Conservation biology of an endangered semi-arid marsupial, the sandhill dunnart (*Sminthopsis psammophila*)

by

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B. Sc (An Sc) Hons

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Thesis Declaration

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Volunteers

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Brain Matthews*
Brett Goodman
Brodie Philp
Carol Dennis
Casey O'Brien*
Chris Malam
Duart McLean
Duncan Crichton
Elinor Hetzel-Bone
Hayley Lewis
Jamie Kohler*#
Jasmin Packer*
Josie McLean
Karen Philp
Kelly Howell
Kyle Holland#
Kyra Evanochko
Lauren Engledow*#
Lee Agars*#
Leticia Johnson#
Luis Verde
Matthew Pearson#
Murray Graetz
Natilia Diaz
Nerida Sweet
Patrick Taggart
Paul Fennell*#
Peter Hatcliffe
Phillip Morgan
Rebecca West
Sally Potter
Sam Clarke
Sarah Mantel
Tiffany Miegel
Ting Wu#
Tony Dingwall*
You Li

* Volunteer had been out on two or more field trips

Volunteer help dig in pitfall traps!

Thesis abstract

Australia has one of the highest rates of extinction in the world, particularly for mammals of the arid zone. Arid and semi-arid species are subject to a number of threatening processes, including predation from introduced cats (*Felis catus*) and foxes (*Vulpes vulpes*), land clearance for agriculture, changing fire regimes post-European settlement and, more recently, increased mining activities and climate change. Unfortunately, the biology, life history and population dynamics of many semi-arid zone mammal species are little known, making effective management and conservation problematic, particularly for those that are considered rare and endangered.

One such species is the nationally endangered sandhill dunnart (*Sminthopsis psammophila*). The species is known from only a small number of individuals inhabiting three disjointed populations; two in South Australia and one in Western Australia. In order to conserve this species, ecological knowledge is required to predict how it is likely to respond to current and future threats, and accordingly what type of management actions are needed to ensure its persistence. This study used a combination of ecological and genetic information from a population in a semi-arid environment to investigate: 1) the influence of a variable environment on the life history and population dynamics of *S. psammophila* during a high and low rainfall year; 2) broad- and fine-scale genetic diversity and connectivity across the species' range and within a population and 3) habitat preferences of the species and the influence rainfall and time since fire may have on the habitat preferences.

One core population west of the Middleback Ranges on the Eyre Peninsula, South Australia, was trapped for two years during a capture-mark-recapture study comprising 23,529 trap nights. Eleven sites were established within an area of approximately 24,000 ha. The vegetation in the region consists of open mallee with an understorey of spinifex (*Triodia* spp.) and a diverse range of shrubs. Tissue samples were taken from individuals caught to examine the fine-scale genetic diversity and connectivity within the study area using 16 newly developed microsatellite markers. Additional tissue samples from the remaining two core populations were collected through collaborations to study the historical connectivity across the species' range using a combination of microsatellite markers and mitochondrial control region sequence data.

The broad scale genetic analyses revealed that the three known core populations of *S. psammophila* are genetically differentiated, but do not show evidence of long-term population isolation. Within the core population the fine-scale genetic analyses and capture-mark-recapture data indicated that both males and females are relatively mobile with no significant genetic structure amongst 107 samples evident within the 24,000 ha study area. In addition, no significant sex-biased dispersal was detected, suggesting it is advantageous for both males and females to disperse from their natal areas.

The study found that the presence and abundance of *S. psammophila* at sites was influenced by rainfall events. During the low rainfall year significantly fewer *S. psammophila* were caught and a higher proportion of individuals were transients. The changes in the population were attributed to a decreased survival rate of dispersing juveniles and second year adults, most likely caused by reduced food (invertebrates) availability during the low rainfall year. In addition, the breeding season may have been delayed or reduced in response to fewer food resources during that year. *S. psammophila* was found to be positively associated with the number of logs and vertical habitat complexity and negatively associated with the average height of spinifex (*Triodia* spp.). These associations likely reflect a preference for areas with increased protection from predators and increased foraging opportunities. We did not detect an effect of time since fire on the presence of *S. psammophila*. However, resident females were observed favouring sites with slightly higher spinifex density during the low rainfall year. This may suggest a preference for areas that provide increased foraging opportunities in microsites, such as areas where leaf litter accumulates, during low resource years.

The relatively high mobility in this species appears to be an adaptation to a system with variable food resources; individuals need to be mobile in order to track food pulses created by rainfall through the landscape. Therefore large areas of suitable habitat will need to be protected in order to maintain a viable *S. psammophila* population. The preference of *S. psammophila* for complex understorey suggests that recently burnt vegetation may be unsuitable for the species. Limiting large scale wildfires will be required to protect the species in the future, especially if climate change leads to an increase in the severity and frequencies of wildfires. The findings from this study have been made available to the Sandhill Dunnart Recovery Team and have contributed to the development of an effective conservation management plan for *S. psammophila*, both regionally and nationally.

CHAPTER 1: General introduction

Sunrise over a dune, west of the Middleback Ranges, S.A. Photo A. McLean

1.1 Loss of biodiversity

Global biodiversity is being lost at an alarming rate, with the current rate of extinction far exceeding that of historical background levels (Mills 2007; Barnosky *et al.* 2011). As of 2014, the IUCN Red List reported that of the 5,513 mammal species assessed globally, 26% (1,199 species) were threatened (i.e. classified as critically endangered, endangered or vulnerable) (IUCN 2014). The major causes of species decline are related to human activities, with the most common being increased human population growth and associated habitat loss and fragmentation (Foley *et al.* 2005; Hoffmann *et al.* 2010). Other causes include overexploitation of animals from unsustainable hunting and fishing, introduction of invasive species (predators and competitors), pollution and climate change (Martens *et al.* 2003). However, extinction patterns are not uniform across geographical areas or taxonomic groups. Mammals are particularly prone to extinction and species are being lost at a rapid rate worldwide (Hoffmann *et al.* 2011). The loss of mammals can have serious consequences for ecosystems as small mammals fill important ecological niches and act as dispersers of seed and spores, pollinators (Murphy *et al.* 2005) and soil engineers (Fleming *et al.* 2014).

In Australia, as with other countries, extinction patterns are unevenly distributed across taxa. Australia has one of the highest rates of mammal extinction in the world, with 29 mammal species becoming extinct within the last 200 years (Woinarski *et al.* 2015) and 39 species now occurring over less than 25 % of their original ranges (Burbidge *et al.* 2009). Contrary to other continents where large mammals have generally suffered the greatest declines (Cardillo *et al.* 2005), in Australia, the most vulnerable groups of mammals are those that reside in areas of low rainfall with small to medium body size within the 35 – 5500 gram weight range (termed the critical weight range) (Short and Smith 1994; Cardillo and Bromham 2001). Significant threats to these groups have been present for a relatively short period of time (~ 200 years) and primarily consist of introduced predators - the domestic cat (*Felis catus*) and red fox (*Vulpes vulpes*), and habitat degradation, largely resulting from changed fire regimes since European settlement (Woinarski *et al.* 2015). Traditional burning practices by Aboriginal people no longer take place and fires are now thought to be more intense and frequent (Yibarbuk *et al.* 2001). These factors interact with other key threats such as habitat loss and fragmentation, introduced herbivores (livestock and feral), diseases, hunting, poisoning by introduced cane toads (northern Australia) and increases in severe weather patterns due to climate change (reviewed in Woinarski *et al.* 2015). The discipline of conservation biology has developed in response to this dramatic loss of species and by definition deals with threats to biodiversity with the aim of preserving biodiversity (biological and genetic).

1.2 Conservation and management

The aim of conservation biology is to understand how threats can be mitigated to reduce or prevent the loss of biodiversity through effective management. Before we can establish effective management strategies we must first understand the biology of target species and their interactions with the environment and other species (Brussard 1991). Important aspects of a species' biology include reproduction, distribution, habitat requirements, genetic structure and connectivity of populations and external threats to the species (Mills 2007). Unfortunately the majority of this information is unavailable for many Australian species, even those that have been extensively studied, making conservation management problematic. Below I focus on three aspects of the biology of animals; life history traits, historic and contemporary genetic structure and habitat preferences, and examine why these are important for the development of an effective management plan for the conservation of a species.

1.2.1 Life history traits

Life history traits are those biological traits of a species that maximise its fitness (Perrin *et al.* 2009). These traits can include longevity, age at sexual maturity, sex-specific growth rates, sex-specific survival rates and intervals between reproductive events. Knowledge of life history traits can indicate how vulnerable a species may be to external threats and help explain why some species are more prone to extinction than others (González-Suárez and Revilla 2013). For example, in a study of butterflies and moths, habitat fragmentation had a greater effect on species that exhibited low mobility, produced fewer eggs and used a narrow variety of food resources compared to their more generalist counterparts (Öckinger *et al.* 2010). Once faced with external threats, life history characteristics can become even more important for the persistence of populations and species (O'Grady *et al.* 2004). For example, species of conilurine rodents in Australia that exhibited high reproductive outputs, as evidenced by a greater average number of litters per year and greater mean number of young produced per year, had a lower extinction risk because their high reproductive rates buffered them against predation (Smith and Quin 1996). In-depth knowledge of life history traits can also provide guidance for various management approaches and increase the cost-efficiency of conservation programs (Foster and Vincent 2004). Specific life stages may be more prone to external threats than others and targeted management actions can have greater success than more general approaches. A targeted approach has been implemented in the management of a range of ground nesting birds, where eggs and chicks are most vulnerable to predation and management techniques have been successful in meeting conservation goals (Smith *et al.* 2011).

1.2.2 Historic and contemporary genetic structure

Molecular methods have become increasingly recognised as important for the conservation and management of species (Moritz 1994; Habel *et al.* 2010). Genetic techniques have proven to be valuable tools in answering a range of questions relating to genetic diversity (Frankham 1997; Keller and Waller 2002), evolutionary history (Potter *et al.* 2012; Spinks *et al.* 2012), population structure (Lancaster *et al.* 2011; Olivares *et al.* 2013) movement patterns (Peakall *et al.* 2003; Chambers and Garant 2010) and mating systems and social organisation (Rossiter *et al.* 2012). The goal of conservation genetics is to maintain fitness of the population or species by maximising its genetic diversity and, thus, evolutionary potential (Frankham 2005). Losses of genetic diversity from populations can lead to an increased risk of local extinction, either directly (e.g., Eldridge *et al.* 1999) or indirectly through demographic and environmental factors (Lande 1988). If a large loss of genetic variation occurs in a naturally outbreeding population, inbreeding depression may develop, drastically reducing the fitness of individuals and therefore the survival of the population (Charlesworth and Willis 2009). For example, a small, island population of koalas (*Phascolarctos cinereus*) exhibited low levels of genetic diversity and males suffered from low sperm concentrations, low sperm motility and testicular aplasia (Seymour *et al.* 2001). Quantification of a species' genetic diversity and patterns of genetic variability can help identify appropriate management options, such as translocations, to restore gene flow and genetic diversity if required (Coleman *et al.* 2013).

Exploration of historical and contemporary genetic structure within a species is valuable for understanding past and present gene flow and defining suitable spatial scales for management (Frankham 2010a). Evolutionarily Significant Units (ESUs) or Management Units (MUs) can be defined using phylogenetic relationships among populations (Moritz

1994) in order to identify key populations within a species, and ensure that the full range of genetic diversity is maintained. ESUs can be defined as groups of species that are reciprocally monophyletic at mitochondrial DNA (mtDNA) haplotypes and show significant divergence of allele frequencies at nuclear loci (Moritz 1994). MUs can be defined as populations within ESUs that show significant divergence of allele frequencies at nuclear and/ or mtDNA loci regardless of phylogenetic relationships (Moritz 1994). However, ecological information should also be considered when assigning populations to ESUs and MUs. Populations may adapt to local environmental conditions, which could prevent survival or interbreeding if individuals are translocated between areas with different environmental conditions (Crandall *et al.* 2000; Weeks *et al.* 2011). Knowledge of ESUs and MUs provide insight into the evolution of a species and can help to identify evolutionary refugia; areas where the species has contracted back to and survived during extreme climatic conditions in the past, such as increased aridity during the Last Glacial Maxima (Byrne 2008). Refugia are of high conservation value because they often contain high levels of genetic diversity, and are presumably areas of high quality habitat and relatively stable climates where the species can hopefully persist in the future (Carnaval *et al.* 2009). In addition, ESUs and MUs can aid in determining if management decisions, such as translocations, re-introductions or genetic rescue are advisable (Weeks *et al.* 2011).

The management of populations at a regional scale can benefit from knowledge of current population processes, which relate to the present population structure, genetic diversity of the population and gene flow (Frankel and Soulé 1981). Analyses of contemporary population processes can also be used to estimate effective population size and levels of connectivity (gene flow) among populations (Schwartz *et al.* 2007), which can help to define suitable spatial scales for management (Cegelski *et al.* 2003). Understanding dispersal patterns and gene flow is important for understanding the social structure of a species and the mechanisms that enable the maintenance of genetic diversity (Greenwood 1980). Knowledge of dispersal patterns and connectivity can increase the effectiveness of management actions (e.g., restricting the spread of disease in a population of Dall’s sheep, *Ovis dalli*; Roffler *et al.* 2014). Genetic techniques can also be used to monitor populations over time and detect changes in movement patterns due to human-induced changes in land use, for example, habitat fragmentation and reduced gene flow in a population of wolverines (*Gulo gulo*) in Montana, USA (Cegelski *et al.* 2003). In addition, genetic monitoring can detect changes in population dynamics and structure (e.g., population size, recruitment of juveniles and migration, Boulanger and McLellan 2001) and loss of genetic diversity over time (Ottewell *et al.* 2014). If changes in gene flow or genetic diversity are detected, appropriate management actions to re-connect populations can be taken.

1.2.3 Habitat preferences

Habitat preferences of a species are determined by a complex interaction between abiotic factors (e.g., rainfall; Dickman *et al.* 1995), and biotic factors, (e.g., intra- and interspecific competition; Falkenberg and Clarke 1998, availability of food resources; Fisher 2000 and predation risk; Broekhuis *et al.* 2013). In addition, species choose habitats through a hierarchical process to fulfil different needs (e.g., food resources vs nesting areas; Martínez *et al.* 2003) and so habitat preferences exist at multiple spatial and temporal scales (McIntyre 1997). Information on why a species is found in a particular location and how habitat preferences may change over time is highly valuable for the development of effective conservation management plans (Finlayson *et al.* 2008). Understanding the habitat requirements of a species can help to inform the configuration and minimum size of reserves at a landscapescale. For example, a study of an endangered ungulate, the takin (*Budorcas taxicolor*) in China discovered that the species needed to move long distances (annual home range of 25 – 98 km^2) to find resources and so required a network of protected areas covering approximately 38,000 km^2 (Guan *et al.* 2015). Habitat preferences can also be used to identify areas of critical habitat. Identification of critical habitat can be highly valuable in the persistence of the species in question and also increase the cost-efficiency of management by using targeted management approaches to protect these areas (Mosser *et al.* 2009). Knowledge of habitat preferences is increasingly being used in species distribution models to predict current distributions, identify areas for translocation or re-introductions, and map potential range shifts due to changes in climate (Guisan *et al.* 2013). Information from these predictive models can increase the effectiveness and success of management strategies for threatened species.

1.3 Arid and semi-arid zones

The arid and semi-arid zones that make up ~ 70 % of Australia (Brown *et al.* 2008) have lost a large number of species, with 43% of endemic mammal species becoming extinct or having experienced significant declines in their distributions since European settlement (Morton 1990). The rapid decline of arid and semi-arid mammals, particularly medium sized mammals, has been attributed to widespread predation by domestic cats (*F. catus*) and red foxes (*V. vulpes*) (Short and Smith 1994; Cardillo and Bromham 2001; Johnson and Isaac 2009). However these regions are also being degraded by land clearance (Fisher *et al.* 2003), introduced herbivores (rabbits, sheep, cattle and goats) and wildfire that cause reductions in vegetation cover and reduced habitat connectivity (McKenzie *et al.* 2007). Global climate change will also have important and unpredictable impacts on arid and semi-arid species as weather patterns change. Changes in small mammal assemblages in response to modified climates have already been recorded in north-central Chile (Meserve *et al.* 2011) and increases in the frequency of large rainfall events and wildfires have been documented in the Simpson Desert in Australia (Greenville *et al.* 2012), which could influence the occurrence of small mammals.

Our knowledge of arid and semi-arid systems is limited compared with that of temperate systems, particularly in the semi-arid ‘mallee vegetation’ regions of southern Australia. While a large body of information is now available from a long-term (+20 years) study in the Simpson Desert of arid Australia (Dickman *et al.* 1999a; Dickman *et al.* 1999b; Dickman *et al.* 2001; Letnic 2002; Letnic 2003; Letnic and Dickman 2005; Dickman *et al.* 2010; Dickman *et al.* 2011; Greenville *et al.* 2012), semi-arid systems have received less attention (although see Woolnough and Carthew 1996; Carthew and Keynes 2000; Bos and Carthew 2001; Bos *et al.* 2002; Bos and Carthew 2003; Bos and Carthew 2007; Bos and Carthew 2008). Like the arid zone, semi-arid zones are characterised by irregular rainfall events that produce pulses of primary resources. However, the average annual rainfall in semi-arid zones is slightly higher (200 - 400 mm) and more predictable than in arid systems (Morton *et al.* 2011). In semi-arid zones, mallee is commonly associated with spinifex (*Triodia* spp.) understorey and both vegetation types are highly flammable (Noble 1984). Wildfires occur after a build-up of plant biomass following rainfall and fire plays an important part in shaping the composition of the vegetation and creating fire mosaics in the landscape (reviewed in Morton *et al.* 2011).

Prior to European settlement Indigenous Australians practiced landscape burning, which is thought by many to have resulted in a fine-scale mosaic of fire ages across the landscape (Bradstock *et al.* 2002). Since European settlement, however, the amount of traditional burning has been drastically reduced and there is some evidence to suggest wildfires have become larger and more frequent. Control burning (purposeful burning of prescribed areas of vegetation) is currently used to create fire mosaics for animal species and prevent large scale wildfires (Penman *et al.* 2011). However, the responses of arid and semi-arid mammals to fire are complex and have not been studied in as much detail as the response of mammals to fire in temperate systems. To date, there is little evidence that fire mosaics increase mammal diversity, with evidence from several species (e.g., common dunnart, *Sminthopsis murina* and western pygmy possum, *Cercartetus concinnus*) showing no apparent preference for habitats of a particular fire age (Letnic *et al.* 2004; Letnic and Dickman 2005; Kelly *et al.* 2011; Kelly *et al.* 2012). If species do show a preference, it appears to be for long-unburnt vegetation (Griffiths and Brook 2014). In addition, climate change may lead to an increase in the variability of rainfall and increase the frequency and intensity of wildfire events (Greenville *et al.* 2012). The unpredictable effects climate change may have on arid and semi-arid regions increases the urgency with which we must gain a better understanding of the ecology of the species that reside in these areas.

1.3.1 Arid and semi-arid dasyurids

Arid and semi-arid dasyurids range in size from the tiny Pilbara ningaui (*Ningaui timealeyi*), weighing between five and nine grams, to the medium sized western quoll (*Dasyurus geoffroii*), weighing up to two kilograms (Menkhorst and Knight 2004). Dasyurids generally live in low densities and in areas that are difficult to access, therefore, relatively little is known about how they survive in these harsh environments. For example, after large rainfall events some species appear to increase in abundance (Rhind and Bradley 2002), while others appear unaffected (Gilfillan 2001a) or even decline (Woolley 1984). Research to date suggests that species may be relatively mobile despite their small size and able to move long distances (up to 12 km recorded for the lesser hairy-footed dunnart, *S. youngsoni*) in search of food resources (Dickman *et al.* 1995). However, the size and connectivity of populations is largely unknown and to the best of my knowledge, no fine-scale genetic analyses of arid and semi-arid dasyurids have been conducted.

The high mobility of some arid and semi-arid dasyurids is thought to have influenced their life histories, and individuals appear to live solitary life styles, coming together during the breeding season and then separating again (Dickman *et al.* 2001; Handley and Perrin 2007). Breeding is usually seasonal and occurs between winter and spring each year (Lee *et al.* 1982). Pouch young are present during late spring and juveniles emerge and disperse during summer when invertebrate numbers peak (Lee *et al.* 1982). Life-spans vary among species, but are generally one to two years for females and 12 to 18 months for males. The diet is considered general and opportunistic and consists of mainly invertebrates with some larger species consuming small reptiles and mammals (Fisher and Dickman 1993a, 1993b).

