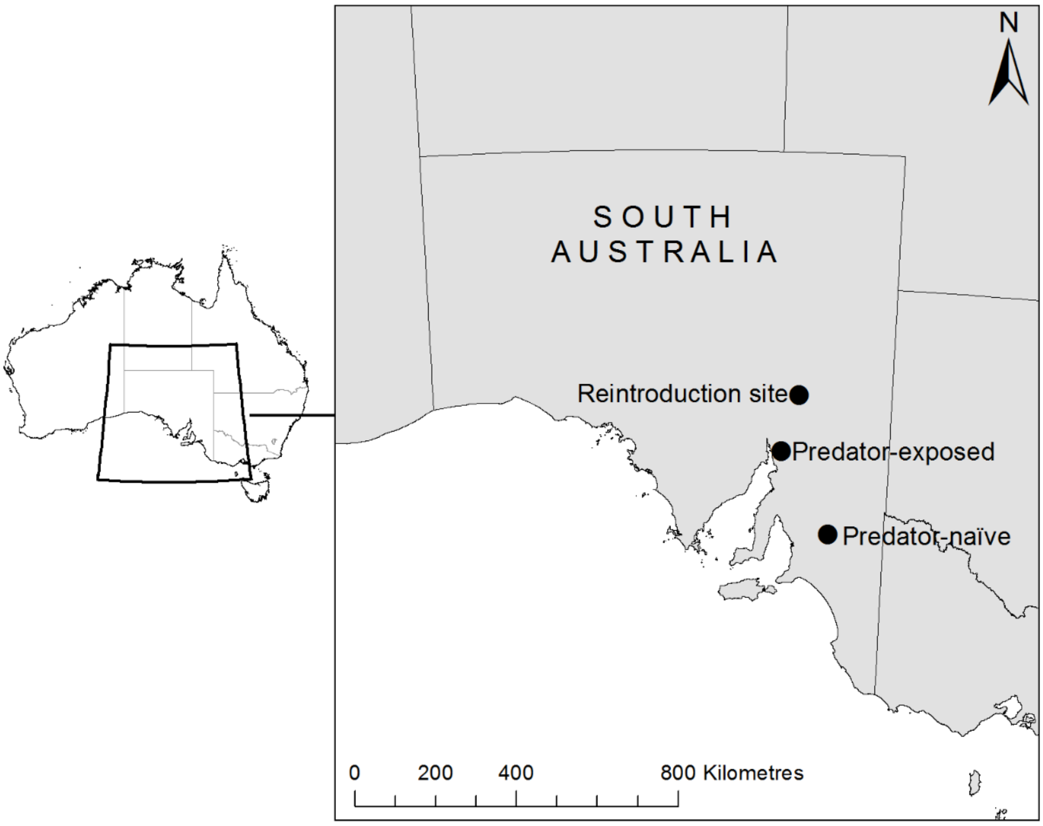

Figure 3.1: Source sites (predator-exposed: southern Flinders Ranges, predator-naïve: Yookamurra Wildlife Sanctuary) where behavioural data was collected for possums prior to translocation, and their reintroduction site (Ikara-Flinders Ranges National Park, predators present) within South Australia. The general location within Australia is shown.

3.3.2 Spotlighting

Prior to any translocations, spotlight surveys took place at both source sites to assess the antipredator responses of possums to the observer. Spotlighting (30V spotlight, Lightforce, Hindmarsh, Australia) was conducted on foot (approximately 3.5 km h^{-1}) or, when surveying along tracks, from a vehicle (approximately 10 km h^{-1}), in areas where possums were known to be present, with both methods used at both source sites. The observer scanned both the canopy and the ground, looking for possums. When spotted, the response of the possum to the spotlight was noted (Table 3.1), as was the height of the possum above the ground (Nikon Forestry Pro rangefinder, Nikon Corporation, Rhodes, Australia). If spotted from a vehicle, the engine was turned off and the observer quietly exited the car. The observer approached the tree to within 10 m and recorded the response of the possum. Tree height, distance to the nearest neighbouring tree, habitat type and whether the canopy was connected to another tree was then recorded. Trees were recorded as connected if branches were < 1.5 m apart because possums are able to jump this distance between trees (authors, pers. obs.). An effort was made to limit sampling along the same access track, transect or creekline to no more than twice to prevent multiple observations of the same individual possums. Responses were scored based on the vulnerability of the possum to predation, assuming the spotlighter was viewed as a potential predator or threat (Table 3.1). For each observation, the initial height of the possum in the tree (or on ground) was categorised as ground level (unsafe), <1.6 m (moderately unsafe) or ≥1.6 m (safe), similar to Mella *et al.* (2014). The response of the possum to the spotlight and the observer's approach was scored 0–2, where higher scores reflected better antipredator responses (Table 3.1). The initial height score and response score were added together to give a total response score per observation, ranging from 0 (worst) to 4 (best).

Table 3.1: Behavioural antipredator responses for possums observed during spotlight surveys. Height scores were determined by the predation risk associated with the possum being found at that height. Response scores were scored based on the possums showing no antipredator response (0), an unsuitable antipredator response (1) or a suitable antipredator response (2). Scores ranged from 0 (worst) to 4 (best).

Initial height	Possum response	Height score	Response score	Total score
Ground	Fled along the ground	0	1	1
	Foraged at an unsafe height <1.6 m	0	0	0
	Climbed a tree to an unsafe height	0	1	1
	Vigilant at an unsafe height	0	1	1
	Retreated to an unsafe shelter	0	1	1
	Climbed tree to a safe height	0	2	2
<1.6 m	Foraged at an unsafe height	1	0	1
	Climbed down tree and fled	1	1	2
	Vigilant at an unsafe height	1	1	2
	Retreated to an unsafe shelter	1	1	2
	Climbed higher	1	2	3
≥1.6 m	Climbed down and fled along the ground	2	0	2
	Foraged at a safe height	2	1	3
	Climbed higher	2	2	4
	Remained vigilant or froze/hid (cryptic) at a safe height	2	2	4
	Retreated into a hollow at a safe height	2	2	4

Statistical analyses were carried out using the program R (R Development Core Team 2018). The response scores of possums from the two source populations were compared using a cumulative link model within the package ‘ordinal’ (Christensen 2015). Total response score, an ordered factor, was the response variable and source population was the explanatory variable. Equidistant thresholds were used. The proportional odds assumption was checked with both a scale test and nominal test (Christensen 2015) and model significance was assessed using a Wald Chi-square test with the package ‘car’ (Christensen 2015; Fox *et al.* 2016).

3.3.3 Habitat use

Because of the difference in habitat at the two source sites, we did not compare habitat use by possums between sources, but within each source. Two habitat types were nested within each of the two source sites. Fifty random points were generated within each habitat type where possums were present (200 points in total) using ArcGIS (Esri 2015)—mallee and shrubland at the predator-naïve source (Yookamurra Wildlife Sanctuary) and creekline and woodland at the predator-exposed southern Flinders Ranges. At each random point, we recorded whether there was canopy cover. We then recorded the distance to the nearest tree (height > 3 m, diameter at breast height (DBH) > 10 cm), the height and genus of the tree, and the distance to the nearest adjacent tree.

For each source site, a binomial generalised linear model was used to compare the connectivity of trees used by possums versus random trees, with habitat type included as a covariate, as well as an interaction term. Similarly, the height of trees used by possums versus random trees was also compared using a generalised linear model, with habitat as a covariate and an interaction term included. The proportion of random points that had canopy cover was compared between all habitat types using a binomial generalised linear model. All generalised linear model significance tests were completed using Chi-square Analysis of Deviance tests.

3.3.4 Supplementary feeders

Supplementary feeders (metal wall-mount plant pots, 20 x 12 x 12 cm) containing rolled oats and sliced apple were deployed at the two source sites prior to translocating possums, to test whether possums were more likely to use feeders at safe rather than risky heights. Eight feeders were used at the predator-naïve source site, while only four were available for the predator-exposed site. Half the feeders were placed at ground level, approximately 1.5 m away from the base of a tree (a ‘risky’ height) while the other half were hung at safe heights (1.6 m, as per Mella *et al.* 2014), using thin rope to tie the feeder to a tree, preferably where there was a fork or horizontal branch the possum could feed from. Feeders at the predator-naïve site were confined to two smaller exclosures (~0.9 ha and 0.16 ha) within the fenced sanctuary, where reintroduced bettongs (*Bettongia* species) could not access feeders, but possums could easily climb in and out of the large pens. The two areas were ~0.6 km apart and within each exclosure the distance between feeders ranged from 15 to 75 m. At the predator-exposed site, feeders were spaced 288–890 m apart. A remote camera (HCO Scoutguard SG560V) monitored each feeder and was set to record three photos per trigger. Data were collected for around 3 weeks at each site. All detections were counted except when it was obviously the same possum as the previous trigger (i.e. the possum was in the same position as the previous photo). The number of detections is likely to be much higher than the number of individual possums that visited, particularly given the close spacing of feeders at the predator-naïve site, but this method ensured consistency as individual possums could not be reliably identified. The number of possum detections at high and low feeders was compared for each site (where possible) using a t-test.

3.3.5 Trapping

To test whether possums avoided predator cues, a choice experiment was conducted whereby treadle-operated cage traps baited with a mixture of peanut butter and rolled oats were set on the ground in groups of three, with alternative scents (cat urine, liquefied kangaroo scat or water) deposited in front of each trap directly onto the ground. Cat urine was collected from feral cats euthanised during routine control operations and was stored in the freezer until several hours prior to use. The solution was diluted by one third because only a small amount was available. Kangaroo scent was prepared by placing fresh kangaroo faeces in a glass jar and adding a small amount of water, then leaving to soak for several days. Both cat urine and kangaroo scat were collected from the IFRNP. Similarly to the feeder experiments, trapping at the predator-naïve site was conducted within two large fenced areas, where possums could easily climb in and out but bettongs could not gain access and saturate traps. For some of the trap sites at the predator-exposed site, both cat and fox (Iron Dog Trapping, Maroochydore, Australia) scents were separately trialled, as both predator species were present in the area and both are known to be predators of possums. Groups of three traps (3–7 groups per exclosure at the predator-naïve site (area = ~1.06 ha), 14 groups at the predator-exposed site (area = ~36 ha)) were set in a line approximately 2.5 m apart and 3 ml of liquid scent was placed 10 cm from the entrance of the trap using a plastic syringe. Traps were all oriented in the same direction. The allocation of scents to traps was random with the proviso that all combinations of scent configuration were presented across the trap sites.

Trapping was conducted according to standard trapping procedures (Petit and Waudby 2012). At the predator-exposed site, an initial 42 trap nights yielded no possum captures. To confirm that possums were not avoiding a larger area (>10 m) around predator cues, we undertook 42 trap nights where traps were set in twos, with the same scent at both traps and with a space between pairs of at least 200 m—again, no possums were captured. Because no predator-exposed possums were captured in cage traps prior to translocation, a targeted trapping effort was made after the translocation of predator-exposed possums to the IFRNP. Three traps with different scents were set at shelter sites currently being used by radio-collared translocated possums 6 weeks after release. The scent avoidance experiment was repeated on predator-naïve possums 12 months after their translocation to the IFRNP to determine whether exposure to predators had altered their behaviour. The proportion of possums captured in traps with each scent was compared using Fisher's Exact Test, analysing captures at the source site and 12 months post-release separately and comparing the proportion of captures at each scent for males and females. Regular trapping was conducted throughout the study and post-release trap success was compared for the two source populations using a binomial generalised linear model. Trap success—the proportion of successful captures relative to trapping attempts for individual possums—was the response variable, with source population as the explanatory variable. Model significance was assessed using a Chi-square Analysis of Deviance.

3.3.6 Survival

A direct comparison of survival was possible after the translocation of possums from predator-exposed and predator-naïve populations in 2016, when 10 possums from each population were radio-collared (VHF M1820, 27 g, Advanced Telemetry Systems) prior to release. The translocation of predator-naïve possums took place 2 weeks after the translocation of predator-exposed possums. A larger cohort of 79 predator-naïve animals had been translocated 1 year prior, and some still remained radio-collared during this study. Radio-collar signals were obtained, where possible, at least once per week, and mortalities (collar inactivity for >10 h) were investigated upon discovery. All 20 possums remained collared for the first 5 months after release, and collars were gradually removed over the ensuing 6 months. Survival comparisons continued until most remaining radio-collars were removed 11 months after release.

Research was conducted according to the Australian Code for the Care and Use of Animals for Scientific Purposes (2013). Animal ethics approvals were issued by The University of Adelaide Animal Ethics Committee (Approval number S-2015-091) and the South Australian Wildlife Ethics Committee (Project number 15/2014).

3.4 RESULTS

The density of possums at the two source sites was not significantly different (*t*-test: $t_{11} = 0.20$, $P = 0.85$), calculated to be 36.8 ± 5.4 possums km^{-2} at the predator-naïve Yookamurra Wildlife Sanctuary and 34.0 ±13.7 possums km^{-2} at the predator-exposed southern Flinders Ranges. Between 10 and 39 predator-naïve possums were sighted nightly at Yookamurra Wildlife Sanctuary, in a survey area of 0.31–1.2 km^2 per night (total sightings = 165, total area = 33.9 km^2). Nine to 30 predator-exposed possums were sighted nightly at the southern Flinders Ranges, surveying an area of 0.17–0.93 km^2 per night (total sightings = 99, total area = 4.03 km^2). It is important to note that the southern Flinders Ranges density estimate is relevant only to our survey sites and will not be representative of possums across the entire region, as possums cannot occur or survive in these densities on cleared farmland and their distribution is patchy.

3.4.1 Predator detections

During a 1 month period (120 camera trap nights) at the southern Flinders Ranges during autumn 2016, remote cameras detected foxes on 4.2% of trap nights and feral cats on 1.7% of trap nights. A pet dog (collared) was also detected. Several foxes were spotted while conducting fieldwork in the area. Using data from four randomly selected remote cameras already deployed at the IFRNP reintroduction site during the same period, foxes were not detected, feral cats were detected on 2.4% of camera trap nights and dingoes were detected on 4.0% of camera trap nights.

3.4.2 Spotlighting

Predator-exposed possums had significantly higher antipredator behaviour scores in response to a spotlighter's approach compared to predator-naïve possums (χ^2_1 = 83.6, $P < 0.0001$, predator-naïve $N = 189$, predator-exposed $N = 59$), when surveyed at both source sites (Fig. 3.2). Predator-naïve possums were observed more frequently on the ground (20.1% of sightings) than predator-exposed possums (6.1% of sightings, Fisher's Exact Test: $P = 0.0069$).

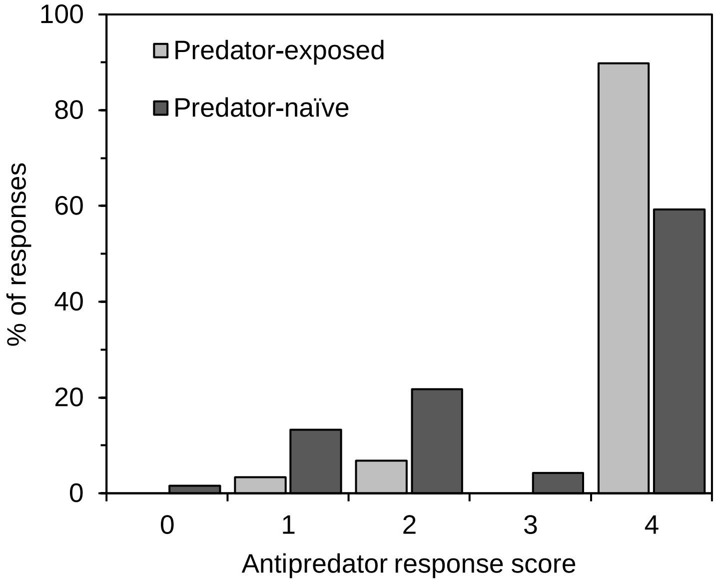

Figure 3.2: The antipredator behaviour response score for possums when observed during spotlight surveys at predator-exposed and predator-naïve source sites, where higher scores represent better antipredator responses.

3.4.3 Habitat use

Predator-exposed possums used trees with connected canopies in a higher proportion to their availability within both creekline and woodland habitat types (Analysis of Deviance (ANODE): treatment (possum observation or random point): $d_1 = 13.6$, $P = 0.00023$, habitat: $d_1 = 0.9$, $P = 0.34$; treatment*habitat: $d_1 = 0.006$, P

= 0.94). In contrast, predator-naïve possums did not preferentially use trees based on their canopy connectivity, and were found using trees that were less connected than randomly sampled trees in the mallee habitat and in similar proportions to their availability within the shrubland habitat (ANODE: treatment: d_1 = 6.7, P = 0.0097, habitat: d_1 = 66.4, P < 0.0001, treatment*habitat: d_1 = 17.3, P < 0.0001, Fig. 3.3).

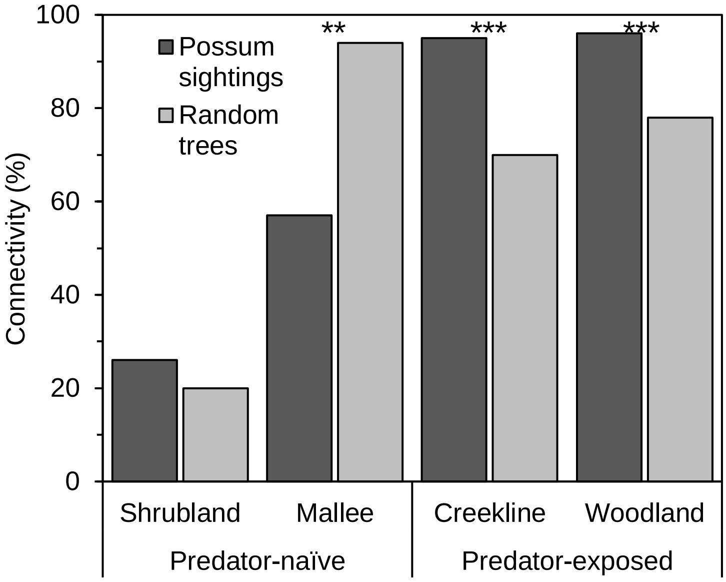

Figure 3.3: The percentage of connected trees used by possums (possum sightings) and the percentage available within each habitat type (random trees) at the predator-naïve and predator-exposed source sites. *indicates significance.

Predator-exposed possums used trees that were a similar height to what was available within each habitat (ANODE: d_1 = 0.80, P = 0.87; treatment*habitat: d_1 = 12.4, P = 0.50, Fig. 3.4) and tree height was significantly different between the two habitat types (ANODE: d_1 = 3286.2, P < 0.0001). Predator-naïve possums used trees that were taller than what was randomly available within both the mallee and shrubland habitats (ANODE: treatment: d_1 = 81.8, P = 0.00011, habitat: d_1 = 187.7, P < 0.0001, treatment*habitat: d_1 = 11.6, P = 0.14, Fig. 3.4). An analysis of the 50 random points surveyed in each habitat at both source sites showed that canopy cover was significantly lower in the shrubland habitat compared to the mallee, creekline and woodland habitats (ANODE: d_3 = 19.3, P = 0.00024).

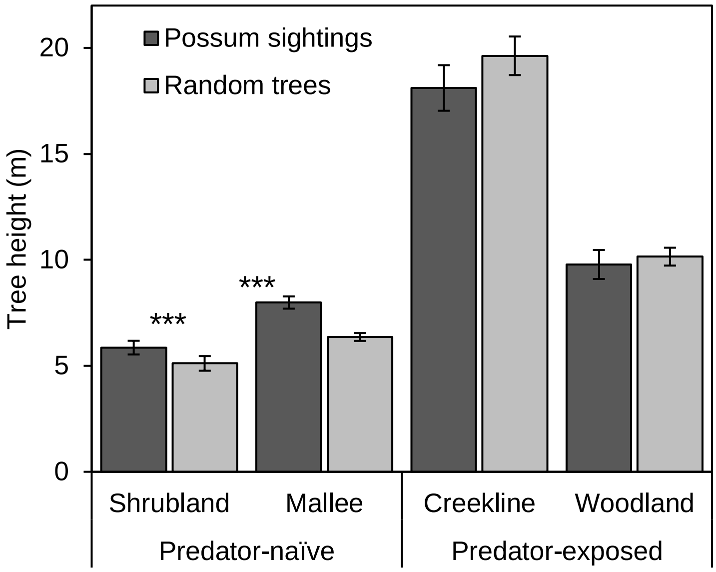

Figure 3.4: The mean height (± 1 standard error) of trees used by possums (Possum sightings) and the mean height of trees within each habitat (Random trees) at the predator-naïve and predator-exposed source populations. *indicates significance.

3.4.4 Supplementary feeders

A total of 335 detections were recorded for predator-naïve possums using feeders at Yookamurra Wildlife Sanctuary. In contrast, no predator-exposed possums were detected using supplementary feeders at the southern Flinders Ranges, despite feeders being placed in areas of known possum occupancy. Predator-naïve possums were detected using ground level feeders significantly more often than at feeders at safe heights (*t*-test: $t_5 = -3.91$, $P = 0.011$, mean detections per feeder: 'risky' height = 79.5, 'safe' height = 5.7). Repeated measures on individuals could not be accounted for as possums were not uniquely identifiable.

3.4.5 Trapping

During predator scent avoidance tests at Yookamurra Wildlife Sanctuary, predator-naïve possums were captured on 72 occasions. Between 8 and 17 unique individuals were caught per night. Some individuals may have been recaptured on subsequent nights—possums were not uniquely marked at the time. Sex was recorded for 57 possums (79%)—the remainder were released without handling. Of the 72 captures, 29%, 38% and 33% were in traps with cat, kangaroo and water scent respectively and there was no avoidance of predator scent (Fisher's Exact Test: $P = 0.74$, Fig. 3.5). Eighteen predator-naïve possums that had been translocated to IFRNP were recaptured 12 months after release in traps with cat (28%), kangaroo (28%) and water (44%) scent—the sex was known for all recaptures (12 male, 6 female). When sexes were pooled, predator-naïve possums had not learnt to avoid predator scent in the 12 months after their translocation to an environment containing mammalian predators (Fisher's Exact Test: $P = 0.73$) and they were caught in equal proportions at each scent when compared to pre-release captures ($\chi^2_2 = 0.04$, $P = 0.98$). There was no significant difference in the proportion of males and females caught at each scent at the source site (Fishers Exact Test: $P = 0.18$), but there was a significant difference between sexes 12 months after release (Fishers Exact Test: $P = 0.029$). Five males but no females were caught in traps with cat scent, although the low capture rate of females ($N = 6$) means this should be interpreted cautiously (Fig.

3.5). At the southern Flinders Ranges, 82 trap nights yielded no captures of predator-exposed possums in predator scent avoidance tests in either of the trap configurations trialled. When these possums were targeted for capture six weeks post-release, just one of the eight targeted possums was captured. Individual predator-naïve possums became more aggressive during handling with time since release (H. Bannister, pers. obs.), although repeated handling is likely to have had an influence. In contrast, all predator-exposed possums were difficult to handle when captured for the first time post-release (H. Bannister, pers. obs.), so repeated handling was not a factor. Predator-exposed possums were more difficult to recapture after translocation compared to predator-naïve possums, with a lower proportion of successful targeted trapping attempts per individual possum (ANODE: $d_{63} = 16.3$, $P < 0.0001$, mean successful attempts: predator-naïve 62.4%, predator-exposed 43.7%).

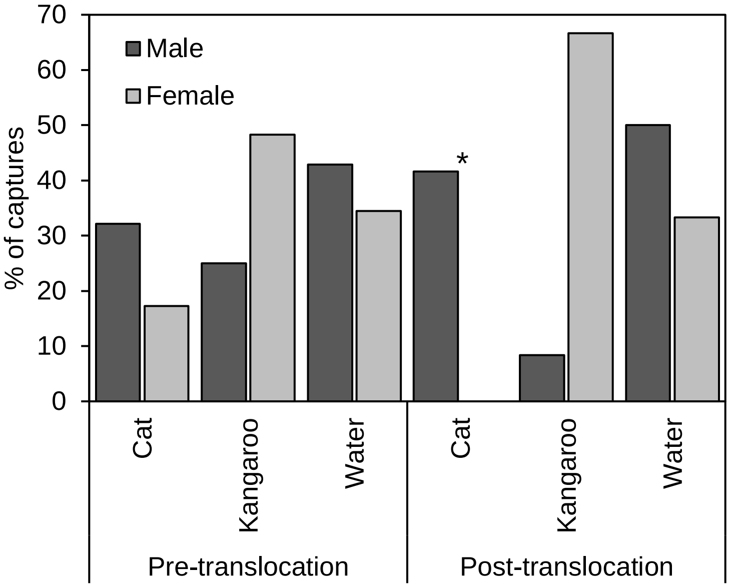

Figure 3.5: The percentage of captures of predator-naïve possums in traps set with three alternate scents (cat, kangaroo and water), with captures made prior to and 12 months after translocation to a low-predator environment. * indicates significance.

3.4.6 Survival

None of the 20 radio-collared possums translocated in 2016 (10 predator-naïve and 10 predator-exposed) died as a result of predation in the first 5 months after release; therefore, there was no significant difference in survival between the predator-exposed and predator-naïve source populations. Although some possums gradually had their collars removed after this time, three predator-exposed and six predator-naïve possums remained collared for 11 months after release and none were predated during this time. However, predation of other radio-collared possums in the study area was recorded before and during the study period (authors, unpubl. data), indicating that predators were present and possums did encounter them.

3.5 DISCUSSION

The present study provides evidence that brushtail possums isolated from mammalian predators show weaker antipredator behaviours compared to possums in higher risk environments where predators are present. Predator-exposed possums were warier, showed neophobic tendencies by avoiding traps and supplementary feeders, were rarely spotted on the ground and when captured were aggressive to handle. They generally responded appropriately to a spotlighter's approach by maintaining or climbing to a safe height or retreating into a hollow. In contrast, predator-naïve possums often showed ineffective antipredator responses when approached during spotlighting surveys, often coming to ground and/or fleeing along the ground rather than climbing a tree. They were generally readily captured in cage traps, did not avoid predator scent at traps, interacted with novel items (supplementary feeders and cage traps), preferred using feeders at ground level, and were often spotted on the ground. Using Banks and Dickman (2007's) prey naïvety model, predator-naïve possums at Yookamurra Wildlife Sanctuary exhibited Level 2 prey naïvety, whereby they recognised a potential threat but responded inappropriately. Predator-exposed possums in the southern Flinders Ranges tended towards Level 3 prey naïvety, whereby they responded to threats appropriately. However the species' widespread decline, largely as a result of predation (Kerle *et al.* 1992; Burrows and Christensen 2002), suggests that the hunting practices of introduced predators are simply superior (Banks and Dickman 2007). There was, however, no significant difference in the post-release survival of the two source populations, despite detectable differences in their antipredator behaviour. An absence of foxes at the reintroduction site probably contributed to the high post-release survival observed, but a small sample of radio-collared animals may have also resulted in undetected mortalities. Had predation pressure been higher, the differences in antipredator behaviours may have translated to differences in survival between the two source populations. Higher predation rates have been demonstrated for predator-naïve captive-bred Vancouver Island marmots (*Marmota vancouverensis*) and thick-billed parrots (*Rhynchopsitta pachyrhyncha*) compared to their predator-exposed (wild-sourced) counterparts (Snyder *et al.* 1994; Aaltonen *et al.* 2009). Alternatively, the behavioural differences observed may not have been true reflections of antipredator behaviour in this species.

Antipredator responses have been rapidly lost under relaxed selection in other species—rock wallabies (*Petrogale lateralis*) expanded their habitat use less than 5 years after fox control was implemented, and tammar wallabies (*Macropus eugenii*) lost group-size effects and weakened their visual predator recognition following ~130 years of isolation from predators (Kinnear *et al.* 1988; Blumstein *et al.* 2004). The reduced antipredator behaviour demonstrated by the predator-naïve possums after as little as 15 years of isolation from mammalian predators supports this, and suggests both that antipredator behaviour for possums is costly to maintain, and that it is quickly reduced when predation pressure is relaxed. Similarly, North Island robins (*Petroica longipes*) quickly lost the ability to recognise stoats (*Mustela erminea*) as predators after being translocated to a predator-free island, and captive bred grey partridges (*Perdix perdix*) showed poor antipredator behaviour compared to wild animals (Rantanen *et al.* 2010; Whitwell *et al.* 2012). While isolation from predators for as little as one generation can cause a loss of some experience-based antipredator behaviours, innate behaviours take longer to be eliminated (Blumstein and Fernandez-Juricic 2010). In addition to intergenerational changes, individuals within a population have the capacity to adapt antipredator responses following exposure to predators; for example, burrowing bettongs (*Bettongia lesueur*) improved their antipredator responses within 18 months of exposure to a low density of feral cats, and captive-bred houbara bustards (*Chlamydotis undulata*) had improved post-release survival if they were first exposed to a live predator (van Heezik *et al.* 1999; West *et al.* 2018). Experience-based learning could explain the increased handling aggression and the avoidance of cat urine (females only) shown by predator-naïve possums after their translocation to an environment where feral cats were present and known to predate adult possums.

The propensity for predator-naïve possums to regularly spend time moving and foraging on the ground is probably a result of them learning to exploit their mammalian predator-free environment, because they are able to access food resources at ground level that are not available in the canopy, with low risk of predation. Rock wallabies (*Petrogale lateralis*) were found to forage further away from rocks after the implementation of fox control, suggesting a more relaxed approach to perceived predation risk or the exploitation of a low-predator environment (Kinnear *et al.* 1988). Possums in areas of low fox density have been shown to travel further along the ground and have lower giving up densities than possums in areas with high fox numbers (Pickett *et al.* 2005). At Ku-ring-gai Chase National Park in eastern Australia, where predators (including foxes) are present, possums were found to spend more time foraging at above-ground feeders than feeders at ground level, but did not avoid predator odours (Mella *et al.* 2014). We found a trend towards female possums learning to avoid cat scent at traps, which may be a result of stronger selection pressure being placed on females compared to males, because they are more susceptible to predation when carrying large pouch young or back young (authors, pers. obs.), and they also need to consider the vulnerability of their young. Resampling several years after the reintroduction event may produce a stronger difference, as could the sampling of possums born into the predator-containing release site. It is unknown whether males will also learn to avoid the scent of cats. The use of only a small amount of scent (3 ml) may have contributed to failing to elicit a response, as this is much less than the natural void of a feral cat (authors, pers. obs.). Other studies testing whether possums avoid the scent of predators at traps suggested they do not (Russell and Banks 2005; Mella *et al.* 2010); however, both experiments were conducted in areas where mammalian predators were excluded, possibly confounding results. An inability to capture any predator-exposed possums in traps prior to translocation precluded our ability to investigate whether they showed any avoidance of predator scents at traps. However, possums displayed wariness by completely avoiding traps and supplementary feeders in pre-release experiments, suggesting neophobic tendencies and heightened antipredator behaviours compared to the predator-naïve population.

To prevent the relaxation of antipredator behaviours in threatened species, the addition of a small number of native (or introduced) predators to fenced conservation areas could be considered, which could ultimately improve reintroduction success outside of fenced areas. Challenges in maintaining low numbers of predators with prey populations may include surplus killing by individual predators (Short *et al.* 2002), limiting the growth of the predator population when prey is numerous and ensuring that fences or neutering do not alter the hunting behaviour of the predators. Despite these obstacles, such actions have been trialled at the Arid Recovery Reserve in South Australia, with burrowing bettongs (*Bettongia lesueur*) modifying their antipredator behaviour following the addition of a low density of predators (West *et al.* 2018), but the practice has not yet been widely adopted (Moseby *et al.* 2016b). Despite reduced predation pressure on California quail (*Callipepla californica*) on Santa Catalina Island compared to their mainland counterparts, a low density of predators was sufficient to maintain antipredator behaviours (Rasheed *et al.* 2018). In our study, all possums showed some response to the threat of predation, and predator-naïve possums showed early indications of having improved their antipredator behaviour following exposure to predators.

Future reintroduction projects should carefully consider whether source populations exhibit prey naïvety behaviour and whether this is likely to influence reintroduction success. An assessment of the antipredator behaviour of a population prior to translocation to an environment where predators are present may aid in predicting whether post-release predation could pose a serious threat to reintroduction success, and could be used to inform practitioners of whether controlled exposure to predators or predator-like stimuli should be undertaken prior to release. Individual variation within populations should also be taken into account; for example, a heterogenous release habitat may allow all individuals to access preferred foraging sites and allows for individuals to adapt to increased predation pressure by shifting their preferred foraging sites to safer ones (McArthur *et al.* 2014; Mella *et al.* 2015). Management of fenced reserves should involve consideration of the importance of maintaining antipredator behaviours in prey species, particularly if fenced populations are to act as source populations for translocations to unfenced areas. Native predators are increasingly being reintroduced to both fenced and unfenced areas, and so threat mitigation for prey species may no longer be limited to the removal of introduced predators, but may extend to improving antipredator responses to cope with native predators that they once co-existed with. Our research demonstrates that environmental predation risk can predict prey naïvety in brushtail possums and that at least some behaviours are able to change in response to altered predation risk. With many threatened species now existing only in feral-predator-free areas, our results have implications for future reintroductions into unbounded areas where feral predators are present.

3.6 ACKNOWLEDGEMENTS

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4. HABITAT

The importance of habitat quality for successful reintroduction: a test using the brushtail possum

Brushtail possum returning to its tree hollow

4.1 CONTEXTUAL STATEMENT

This chapter provides a broad summary of the post-release habitat use and movement of brushtail possums reintroduced to the Ikara-Flinders Ranges National Park, with a particular focus on assessing whether the degraded habitat of the park was likely to influence reintroduction success. Changes in body mass, body condition and reproduction with time since release were assessed, with data collected from 148 released animals and 65 recruits captured within the 33 month study period. Post-release survival and home ranges are given and sex differences are highlighted. Habitat use and selection by possums is discussed, with particular attention given to whether habitat quality is important for reintroduction success and population persistence. The use and availability of preferred hollow-bearing tree species is described and the current demography of these species is discussed. Brushtail possums have been extirpated from the outback region of South Australia and indeed most of Australia's arid and semi-arid zones, therefore this study provides insights into important aspects of the species' ecology and likely causes of decline, as well as highlighting factors that may need to be addressed to ensure long-term population persistence. This chapter has been submitted to the journal *Austral Ecology*.

4.2 STATEMENT OF AUTHORSHIP

Title of paper	The importance of habitat quality for successful reintroduction: a test using the brushtail possum			
Publication status	☐ Published	☐ Accepted for publication	☒ Submitted for publication	☐ Publication style
Publication details	Submitted to *Austral Ecology*, January 2019			

Author contributions

By signing the Statement of Authorship, each author certifies that the stated contributions to the publication are accurate, and that permission is granted for the candidate to include the publication in the thesis.

Primary author	Katherine Moseby		
Contribution to the paper	Designed the experiment, collected data, analysed data, wrote the manuscript.		
Overall percentage	40 %		
Signature		Date	21/01/2019

Co-author	Robert Brandle		
Contribution to the paper	Assisted with experimental design, assisted with data collection, reviewed the manuscript.		
Signature		Date	20/01/2019

Co-author	Patrick Hodgens		
Contribution to the paper	Assisted with data collection, reviewed the manuscript.		
Signature		Date	20/1/2019

Co-author (candidate)	Hannah Bannister		
Contribution to the paper	Assisted with experimental design, collected data, analysed data and prepared figures, assisted with writing the manuscript, reviewed the manuscript.		
Overall percentage	40 %		
Signature		Date	20/01/2019

4.3 ABSTRACT

Habitat degradation contributes to species decline, and habitat quality is an important factor influencing reintroduction success globally. However, in arid Australia, introduced predators are thought to be the primary cause of mammal extinction and reintroduction failure. Brushtail possums are one arid Australian marsupial close to regional extinction. To understand whether habitat quality was limiting their recovery, we reintroduced 148 brushtail possums into an area where introduced foxes were controlled but historic overgrazing had degraded vegetation. Sixty-seven released possums and 26 post-release recruits were radio-collared to provide information on parameters potentially influenced by habitat quality.

Post-release survival of radio-collared possums was high after 12 months (0.70), and there were no deaths from starvation. Predation by feral cats was the most common cause of mortality, and the open, degraded habitat may have exacerbated predation risk. Continuous breeding, good body condition and comparative home ranges with other sites suggested that food resources were not limiting. Possums used natural hollows in *Eucalyptus* spp with no use of artificial nest-boxes. Results suggest that degraded habitat was no barrier to short term survival and reproduction when foxes were controlled and natural hollows were plentiful. However, demographic data suggests a possible future decline in availability of hollow bearing trees. These factors, combined with the unknown effects of drought, and synergistic effects of predation and poor quality habitat, suggests long term reintroduction success (population increase and persistence) may require improved habitat and broader predator control.

Key words: Australia, habitat quality, mammal, marsupial, reintroduction success, translocation

4.4 INTRODUCTION

Habitat quality is recognised globally as one of the most important factors influencing reintroduction success (Griffith *et al.* 1989; Wolf *et al.* 1996; Powell *et al.* 2012; Stadtmann and Seddon 2018). Habitat quality is often measured *a priori* to decide whether to proceed with reintroductions (Cheyne 2011), as reintroductions into areas where habitat quality is poor are less likely to succeed (Griffith *et al.* 1989; Moorhouse *et al.* 2009). Poor quality habitat can be a result of vegetation clearance, introduction of pest species, fragmentation or inappropriate fire regimes. In Australia, habitat degradation from vegetation clearance and overgrazing by introduced herbivores is a contributing factor in the decline and extinction of many mammal species including terrestrial and arboreal marsupials (Woinarski *et al.* 2014). However, introduced cats (*Felis catus*) and foxes (*Vulpes vulpes*) are implicated in the widespread decline of Australian mammal fauna following European settlement (Burbidge and McKenzie 1989; Woinarski *et al.* 2015). Additionally, predation by introduced predators is the major cause of reintroduction failure in Australia (Fischer and Lindenmayer 2000; Moseby *et al.* 2011), responsible for 80% of translocation failures (Short 2009). The relative contribution of poor vegetation availability and structure, and predation to mammal decline and reintroduction failure is difficult to quantify and is likely to be synergistic (Bennett *et al.* 2013; Doherty *et al.* 2015b; Woinarski *et al.* 2015). For example, predation rates have been found to be higher in open habitats where predators may find it easier to hunt (McGregor *et al.* 2015); lower ground foraging habitat quality may increase predation risk as animals spend more time seeking refuge (Bennett *et al.* 2013); and foxes are more common in cleared areas than intact habitat (Towerton *et al.* 2011).

The brushtail possum (*Trichosurus vulpecula*, hereafter ‘possum’) is a medium-sized (1–4 kg, Kerle 2001), arboreal marsupial native to Australia. Possums are within the “Critical Weight Range” (55 g – 5.5 kg, Burbidge and McKenzie 1989) of Australian mammals most susceptible to decline and extinction. The species formerly occupied nearly all of the Australian mainland but has disappeared from more than 50 % of its historic distribution since European settlement. In arid central Australia, possums only persist in small, widely scattered populations (Kerle *et al.* 1992; Foulkes 2001). Despite being listed internationally as “Least Concern”, their population trend is declining (Morris *et al.* 2008; Woinarski *et al.* 2014), especially in arid and semi-arid areas (Kerle *et al.* 1992; Kerle 2004). Possums are nocturnal and spend the day usually in tree hollows (Burbidge *et al.* 1988; How and Hillcox 2000). Large hollow-bearing trees are an important component of their preferred habitat (Whitford 2002; Cruz *et al.* 2012a). The general decline of brushtail possums in Australia has been attributed to predation by introduced predators, particularly foxes, and a decline in habitat quality through the removal of large hollow bearing trees and natural food plants caused by factors such as clearance, altered fire regimes and degradation by introduced herbivores. Drought refuges are considered vital to the survival of possums, and indeed other fauna in the arid zone (Morton 1990; Pavey *et al.* 2017) and are located in the most nutrient rich and moisture prone soils within the landscape that also support good hollows and food resources (Foulkes 2001). Exotic herbivores contribute to the degradation of these refuges, increasing vulnerability of possums to predation from introduced predators, which can lead to local extinctions (Kerle *et al.* 1992; Kemper and Foulkes 1997). This theory that decline is caused by a combination of habitat degradation and predation is supported by other research on possums in mesic areas (Pickett *et al.* 2005) as well as other species from arid Australia (Burbidge and McKenzie 1989; Morton 1990).

To investigate the importance of habitat quality in reintroduction programs, we monitored the habitat quality and post release parameters during a reintroduction of the brushtail possum into the semi-arid zone in Australia, where predator management was implemented. The release occurred within the Ikara-Flinders Ranges National Park, where possums were reported to have become extinct between 1926 and the 1940’s (Tunbridge 1991; Kerle *et al.* 1992). The Flinders Ranges was once a refuge for a range of arid species due to its habitat diversity and complexity, including the abundance of reliable springs and long lived hollow bearing trees. However, vegetation quality has been severely compromised, initially through unsustainably high sheep stocking rates followed by the invasion of European rabbits (Medlin 1993), and more recently by large populations of feral goats and native kangaroos. The red fox, known to be the main predator of possums in previous translocations (Pietsch 1995; DEC 2012), has been successfully controlled on the Park using poison baits (Brandle *et al.* 2018). Feral cats were present but were not considered high risk predators to adult possums given co-existence on islands with dense feral cat populations (Bengsen *et al.* 2011). We asked whether possums could be successfully released into an historically degraded environment if foxes were controlled. If poor vegetation quality was affecting post release parameters, we expected that possums might exhibit poor body condition and limited breeding compared with known parameters from other sites, along with inflated home range sizes, long distance and extended post-release dispersal as they searched for better habitat, mortalities from malnutrition and high use of supplementary shelter sites. Predation was not expected to significantly affect reintroduction success because of ongoing fox control (Brandle *et al.* 2018), although other possible predators such as feral cats, dingoes (*Canis lupus dingo*), carpet pythons (*Morelia spilota*), western quolls (*Dasyurus geoffroii*) and wedge-tailed eagles (*Aquila audax*) were present.

4.5 METHODS

4.5.1 Study site and historic impacts on habitat quality

The Ikara-Flinders Ranges National Park (IFRNP, 31° 31’ 43” S, 138° 36’ 13” E) is an iconic, rugged range situated in semi-arid South Australia (Fig. 4.1). Vegetation complexes comprised of river red gum (*Eucalyptus camaldulensis)* creeklines, woodlands comprised of river red gum flood out areas or mixed native pine (*Callitris glaucophylla*) and gum coolibah (*E. intertexta*), shrubland (*Acacia* and *Allocasuarina* spp.), mallee (*Eucalyptus* spp.), and open grassland. Only two species of large hollow bearing trees are common in the area; river red gum and gum coolibah, the former occupying creeklines and woodland flood outs and the latter occupying woodlands with mixed native pine.

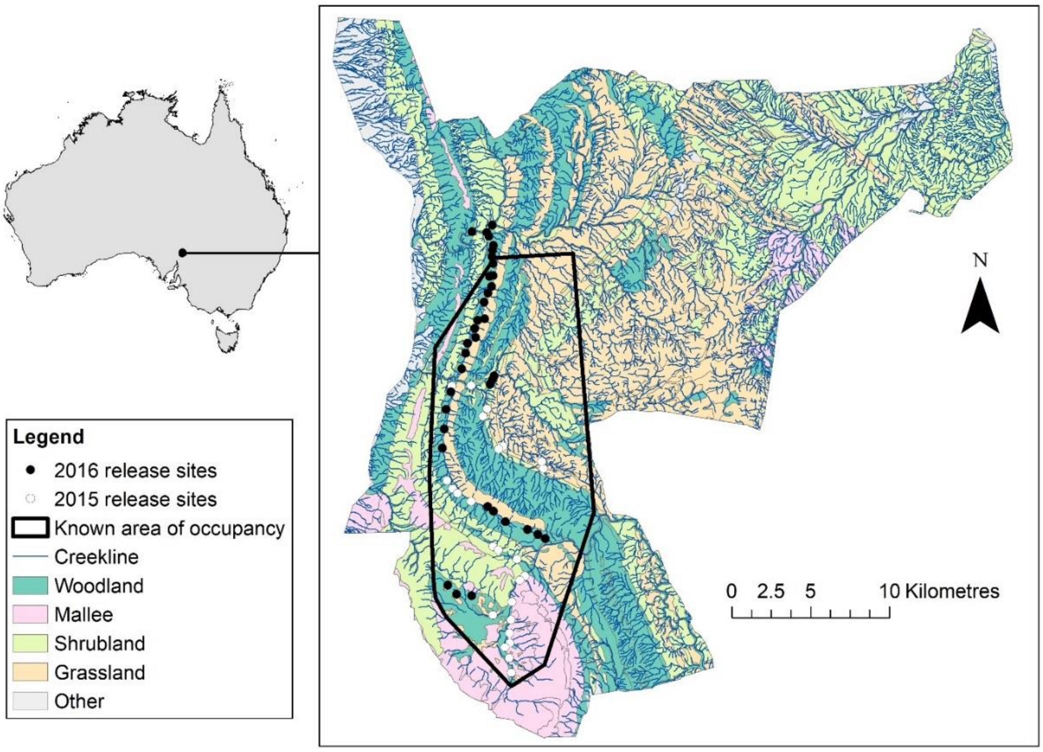

Figure 4.1: Map of the Ikara-Flinders Ranges National Park, showing possum release sites (2015 and 2016), habitat types found within the park and the known area of occupancy at the end of the study in March 2018.

Europeans began to take up pastoral leases in the Flinders Ranges from the 1850s to graze sheep and other domestic stock on the native grasses and chenopod shrubs (Mincham 1996). Initial minimum stocking rates were set at a grossly unsustainable level (Brandle 2001), which decimated palatable perennial shrubs, grasses and ground cover, especially during periodic droughts (Medlin 1993; Mincham 1996; Robinson 2012). The result was widespread severe soil erosion and reduced productivity (DENR 1995). Excessive trampling by ungulates impacted river red gum communities through degradation of soil structure, reduced water infiltration, accelerated erosion and diminished soil nutrient levels (Yates *et al.* 2000; Souter 2009). Habitat quality was further reduced by subsequent rabbit and goat invasions that suppressed regeneration of vegetation and exacerbated soil erosion (Smith 1996; Souter 2009; DEWNR 2012). The local extinction of more than 30 native mammals occurred by the 1930's (Tunbridge 1991; Medlin 1993).

The IFRNP was proclaimed a national park in 1970 and a pest management program, "Bounceback", was initiated in 1992 focussing on fox, goat and rabbit control (Alexander *et al.* 1997; Robinson 2012). Although there have been some improvements in habitat quality, land condition is still considered poor to fair (DEWNR 2012). Introduced herbivores, whilst managed, are still present, and combine with excessive kangaroo (*Macropus* spp.) densities to prevent recovery of native grasses, forbs and palatable shrubs (Brandle *et al.* 2018). Quarterly fox baiting was initiated in 1992 (Brandle *et al.* 2018) and average fox detection rates per month (total detections > 10 minutes apart divided by total camera trap nights x 100) on 30 remote cameras set in the possum release area for 1 year prior and 3 years after reintroduction averaged 0.005 %, suggesting that fox control was highly effective. Cat detection rates averaged 2 % per month during the same period, and dingoes and reintroduced western quolls both averaged 2.5 %.

The 33 month study period began in June 2015 with the first release of possums and ended in March 2018. Average rainfall at Wilpena Pound in the IFRNP is 440mm but fluctuates significantly over time; below average rainfall was received in the two years prior to release and average or above average rainfall during the two releases in 2015 and 2016 (Fig. 4.2).

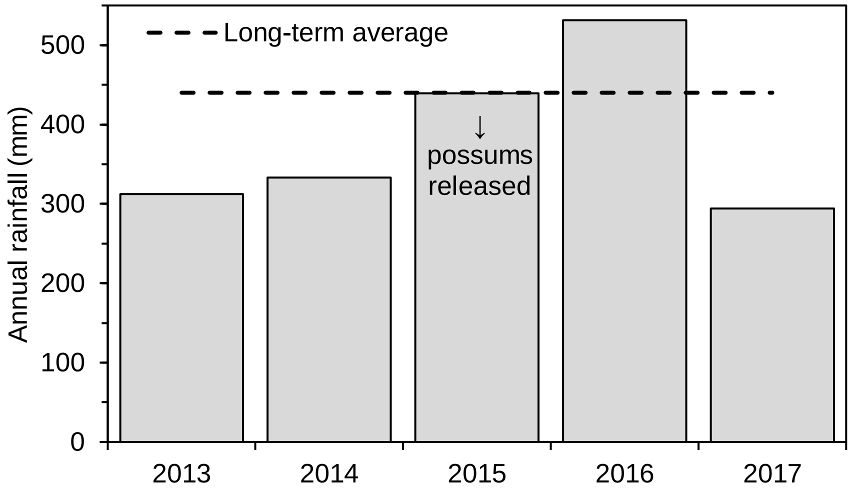

Figure 4.2: Average rainfall at the reintroduction site (Wilpena Pound) and annual rainfall received prior to and after the initial release. Rainfall statistics from Bureau of Meteorology (2018).

4.5.2 Measures of habitat quality

Although vegetation quality of the study site was known to be degraded from over 100 years of overgrazing, we measured three attributes in order to understand their possible effects. We assessed the availability and demography of hollow bearing trees, cover of mid storey vegetation and availability of known preferred food plants of possums in arid systems. The study area was approximately 22,000 ha as defined by the known area of occupancy by possums (100% Minimum Convex Polygon) at the end of the study period based on radio-tracking, capture locations and camera detections. Hollow availability in different habitat types was measured using 1 km belt transects. The number of four hollow-bearing species or species groups (river red gum, gum coolibah, native pine and mallee *Eucalyptus spp*.) were counted within a 20 m wide belt. Gum coolibahs are occasionally present in mallee form but were counted as gum coolibahs not mallee. For all river red gum and gum coolibah trees we measured DBH (diameter at breast height), living status and whether they were hollow-bearing. Transects were conducted in each of the two main habitat types used by the possums as evidenced from radio-tracking data; 10 in river red gum creeklines and 19 in mixed woodland (stratified into river red gum floodout and native pine/gum coolibah woodland, with 6 and 13 transects conducted in each sub-habitat respectively). For the purposes of this study, "young" trees were considered to be those not yet successfully recruited into the population, classified as those ≤ 10 cm for gum coolibah and slightly wider in river red gums (≤ 15 cm as per Ellis *et al.* 2017) due to their ability to reach much wider DBH.

The midstorey vegetation structure around shelter trees was recorded by measuring the percentage cover of midstorey species within circular plots of 50 m radius around random shelter trees, with 84 unique sites surveyed in the 12 months after release. Midstorey was defined as shrubs within a height range of 0.5 to 3 m which would provide cover, an escape from predators, and food. Previously identified preferred and/or nutritious plant species that were present at other arid zone possum sites (Evans 1992; Foulkes 2001) were noted with their availability extracted from midstorey surveys.

4.5.3 Possum reintroduction

A total of 148 possums were released into the IFRNP in 2015 (79) and 2016 (69) (Fig. 4.1). In 2015, possums were translocated from Yookamurra Wildlife Sanctuary (34° 32' 22" S, 139° 28' 33" E), a fenced, feral-predator free conservation reserve owned by the Australian Wildlife Conservancy (Australian Wildlife Conservancy 2018). In 2016, individuals were sourced from Yookamurra (50), and the closest extant population of brushtail possums, in the southern Flinders Ranges (32° 38' 49" S, 138° 05' 45" E) (19). Both introduced foxes and feral cats were present in the area. Approximately even numbers of each sex were released. Possums were captured using handheld spotlights, flags and nets (Whisson and Carlyon 2010) or in baited cage traps. Possums were weighed, checked for reproductive condition (presence or absence and size of pouch young, or evidence of lactation) and body condition and given a unique eartag and microchip. A proportion of possums (48 in 2015 and 20 in 2016) were fitted with VHF radio-collars (V5C-161E, 35 g or V5C-162E, 41 g, Sirtrack, New Zealand, or M1820, 27 g, Advanced Telemetry Systems, Australia). Several GPS collars (VHF/GPS datalogger collar, 45g, Sirtrack, New Zealand) were fitted to possums for various lengths of time (usually ca.1 month).

Possums were released at night in pairs at the base of adjacent hollow-bearing trees. Prior to release, 75 nest-boxes were attached to river red gums in creeklines or occasionally to native pines at a height of ~ 3 m. In 2015, a sample of possums were released into delayed release pens (n = 16) or nest-boxes (n = 16) as part of a release methods study (Bannister *et al.* 2018). We developed potential short- and long-term reintroduction success criteria (Table 4.1); long-term success criteria were not tested within the time frame of this study.

Table 4.1: Potential indicators of short- and long-term reintroduction success and evidence requirement to assess achievement. Long-term success criteria have not yet been measured.

Criteria type	Criteria	Criteria met	Evidence
Short	Survival of 50% of individuals from each released population in first 3 months	Yes	Kaplan Meier survival of radio-collared possums in first 3 months (0.99)
Short	Maintenance or increase in body condition and mass after release	Yes	Body condition and weights of possums stable or increasing ca.60 days post-release following initial decrease
Short	Survival of 25% of released individuals in first 12 months	Yes	Kaplan Meier survival of radio-collared possums after 12 months (0.70)
Short	Survival of at least some emergent pouch young in first 12 months and F2 generation produced in first 3 years	Yes	Survival of radio-collared recruits (65%). Proportion of adult females captured with pouch young in the 3 years after release (87%). Proportion of females reintroduced with pouch young where young survived to pouch exit (94%). F2 generation produced.
Long	Increase in extent of occurrence and abundance over a 5 year period	N/A	Annual cage trapping across the IFRNP, detection rates on cameras set inside and outside known area of occupancy
Long	Population recovery after drought	N/A	Annual cage trapping across the IFRNP, detection rates on cameras set inside and outside known area of occupancy

4.5.4 Effects of habitat quality

The influence of habitat quality on possum survival was assessed using the following criteria; mortality rates and cause of death, body condition, reproduction, the use of natural hollows compared with nest-boxes, movement and home range size.

4.5.4.1 Mortality

Radio-collared possums were tracked by plane or on ground every 1-2 days for the first month and approximately weekly thereafter. Most possums were radio-collared for up to 6 months after release, but a small number of individuals were radio-tracked for almost 2 years. Any possums found recently dead were autopsied by wildlife vets (Zoos SA). DNA samples were taken from radio-collars and puncture wounds with a cotton swab dipped in Tissue Digest (DXT) (Qiagen). DNA swabs were stored in the freezer and then sent to the Wildlife Genetics Lab (Institute for Applied Ecology, University of Canberra) or Helix Molecular Solutions (Perth) to identify whether DNA of cats, foxes or dingoes was present (further details in Moseby *et al.* 2015).

Kaplan Meier survival analysis was conducted for released radio-collared possums. Survival curves were compared between sexes and between release cohorts (2015 Yookamurra, 2016 Yookamurra, 2016 South Flinders). Two deaths after release were caused by poorly designed radio-collars and were excluded from survival analyses. Twenty-six possums born after release or translocated as small pouch young were radio-collared once they had emerged from their mother's pouch to assess survival of recruits within the reintroduced population (further details in Bannister *et al.* 2019). Recruits were radio-tracked approximately weekly until a maximum age of 610 days (Bannister *et al.* 2019). The proportion of surviving recruits was compared with released adult survival using a Fisher's Exact Test.

4.5.4.2 Body condition and reproduction

Uncollared possums were captured opportunistically but radio-collared possums were trapped every 4–12 weeks to check reproductive and body condition. A linear mixed effects model within the R package lme4 (Bates *et al.* 2015) was used to test whether the proportional change in adult body mass after release varied by sex, release cohort or time since release (grouped by season and year). Records from < 1 month after release were omitted as some possums were known to have rapidly lost weight during this period (Bannister *et al.* 2018). Possums with less than three records were omitted. Model interaction terms were included for time and sex, and time and release cohort. Possum identity was included as a random effect. Model significance was assessed using an Analysis of Deviance.

Body condition was scored on a scale of 1 (poor) to 5 (excellent) based on the amount of fat felt around the pelvis and backbone. Body condition for all captured adult possums was compared over time using a linear mixed effects model. Two separate models were run, as there were too many variables for the given sample size. Body condition was the response variable, and time since release, sex, and an interaction between the two were explanatory variables. Possum identity was included as a random effect. In the second model, release cohort was swapped with sex. Juvenile and subadult possums (males: testes length ≤18mm, females: pouch shallow, clean) were excluded from the analysis.

4.5.4.3 Tree hollows

Hollow use was assessed by investigating attributes of natural shelter sites used by radio-collared possums after release, and comparing natural hollow use with the use of artificial nest-boxes. Radio-collared possums were tracked to their diurnal shelter site approximately weekly. For each site, the location and type of hollow (nest-box or natural hollow) was recorded. For natural hollows, tree species, DBH, live/dead status and habitat type were recorded. Shelter sites used within the first month of release were excluded from analyses as they may not be representative of normal behaviour (Bannister *et al.* 2018). The height (using a range finder) of 56 randomly selected Eucalypt shelter trees was compared to the closest Eucalypt that had not been identified as a used shelter site. For hollows used by radio-collared possums, the tree species, the DBH of the tree and the proportion of live to dead trees used as shelter sites was compared with available hollow information taken from transect data using chi-square tests and unpaired student t tests. Transect data were extrapolated to estimate hollow availability across the possums' area of occupancy.

4.5.4.4 Movement, home range size and habitat use

Dispersal distances were obtained for 67 radio-collared possums across the three release cohorts (n = 47, Yookamurra 2015; n = 10, Yookamurra 2016; n = 10, South Flinders 2016) four weeks after release, when most possums had settled (regularly returning to the same shelter sites and no longer making unidirectional movements). Three males had not settled after four weeks and we calculated their dispersal distance using their actual settling date. Distances were log-transformed to meet model assumptions. A generalised linear model was used to investigate whether there was an effect of sex or release cohort on dispersal distance, with an interaction term between the two.

For 58 adult possums, at least 20 locations (daytime shelter, trap site, night time radio-tracking or GPS fix) were recorded during the study. For these possums, 100, 95 and 50 % minimum convex polygons (MCPs) were calculated using the R package adehabitatHR (Calenge 2006). For 100 % MCPs, 1000 iterations of incremental additions of fixes (5 at a time) were run, to determine whether the home range reached an asymptote. An estimated asymptote value was then produced for each possum. We considered possums that were within 20 % of the predicted asymptote value to be within an acceptable range for inclusion in further analysis. 95, 90 and 50 % kernel density estimates (KDEs) were calculated using the HRT 2.0 extension in ArcMap (Rodgers *et al.* 2015). Non-parametric Wilcoxon Rank Sum Tests were used to test for differences in home range size based on sex.

For possums with GPS data that had reached acceptable asymptotes, the proportion of their home range (*r*) falling within each vegetation type (creekline, woodland, grassland, mallee and shrubland taken from www.data.environment.sa.au/naturemaps) was compared with availability (*p*) as calculated within all of the possums' collective area of occupancy, using ArcMap 10.3.1 (ESRI, California). Habitat selectivity (*D*) was calculated using the Jacob's preference index (Jacobs 1974), where $D = (r–p) / (r + p – 2 \times r \times p)$. A non-parametric Wilcoxon Rank Sum Test was then used to compare the selectivity index to zero to test whether a habitat type was preferred or avoided relative to its availability. Positive values indicate a preference while negative values indicate avoidance relative to availability. For all statistical analyses, the significance level (alpha) was set at 0.05.

4.6 RESULTS

4.6.1 Measures of habitat quality

Twenty-nine transects (27.5 km) were surveyed. The density of hollow bearing trees was 27.3 per hectare in river red gum creekline and 5.7 per hectare in woodland. River red gums comprised the majority of trees bearing hollows in creeklines, and river red gums and gum coolibah were in similar proportion in woodlands (Table 4.2). The total number of hollow bearing trees available in the release area was calculated by multiplying the density of hollow bearing trees per hectare in each vegetation type by the proportion of that vegetation type within the possums' area of occupancy. An estimated total of 65,092 river red gums, 17,564 gum coolibah and 666 pines with hollows were present within the 21,000 ha area of occupancy, at an overall density of 3.96 hollow bearing trees per hectare.

Table 4.2: Density of hollow bearing trees (per hectare) in each vegetation type across the study area.

Vegetation type	River red gum	Gum coolibah	Native pine	Total
Creekline	27.2	0.05	0.05	27.3
Woodland	3.0	2.6	0.09	5.7

Frequency histograms of DBH suggested that all age classes were present (Fig. 4.3). River red gum frequency distribution indicated a high density of young trees suggesting recent germination events. However, a lower frequency of occurrence was recorded in the middle size classes. In comparison, gum coolibahs had lower frequency in smaller age classes suggesting low recent recruitment. Hollows were present in river red gums from as small as 25 cm DBH but were more reliably present in trees with DBH > 100 cm. Hollows were regularly recorded in gum coolibahs with a DBH of more than 60 cm. Native pines were the most common tree, present on 91 % of transect segments, with river red gums present on 61 %, gum coolibah present on 26 % and mallee present on 5 % of transect segments. Of the transect segments that contained gum coolibahs only 18% of these also contained young gum coolibahs (<10 cm DBH, 13 of 72 segments) compared with 44% for river red gum (< 15 DBH, 73 of 167 segments).

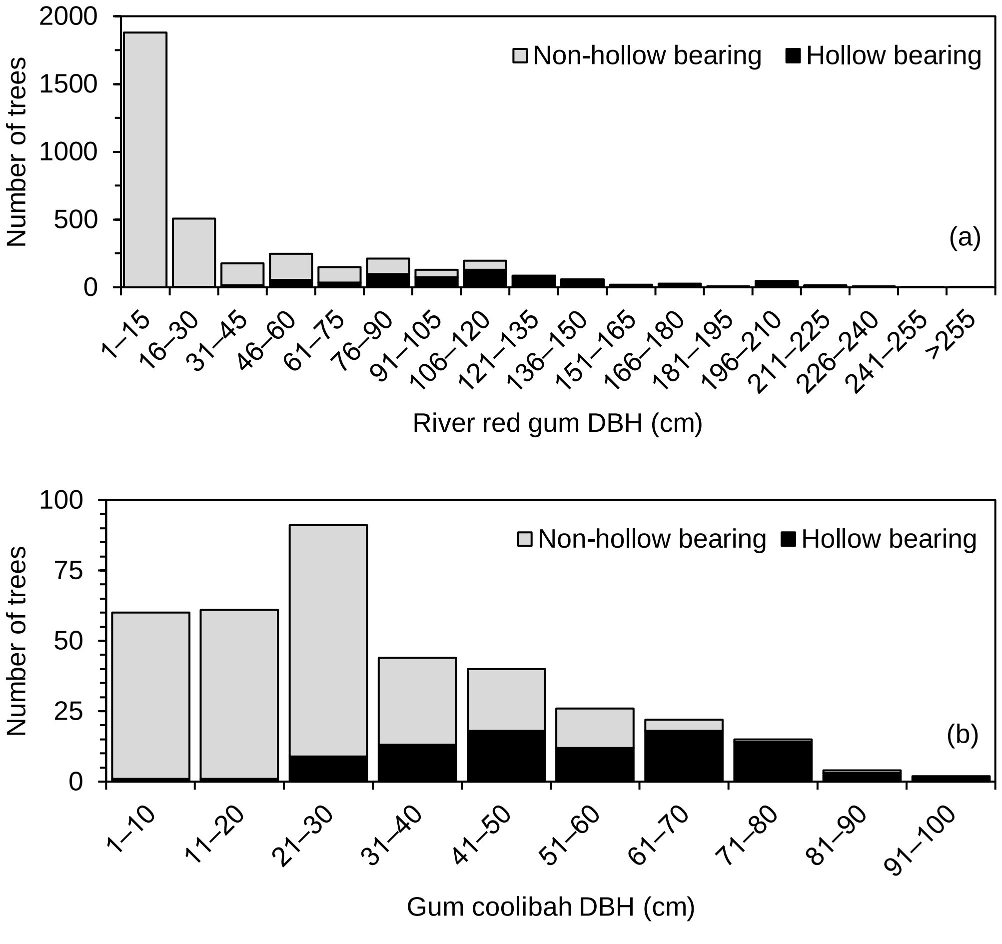

Figure 4.3: Histogram showing frequency of Diameter Breast Height (DBH) classes for river red gum (a) and gum coolibah (b) in the study area from transect data

Midstorey cover at vegetation survey sites around shelter trees ranged from 0 to 65 % with an average of only 12.9 % (± 1.5). Genera providing the most cover included *Acacia* (mean cover 3 % ± 0.6), *Dodonaea* (3 % ± 0.5), *Olearia* (2.1 % ± 0.4) and *Senna* (2 % ± 0.3). Combined, these species made up more than 78% of midstorey cover. Preferred foods identified by previous arid zone possum diet studies (Evans 1992; Foulkes 2001) comprised on average less than 4% cover in vegetation surveys in the IFRNP (Table 4.3). Whilst acacias were found in almost half of the quadrats sampled, the remaining genera were in low frequency of occurrence. Whilst 64 % of survey sites contained one or more known preferred food species, only 25 % contained a known preferred food plant other than *Acacia*.