Previous studies on the habitat preferences of arid and semi-arid dasyurids have reported weak correlations between species abundance and vegetation structure (e.g., Letnic *et al.* 2004; Haythornthwaite and Dickman 2006a). The lack of strong correlations to vegetation structure may reflect the high mobility of individuals and the strong influence of rainfall in the system (Masters 1993; Letnic and Dickman 2010). However, spinifex (*Triodia* spp.) has been suggested as an important habitat component for a number of species, such as the lesser hairy-footed dunnart, *S. youngsoni* (Dickman *et al.* 2001), mallee ningaui, *Ningaui yvonneae* (Bos *et al.* 2002), wongai ningaui, *N. ridei* (Masters 1993) and brush-tailed mulgara, *Dasycercus blythi* (Masters 1993). This association presumably exists as spinifex provides protection from predators and possible nesting sites. However, further study on the habitat preferences of arid and semi-arid dasyurids is required to understand why species occur in particular areas and to identify areas of critical habitat for protection.

1.4 The sandhill dunnart – what do we know?

The sandhill dunnart (*Sminthopsis psammophila*) is a small carnivorous dasyurid marsupial (30-55 grams) found in the arid and semi-arid regions of Australia (Menkhorst and Knight 2004). *S. psammophila* is the second largest dunnart of the 19 species within the *Sminthopsis* genus. It was discovered in the Northern Territory near Lake Amadeus during the Horn Scientific Expedition on the 18th of June 1894 (Spencer 1896). Since then, the species remained undetected until 1969 when five dunnarts were caught at two separate properties on the northern Eyre Peninsula, South Australia during land clearance activities (Aitken 1971). During 1985, four individuals were caught near Mulga Rock in the south-west Great Victoria Desert, Western Australia and in 1987 five more *S. psammophila* were caught in the Yellabinna Region of the Great Victoria Desert. The species has also been detected in large remnant vegetation patches in central Eyre Peninsula, Pinkawillinie Conservation Park (CP) (J. Lee, J. Read and K. Moseby, unpublished data), Hambridge CP (Churchill 2001b) and Hinks CP (D. Driscoll unpublished data), as well as west of the Middleback Ranges. These records indicate the current distribution of the species, with hundreds of kilometres separating the three core populations; Middleback Ranges region, Eyre Peninsula, South Australia; Yellabinna Regional Reserve area, Great Victoria Desert, South Australia; south-western Great Victoria Desert, Western Australia (Churchill 2001b) (Figure 1.1). Although surveys have been conducted in the Northern Territory the species has not been detected since the type specimen was collected in 1894 and is considered locally extinct.

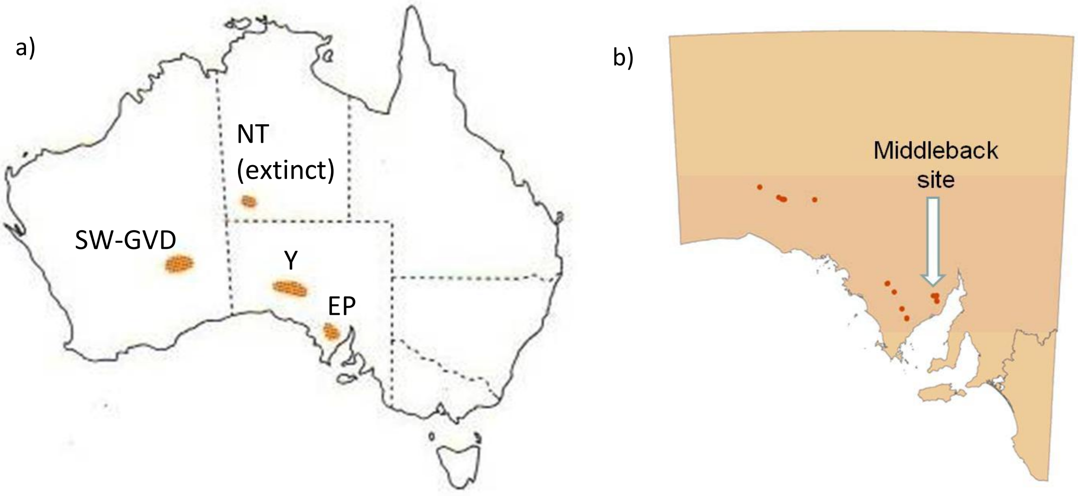

Figure 1.1: The a) national (Menkhorst and Knight 2004) and b) South Australian (Way 2008) distribution of *Sminthopsis psammophila*. The national distribution shows the three extant core populations; south-west Great Victoria Desert, Western Australia (SW-GVD); Yellabinna Regional Reserve, South Australia (Y) and Eyre Peninsula, South Australia (EP) and the assumed extinct population in the Northern Territory (NT). The South Australian distribution shows the locations where *S. psammophila* have been caught (red dots) in South Australia and the location of the Middleback Ranges study site on Eyre Peninsula.

Sminthopsis psammophila is classified as Endangered on the IUCN Red List (Criteria B2ab (ii,iii,iv,v); C1) (IUCN 2013). This classification reflects the lack of knowledge of the species, its small current distribution (< 500 km^2) and a decline in range of ~50 % since European settlement, with cause(s) unknown. Current threats to *S. psammophila* are thought to include predation, changing fire regimes, habitat degradation and fragmentation from agriculture, increased mining activities across its known distribution (Churchill 2001a) and climate change. However, comprehensive management plans require more detailed knowledge on these threats before management actions can be designed and implemented.

1.4.1 Life history

The most comprehensive information on the life history characteristics of *S. psammophila* comes from a captive study at Perth Zoo, Western Australia, which classified the species as having a Life Strategy V (Lambert *et al.* 2011) as per Krajewski *et al.* (2000) and Lee *et al.* (1982). Six life history strategies have been been classified by Lee *et al.* (1982) for dasyurids (detailed in Chapter 2). Strategy V is characterised by polyoestrus (multiple oestrus cycles) in the females (22 - 23 days between cycles in *S. psammophila*) and a seasonal but extended breeding period. Males can live for more than one year and potentially breed in consecutive years. Both males and females reach sexual maturity between eight and 11 months of age and exhibit a seasonal but extended breeding period (Lambert *et al.* 2011). In captivity, *S. psammophila* bred between June and November each year and this concurs with opportunistic field observations of mating between August/ September, pouch young during September/ October and juveniles emerging December/ January (Churchill 2001b). The maximum number of pouch young born per female in captivity was eight (female *S. psammophila* have eight teats), although only up to five pouch young per female have been recorded in the wild (Churchill 2001b). In captivity pouch young spent approximately 45 days in the pouch before they began to relinquish the teat. The captive study provided detailed information about reproduction in *S. psammophila*, however, a detailed study on the life history of *S. psammophila* in the wild is needed as captive animals do not necessarily reflect their wild counterparts in this area (Lambrechts *et al.* 1999). In particular, we lack information on how variable environmental conditions, such as rainfall, may influence the population size and possibly the timing and volume of breeding each year in *S. psammophila*. Information on the life history of *S. psammophila* in the wild will aid in directing management actions by providing insights into the vulnerability of the species to present threats, such as predation from domestic cats (*F. catus*) and red foxes (*V. vulpes*), and future threats, such as increased weather variability due to climate change.

1.4.2 Habitat preferences

Broad surveys have been conducted by the South Australian Department of Environment, Water and Natural Resources in all three known locations of *S. psammophila* to detect additional populations and gain baseline information on the ecology of the species (Churchill 2001b; Ward 2008; Ward 2009). *S. psammophila* has generally been found either in or near sand dunes (usually parallel sand dunes), ranging from 5 m to 30 m high (Churchill 2001b). The vegetation in these areas is typically made up of open mallee (e.g., *Eucalytpus oleosa* and *E. socialis*) with an understory of a diverse range of shrubs (e.g., *Acacia* spp., *Hakea* spp.) and *Triodia* species representing 10 % to 70 % of the ground cover. Churchill (2001b) suggested that *S. psammophila* has a strong affinity with *Triodia* and was observed to nest in large hummocks that had begun to die off in the middle (Stage 3, Figure 1.2). The use of *Triodia* for nesting presumably provides *S. psammophila* with protection from predators (aerial and terrestrial) and variations in extreme temperatures that occur in semi-arid and arid regions (Churchill 2001b). However, as stated previously, *Triodia* is susceptible to fire, and as a result, fire has a significant influence on the structure and composition of *Triodia* stages in the landscape.

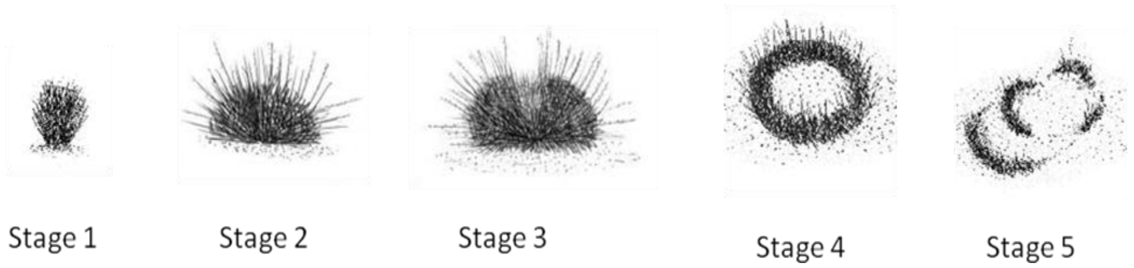

Figure 1.2: Life stages of *Triodia* spp. as per Churchill (2001b). At Stage 1 the *Triodia* is a small tusk of grass. It then grows into a dense hummock by Stage 2. At Stage 3, the *Triodia* starts to die off in the middle and continues to grow outwards until it reaches a ring (Stage 4), which breaks down into fragments (Stage 5).

A wildfire event temporarily removes most, if not all, *Triodia* in the burnt area (Wright and Clarke 2007). After a fire, *Triodia* re-colonises the burnt area from seed or possibly from regeneration of basal meristems, and as a result the majority of *Triodia* in an area is of a similar age (Noble and Vines 1993). *Triodia* reaches its maximum size approximately 20 to 30 years post-fire in semi-arid mallee communities (Haslem *et al.* 2011). As *S. psammophila* appears to have a close affinity to *Triodia* and utilises large hummocks for nesting, Churchill (2001b) suggested that *S. psammophila* will not utilise habitat more than 30 years post-fire and will favour habitats five to 20 years post-fire. However, most *Triodia* plants found in *S. psammophila* habitat in the Great Victoria Desert are older plants (Stage 4-5, Figure 1.2) and *S. psammophila* have been observed to use burrows under *Triodia* plants rather than build nests within *Triodia* (Churchill 2001b). We currently lack detailed information on the habitat preferences of *S. psammophila* and almost no information is available on how time since fire may influence the presence and abundance of the species. Information on the habitat preferences of *S. psammophila*, including its preference for a particular successional stage of vegetation post-fire, is needed to 1) protect suitable habitat for the species, 2) help to inform control burning practices and 3) identify suitable habitat for future surveying efforts to find additional *S. psammophila* populations.

1.4.3 Broad and fine-scale genetic structure

Genetic methods are valuable for defining suitable areas and/ or populations for conservation and management of the species, both nationally and regionally. However once again, there is no information on the fine and broad-scale gene flow and genetic diversity of *S. psammophila*. The three core populations of *S. psammophila* are most likely separate populations given the large distances between the regions (+800 km), but investigation into both current and historical connectivity is needed to identify ESUs and MUs within *S. psammophila*. Investigation into the fine-scale genetic structure and gene flow within a core population of *S. psammophila* will provide valuable information on genetic diversity and dispersal patterns of the species. Knowledge of the genetic structure within a population will enable definition of a suitable area for the management of the population on a local scale. In addition, very few fine-scale genetic studies have been conducted on arid or semi-arid species. A population genetic study on *S. psammophila* will provide new information on dispersal patterns and the maintenance of genetic diversity in a semi-arid dasyurid marsupial and potentially provide evidence for how the species (and other similar species) persists in an environment with variable resources.

Project aims

My study used multiple approaches to investigate aspects of the biology of the endangered sandhill dunnart (*Sminthopsis psammophila*) deemed important for developing effective conservation plans. Capture-mark-recapture methods were combined with molecular and habitat modelling techniques to provide a comprehensive overview of the biology of *S. psammophila* in one core population in a semi-arid environment. The information gathered by this study will not only aid in the development of an effective management plan for the conservation of *S. psammophila,* but will also provide valuable information on how dasyurids persist in a semi-arid environment. The results of my study have been made available to the Sandhill Dunnart Recovery Team formed by the Department of Environment, Water and Natural Resources (DEWNR) in South Australia and have been used to develop management objectives incorporated into the Sandhill Dunnart Recovery Plan.

Aim 1 (Chapter 2): To investigate the life history and population dynamics of *S. psammophila* in response to variable rainfall in one core population west of the Middleback Ranges, Eyre Peninsula.

Aim 2 (Chapter 3 and 4): To ascertain population genetic information of *S. psammophila* at two spatial scales. In particular, I aim to investigate current population processes that have led to present levels of genetic diversity, gene flow and population structure of *S. psammophila* west of the Middleback Ranges, and to determine potential Evolutionarily Significant Units and Management Units for *S. psammophila* across the species' range.

Aim 3 (Chapter 5): To investigate the habitat preferences of *S. psammophila* and determine whether habitat preferences are influenced by rainfall and time since fire in one core population west of the Middleback Ranges, Eyre Peninsula.

CHAPTER 2: Dunnarts, downpours and deserts: Influence of rainfall on the life history of a rare semi-arid dasyurid marsupial

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Sminthopsis psammophila pouch young approximately 21 days old. Photo J. McLean

Statement of Authorship

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By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate's thesis.

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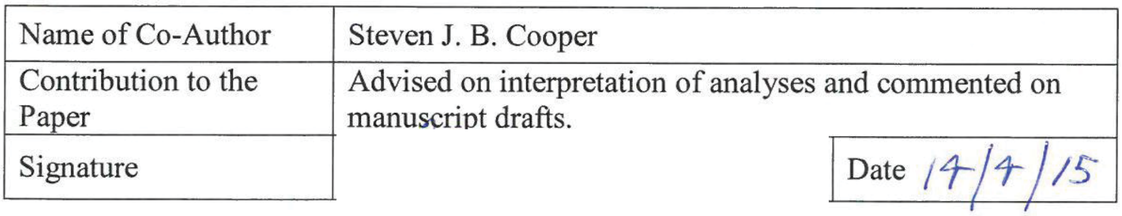
Contribution to the Paper	Designed project, collected data, preformed analyses, interpreted analyses and wrote manuscript.	
Signature		Date

Name of Co-Author	Melanie L. Lancaster	
Contribution to the Paper	Advised on interpretation of analyses and commented on manuscript drafts.	
Signature		Date 14/4/15



Name of Co-Author	Steven J. B. Cooper	
Contribution to the Paper	Advised on interpretation of analyses and commented on manuscript drafts.	
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Signature		Date 14/4/15

Abstract

The Australian arid and semi-arid systems are driven by unpredictable rainfall events that create variable resource pulses in time and space. As a result, mammal populations fluctuate, sometimes dramatically, within and between years. Dasyurid marsupials are conspicuous in the arid and semi-arid zones, however, many species are naturally rare and little is known about the life history and ecology of these species. It is unclear how they persist in regions with irregular rainfall and variable resources, particularly when they have relatively fixed life histories compared to the more flexible life histories of sympatric rodents. This study investigated the life history of the endangered sandhill dunnart (*Sminthopsis psammophila*) during a two year trapping program on the Eyre Peninsula (South Australia) that included a high and low rainfall year. The study aimed to determine if the population size and timing of breeding of *S. psammophila* was affected by low rainfall in a semi-arid environment and how these findings may affect its ability to persist in a changing climate. Capture-mark-recapture data for *S. psammophila* were compared for a year of above average rainfall (high resource year) and a year of below average rainfall (low resource year). The *S. psammophila* population fluctuated during the study with significantly lower capture rates and fewer proportions of resident individuals (particularly males) caught during the low rainfall year. We attributed the lower capture rate to a decreased survival rate of predominantly second year adults and dispersing juveniles, most likely caused by a reduction in food resources during the low rainfall year. Breeding was relatively fixed to a two to three month period each year; however, the timing of mating may have been delayed or the number of breeding animals reduced during the low rainfall year. *S. psammophila* appears to fluctuate in response to variable rainfall, with lower rainfall producing a decrease in population size, density and an increase in the proportion of transient individuals. In order to conserve the species, it is imperative that we identify critical habitat and possible habitat refuges for the species. Climate change, with increased rainfall variability and wildfires, may pose one of the greatest threats to *S. psammophila* survival. Future management should focus on and protecting large areas of continuous suitable habitat.

Keywords: *Sminthopsis psammophila* – Semi-arid – Dasyuridae – Endangered species – Marsupial – Population dynamics – Rainfall

2.1 Introduction

The Australian arid and semi-arid zones are home to a range of species uniquely adapted to environments that experience high day time temperatures and low annual rainfall. A driving factor in these regions is the irregular rainfall events that produce sudden ‘pulses’ of primary resources in the system (Dickman *et al.* 2001; Holmgren *et al.* 2006; Letnic and Dickman 2010). Mammal species inhabiting these areas have thus evolved life histories that enable them to exploit unpredictable resources. For example, the flexible timing of breeding in rodent species such as sandy inland mouse (*Pseudomys hermannsburgensis*) and spinifex hopping mouse (*Notomys alexis*) allows for population explosions during resource rich years (Southgate and Masters 1996). However, unlike their rodent counterparts, arid zone marsupials tend to exhibit relatively fixed breeding times. Members of the family Dasyuridae (carnivorous marsupials) primarily occur in arid and semi-arid regions, with just over half of the 55 species occurring entirely or partially here (Menkhorst and Knight 2004). They feed predominantly on invertebrates and range in size from the tiny Pilbara ningaui (*Ningaui timealeyi*), weighing between five and nine grams to the medium sized western quoll (*Dasyurus geoffroii*) weighing up to two kilograms (Menkhorst and Knight 2004). Breeding in dasyurids is generally seasonal, with juvenile emergence usually coinciding with increases in insect (primary food source) numbers during summer, presumably to maximise the survival of juveniles (Lee *et al.* 1982). Given the seasonality of their breeding cycles, it is not known how flexible dasyurids can be in responding to variation in the external environment and their flexibility (or lack of) may have important implications for their long-term resilience in response to environmental change.

Studies to date have reported inconsistent results in the response of arid dasyurids to large rainfall events. Some studies have detected population increases due to large rainfall events, such as in the brush-tailed mulgara (*Dasycercus blythi*) (Dickman *et al.* 2001). However, other studies have found relatively constant population levels, despite increases in rainfall, such as in the fat-tailed false antechinus (*Pseudantechinus macdonnellensis*) (Gilfillan 2001a) and the wongai ningaui (*Ningaui ridei*) (Dickman *et al.* 2001) or even declines in population size, such as the kultarr (*Antechinomys laniger*) (Woolley 1984). The reasons behind population fluctuations appear to be complex and are most likely a combination of environmental conditions (e.g., rainfall and temperature), characteristics of the individual species (e.g., size, energy requirements, habitat preferences, diet and life histories) and interactions with other species (e.g., competition and predation) (Haythornthwaite and Dickman 2006b; Masters and Dickman 2012).

Understanding the life history of a species and how it responds to variable environmental conditions is valuable in predicting the response of vulnerable species to external threats, such as climate change. Our study species, the sandhill dunnart (*Sminthopsis psammophila*), is little known and classified as Endangered (IUCN 2013). The small (25-55 grams) carnivorous dasyurid marsupial, found in the semi-arid and arid regions of southern Australia (Menkhorst and Knight 2004), is currently known from only three geographically small and disjointed populations; Eyre Peninsula, South Australia; Yellabinna Regional Reserve, South Australia and south-west of the Great Victoria Desert, Western Australia (Churchill 2001b). External threats likely to be significant to *S. psammophila* include predation by introduced domestic cats (*Felis catus*) and red foxes (*Vulpes vulpes*), habitat degradation and loss due to agriculture and open cut mining operations, changing fire regimes, stochastic events that may impact small, isolated populations (Churchill 2001a) and climate change. Previous research of a captive population of *S. psammophila* has led to the classification of its life history as Strategy V (Lee *et al.* 1982; Lambert *et al.* 2011), defined by multiple oestrus cycles and a seasonal but extended breeding season. These features of the life history may allow for some flexibility in the timing of mating, as observed in the brush-tailed mulgara (*Dasycercus blythi*) (Masters and Dickman 2012) and potentially multiple litters within a single breeding season, such as observed in the fat-tailed dunnart (*Sminthopsis crassicaudata*) (Morton 1978b) and the lesser hairy-footed dunnart (*Sminthopsis youngsoni*) (Dickman *et al.* 2001). However, the life history of *S. psammophila* needs to be defined in the wild as important life history events (e.g., timing of breeding) may differ between captive and wild populations due to natural changes in resources, geographical location or other factors (e.g., Lambrechts *et al.* 1999).