Table 4.3: The availability of preferred food plants within IFRNP (± 1 standard error). Frequency of occurrence = percentage of vegetation surveys the genus was detected in.

Genus	Mean % cover	Frequency of occurrence
Acacia (Wattles)	2.95 ± 0.5	45.5%
Amyema (Mistletoe)	0.090 ± 0.04	5.4%
Euphorbia	0.15 ± 0.04	11.6%
Lysiana (Mistletoe)	0.054 ± 0.03	3.6%
Rhagodia (Salt bushes)	0.21 ± 0.1	5.4%
Santalum (Plums Cherrys)	0.11 ± 0.08	1.8%
Solanum (Nightshades)	0.071 ± 0.03	5.4%
TOTAL	3.635	64.3%

4.6.2 Effect of habitat quality

4.6.2.1 Survival

Sixty eight released adult possums and 26 recruited possums were radio-collared for an average of 234 days (± 17.75, range 11-714 days). Twenty one percent (15) of collared adults died during the study period. The most common cause of death was predation (6), followed by natural/unknown causes (4) and non-target 1080 poisoning during routine fox and experimental cat control operations conducted by DEW (3, Table 4.4). Autopsy results indicated that no possums died from a result of malnutrition.

Table 4.4: Causes of mortality in radio-collared possums after release into the IFRNP, grouped by released animals and animals reared in the IFRNP (recruits).

		Released	Recruits	Method of determination
Number radio-collared		68	26	
Cause of Death				
Predation	Cat	3	5	DNA swab of carcass, direct observation
	Dingo	1	0	DNA swab of carcass
	Suspected quoll	1	1	Observation at carcass site
	Suspected cat	1	1	Remains found in cat lair
1080 poisoning		3	0	Autopsy/organ testing
Collar		2	0	Carcass found with wedged collar
Unknown		1	1	Autopsy - no obvious cause of death
Natural		3	1	Autopsy – not predation
Total deaths		**15**	**9**	

Kaplan Meier survival analysis found no significant difference in survival between males and females (*P* = 0.72) or between release cohorts (*P* = 0.28). When animals were pooled to determine overall survival probability, survival of radio-collared released animals was estimated at 0.93 (95% CI 0.81–0.97) at six months post release and 0.70 (95% CI 0.48–0.84) at 12 months post release (Fig. 4.4).

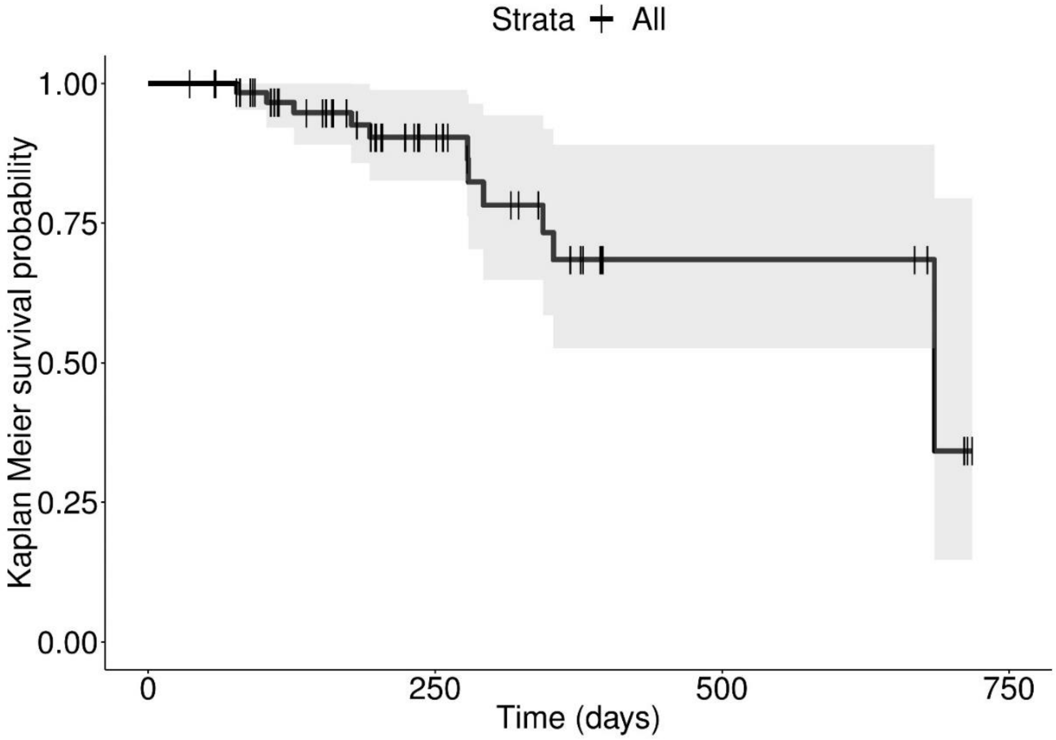

Figure 4.4: Kaplan-Meier survival curve for possums reintroduced to the Ikara-Flinders Ranges National Park, based on radio-tracking data. Markers denote either collar removal or death.

Of the 26 recruits radio-collared, 65 % survived to maturity. Two recruits died from natural or unknown causes and a higher proportion of recruits died from predation (27 %) than did radio-collared released adults (9 %), however this was not statistically significant (odds ratio 1.9, $P = 0.26$). Detailed analyses of juvenile survival are given by Bannister *et al.* (2019).

4.6.2.2 Reproductive condition and body condition

Of the 24 radio-collared females released in 2015, 20 (83 %) had pouch young at the time of release. The fate is known for 17 of these young, of which 16 (94%) survived to pouch exit. After release possums bred continuously with only 10 out of 293 captures of adult female possums (or 7 out of 54 individual females) not carrying pouch young or lactating at any time over the 33 month study period. Of the adult females regularly trapped and monitored over the study period, all successfully produced at least one young per year and up to 5 young during the study. Sixty five new recruits were captured during the study period. The sex ratio of possums born after release (20 females and 27 males) and translocated as pouch young in 2015 (14 females and 14 males) bordered on parity.

Overall, possums increased in weight after release (Fig. 4.5). The body mass of male and female possums changed significantly in relation to time since release ($\chi^2 = 57.0$, df = 10 $P < 0.0001$, Fig. 4.5), release cohort ($\chi^2 = 16.5$, df = 2, $P = 0.00026$) and sex ($\chi^2 = 6.5$, df = 1, $P = 0.011$). There was a significant interaction between time since release and sex ($\chi^2 = 28.6$, df = 10, $P = 0.0014$), but not time since release and release cohort ($\chi^2 = 0.2$, df = 2, $P = 0.89$). Post-hoc comparisons revealed that males gained weight at a faster rate than females, and there was a significant difference only between the South Flinders 2016 and Yookamurra 2015 release cohorts. The 2015 and 2016 Yookamurra release animals increased in weight or remained stable after the release whilst the 2016 source animals from the South Flinders animals lost weight.

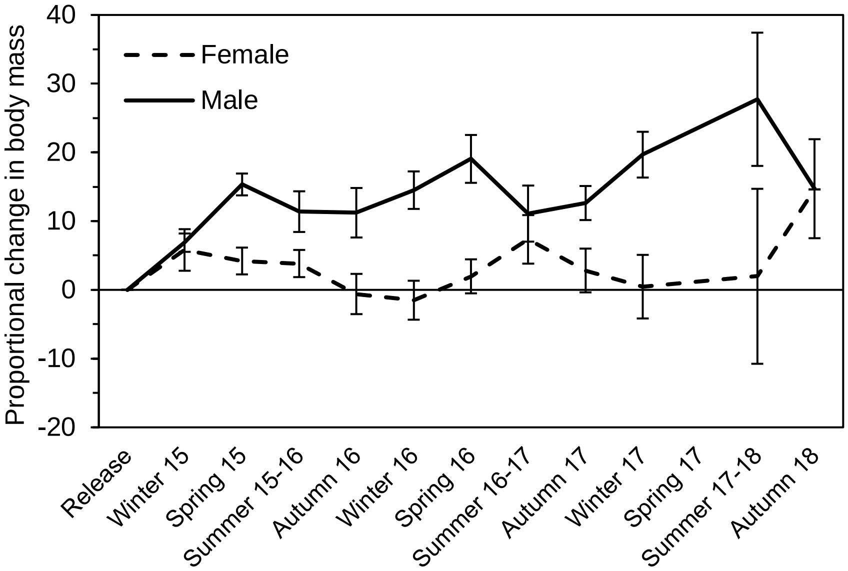

Figure 4.5: Proportional change in body mass (%, ± 1 standard error) for possums released into the IFRNP, where zero represents no change. Female *n* range =1-52 (mean = 19), Male *n* range = 4-35 (mean = 16).

Body condition did not significantly change over time (χ^2_{10} = 14.5, *P* = 0.15, Fig. 4.6), but males were generally in better condition than females (χ^2_1 = 14.9, *P* = 0.00011) and fluctuated more than females (time*sex χ^2_{10} = 25.4, *P* = 0.0045, Fig. 4.6). There was no effect of release cohort (χ^2_2 = 0.25, *P* = 0.88), but there was an interaction between cohort and time (χ^2_{12} = 23.0, *P* = 0.028), with all cohorts fluctuating but at different times.

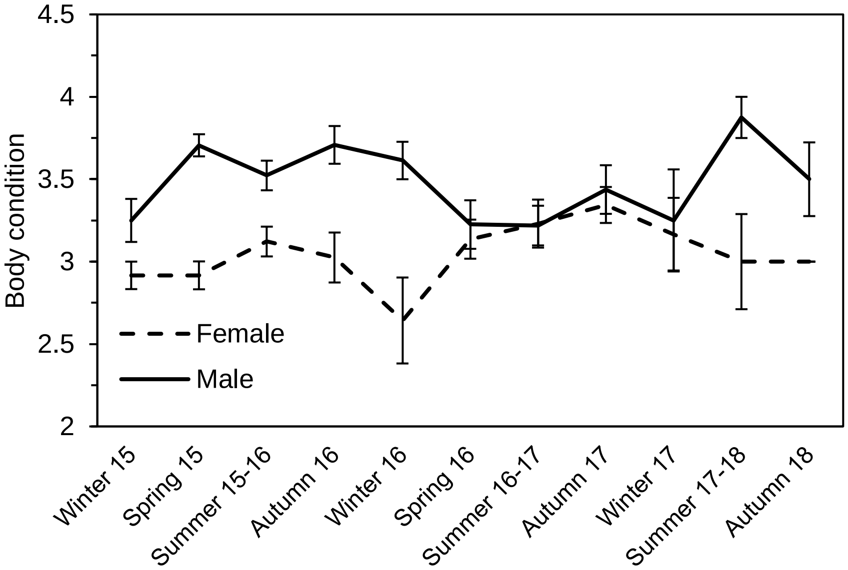

Figure 4.6: Body condition for possums over time, where higher values represent better body condition. Female *n* range = 1–45 (mean = 16*),* male *n* range = 4–34 (mean = 15).

4.6.2.3 Movement, home range and habitat use

Post-release dispersal distances ranged from 64 – 17,108 m, averaging 2,090 m (± 393). Dispersal distance was not significantly influenced by sex ($\chi^2 = 0.2$, *df* = 1, *P* = 0.63, F mean 2304 ± 557 m, M mean 1754 ± 511 m) or release cohort ($\chi^2 = 3.5$, *df* = 2, *P* = 0.17), and there was no significant interaction between sex and release cohort ($\chi^2 = 2.8$, *df* = 1, *P* = 0.097, Fig. 4.7).

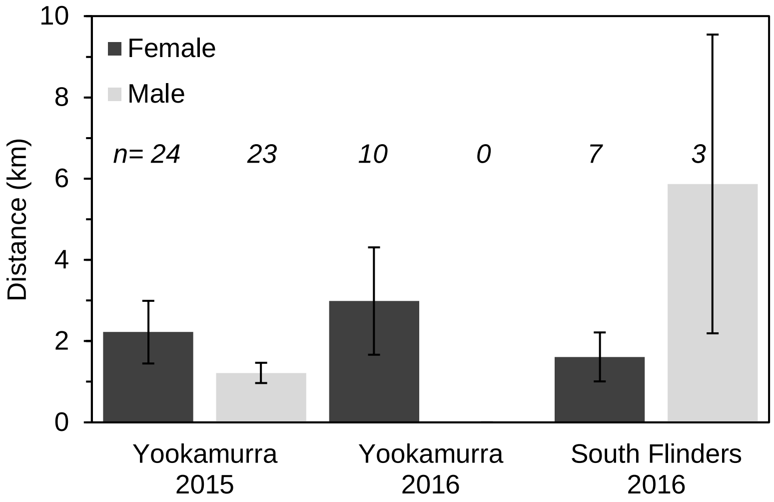

Figure 4.7: Average post-release dispersal distance (4 weeks after release) for radio-collared possums released in three cohorts (± 1 standard error).

Thirty-six of the 58 radio-collared possums with more than 20 fixes were within 80 % of a predicted home range asymptote (30F, 6M) and so were included in home range analysis. The home range of females (*n* = 30) was around half that of males (*n* = 6) (95 % MCP 21.5 ± 3.4 ha and 46.0 ± 13.0 ha respectively), but the difference was not significant at the 0.05 level, probably due to a small sample size for males and large variance (*P* = 0.086, Table 4.5). Of the 11 possums with GPS data, 8 (73 %) reached an asymptote. Habitat selectivity (Jacob's Index) was calculated for those possums as the GPS data enabled information to be obtained on night time foraging and movement. Vegetation mapping (Fig 4.1) showed that woodland, grassland and shrubland habitats were most commonly available, while creekline and mallee habitats were available in lower proportions (Table 4.6). Shrubland and grassland were strongly avoided (*P* = 0.0078 and *P* = 0.0082 respectively) whilst creekline and mallee habitats were accessed in the same proportions as they were available (Table 4.6). There was a non-significant trend towards possums selecting for woodland habitat more than its availability (*P* = 0.082, Table 4.6), a larger sample size would likely strengthen the result.

Table 4.5: Average range size (mean hectares ± 1 standard error) for VHF and GPS collared possums whose 100% MCP was within 20% of the predicted asymptote value. Non-parametric comparisons (Wilcoxon Rank Sum Test) were made between sexes. MCP = Minimum Convex Polygon, KDE = Kernel Density Estimate.

	n	100% MCP	95% MCP	50% MCP	95% KDE	90% KDE	50% KDE
Female	30	30.2 ± 4.6	21.5 ± 3.4	4.3 ± 1.0	88.7 ± 14.9	69.1 ± 11.7	19.7 ± 3.6
Male	6	61.0 ± 15.9	46.0 ± 13.0	9.8 ± 5.2	218.6 ± 61.4	171.9 ± 49.3	52.0 ± 16.1
Significance		*W* = 134 *P* = 0.065	*W* = 131 *P* = 0.086	*W* = 117.5 *P* = 0.25	*W* = 134 *P* = 0.064	*W* = 133 *P* = 0.071	*W* = 132 *P* = 0.078

Table 4.6: Habitat selectivity derived from 8 GPS collared possums. The proportion of available vegetation types are given along with use by possums (± 1 standard error). A positive Jacob's Index value indicates a preferred habitat type and a negative value indicates avoidance. Wilcoxon Rank Sum tests were used to determine significance compared to a value of zero. *= trend but not significant

Vegetation type	Availability (%)	Use (mean %)	Jacob's Index	Significance	Selectivity
Creekline	8	10.9 ± 3	0.09 ± 0.1	*W*=24, *P*=0.40	None
Grassland	30	12.1 ± 5	-0.57 ± 0.2	*W*=8, *P*=0.0082	Avoided
Mallee	10	16.5 ± 9	-0.35 ± 0.3	*W*=24, *P*=0.39	None
Shrubland	21	5.4 ± 4	-0.76 ± 0.2	*W*=8, *P*=0.0078	Avoided
Woodland	32	55.1 ± 9	0.37 ± 0.2	*W*=48, *P*=0.082	Preferred*

4.6.2.4 Shelter sites

Over 2,600 shelter site records comprising 628 unique shelters were recorded over the study period. No artificial nest-boxes were used during the study despite possums being regularly found sheltering in natural hollows nearby. Tree hollows comprised more than 98% of the shelter sites used with river red gum and gum coolibah being the dominant tree species, making up 55 % and 39 % of total shelter sites used respectively. Native pine hollows made up 1 % of shelter sites, while 2 % of tree hollows were in unidentified species. Hollow logs (2 %), mallee hollows (< 1 %), burrows (< 1 %) and rock crevices (< 1 %) were also occasionally used for shelter. A chi square test was used to determine whether possums were using hollow bearing tree species relative to their availability in the study area. The result was highly significant ($\chi^2 = 59.2$, $df = 2$, $P < 0.0001$) with possums using more gum coolibah hollows than expected by chance and fewer river red gums in relation to availability. Although possums showed a preference for gum coolibah hollows, the average re-use rate of tree hollows was similar for all three tree species with each hollow used an average of 4.2 to 4.5 times. Possums used hollow bearing trees with a DBH of between 25 and 450 cm, the average DBH for river red gums and gum coolibahs used by possums was 140 cm and 79 cm respectively and possums selected gum coolibah and river red gum trees with a significantly higher DBH than randomly available hollow bearing trees (river red gum $t = 6.58$, $df = 1$, $P < 0.0001$; gum coolibah $t = 6.78$, $df = 1$, $p < 0.0001$). Possums used hollows in both live (506) and dead (77) trees, in proportion to their availability ($\chi^2 = 1.0$, $df = 1$, $P = 0.32$).

River red gum shelter sites were located in creekline (83 %), floodplain (15 %) and occasionally open woodland (3 %) habitat while gum coolibah shelter trees were recorded almost exclusively in open woodland (98 %). The average height of 18 river red gum and 38 gum coolibah shelter trees was 18.4 m (± 0.8) and 13.2 m (± 0.4) respectively and this did not differ from non-hollow bearing control trees (18.4m ± 1.2 and 12.4m ± 0.6).

4.7 DISCUSSION

Despite significant historic damage and ongoing impacts to habitat within the IFRNP, short-term reintroduction criteria for brushtail possums were met. Possums had high survival after release, bred continuously and successfully reared young. Following an initial post-release decline (Bannister *et al.* 2018), body condition and body mass were maintained or improved after release, thus food availability was not a limiting factor. Possums dispersed an average of 2 km from their release site and settled within one month of release, establishing home ranges. There were sufficient natural hollows present for use by the reintroduced population, with no use of artificial shelters.

Female home range size (21 ha, 100 % MCP) was comparable to studies at other resident (32 ha, Foulkes 2001) and reintroduced ((32 ha, Short and Hide 2014) arid / semi-arid sites. Male home ranges (46 ha, 100 % MCP), however, were slightly larger (resident: 30 ha (Foulkes 2001), reintroduced: 36.1 ha (Short and Hide 2014)). The low number of previous home range studies at arid zone sites combined with a low sample size for males in the current study makes it difficult to determine whether male home ranges were inflated within the IFRNP, and if so whether this was due to vegetation quality or simply due to reintroduction into unoccupied habitat. However, the similarity in female home ranges suggests inflation is unlikely.

No nest-boxes were used by possums after release despite being readily used by possums in some other areas (Harper *et al.* 2005; Lindenmayer *et al.* 2015). The low use of nest-boxes and the high estimated density of hollows available in the release area suggests natural hollow density is sufficient and unlikely to restrict possum density growth in the medium term. Hollows are the preferred shelter site for possums and availability has been shown to be an important factor determining density and distribution (Lindenmayer *et al.* 1990; Lindenmayer *et al.* 1991; Smith and Lindenmayer 1992; Wormington *et al.* 2002). The density of 3.96 hollows per hectare in our release area is lower than the 6 hollows per hectare found by Wormington *et al.* (2002) to support the maximum abundance of arboreal mammals in south-eastern Queensland eucalypt forests, but our study area is considerably more arid. However, whilst hollow availability is high, it is patchily distributed and almost exclusively restricted to two vegetation types (creekline and woodland). Significantly higher hollow density was recorded in creeklines which comprised only 8% of available vegetation. Possum distribution and diurnal and nocturnal ranges within the release area were predominantly focused within these vegetation types, reducing the actual available habitat to 40% of the area of occupancy. Results suggest that possums are closely associated with hollow bearing tree habitat, which should be taken into account when estimating carrying capacity at reintroduction sites.

Our possums used hollow bearing trees with a DBH usually > 45 cm for gum coolibahs and > 80 cm for river red gums compared with >55 cm (Kerle 2001) and >80 cm (Pausas *et al.* 1995) in other studies. Estimating the health of hollow bearing tree populations using the relative frequency of different size classes is difficult but has been used by many researchers due to the absence of accurate ageing data (Kohira and Ninomiya 2003; George *et al.* 2005; Ellis *et al.* 2017). Tree species with continuous recruitment should produce “inverse -J” shaped histograms (Smith *et al.* 1997; Kohira and Ninomiya 2003) where the majority of trees should be in lower size categories with a gradual decline through the age classes because young trees have a higher mortality rate, particularly in thick stands where they thin out (Smith *et al.* 1997). Although river red gum recruitment is thought to be driven by flooding (Di Stefano 2002), the high densities of saplings and young river red gum trees recorded was encouraging but the low and constant frequency of trees in the middle size classes suggests that hollows may become less abundant in the medium term. Seedling survival is impacted by domestic stock, rabbits and kangaroos (Jansen and Robertson 2001) but this is usually only significant during drought years (Dexter 1970). The relatively slow growth of river red gums (Taylor *et al.* 2014; Ellis *et al.* 2017) and their long life span (500–1000 years (Jacobs 1955; Colloff 2014)) suggests that any reduction in density of hollow bearing trees may not be noticeable for many years. There may be a hiatus during which older trees die and younger trees have not yet formed suitable hollows.

Of more concern is the low recruitment of the gum coolibah, a preferred shelter tree and one that is not as reliant on flooding for recruitment events. The relative frequency of small trees was substantially lower than other size classes and this was reflected in the low number of transect segments that contained young trees. Given the above average cumulative rainfall since the 1970s (Bureau of Meteorology www.bom.gov.au) it is most likely that seedlings are being removed, probably by introduced herbivores including rabbits and goats, and three species of native kangaroos (*Macropus spp*.) that were in high abundance during the period of this study (DEWNR 2017; DEW, unpubl. data). Current recruitment may not be sufficient to maintain hollow density in the long term (Gibbons *et al.* 2008). Relationships between tree growth, habitat variables and hollow formation are complex (Ellis *et al.* 2017) and more research is needed to understand the trajectories of these important hollow bearing trees and ensure adequate hollows into the future.

Due to the potential lag effects of hollow availability, the three measures of vegetation quality (hollow availability, midstorey cover and preferred food plants) showed inconsistent trends. Current hollow availability was high in woodland and creekline vegetation but long term hollow availability may be compromised. Midstorey cover and the availability and cover of preferred food plants was low (Table 4.3). The current availability of tree hollows may have been a more important determinant of short-term reintroduction success than cover or availability of preferred food plants. Possums are flexible in their diet and feed on a wide variety of leaves, stems, flowers and fruit, and can include a high percentage of *Eucalyptus* leaves which are ubiquitous throughout the park (Kerle 1984; Foulkes 2001). However, brushtail possums have high nutritional requirements in comparison with other arboreal mammals and a high diversity of food resources is considered advantageous to persistence (Marsh *et al.* 2006). Other arboreal mammals have been found to have higher abundance where they have access to a wide range of food items to allow for seasonal availability (Braithwaite *et al.* 1983; McElhinny *et al.* 2006), and Foulkes (2001) found high quality food plants were important predictors of population persistence for resident brushtail possums in central Australia. Dietary studies conducted during our release indicate that three of the four dominant midstorey species (*Dodonaea, Olearia* and *Senna*) were avoided by possums (H. Bannister, unpub. data). Poor midstorey cover and low occurrence of preferred plant species, despite above average rainfall conditions in recent decades (Bureau of Meteorology 2018), likely reflects high herbivore pressure. Overgrazing can remove shrub and understorey cover, reduce water infiltration, accelerate erosion and arrest recruitment of trees (Yates *et al.* 2000; Souter 2009), potentially impacting on long term population persistence of possums, particularly during droughts.

There were no known possum deaths from malnutrition or starvation and consistent body condition and weight gain/maintenance suggests conditions at the release site were suitable for survival and breeding. The most significant cause of mortality was predation, predominantly by feral cats. Predation has been shown to be the most significant cause of post-release mortality for other reintroductions of wild possums (Short and Hide 2014) including Cape Range and Paruna in Western Australia where 74% and 30% of possums were killed by predators within a few months of release (DEC 2012; May *et al.* 2016). Even in areas where habitat quality is high, reintroduction failure in translocated urban brushtail and ringtail possums has been attributed to predation (Pietsch 1995; Augee *et al.* 1996; Smith *et al.* 2003). Predation by feral cats is often overlooked when foxes remain present, despite this species being known to predate possums (Kerle *et al.* 1992; Doherty *et al.* 2015a). There are likely to be synergistic effects of poor vegetation quality and predation rates due to increased encounter rates between possums and predators when midstorey cover and canopy connectivity is low (Didham *et al.* 2007; Doherty *et al.* 2015b). Cats are known to have improved hunting efficiency in open landscapes (McGregor *et al.* 2015) and the 30–60 ha home range of possums in the IFRNP combined with poor canopy connectivity in the release area (Menadue 2014) suggests they spend considerable time on the ground at night where they would be exposed to predators. For this reason, predation by cats should be considered a threat that needs monitoring and potentially managing when considering future reintroductions into semi-arid and arid locations.

The reintroduction of the brushtail possum into the IFRNP is considered successful in the short-term likely due to high hollow density, sufficient food resources and effective fox control. The recorded predation rates on possums (Bannister *et al.* 2019), low midstorey cover, and low presence and abundance of high quality plants suggests that feral cat and herbivore control may be required to improve the growth and expansion of reintroduced populations. Plant species diversity could be enhanced through effective herbivore management, which would also promote the establishment of a more diverse and palatable understorey and reduce pressure on seedlings of hollow-bearing trees. Ensuring the survival and replacement of hollow bearing trees will be important for ensuring long-term population persistence which is unlikely to be measurable until after extended drought conditions and senescence of current hollow bearing trees. Our study suggests that reintroductions into degraded habitats may still achieve short-term success, but that longer term population establishment may require more intensive restoration intervention.

4.8 ACKNOWLEDGEMENTS

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5. DIET

Time to adjust: changes in the diet of a reintroduced marsupial after release

Brushtail possum in an Acacia

5.1 CONTEXTUAL STATEMENT

Because of the widespread decline of brushtail possums throughout the arid and semi-arid zones (Kerle *et al.* 1992), there is little detailed knowledge of their diet within these areas. In addition, for a reintroduction to be considered successful it is implicit that released animals can locate and consume sufficient amounts of quality, naturally available food (Griffith *et al.* 1989; Stamps and Swaisgood 2007). The time taken to do so is rarely documented, but inferred via alternate measures such as reproduction and body mass. This chapter documents the availability of plant species within the possums' area of occupancy over a 12 month period, and compares this to the consumption of these plant species by possums with evidence from 253 samples collected from adult possums, analysed using next-generation DNA sequencing. The consumption and availability of preferred food plants is discussed, and we investigate changes in diet with time since release. We discuss the acclimatisation period indicated by diet compared to other typical acclimatisation measures. Results highlight the importance of using multiple methods to determine acclimatisation times. Results can be used to inform future mammal reintroductions as well as broadening our knowledge of the ecology of the brushtail possum in drier regions of Australia. This chapter has been submitted to the journal *Oryx*.

5.2 STATEMENT OF AUTHORSHIP

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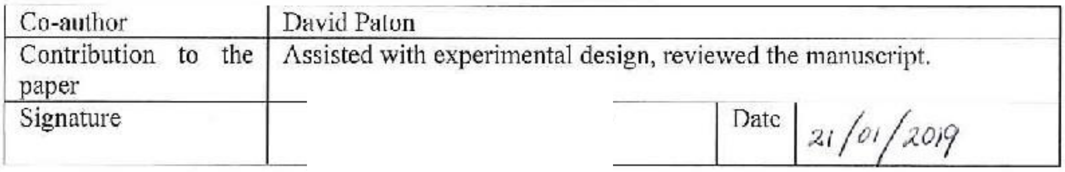
Author contributions

By signing the Statement of Authorship, each author certifies that the stated contributions to the publication are accurate, and that permission is granted for the candidate to include the publication in the thesis.

Primary author	Hannah Bannister		
Contribution to the paper	Designed the experiment, collected the field data, assisted with lab work, analysed the data and prepared the figures, wrote the manuscript.		
Overall percentage	60 %		
Signature		Date	19/01/2019

Co-author	Adam Croxford		
Contribution to the paper	Conducted the lab work, assisted with writing the manuscript, reviewed the manuscript.		
Signature		Date	20/01/2019

Co-author	Robert Brandle		
Contribution to the paper	Assisted with experimental design, assisted with data collection, reviewed the manuscript.		
Signature		Date	20/1/2019



Co-author	David Paton		
Contribution to the paper	Assisted with experimental design, reviewed the manuscript.		
Signature		Date	21/01/2019

Co-author	Katherine Moseby		
Contribution to the paper	Assisted with experimental design, assisted with data collection, reviewed the manuscript.		
Signature		Date	19/01/2019

5.3 ABSTRACT

An important component of reintroductions is acclimatisation to the release site. Movement parameters and breeding are common metrics used to infer the end of the acclimatisation period, but the time taken to locate preferred food items is another important measure. We studied the diet of a reintroduced population of brushtail possums *Trichosurus vulpecula* in semi-arid South Australia over a 12 month period, investigating changes over time as well as the general composition of the diet. Next-generation DNA sequencing was used to determine the contents of 253 scat samples collected from adult possums, after creating a local plant reference library. Vegetation surveys were conducted monthly to account for availability. Dietary diversity and richness decreased significantly with time since release, after accounting for availability. Jacob's Index was used to assess selectivity; just 13.4 % of available plant genera were significantly preferred overall, relative to availability. The mean proportion of preferred plant genera contained within individual samples increased significantly with time since release, but the frequency of occurrence of preferred plants did not. Five genera (*Eucalyptus*, *Petalostylis*, *Maireana*, *Zygophyllum* and *Callitris*) were present in more than half of samples. There was no significant difference in dietary preferences between sexes (overlap = 0.73). The diet continued to change 12 months after release, in contrast to reproduction, body mass and post-release movement parameters that stabilised or improved after < 6 weeks. Reintroduction projects should aim to extend post-release monitoring beyond the period in which the diet stabilises relative to availability, and for dry climates, monitor the diet through a drought period.