Our study investigated the life history of *S. psammophila* in the wild during a two year trapping program on the Eyre Peninsula (South Australia) that included a high and low rainfall year. We aimed to determine if population size and timing of breeding in *S. psammophila* were influenced by low rainfall in a semi-arid environment and discuss whether these findings may affect its ability to persist in a changing climate. We predicted that the abundance of *S. psammophila* would decline during the low rainfall year due to a reduction in food resources, which would cause increase stress for lactating females, and potentially lower the survival rate of pouch young and reduce juvenile recruitment into the population. If the life history strategy of *S. psammophila* exhibits similar flexibility in the timing of breeding as observed in *D. blythi,* we predicted that the timing of breeding may be delayed or fewer individuals may breed during resource poor (low rainfall) years.

2.2 Methods

2.2.1 Study site

The study was conducted within relatively intact mallee vegetation on the western side of the Middleback Ranges, Eyre Peninsula, South Australia (33°09′S, 137°07′E) (Figure 2.1). The region has a semi-arid climate, with relatively hot dry summers and cold winters. Mean rainfall in this region is approximately 250 mm per year, with most rainfall occurring during winter, and up to 20 % during summer (Schwerdtfeger 1985). The western side of the Middleback Ranges is characterised by parallel sand dunes ranging from 10 to 20 meters (m) high. The main plant species include mallee species (*Eucalyptus socialis, E. gracilis, E. incrassata, E. oleosa* and *E. brachycalyx*), with an understorey dominated by *Triodia irritans* and other shrubs such as *Alyxia buxifolia, Eremophila scoparia, Senna artemissioides, Hakea francisiana Melaleuca lanceolata* and *Dodonaea viscosa* (Bos and Carthew 2001).

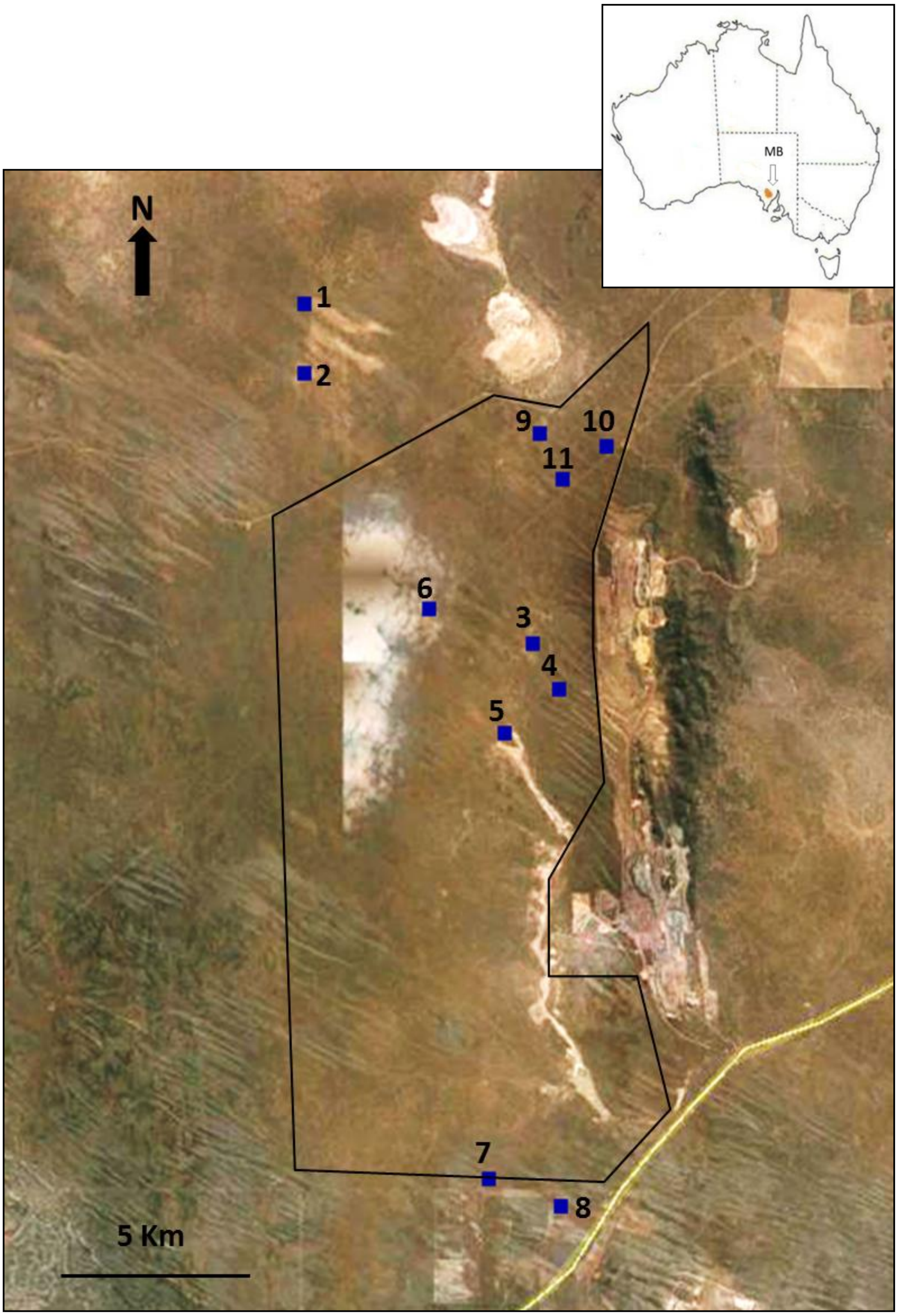


Figure 2.1 Location of study site west of the Middleback Ranges (MB) on the Eyre Peninsula, South Australia and location of the 11 *S. psammophila* sites within the 24,000 ha study area. Eight of the sites were situated within the Ironstone Hill Conservation Park (black line = the boundary of conservation park) and three sites were on adjacent private property, Site 1 and 2 were situated on Cooyerdoo Station and Site 8 was situated on Pine Hill. *Source*: “Middleback Ranges”. 33°09′S and 137°07′E. **Google Earth**. April 20th, 2011. August 3rd, 2011.

2.2.2 Trapping protocol

Eleven trapping sites were established within Ironstone Hill Conservation Park and surrounding private property (Pine Hill and Cooyerdoo Stations), covering approximately 24,000 ha (Figure 2.1). All sites were at least 1.5 km apart to ensure that all sites were independent of each other. Sites were established in areas with sandy soils with *Triodia irritans* present, as past surveys have suggested *S. psammophila* exhibits a close affinity with this plant species (Churchill 2001b; Way 2008; Ward 2009). Each site was comprised of four parallel transects, with transects alternatively using aluminium box treadle traps (12, Elliott traps, Type A) and deep pitfall traps (6 permanently installed PVC pipe with lids, 600 mm deep and 230 mm diameter; Figure 2.2 and Figure 2.3). Transects were 20 m apart with 20 m separating each trap along transects. Trapping grids were positioned along the length of a dune with the centre of the grid on its crest. Each grid covered an area of approximately 16,000 m^2. Timing of trapping was designed to capture the life history of *S. psammophila* in the wild. All sites were trapped seasonally (summer, autumn, winter, spring – eight trapping sessions) with six of these sites trapped monthly (excluding February and December 2011 and May 2012 – 12 trapping sessions). All trapping sessions took place during the new moon phase of each month to increase capture rate. Moonlight has been observed to decrease movement of *S. psammophila* (Churchill 2001b) and Mitchell's hopping mouse (*Notomys mitchellii*) (S. Carthew unpublished data), likely due to the increased susceptibility to predation. Trapping was conducted for six nights each session, with Elliott traps closed on alternate nights to reduce the chance of recaptures.

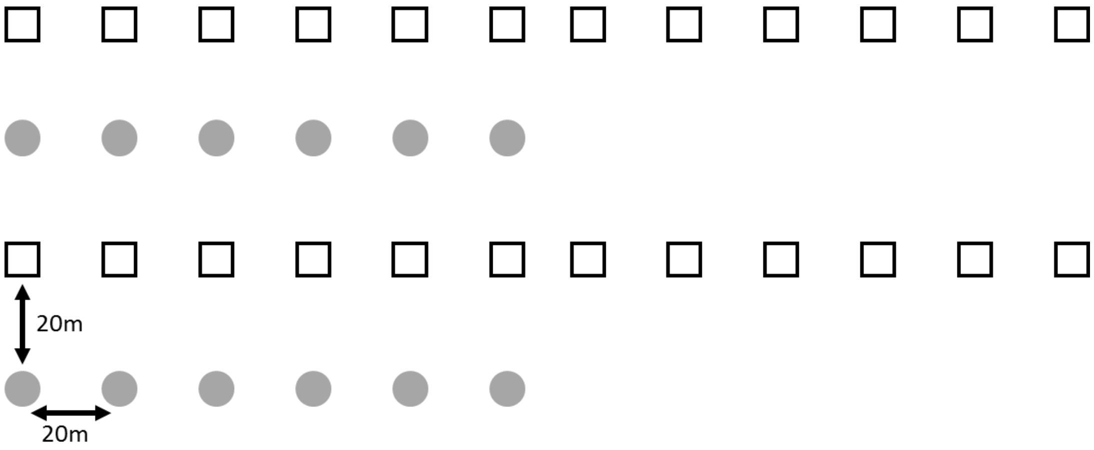


Figure 2.2 The design of the trapping grid used at each site. Each trapping grid was positioned along the length of the dune and comprised of 24 Elliott traps (open squares) and 12 pitfall traps (closed circles). The traps were arranged in four transects, alternating between Elliott trap and pitfall trap transects. The distance between each transect and each adjacent trap along each transect was 20 m and traps spanned a total area of approximately 10,800 m^2, (60 m x 100 m) + (40 m x 120 m).

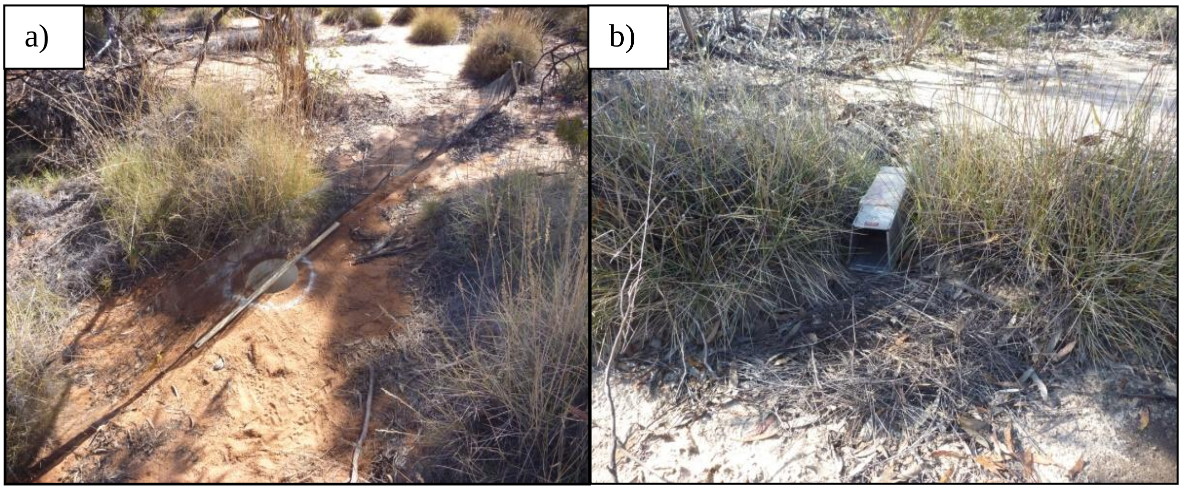


Figure 2.3 Trap set up of a) permanent pitfall trap, 600 mm deep and 230 mm diameter (with 7 m long drift net) and b) baited Elliott trap (Type A) with a plastic bag placed on the outside to prevent rain for entering it and situated within *Triodia* to increase captures of *S. psammophila*.

Elliott traps were baited with a mixture of peanut butter and oats, and a small amount of bedding (pieces of hessian bag) was added to each trap. During the winter months, a plastic bag was placed around Elliott traps to prevent rain entering. A small piece of PVC pipe was placed in the bottom of each pitfall trap to provide protection for animals captured. Alternate pitfall traps in each transect were fitted with 7 m long permanent drift fences (3.5 m each side of the pitfall trap), dug approximately 10 cm into the ground (Friend *et al.* 1989).

All animals captured were identified to species and released with minimal handling. *S. psammophila* were measured (left pes length, tail length, head length), weighed to the nearest 0.5 g, sexed and a small ear notch taken for genetic analysis. Each *S. psammophila* was implanted with a Trovan Unique ID100 (1.25) nanotransponder (7 mm long x 1.25 mm diameter) for individual identification. The microchip was pre-sterilized and preloaded into a needle and syringe for ease of implantation and was inserted under the skin in the scruff of the animal’s neck.

2.2.3 Life history strategies and reproduction

Six life history strategies have been defined by Lee *et al.* (1982) within members of the family Dasyuridae, based on the frequency of oestrus in females, timing and length of reproduction in the males, seasonality of mating and the age that animals reach sexual maturity (Table 2.1). Arid zone species studied to date have been classified as either Strategy IV or V. These life histories appear to be adapted to environments where resources are unpredictable, and exhibit ‘safe guards’ against reproductive failure by evolving an extended, but seasonal breeding period and polyoestrus in the females (Lee *et al.* 1982; Friend *et al.* 1997).

Table 2.1 Details of the six life history strategies of dasyurid marsupials as defined by Lee *et al.* (1982). Each life history strategy was defined in relation to the oestrus pattern of the female, the number of breeding seasons a male can live for, the duration of the breeding season, the seasonality of the breeding and the age at which males and females become sexually mature. Table is taken from Krajewski *et al.* (2000).
* In some taxa males and females mature at different ages
** *Sarcophilus harrissi* matures at 2 years but is identified as Strategy II based on the four other reproductive traits

Strategy	Oestrus pattern	Seasons per male	Duration of breeding season	Seasonality of breeding	Age at sexual maturity months*
I	Monoestrus	Annual	Restricted	Seasonal	11
II	Monoestrus	Perennial	Restricted	Seasonal	11**
III	Facultatively Polyoestrus	Perennial	Restricted	Seasonal	11
IV	Polyoestrus	Perennial	Extended	Seasonal	6
V	Polyoestrus	Perennial	Extended	Seasonal	8 - 11
VI	Polyoestrus	Perennial	Extended	Aseasonal	8 - 11

Reproductive condition was assessed for both male and female *S. psammophila* caught. Pouch condition in female *S. psammophila* was scored from one to six based on pouch development descriptions of Woolley (1990a) and Godfrey (1969) for the stripe-faced dunnart (*Sminthopsis macroura*) and Smith (1984) for the yellow-footed antechinus (*Antechinus flavipes*). Appendix 1 details pouch development stages used in this study. Pouch young present were measured from crown to rump (C-R length) whilst in the pouch. The age of pouch young was estimated by comparing the C-R length with that of pouch young of known age from a captive study (Lambert *et al.* 2011). The testes width was measured in males to determine timing of breeding, as testes width has been documented to reach a maximum at the onset of breeding in other dasyurid species (e.g., the mallee ningaui, *Ningaui yvonneae*; Bos and Carthew 2001 and the spotted-tail quoll, *Dasyurus maculatus*; Glen 2008) and provides an indication of spermatogenic activity in males (Woolley 1966; Dickman 1985).

2.2.4 Environmental conditions

Rainfall was used as a predictor of resource availability, as rainfall is known to stimulate increases in primary resources in arid and semi-arid systems (Dickman *et al.* 2001; Letnic and Dickman 2010; Morton *et al.* 2011). To investigate the flexibility of the life history of *S. psammophila*, capture rates and timing of breeding were compared between a high rainfall year (2011) and a low rainfall year (2012). Rainfall data were obtained from the Bureau of Meteorology using the closest weather station to the field site, which was approximately 15 km away (Whyalla; Moola, station number 018117). Rainfall data were available from 1958 to present (2012) and the average annual rainfall (± S.E.) between 1958 and 2012 was 274.7 ± 20.2 mm (Bureau of Meteorology 2012a). The average monthly rainfall between January 2010 and December 2012 was used to investigate the influence of rainfall on *S. psammophila* (Figure 2.4). Maximum and minimum daily temperature data were obtained from the Bureau of Meteorology weather station at Kimba (station number 018040) as Moola did not have temperature data available and Kimba was the next closest inland weather station to the field site (approximately 60 km away). Temperature data were available from 1920 to present (2012) and the average maximum and minimum daily temperature for each month during the study was used (Bureau of Meteorology 2012b, 2012c) (Figure 2.5).

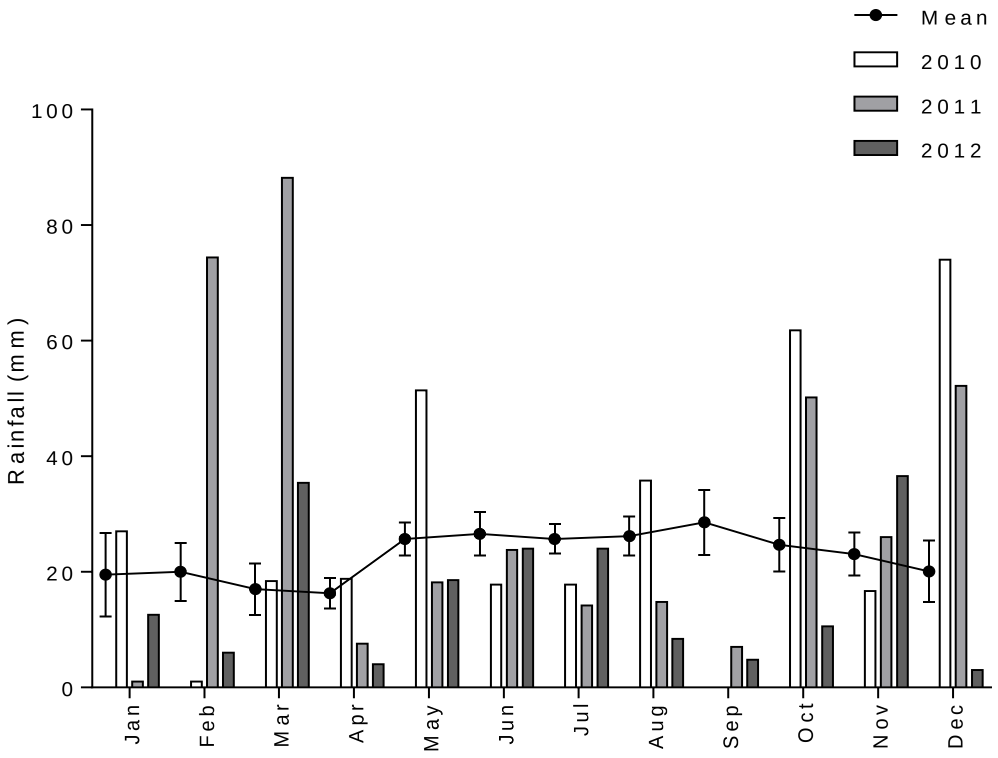


Figure 2.4 Monthly rainfall recorded during 2010, 2011 and 2012 (bars) and mean monthly rainfall (± S.E.) (line) recorded from 1958 to 2012 at the closest weather station to the Middleback Ranges study site, Whyalla (Moola), weather station number 018117 (33.11°S 137.17°E) (Bureau of Meteorology 2012a).

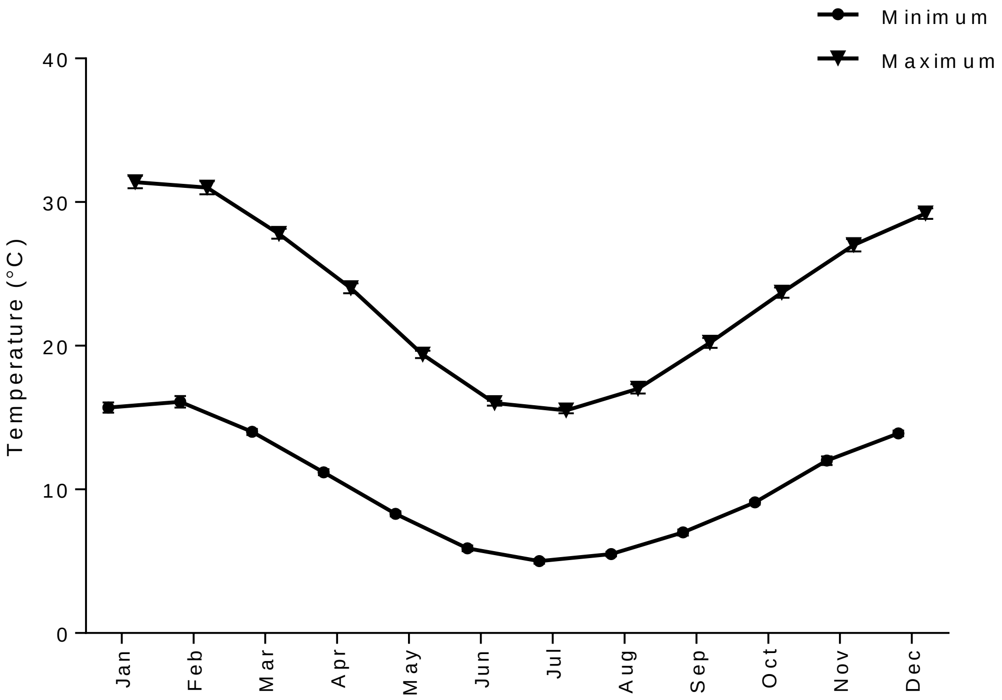


Figure 2.5 Mean monthly minimum (circle) and maximum (triangle) monthly temperatures (± S.E.) recorded from 1920 to 2012 at the closest weather station with temperature date to the Middleback Ranges study site, Kimba, weather station number 018040 (33.14°S 136.41°E) (Bureau of Meteorology 2012b, 2012c).