Key words: acclimatisation, brushtail possum, diet, marsupial, reintroduction, translocation, *Trichosurus vulpecula*

5.4 INTRODUCTION

Acclimatisation is defined as both physical and behavioural responses to changes in environmental factors or conditions (Oxford Dictionary). In a reintroduction context, acclimatisation can be defined as the period of time that released animals take to exhibit normal physiological processes or condition, and normal behaviour, and may include producing young, maintaining or increasing body mass, establishing normal movement patterns (often a stable home range), sheltering in suitable locations, displaying normal activity patterns, locating conspecifics, and consuming a typical diet (Armstrong *et al.* 2017; Stadtmann and Seddon 2018). If many individuals fail to do so, the reintroduction will fail. Typically, the acclimatisation of released animals is measured by monitoring changes in body mass, post-release movement, reproductive status and the cause of death for released animals that have died (Hardman and Moro 2006; Hamilton *et al.* 2010; Short and Hide 2015). Starvation or malnutrition can occur when released animals fail to locate food resources soon after release (Islam *et al.* 2008; Jule *et al.* 2008); thus, post-release diet is an important, yet often overlooked, component of reintroduction biology, particularly for herbivores. In addition to short-term survival, the availability of stable or seasonally-reliable food resources is critical for reproduction and long-term persistence (Nolet *et al.* 2005; Moorhouse *et al.* 2009; Carlson *et al.* 2014).

The post-release acclimatisation period depends on a species' dietary breadth and movement patterns, and could take days, weeks or months. For example, European mink (*Mustela lutreola*) took around one month after release to shift from an atypical to a typical diet (Põdra *et al.* 2013), and Gilbert's potoroos (*Potorous gilbertii*) increased the number of truffles in their diet with time since release, presumably as they were able to locate new food sources (Bougher and Friend 2009). Other post-release diet studies have assessed diet at various time points after release, rather than monitoring changes over time. For example, 15 months after release, the diet of captive-bred houbara bustards was the same as their wild-born counterparts (Bourass and Hingrat 2015), however the time taken for the birds to adjust their diets is unknown. Many practitioners provide supplementary food or water during the acclimatisation period in an attempt to ease the transition, but the usefulness of this is often debated (Rickett *et al.* 2013; Moseby *et al.* 2014). Understanding the diet of a reintroduced species and how it changes over time is useful in assessing whether dietary components are available in sufficient quantities for long-term population persistence. Dietary studies can contribute to both understanding the ecology of a species as well as improving reintroduction success of future projects.

Our study investigated the diet of a reintroduced population of brushtail possums *Trichosurus vulpecula* (hereafter 'possums') in semi-arid South Australia over a 12 month period following reintroduction. Possums are a widely distributed Australian marsupial, but have disappeared from more than 50 % of their historic range since European settlement, with declines most pronounced in the arid zone (Kerle 1984; Kerle *et al.* 1992). Predominantly arboreal, possums usually forage in the canopy, consuming plants such as *Eucalyptus*, *Acacia*, *Agonis* and *Santalum*, but sometimes forage on the ground, consuming grasses, herbs and fungi (Fitzgerald 1984; Kerle 1984; Evans 1992; How and Hillcox 2000). Dominant plant species in their diet varies with location and environment. Possums occasionally consume invertebrates and birds' eggs (Brown *et al.* 1993; Foulkes 2001; Cruz *et al.* 2012b). In the arid zone, possums prefer plants that are high in moisture, nutrients and dry matter digestibility, with low levels of toxins (Foulkes 2001). Possums were introduced to New Zealand, where their diet has since been well studied (Brown *et al.* 1993; Owen and Norton 1995), but due to differences in habitat as well as a differing niche position we make limited comparisons.

Using next-generation DNA sequencing to identify dietary components, we investigated whether possum diet changed with time since release, taking into account variation in food availability. We hypothesised that after accounting for availability, the diet would initially contain a high diversity and richness of food items as possums explored their new environment, but that this would decrease over time as preferred foods were located, thus increasing selectivity. The diet should stabilise, relative to availability, once possums have acclimatised to the release site. We also aimed to investigate sex effects.

5.5 STUDY SITE

Brushtail possums were reintroduced to around 20 % of the 93,400 ha Ikara-Flinders Ranges National Park (IFRNP, 31° 31' 43" S, 138° 36' 13" E, Fig. 5.1) in semi-arid South Australia in June 2015 (Bannister *et al.* 2018). The species became regionally extinct around the 1940s (Kerle *et al.* 1992). Prior to being declared a National Park in 1970, significant land degradation occurred as a result of overgrazing by domestic stock (from the 1850s) and introduced herbivores (Mincham 1996; Robinson 2012). The ‘Bounceback’ Project was initiated in 1992 and involved the removal of introduced foxes *Vulpes vulpes*, goats *Capra hircus* and rabbits *Oryctolagus cuniculus* (Alexander *et al.* 1997; Robinson 2012), however goats and rabbits remain present (Smith 1996; Brandle *et al.* 2018) along with overabundant native macropods (*Macropus rufus, M. robustus* and *M. fuliginosus*), arresting the regeneration and recruitment of many plants. Vegetation types consist of open woodlands (*Callitris glaucophylla* interspersed with *Eucalyptus intertexta*, or *E. camaldulensis* floodouts), *E. camaldulensis* creeklines, mallee (*Eucalyptus* spp), shrubland and grassland.

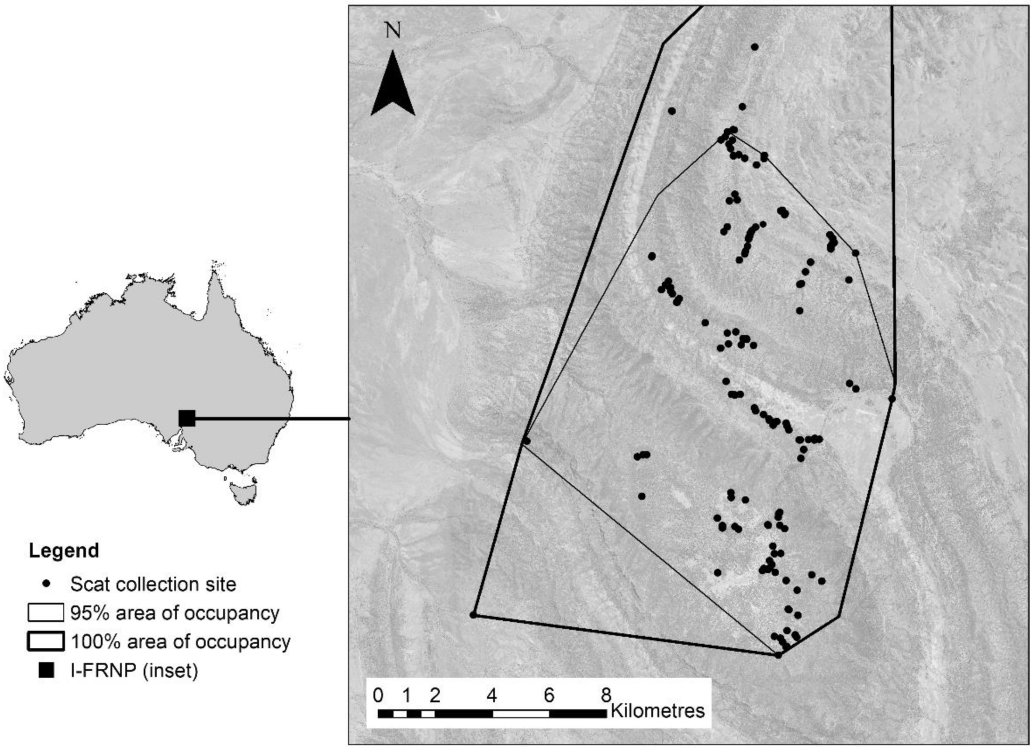


Figure 5.1: Sites where possum scats were collected within the IFRNP, and the location of the IFRNP within Australia. The known area of occupancy (95 % and 100 % minimum convex polygons) for possums during the study period is indicated.

5.6 METHODS

The possums’ diet was studied over a 12 month period, from August 2015 to July 2016, commencing one month after animals had been released. Scats were collected from trapped possums (baited with peanut butter and rolled oats or apple and peanut butter), with an average of 44 (SE ± 3) days between collections from the same individual. The location of collected scats was recorded using a handheld GPS (Fig. 5.1) and the identity, sex, age, body mass, body condition and reproductive status of the possum was also recorded. Because of the shelter site habits of the possums, some collections were made from the same sites multiple times during the study period. Samples were temporarily stored at -4° C after collection and were then transferred to a -20° C freezer where they were stored until being analysed.

To determine the environmental availability of plant genera, vegetation surveys were conducted monthly. Surveys were conducted within the two habitat types used by possums for shelter: creekline and woodland (including floodouts). Each survey involved recording the presence and a visual estimate of percentage cover for each plant species within a 50 m radius of a shelter tree, usually also a trap site. When identification was not possible in the field a photo and sample was taken for subsequent identification. Plant samples were also collected for a DNA reference library. The availability of perennial species was averaged across the year as differences between months were more likely due to the varied locations of survey sites. The percent of canopy that was new growth was not accounted for. The availability of annuals was calculated monthly. Where there was any doubt about the life history of a species, it was considered annual. Because the vegetation survey method used resulted in recording eucalypts (used as shelter sites) in all surveys, the availability of eucalypts was assessed using transect data from another study conducted simultaneously (Moseby *et al.* subm.); the proportion of belt transect segments (100 m long, 20 m wide, location randomly selected, stratified by habitat type) containing eucalypts was calculated, based on 27.5 km worth of transects surveyed within possum habitat.

5.6.1 Local plant DNA-barcode reference library

A plant DNA reference library was developed for the study site which included 165 plant species (Supplementary data S10.5.1), as well as bait used in traps. Leaf samples were freeze-dried for two days prior to being homogenised with tungsten-carbide beads in a TissueLyser (Qiagen), and DNA was extracted using an ISOLATE II Plant DNA Kit (Bioline) according to the manufacturer's instructions. The dual locus barcoding approach of Wilkinson *et al.* (2017) was used to develop the local reference library for the *rbcL* (Kress and Erickson 2007) and *ndhJ* (Schmitz-Linneweber *et al.* 2001) barcodes and sequenced on the MiSeq platform (Illumina) at the University of Adelaide.

5.6.1.1 Scat analysis: plants

A modification of the two-step PCR strategy described by Bell (2011) was used for the amplification of *rbcL* and *ndhJ* barcodes from scat samples. Scats (2–3 per sample) were freeze-dried and homogenised with tungsten-carbide beads in a TissueLyser (Qiagen) and DNA was extracted using an ISOLATE II Plant DNA Kit according to the manufacturer's instructions. The first amplification was performed in 20µl reaction volume consisting of 1x MyFi Buffer (Bioline), 0.2 nM of each forward and reverse primer, 1.6 U MyFi Polymerase (Bioline) and 20 ng of DNA. PCRs were performed on a RotorGene RG-6000 machine (Corbett Life Science) using the following thermocycling conditions: for *rbcL*, 95° C for 1 minute followed by 35 cycles of 95° C for 15 seconds, 55° C for 15 seconds, 72° C for 15 seconds; and for *ndhJ*, 95° C for 1 minute followed by 35 cycles of 95° C for 15 seconds, 50° C for 15 seconds, 72° C for 15 seconds. Amplification products were then purified using the Agencourt AMPure XP system (Beckman Coulter) at a ratio of 0.8x beads to PCR product.

The second PCR was performed using Nextera 96 index adapter sequences (Illumina) to add identifying sequences to the amplify products from the first PCR. This was achieved by adding the following into a 12.5 µL reaction volume: 1x MyFi Buffer (Bioline), 1.6U MyFi Polymerase (Bioline), 0.4 nM of paired Nextera 96 Index Sequences and 4 µL of purified PCR product. The amplification conditions consisted of 95° C for 1 minute followed by 5 cycles of 95° C for 5 seconds, 55° C for 10 seconds and 72° C for 10 seconds. Amplified products were then performed using the Agencourt AMPure XP PCR Purification beads at a ratio of 0.6x beads to PCR product and quantified by qPCR with reference to known PhiX standards (Illumina) using the SYBR FAST qPCR Kit (Kapa Biosystems) on a RotorGene RG-6000 machine (Corbett).

The pooled library was then diluted and a 16pM aliquot was paired-end sequenced on a MiSeq V3 sequencer, using a 600-cycle Version 3 kit (Illumina) according to the manufacturer's instructions. The MiSeq Bcl output files were demultiplexed and converted to fastq files using MiSeq Reporter v2.6 software (Illumina).

The *ndhJ* locus raw sequences were merged using the BBMerge Paired Read Merger Version 37.64 software (Bushnell *et al.* 2017) and aligned to the local DNA reference database using a pairwise match of > 99 % in Geneious v11.1.1 (https://www.geneious.com) identified to genus level. Sequences that were < 99 % similar were identified to genus, but the confidence was lower. For the *rbcL* sequences, reads were trimmed and quality-filtered, and only reads of 300bp with QF > 30 were used for alignment to the *rbcL* reference database with a pairwise match of > 99 % (Bushnell *et al.* 2017).

5.6.1.2 Scat analysis: invertebrates and birds

Possum scats were analysed for the presence of invertebrate and bird DNA using a similar approach as described for plant DNA, using invertebrate (Hebert *et al.* 2004a; Foottit *et al.* 2008) and bird specific COI primers (Hebert *et al.* 2004b). Amplification products were assessed by visualisation following electrophoresis on a 1 % agarose gel and products sequenced on the Illumina MiSeq platform using a 600-cycle v3 kit (Illumina), as described previously.

5.6.2 Data analysis

Data analysis was conducted using R version 3.5.0 (R Development Core Team 2018). Genera making up < 1 % of reads within a sample were removed from analyses to reduce the inclusion of material resulting from incidental ingestion or environmental contamination. Bait items were also omitted from results. The plant component of the diet of possums in the IFRNP was investigated by calculating the frequency of occurrence of each genus in scats (the number of scats containing each genus), both monthly and pooled across the whole study period. We also calculated relative abundance of genera within samples by measuring the proportion of each genera contained within each sample (i.e. the number of reads for a particular genera, divided by the total number of reads for that sample). Selectivity values were calculated monthly as well as overall for each genus (Jacobs 1974). We calculated an average pairwise Pianka's niche overlap index to test for sex effects (Pianka 1974).

To investigate the influence of time since release on possum diet, we calculated selectivity, frequency of occurrence in scats and proportions within scats over time (monthly). Selectivity was calculated using Jacob's Index (Jacobs 1974), which assesses plant preference or avoidance relative to environmental availability:

$$\text{Jacob's Index } (D) = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

Where r_i = the proportion of genera i within the diet (frequency of occurrence within scats), and p_i = the proportion that genus i is available (frequency of occurrence within the environment). Maximum preference is a Jacob's Index value of + 1, and maximum avoidance is -1. Genera present in less than 5 % of both scats and vegetation surveys were omitted from the selectivity analysis to avoid heavily skewing selectivity results because of low detectability. A linear mixed-effects model with a gaussian distribution was used to test whether the frequency of occurrence (number of scats the genera was present in, for each month) of genera in samples changed over time (monthly) based on preference (where > 0 = preferred, < 0 = non-preferred). Frequency of occurrence was the response variable, with preference, time and an interaction between preference and time as explanatory variables. Genus was included as a random effect as there were multiple values for the same genera included over time. Similarly, the mean proportion of each genus contained within a sample (response variable), per month, was analysed using a linear mixed-effects model with a gaussian distribution, with preference, time and an interaction between preference and time as explanatory variables. A random effect was included for genus.

To determine whether dietary richness (number of genera in a sample) changed with time since release, we ran a linear mixed-effects model with the number of genera within a scat as the response variable, and time since release (months), sex, number of genera available (derived from vegetation surveys), and an interaction between time since release and number of genera available as explanatory variables. Possum identity was included as a random effect. The same factors were included in another model with Shannon's diversity (per sample) as the response variable. The height of plants (< 0.5 m, 0.5–2.5 m or > 2.5 m) falling into each preference category (calculated overall rather than monthly) was calculated along with the overall frequency of occurrence in scats for plants in those height classes.

We tested for a relationship between rainfall in the previous month (response variable, log-transformed to meet model assumptions) and the number of annual genera available (fixed effect) using a generalised linear model with a poisson distribution.

Where relevant, means are presented with ± 1 standard error.

5.7 RESULTS

An average of 21.1 scat samples (± 2.8) were collected monthly during the study period (August 2015–July 2016), from a total of 55 adult possums (26 female, 29 male) of known identity, totalling 253 samples. An average of 5.3 (± 0.7) and 4.0 (± 0.6) samples were collected from individual females and males, respectively, over the study period. Samples were collected from across the possums' area of occupancy (Fig. 5.1). A total of 112 vegetation surveys were conducted (mean number of surveys per month = 9.3, range: 7–12) during the same period, in both of the habitat types possums used for shelter; 57 in woodland habitat and 55 in creekline habitat. The IFRNP received 466mm of rain during the study period, comparable to the 440mm annual mean (Bureau of Meteorology 2018; Fig. 5.2). The number of annual genera available was not significantly related to rainfall in the preceding month ($\chi^2_1 = 2.7$, $p = 0.098$; Fig. 5.2), although there was a positive trend.

5.7.1 Time since release

Possums significantly decreased dietary richness with time since release (χ^2_1 =10.8, $p < 0.0010$, Fig. 5.3), regardless of the number of genera available (χ^2_1 = 1.4, p = 0.24) and with no effect of sex (χ^2_1 = 0.7, p = 0.40). There was a significant interaction between time since release and number of genera available (χ^2_1 = 18.9, $p < 0.00001$). Similarly, dietary diversity decreased with time since release (χ^2_1 = 10.1, p = 0.0015), with no significant effect of sex (χ^2_1 = 1.5, p = 0.21) or genera available (χ^2_1 = 0.5, p = 0.47). In contrast to the dietary richness model, there was no significant interaction between time since release and genera available (χ^2_1 = 0.1, p = 0.75). Frequency of occurrence of genera within the diet changed significantly with time since release (χ^2_1 = 5.9, p = 0.015) and preferred genera were present in a higher proportion of scats than non-preferred genera (χ^2_1 = 185.6, $p < 0.0001$). The interaction between time and preference was not significant (χ^2_1 = 1.8, p = 0.18). Proportional consumption was significantly different based on preference (χ^2_1 = 20.2, $p < 0.0001$), with preferred genera making up a larger proportion of reads within each scat than non-preferred genera, but did not change significantly over time (χ^2_1 = 0.3, p = 0.60), however there was a significant interaction between preference and time (χ^2_1 = 6.0, p = 0.014), with preferred species making up a larger proportion of reads within individual scats over time, with a decline in the number of reads for non-preferred plants.

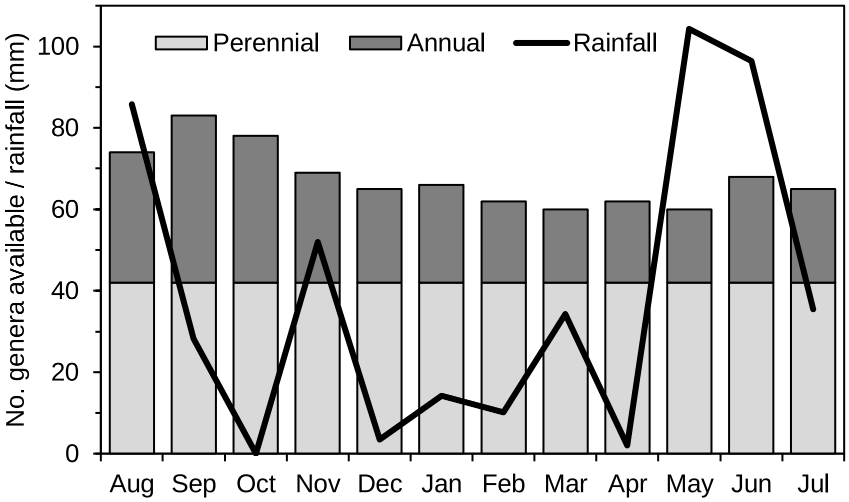


Figure 5.2: Rainfall and the number of genera available per month during the study period, August 2015–July 2016. The number of annuals available was not significantly related to rainfall in the preceding month, but there was a positive trend.

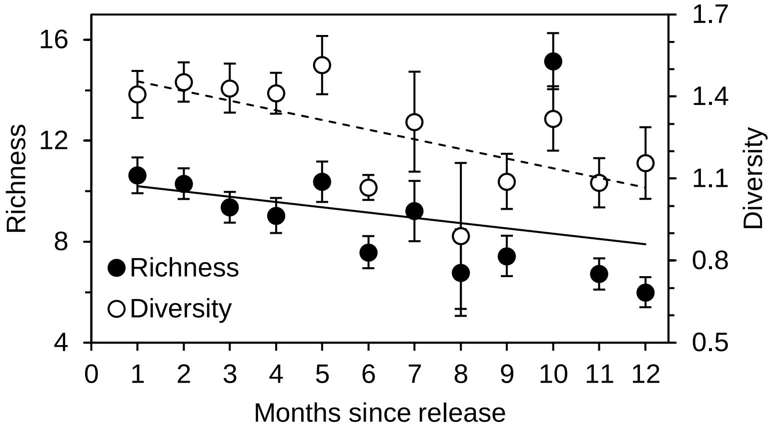


Figure 5.3: Dietary richness (primary y-axis) and Shannon's diversity (secondary y-axis) for plant genera consumed by possums after their release (study period August 2015–July 2016), ± 1 standard error. Both relationships are statistically significant.

5.7.2 General diet

One hundred and one plant genera were detected in at least one sample during the study period, and 88 were present in at least five samples. Twelve genera were present in more than 20 % of samples: *Eucalyptus*, *Petalostylis*, *Maireana*, *Zygophyllum*, *Callitris*, *Acacia*, *Silene*, *Austrostipa*, *Stackhousia*, *Melaleuca*, *Senna* and *Sonchus* (Table 5.1). Only four of those were not readily available at the source site (Yookamurra Wildlife Sanctuary) prior to translocation: *Petalostylis*, *Silene*, *Stackhousia* and *Sonchus* (H. Crisp, pers. comm.).

Table 5.1: Genera detected in more than 20 % of adult possum scats and the mean proportion of those genera found in each scat using two primers (*ndhJ* and *rbcL*). Mean selectivity values (Jacob's Index) for the study period and whether they significantly deviate from zero (*P*) is indicated for each genera; negative values indicate avoidance (non-preferred) relative to availability, positive values indicate preference. FOO = frequency of occurrence in scats (% of samples containing the genus).

Genus	FOO	*ndhJ*	*rbcL*	Jacob's Index	*P*	Preference
Eucalyptus	78.5	38.1	8.8	-0.013±0.2	0.15	Neutral
Petalostylis	72.3	3.2	32.2	1±0	<0.0001	Preferred
Maireana	59.1	5.5	2.5	0.55±0.1	0.00024	Preferred
Zygophyllum	51.5	1.7	0.9	0.94±0.03	<0.0001	Preferred
Callitris	50.7	3.2	18.4	-1±0	<0.0001	Non-preferred
Acacia	36.5	3.6	2.8	-0.090±0.2	0.48	Neutral
Silene	34.7	6.7	5.4	0.15±0.2	0.48	Neutral
Austrostipa	33.6	0	2.0	0.21±0.2	0.15	Neutral
Stackhousia	33.6	4.9	0	0.58±0.2	0.026	Preferred
Melaleuca	31.4	1.9	5.2	1±0	<0.0001	Preferred
Senna	29.6	2.3	2.2	-0.39±0.1	0.029	Non-preferred
Sonchus	27.0	3.7	0	0.69±0.1	0.00021	Preferred

The diet of males and females did not differ greatly throughout the year (Pianka overlap (overall) = 0.73, monthly overlap values 0.65–0.84). Overall, nine (13.4 %) genera were preferred, occurring in a significantly higher proportion of scats than expected based on their availability at the study site, 22 (32.8 %) genera were consumed in the same proportion as their availability (neutral), and 36 (53.7 %) genera were non-preferred, being consumed in significantly lower proportion than their availability (Fig. 5.4). Of the nine preferred genera, four were readily available at the source site (*Melaleuca*, *Zygophyllum*, *Pittosporum* and *Maireana*, H. Crisp, pers. comm).

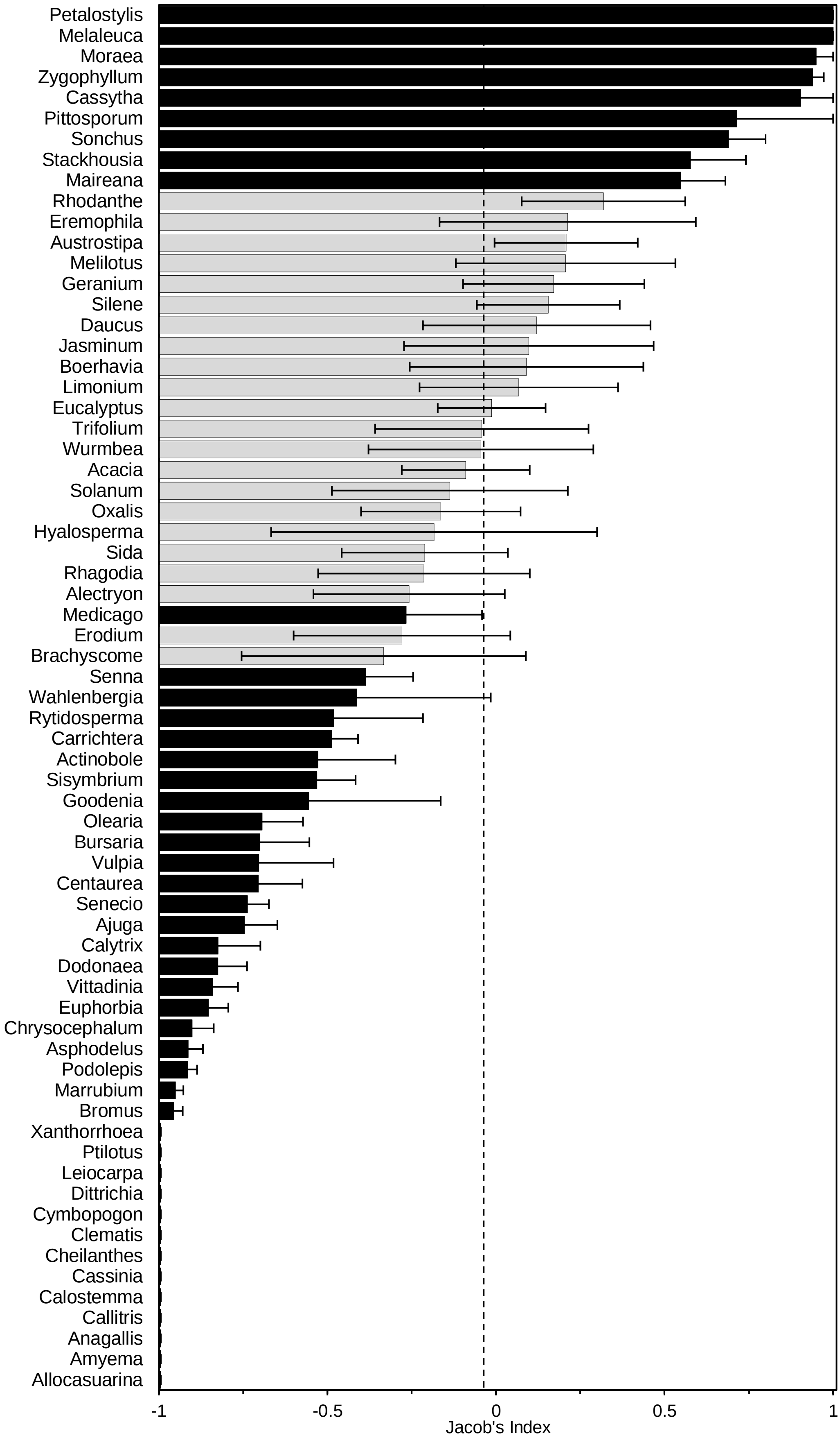


Figure 5.4: Selectivity preferences for genera within the possums' diet, averaged across the 12 month study period, where negative values indicate selectivity against a genera and positive values indicate preference; a value of zero suggests consumption at the same rate as availability. Dark bars denote values that significantly deviate from zero.

5.7.3 Foraging habits

Of the plant genera recorded in the possums' diet, most (72 %) were < 0.5 m in height. However, these genera made up a relatively small proportion of diet (frequency of occurrence in scats 11.4 %), along with midstorey plants (0.5–2.5 m, frequency of occurrence in scats 9.5 %), which made up 21 % of plant genera consumed. The highest frequency of occurrence in scats was for genera taller than 2.5 m (32.6 %, Fig. 5.5), despite making up only 7 % of genera available. Although taller plants made up a low proportion of genera, percent cover was relatively similar to that of small plants (> 2.5 m, mean % cover: 41.7 % ± 1.8, < 0.5 m, mean % cover: 45.9% ± 5.6), with midstorey plants providing considerably lower percent cover (0.5–2.5 m, mean % cover: 13.4 % ± 1.8). However, eucalypts (> 2.5 m category) are likely to be overrepresented because the survey design was centred around shelter trees. Midstorey genera including *Acacia*, *Pittosporum* and *Eremophila* were found in a higher proportion of scats with increasing time since release.

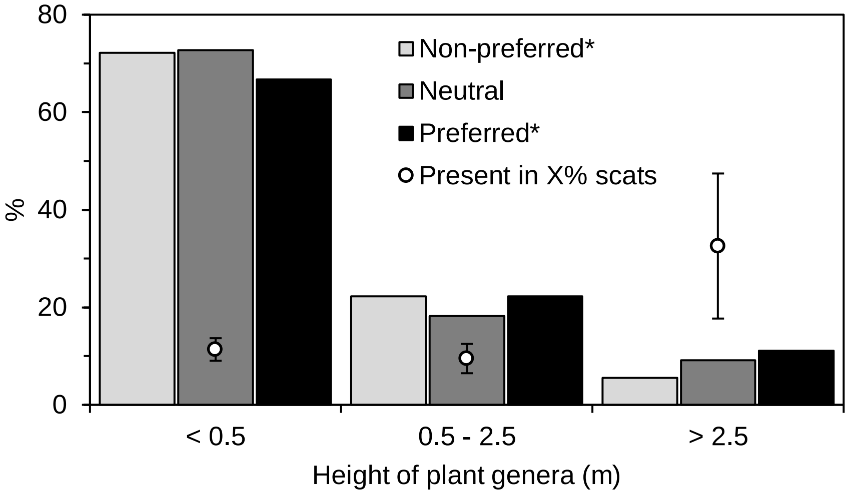


Figure 5.5: The height distribution of plants grouped by dietary preference (Jacob's Index values compared to zero, calculated for the year), and the mean proportion of scats containing genera in those size classes (± 1 SE). Genera contained in < 5 % of both scats and vegetation surveys were omitted, likely reducing the number of non-preferred plants included.

No bird DNA was detected in any of the possum scats. We were unsuccessful in amplifying invertebrate DNA and thus the consumption of invertebrates by possums in the IFRNP remains unknown.

5.8 DISCUSSION

The diet of reintroduced brushtail possums changed significantly with time since release, independent of changes in the availability of genera. Presumably, possums consumed a wider variety of foods (higher dietary richness and diversity) after release because the location of preferred and nutritious food plants was unknown. Flora at the source site (Yookamurra Wildlife Sanctuary) varied somewhat to the release site, although many of the same genera were available (H. Crisp, pers. comm). Over time, possums likely discovered sources of preferred plants within the release area. An investigation of the diet from the time of release, rather than one month later, may have uncovered stronger changes, however scats from the first month after release were not collected because of the supplementary feeding of some animals (Bannister *et al.* 2018). Trends suggested that either the acclimatisation period had not ended 12 months after release, or that seasonal effects on food consumption were taking place. Both explanations suggest that the diet of the possum is flexible and varied, and thus can adapt to changes in the availability of food resources.

Post-release acclimatisation time is often measured using metrics such as reproduction, movement (establishment of a stable home range) and body mass (Bright and Morris 1994; Hardman and Moro 2006; Facka *et al.* 2010). Possums released into the IFRNP retained all pouch young and continued to breed after release, despite initial loss of body mass (Bannister *et al.* 2018; Moseby *et al.* subm.). Mass was generally regained (or increased) within 30–60 days of release and possums settled into home ranges within 2–6 weeks (Bannister *et al.* 2018). However, the current study suggests that although many post-release acclimatisation parameters had been met relatively quickly, changes in the diet were still occurring 12 months after release, thus total acclimatisation was incomplete, although not a barrier to short-term reintroduction success (Table 5. 2). An alternative explanation is that the diet is highly variable and thus the concept of dietary acclimatisation does not apply—however, the direction of change suggests this is unlikely. Research usually focuses on the initial post-release period, when starvation is most likely, and during this period body condition may provide a more informative and rapid measure of foraging success than an investigation of diet (Soderquist 1995). In addition to avoiding starvation, nutritional requirements for reproduction and maintaining immunocompetence may be more complex. Some nutrients may have been acquired and stored prior to release, resulting in a delay in the symptoms of malnutrition. Good food resources and successful breeding are vital for long-term population persistence through difficult conditions such as drought, and thus diet should be viewed as an important metric for measuring population viability and reintroduction success. For brushtail possums, total acclimatisation was not required for successful post-release reproduction. Given their flexibility in diet post-release and the usually limited amount of funding for reintroduction projects, an investigation into post-release diet for brushtail possums may only be necessary when and if other indicators of malnutrition such as the cessation of breeding or loss of body mass become apparent.

Table 5.2: The time taken by reintroduced brushtail possums to achieve acclimatisation measures. Additional data from Bannister *et al.* (2018) and Moseby *et al.* (subm.).

Acclimatisation measure	Time taken
Successfully reproduce	0 days
Select safe, suitable shelter sites	3 weeks
Establish a stable home range	2–6 weeks
Maintenance or gain of body mass	30–60 days
Consume a natural, stable diet, relative to availability	> 12 months

Post-release diet studies can be used to investigate the diet of species reintroduced to areas where knowledge of their local diet may be limited, or when the feasibility of the translocation is unknown. The diets of the red-tailed phascogale *Phascogale calura* and mala *Lagorchestes hirsutus* were investigated as part of trial releases to determine the feasibility of reintroductions to other nearby areas (Stannard *et al.* 2010; Clayton *et al.* 2015), and the diet of translocated Gilbert’s potoroos *Potorous gilbertii* was studied to determine whether sufficient fungi was present for population establishment and reproduction (Bougher and Friend 2009). Dietary studies can thus be used to inform acclimatisation time, the feasibility of population establishment, the suitability of additional release locations and the species' ecology.

Eucalypts had both the highest frequency of occurrence in scats (78.5 %) and the highest proportions within samples (making up an average of 23.5 % of DNA extracted from scats) for scats collected in the IFRNP. Possums cannot consume an exclusively eucalypt diet: eucalypts are high in fibre, relatively indigestible and contain terpenes (Foley and Hume 1987; Boyle and McLean 2004). A varied diet is therefore needed to meet their nutritional needs and energy demands (Marsh *et al.* 2006). The low number of preferred genera combined with the relatively high frequency of non-preferred genera in the possums' diet suggests that they feed opportunistically in small amounts, while consuming large amounts selectively. Drought conditions—not experienced during our study period, may exacerbate the need for possums to locate easily digestible, moist food plants. Foulkes (2001) found that the moisture content of mature foliage was the only reliable predictor of possum occupancy in arid central Australia. Low availability of traditionally preferred plants such as *Santalum* may explain low consumption (without noticeable consequence), but the importance of such nutritious and moist plants (Foulkes 2001) may differ under drought conditions. In arid systems, drought can negatively affect reintroduction success, as occurred for black-tailed prairie dog (*Cynomys ludovicianus*) populations in the Chihuahuan Desert (Facka *et al.* 2010), and red-necked ostriches in Saudi Arabia (Islam *et al.* 2008). Possums are well known for their plasticity and ability to adapt to different environments (Kerle 1984; Kerle *et al.* 1991) and in this study have demonstrated persistence in an area where previously identified preferred food plants are uncommon. The diet of possums in the IFRNP should be monitored through the next drought period to assess whether plants containing high moisture and nutrients are available in sufficient quantities to enable persistence.

The majority of the genera present in the possums' diet were ground cover plants < 0.5 m in height, however their combined frequency of occurrence in scats was low, suggesting they were only occasionally eaten, despite being the most diverse height class. Palatability was not accounted for, and many herbs and grasses were present but dry/senesced at various times during the study period. In contrast, few tall genera (> 2.5 m height) were available compared to shrubs and annuals, but the frequency of occurrence within scats was high. This suggests that possums may spend more time foraging in the canopy than on the ground, a result supported by previous studies into possum foraging and movement, where diet is dominated by canopy species (Foulkes 2001; Cruz *et al.* 2012b; Gloury and Handasyde 2016). This could be due to the avoidance of predators at ground level, the quality of food in the canopy, or a combination of both.

We found no sex effects in the diet of brushtail possums. Combined with the presence of pouch young at all times during the study period (Bannister *et al.* 2018; Moseby *et al.* subm.), this suggests that lactation demands do not extend to detectable differences in the diet of breeding and non-breeding individuals. We suggest post-release diet studies should, at minimum, span one full breeding season after release, to assess whether food resources are adequate for breeding and the survival of juveniles, and to investigate whether food requirements differ between breeding and non-breeding individuals, or by sex.

5.8.1 Limitations

Unfortunately, we were unsuccessful in identifying invertebrate DNA in possum scats and therefore do not know the importance of invertebrates in their diet at our study site. Fungi intake was not measured, but was present in the diet of possums in southwest Australia (How and Hillcox 2000). The use of two genetic markers, as per Wilkinson *et al.* (2017), enabled the detection of a higher number of genera within the diet than the use of one marker alone, but the sensitivity of each marker to different genera varied; some genera were only detected by one of the markers. Next-generation DNA sequencing is increasingly being used to study animal diets (e.g. Hibert *et al.* 2013; Thomas *et al.* 2014). However, limitations include not being able to determine which parts of plants are being eaten, an often low resolution of diet content to family or genus, inaccurate proportions of genera within samples, and reliance on a comprehensive and accurate reference library (Hibert *et al.* 2013; Thomas *et al.* 2014). Some species identified as having a high frequency of occurrence in scats using DNA (e.g. *Petalostylis*) were uncommon at our study site and may in fact be closely related genera. Diet studies of any method are not immune to error and we urge caution in relying solely on DNA studies of diet. Selectivity analyses are subject to the accuracies of the proportions given by the two markers, as well as plant availability data. Finally, with the benefit of hindsight, our study should have extended beyond 12 months, given that the possums' diet had not stabilised within this period. Monitoring the diet over multiple years and comparing to the diet of an established, non-reintroduced possum population would also enable seasonal effects to be teased out from effects of post-release acclimatisation.

5.8.2 Conclusions

The interaction between diet and time since release in reintroductions has been largely overlooked in the published literature. Our study demonstrates that a reintroduced population can, over time, decrease dietary richness and diversity, while increasing the consumption of preferred foods within the diet. This acclimatisation period is longer than that recorded using movement, body condition and reproductive data and suggests a range of indicators should be used to measure acclimatisation at different time scales to ensure ecological relevance. However, the importance of a stable diet in a non-drought period may have been overestimated. While only a small number of genera made up the bulk of each sample, a large number of genera were ingested, suggesting some opportunistic feeding and a relatively high consumptive diversity. The availability and consumption of plant species at our site was not a barrier to reintroduction success in the short- or medium-term but drought conditions were not experienced during our study and may impact longer term establishment. We suggest that the acclimatisation period should extend past the first drought period for arid zone species to ensure that suitable food plants can be sourced under stressful conditions.

5.9 ACKNOWLEDGEMENTS

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6. JUVENILES

Offspring sex and maternal effects influence the development and natal dispersal of an arboreal marsupial

Female brushtail possum with her 5 ½ month old offspring

6.1 CONTEXTUAL STATEMENT

The final data chapter presents the results from intensive monitoring of the growth, movement (including dispersal), and survival of juvenile possums through to adulthood, within the reintroduced population. For population persistence to be achieved, it is essential that a sufficient proportion of juveniles survive to reproduce. Data were collected from 40 juvenile possums during the study (26 of which were radio-collared), as well as thirteen mothers translocated as part of the founding population. Previous studies have demonstrated various effects of sex, maternal behaviour and environmental factors on the growth, movement and survival of juveniles of various species (Howard 1960; Clobert *et al.* 2009; Duputié and Massol 2013), and are considered in this study along with interactive effects between such factors. This chapter has been published by the *Journal of Mammalogy*.

6.2 STATEMENT OF AUTHORSHIP

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Author contributions

By signing the Statement of Authorship, each author certifies that the stated contributions to the publication are accurate, and that permission is granted for the candidate to include the publication in the thesis.

Primary author	Hannah Bannister		
Contribution to the paper	Designed the experiment, collected data, analysed the data and prepared the figures, wrote the manuscript and responded to reviewer comments.		
Overall percentage	80 %		
Signature		Date	25/03/2019

Co-author	Patrick Hodgens		
Contribution to the paper	Assisted with data collection, reviewed the manuscript.		
Signature		Date	25/03/2019

Co-author	Katherine Moseby		
Contribution to the paper	Assisted with experimental design, assisted with data collection, advised on and reviewed the manuscript.		
Signature		Date	25/03/2019

6.3 ABSTRACT

Natal dispersal is influenced by many environmental and biological factors, and can be a time of elevated mortality risk. We aimed to understand how physical, behavioural and demographic traits of mothers and juveniles influenced natal dispersal by studying a population of brushtail possums (*Trichosurus vulpecula*) reintroduced to their former range. We used radio-tracking and trapping to intensively monitor the growth, survival, shelter use and movement of juveniles and their mothers from pouch young to adulthood over a 22-month study period. We recorded multiple dispersal movement phases, with males undergoing more phases than females (6 versus 4) and dispersing 16 times farther. Dispersal age was positively related to maternal body mass for males but not females. Mothering behaviour varied with offspring sex, with mothers tending to shelter daughters in a higher proportion of new shelter sites compared to sons. Females matured at a younger age and mass than males, and possums that left their mother at an earlier age reached sexual maturity earlier, regardless of sex. The timing of dispersal by males was not influenced by body mass, age, sexual maturity, rainfall, or the age of their younger sibling. Survival of juveniles (63 %) was not related to sex or dispersal phase but instead sexual maturity, suggesting an effect of experience. Sex, maternal effects and an interaction between the two influenced the development and movement of juvenile possums, suggesting that at least some sex-related differences in natal dispersal may be influenced by the mother rather than simply being the innate behaviour of offspring. Although sex effects on dispersal have been reported in marsupials, the interaction with maternal characteristics has been previously overlooked.

Key words: brushtail possum, male-biased dispersal, maternal effects, mothering behaviour, natal dispersal, predation, reintroduction, sex-bias, survival

6.4 INTRODUCTION

Natal dispersal (hereafter referred to as dispersal) is defined as permanent movement away from the natal range, and can be classified as innate or environmental (Howard 1960). Innate dispersal occurs in offspring regardless of the available habitat or range and is density independent, while density-dependent (environmental) dispersal occurs in response to environmental conditions—both are assumed to be inherited and are usually related to sexual maturity (Howard 1960). Innate dispersal may act to prevent inbreeding, extend a species' range, reduce intraspecific conflict, ensure efficient utilisation of resources or geographically spread traits that may one day be advantageous (Howard 1960; Lawson Handley and Perrin 2007). In mammals, innate dispersal is usually male-biased, however female-biased dispersal occurs in some species and both sexes disperse in equal proportions in a number of species as well (Howard 1960; Greenwood 1980; Lawson Handley and Perrin 2007; Clutton-Brock and Lukas 2012). Mating systems and social dynamics are known to influence the direction of sex-biased dispersal, however the patterns and mechanisms remain complex (Lawson Handley and Perrin 2007; Clutton-Brock and Lukas 2012). Generally, male-biased dispersal is linked to polygynous mating systems, inbreeding avoidance, and the avoidance of sexual or resource competition with kin (Greenwood 1980; Lawson Handley and Perrin 2007; Brom *et al.* 2016).

Although sex appears to be the dominant factor affecting dispersal, other influencing factors can include hormone levels, energy stores, diet, natal resource availability, population density, litter size, species body mass and home range size (Nunes *et al.* 1999; Sutherland *et al.* 2000; Bowman *et al.* 2002; Ferreras *et al.* 2004; Fisher 2005; Whitmee and Orme 2013; Edelman 2014). The natal environment can also affect the development, survival and dispersal of young (English *et al.* 2014; Van Allen and Bhavsar 2014). Removal of a mother can alter the dispersal process, probability of dispersal or range establishment for offspring (Cockburn *et al.* 1985; Blackie *et al.* 2011; Sakamoto *et al.* 2015). Aside from using removal experiments, specific behaviours shown by mothers are difficult to study, but are likely to influence the dispersal process. Physical aspects of mothers can also influence dispersal, for example the maternal body mass of Mt Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in spring influenced the dispersal distance of juveniles, but the effect varied with offspring sex probably because of an interaction between sex, philopatry and condition (Merrick and Koprowski 2017). The interaction between offspring sex and the physical and behavioural characteristics of the mother have received little attention in the published literature, and sex-biased mothering behaviour could add to current explanations for sex-biased dispersal.

Costs of dispersal can include energy expenditure, opportunity (time) costs, increased mortality and the risk of settling in unfavourable habitat (Bonte *et al.* 2012). Dispersal has been associated with elevated mortality for a suite of mammal and bird species (Ferreras *et al.* 2004; Estes-Zumpf and Rachlow 2009; Serrano and Tella 2012). Even prior to dispersal, juveniles are often more susceptible to predation than adults due to their smaller size and inexperience (Barja 2009; O'Kane and Macdonald 2016), and thus natal dispersal is likely to be a time of significant mortality risk. Sex-biased juvenile survival has been found for birds including snowy plovers (*Charadrius nivosus*) (Eberhart-Phillips *et al.* 2017) and the Seychelles warbler (*Acrocephalus sechellensis*) (Kingma *et al.* 2017). Theoretically, the dispersing sex should incur a higher mortality rate as they travel farther and are thus more likely to encounter predators, as well as expending considerable energy while entering unfamiliar habitat where resource quality and availability may be suboptimal (Bonte *et al.* 2012).

Few studies of natal dispersal have been conducted in Australia on native marsupials and most rely on genetic information (e.g., Hazlitt *et al.* 2006; Stow *et al.* 2006) or trapping (e.g., Cockburn *et al.* 1985; Fisher 2005), rather than specific movement patterns recorded using radio-telemetry. However, combined telemetry and trapping studies on the brush-tailed phascogale (*Phascogale tapoatafa*), western quoll (*Dasyurus geoffroii*) and burrowing bettong (*Bettongia lesueur*) (Soderquist and Lill 1995; Soderquist and Serena 2000; Parsons *et al.* 2002), provided detailed movement information that suggested male-biased dispersal. We investigated sex and maternal effects on the dispersal and survival of a population of common brushtail possums (*Trichosurus vulpecula*, hereafter, possum) reintroduced to Australia's semi-arid zone after an absence of at least 75 years (Kerle *et al.* 1992). Possums are semi-arboreal, nocturnal marsupials weighing 1–4 kg, that vary considerably in their morphology and physiology across their range (Kerle 1984, 2001). Once widespread across Australia, possums have suffered a > 50 % decline in range following European settlement due to predation by introduced predators, habitat loss and alteration, competition with introduced herbivores, altered fire regimes, and hunting (Kerle *et al.* 1992; Kerle 2001).

Predation by introduced predators, particularly foxes (*Vulpes vulpes*), has been the dominant cause of translocation failure (Pietsch 1995; DEC 2012), and in some areas where foxes are controlled, possum activity has subsequently increased (Burrows and Christensen 2002; Kinnear *et al.* 2002).

Within their native range, dispersal by possums has only been studied in detail using genetic information from an urban population, which revealed male-biased dispersal, generally < 900 m (Stow *et al.* 2006). The dispersal patterns of brushtail possums have been studied in New Zealand, where the species is an introduced pest, and is generally reported to be male-biased, although with some exceptions (Clout and Efford 1984; Cowan *et al.* 1996; Ji *et al.* 2001). The ongoing removal of individuals for population control in New Zealand is likely to influence their movements and behaviour (Blackie *et al.* 2011; Rouco *et al.* 2017), therefore we make limited comparisons to these populations. To our knowledge, telemetry has not been used to study natal dispersal of possums within their native range, despite their widespread distribution.

We aimed to understand potential sex effects on the natal dispersal of possums including differences in survival, movement, timing, and distance, as well as any interactions between juvenile sex and maternal effects. We predicted that possums would exhibit male-biased dispersal, and that sex would influence movement patterns and the timing of dispersal. We predicted that the dispersing sex would have higher mortality than the non-dispersing sex. We explored whether sex-biased dispersal led to differences in mothering behaviour towards male and female offspring, and whether the physical characteristics of the mother influenced dispersal characteristics differently in each sex. Finally, because we were studying a reintroduced population, we investigated whether there was a sex-bias in offspring produced post-release, and whether this was related to maternal body mass or time since release. Sex-biases in offspring produced have been previously reported for the species (Johnson *et al.* 2001; Johnson and Ritchie 2002). Our study site supported a low density of possums, released at a density of 0.012/ha (79 possums into a release area of 6,500 ha), compared to other sites where densities can be, for example, 2–3/ha (How and Hillcox 2000), 0.09–7.2/ha (Isaac and Johnson 2003), and 16.7/ha (Brockie *et al.* 1997). This provided us with an opportunity to study dispersal patterns of the species without the confounding effects of high population density and the ongoing removal of individuals, as occurs in New Zealand.

6.5 MATERIALS AND METHODS

6.5.1 Study site

Seventy-nine brushtail possums were reintroduced to a 65-km² area in the semi-arid Ikara-Flinders Ranges National Park (IFRNP, 31° 31’ 43” S, 138° 36’ 13” E) in June 2015 (Bannister *et al.* 2018). The area receives an average annual rainfall of 440 mm (Station 19070, Bureau of Meteorology 2018). Habitats within the park consist creeklines and floodouts dominated by *Eucalyptus camaldulensis* interspersed with open eucalypt (*E. intertexta* or *E. camaldulensis*) or mixed eucalypt–*Callitris glaucophylla* woodlands, mallee (*Eucalyptus* spp.), shrubland (*Acacia*–*Allocasuarina*) and grassland. Introduced foxes were well controlled within the park (Brandle *et al.* 2018), however feral cats (*Felis catus*) and dingoes (*Canis lupus dingo*) were present but subject to control, and a reintroduced population of western quolls was also present; all species are known to depredate possums where they co-exist (Kerle *et al.* 1992; Glen *et al.* 2010; DEWNR 2012).

6.5.2 Data collection

Data were collected using a combination of trapping (to collect growth and development information) and radio-telemetry (to collect movement and survival data) over a 22-month study period, commencing 4 months after the reintroduction of possums to the IFRNP. Possums had settled within 1–6 weeks of release and although body mass was initially lost, it was regained (or increased) within 30–60 days (Bannister *et al.* 2018). Therefore, we expected the behaviour of possums at our study site to be relatively normal by this time. We chose to intensively monitor 13 released adult female possums, investigating the survival, growth, and movements of their offspring as well as aspects of mothering behaviour. Typically, female possums give birth to a single joey that spends around 5 months inside the pouch before advancing to back young (being carried on their mothers' back), young-at-foot and eventually independence (Pilton and Sharman 1962). Twelve of the females were carrying small pouch young at the time of release, and the 13th gave birth around 6 weeks later. Treadle-operated cage traps (22 x 22 x 55 cm) baited with peanut butter and rolled oats were used to capture adults and subadults. Larger traps (45 x 50 x 1,200 cm) proved more successful for capturing large back young and young-at-foot, as juveniles as large as 1,075 g were able to be captured in the same trap as their mother. Adult females were fitted with VHF radio-collars (V5C-161E, 35 g or V5C-162E, 41 g; Sirtrack, Havelock North, New Zealand, or M1820, 27 g; Advanced Telemetry Systems Australia, Gold Coast, Australia) for the duration of the study. Juveniles were first monitored as pouch young through the routine capture of adult females, and were fitted with lightweight radio-collars (RI-2DM, 7 g; Holohil, Carp, Canada) upon their first capture after exiting the pouch. Collars were attached to juveniles using three strands of crochet cotton threaded through silicone tubing. Collars fell off after 4–6 weeks if the juvenile was not recaptured and the collar re-strung beforehand. Once juveniles were $\geq$ 800 g, collars were switched to the larger collars also used for adult females. One young male had a GPS collar (Argos G3C; Sirtrack, Havelock North, New Zealand) fitted for a period of 1 month during dispersal. All radio-collars had mortality sensors that would activate following 10 h of inactivity.

Radio-collared possums were trapped every 4–12 weeks (occasionally longer intervals), depending on their age, by setting traps at shelter trees identified via radio-tracking. We measured the short *pes* (length between heel and tip of pad), head and testes length (males only) of captured possums, and new animals were given a unique microchip. Weights were measured using 1 kg (± 0.005), 2 kg (± 0.02), or 5 kg (± 0.025) spring scales, using the smallest where possible, and body condition was assessed on a scoring system of 1 (poor) to 5 (excellent). The reproductive condition of females was assessed by checking for the presence of pouch young, teat condition, pouch staining, and pouch depth. The head length of pouch young was estimated (very small young) or measured (larger young). Most joeys were first recorded within 6 weeks of birth, enabling an accurate estimate of age to be determined. Three equations were used to determine the birth date of pouch young based on head length (Kerle and Howe 1992; Clinchy 1999; Isaac and Johnson 2003), and the mean result from these equations was used; all equations produced similar results. Additional biological data were collected from other juveniles of known age and maternity that were trapped throughout the study period.

We aimed to radio-track both adult females and juveniles to their shelter site a minimum of once per week. Efforts were intensified around the time of dispersal, with tracking undertaken more regularly (where possible) for dispersing possums. Several discrete dispersal movement phases were identified and are discussed further in the results section. When radio-collar signals indicated a mortality, the carcass or remains were retrieved. Cause of death was determined, where possible, using a combination of carcass condition, searching a 50-m radius to look for further evidence (e.g. scattered entrails, fur, cached carcasses) and swabbing the radio-collar and carcass to test for predator DNA (see Moseby *et al.* 2015 for details of the method). Fresh carcasses were sent to Zoos SA (Adelaide, Australia) for autopsy. For surviving juveniles, collars were removed once they had dispersed, settled into an area (regularly returning to familiar shelter trees), reached sexual maturity, and, for females, given birth. Some collars remained fitted for longer than this and several former juveniles were recaptured months after their collars had been removed, including several captures beyond the defined study period. All radio-collars were removed at the end of the study. Female possums were classified as sexually mature when their pouch became deep and slightly moist or stained, in stark contrast to the shallow, clean pouches of juveniles and subadults. Males were classed as adult when testes length was ≥ 18 mm (Tyndale-Biscoe 1955) and the epididymis was prominent.

Research followed ASM guidelines (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016) and was conducted under the Australian Code for the Care and Use of Animals for Scientific Purposes (2013), with approvals from the South Australian Wildlife Ethics Committee (Project number 15/2014) and the University of Adelaide's Animal Ethics Committee (Approval number S-2015-091).

6.5.3 Data analysis

Statistical analyses were undertaken using the program R (R Development Core Team 2018). We tested the fixed effects of maternal body mass and time since release on the sex ratio of joeys born during the study (response variable), using a binomial generalised linear model (GLM). A linear mixed effects model (LMER) within the package lme4 (Bates *et al.* 2015) was used to investigate the fixed effect of maternal body mass on the age at which offspring reached sexual maturity (response variable), including the mother's identity as a random effect. The proportion of new shelters used by mothers (fixed effect) when they had male or female young-at-foot (response variable) was compared using a generalised linear mixed model (GLMM) with a betabinomial distribution (Fournier *et al.* 2012), which accounted for overdispersion encountered in earlier models. Time since release was also included as a fixed effect and the mother's identity was the random effect. An effect size (Hedges's g) was also calculated. The proportion of previously used versus previously unused shelter sites used by juveniles during their exploratory phase (fixed effect) was compared between sexes (response variable) using a GLMM with a betabinomial distribution, as was the fixed effect of the number of different trees used (as a proportion of tracking events).

Using the Home Range Tools extension in ArcGIS (Esri 2015, version 10.3.1; Rodgers *et al.* 2015), 100% minimum convex polygons (MCPs) were created for juveniles and their mothers for at-foot, exploratory, and settled movement phases. The extent of overlap of home ranges of mothers and offspring was calculated for the three phases.

Cumulative distance travelled (CDT) for dispersing males was calculated by adding the distances between successive radio-tracking fixes from the time they began long-distance dispersal until the time at which they settled. Despite obtaining irregular numbers of fixes for different individuals while dispersing, number of fixes and CDT were not strongly related ($R^2 = 0.29$). Net dispersal distance (NDD) was calculated for both sexes by measuring the distance from the centre of the possum's 100% MCP when settled compared to that of their maternal range. Because only a small number of males achieved long-distance dispersal ($n = 7$), we limited most of our analyses of factors influencing dispersal to the calculation of R^2 values, investigating the influence of age and body mass (correlated with testes length) at the time of long-distance dispersal on CDT and NDD, rainfall in the previous 30 days on age at dispersal, and time spent dispersing on CDT and NDD.

Kaplan–Meier survival curves created using the package 'survival' (Therneau 2015) tested for differences in survival by movement phases (using time since the phase began), sex, maternal dependence, and sexual maturity. Fisher's Exact Test was used to test for differences in the proportion of possums dying in each category, and to compare mortality rates between juveniles and their mothers.

Where relevant, results are presented as means with standard error. Given the relatively small sample sizes within our study, we discuss trends where $P < 0.01$, noting that these results should be further validated by future studies.

6.6 RESULTS

Over the 22-month period, data were collected for 40 juvenile possums, 26 of which were radio-collared. Juveniles were radio-collared at a mean weight of 556 ± 36 g, and a mean age of 178 ± 8 days. Collared juveniles were radio-tracked to shelter sites or occasionally active locations (at night) an average of 30 ± 4 times and were trapped an average of 6 ± 1 times. Juveniles were collared for an average of 201 ± 22 days, although many were recaptured again after collars were removed. Mothers were captured an average of 14 ± 2 times and radio-tracked an average of 67 ± 10 times, noting that surviving mothers were collared for the duration of the study period.

The body mass, head length, testes length, *pes* length and age of juveniles were all positively related (Supplementary data S10.6.1); biological data from uncollared juveniles of known age and maternity were included in these results. We identified three phases for dependent young: pouch young, at-foot and exploratory phases. We then identified a fourth phase for independent females (settled), and an additional three phases for independent males (pre-dispersal, long-distance dispersal, and settled; Fig. 6.1).

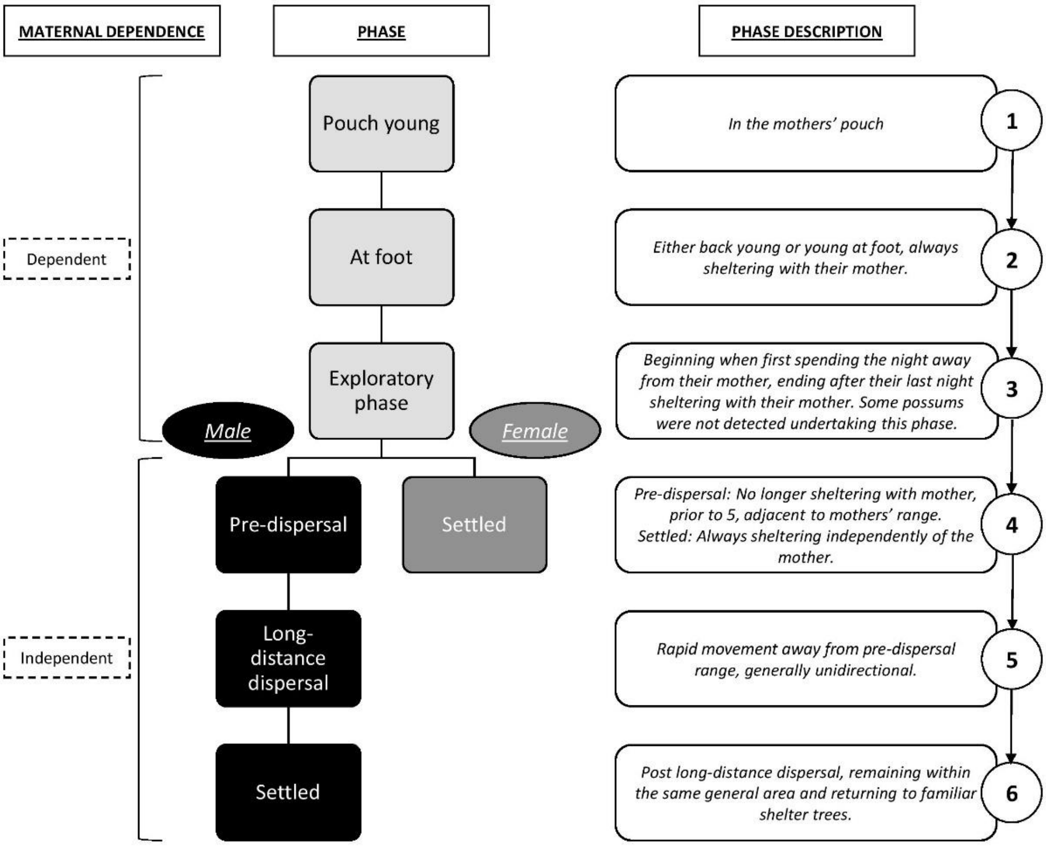


Figure 6.1: Development and movement phases for brushtail possums (*Trichosurus vulpecula*) from birth through to adulthood. Females undertook four phases while males undertook six.

6.6.1 Dependent phases

Pouch young—The 13 adult females always had either pouch young, young-at-foot, or dependent young during the study period, with a mean length of time between the birth of consecutive young of 186 ± 6 days. Each female raised or gave birth to 2–5 joeys during the study. Twelve of the 40 joeys with data collected were translocated to the IFRNP as pouch young. The sex ratio of joeys born post-release was close to parity (16 M, 14 F, Proportions Test: $\chi^2_1 = 0.067$, $P = 0.80$) and not influenced by the mother's body mass ($\chi^2_1 = 0.42$, $P = 0.52$) or time since release ($\chi^2_1 = 0.52$, $P = 0.47$). Joeys were recorded in the pouch up to a maximum of 152 days of age and as large as 310 g.

At foot—The 'at-foot' stage (Fig. 6.1) began as back young as early as 142 days of age and as small as 230 g. Mothers tended to use a higher proportion of new shelter sites when they had female young-at-foot compared to males (F 43 ± 8 %, M 26 ± 9 %; $\chi^2_1 = 2.76$, $P = 0.097$; Fig. 6.2, Table 6.1). On average, young females re-used 31.5 ± 12 % of these shelter trees as adults. There was no significant difference in the total number of trees used by mothers based on offspring sex, when tracking effort was accounted for (F 42 ± 5 %, M 39 ± 6 %, Table 6.1). Young-at-foot sheltered with their mother in tree hollows during the day.

Table 6.1. The effects of sex and maternal traits on the development and dispersal of juvenile brushtail possums (*Trichosurus vulpecula*). *Indicates significant relationship ($P \leq 0.05$), ^indicates trend ($P = 0.051–0.01$). RE = random effect. LMER = linear mixed-effects model, GLMM = generalised linear mixed model.