2.2.5 Data analysis

All captures were standardised to 100 trap nights (trap nights (TN) = number of traps open x number of nights) prior to further analyses. Minimum number of *S. psammophila* known to be alive (KTBA) was estimated for males and females separately using the program DENSITY v 5.0.2 (Efford 2012) by selecting the ‘Open population’ model and the MNA (minimum number alive) option within this model. All other analyses were conducted in the statistical program R (R Core Team 2013) and non-parametric tests were used when data were determined to be non-normally distributed. Differences in capture rates of *S. psammophila* between months for each year were investigated using a Kruskal-Wallis rank sum test with a post-hoc pairwise Wilcoxon rank sum test. Differences in capture rates and KTBA between the high rainfall year (2011) and low rainfall year (2012) were investigated using a Wilcoxon rank sum test. A Kruskal-Wallis rank sum test with a post-hoc pairwise Wilcoxon rank sum test used to determine if the number of juvenile male and female *S. psammophila* caught differed between the years.

First year animals were identified as such when caught as juveniles during January or if their body weights were within one standard deviation of the mean monthly body weight of known first year individuals as per Gilfillan (2001b). Second year animals were generally heavier than first year animals and pouch condition (if the female had bred previously) was also used to differentiate between first and second year females. Based on the results of this study, we used an approximate birth date of September to provide an estimated age of captured animals. Individuals were placed into age classes and cohorts based on their estimated ages. Testes width and body weights were pooled across the two years and plotted as monthly data over a 12 month period. Resident individuals were defined as an individual caught at the same site during two or more trapping sessions as per Marchesan and Carthew (2004) and Masters and Dickman (2012) and ignoring same session recaptures. An individual was assumed to be transient if it was only caught during one trapping session. The time residents spent at a site was calculated as the time between the first and last capture of the resident at the site.

2.3 Results

A total trap effort of 23,529 trap nights resulted in 241 captures of 107 individual *S. psammophila*; 46 females and 61 males. The overall capture rate of *S. psammophila* during the study was 1.0 %. Capture rates varied between months and years and ranged from 0.0 % to 6.3 %.

2.3.1 Life history characteristics of S. psammophila

2.3.1.1 Males

Mean testes width in males increased from January to July as juveniles became adults (Figure 2.6). Maximum mean testes width was reached during July and then decreased from August onwards, a common sign in dasyurids that breeding had commenced (e.g., Calaby and Taylor 1981; Woolley 1990b; Friend *et al.* 1997; Bos and Carthew 2001). Body weights of first year males increased from January to August when they reached a maximum average body weight of 49.2 ± 0.9 grams (n = 28) and then declined after August (Figure 2.7). The increase in body weight and then decline is another sign of the onset of the breeding season in dasyurids (e.g., Calaby and Taylor 1981; Friend *et al.* 1997). Further evidence that breeding had commenced was the two instances of aggression we observed between male *S. psammophila* caught in the same pitfall trap, which resulted in the biting of tails and removing the hair from the rump. Similar acts of aggression were observed between males in captivity at the onset of the breeding season (Lambert *et al.* 2011). Male capture rates peaked during August 2011 (3.6 males/ 100 TN) and then declined during September to November (September – November capture rate = 1.3 – 0.9 males/ 100 TN). New (not previously caught) males were captured between January and September 2011 and between January and July 2012.

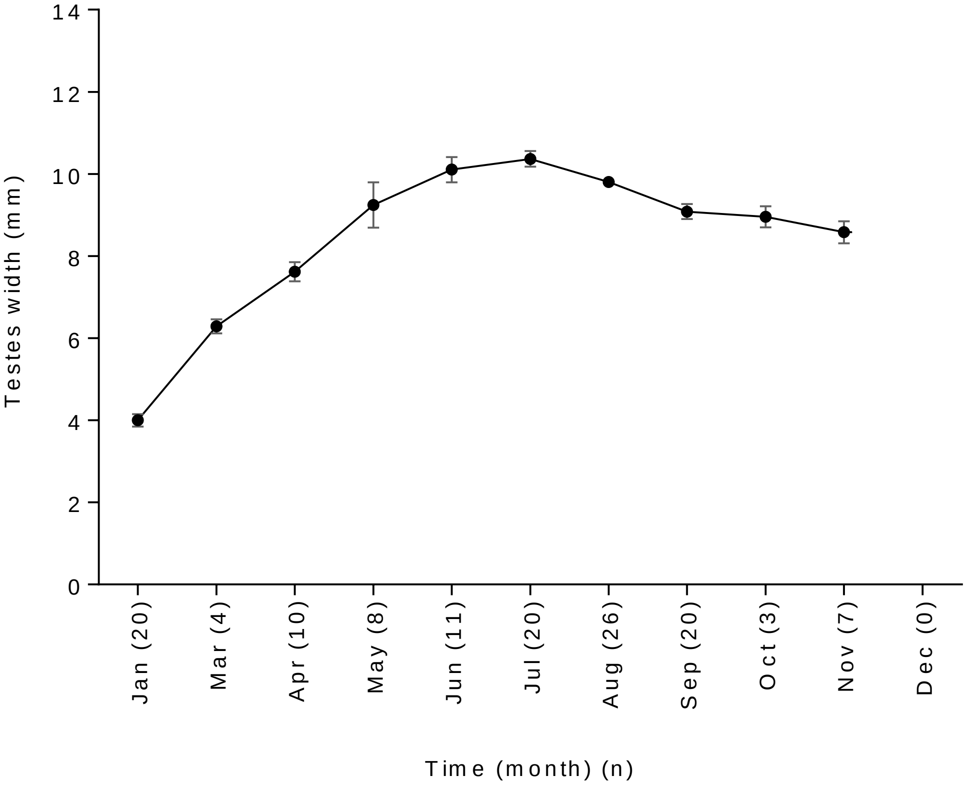


Figure 2.6 Mean testes width (mm) ± S.E. of first year male *S. psammophila* caught during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia. Data for both years (2011 and 2012) were pooled per month and the number in brackets represents the sample size.

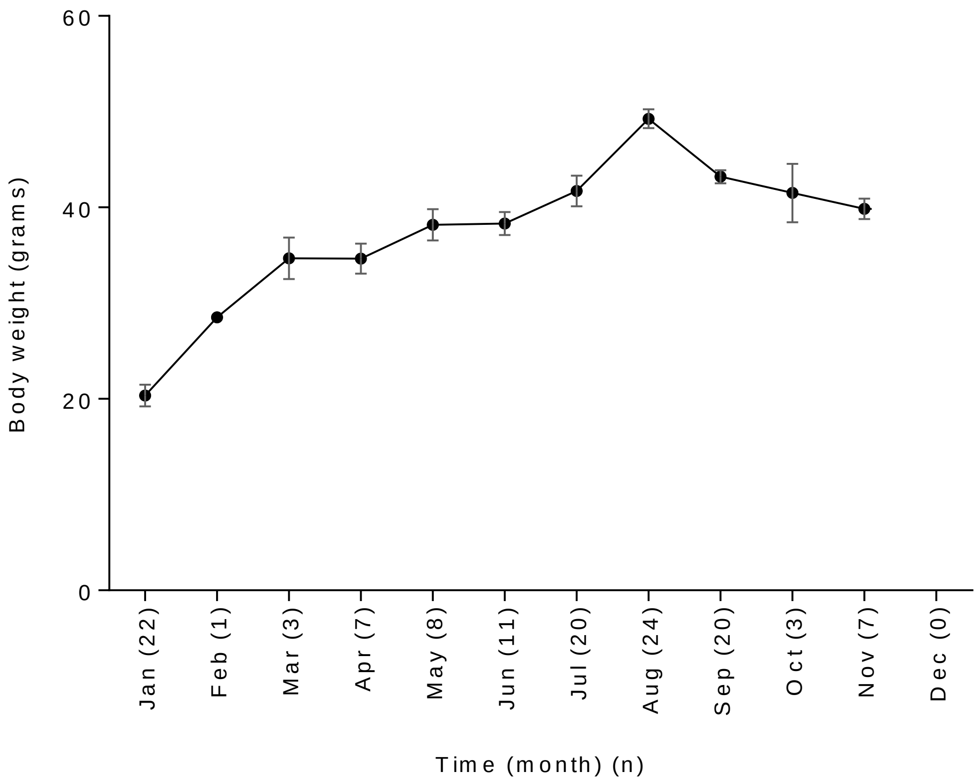


Figure 2.7 Mean body weight (grams) (± S.E.) of first year male *S. psammophila* caught during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia. Data for both years (2011 and 2012) were pooled for each month and number in brackets represents the sample size.

2.3.1.2 Females

Pouches of all females caught developed slowly between January and July and reached Stage 2 (development of middle and edge skin flaps and teats becoming more visible, Appendix 1) during August of both years. During September 2011 and October 2011 all pouches were fully developed (development of skin flaps and enlargement of teats) and pouch young were present (Stage 4, Appendix 1). Pouches remained developed through November 2011, although pouch young were no longer present (Stage 5, Appendix 1), suggesting that females were still lactating and the young had been placed in the nest. From January onwards, the pouches of females began to regress. The body weights of first year females showed a similar pattern to that of the males and increased from January, reaching their mean maximum body weight (without pouch young) during August (37.1 ± 1.2 grams, *n* = 24) (Figure 2.8).

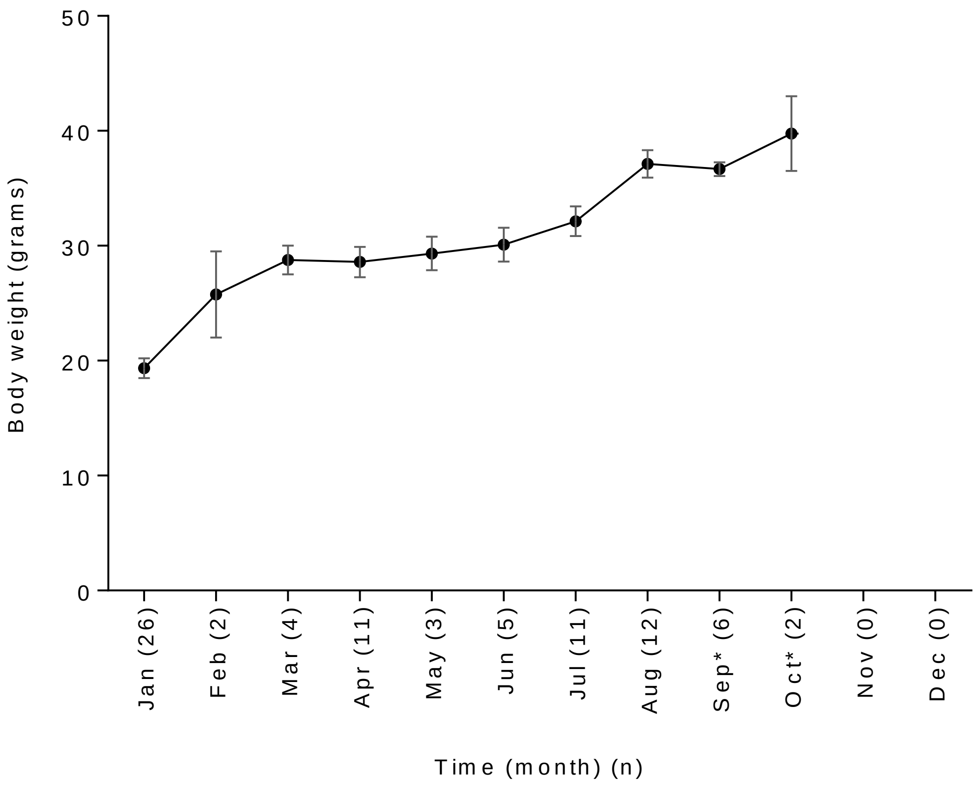


Figure 2.8 Mean body weight (grams) (± S.E.) of first year female *S. psammophila* caught during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia. Data for both years (2011 and 2012) were pooled for each month and the number in brackets represents the sample size.
* Females with pouch young included.

Capture rates of *S. psammophila* females increased at the onset of the breeding season (August capture rate = 1.4 females/ 100 TN) and then declined during September to November (September – November capture rate 0.5 - 0.3 females/ 100 TN). New females were captured from January to August 2011 (excluding May 2011), however, no new females were caught after the breeding season commenced. New females were caught between January and April 2012 and also during September 2012. During the study a total of six adult females were caught with seven to eight pouch young each (mean number of pouch young per litter ± S. E. = 7.6 ± 0.3) during November 2010 and September and October 2011 (Table 2.2). During September 2011 five adult females were caught without pouch young, but during October and November 2011, all females caught had pouch young (October) or had pouches indicating they had bred (November). The timing of conception for pouch young caught during 2011 was estimated to be between the 7th and 19th of September, based on a gestation length of 16 - 19 days (Lambert *et al.* 2011). The age of pouch young at capture ranged from zero to six days in September 2011, 21 days in October 2011 and 33 days in October 2010. These estimates suggest that the breeding period lasted approximately three weeks and female oestrus was synchronised within each year. Discrepancies between captive and wild populations are common (e.g., Morton 1978b) and we detected one instance where the age of pouch young was underestimated by at least three days. One female (F20) with pouch young was caught twice, three days apart (Table 2.2). However, when the measurements of the pouch young were compared to the measurements from the captive study, the captive data suggested that the pouch young were zero days old at both captures, indicating an underestimation of pouch young age of at least three days at the second capture.

Table 2.2 Information on female *S. psammophila* captured with pouch young during a two year field study west of the Middleback Ranges on the Eyre Peninsula, South Australia. Data includes the date and site of capture for each *S. psammophila* mother, the number of pouch young in each litter, pouch young crown to rump (C-R) length (mm) and mean C-R length (mm) (± S.E.) for each litter. Age, date of birth, date of mating and weaning date were estimated based on growth data of pouch young from a captive study of *S. psammophila* by Lambert *et al.* (2011). Gestation in *S. psammophila* is estimated as 16 - 19 days and juveniles are weaned at approximately 60 days of age (Lambert *et al.* 2011).

* Values estimated based on information from Lambert *et al.* (2011).

Underestimation of pouch young age by at least three days.

Date	Mother	Site	No. of pouch young	C-R length (mm)	Average C-R length ± S.E. (mm)	Age* (days)	Date of mating*	Date of birth*	Date weaned*
28/11/2010	F8903	9	8	16.6 16.4	16.5 ± 0.1	33	12th - 16th Oct	26th Oct	23rd Dec
29/09/2011	F20	3	8	3.8 4.1	3.9 ± 0.3	0	10th - 14th Sep	29th Sep	27th Nov
1/10/2011	F20	3	8	4.7 4.8	4.8 ± 0.1	0#	10th - 14th Sep	29th Sep	27th Nov
2/10/2011	F829B	6	8	7.5 7.9 7.1	7.5 ± 0.2	6	7th - 10th Sep	26th Sep	25th Nov
26/10/2011	F6374	3	7	9.6 9.4 9.7	9.6 ± 0.1	21	16th - 19th Sep	5th Oct	4th Dec
26/10/2011	F17	9	7	10.0 9.6	9.8 ± 0.2	21	16th - 19th Sep	5th Oct	4th Dec
26/10/2011	F8903	9	8	9.2 9.5	9.3 ± 0.1	21	16th - 19th Sep	5th Oct	4th Dec

2.3.2 Population age structure and individual longevity

The variation in capture rate and KTBA observed within each year appeared to be based on the approximate 12 month life history cycle of *S. psammophila*. The population was dominated by a single cohort each year, based on body weight and reproductive characteristics (Figure 2.9 and Figure 2.10). Individuals caught in January were considered juveniles, those caught between April and June were considered sub-adults and individuals caught from July onwards were considered adults. Each year the transition between the cohorts occurred during January as juveniles born the previous September dispersed from their natal areas (Figure 2.9). At this time of year (January), captures were comprised of mostly juveniles (2011 = 81 %, *n* = 26 individuals and 2012 = 100 %, *n* = 21 indiviudals) as well as second year adults (2011 = 19%, *n* = 5 individuals and 2012 = 0 %, *n* = 0). After January capture rates declined suddenly and then remianined relatively stable between April and June (2011 = 1.3 captures/ 100 TN and 2012 = 0.6 captures/ 100 TN). Capture rates then increased during mating (July to September, 2011 = 2.8 captures/ 100 TN and 2012 = 0.4 captures/ 100 TN), and then declined after mating (October to December 2011 = 0.6 captures/ 100 TN and 2012 = 0 captures/ 100 TN).

The average (± S.E.) life span of each cohort was 19.3 ± 2.9 months. Male and female juveniles reached sexual maturity at approximately 10 to 11 months of age and bred in the year following their birth. Second year animals were easily distinguishable from the dominant cohort between January to April by their larger body weights and females by their pouch condition. Four second year males were caught during the study but were not detected after April, with the exception of one male trapped twice, during July and August. Eight second year females were caught during the study, of these, four females were observed to breed in their second year (two were caught with pouch young and two with pouches that indicated nest young). These observations indicate that males can live up to ~18 months of age and females up to ~25 months of age.

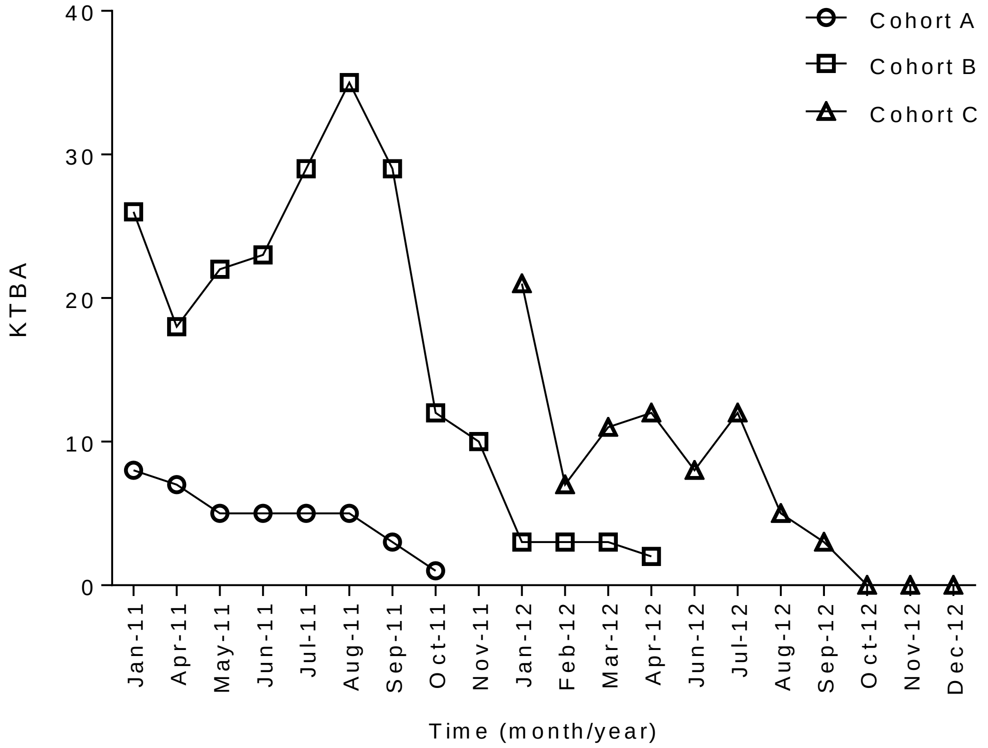
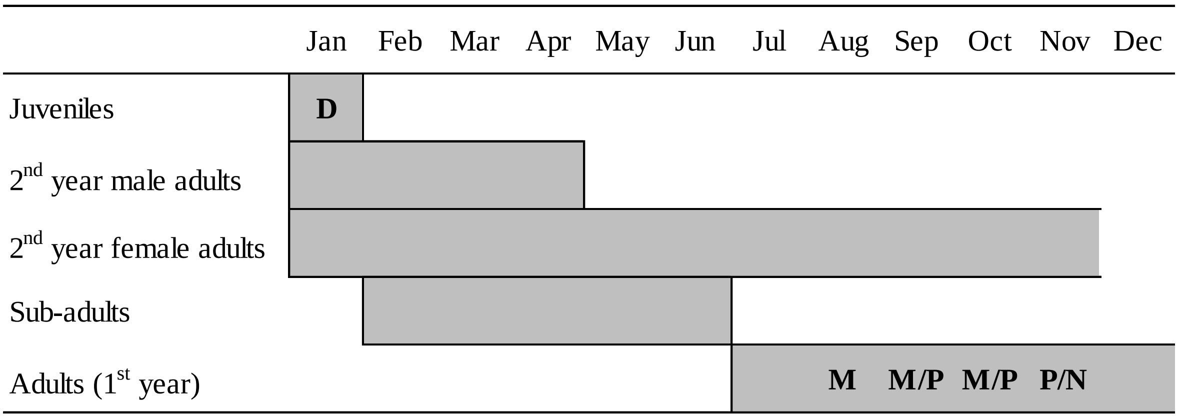


Figure 2.9 Minimum number of *S. psammophila* individuals known to be alive (KTBA) per trapping session (month/ year) for each cohort (A, B and C) encountered during a two year field study west of the Middleback Ranges on the Eyre Peninsula, South Australia.