Fixed effect	Response variable	Co-variate(s)	Interaction terms	Analysis	Trend	Statistical significance
Maternal effects						
Mother’s body mass	Age at sexual maturity	Sex RE=Mother’s identity	Mass*Sex	LMER	Sons of heavier mothers reached sexual maturity sooner. No effect for daughters.	Mass: $\chi^2_1 = 0.8$, $P = 0.36$ Sex: $\chi^2_1 = 15.3$, $P < 0.0001$* Mass*Sex: $\chi^2_1 = 5.5$, $P = 0.019$*
% of previously unused shelter sites used by mothers	Sex of young-at-foot	Sex Time since release RE=mother’s identity		GLMM Effect size (Hedge’s g)	Higher proportion of unfamiliar shelter sites used with female offspring than male (F offspring 43 ± 8 %, M offspring 26 ± 9 %)	$\chi^2_1 = 2.8$, $P = 0.097$^ Hedge’s g = 0.6
Age when ceased sheltering with mother	Age at sexual maturity	Sex RE=mother’s identity	Age ceased*Sex	LMER	Those that ceased sharing at a younger age reached sexual maturity at a younger age. No interaction with sex.	Age: $\chi^2_1 = 3.7$, $P = 0.056$^ Sex: $\chi^2_1 = 3.4$, $P = 0.067$^ Age*Sex: $\chi^2_1 = 1.7$, $P = 0.19$
Exploratory behaviour						
% of previously unused shelter sites used by juveniles in the exploratory phase	Sex			t-test	Females used a significantly higher proportion of unfamiliar shelter sites than males (F 77.0 ± 10 %, M 44.0 ± 12 %)	$\chi^2_1 = 3.8$, $P = 0.050$*
Overlap with at foot area (100% MCP) when undergoing exploratory phase	Sex			Wilcoxon rank-sum test	(F 33.4 ± 17 %, M 33.6 ± 12 %)	$W = 22$, $P = 0.80$
Number of trees used during exploratory phase (proportion of tracking events)	Sex			GLMM	(F 0.42 ± 0.05, M 0.39 ± 0.06)	$\chi^2_1 = 1.2$, $P = 0.28$
Sexual maturity						
Age at sexual maturity	Sex			t-test	Males were significantly older than females (F 290 ± 18 days, M 359 ± 22 days)	$t_{14} = -2.5$, $P = 0.026$*
Weight at sexual maturity	Sex			t-test	Males were significantly heavier than females (F1144 ± 63 g, M 1449 ± 36 g)	$t_{14} = -3.9$, $P = 0.0017$*

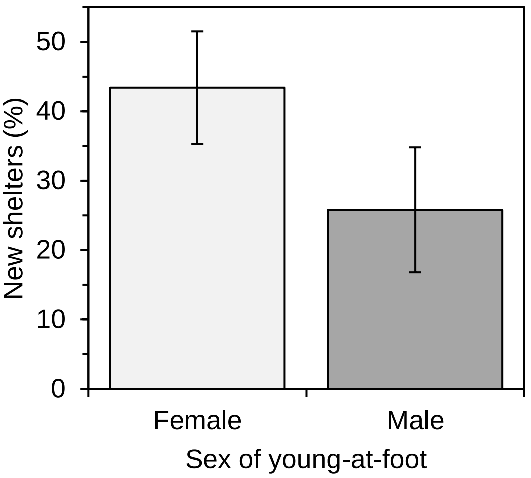


Figure 6.2: The percentage of new shelter sites used by mother brushtail possums (*Trichosurus vulpecula*) when they had either female or male young-at-foot (± 1 SE).

Exploratory phase—The exploratory phase was characterised by a period of time when juveniles moved between sheltering independently and sheltering with their mother. Sixty-seven percent of juveniles were recorded undertaking this exploratory movement (M 73%, F 60%; Fisher's Exact Test: $P = 0.66$, odds ratio = 1.7). The remaining 33% were not recorded sheltering with their mother after the first time they were recorded separately, but it is likely that some movements remained undetected as juveniles were not always able to be tracked daily during that time. Juvenile females used a significantly higher proportion of unfamiliar shelter sites during their exploratory phase than did males (F 77 ± 10 %, M 44 ± 12 %; Fig. 6.3, Table 6.1), but both sexes overlapped with the area (100% MCP) they had used when at foot in similar proportions (F 33.4 ± 17 %, M 33.6 ± 12 %; Table 6.1). Females re-used an average of 66.7 ± 19 % of these trees as adults; males did not re-use these trees post-dispersal.

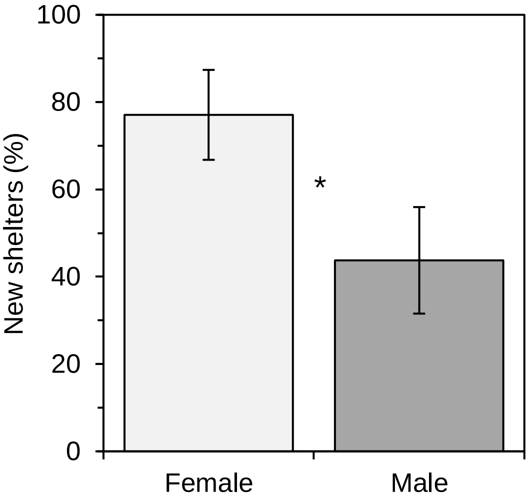


Figure 6.3: The percentage of previously unfamiliar shelter sites used by brushtail possums (*Trichosurus vulpecula*) during their exploratory stage (± 1 SE). *Indicates significance ($P \leq 0.05$).

6.6.2 Independent phases

Sexual maturity—Maternal body mass did not influence the age at which juveniles ceased contact with their mother, but those that left earlier reached sexual maturity at a younger age, regardless of sex (Fig. 6.4, Table 6.1). Females took around 47 ± 14 days (range -11–93) to reach sexual maturity after achieving independence and males took around 58 ± 21 days (range -25–168). Males showed a large degree of variation in age at sexual maturity, and some were still sheltering with or near their mother (at foot, exploratory or pre-dispersal phase), while others dispersed prior to becoming sexually mature. Males were significantly older (M 359 ± 22 days, F 290 ± 18 days) and heavier (M 1,449 ± 36 g, F 1,144 ± 63 g) than females when they reached sexual maturity (Fig. 6.5, Table 6.1). Heavier mothers produced sons that attained sexual maturity earlier than sons of lighter mothers, whereas the same effect was not observed for daughters (Table 6.1). These sons also commenced long-distance dispersal sooner than sons of lighter mothers.

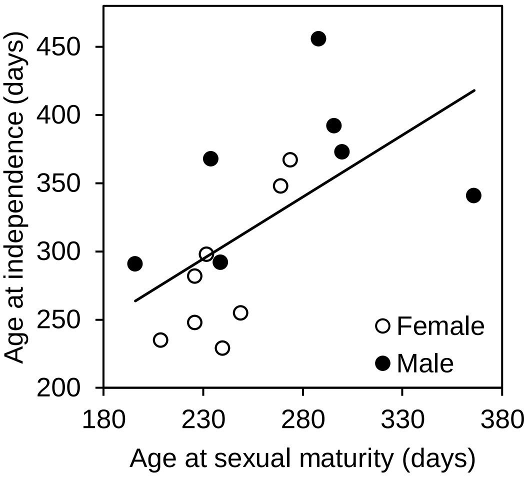
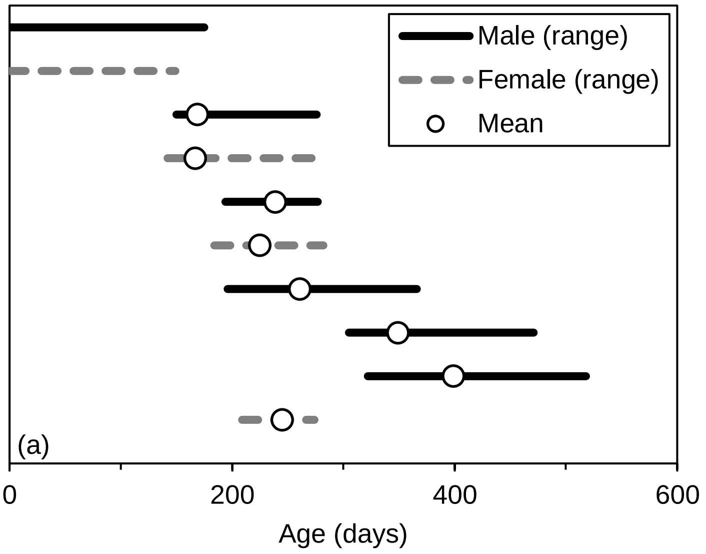


Figure 6.4: The relationship between age at which juvenile brushtail possums (*Trichosurus vulpecula*) ceased sheltering with their mother (age at independence) and age at sexual maturity.

Dispersal by females—Following the exploratory phase, young females immediately settled into an area adjacent to (36 % of females) or slightly overlapping (64 % of females) with their mother (mean overlap 18.2 ± 8 %), but no longer sheltering with her. At this point female possums were considered independent from their mothers and "settled". Seventy percent of females established a range that included part of the area they had used when at foot (mean overlap 19.2 ± 10 %), while no males did ($W = 59.5$, $P = 0.0074$).



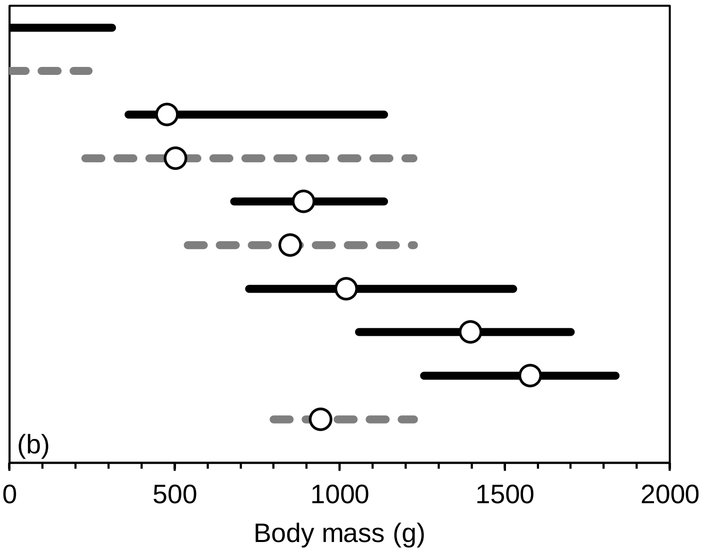


Figure 6.5: The mean age (a) and weight (b) at which movement and development milestones were reached by brushtail possums (*Trichosurus vulpecula*), based on sex, with lines indicating range. *** indicates significance, ^ phase only relevant to males.

Male dispersal—Following the exploratory phase, males behaved in a similar manner to settled females, sheltering in an adjacent or overlapping area to their mother but not sharing daytime shelter sites. This "pre-dispersal" phase lasted anywhere from 7 to 183 days (Fig. 6.5). At least three subadult males undertook overnight forays of 1.4–2.09 km (linear distance) away from their normal range of shelters, returning to their usual range the following night. Following the pre-dispersal phase, males commenced a long-distance dispersal phase that took on average 49 ± 15 days (range 14–126, $n = 7$) to complete. Once commencing long-distance dispersal, males did not return to their pre-dispersal range. Males dispersed an average net distance of 6.45 ± 0.82 km (range 2.80–10.06), 16 times further than females (0.40 ± 0.06 km, range 0.12–0.83, $t_{15} = -8.9$, $P < 0.0001$). Males settled into their own range at a larger body mass than females ($t_{15} = -6.9$, $P < 0.0001$) and were around 150 days older ($t_{14} = -6.3$, $P < 0.0001$, Fig. 6.5).

Factors influencing dispersal by males—Just 43% of males were classified as adult prior to commencing long-distance dispersal. The age at which males commenced dispersal was not significantly related to the age or weight at which sexual maturity was reached, or by rainfall in the previous 30 days (Table 6.2). Older male dispersers had, as intuitively expected, younger siblings that were older than the siblings of younger dispersers; the age of the next young therefore did not influence the timing of dispersal (Table 6.2). Males known to have unrelated females nearby still dispersed away from their natal range, and some were known to pass through the ranges of female possums on their travels; the presence of resident adult males in those areas was less well known. The presence of adult males also appeared to have no effect on the timing of dispersal. One 1.13 kg subadult male was found sheltering with his mother and another likely unrelated adult male (both radio-collared) on one occasion, suggesting aggression from resident males is unlikely to be the sole driver of male-biased dispersal in possums. Adult males were sometimes captured in traps set for young males that had not dispersed, without a subsequent rapid movement of the young male, showing some overlap of their range and tolerance for one another.

The mean cumulative distance travelled (CDT) by dispersing males was 15.66 ± 4.20 km (range 5.80–35.11). Maternal body mass had no significant effect on net dispersal distance (NDD) or CDT (Table 6.2). Older males had higher CDT than younger males, but age was not related to NDD. Neither body mass nor testes length explained CDT or NDD (Table 6.2).

Time taken to settle was not related to CDT or NDD (Table 6.2). The farthest overnight movement recorded was 3.56 km (linear distance). There was no discernible pattern in the direction of travel by dispersing males (Supplementary data S10.6.2), although possums often sheltered in tree hollows found in creeklines. Males did not appear to have lost weight or condition after long-distance dispersal, although we avoided trapping possums immediately upon settling.

6.6.3 Survival

Eleven sexually immature possums (juveniles) died during the study (37 %, n = 30); eight were dependent and three were recently independent. In comparison, six of the 13 adult females (46%) died during the study period; the survival of adult females was not significantly different from the survival of juvenile possums (Fisher's Exact Test: P = 0.74, odds ratio = 0.68). Sixty-four percent of deaths of juveniles were confirmed as predation by feral cats and another 18% of deaths were suspected to be predation by feral cats or western quolls. Two young-at-foot died along with their mothers in one confirmed and one suspected predation event. All deaths of pouch young were a result of the death of the mother, three (75 %) of which were due to predation. All remaining pouch young survived to pouch exit (90 % survival, n = 39). One male was killed by a feral cat after completing long-distance dispersal and settling as an adult and was not included in the juvenile mortality rate.

Table 6.2. The effects of different variables on long-distance dispersal by male brushtail possums (*Trichosurus vulpecula*). LDD = long-distance dispersal, CDT = cumulative distance travelled, NDD = net dispersal distance, LMER = linear mixed-effects model. *Significant relationship ($P \leq 0.05$).

Fixed effect	Response variable	Random effect	Analysis	Trend	Statistical significance
Mothers' physical traits					
Maternal body mass	Age commenced LDD	Mother's identity	LMER	Sons of heavier mothers commenced LDD at a younger age.	$\chi^2_1 = 5.4$, $P = 0.021$*
Maternal body mass	NDD	Mother's identity	LMER	None	$\chi^2_1 = 1.1$, $P = 0.28$
Maternal body mass	CDT	Mother's identity	LMER	None	$\chi^2_1 = 1.8$, $P = 0.18$
Age related traits					
Age when LDD commenced	Age at sexual maturity		Linear regression	Positive relationship (weak)	$R^2 = 0.48$
Age when LDD commenced	Weight at sexual maturity		Linear regression		$R^2 = 0.044$
Age when LDD commenced	Age of younger sibling		Pearson's correlation	Older males had older siblings (i.e. no effect)	$t_5 = 4.9$, $P = 0.0046$*
Age when LDD commenced	NDD		Linear regression	None	$R^2 = 0.11$
Age when LDD commenced	CDT		Linear regression	Positive relationship	$R^2 = 0.84$*
Physical traits					
Body mass when LDD commenced	NDD		Linear regression	Positive relationship (weak)	$R^2 = 0.42$
Body mass when LDD commenced	CDT		Linear regression	None	$R^2 = 0.20$
Testes length when LDD commenced	NDD		Linear regression	Positive relationship (weak)	$R^2 = 0.48$
Testes length when LDD commenced	CDT		Linear regression	Positive relationship (weak)	$R^2 = 0.43$
CDT	Time to settle		Linear regression	None	$R^2 = 0.01$
NDD	Time to settle		Linear regression	None	$R^2 = = 0.01$
Environmental factors					
Age when LDD commenced	Rainfall in previous 30 days		Linear regression	None	$R^2 = 0.02$

The proportion of juveniles dying within each phase was not significantly different (Fisher's exact test: $P = 0.93$, Kaplan–Meier: $P = 0.82$), however no mortalities were recorded for males undergoing long-distance dispersal. Similarly, there was no significant difference in survival probability based on sex (Fisher's Exact Test: $P = 1$, odds ratio = 1.3, Kaplan–Meier: $P = 0.62$) or maternal dependence (Fisher's Exact Test: $P = 0.53$, odds ratio = 1.6, Kaplan–Meier: $P = 0.60$). However, the mortality of sexually immature possums (regardless of maternal dependence) was higher than that for sexually mature possums (Fisher's Exact Test: $P = 0.017$, odds ratio = 10.0, Kaplan–Meier: $P = 0.16$, Fig. 6.6), noting that the 13 mothers were not included in that analysis as their age was unknown. Survival, movement, and milestone information for individual possums can be found in Supplementary data S10.6.3 and S10.6.4.

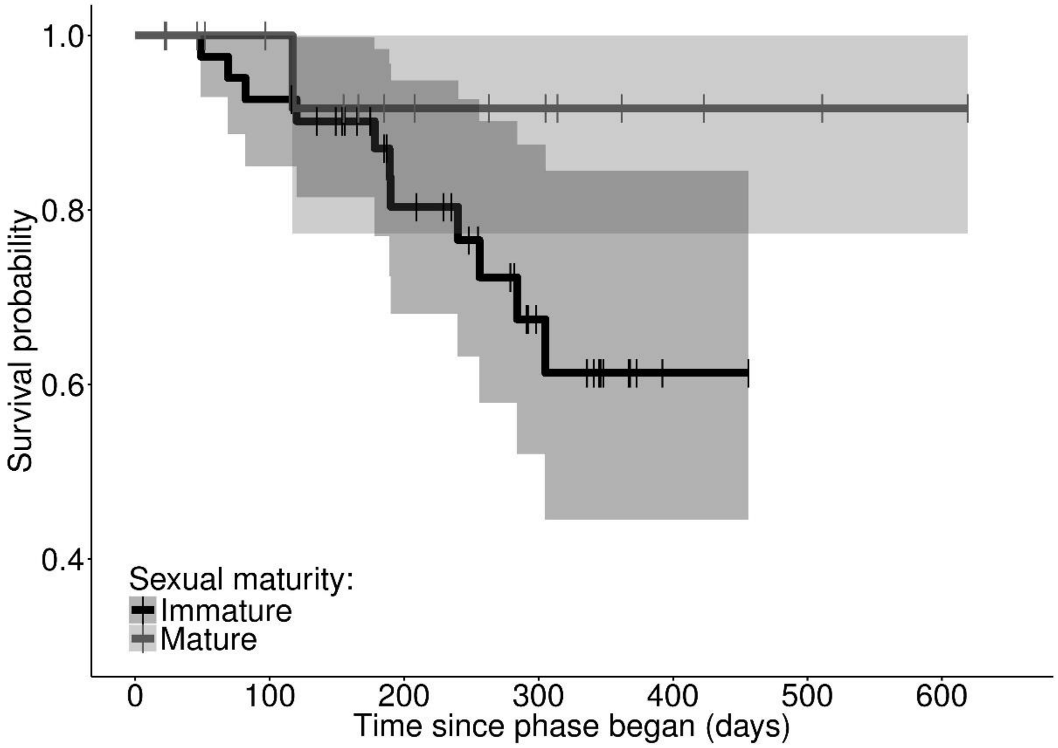


Figure 6.6: Kaplan-Meier survival probabilities for young brushtail possums (*Trichosurus vulpecula*) based on sexual maturity, with 95 % confidence intervals. The symbol | denotes times at which animals were removed from the study (i.e. died or last known to be alive).

6.7 DISCUSSION

Sex effects were found for the growth, movement, and mothering behaviour of brushtail possums, but not survival which was instead related to sexual maturity. In addition, discrete movement phases during natal dispersal differed by sex. Two-phase dispersal was recorded using telemetry for western quolls, with males dispersing farther than females; however in contrast to possums, quolls dispersed within just 3–18 days of ceasing contact with their mother (Soderquist and Serena 2000). Male possums must gain some advantage by waiting sometimes lengthy periods of up to 183 days between ceasing to shelter even occasionally with their mother, and commencing long-distance dispersal. The importance and advantages of multiple movement phases during dispersal could be a focus of future studies, for applicable species, with the underlying driving forces currently unknown.

We recorded an interaction between the behavioural and physical traits of the mother and the sex of a juvenile. There was a strong trend towards mothers using a higher proportion of previously unused shelter trees with daughters compared to sons, although the trend was not significant at the alpha 0.05 level, possibly due to small sample size. Sex-biased mothering remains relatively unexplored in research. Juvenile females continued to investigate available shelters during their exploratory phase, using a higher proportion of unfamiliar shelters than did juvenile males. Maternal body mass had more of an influence on the development and movement of males than females; heavier mothers produced sons that reached sexual maturity at a younger age and commenced long-distance dispersal earlier. Early dispersers may be able to begin breeding at a younger age, although we did not measure this for males. The body mass of female Mt Graham red squirrels influenced the dispersal movements of sons and daughters in opposite ways (Merrick and Koprowski 2017), while maternal age influenced the growth of juvenile meerkats (*Suricata suricatta*) (English *et al.* 2014). We found that possums that ceased sheltering with their mother at an earlier age reached sexual maturity earlier, regardless of sex, suggesting a possible physiological response to the presence of the mother. While the influence of maternal condition appears to be inconsistent across species, our study adds to a growing body of evidence suggesting that both physiological and behavioural maternal traits should be considered when studying natal dispersal.

As expected, possums displayed male-biased dispersal, whereby males exhibited a bout of long-distance dispersal away from their natal site, whereas females were philopatric, remaining adjacent to and occasionally overlapping with their mother. This somewhat contrasts with studies in New Zealand, where not all male possums dispersed long distances, and some females did disperse away from their natal range (Clout and Efford 1984; Cowan *et al.* 1996). However, the constant removal of individuals at the New Zealand study site is likely to influence these movements (Blackie *et al.* 2011). An Australian study using genetic samples found that while dispersal was male-biased, possums rarely dispersed beyond 900 m. However, the study environment was urban and the population was resident, which could account for the much shorter distances than recorded in our reintroduced population in a semi-arid environment (Stow *et al.* 2006). We suggest therefore that density and resources are likely to influence dispersal distance in possums.

Aside from maternal body mass, other biological and environmental factors were unable to predict the timing of dispersal, and so we suggest that long-distance dispersal by male possums is innate (Howard 1960). While sexual maturity is thought to be related to the timing of dispersal by possums in New Zealand (Cowan and Rhodes 1993; Cowan *et al.* 1996), our data does not show strong evidence of this pattern. Around one-half of the males were sexually mature prior to dispersal and one-half were not; while undoubtedly the long-term goal of dispersal is to breed with unrelated females, several immature males dispersed with no immediate prospect of siring offspring. In addition, the castration of males has not been found to prevent dispersal (Cowan *et al.* 1997). In various species of *Antechinus,* the onset of male-biased dispersal is driven by the presence or absence of the mother (Cockburn *et al.* 1985; Fisher 2005). It has not been determined whether this is due to maternal behaviour in driving out sons or an innate response by sons to the continued presence of their mother. These results support the suggestion that maternal effects, both physiological and behavioural, may strongly influence dispersal, but further research is needed to continue uncovering the mechanisms and effects.

Generally, dispersal is considered to be a high-risk phase (Estes-Zumpf and Rachlow 2009; Serrano and Tella 2012) and previous studies anecdotally suggested that the mortality of dispersing possums was greater than that for resident adults (How 1981; How and Hillcox 2000). However, we recorded no mortalities for dispersing males at our study site, although the sample size was small. The ongoing control of introduced predators, particularly foxes, in the IFRNP is likely to have contributed to the survival of many juveniles and adults, with predation by feral cats now posing the biggest threat. We found that sexually immature possums suffered a higher mortality rate than sexually mature but young possums, suggesting an age or experience effect rather than differential risk based on movement. Nearly one-half of the mothers died over the study period and this was not significantly different from juvenile mortality, suggesting body mass and site familiarity are unlikely to be the main factors influencing juvenile mortality. Mothers have a significant handicap when carrying large pouch young or back young and this could influence survival. The low population density may have influenced the survival of juveniles; dispersing banner-tailed kangaroo rats (*Dipodomys spectabilis*) had lower survival when population densities were high compared to when densities were low (Jones 1988). Philopatric Arctic ground squirrels (*Urocitellus parryii*) had higher survival than dispersing individuals (Byrom and Krebs 1999), suggesting an advantage in being familiar with the local environmental or in avoiding long-distance movements; however, environmental familiarity did not appear to influence possum survival, with no sex difference recorded, despite young females being familiar with a larger number of shelter trees within their natal range than males. Longer dispersal distances can further elevate mortality (e.g., Byrom and Krebs 1999; Johnson *et al.* 2009), but again we found no evidence of this for possums. In contrast, swift foxes (*Vulpes velox*) and prairie voles (*Microtus ochrogaster*) that dispersed had higher survival than non-dispersing animals (Lin and Batzli 2004; Ausband and Foresman 2007), suggesting the benefits and costs of dispersal probably vary by species.

By combining intensive trapping with radiotelemetry, we were able to uncover sex differences in the movement, growth, and mothering behaviour of possums, as well as identify and eliminate factors influencing mortality. In contrast to most studies of natal dispersal, we recorded no deaths of long-distance dispersers, and instead found that mortality risk decreased when sexual maturity was reached and is probably related to age and thus experience or behaviour. Our results suggest that dispersal, dispersal distance, sex and sex differences in maternal care do not necessarily influence mortality of the young of marsupials. Sex-dependent mothering behaviour and the influence of maternal physiological traits on offspring are largely unexplored in the literature, despite the vast potential for mothers to influence the survival, development, and movement of juveniles. A shift to more-intensive field studies is required for these relationships to be investigated in marsupials and other mammals.

6.8 ACKNOWLEDGMENTS

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7. GENERAL DISCUSSION

This thesis has investigated the influence and importance of release protocols and release environment on reintroduction success, using the brushtail possum as a study species.

Release methods were found to have little measurable impact on reintroduction outcomes when key predators were intensively managed and rainfall was ≥ average. While possums did initially lose body mass after release, all release treatment groups regained mass relatively quickly (30–60 days) at an equal rate. Additionally, no females in any treatment lost pouch young as a result of the translocation. Temporary confinement and the provision of supplementary food and shelter did not influence post-release dispersal distance and the use of supportive provisions (supplementary food and shelter) was poor. While hyperdispersal and loss of mass experienced in this and previous possum releases suggests that alternative release methods should be trialled, the delayed and nest-box release methods tested in this study had no effect on these parameters compared to immediate release animals. Low predation pressure at the release site may have reduced the potential for these issues to drive post-release mortality. Hyperdispersal was known to be an issue for other possum reintroductions to areas where predators had not been effectively controlled. Our study was consistent with possum releases where dispersal was monitored, with hyperdispersal recorded in all cases (Pietsch 1995; Short and Hide 2014; May *et al.* 2016), even when delayed release methods were used (Tribe *et al.* 2005). Despite conducting the first experimental comparison of release methods for brushtail possums, this study was unable to identify a technique that would successfully limit hyperdispersal, and this should be accounted for in future releases of the species if areas surrounding release sites have threatening processes that may impact on the reintroduction (e.g. higher predator numbers or drought conditions that impact on understorey cover). Sometimes, hyperdispersal can be positive, as animals may locate more suitable habitat (Richardson *et al.* 2015b). While hyperdispersal for unfenced possum releases cannot be controlled, it should be accounted for by either compensating and releasing a larger number of animals, or intensively monitoring animals after release and moving them back to the release area if necessary. We found that two possums that had hyperdispersed and were recaptured and returned to the release area quickly settled where re-released.

Significant differences in antipredator behaviour were found between predator-exposed and predator-naïve source populations, with predator-exposed possums showing more suitable antipredator behaviours. Predator-exposed possums were wary, difficult to trap (and handle), showed neophobic tendencies and used their habitat in a way that minimised predation risk. Consistent with the release methods study, however, effective predator control at the release site was found to be a more important factor, with previous exposure to predators having no discernible impact on post-release survival during the study period. Pickett *et al.* (2005) also found that the presence of predators influenced habitat use (time spent on the ground, movement and giving-up densities) by brushtail possums, but only in some habitat types. Interactions between habitat and predation risk are well documented (Didham *et al.* 2007; Doherty *et al.* 2015b; McGregor *et al.* 2015) and in this case may be applicable to prey behaviour as well as predator behaviour. The results from this thesis demonstrate that the antipredator responses of brushtail possums can be relaxed relatively quickly when prey are isolated from predators. While in theory this could influence post-release survival, effective predator control at release sites can offset these risks.

Degraded habitat was not found to be a barrier to short-term reintroduction success, despite being cited as a common cause of reintroduction failure for a range of fauna (Griffith *et al.* 1989; Wolf *et al.* 1996; Powell *et al.* 2012; Stadtmann and Seddon 2018). The high availability of tree hollows combined with successful fox control and ongoing feral cat removal outweighed any negative impacts associated with habitat degradation by introduced feral and overabundant native herbivores. Similarly, in another study, the exclusion of predators was sufficient to enable the survival of reintroduced eastern barred bandicoots (*Perameles gunnii*) despite degraded habitat (Winnard *et al.* 2013). Predation was also found to be the most important factor for reintroductions of water voles (*Arvicola terrestris*), with habitat quality having a lesser effect (Moorhouse *et al.* 2009). The ubiquitous presence of hollow bearing eucalypts at the release site may have been essential for population establishment, with eucalypts providing the majority of shelter sites and a food staple. The low recruitment of some of these species, particularly *E. intertexta*, may influence population persistence in future if the issue is not addressed, with impacts on food resources as well as hollow availability. The high proportion of eucalypts recorded in the diet could also be a reflection of a limited number of alternative food plants compared to some other sites where eucalypt consumption is much lower (Fitzgerald 1984; Evans 1992). A large number of ground level species were also recorded in the diet. Should predator control be relaxed or become ineffective, ground foraging may leave possums susceptible to higher predation rates. The interaction between ground versus canopy foraging, drought, and vegetation quality was not investigated in this study, and under drought circumstances it is likely that vegetation may play a stronger role in population persistence through both diet and predation risk.

Consistent with studies conducted in New Zealand (Clout and Efford 1984; Cowan *et al.* 1996; Ji *et al.* 2001), natal dispersal was male-biased. However, dispersal distances were much further than anticipated, with distances of up to 35 km travelled and net dispersal distances occasionally exceeding 10 km. Only one previous dispersal study is available for comparison within the possums' native range (Australia), with dispersal distances ascertained from genetic analysis suggested to be less than 900 m (Stow *et al.* 2006), less than 14 % of the mean male dispersal distance recorded in our study. Shorter dispersal distances found by Stow *et al.* (2006) were likely due to the population being urban, resident, and at a higher density, compared to our population which was semi-arid, reintroduced, and at a low density. The method used to determine dispersal distance is likely to influence precision.

Despite feral cats causing several mortalities, juvenile survival maintained at the current rate (63 % survival) suggests that population persistence is feasible. Given the somewhat previously overlooked impact of feral cats on brushtail possums, combined with the known impacts of foxes, it is likely that predation rates on juveniles within other populations where introduced predators are not controlled may be unsustainable. Two dispersing males travelled outside the national park, highlighting the importance of feral predator control in areas surrounding release sites (i.e. a buffer zone). The high survival of dispersing males in our study was promising, however, for both population persistence and for an increase in the area of occupancy for the population.

Despite post-release hyperdispersal and weight loss, a variable diet and predator-naïve behaviour, the possum reintroduction met short-term reintroduction success criteria and thus these measures may be poor predictors of reintroduction outcomes, or poor indicators of acclimatisation. For short-term population establishment and persistence, this study has demonstrated that release site features including hollow availability and predator control are more important than release protocols, notably release method and source population. The relative influence of release site features on long-term establishment or persistence through drought may differ to those experienced under short-term establishment under non-drought conditions. However, the impact of release site features on long-term persistence, particularly through drought conditions, remains untested and should be the focus of future research.

7.1 CONTRIBUTIONS TO KNOWLEDGE

Very little research has been published on possums in Australia's arid and semi-arid zones, despite these areas being of the highest conservation importance. Much of the research that has been undertaken within these regions remains unpublished as reports (Foulkes and Kerle 1989; DEC 2012) or theses (Foulkes 2001). Some notable exceptions exist (Evans 1992; Kerle *et al.* 1992; Short and Hide 2014), but this thesis provides the first experimental-based reintroduction of brushtail possums to the semi-arid zone, testing release methods and release site attributes. The finding that immediate releases are suitable in low predator areas where natural food and shelter is plentiful can be used to guide future reintroductions of the species to other areas, and can form the basis of hypotheses for translocations of other species. Previous predator exposure was not found to influence post-release survival, and given that other possum releases have experienced high rates of post-release predation regardless of source, this suggests that predator control is one of the most important factors in reintroduction success, and if achieved can provide flexibility in the selection of source animals and source sites. The behaviour of possums in semi-arid environments, where habitat differs from temperate regions and is likely to influence behaviour, had not been previously assessed.