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Juveniles	▨ **D**											
2nd year male adults	▨	▨	▨	▨								
2nd year female adults	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Sub-adults		▨	▨	▨	▨	▨						
Adults (1st year)							▨	▨ **M**	▨ **M/P**	▨ **M/P**	▨ **P/N**	▨

Figure 2.10 Phenology and population structure of *S. psammophila* based on observations made during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia. Population structure present each month is indicated by the shaded areas. Important life history events that occur during a 12 month period in *S. psammophila* are indicated by capital letters; D = dispersal; M = mating; P = pouch young and N = nest young and the timing of these events are indicated by the month in which they occur.

2.3.3 *The influence of a variable environment on population processes in* S. psammophila

During 2011 (high rainfall year) the region received 102.6 mm above the average annual rainfall of 275 mm (377.6 mm), whereas during 2012 (low rainfall year) the region received 87 mm less than the average annual rainfall (188.0 mm) (Bureau of Meteorology 2012a). The main difference between the years was the high summer and autumn rainfall during 2011 (total summer and autumn rainfall = 263.4 mm) that did not occur during 2012 (total summer and autumn rainfall = 116.2 mm) (Figure 2.4 & Table 2.3). Maximum daily temperature and minimum daily temperature also fluctuated seasonally and annually (Figure 2.5 & Table 2.3). Overall, environmental conditions were wetter during 2011, with slightly cooler day time temperatures (average annual temperature ± S.E. = 23.3 ± 0.7 °C) and warmer night time temperatures (average annual temperature ± S.E. = 10.8 ± 0.6 °C) than average (Bureau of Meteorology 2012b, 2012c). In comparison, 2012 was drier, with slightly hotter day time temperatures (average annual temperature ± S.E. = 23.6 ± 0.7 °C) and cooler night time temperatures (average annual temperature ± S.E. = 10.1 ± 0.6 °C) than average.

Table 2.3 Differences between the mean rainfall (mm), and maximum and minimum temperature (°C) for each season and the long-term seasonal mean for each parameter for a two year period (2011 to 2012) west of the Middleback Ranges on Eyre Peninsula, South Australia. The long-term mean of each parameter was calculated from data collected between 1958 and 2012 for rainfall and between 1967 and 2012 for temperature. Rainfall data were taken from Whyalla (Moola) weather station number 018117 (33.11°S 137.17°E) (Bureau of Meteorology 2012a) and temperature data were taken from the Kimba weather station number 018040 (33.14°S 136.41°E) (Bureau of Meteorology, 2012b, 2012c).

	2011				2012			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Rainfall (mm)	25.9	20.9	-7.6	0.7	-0.3	2.3	-6.4	-9.7
Max. temp. (°C)	-0.3	-2.2	0.1	0.4	-0.8	-0.5	-1.0	2.1
Min. temp. (°C)	0.4	0.0	0.4	0.4	0.2	-0.5	-0.3	-0.2

2.3.3.1 Effect of rainfall on capture rate & population size of S. psammophila

Capture rate and minimum number of *S. psammophila* known to be alive (KTBA) were significantly lower during the low rainfall year compared to the high rainfall year (Wilcoxon rank sum test, Capture rate W = 246.5, $P < 0.001$ and KTBA W = 364, $P < 0.001$) (Figure 2.11). Capture rate and KTBA also differed significantly between months (Kruskal-Wallis rank sum test, capture rate $\chi^2 = 34.844$, *d.f.* = 19, P = 0.015 and KTBA $\chi^2 = 35.869$, *d.f.* = 19, P = 0.011), however after Bonferroni corrections the monthly differences became non-significant (pairwise Wilcoxon rank sum test, $P > 0.05$). Proportionally more males than females were caught during 2011 (males = 61 %, *n* = 44 and females = 39 %, *n* = 28), whereas in 2012, the sex ratio was almost equal (males = 49 %, *n* = 17 and females = 51%, *n* = 18).

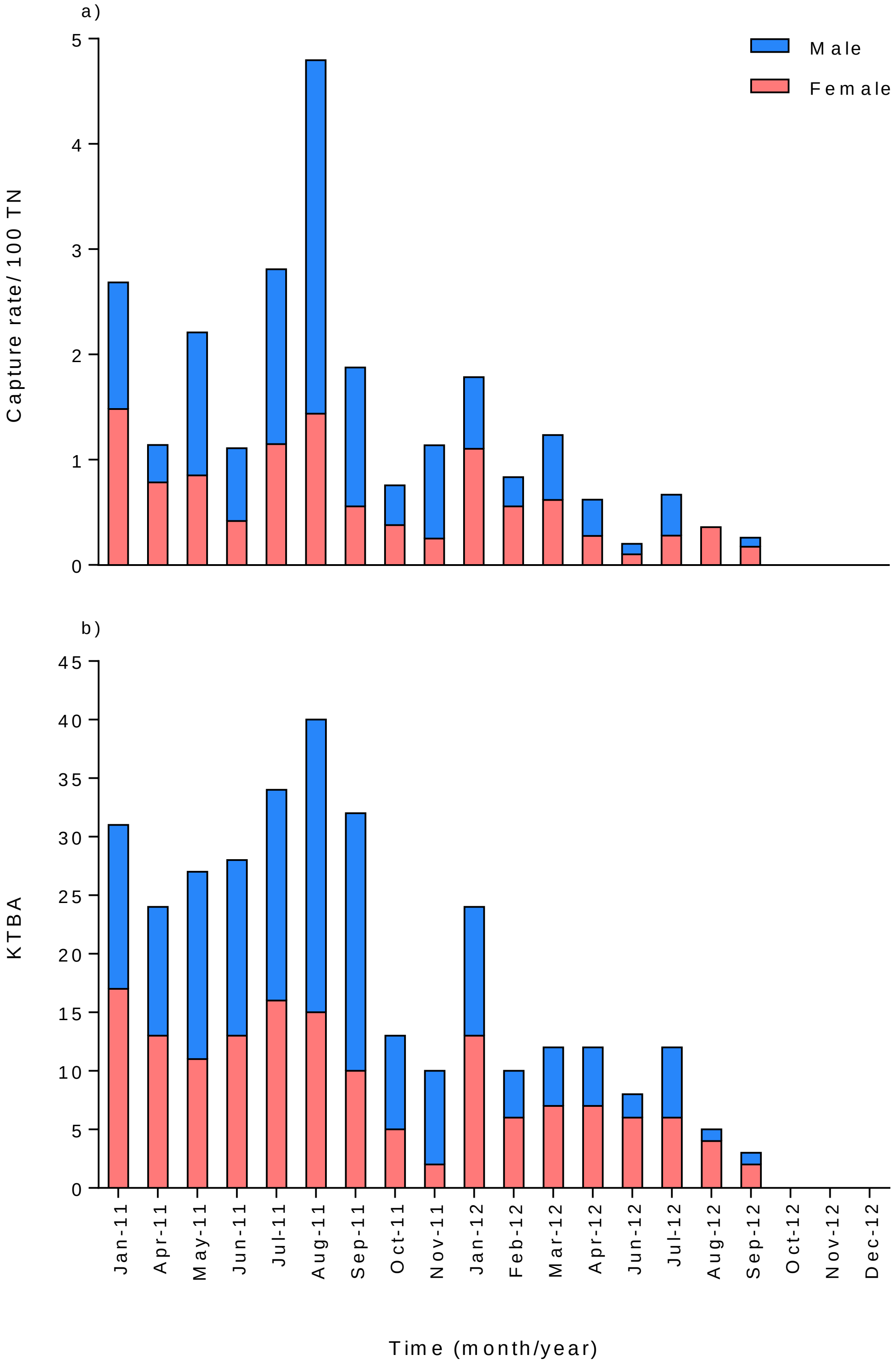


Figure 2.11 Monthly and yearly variation in a) capture rate per 100 trap nights (TN) (same session recaptures excluded) and b) KTBA (known to be alive) of male (blue) and female (pink) *S. psammophila* caught during each trapping session of a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia.

Fewer *S. psammophila*, both males (2011 *n* = 44 and 2012 *n* = 17) and females (2011 *n* = 28 and 2012 *n* = 18), were present in the population during 2012 than 2011 (Figure 2.9 and Table 2.4). In addition, a greater proportion of residents were caught during 2011 (54 %) compared to 2012 (37%). Residents were recorded at fewer sites (2011 = 8 sites and 2012 = 6 sites) and sites with residents had fewer residents per site during 2012 (mean residents/ site ± S.E., 2011 = 4.8 ± 1.8 and 2012 = 2.2 ± 0.4) (Table 2.4). In addition, the length of time residents remained at the site was longer during 2011 (mean time ± S.E. = 5.3 ± 0.6 months) compared to 2012 (mean time ± S.E. = 4.1 ± 0.7 months). During 2011 the average time that male and female residents spent at sites was the same (5.3 ± 0.6 months), but during 2012 males spent half as much time at sites than females (males, mean time ± S.E. = 2.3 ± 0.5 months and females, mean time ± S.E. = 5.0 ± 0.8 months). There was a reduction in the number and percentage of resident females during 2012 (2011 = 61% and 2012 = 44 %), but similar numbers of transient females were caught during both years (Table 2.4). In contrast, there was a notable reduction in the number of both resident (2011, *n* = 22 and 2012, *n* = 5) and transient (2011, *n* = 22 and 2012, *n* = 12) males caught during 2012 (Table 2.4).

Table 2.4 Variation in the number of resident and transient male and female *S. psammophila* caught during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia that included a high rainfall (2011) and low rainfall (2012) year.
A resident was defined as an individual captured at least twice at the same site during two or more trapping sessions, same session recaptures excluded and an individual was assumed to be transient if it was only captured during one trapping session. Data shown includes differences in the capture rate per 100 trap nights (TN), number of resident individuals, transient individuals, total number of individuals caught, percentage of resident/recaptured individuals, number of sites with residents animals, mean (± S. E.) residents per site (range in brackets) and the mean (± S. E.) time (months) residents were present at the same site (i.e., duration between first and last capture) between females, males and years.

	Capture rate/ 100 TN	No. of residents	No. of transients	Total caught	% of individuals recaptured	Sites with residents	Mean residents/ site (± S. E.) (range)	Mean time (months ± S.E.) residents were present (range)
Males								
2011	1.2	22	22	44	50	6	3.5 ± 1.6 (1 -11)	5.3 ± 0.8 (1 - 14)
2012	0.2	5	12	17	29	4	1.3 ± 0.3 (1 - 2)	2.3 ± 0.5 (1 - 3)
Females								
2011	0.8	17	11	28	61	8	2.1 ± 0.6 (1 - 5)	5.3 ± 0.7 (1 - 12)
2012	0.2	8	10	18	44	5	1.6 ± 0.4 (1 - 3)	5.0 ± 0.8 (1 - 7)
Total								
2011	1.0	52	55	107	49	9	4.8 ± 1.8 (1 - 11)	5.3 ± 0.6 (1 - 14)
2012	0.4	13	22	35	37	6	2.2 ± 0.4 (1 - 3)	4.1 ± 0.7 (1 - 7)

During 2011 substantially more second year animals were caught than during 2012 (2011, $n = 10$ and 2012, $n = 2$) with second year animals making up 14 % of the population during 2011 and only 5 % during 2012 (Figure 2.9). In particular, no second year females were caught during 2012, whereas eight were caught during 2011. The apparent lack of second year females during 2012 resulted in the reduction of Cohort B's life span (~18 months) compared to Cohort A (~25 months). Cohort A (born 2009) appeared to be the longest living cohort of the three encountered during the study with second year females living until at least October 2011.

2.3.3.2 Effect of rainfall on the timing of mating and juvenile recruitment

During 2011, mating commenced during late August and lasted approximately three weeks. During 2012, potentially due to a smaller population size overall, no females with pouches fully developed, pouch young or lactating were caught to confirm the onset of the breeding season. However, reproductive indicators (pouch development in females and increase in testes width in males, Figure 2.12) were concordant with 2011, and juveniles were captured in January 2013 (within 1 km of our sites), suggesting that the timing of breeding was similar, September/ October (K. Moseby and J. Read, unpublished data).

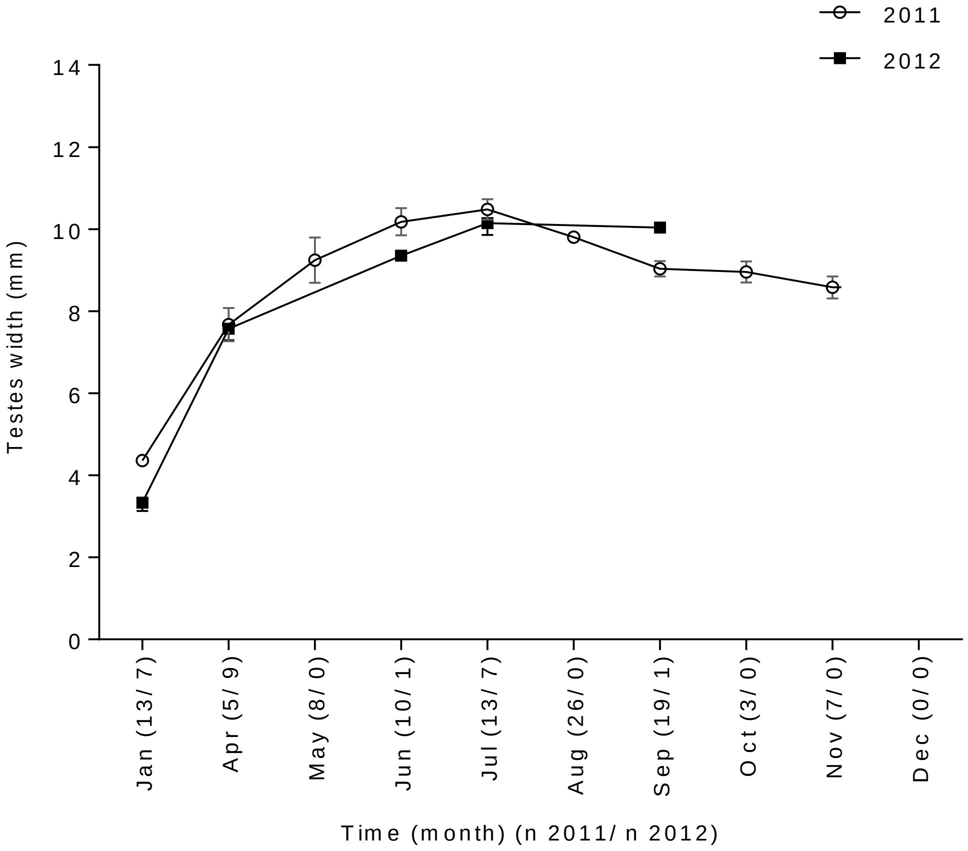


Figure 2.12 Mean testes width (mm) ± S.E. of first year male *S. psammophila* caught each trapping session (month) during 2011 and 2012 during a two year field study west of the Middleback Ranges on Eyre Peninsula, South Australia. Number in brackets represents the sample size for each year (2011/ 2012).

Slightly fewer juveniles were captured in 2012 than 2011 (2011, *n* = 26 and 2012, *n* = 21), however, substantially fewer juveniles were recaptured after January 2012 as sub- adults or adults that same year (58 % in 2011, *n* = 14 *cf* 29 % in 2012, *n* = 6). During 2011 the proportion of male and female juveniles caught was the same (13 of each sex), but during 2012 more females were caught than males (males = 38 %, *n* = 8; females 62 % *n* = 13). However no significant differences in captures based on either sex or year were evident (Kruskal-Wallis rank sum test, χ^2 = 1.849, P = 0.604). A similar trend was observed when the proportions of juveniles recaptured after January as either sub-adults or adults were investigated. Similar proportions of males and females were recaptured as sub-adults or adults during 2011 (males = 54 %, *n* = 7 and females = 58%, *n* = 7), but substantially fewer males were recaptured than females during 2012 (males = 13 %, *n* = 1 and females = 38 %, *n* = 5).

2.4 Discussion

The abundance of *S. psammophila* fluctuated during the study, with significantly lower capture rates observed during the low rainfall year (2012) compared to the high rainfall year (2011). As explained further below, this variation in population size was attributed to a decreased survival rate of predominantly juveniles and second year adults during the low rainfall year. In addition, there appeared to be either a delay in the timing of mating or a reduction in the number of individuals that bred during the low rainfall year. The decline in *S. psammophila* abundance and possible reduction in breeding were most likely in response to a reduction in food resources, mainly invertebrates, caused by low rainfall (e.g., James 1991; Langlands *et al.* 2006).

2.4.1 Influence of rainfall on the abundance of S. psammophila

Arid and semi-arid systems are driven by rainfall events that create primary resource pulses (Holmgren *et al.* 2006; Morton *et al.* 2011). A reduction in rainfall reduces both plant growth and invertebrate populations, while large rainfall events increase plant biomass and invertebrates. Food availability is thought to be a limiting factor in determining the population size of species (Wynne-Edwards 1962; White 1978), with some relevant examples including the semi-arid mouse-opossum (*Thylamys elegans*) in Chile (Lima *et al.* 2002) and rodent species in the Simpson Desert, Australia (Predavec 1994; Dickman *et al.* 1999b). *S. psammophila* is unlikely to be an exception and population size is most likely determined by food availability. Invertebrates are the main food source for *S. psammophila* (Churchill 2001b) and although variability in invertebrate numbers or diversity were not specifically measured in this study, based on other studies rainfall is likely to have influenced the abundance of invertebrates over the two years (James 1991; Langlands *et al.* 2006; Letnic and Dickman 2010).

The timing and total amount of rainfall can be important for stimulating increases in invertebrate abundances. For example, a study in the USA tested two different irrigation treatments (irrigation during autumn and spring or summer) and a control (ambient precipitation) on sagebrush in an arid system, and found that irrigation of plots during autumn and spring produced the greatest abundance and diversity of invertebrates during early summer (Wenninger and Inouye 2008). However, after early summer both irrigation treatments produced more invertebrates than ambient rainfall. The timing of rainfall may also be important in determining if dasyurids, with their relatively fixed life histories, are able to take advantage of the increase in food resources following large rainfall events. Kelly *et al.* (2013) noted that although the common dunnart (*Sminthopsis murina*) responded positively to rainfall, it did not respond to all large rainfall events. The authors speculated that *S. murina* could only benefit from high rainfall if it occurred at a particular time of year, such as before the winter/spring breeding period. In a similar vein, a previous study of a temperate dasyurid, the yellow-footed antechinus (*Antechinus flavipes*), documented a large decline in population size after several years of drought conditions (Lada *et al.* 2013). A reduction in both the recruitment of juveniles and capture rate of second year females was strongly correlated with low rainfall during September (the time of lactation) the previous year. The authors suggested that a reduction in food resources during a period of increased energy requirements for females resulted in a reduced survival rate of females in the following year and also reduced the survival of the offspring (Lada *et al.* 2013). During our study, above average rainfall occurred during autumn 2010, spring 2010 and summer/autumn 2011, which most likely stimulated an increased in invertebrate abundance during early 2011, as it did in the experimental study of Wenninger and Inouye (2008). An increase in food resources at a time when adult females were lactating (spring 2010) and juvenile *S. psammophila* were emerging and dispersing (summer 2011) may have aided in the survival of juveniles during 2011. Conversely low rainfall during 2012 would have reduced food resources and potentially decreased juvenile and second year animal survival. Interestingly, in the present study rainfall was above average during spring 2011 when females were lactating, however very low rainfall occurred during summer 2012 when juveniles were dispersing. The continued below average rainfall during 2012, regardless of conditions during lactation, may have negatively affected the survival of second year animals, as none were captured after April 2012. A study of another dasyurid, the brush-tailed mulgara (*Dasycercus blythi*) also documented fewer second year animals captured during ‘poor’ resource years (low rainfall) than during ‘high’ resource years (high rainfall) (Masters and Dickman 2012). The results of our study may suggest that low rainfall during summer/autumn when juveniles are dispersing and maturing and second year females are recovering from raising young, may strongly influence survival and population size, regardless of the high rainfall (high resources) during lactation.

An alternative or an additional explanation for a reduction in juvenile and second year animal recaptures, is that individuals were travelling further afield in order to find adequate food resources, and so were less likely to be trapped during the low rainfall year. During 2012 we observed an increase in the proportion of transient individuals, particularly males, captured compared to 2011, and a reduction in both the number of residents and transients per site. Fewer food resources in a particular area would result in a reduction in the number of residents that the area could support and individuals may have roamed further afield and/ or expand their 'home ranges' to find adequate resources. Although we do not have data on how far individuals travelled, the increased proportion of transients and the decreased time residents spent at sites during the low rainfall year suggests that individuals were moving around more and possibly travelling further. Males appeared to be more mobile than females, with a greater proportion of male transients observed during 2012 than 2011. This may suggest that male *S. psammophila* move further than females, a trend that has been observed in other dunnart species, such as the little long-tailed dunnart (*Sminthopsis dolichura*) (Friend *et al.* 1997). Given that we observed resident individuals remaining in the area for up to 14 months during the high rainfall year (2011) and seven months during the low rainfall year (2012), this may suggest that animals do establish a semi-stable home range, but may move their home ranges once resources in the area have been depleted. However, the rate of home range movement may not be as high as in other arid species. Read (1984) documented a high proportion of transient individuals and rare recaptures of individuals after 25 weeks (from original capture) in three arid dasyurids, the fat-tailed dunnart (*Sminthopsis crassicaudata*), Giles' planigale (*Planigale gilesi*) and the narrow-nosed planigale (*P. tenuirostris*), and suggested that individuals were continually changing their home ranges (termed 'drifting home range'). Churchill (2001b) documented a female *S. psammophila* moving her home range 400 m to the west between two radio-tracking periods eight months apart, which gives some evidence for limited home range movement in *S. psammophila*. In support of this, studies on other arid mammals have found that during resource poor years individuals move further than usual to find adequate resources, for example, the spinifex hopping mouse (*Notomys alexis*) (Dickman *et al.* 2011) and the sandy inland mouse (*Pseudomys hermannsburgensis*) (Dickman *et al.* 2010) were observed to move greater distances when food was limited. A study on the banner-tailed kangaroo rat (*Dipodomys spectabilis*) in the USA discovered that in addition to an increased dispersal distance, the proportion of long distance dispersers in the population also increased during resource poor years when the population density was low (Waser and Elliott 1991; Waser *et al.* 2006). Overall, we suggest that the low capture rate observed during the low rainfall year was due to a reduced population size and individuals travelling further afield to track resources across the landscape. However, a long-term study comparing changes in *S. psammophila* abundance during multiple high and low rainfall years would be beneficial to confirm the observations of this study.

2.4.2 Influence of rainfall on timing of reproduction

The sequence of events leading up to the breeding season of 2012 is unknown as no animals were caught breeding during 2012, however, juveniles were trapped during late-January the following year (2013) at sites within 1 km of our sites, indicating that at least some of the population bred during 2012 (K. Moseby and J. Read unpublished data). Our results provide evidence for two scenarios that may have occurred during the 2012 breeding season. The first possibility is that a reduction in rainfall may have reduced the number of females that bred during the low rainfall year and with a reduced population size, the chances of catching a breeding female were lowered. A similar scenario was documented in a temperate study of the agile antechinus (*Antechinus agilis*), where a reduction in food resources due to drought conditions reduced the number of female *A. agilis* that bred during the drought year, and also reduced the number of pouch young in each litter (Parrott *et al.* 2007).

The second possibility is that the breeding period was delayed during the low rainfall year. The breeding period of *S. psammophila* appeared relatively fixed (Strategy V) (Lambert *et al.* 2011). However, the extended breeding season of *S. psammophila* may allow for limited flexibility in the timing of mating between years as mating can occur within a two to three month period. Conversely, the smaller mallee ningaui (*Ningaui yvonneae*), which is sympatric with *S. psammophila* at our site and also has a Strategy V life history, appears to be relatively unaffected by rainfall events. Bos and Carthew (2001) found that the majority of females conceived during October each year and the population size remaining relatively constant despite fluctuations in rainfall. In contrast, the arid brush-tailed mulgara (*D. blythi*) (Strategy V) was observed to breed anytime within a three to four month period each year, but during low rainfall years, breeding occurred later than during high rainfall years, possibly due to a delay in the onset of oestrus (Masters and Dickman 2012). A temperate study of *A. agilis* also found that drought conditions negatively affected the breeding of the population and pouch young were placed in the nest two weeks later than usual (Parrott *et al.* 2007). The authors suggested that oestrus, ovulation or the births may have occurred later than usual or that the lactation period was extended during the drought year. A similar delay in either the onset of oestrus or ovulation may have occurred in *S. psammophila,* as changes in testes width and pouch development during August and September 2012 were comparable to the lead up to the 2011 breeding season. However, no animals were caught after September 2012 to confirm if they did breed and a long-term study incorporating multiple high and low rainfall years is needed to determine the influence rainfall has on the breeding of *S. psammophila*.

The mating period within a year appeared to be synchronised between females, with females giving birth within approximately two weeks of each other during 2011. Although we did not capture any females breeding during 2012, both the captive study (Lambert *et al.* 2011) and field observations from other *Sminthopsis* species (e.g., Morton 1978b; Dickman *et al.* 2001) indicate that our assumption of a synchronised mating period within each year for *S. psammophila* is appropriate. A synchronised mating period would maximise the chance of males finding females and potentially provide females with a greater selection of males to choose from, either pre and/ or post copulation (sperm competition). Sperm competition has been reported in other dasyurid species where sperm can be stored in the female for several weeks (e.g., brown antechinus, *Antechinus stuartii*, Taggart and Temple-Smith 1991), with this long storage period presumably facilitating sperm competition. However, the length of sperm storage in *Sminthopsis* species is relatively short; for example, sperm storage of three days was reported in the stripe-faced dunnart (*S. macroura*) and fat-tailed dunnart (*S. crassicaudata*) (Selwood 1987). *S. psammophila* appears to have a similar sperm storage time (~ three days) (Lambert *et al.* 2011), which suggests that sperm competition may be limited in this and other *Sminthopsis* species (Taggart *et al.* 1997). If *S. psammophila* has a promiscuous mating system like other dasyurid species (e.g., agile antechinus, *A. agilis*; Kraaijeveld-Smit *et al.* 2002) a synchronised mating period may aid in achieving multiple paternity within litters, which may increase genetic diversity and survival of the young. Synchronisation also allows pregnancy/lactation and juvenile dispersal to occur during spring and summer respectively, when invertebrate numbers are increasing (Lee *et al.* 1982). This strategy presumably increases both the survival of adult females and pouch young, as well as dispersing juveniles during summer. Further study into the reproductive biology of *S. psammophila* is needed to determine if synchronisation of the breeding period facilitates sperm storage/ competition or multiple paternity of litters in this species.

2.4.3 Conservation concerns

Climate change may pose one of the greatest threats to the long-term persistence of *S. psammophila*. Based on current predictions, climate change will result in increased temperatures, lower rainfall and greater variability of climatic conditions worldwide (IPCC 2013). Climatic data from the Simpson Desert have shown that the average temperature and rainfall variability have increased over the past 100 years (Greenville *et al.* 2012). Greenville *et al.* (2012) suggested that an increase in the frequency of large rainfall events in arid regions of Australia will lead to an increase in plant biomass and more frequent irruptions of small mammal populations, particularly rodents. As this study has shown, *S. psammophila* populations may also increase during high rainfall years. It should be noted that during high rainfall events an increase in prey species, such as rodents and small dasyurids, can lead to an increase in both native and introduced (cats and foxes) predators (Letnic *et al.* 2005). Increased predator numbers can be particularly problematic when conditions become dry again and prey species populations ‘crash’, the increased predator population may cause over-hunting of the prey species and drive the populations down to unsustainably low levels. The scope of this study did not allow for the examination of the impact of predation on the target species. However further study on the degree to which *S. psammophila* is affected by feral predators, with a particular focus on high and low rainfall years, would be beneficial. *S. psammophila* may be able to tolerate low levels of predation, but high levels could have negative consequences for the survival of the local population and should not be over-looked in management plans. Populations reduced by high levels of predation will then be at greater risk from stochastic events, genetic problems (e.g., inbreeding) and local extinction (Lande 1988).

The relatively high levels of mobility apparent in both male and female *S. psammophila* indicate that large areas of suitable habitat will need to be maintained to ensure that individuals can find adequate food resources during low rainfall years. Habitat preferences of *S. psammophila* will need to be determined and areas of critical habitat identified and protected. In order to determine area requirements for the management of *S. psammophila*, the level of connectivity (gene flow) within the study area also needs to be investigated. Further research into the dispersal patterns of *S. psammophila* will also provide insights into how the endangered dasyurid marsupial maintains genetic diversity within the population.

2.5 Conclusion

This study has shown that in a semi-arid system *S. psammophila* responds quickly and negatively to low rainfall. During the low rainfall year we observed a significant reduction in population size, which was attributed to a decline in the survival of juveniles and second year animals, presumably caused by a reduction in food resources (invertebrates). In addition, the population appeared to become more mobile during the low rainfall year, which may have been due to individuals tracking food resources across the landscape. The lower rainfall may have also influenced the breeding of *S. psammophila* by delaying the onset of the breeding period and/ or reducing the number of animals that bred. Further long-term study on the population dynamics of *S. psammophila* and fluctuations in its food resource (invertebrates) during multiple high and low rainfall years is needed to confirm the findings of this study. Management strategies to consider for the long-term persistence of *S. psammophila* include controlling predator numbers; especially after high rainfall years and protecting large areas of continuous habitat. To aid in management decisions, future research should focus on determining the habitat preferences and investigating dispersal patterns of *S. psammophila*.

CHAPTER 3: Development of 16 microsatellite loci for the endangered sandhill dunnart (*Sminthopsis psammophila)*

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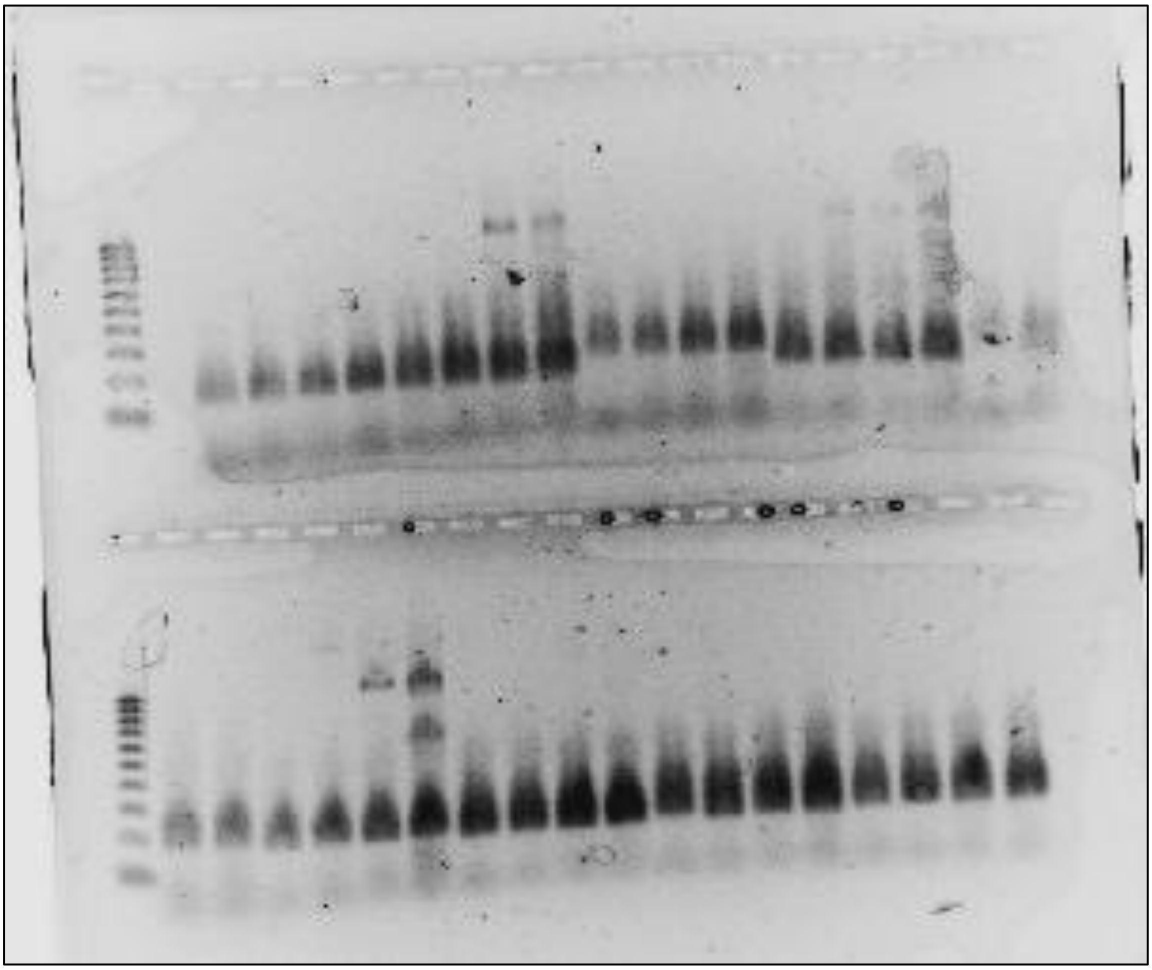


Initial screening of microsatellite loci performed on an agarose gel.

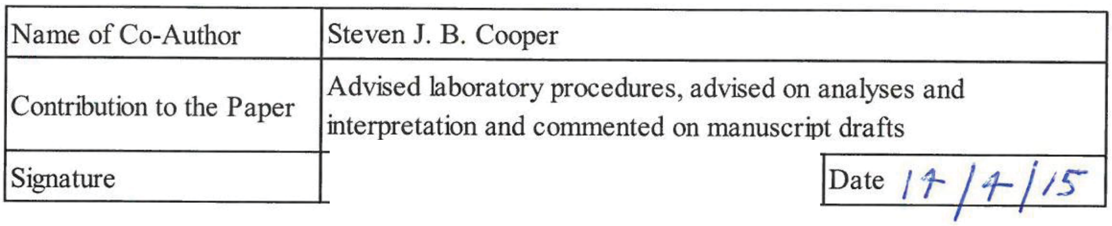
Statement of Authorship

Title of paper	Development of 16 microsatellite loci for the endangered sandhill dunnart (*Sminthopsis psammophila*)							
Publication status	☑	Published	☐	Accepted for publication	☐	Submitted for publication	☐	Publication style
Publication details	McLean, AL, Cooper, SJB, Lancaster, ML, Carthew, SM (2014) Development of 16 microsatellite loci for the endangered sandhill dunnart (*Sminthopsis psammophila*). *Conservation Genetics Resources* **6**, 323-326.							

<u>Author contributions</u>

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate’s thesis.

Name of Principle author	Amanda L. McLean	
Contribution to the Paper	Collected tissue samples, performed laboratory procedures, analyses, interpretation of analyses and wrote manuscript.	
Signature		Date



Name of Co-Author	Steven J. B. Cooper	
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Signature		Date 17/4/15

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Development of 16 microsatellite loci for the endangered sandhill dunnart
(*Sminthopsis psammophila*).
Conservation Genetics Resources, v. 6 (2), pp. 323-326

CHAPTER 4: Small marsupial, big dispersal? Genetic structure of a semi-arid dasyurid

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Sandhill dunnart (*Sminthopsis psammophila*) amongst *Triodia*. Photo A. McLean

Statement of Authorship

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Author contributions

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate’s thesis.

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Contribution to the Paper	Advised laboratory procedures, advised on analyses and interpretation and commented on manuscript drafts	
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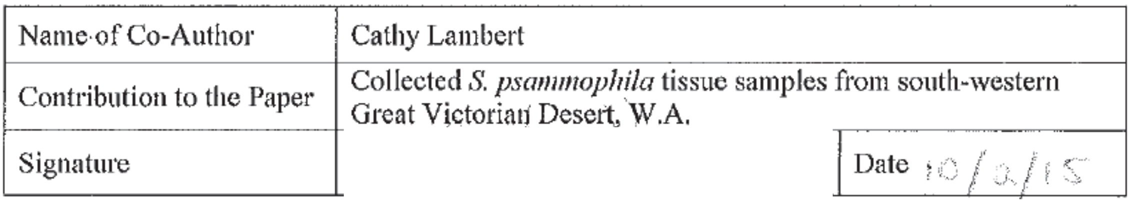

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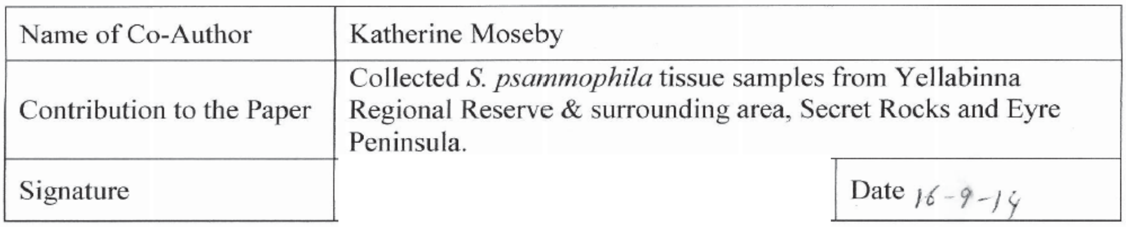

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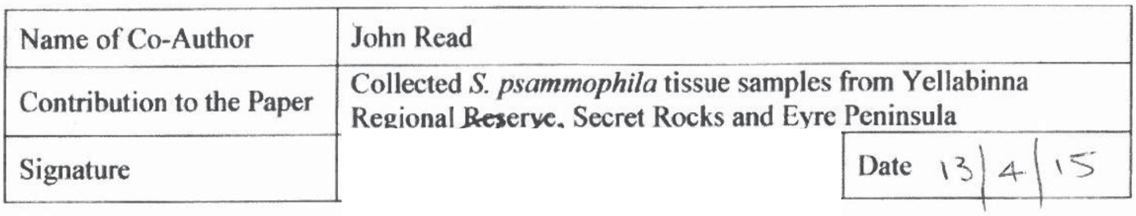
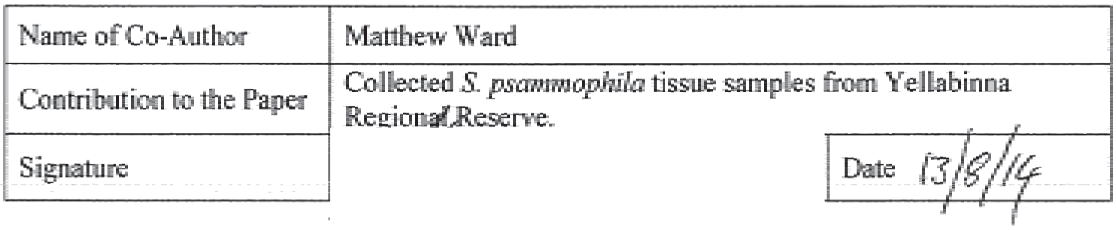
Signature		Date 16-9-14



Name of Co-Author	John Read	
Contribution to the Paper	Collected *S. psammophila* tissue samples from Yellabinna Regional Reserve, Secret Rocks and Eyre Peninsula	
Signature		Date 13/4/15



Name of Co-Author	Matthew Ward	
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Signature		Date 14/4/15

Abstract

Arid and semi-arid regions are known for having harsh climates with low rainfall and high temperatures. The unpredictable nature of rainfall in the Australian arid and semi-arid zones results in a heterogeneous distribution of resources in both time and space. The mammal species that reside in these regions are uniquely adapted to these climatic conditions, however little is known of broad and fine-scale movement patterns of arid and semi-arid marsupials. This study used molecular methods to investigate 1) broad-scale genetic structure and 2) fine-scale movement patterns of a semi-arid and arid marsupial, the sandhill dunnart (*Sminthopsis psammophila*). Analyses of mitochondrial *CR* sequences and microsatellite loci indicated that the three known core populations of *S. psammophila* were genetically differentiated, but did not show evidence of long-term population isolation. At the fine-scale, no significant genetic structure or sex-biased dispersal was detected within the study site of 24,000 ha. These findings suggest that both sexes are highly mobile which allows individuals to locate resource patches when they become available. This study is the first genetic study on *S. psammophila* and one of only a few fine-scale genetic studies on a semi-arid mammal. The results of the study contribute to our knowledge of fine-scale movement patterns of *S. psammophila* and other arid and semi-arid marsupials.