Effective fox control, combined with the ongoing removal of feral cats, appears sufficient to facilitate short-term reintroduction success for possums, provided that food and shelter is available. Poor understorey did not appear to significantly influence reintroduction outcomes, although it could have affected predation rates. This study has perhaps drawn more attention to the potential impact that feral cats can have on possums. While feral cats are known to be predators of possums (Jones and Coman 1981; Cruz *et al.* 2013; Doherty *et al.* 2015a), their impact may have previously been underestimated given the comparatively heavy impacts caused by foxes (Saunders *et al.* 1995; Burrows and Christensen 2002; Robley *et al.* 2014), and the fact that possums and cats co-exist in many areas such as Kangaroo Island and Tasmania. In semi-arid environments, possums probably need to spend more time on the ground foraging, thus increasing their predation risk compared to temperate environments where canopy connectivity is higher. Despite habitat quality being highlighted as essential for reintroduction success globally (Griffith *et al.* 1989; Wolf *et al.* 1996; Stadtmann and Seddon 2018), our results suggest that the control of feral predators may be more critical for this species. Landscape scale fox control is likely to improve the population health of remnant populations of possums in other areas.

The mothering behaviour of brushtail possums has not been assessed previously, and initial results suggest that some aspects may be sex-biased. This phenomenon has been rarely described for any species and these results warrant further investigation, having potential implications for dispersal theory more widely. This thesis also provides the first dedicated study of possum dispersal that uses a combination of trapping and radio-tracking within their native range. This was somewhat surprising, given the species' widespread distribution and relatively high abundance in some areas and significant declines (thus, conservation concern) in others.

The original causes of decline and local extinction of possums in Australia were attributed to predation by introduced foxes (Paull and Date 1999; Foulkes 2001; Burrows and Christensen 2002) and feral cats (Jones and Coman 1981; Foulkes 2001; Cruz *et al.* 2013) as well as the naturalised dingo (Foulkes 2001; Davis *et al.* 2015), habitat loss and alteration (Abbott and Whitford 2002; Anderson *et al.* 2010), competition with introduced and domestic herbivores (Evans 1992; Foulkes 2001), altered fire regimes (Burbidge *et al.* 1988; Foulkes 2001) and hunting and persecution (Kerle 2001; Gordon and Hrdina 2005). Anecdotal evidence suggests disease may have caused some sudden decreases in population size as well (Kerle 2004; Abbott 2006). The results presented in this thesis support the suggestion that arid zone possums have fallen into a 'predator pit', whereby numbers have become so low that they are unable to increase even under favourable conditions (Walker and Noy-Meir 1982; Newsome 1990; Kerle *et al.* 1992). The control of foxes (and to a lesser extent feral cats and dingoes), despite habitat quality being degraded, was sufficient to enable short-term population establishment in the IFRNP. Whilst results suggest that feral predators may be the major cause of decline, the combined effect of so many threatening processes is likely to have had a synergistic effect, thus further increasing the impact of the threats (Morton 1990; Kerle *et al.* 1992; Didham *et al.* 2007). For example, where vegetation is sparse, possums may be more at risk of predation as they are forced to spend more time on the ground.

The chapters within this thesis provide the first quantitative research on the release and ecology of brushtail possums in the semi-arid zone of South Australia. These findings may be used for the conservation of *in situ* possum populations as well as applied to future translocations of the species (see 7.4 Recommendations).

7.2 LIMITATIONS

This study encountered the usual slew of problems associated with conducting large amounts of fieldwork with a reintroduced species—unfavourable and unseasonal weather, small sample sizes, difficulty recapturing collared animals, technical issues with both VHF and GPS radio-collars and financial and logistic costs. Many of these challenges, despite being frustrating, were actually advantageous for the possums—higher than average rainfall and heavy downpours increased food availability for possums and at times provided free water; trap-shy possums may have better anti-predator behaviours than those that were trap happy, and; despite having to conduct fieldwork through the hot summers, it was evident that the reintroduced population could tolerate both the hot summers and cold winters experienced in the IFRNP. Whilst not a study limitation *per se*, a major challenge was the huge logistic effort required to radio-track and trap possums at regular, sometimes intensive, intervals. Trap-shyness and dispersal into difficult to access areas by some animals confounded this.

The comparison of the behaviour and post-release survival of predator-naïve and predator-exposed possums was problematic because only one population was available of each, and the habitat at each site was considerably different. Originally, a comparison of possums inside and outside the fence at Yookamurra Wildlife Sanctuary was to be made, where the habitat was identical and the only differing factor was predator exposure. However, a pilot study only recorded two possums outside the fence, meaning a suitable sample size for comparisons was not achievable and possums could not be translocated from there. The difference in the abundance of possums inside and outside the fence at Yookamurra is probably testament to the impact that introduced predators have on the species. The southern Flinders Ranges was then selected as an alternative predator-exposed site, as possums were known to be present and introduced predators were relatively commonly sighted. Differences in habitat and vegetation at the two source sites (creekline and woodland habitats at the Southern Flinders Ranges, and mallee and shrubland at Yookamurra Wildlife Sanctuary) was obviously problematic and mostly resulted in within-treatment comparisons rather than between-treatment. However, the large dataset produced consistent and convincing results, and this information may be used for the management of predator-free populations. The addition of mammalian predators to fenced reserves is likely to be important if those populations are to be used as sources for reintroductions to unfenced areas where introduced predators are present.

Next-generation DNA sequencing is a relatively new method for diet studies. I had to collect as many plant species as possible from the study site to form a local reference library, which relied on me being able to find species and then correctly identify them. Some species found at the study site did not make it into the reference library. In addition, genetic material was not able to be extracted from a small number of reference samples. The ability of the method to quantify the proportion of each plant species within each sample was probably overestimated at the beginning of the study, and this became a limitation when interpreting the results. Originally, a comparison of two methods (traditional microhistological analysis and next-generation DNA sequencing) was planned, however undertaking both methods within the PhD timeframe was ultimately not feasible. The diet study was conducted using samples from a one year period, which precluded seasonal effects from being investigated.

7.3 FUTURE DIRECTIONS

This study has uncovered several knowledge gaps and possibilities for future research. Brushtail possums in the semi-arid and arid zones of Australia have not been intensively studied, despite their declining trajectory in many areas. Causes of decline should continue to be investigated. Perhaps the most pertinent outcome from this study is the need to study this and/or other semi-arid or arid possum populations through a drought period. Drought is likely to affect food availability, nutritional requirements, predation risk via the decline in alternative prey and an increased sparseness of understorey, reproduction and ultimately, population persistence.

Hyperdispersal and loss of body mass (and even death due to lack of resources) are commonly experienced in reintroductions of possums (Pietsch 1995; Miller *et al.* 2010; Short and Hide 2014; May *et al.* 2016) and other species (Hardman and Moro 2006; Matějů *et al.* 2012; Moseby *et al.* 2014). Research should continue to test methods of reducing post-release dispersal and loss of body mass for possums and other species. In particular, research should focus on novel ways to increase the uptake of post-release assistance, as this was found to be an issue with possums. While release protocols are rarely a one-size-fits all solution (Moseby *et al.* 2014), effective methods could be determined and then trialled for a variety of other species.

Given the increasing recognition of feral cats as a key threatening process for many native species (Australian Government 2018) and the well documented difficulties in achieving effective control, future research should continue to investigate alternative methods of cat control (e.g. Read *et al.* 2014; Read *et al.* 2016; Moro *et al.* 2018). Successful methods will likely provide benefits for a suite of species, as has been demonstrated following successful fox control (Burrows and Christensen 2002; Robley *et al.* 2014).

As the use of genetics for diet analysis becomes more popular, comparisons to other analysis methods should continue to be made, as well as investigating digestive biases and the accuracy of identifying proportions consumed by undertaking captive feeding trials (Deagle *et al.* 2010; Peters *et al.* 2015). This would enable the method's strengths and weaknesses to be uncovered, and if error levels can be calculated then quantitative comparisons to studies using different methods may be possible. All dietary analysis methods have imperfections, but as long as these are understood they still provide valuable information on the ecology of a species. The possums' diet in the IFRNP should also be investigated over multiple years, to provide information on seasonal changes and drought effects. If/when drought conditions are experienced, sex and/or reproductive effects on diet may become apparent.

The newly formed IFRNP possum population provides many opportunities for ongoing and future research. Assuming the population continues to increase, the effects of density and time since release on home range size and habitat utilisation could be investigated. Potential changes over time could either arise from changes within individual behaviour (i.e. an individual's home range decreases or increases over time) or changes between generations. Given the initial suggestion of a modification in antipredator behaviour by predator-naïve possums (the avoidance of cat urine by female possums one year after release), antipredator behaviour of the population could be periodically assessed to ascertain how long it takes for predator-naïve possums to achieve the same level of antipredator behaviours as their predator-exposed counterparts. The retention of some predators at the reintroduction site (feral cats are unlikely to be functionally removed in the near future) may have the benefit of maintaining/enhancing these antipredator behaviours. Another research focus could be the investigation of traits influencing paternity; do all males contribute to the population evenly, are some males dominant, and do females breed with the same male on multiple occasions? Given the results presented in this thesis, the reintroduced IFRNP possum population is likely dependent on the maintenance of intensive predator management across the Park; effective fox control must continue or the population is unlikely to remain sustainable, and feral cat control should continue and, ideally, become more effective.

Given the limited research into the survival and dispersal of juvenile possums within their native range, and the interesting results to come from this study, future research should continue to investigate this aspect of possum ecology. We recorded male dispersal distances much further than was recorded in the only other natal dispersal study of possums within their native range (Stow *et al.* 2006), and found that all males and no females completed long-distance dispersal, which was inconsistent with dispersal studies in New Zealand, where dispersal has been better studied because of the species' pest status (Clout and Efford 1984; Cowan and Rhodes 1993; Cowan *et al.* 1997). The many movement stages we found from birth to settling has not been described for this species and we found no evidence of any other species undergoing as many stages. We have highlighted the importance of incorporating maternal behaviour into dispersal studies and our result of sex-specific mothering behaviour could provide a promising direction for future research. If mothers alter one behavioural aspect based on the sex of their offspring, it is likely that other aspects (undetected in the current study) are also altered. Other research into juvenile dispersal could include how time since release influences dispersal distance, home range size, the proportion of overlap between females and their mothers, and how inbreeding avoidance is achieved given that females can breed at a young age relative to their lifetime.

7.4 MANAGEMENT IMPLICATIONS

7.4.1 Predators

Predator control is likely to be the most important factor for the reintroduction of possums and the conservation of existing populations. Fox control is undoubtedly the most important factor, but feral cat control should also be implemented effectively; feral cats were the primary cause of death for possums in our reintroduced population. Juvenile possums can disperse significant distances and thus predator management should include buffer areas around core populations. Similarly, reintroductions to unfenced areas should also consider buffer zones for the surrounding areas of release sites as a proportion of the population is likely to hyperdisperse, and this may result in leaving the predator-managed area. Finally, maintaining herbivore populations (including those within fences) with a sustainable level of predators will aid in retaining antipredator behaviours and may be more likely to result in successful translocations to areas where predators are present.

7.4.2 Translocations

If predators are absent or well controlled, then immediate releases are most suitable for possum translocations given the fast settling time and inability for supplementary food to prevent loss of body mass. Under these conditions, previous exposure to predators is not likely to influence post-release survival. If exposed to low numbers of predators, antipredator behaviour could improve over time. Previous studies combined with the current research suggests that translocations should not proceed in areas where predators are not subject to any level of control, or where control is ineffective. However, if for some reason this does occur, delayed releases may offer some protection while possums acclimate and occasionally utilise 'risky' shelters. Predator-naïve animals should not be used as source populations for these (unlikely) translocations given their relaxed antipredator behaviour compared to their predator-exposed counterparts.

7.4.3 Habitat

Possum releases into degraded habitat are possible *if* tree hollows are abundant, and predators are subject to control. If these requirements are not met, then it is possible that predation rates may attain unsustainable levels as possums are forced to spend more time on the ground and use more exposed shelter sites. Reintroductions to areas where plant diversity has been reduced compared to historic levels is possible, however the impact of drought conditions on dietary requirements are yet to be tested and should be considered when reintroducing animals to arid and semi-arid environments. The recruitment of hollow-bearing trees as well as quality food plants should be ensured if long-term population persistence is to be achieved; thus, the control of feral herbivores (goats and rabbits) and overabundant native species (kangaroos) within the IFRNP should be of immediate management concern. This is likely to be reflected across other areas, including central Australia where possum populations are declining (or locally extinct).

7.5 CONCLUSIONS

This thesis provides evidence that release site features (habitat quality and predators) may be more important than release protocols (release methods and source population). I have demonstrated that, when key predators are controlled and natural hollows are plentiful, immediate release methods are suitable for possums, with the source of the released animals not being of critical importance. However, these results are likely to vary under drought conditions or when predator numbers are higher. Degraded habitat does not preclude short-term reintroduction success, provided that hollow-bearing trees are numerous and at least some preferred food plants are available. Effective fox control combined with feral cat removal can facilitate juvenile survival that is sufficient to enable population growth and, ultimately, persistence.

Overall, brushtail possum populations in Australia are declining, particularly in the arid and semi-arid zones; the species has already disappeared from more than 50 % of it's historic distribution (Kerle *et al.* 1992; Dickman *et al.* 1993; Kerle 2001; Kerle 2004; Gordon and Hrdina 2005; Morris *et al.* 2008). The significant decline of the species prior to the last 10 years combined with their widespread (but patchy) distribution makes them ineligible for threatened species status (IUCN 2001). Sadly, much of the attention the species receives is focused on areas where they are overabundant, considered a nuisance or pose a threat to a commercial industry—usually, these are urban environments, islands or plantations (Statham 1984; Hill *et al.* 2007; Russell *et al.* 2011; DEPIPWE 2015). Few studies have been conducted on possums in semi-arid and arid areas, and without an understanding of their ecological requirements and the reasons for their ongoing decline in these areas, effective conservation strategies cannot be developed. Additional research could facilitate recovery of the species, before possums in central Australia join the long list of critical weight range mammals to disappear.

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The Possum Mobile

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10. SUPPLEMENTARY MATERIAL

Supplementary data S10.2.1: The outcomes of previous brushtail possum translocations.

S = source population (W = wild, U = urban, R = rehabilitated, C = captive); DR = delayed release, SF = supplementary feeding reported, F = fenced release site free of mammalian predators; FC = fox control, M = post-release monitoring, H = hyperdispersal, n = total number of possums released, EP = existing population at the release site, MR = multiple releases reported. If multiple releases occurred, 'year' refers to the first reported release at that location. Blank spaces indicate unknown information. Y = yes, N = no.

Location	Year	S	DR	SF	F	FC	M	H	*n*	EP	MR	Outcome	Comments	Reference
Arkaroola, SA	1968		N		N		N		14	N		Unsuccessful		Papenfus (1990)
Cape Range NP, WA	2010	W	N		N	Y	Y		104	N	Y	Unsuccessful	Failed due to fox predation, despite baiting	DEC (2012)
Ernabella, SA	1976	U	N		N		N		12	N		Unsuccessful		Papenfus (1990)
Gold Coast, Qld	1995	R	Y	Y	N		Y	Y	13	Y	Y	Successful?	No mortalities by introduced predators. Python predation. Some were humanised. Short term monitoring/success criteria.	Tribe *et al*. (2005)
Humbug Scrub, SA	1980s	U	N		N		N				Y			Papenfus (1990)
Karakamia, WA	1994	C(R)	N	N	Y	Y	Y		8	Y	Y	Successful	Orphaned (hand-reared) possums, supplemented existing population	Australian Wildlife Conservancy (unpub. data)
Katarapko Island, SA	1970s	W	N		N		N			Y				Papenfus (1990)
Lorna Glen, WA	2007	W	N	Y	Y	Y	Y		95	N	Y	Successful	Some deaths due to lack of resources and raptor predation.	Miller *et al*. (2010)
Mambray Creek, SA	1972	U,W	N		N		N		16	?	Y	Unsuccessful		Papenfus (1990)
Melbourne, Vic	1992	U(R)	N	N	N		Y	Y	64	Y	Y	Unsuccessful	Naivety, fox predation, stress.	Pietsch (1995)
Murray Bridge, SA	1980s	W	N		N		N							Papenfus (1990)
New Zealand	1993	W	N	N	N	-	Y	Y	43	Y	Y	-	Several were shot (pest status in NZ, introduced species)	Cowan (2001)
Oraparinna Mine, SA	1961	W(R)	N	Y	N		N		12	N	Y	Unsuccessful		Papenfus (1990)
Paruna, WA	2000	W	N	N	N	Y	Y	Y	118	Y	Y	Semi-successful	Numbers stable but not increasing. Predation by foxes/cats, pythons, raptors.	May *et al*. (2016), Australian Wildlife Conservancy (unpub. data)
Quorn, SA	1974	U	N		N		N		30+		Y	Successful		Papenfus (1990); SA DELM in Copley (1995)
Sandilands, SA	1970s	W	N		N		N				Y	Not reported	Translocation distance 30km	Papenfus (1990)
Stony Creek, SA	1974	U	N		N		N		>20		Y	Successful	Additional possums released at nearby Wilmington in the following years	Papenfus (1990); pers. obs.
Wadderin, WA	2008	W, U(R)	N	N	Y	Y	Y	Y	9	N		Successful	3 released in nest-boxes	Short and Hide (2014)
Wilmington, SA	1985		N		N		N		5			Successful		SA DELM in Copley (1995); pers. obs.
Wilpena, SA	1961	W(R)	N	Y	N		N		4	N	Y	Unsuccessful	Small release number	
Yookamurra, SA	1990s				Y	Y	Y			Y		Successful	Now at a high density	Australian Wildlife Conservancy (unpub. data)

Supplementary data S10.2.2: Release method, sex and dispersal distance for possums that hyperdispersed (moved more than 3x the mean range length of 0.88 km) away from their release site. Distances were obtained six weeks after release, when possums had stabilised their distance from release site.

Release method	Sex	Distance (km)
Immediate	Male	4.09
Delayed	Male	3.35
Delayed	Female	2.99
Delayed	Female	4.88
Nest-box	Female	4.22
Nest-box	Female	9.55
Nest-box	Female	17.02

Supplementary data S10.5.1: Plant species included in the DNA barcode reference library. Bold text indicates bait (apple, peanut butter and oats).

Abutilon leucopetalum
Abutilon otocarpum
Acacia beckleri
Acacia calamifolia
Acacia continua
Acacia halliana
Acacia havilandiorum
Acacia iteaphylla
Acacia ligulata
Acacia pycnantha
Acacia rigens
Acacia rivalis
Acacia tetragonophylla
Acacia victoriae
Acaena sp.
Actinobole uliginosum
Aira cupaniana
Ajuga australis
Alectryon oleifolius
Allocasuarina muellariana
Allocasuarina sp.
Allocasuarina verticillata
Amyema miquelii
Amyema preissii
Anagallis arvensis
Arachis hypogaea
Austrostipa nodosa
Austrostipa scabra
Austrostipa sp.
Avena sativa
Boerhavia sp.
Brachyscome ciliaris
Brachyscome sp.
Bursaria spinosa
Callistemon teretifolius
Callitris glaucophylla
Calostemma purpureum
Calotis sp.
Calytrix tetragona
Carrichtera annua
Cassinia complanata
Cassinia laevis
Cassytha sp.
Centaurea calcitrapa
Centaurea lanatus
Centaurea melitensis
Centaurium tenuifolium
Centipeda crateriformis
Cheilanthes sp.
Chrysocephalum semipapposum
Clematis microphylla
Crepis sp.
Cymbopogon ambiguus
Cyperus alterniflorus
Daucus glochidiatus
Daviesia spp.
Dianella revoluta
Dichelachne rara
Dittrichia graveolens
Dodonaea baueri
Dodonaea lobulata
Dodonaea viscosa
Eragrostis sp.
Eremophila alternifolia
Eremophila longifolia
Erodium sp.
Eucalyptus camaldulensis
Eucalyptus dumosa
Eucalyptus flindersii
Eucalyptus intertexta
Eucalyptus leptophylla
Eucalyptus polybractea
Eucalyptus porosa
Eucalyptus socialis
Euphorbia tannensis
Exocarpos aphyllus
Galium sp.
Geranium sp.
Glischrocaryon flavescens
Glycine canescens
Glycine rubiginosa
Goodenia albiflora
Goodenia fascicularis
Gypsophila tubulosa
Hyalosperma glutinosum
Hybanthus floribundus
Indigofera australis
Isoetopsis graminifolia
Jasminum didymum
Lavatera plebia
Leiocarpa semicalva
Leiocarpa websteri
Limonium lobatum
Lophochloa sp.
Lysiana exocarpi
Maireana enchylaenoides
Malus domestica
Marrubium vulgare
Melaleuca lanceolata
Melilotus indicus
Mentha satureioides
Millotia myosotidifolia
Morea setifolia
Myoporum montanum
Neatostema apulum
Nicotiana velutina
Olearia decurrens
Olearia pimeleoides
Oxalis sp.
Petalostylis labicheoides
Phyllanthus saxosus
Pimelea micrantha
Pimelea microcephala
Pimelea simplex
Pimelea stricta
Pittosporum angustifolium
Plantago varia
Pleurosorus rutifolius
Podolepis capillaris
Pomax umbellata
Prostanthera striatiflora
Pterocaulon sphacelatum
Ptilotus obovatus
Ptilotus spathulatus
Rhagodia parabolica
Rhodanthe polygalifolia
Rhodanthe pygmaea
Rhodanthe stricta
Rostraria pumila
Rytidosperma caespitosa
Santalum acuminatum
Santalum lanceolatum
Senecio glossanthus
Senecio lautus
Senecio magnificus
Senecio quadridentatis
Senna artemisioides
Senna artemisioides petiolaris
Sida corrugata
Silene nocturna
Solanum nigrum
Solanum quadrilocatum
Solanum simile
Sonchus oleraceus
Spyridium phlebophyllum
Stackhousia monogyna
Stuartina muelleri
Teucrium corymbosum
Teucrium racimosum
Thysanotus baueri
Trifolium angustifolium
Trifolium arvense
Trifolium campestre
Trifolium sp.
Trifolium tormentosum
Triodia sp.
Triptilodiscus pygmaeus
Vittadinia blackii
Vittadinia gracilis
Vittadinia spp.
Vulpia bromoides
Vulpia muralis
Vulpia myuros
Wahlenbergia sp.
Wurmbea sp.
Xanthorrhoea quadrangulata
Xerochrysum bracteatum
Zygophyllum apiculatum

Supplementary data S10.5.2: Composition of adult possum scats, by genera (mean % of number of reads per scat), using two different primers (n = *ndhJ* and r = *rbcL*).

	August		**September**		**October**		**November**		**December**		**January**		**February**		**March**		**April**		**May**		**June**		**July**		**Annual**	
Genus	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*
Eucalyptus	32.1	17.9	19.9	4.8	52.6	14.2	30.4	5.2	22.9	2.8	70.7	4.5	46.5	17.6	26.1	1.1	52.9	2.2	27.3	0.0	31.7	3.7	32.7	26.6	38.1	8.8
Petalostylis	0.0	1.8	0.0	3.5	0.0	27.2	0.0	12.0	4.3	29.8	5.9	82.4	0.0	22.8	0.0	6.3	0.6	48.4	17.9	86.7	14.0	67.6	1.9	16.4	3.2	32.2
Callitris	1.7	20.9	11.7	52.1	0.8	16.2	5.9	30.4	0.9	17.1	0.1	0.5	0.3	0.6	0.1	9.2	0.1	2.0	0.4	1.5	1.8	7.9	6.2	21.5	3.2	18.4
Silene	1.8	4.2	10.8	7.5	1.4	1.4	3.3	3.2	20.6	9.7	1.7	0.0	1.5	3.4	34.2	31.0	18.7	18.9	1.0	0.3	0.0	0.0	3.6	1.9	6.7	5.4
Maireana	6.0	4.0	6.7	0.7	2.9	2.8	10.8	3.1	2.5	0.3	1.8	0.0	3.8	4.1	1.3	0.3	4.0	0.3	7.0	0.0	12.8	12.7	4.7	2.9	5.5	2.5
Trifolium	0.0	0.0	0.0	0.2	0.0	1.2	0.0	0.0	31.3	0.1	33.3	1.7	0.0	0.0	0.0	0.0	0.0	1.7	23.5	0.2	0.0	0.7	0.0	0.0	6.9	0.5
Melaleuca	0.0	10.3	0.0	4.1	0.9	8.6	1.3	5.8	2.8	1.4	3.2	1.6	0.0	10.8	0.0	1.6	0.0	0.2	0.2	1.0	5.0	8.5	10.1	5.5	1.9	5.2
Acacia	0.0	0.0	0.4	2.3	0.9	6.1	1.6	1.4	4.1	0.9	4.2	0.1	0.6	7.0	4.1	15.4	3.4	8.1	17.7	0.2	15.5	0.0	0.3	0.0	3.6	2.8
Stackhousia	4.2	0.0	7.1	0.0	9.9	0.0	1.4	0.1	5.5	0.0	1.1	0.0	9.8	0.0	7.7	0.0	5.0	0.0	0.4	0.0	0.1	0.0	6.8	0.0	4.9	0.0
Senna	1.1	1.0	4.0	5.1	3.3	2.7	6.8	4.4	7.9	7.9	0.0	0.0	0.0	0.7	0.9	1.8	0.0	0.2	0.8	0.0	0.3	0.7	0.1	0.1	2.3	2.2
Sisymbrium	1.7	0.9	1.0	0.5	5.4	2.3	1.2	0.6	0.1	0.0	0.5	0.0	11.0	9.4	10.3	19.6	0.1	0.1	0.3	0.0	0.0	0.0	3.7	0.7	2.4	1.8
Sonchus	6.0	0.0	9.4	0.0	3.3	0.0	2.8	0.0	7.0	0.0	1.4	0.0	0.7	0.0	3.0	0.0	1.8	0.0	0.9	0.0	1.6	0.0	1.0	0.0	3.7	0.0
Carrichtera	4.3	3.3	0.4	0.1	0.5	0.1	0.3	0.1	0.1	0.0	0.2	0.0	1.2	0.3	0.1	0.2	0.5	0.0	5.8	1.2	0.3	0.2	11.1	11.7	1.9	1.4
Zygophyllum	3.4	0.0	2.1	0.0	0.9	0.9	3.0	0.5	3.2	0.8	0.4	2.5	0.9	1.0	1.4	0.1	0.5	1.1	1.3	2.8	3.7	1.5	0.0	0.1	1.7	0.9
Solanum	0.0	0.0	1.8	0.0	5.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	6.8	6.4	0.0	0.0	0.0	0.0	0.0	0.0	10.5	0.0	0.0	0.0	2.1	0.5
Oxalis	0.0	2.6	0.0	2.6	0.0	3.0	0.0	0.5	0.0	2.1	0.0	0.0	0.0	7.1	0.0	1.2	0.0	4.1	0.0	0.0	0.0	0.1	0.0	1.5	0.0	2.0
Austrostipa	0.0	1.7	0.0	1.9	0.0	3.9	0.0	5.6	0.0	3.0	0.0	0.1	0.0	3.2	0.0	1.3	0.0	1.1	0.0	0.0	0.0	0.3	0.0	0.4	0.0	2.0
Geranium	0.0	2.3	0.0	2.7	0.0	1.6	0.0	5.9	0.0	3.1	0.0	0.0	0.0	0.1	0.0	2.3	0.0	1.2	0.0	0.0	0.0	0.0	0.0	1.8	0.0	1.9
Cassytha	0.0	0.7	0.0	0.4	0.0	2.2	0.0	1.9	0.0	15.2	0.0	0.4	0.0	0.8	0.0	5.6	0.0	0.3	0.0	0.1	0.0	0.1	0.0	0.0	0.0	1.8
Senecio	3.4	0.0	5.1	0.0	0.9	0.0	1.4	0.0	0.2	0.0	0.2	0.0	0.9	0.0	0.0	0.0	0.2	0.0	0.7	0.0	0.2	0.0	3.0	0.0	1.7	0.0
Centaurea	2.5	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	1.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	5.8	6.1	0.8	0.5
Medicago	0.7	0.0	2.0	0.0	1.6	0.0	0.6	0.0	5.2	0.0	0.3	0.0	0.0	0.0	8.9	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	1.3	0.0
Rhodanthe	3.5	0.1	0.1	0.0	0.1	0.0	4.3	0.0	0.0	0.0	0.4	0.0	0.3	0.3	0.1	0.0	0.5	0.0	0.9	0.0	0.1	0.0	2.8	0.5	1.2	0.1
Moraea	7.2	0.0	1.5	0.0	0.1	0.0	0.8	0.2	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.1	1.7	0.0	1.2	0.0
Erodium	0.0	3.4	0.0	2.1	0.0	0.0	0.0	4.4	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	1.2
Limonium	0.1	0.0	2.1	0.6	0.1	0.0	4.9	0.3	3.2	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	1.0	0.2
Acaena	0.0	0.0	0.7	1.0	0.0	0.0	2.6	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7
Actinobole	1.9	0.0	0.7	0.0	2.1	0.1	1.6	2.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.7	0.2
Pimelea	1.0	1.0	0.0	0.7	0.2	0.2	0.4	1.5	0.0	0.0	0.6	1.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.0	0.7	0.5	0.3	0.6
Daucus	2.2	0.0	0.3	0.0	0.2	0.0	0.2	0.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	2.9	0.0	0.7	0.0
Wurmbea	3.2	2.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.0	0.7	0.0	0.0	0.0	0.1	0.1	0.4	0.2
Sida	0.8	0.0	0.1	0.0	0.1	0.0	0.7	0.0	0.0	0.0	0.1	0.0	5.4	0.2	0.0	0.0	0.0	0.0	0.8	0.0	0.2	0.0	0.0	0.0	0.5	0.0
Vulpia	0.9	0.0	2.3	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Rhagodia	0.7	1.9	0.0	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	1.2	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4

S10.5.2 contd.	**August**		**September**		**October**		**November**		**December**		**January**		**February**		**March**		**April**		**May**		**June**		**July**		**Annual**	
Genus	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	ndhJ	rbcL
Olearia	0.6	0.0	0.4	0.0	0.0	0.0	2.0	0.0	0.7	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.2	0.0	0.0	0.0	0.5	0.0
Millotia	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2
Pittosporum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	1.7	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.6	0.0	0.4	0.0	0.0	0.0	0.4
Euphorbia	0.1	0.0	0.2	0.0	0.0	0.0	3.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Vittadinia	1.4	1.3	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.9	0.2	0.2
Hybanthus	0.0	0.0	0.0	0.0	0.2	2.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.3	0.0	0.1	0.0	0.1	0.0	0.3
Lysiana	0.0	0.1	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Jasminum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0	1.3	0.0	0.0	0.0	0.3	0.0
Podolepis	0.1	0.0	0.8	0.0	0.1	0.0	1.6	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.0
Dodonaea	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.2	0.0	1.0	0.0	0.0	0.0	0.8	0.0	0.5	0.0	0.5	0.0	0.0	0.0	0.3	0.0
Eremophila	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.6	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Asphodelus	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Marrubium	1.2	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Ajuga	0.0	0.0	0.3	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	1.0	0.0	0.0	0.0	0.2	0.0
Melilotus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.1
Teucrium	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.7	0.0	0.0	0.0	0.6	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.2	0.0
Boerhavia	0.0	0.0	0.0	0.2	0.0	0.2	0.5	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.1
Rytidosperma	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Bromus	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Crepis	0.0	0.3	0.0	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Brachychiton	0.0	0.6	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.1
Bursaria	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.6	0.1	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Wahlenbergia	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Triodia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.7	0.0	0.1	0.0	0.0	0.0	0.1	0.0
Heliotropium	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Callistemon	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Eragrostis	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Lavatera	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Isoetopsis	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
Alectryon	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Chrysocephalum	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hyalosperma	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleurosorus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nicotiana	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Myoporum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0

S10.5.2 contd.	**August**		**September**		**October**		**November**		**December**		**January**		**February**		**March**		**April**		**May**		**June**		**July**		**Annual**	
Genus	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	*ndhJ*	*rbcL*	ndhJ	rbcL
Goodenia	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rostraria	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spyridium	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Santalum	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gypsophila	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calytrix	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Galium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pterocaulon	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Brachyscome	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prostanthera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Supplementary data S10.5.3: Frequency of occurrence (% of scats containing the genus), detected via either of the two primer methods used (*ndhJ* or *rbcL*).