Keywords: *Sminthopsis psammophila* – Semi-arid – Marsupial – Microsatellites – Mitochondrial sequence – Endangered species – Dasyuridae – Movement patterns – Dispersal

4.1 Introduction

Arid and semi-arid zones occur globally and are typically areas of low annual rainfall and high temperatures. The extensive arid regions of Australia formed over millions of years and underwent many glacial and interglacial cycles during the Pleistocene (Byrne *et al.* 2008). The last glacial maximum (LGM) (21000 ± 2000 years) was a particularly dry period and has influenced the arid zones of today. The Australian arid zone now occupies the majority (70 %) of the continent and is characterised by unpredictable rainfall (100 mm to 250 mm per year), with moderate seasonality and poor soil quality (Stafford Smith and Morton 1990; Brown *et al.* 2008; Byrne *et al.* 2008). The unpredictable nature of rainfall makes the Australian arid zone significantly different to its northern hemisphere counterparts in North America and the Mediterranean, where the majority of literature on arid systems has come from to date (Morton *et al.* 2011).

The Australian arid and semi-arid zones are home to a range of species that have evolved unique adaptations to cope with the extreme temperatures and limited water of these environments. Small mammals are strongly dependent on localised resource pulses (Dickman *et al.* 1999a; Dickman *et al.* 1999b; Letnic *et al.* 2005) that vary both temporally and spatially due to irregular rainfall events that create these primary resources (Holmgren *et al.* 2006; Morton *et al.* 2011). To utilise these changes in resources, individuals must be able to move towards resource-rich areas and/or have a flexible life history that allows for large increases in population size '*in situ*' during resource rich years, to guard against local extinction during resource poor years. Rodent species are well known for their 'boom and bust' life histories (Dickman *et al.* 1999b). However, many successful arid marsupials have comparatively fixed and predictable life histories (Lee *et al.* 1982). Previous mark-recapture studies suggest that arid marsupials may be capable of moving long distances to exploit resource pulses (Dickman *et al.* 1995; Haythornthwaite and Dickman 2006b), yet relatively little is known about fine-scale movement patterns of many marsupials and how they persist in these environments.

Molecular methods are valuable tools for exploring evolutionary processes that have shaped the genetic structure within species (e.g., Potter *et al.* 2012) and for investigating fine-scale movement patterns within populations (e.g., Olivares *et al.* 2013). Genetic methods can often reveal cryptic genetic structure and processes that would go unnoticed using traditional techniques (e.g., capture-mark-recapture); for example, in a species of banner-tailed kangaroo rat (*Dipodomys spectabilis*) assumed to be highly philopatric, long distance dispersal events were detected using genetic methods (Waser *et al.* 2006). However, relatively few genetic studies have been conducted on arid mammal species and most studies have focused on broad-scale phylogenetic patterns within species (e.g., Faleh *et al.* 2012; Mantooth *et al.* 2013) rather than investigating fine-scale population processes (e.g., Meyer *et al.* 2009; Marin *et al.* 2013).

This study used a combination of mitochondrial DNA sequence data and microsatellite loci data collected on a semi-arid/arid marsupial, the sandhill dunnart (*Sminthopsis psammophila*). *S. psammophila* is a small (25 – 55 grams) carnivorous marsupial found in the semi-arid and arid regions of Australia (Menkhorst and Knight 2004). Historically, the range of *S. psammophila* appears to have extended from the south-west of the Great Victoria Desert, Western Australia across to the Eyre Peninsula, South Australia and up to Lake Amadeus in the Northern Territory (Spencer 1896). However, the species has not been captured in the Northern Territory since the late 1800s and is now known from only three disjunct core populations. Given the elusive nature of *S. psammophila*, it is possible that unidentified populations remain in between the known core populations. However, due to a perceived range reduction of ~50% *S. psammophila* has been classified as Endangered (IUCN 2013).

The aims of this study were to investigate i) broad-scale population structure and ii) fine-scale population structure and movement patterns within a semi-arid population of the species. We predicted that although the three known core populations of *S. psammophila* may have been connected historically, given the large distances between the populations (500+ km), it is likely that the core regions are now genetically differentiated. We also predicted that individuals will move relatively long distances to utilise resource pulses that are created by irregular rainfall events. If individuals are highly mobile (Chapter 2) and move away from their natal areas, these movement patterns are likely to result in high levels of gene flow within the study area.

4.2 Methods

4.2.1 Study sites

Tissue samples were collected from the three known core populations across the range of *S. psammophila*: Eyre Peninsula, South Australia (EP), (33°12.938′S, 137°3.002′E); south-eastern Great Victoria Desert including Yellabinna Regional Reserve and surrounding area (Y), South Australia (30°49.905’S, 132°25.838’E); and south-western Great Victoria Desert (SW-GVD) including Queen Victoria Springs Nature Reserve and northern Pulmridge Lakes Nature Reserve, Western Australia (29°58.827'S, 124°00.870'E) (). All three locations are characterised by sand dunes with the vegetation dominated by mallee (e.g., *Eucalytpus oleosa* and *E. socialis*) and an understory of *Triodia* species and other shrubs (Churchill 2001b). EP is situated approximately 508 km from Y and is characterised as a semi-arid climate with an average annual rainfall of approximately 250 mm (Schwerdtfeger 1985). The majority of rainfall occurs during winter, however, up to 20% of the year’s total rainfall can occur during the summer. Mean monthly maximum temperatures range from 16 °C to 31 °C (Bureau of Meteorology 2014a, 2014b) during winter and summer respectively. Y and SW-GVD are situated approximately 815 km apart in the Great Victoria Desert (GVD). Y is a large reserve covering 2,522,700 ha and the northern part of the reserve (where tissue samples were collected) has an arid climate while the southern part has a semi-arid climate (Department of Environment and Heritage 1999). Rainfall is usually low and unpredictable during the year and the average annual rainfall ranges between 230 mm in the upper northwest to 172 mm in the upper northeast of the reserve (Department of Environment and Heritage 1999). Mean monthly maximum temperatures range from 19 °C during winter to 33 °C in summer. Queen Victoria Springs Nature Reserve covers approximately 270,000 ha, although only 54,000 ha is suitable *S. psammophila* habitat (Gaikhorst and Lambert 2014), and is an arid climate with an unpredictable and unseasonal mean annual rainfall of approximately 150 mm (Department of Conservation and Land Management 1994). Mean maximum temperature ranges from 18.6 °C to 33.7 °C in winter and summer respectively (Bureau of Meteorology 2014b).

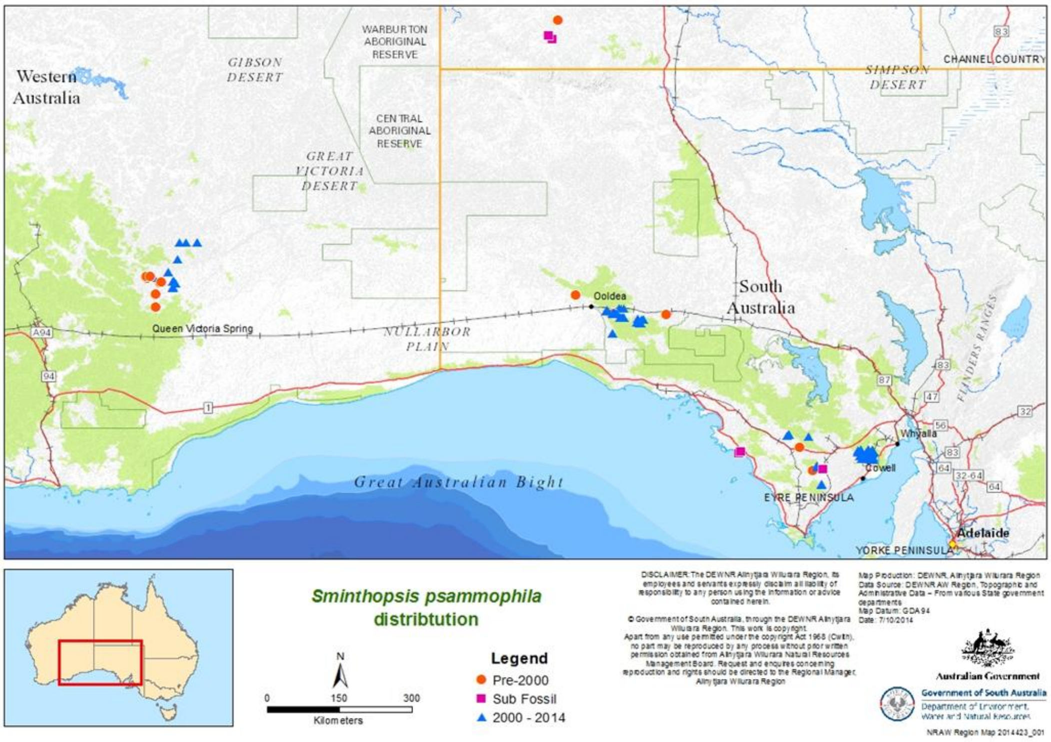

Figure 4.1 Historical (orange and pink) and current distribution (blue) of *S. psammophila* showing the three core populations sampled during this study: Eyre Peninsula, South Australia, South-eastern Great Victoria Desert, Yellabinna Regional Reserve, South Australia, and south-western Great Victoria Desert, Western Australia. *Source*: Department of Environment Water and Natural Resources (in review).

4.2.2 Sample collection

A total of 188 tissue samples (ear biopsies and tail tips) were collected using a combination of deep pitfall (600 mm) and Elliott traps (Type A; 30 x 10 x 9 cm) between 1987 and 2012. Samples used in the broad-scale analyses were collected during surveys in 1997 and 2005 at SW-GVD; 1987, 2008, 2011 and 2012 at Y; and 2000, 2010, 2011 and 2012 at EP (Table 4.1). The largest known *S. psammophila* population on the EP is found west of the Middleback Ranges in upper Eyre Peninsula (hereafter referred to as Middleback) and this population was used for the fine-scale analyses. A total of 107 samples were collected within Middleback during 23,529 trap nights (Table 4.2). Preliminary trapping occurred here during October and November 2010 prior to more intensive trapping between January 2011 and December 2012. During the more intensive sampling, all sites were trapped seasonally (summer, autumn, winter, spring) in both years, with six of these trapped monthly (excluding February and December 2011 and May 2012) to investigate the life history of *S. psammophila* in the wild (Chapter 2). A total of 11 permanent trap sites were used, consisting of 36 traps per site (24 Elliott traps and 12 pitfall traps) in four parallel transects covering an area of approximately 16,000 m^2. Eight of the 11 sites were situated in Ironstone Hill Conservation Park and three sites were situated on surrounding private property; one on Pine Hill and two on Cooyerdoo Station. All sites were at least 1.5 km apart and covered an area of approximately 24,000 ha (Figure 4.2). On capture all *S. psammophila* were measured, weighed, ear notched for genetic analysis, micro-chipped for individual identification and assessed for reproductive condition (for more information on trapping protocol refer to Chapter 2). Tissue samples were immediately placed into vials containing 100 % ethanol.

Table 4.1 Number and distribution of *S. psammophila* tissue samples collected for broad spatial scale genetic analyses across the distribution of the species. Total number of samples collected (Total *n*), number of samples sequenced for mtDNA control region (*n* mtDNA seq.) and number of samples genotyped at 16 microsatellite loci (*n* microsat. loci). Location refers to the three core populations of *S. psammophila*, EP = Eyre Peninsula, South Australia; Y = Yellabinna Regional Reserve, South Australia; SW-GVD = South-western Great Victoria Desert, Western Australia. Latitude and longitude coordinates and date of collection are provided for each site within the three locations.

Location	Latitude	Longitude	Site	Year	Total *n*	*n* mtDNA seq.	*n* mircosat. Loci
EP	33° 10.116' S	137° 05.870' E	Ironstone Hill CP	2000	7	7	
				2010	3	2	3
				2011	60	5	60
				2012	25	1	25
	33° 19.705' S	137° 05.249' E	Pine Hill	2000	1	1	
				2008	1	1	
				2011	4	1	4
				2012	1		1
	33° 08.167' S	137° 01.168' E	Cooyerdoo station	2011	13		13
				2012	12	2	12
	33° 17.786' S	136° 54.790' E	Secret Rocks	2011	6	2	6
	33° 48.583' S	136° 08.727' E	Hinks CP	2005	2	2	
	32° 57.394' S	135° 47.639' E	Pinkawillinie CP	2012	1	1	
EP total					**136**	**25**	**124**
Y	30° 35.150' S	132° 14.517' E	Immara siding	1987	3	3	
	30° 14.517' S	131° 32.317' E	Maralinga	1987	1	1	
	30° 36.933' S	133° 13.950' E	Mount Christie Siding	1987	1	1	
	30° 35.332' S	132° 18.111' E	SHD001	2008	1		1
				2012	3		3
	30° 35.277' S	132° 16.994' E	SHD002	2008	2		2
				2011	3		3
				2012	3	1	3
	30° 35.091' S	132° 15.823' E	SHD003	2008	4		4
				2011	2	1	2
	30° 35.012' S	132° 14.598' E	SHD004	2008	4		4
				2011	8	1	8
				2012	5		5
	30° 31.855' S	132° 06.938' E	SHD005	2012	1	1	1
	30° 32.144' S	132° 06.739' E	SHD006	2012	1	1	1
	30° 35.373' S	132° 18.400' E	SHD007	2012	1		1
	30° 49.656' S	132° 30.792' E	YRR	2012	1	1	1
	30° 49.656' S	132° 27.586' E	YRR	2012	1	1	1
Y total					**45**	**12**	**40**
SW-GVD	29°58.827' S	124°00.870' E		1997	4	4	4
	29°58.827' S	124°00.870' E		2005	3	3	3
SW-GVD total					**7**	**7**	**7**

Table 4.2 Number of *S. psammophila* tissue samples collected from the 11 sites west of the Middleback Ranges, South Australia, for the fine-scale genetic analyses. Sites 1 and 2 were situated in Cooyerdoo Station, Site 8 was situated in Pine Hill and the remaining sites were situated in Ironstone Hill Conservation Park. Latitude and longitude coordinates, number of trap nights and year samples were collected are provided for each site. NA = sites not trapped during the 2010 preliminary trapping session.

Site	Latitude	Longitude	Total trap nights	2010	2011	2012	Total
1	33° 08.167' S	137° 01.168' E	1188	NA	5	7	12
2	33° 09.105' S	137° 01.141'E	1104	NA	4	4	8
3	33° 12.582' S	137° 04.644' E	3000	0	10	5	15
4	33° 13.347' S	137° 05.121' E	1236	NA	2	0	2
5	33° 13.765' S	137° 04.242' E	2844	0	9	1	10
6	33° 12.178' S	137° 03.021' E	3315	0	9	5	14
7	33° 19.477' S	137° 04.132' E	978	0	0	5	5
8	33° 19.705' S	137° 05.249' E	1062	NA	4	0	4
9	33° 09.817' S	137° 04.749' E	3072	2	17	3	22
10	33° 10.116' S	137° 05.870' E	2844	0	3	1	4
11	33° 10.615' S	137° 05.136' E	2886	1	6	4	11
Total			23529	3	69	35	107

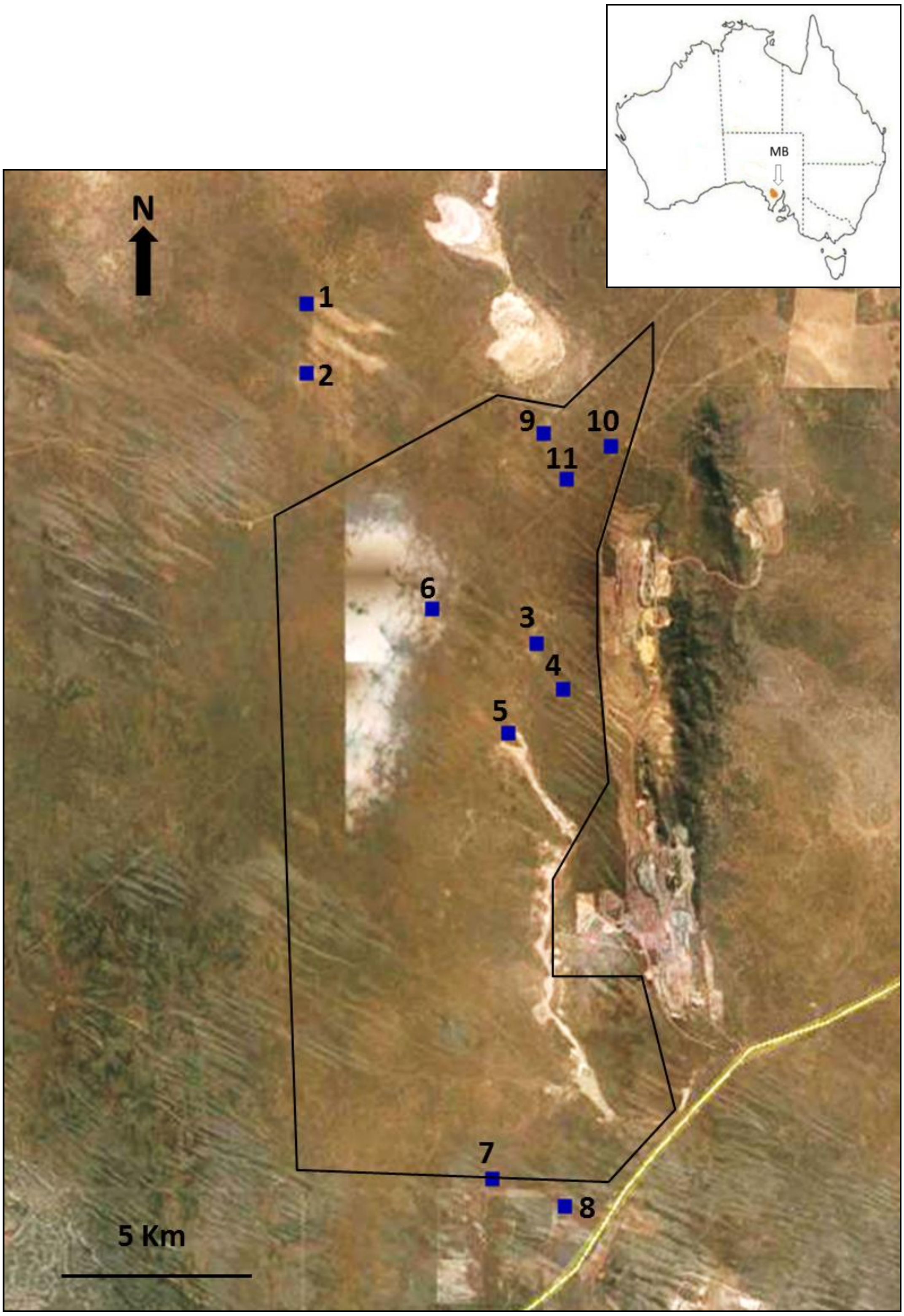

Figure 4.2 Distribution of the 11 *S. psammophila* study sites west of the Middleback Ranges on Eyre Peninsula, South Australia used for fine-scale population genetic analyses of *S. psammophila*. Black line represents Ironstone Hill Conservation Park. *Source*: "Middleback Ranges". 33°09′S and 137°07′E. **Google Earth**. April 20th, 2011. August 3rd, 2011.

4.2.3 DNA extraction

S. psammophila genomic DNA was extracted from ear tissue using the Gentra Puregene extraction kit (Qiagen) and procedures specified by the manufacturer.

4.2.4 Mitochondrial sequencing

A total of 44 samples were selected from across the geographical distribution of *S. psammophila* (EP: *n* = 25; Y: *n* = 12; SW-GVD: *n* = 7) (Table 4.1) and sequenced for 306 bp of the mitochondrial control region (*CR*) using primers M20 (5′-CCTCACCATC AGCACCCAAGC-3′) and M119 (5′-TGCTGATCTCTCG TGAGTTG-3′) (Blacket *et al.* 1999). These primers and the *CR* locus have previously been used in phylogenetic studies of the *Sminthopsis* genus and population genetic studies of several *Sminthopsis* species, where it shows high levels of genetic variation (Blacket *et al.* 1999; Cooper *et al.* 2000; Blacket *et al.* 2001; Kemper *et al.* 2011; Pavey *et al.* 2012).