Genus	August	September	October	November	December	January	February	March	April	May	June	July	Annual
Eucalyptus	81.5	52.5	100.0	61.5	56.3	100.0	86.7	70.0	85.0	82.4	73.7	90.5	78.5
Petalostylis	51.9	45.0	97.0	69.2	62.5	100.0	93.3	50.0	95.0	100.0	73.7	33.3	72.3
Maireana	66.7	57.5	84.8	73.1	43.8	36.7	53.3	20.0	50.0	82.4	68.4	42.9	59.1
Zygophyllum	33.3	35.0	48.5	50.0	56.3	100.0	40.0	20.0	50.0	100.0	73.7	4.8	51.5
Callitris	55.6	95.0	45.5	76.9	68.8	16.7	26.7	50.0	25.0	52.9	21.1	38.1	50.7
Acacia	3.7	15.0	33.3	38.5	50.0	50.0	60.0	50.0	40.0	94.1	47.4	9.5	36.5
Silene	37.0	62.5	24.2	30.8	68.8	13.3	20.0	90.0	40.0	11.8	0.0	33.3	34.7
Austrostipa	40.7	37.5	72.7	61.5	37.5	3.3	60.0	40.0	20.0	0.0	5.3	4.8	33.6
Stackhousia	63.0	47.5	45.5	26.9	43.8	6.7	40.0	40.0	25.0	11.8	5.3	33.3	33.6
Melaleuca	25.9	27.5	54.5	30.8	31.3	13.3	60.0	20.0	5.0	41.2	31.6	38.1	31.4
Senna	37.0	52.5	33.3	42.3	50.0	3.3	33.3	40.0	5.0	23.5	10.5	14.3	29.6
Sonchus	44.4	40.0	27.3	26.9	56.3	10.0	13.3	30.0	25.0	17.6	5.3	19.0	27.0
Carrichtera	25.9	17.5	15.2	7.7	6.3	13.3	26.7	20.0	5.0	23.5	15.8	38.1	17.5
Pittosporum	0.0	2.5	0.0	0.0	25.0	70.0	0.0	0.0	45.0	52.9	21.1	0.0	17.5
Oxalis	37.0	25.0	21.2	7.7	31.3	0.0	40.0	10.0	15.0	0.0	5.3	9.5	17.2
Senecio	37.0	25.0	6.1	15.4	6.3	6.7	6.7	0.0	5.0	35.3	10.5	28.6	16.4
Medicago	11.1	35.0	24.2	11.5	56.3	10.0	0.0	20.0	5.0	5.9	0.0	0.0	16.1
Sisymbrium	22.2	22.5	18.2	19.2	6.3	10.0	33.3	30.0	5.0	11.8	0.0	14.3	16.1
Geranium	25.9	25.0	6.1	38.5	18.8	0.0	6.7	30.0	10.0	0.0	0.0	9.5	14.6
Trifolium	0.0	5.0	3.0	0.0	25.0	56.7	0.0	0.0	35.0	23.5	26.3	0.0	14.6
Moraea	29.6	30.0	3.0	30.8	12.5	0.0	6.7	0.0	5.0	0.0	10.5	4.8	13.1
Cassytha	7.4	7.5	12.1	15.4	31.3	20.0	6.7	40.0	15.0	5.9	5.3	0.0	12.4
Rhodanthe	14.8	5.0	3.0	11.5	0.0	6.7	20.0	10.0	15.0	47.1	5.3	9.5	10.9
Erodium	22.2	22.5	0.0	19.2	18.8	0.0	0.0	0.0	0.0	17.6	0.0	0.0	9.5
Centaurea	33.3	12.5	0.0	0.0	6.3	3.3	6.7	10.0	5.0	0.0	0.0	28.6	9.1
Olearia	14.8	10.0	3.0	3.8	18.8	0.0	6.7	0.0	0.0	47.1	5.3	0.0	8.4
Wurmbea	40.7	5.0	0.0	0.0	0.0	0.0	6.7	0.0	5.0	35.3	0.0	9.5	8.4
Jasminum	0.0	0.0	0.0	0.0	18.8	16.7	0.0	0.0	0.0	58.8	21.1	0.0	8.0
Dodonaea	0.0	7.5	6.1	0.0	12.5	10.0	6.7	0.0	5.0	41.2	10.5	0.0	7.7
Daucus	18.5	5.0	3.0	7.7	12.5	0.0	0.0	0.0	0.0	5.9	0.0	23.8	6.6
Sida	3.7	2.5	3.0	7.7	0.0	10.0	20.0	0.0	0.0	35.3	5.3	0.0	6.6
Ajuga	0.0	10.0	3.0	3.8	0.0	6.7	0.0	0.0	0.0	23.5	15.8	0.0	5.5
Limonium	7.4	10.0	3.0	15.4	12.5	0.0	0.0	0.0	0.0	11.8	0.0	0.0	5.5
Eremophila	0.0	0.0	3.0	0.0	6.3	6.7	0.0	0.0	10.0	47.1	0.0	0.0	5.1

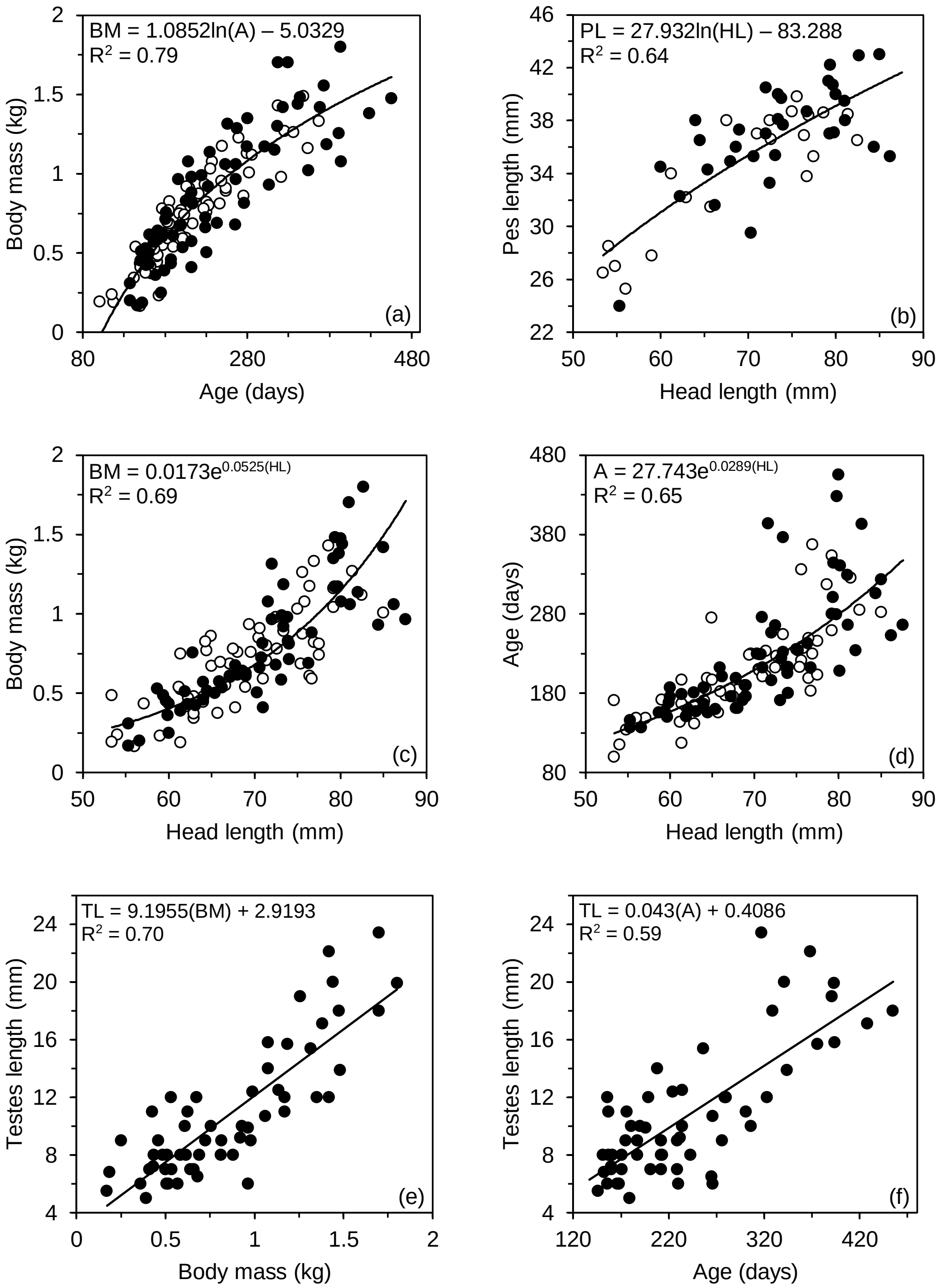
S10.5.3 contd.	**August**	**September**	**October**	**November**	**December**	**January**	**February**	**March**	**April**	**May**	**June**	**July**	**Annual**
Actinobole	7.4	10.0	3.0	15.4	6.3	0.0	0.0	0.0	0.0	5.9	0.0	0.0	4.7
Hybanthus	0.0	0.0	6.1	0.0	0.0	16.7	0.0	0.0	10.0	11.8	5.3	4.8	4.7
Pimelea	7.4	5.0	6.1	7.7	0.0	3.3	0.0	0.0	5.0	5.9	0.0	9.5	4.7
Boerhavia	0.0	7.5	9.1	11.5	0.0	0.0	0.0	10.0	0.0	0.0	10.5	0.0	4.4
Rytidosperma	18.5	10.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.0	0.0	4.4
Triodia	0.0	2.5	0.0	3.8	12.5	0.0	6.7	0.0	0.0	35.3	5.3	0.0	4.4
Vulpia	22.2	10.0	3.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	4.4
Lysiana	7.4	12.5	0.0	0.0	12.5	3.3	0.0	0.0	5.0	0.0	0.0	0.0	4.0
Teucrium	0.0	5.0	0.0	0.0	0.0	3.3	20.0	0.0	10.0	11.8	5.3	0.0	4.0
Rhagodia	11.1	2.5	6.1	11.5	0.0	0.0	6.7	0.0	0.0	0.0	0.0	0.0	3.6
Callistemon	0.0	2.5	3.0	0.0	0.0	3.3	13.3	0.0	5.0	17.6	0.0	0.0	3.3
Marrubium	3.7	7.5	0.0	0.0	6.3	3.3	13.3	0.0	0.0	5.9	0.0	0.0	3.3
Melilotus	3.7	0.0	0.0	7.7	6.3	6.7	0.0	0.0	0.0	11.8	5.3	0.0	3.3
Podolepis	3.7	7.5	3.0	3.8	0.0	3.3	6.7	0.0	0.0	0.0	5.3	0.0	3.3
Asphodelus	0.0	0.0	12.1	0.0	0.0	6.7	6.7	0.0	0.0	5.9	0.0	0.0	2.9
Bursaria	0.0	0.0	0.0	3.8	6.3	0.0	13.3	0.0	0.0	23.5	0.0	0.0	2.9
Solanum	0.0	2.5	9.1	0.0	0.0	0.0	13.3	0.0	0.0	0.0	10.5	0.0	2.9
Vittadinia	11.1	0.0	3.0	3.8	0.0	0.0	0.0	0.0	0.0	5.9	0.0	9.5	2.9
Alectryon	0.0	2.5	3.0	0.0	6.3	0.0	6.7	0.0	0.0	5.9	5.3	0.0	2.2
Brachychiton	14.8	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.3	0.0	2.2
Acaena	0.0	5.0	0.0	7.7	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	1.8
Chrysocephalum	7.4	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.0	0.0	1.8
Crepis	11.1	2.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8
Bromus	3.7	5.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Eragrostis	3.7	7.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Euphorbia	3.7	2.5	0.0	3.8	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	1.5
Heliotropium	0.0	0.0	3.0	0.0	6.3	0.0	0.0	0.0	10.0	0.0	0.0	0.0	1.5
Hyalosperma	0.0	5.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	5.9	0.0	0.0	1.5
Lavatera	0.0	7.5	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	1.5
Myoporum	0.0	0.0	0.0	0.0	12.5	3.3	0.0	0.0	0.0	5.9	0.0	0.0	1.5
Nicotiana	3.7	0.0	9.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Spyridium	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	17.6	0.0	0.0	1.5
Calytrix	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	11.8	0.0	0.0	1.1
Isoetopsis	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	5.3	0.0	1.1
Millotia	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	1.1
Wahlenbergia	7.4	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1

S10.5.3 contd.	**August**	**September**	**October**	**November**	**December**	**January**	**February**	**March**	**April**	**May**	**June**	**July**	**Annual**
Brachyscome	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	5.9	0.0	0.0	0.7
Galium	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	0.0	0.0	0.7
Goodenia	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0	0.7
Prostanthera	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	5.9	0.0	0.0	0.7
Pterocaulon	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	5.3	0.0	0.7
Rostraria	0.0	0.0	3.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Cyperus	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Gypsophila	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Pleurosorus	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Santalum	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4

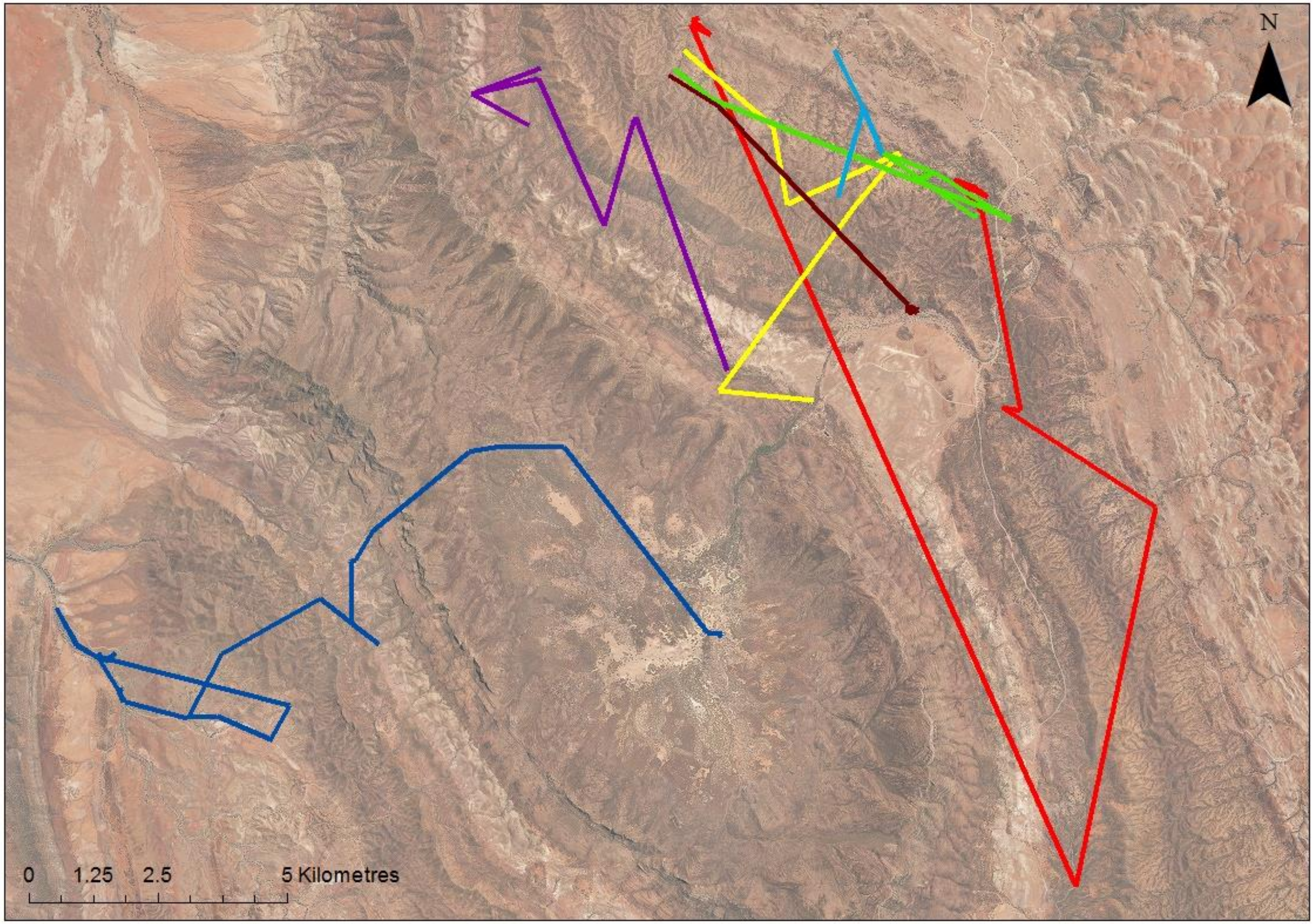
Supplementary data S10.5.4: Jacob's Index values for genera detected in >1 scat, averaged for each month. Genera detected in less than five scats *and* less than five vegetation surveys were omitted. Positive values indicate a preference relative to availability, negative values indicate avoidance.

Genus	August	September	October	November	December	January	February	March	April	May	June	July	Mean
Acacia	-0.90	-0.64	-0.14	-0.41	0.56	0.20	0.80	0.50	-0.29	0.88	-0.77	-0.87	-0.09
Actinobole	-0.72	-0.89	-0.96	0.24	1.00	-1.00	-1.00	-1.00	-1.00	1.00	-1.00	-1.00	-0.53
Ajuga	-1.00	-0.76	-0.86	-0.72	-1.00	-0.56			-1.00	-0.04	-0.52	-1.00	-0.75
Alectryon	-1.00	1.00	-0.56		-0.30	-1.00	1.00	-1.00		1.00	-0.71	-1.00	-0.26
Allocasuarina	-1.00	-1.00									-1.00	-1.00	-1.00
Amyema			-1.00	-1.00					-1.00		-1.00	-1.00	-1.00
Anagallis	-1.00	-1.00	-1.00	-1.00	-1.00		-1.00				-1.00	-1.00	-1.00
Asphodelus	-1.00	-1.00	-0.51	-1.00	-1.00	-0.81	-0.83	-1.00	-1.00	-0.81	-1.00	-1.00	-0.91
Austrostipa	1.00	0.66	0.72	0.87	0.66	-0.53	1.00	0.33	0.06	-1.00	-0.89	-0.38	0.21
Avena	1.00	1.00	1.00	1.00	1.00	1.00			1.00	1.00	1.00		1.00
Boerhavia		1.00	-0.05	-0.31		-1.00		1.00	-1.00		1.00		0.09
Brachyscome	-1.00	-1.00	-1.00	-1.00		1.00				1.00			-0.33
Bromus	-0.79	-0.92	-1.00	-1.00	-1.00	-0.93	-1.00	-1.00					-0.96
Bursaria	-1.00	-1.00	-1.00	-0.72	-0.30	-1.00	-0.04		-1.00	0.37	-1.00	-1.00	-0.70
Callitris	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Calostemma	-1.00	-1.00	-1.00			-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Calytrix	-1.00	-1.00	-0.56	-1.00					-1.00	-0.03	-1.00	-1.00	-0.82
Carrichtera	0.02	-0.40	-0.58	-0.78	-0.76	-0.47	-0.35	-0.60	-0.83	-0.53	-0.52	-0.04	-0.49
Cassinia	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00		-1.00	-1.00	-1.00	-1.00	-1.00
Cassytha	-0.06	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		0.90
Centaurea	0.43	-0.56	-1.00	-1.00	-0.90	-0.90	-0.94	-0.80	-0.75	-1.00	-1.00	-0.03	-0.71
Cheilanthes		-1.00				-1.00	-1.00	-1.00		-1.00	-1.00	-1.00	-1.00
Chrysocephalum	-0.43	-0.96	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-0.43	-1.00	-1.00	-0.90
Clematis	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00		-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Cymbopogon			-1.00	-1.00	-1.00	-1.00	-1.00		-1.00	-1.00		-1.00	-1.00
Daucus	1.00	-0.41	-0.86	1.00	1.00					1.00	-1.00	-0.76	0.12
Dittrichia			-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Dodonaea	-1.00	-0.92	-0.92	-1.00	-0.79	-0.86	-0.70	-1.00	-0.92	0.08	-0.87	-1.00	-0.83
Eremophila	-1.00		-0.78		1.00	1.00			0.05	1.00			0.21
Erodium	-0.75	-0.85	-1.00	0.36	1.00					1.00	-1.00	-1.00	-0.28
Eucalyptus	-0.84	-0.65	1.00	0.53	-0.60	1.00	0.11	-0.38	0.04	-0.05	-0.30	0.29	-0.01
Euphorbia	-0.68	-0.66	-1.00	-0.72	-1.00	-1.00	-1.00	-1.00	-0.62				-0.85
Geranium	0.27	-0.41	1.00	1.00	1.00	-1.00	1.00	1.00	1.00	-1.00	-1.00	-0.81	0.17
Goodenia	-1.00		-0.78	-1.00					1.00			-1.00	-0.56

S10.5.4 cont.	**August**	**September**	**October**	**November**	**December**	**January**	**February**	**March**	**April**	**May**	**June**	**July**	**Mean**
Hyalosperma	-1.00	-0.92	-1.00			1.00				1.00			-0.18
Jasminum	-1.00				0.30	0.29				1.00	1.00	-1.00	0.10
Leiocarpa		-1.00	-1.00								-1.00	-1.00	-1.00
Limonium	1.00	-0.06	-0.78	0.24	0.07	-1.00				1.00			0.07
Maireana	0.71	0.04	0.70	1.00	0.46	0.68	1.00	1.00	0.27	0.87	0.37	-0.51	0.55
Marrubium	-0.93	-0.72	-1.00	-1.00	-0.90	-0.96	-0.95	-1.00	-1.00	-0.96	-1.00	-1.00	-0.95
Medicago	-0.92	-0.73	-0.35	-0.31	0.82	1.00	-1.00	1.00	-0.31	-0.39	-1.00	-1.00	-0.27
Melaleuca	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Melilotus	1.00	-1.00	-1.00	-0.14	1.00	1.00		-1.00		1.00	1.00		0.21
Moraea	1.00	0.55	1.00	1.00	1.00		1.00		1.00		1.00	1.00	0.95
Olearia	-0.48	-0.76	-0.86	-0.83	-0.55	-1.00	-0.40	-1.00	-1.00	0.45	-0.89	-1.00	-0.69
Oxalis	-0.10	-0.41	0.04	-0.85	0.23	-1.00	1.00	1.00	1.00	-1.00	-0.96	-0.91	-0.16
Petalostylis	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Pittosporum		1.00			1.00	1.00		-1.00	1.00	1.00	1.00		0.71
Podolepis	-0.90	-0.82	-0.91	-0.92	-1.00	-0.90	-0.70	-1.00	-1.00	-1.00	-0.83	-1.00	-0.91
Ptilotus		-1.00	-1.00	-1.00	-1.00						-1.00	-1.00	-1.00
Rhagodia	1.00	-0.66	-0.27	1.00	-1.00		1.00	-1.00	-1.00		-1.00		-0.21
Rhodanthe	-0.78	-0.69	-0.56	1.00		1.00	1.00	1.00	1.00	1.00	-0.44	-0.03	0.32
Rytidosperma	1.00	1.00	-0.78	-1.00	-1.00	-1.00		-1.00	-1.00	-0.03	-1.00		-0.48
Senecio	-0.79	-0.83	-0.92	-0.69	-0.85	-0.87	-0.83	-1.00	-0.88	-0.29	-0.48	-0.43	-0.74
Senna	-0.67	0.16	-0.65	-0.15	0.11	-0.76	-0.45	0.65	-0.83	-0.32	-0.92	-0.80	-0.39
Sida	-0.41	1.00	-0.78	-0.50	-1.00	1.00	1.00	-1.00	-1.00	0.58	-0.44	-1.00	-0.21
Silene	1.00	0.54	-0.52	0.28	0.28	-0.73	-0.50	0.80	-0.29	1.00	-1.00	1.00	0.15
Sisymbrium	-0.27	-0.47	-0.06	0.36	-0.76	-0.86	-0.45	-0.75	-0.88	-0.43	-1.00	-0.80	-0.53
Solanum		1.00	1.00	-1.00	-1.00	-1.00	1.00		-1.00		-0.10		-0.14
Sonchus	1.00	0.40	0.54	0.19	0.82	1.00	-0.04	1.00	1.00	1.00	1.00	0.36	0.69
Stackhousia	0.55	-0.16	-0.09	1.00	1.00	1.00	1.00	1.00	1.00	1.00	-0.44	0.08	0.58
Trifolium	-1.00	-0.95	-0.91	-1.00	-0.20	0.68			1.00	1.00	1.00		-0.04
Vittadinia	-0.45	-1.00	-0.94	-0.89	-1.00	-1.00	-1.00	-1.00	-1.00	-0.39	-1.00	-0.41	-0.84
Vulpia	1.00	-0.44	-0.91	-1.00	-1.00	-0.98	-1.00	-1.00	-1.00				-0.70
Wahlenbergia	-0.06	1.00	-1.00			-1.00				-1.00			-0.41
Wurmbea	-0.34	-0.69					1.00		1.00	0.58	-1.00	-0.87	-0.04
Xanthorrhoea	-1.00	-1.00		-1.00			-1.00				-1.00	-1.00	-1.00
Zygophyllum	0.69	1.00	0.79	0.80	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94



Supplementary data S10.6.1 (a–f): The relationship between various physical traits for juvenile brushtail possums (*Trichosurus vulpecula*), where A = age (days), BM = body mass (kg), PL = short *pes* length (mm), HL = head length (mm) and TL = testes length (mm). The equation and strength of the relationship (R^2 value) is given. ○ = female ● = male



Supplementary data S10.6.2: The dispersal paths of seven dispersing male brushtail possums (*Trichosurus vulpecula*). Each coloured line represents a different individual.

Supplementary data S10.6.3: The growth and fate of selected individual radio-collared juvenile brushtail possums (*Trichosurus vulpecula*) in the IFRNP. Possums that were translocated to the IFRNP as pouch young are indicated by *. Age = days, body mass = g, testes length = mm. LDD = long-distance dispersal (males only).

ID	Sex	Mum	Born	Age when next joey born	Survived to sexual maturity?	Sexually mature		Produced first joey (F only)		Testes length at time of LDD	Fate
						Age	Weight	Age	Weight		
Clyde*	M	Nougat	Apr-15	166	Y	292	1492			22.8	Last caught 606 days, 2220 g
Dukie	M	Nougat	Oct-15	148	N						Predated by cat as a subadult, 256 days, 990 g
Eric	M	Nougat	Mar-16	147	Y	291	1510				Collar removed pre- long-distance dispersal, 476 days, 1825 g
Frankie	F	Nougat	Jul-16	159	Y	235	1030	270	1160		Last caught 597 days, 1750 g, with ≥2nd joey
Caesar*	M	Sage	Apr-15	184	Y	341	1440			19.0	Dispersed off park, moved him back, last caught 960 days, 2285 g
Dill	F	Sage	Oct-15	172	Y	248	955	NA	NA		Last caught 511 days, 1800 g, with second joey
Delilah	F	Spice	Sep-15	184	Y	298	1200	298	1200		Last caught 809 days, 1820 g, with ≥3rd joey
Falafel	M	Spice	Sep-16	144							Collar removed pre-dispersal, 279 days, 1170 g
Cadence	F	Sunny	Aug-15	223	Y	367	1330	392	1450		Last caught 672 days, 1575, with second joey
Coco*	F	Hazel	May-15	200	Y	282	1005	311	1060		Last caught 379 days, 1330 g, with first joey
Dilbert	M	Nancy	Sep-15		N						Died with mum inside tree hollow, 189 days old, 360 g, quoll predation/scavenging
Chechnya*	F	Sasha	May-15	185	N						Predated by cat as a subadult, 305 days, 890 g
Dasha	F	Sasha	Dec-15	171	N						Predated by cat as dependent young, 190 days, 590 g
Eddie	M	Sasha	May-16	238	Y	373	1550			11.0	Last caught 396 days, 1550 g
Danny	M	Nina	Nov-15	230	Y	NA	NA			13.0	Predated by cat as an adult, 462 days, 1800 g
Echo	F	Nina	Jul-16	181							Collar removed prior to reaching sexual maturity, 336 days, 1260 g
Chilli*	M	Nutmeg	Apr-15	182	Y	456	1475			18.0	Last caught 611 days, 1850 g
Dukkah	M	Nutmeg	Oct-15	218	Y	392	1255			12.9	Last caught 600 days old, 1705 g
Eggnog	M	Nutmeg	May-16	150	Y	368	1420			12.0	Last caught 390 days old, 1775 g
Cupcake*	F	Nissa	May-15	333	N						Died as a subadult, cause unknown, 284 days, 1040 g
Cecil*	M	Nanna	May-15	162	N						Died as subadult, predated/scavenged, 240 days, 725 g
Esme	F	Nanna	Apr-16	170	Y	229	930	243	930		Last caught 423 days, 1260 g
Comet*	F	Helga	Apr-15	170	Y	348	1510	373	1510		Last caught 394 days, 1530 g, with first joey
Dipper	F	Helga	Oct-15		N						Predated with mum by a cat, 178 days, weight unknown
CD*	F	Asha	Apr-15	177	Y	346	1160	346	1160		Last caught 398 days, 1410 g, with first joey
Effie	F	Asha	Apr-16	182	Y	255	1175	275	1300		Last caught 421 days, 1775 g, with first joey

Supplementary data S10.6.4: Movement information for individual radio-collared juvenile brushtail possums (*Trichosurus vulpecula*) in the IFRNP. Possums that were translocated to the IFRNP as pouch young are indicated by *. Long-distance dispersal (LDD) and time to settle was only applicable to males. Time = days, distance = m, age = days, weight = g.

ID	Sex	Mum	Commenced exploratory phase		Ceased sheltering with mother (independent) (1)		First used unfamiliar shelter (age)	Time between (1) and LDD	Adult prior to LDD	LDD commenced		CDT	NDD	Time to settle	100% MCP overlap with mother (%)
			Age	Weight	Age	Weight				Age	Weight				
Clyde*	M	Nougat			239	1135	267	81	Y	320	1700	13,850	7,458	71	0
Dukie	M	Nougat	200	755	223	990	215								
Eric	M	Nougat	194	965	196	965	201								
Frankie	F	Nougat	188	770	209	980	188						450		2.1
Caesar*	M	Sage	238	835	366	1525	332	13	Y	379	1525	26,932	10,061	20	0
Dill	F	Sage			226	830	250						464		13.5
Delilah	F	Spice	188	540	232	800	189						827		0.9
Falafel	M	Spice	205	810	211	810	231								
Cadence	F	Sunny	184	550	274	860	296						325		0
Coco	F	Hazel			226	875	231						483		0
Chechnya*	F	Sasha	229	820	264	890	229								
Eddie	M	Sasha	277	1025	300	1170	280	7	N	307	1170	5,802	2,804	15	0
Danny	M	Nina	269	1060	298	1060	269	7	N	305	1430	11,954	6,275	126	0
Echo	F	Nina	205	590	257	850	205						125		34.8
Chilli*	M	Nutmeg	274	815	288	915	324	183	Y	471	1475	35,105	6,230	47	0
Dukkah	M	Nutmeg	277	680	296	930	277	41	N	337	1058	9,194	5,728	52	0
Eggnog	M	Nutmeg			234	980	243	93	N	327	1420	6,788	6,586	14	0
Cupcake*	F	Nissa	282	1040			282								
Cecil*	M	Nanna			225	725	225								
Esme	F	Nanna			240	930	240						425		21.6
Comet*	F	Helga			269	1225	286						345		42.8
CD*	F	Asha											466		0
Effie	F	Asha	243	1175	249	1175	243						116		84.2