Each initial PCR amplification of 25 µl contained 10 ng DNA, 5µM forward (light strand) primer (M20), 5 µM reverse (heavy strand) primer (M119), 0.15 U Immolase DNA polymerase (Bioline, Luckenwalde, Germany) and 1 X MRT (multiplex-ready-technology) buffer. PCR amplifications consisted of an initial denaturing phase of 95 °C for 10 min followed by 34 cycles of 94 °C for 45 s, 55 °C for 45 s and a final extension period of 72 °C for 10 min. PCR products were cleaned using a Millipore vacuum plate (Multi Screen PCR µ96 Plate) and manifold (Multi ScreenHTS Vacuum Manifold) and were diluted prior to the sequencing reaction. Each sample was sequenced for both the forward and reverse primer using the BigDye® Terminator v 3.1 Cycle Sequencing Kit (Applied Biosystems) and following standard protocols. The sequencing program was as follows: 24 repeats of 30 s at 96 °C, 15 s at 50 °C, 4 min at 60 °C followed by one cycle of 2 min at 25 °C. Products were cleaned using a Millipore vacuum plate (Multi Screen SEQ µ96 Plate) and manifold (Multi ScreenHTS Vacuum Manifold) prior to sequencing via capillary separation on an ABI 3730 DNA Analyser (Applied Biosystems) at the Australian Genome Research Facility (AGRF). Sequences were edited using Geneious v 6.1.6 (Biomatters) and aligned in MEGA v 5.2 using ClustalW (Tamura *et al.* 2011).

4.2.5 Microsatellite genotyping

A total of 172 samples from across the species range (Middleback, *n* = 124, Y, *n* = 40 and SW-GVD, *n* = 7) (Table 4.1) were genotyped using a suite of 19 loci; 16 developed for *S. psammophila* (Chapter 3) and three isolated from the Julia Creek dunnart (*Sminthopsis douglasi*) (Spencer *et al.* 2003) and optimised for *S. psammophila* (Chapter 3). The five samples collected during 1987 were excluded in the analyses due to the possibility that there had been temporal changes in allele frequencies. In addition, the two samples from Hinks CP and the single sample from Pinkawillinie CP were excluded because of the small number of samples from these locations. PCR-amplifications were performed as per Chapter 3. Alleles were scored using GeneMapper® v 3.7 (Applied Biosystems) and 10 % of samples were repeated to assess errors in scoring.

4.2.6 Genetic diversity

4.2.6.1 Mitochondrial sequence

DNASP v 5.1 (Labrado and Rozas 2009) was used to determine the number of polymorphic sites and haplotype diversity (*h*) of the *CR* data. The number and distribution of haplotypes and nucleotide diversity (π) were determined using Arlequin v 3.5.1.2 (Excoffier and Lischer 2010).

4.2.6.2 Microsatellite loci

Prior to further analysis microsatellite loci were checked for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). Scoring errors and presence of null alleles were investigated using MICRO-CHECKER v 2.2.3 (Van Ossyerhout *et al.* 2004). Significance values were adjusted using sequential Bonferroni corrections for multiple comparisons (Rice 1989).

Temporal changes in allele frequencies can occur when samples are collected from the same location over several years and can cause problems if samples with different allele frequencies are pooled (Waples 1989; Balloux and Lugon-Moulin 2002). An exact G-test with significance determined using Fisher's method in Genepop v 4.2 (Raymond and Rousset 1995) was used to check if samples collected from the same site over a two and a half year period within Middleback differed significantly in allele frequency (Goudet *et al.* 1996; Lugon-Moulin *et al.* 1999). Samples were separated into site and collection year;

either 2011 or 2012 for the exact G-test (only three samples from three different sites were collected during 2010 so these were excluded due to low sample size). No significant ($P > 0.05$) temporal differences in allele frequencies were detected at any site within Middleback; therefore, samples were pooled from all years for further analyses.

Genetic diversity between core populations and at each sampling site within Middleback was estimated by calculating observed (H_O) and expected (H_E) heterozygosity and allelic diversity (*AD*; average number of alleles per locus) in Arlequin v 3.5.1.2 (Excoffier and Lischer 2010). Allelic richness (A_R), which corrects for sample size, and the inbreeding coefficient (F_{IS}) were calculated using the program FSTAT (Goudet 1995). Significant differences in H_O, H_E, A_R and F_{IS} between sampling locations were tested using a Kruskal-Wallis rank sum test with a post-hoc pairwise Wilcoxon rank sum test (as data were non-normally distributed) in the statistical program R (R Core Team 2013). Differences in allelic diversity were not compared between sampling locations as this parameter is strongly influenced by sample size.

4.2.7 Genetic structure

4.2.7.1 Mitochondrial structure within S. psammophila

An analysis of molecular variance (AMOVA) performed in Arlequin v 3.5.1.2 (Excoffier and Lischer 2010) was used to investigate genetic variation within and between the three core populations. Genetic differentiation between the populations was investigated using pairwise mitochondrial differentiation (Φ_{ST}) and pairwise *F*-statistics (Nei and Li 1979) performed in Arlequin v 3.5.1.2. A Mantel test in the program IBDWS was used to investigate isolation by distance between the populations (Jensen *et al.* 2005). Default parameters of 1000 randomizations and genetic distance (Φ_{ST}) against geographical distance were used. Phylogenetic reconstruction was initially carried out using a neighbour-joining (NJ) analysis of a matrix of pairwise p-distances among taxa, using MEGA (Tamura *et al.* 2011). A related taxon to *S. psammophila*, the grey-bellied dunnart (*Sminthopsis griseoventer*), was used as the outgroup for the analysis. In addition to the phylogenetic tree, a haplotype network was derived using the program TCS (Clement *et al.* 2000).

4.2.7.2 Population structure of S. psammophila based on microsatellite loci

Population differentiation across the species' range and Middleback was investigated using pairwise F_{ST} in Arlequin v 3.5.1.2 (Excoffier and Lischer 2010) and pairwise Jost's D_{est} (Jost 2008) using the 'DEMEtics' package (Gerlach *et al.* 2010) in the statistical program R (R Core Team 2013). Jost's D_{est} was used in conjunction with $F_{ST,}$ as F_{ST} may underestimate population differentiation due to the high mutation rates of microsatellites, especially when migration is low (Balloux and Lugon-Moulin 2002).

The programs STRUCTURE v 2.3.3 (Pritchard *et al.* 2000) and TESS v 3.1 (Chen *et al.* 2007) were used to estimate the number of genetic clusters across the species' range and within Middleback. STRUCTURE uses a Bayesian assignment method to group individuals into genetically similar clusters without any prior knowledge of the geographical origin of the sample (Pritchard *et al.* 2000). Conversely, TESS uses a combination of genotypic and spatial (geographical location) data to determine if differences in genotypic structure are influenced by the geographical location of individuals. To ensure that the number of genetic clusters was not underestimated, each sampling location was assumed to be a potential genetic cluster, therefore the maximum number (K) of genetic clusters was set at 16, with 10 iterations of each K value. The analyses were re-run with samples from Middleback only to investigate fine-scale genetic structure that may have been overwhelmed by strong structure within the species. STRUCTURE simulations were run with the following parameters; a burn-in period and MCMC repeats of 200,000 each, mixed ancestry assumed between sampling sites and correlated allele frequencies. The number of genetic clusters was determined using the ΔK approach (Evanno *et al.* 2005). TESS simulations were run using 10,000 sweeps and 5000 burn-in sweeps, the level of spatial influence was set to ‘admixture’ and the admixture model chosen was the CAR (conditional autoregression) model. The number of genetic clusters was determined by plotting K against the averaged DIC value over the ten iterations for each K. The final value of K was chosen as the value at which the DIC curve sharply decreased (lowest DIC), as per the TESS manual.

4.2.7.3 Isolation by distance within Middleback

The distance between the furthest sites sampled in Middleback was 22 km and since the study species is a small mammal with unknown dispersal capabilities, isolation by distance was examined for each pair of sites using a Mantel test in the program IBDWS (Jensen *et al.* 2005). Site 4 was excluded from the analysis due to a low sample size (*n* = 2). All individuals were initially analysed together and then males and females were analysed separately. Default parameters of 1000 randomizations and genetic distance (F_{ST}) against geographical distance were used.

Spatial autocorrelation in GenAlEx v 6.5 (Peakall and Smouse 2006) was also used to investigate genetic structure within Middleback as per Smouse and Peakall (1999). Variable distance classes of 1 km (within sites), 3 km, 8 km, 12 km and 22 km were used as these distances represented the major distance classes between the sampling sites (Figure 4.3). The nonparametric heterogeneity test of Smouse *et al.* (2008) was used to test the null hypothesis that there was no significant spatial structure across the spatial correlogram graph. An Omega (ω) value and P-value was produced, with the null hypothesis rejected at $P < 0.01$ as per Banks and Peakall (2012). The 95 % upper and lower confidence intervals around the null hypothesis were determined by 999 permutations and the upper and lower error bars around the *r* value were determined by 999 bootstraps.

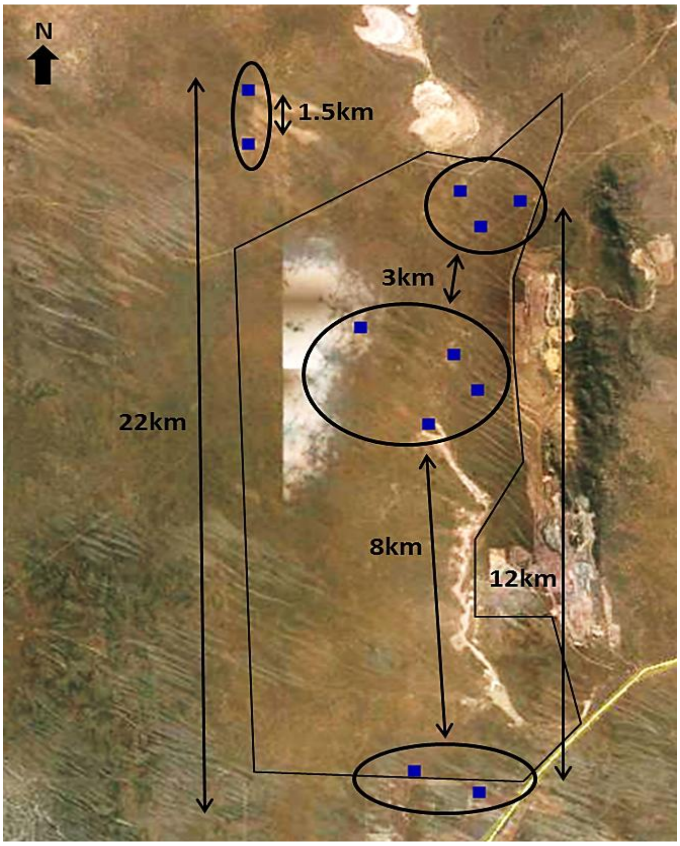

Figure 4.3 Distribution of the 11 *S. psammophila* study sites in the Middleback Ranges region on Eyre Peninsula, South Australia showing the major distance classes between the sites used for the spatial autocorrelation analyses. Black line represents Ironstone Hill Conservation Park. *Source*: “Middleback Ranges”. 33°09′S and 137°07′E. **Google Earth**. April 20th, 2011. August 3rd, 2011.

4.2.8 Relatedness & sex biased dispersal

Dispersal patterns are important for understanding how genetic diversity is maintained in a population. Sex-biased dispersal can influence the fine-scale genetic structure observed within males and females and can provide insight into the social structure and inbreeding avoidance strategies of the species. Sex-biased dispersal was investigated by comparing spatial autocorrelation results for each sex as per Banks and Peakall (2012). Only post-dispersal males and females were used, as pre-dispersal juveniles can distort the signal of sex-biased dispersal (Balloux and Lugon-Moulin 2002). Initially, adults caught during 2011 and 2012 were analysed separately to ensure relatedness between parents and any offspring did not bias the results. Analyses were then re-run with adults from both years pooled. A squared paired-sample t-test statistic (T2) for each distance class was used to test the null hypothesis that both sexes were homogeneous at that particular distance class. The correlograms for each sex were then compared using the T2 statistics and P-values from the previous tests. The null hypothesis was rejected when $P < 0.01$ as per Banks and Peakall (2012).

Sex-biased dispersal was further explored by comparing genetic relatedness within adult males and females as sex-biased dispersal should result in a higher relatedness value for the philopatric sex (e.g., Banks *et al.* 2002; Coulon *et al.* 2006). Pairwise relatedness estimates (*Relatedness*) were calculated as per Queller and Goodnight (1989) in GenAlEx v 6.5 for adult males and females at each site separately. To test the null hypothesis that the mean relatedness value for individuals caught within each site was not statistically different to the mean relatedness value expected by chance (i.e. unrelated individuals), upper and lower 95% confidence intervals around the *Relatedness* values were produced based on 999 permutations and error bars around the mean relatedness value were produced using 999 bootstraps. All males and females from across all sites were pooled and the mean pairwise relatedness value for males and females was calculated in KINGROUP v 2 (Konovalov *et al.* 2004). The difference in relatedness between the sexes was tested using a Wilcoxon Rank Sum test in the statistical program R (R Core Team 2013).

4.3 Results

4.3.1 Microsatellite loci testing

A final panel of 16 polymorphic loci were retained after testing for deviations from HWE, LD and null alleles. Sp2 was removed as it showed very little variation and was monomorphic in Y and SW-GVD. Sp4 and Sd2 were removed due to inconsistencies in scoring and detection of putative null alleles. All other loci were retained as any deviations from HWE detected or significant LD were not consistent between populations (see below for details), which suggests that population processes are more likely to be driving these deviations. Average scoring error was 1.1 % per locus (range of 0.0 % to 5.6 %) for all 19 loci and 0.8 % for the final panel of 16 loci.

In Middleback (2011 and 2012 pooled), five loci deviated from HWE (Sp2, Sp4, Sp11, Sd2 and Sd25) and three pairs of loci (Sp12/Sp16; Sp10/Sp15 and Sp6/Sp12) showed significant LD. Putative null alleles were detected in six loci (Sp4, Sp11, Sp16, Sd2, Sd4 and Sd25). In Y two loci deviated from HWE (Sp18 and Sd4) and Sp2 was monomorphic. No significant LD was found between any pairs of loci. Putative null alleles were detected in five loci (Sp1, Sp11, Sp16, Sp18, Sd2 and Sd4). In SW-GVD one locus (Sd4) deviated from HWE and Sp2 was monomorphic. No significant LD was detected between any pair of loci, however putative null alleles were detected in two loci (Sp4 and Sd4).

4.3.2 <u>Genetic diversity</u>

4.3.2.1 Mitochondrial sequences

Eleven polymorphic sites and nine haplotypes were identified from the *CR* sequence data and multiple haplotypes were found in each population (Table 4.3). Haplotype diversity was highest in SW-GVD (h = 81 %) and nucleotide diversity was similar for both SW-GVD and EP, π = 0.72 % and π = 0.75 % respectively. AMOVA results revealed significant ($P < 0.001$) partitioning of genetic variation among populations with 54.8 % of genetic variation within the species found among populations. The Mantel test did not reveal any evidence of isolation by distance between the populations (Mantel test, Z = 1267.894, P = 0.665).

Table 4.3 Details of haplotypes identified from the *CR* sequence data for each of the three core *S. psammophila* populations sampled; EP = Eyre Peninsula, South Australia, Y = Yellabinna Regional Reserve, South Australia and SW-GVD = South-western Great Victoria Desert, Western Australia. Details include the number and distribution of *CR* haplotypes, haplotype diversity (h) ± S.D., nucleotide diversity (π) ± S.D and samples size (n).

Population	n	Haplotypes	h (± S. D)	π (± S. D)
EP	25	3	0.477 ± 0.085	0.00750 ± 0.00475
Y	12	3	0.621 ± 0.118	0.00543 ± 0.00387
SW-GVD	7	4	0.810 ± 0.130	0.00721 ± 0.00517

4.3.2.2 Microsatellite loci

Allelic diversity ranged from 6.063 alleles per locus in SW-GVD to 10.063 alleles per locus in Y (Table 4.4). There was no significant difference in the observed heterozygosity (range = 0.678 - 0.757) among the population means as determined by a Kruskal-Wallis rank sum test χ^2 = 6.266, *d.f.* = 2, P = 0.044 and post-hoc pairwise Wilcoxon rank sum test, P > 0.05. However, a significant difference was detected in the expected heterozygosity (range = 0.711 - 0.825), and allelic richness, based on four diploid individuals (range = 3.749 to 4.822), among the population means based on a Kruskal-Wallis rank sum test (H_E χ^2 = 14.224, *d.f.* = 2, P = 0.001 and A_R χ^2 = 17.798, *d.f.* = 2, P > 0.001). A post-hoc Wilcoxon rank sum test revealed that mean expected heterozygosity and mean allelic richness were significantly lower in EP compared with the other two populations (Wilcoxon rank sum test, H_E SW-GVD/EP, P = 0.012 and Y/EP, P = 0.001; A_R SW-GVD/EP, P = 0.003 and Y/EP, P > 0.001). However, mean expected heterozygosity and mean allelic richness were not significantly different between SW-GVD and Y (Wilcoxon rank sum test, H_E P = 1.00 and A_R P = 1.00). The inbreeding coefficient (F_{IS}) ranged from 0.046 to 0.097 and did not differ significantly from zero in any population, nor was there any significant difference among population means (Kruskal-Wallis rank sum test, χ^2 = 1.448, *d.f.* = 2, P = 0.485).

Table 4.4 Genetic diversity detected from 16 polymorphic microsatellite loci within the three core populations of *S. psammophila*; EP = Eyre Peninsula, South Australia; Y = Yellabinna Regional Reserve, South Australia; SW-GVD = South-western Great Victoria Desert, Western Australia. Genetic diversity parameters reported include allelic diversity (*AD*), observed (H_O) and expected (H_E) heterozygosity, allelic richness (A_R) based on four diploid individuals and inbreeding coefficient (F_{IS}) from individuals (*n*) collected from the three core populations. F_{IS} did not differ significantly from zero within any population. Differences in genetic diversity parameters among population means were tested for using Kruskal-Wallis rank sum test with a post hoc pairwise Wilcoxon rank sum test.
^{a,b} denote significant differences among populations for each parameter.

Population	*n*	*AD*	H_O	H_E	A_R	F_{IS}
EP	124	7.813	0.678^a	0.711^a	3.749^a	0.046^a
Y	40	10.063	0.745^a	0.825^b	4.822^b	0.098^a
SW-GVD	7	6.063	0.757^a	0.803^b	4.677^b	0.064^a

There was no significant difference among the genetic diversity parameters among sites within Middleback as determined by Kruskal-Wallis rank sum tests for each parameter (Kruskal-Wallis rank sum test, H_O, χ^2 = 10.004, *d.f.* = 9, P = 0.350; $H_{E,}$ χ^2 = 10.004, *d.f.* = 9, P = 0.678; A_R, χ^2 = 8.698, *d.f.* = 9, P = 0.466; $F_{IS,}$ χ^2 = 13.411, *d.f.* = 9, P = 0.145) (Table 4.5). Observed and expected heterozygosity ranged from 0.646 to 0.763 and 0.667 to 0.750, respectively. Allelic diversity ranged from 3.313 to 7.750 alleles per locus and allelic richness, based on three diploid individuals, ranged from 3.011 to 3.463. The inbreeding coefficient ranged from -0.054 to 0.135 and did not differ significantly from zero at any site.

Table 4.5 Genetic diversity parameters calculated from 16 microsatellite loci across 10 sites (Site 4 was excluded due to small sample size, *n* = 2) west of the Middleback Ranges (Middleback), South Australia. Parameters reported include sample size (*n*) allelic diversity (*AD*), observed (H_O) and expected (H_E) heterozygosity, allelic richness (A_R) based on three diploid individuals and inbreeding coefficient (F_{IS}). Differences in mean genetic diversity parameters among sites were tested for using Kruskal-Wallis rank sum test, however no parameter means were found to differ among sites ($P < 0.05$). Site numbers are as shown in Figure 4.3, and F_{IS} did not differ significantly from zero at any site.

Site	*n*	*AD*	H_O	H_E	A_R	F_{IS}
1	13	5.250	0.763	0.725	3.320	-0.054
2	8	4.750	0.656	0.706	3.278	0.060
3	15	5.438	0.646	0.722	3.296	0.113
5	10	4.625	0.670	0.676	3.128	0.014
6	13	5.188	0.737	0.717	3.293	-0.028
7	5	4.313	0.650	0.750	3.463	0.135
8	4	3.938	0.672	0.714	3.404	0.059
9	22	5.750	0.646	0.698	3.214	0.079
10	4	3.313	0.688	0.678	3.011	-0.029
11	11	4.688	0.649	0.667	3.075	0.014

4.3.3 Genetic structure

4.3.3.1 Broad-scale structure within S. psammophila

Pairwise sequence divergence (p-distance) between the nine haplotypes identified within *S. psammophila* ranged from 0.3 % to 2.7 %. Average sequence divergence was 0.8 % between SW-GVD/Y, 1.6 % between EP/SW-GVD and 1.7 % between Y/EP. Phylogenetic reconstruction produced a phylogenetic tree with a single monophyletic group comprising the nine haplotypes within *S. psammophila* relative to the outgroup *S. griseoventer,* but nodes within the *S. psammophila* group were poorly defined with low bootstrap confidence (tree not shown). Due to the low resolution of nodes, a haplotype network was produced to show relationships among the haplotypes (Figure 4.5). The haplotype network shows few substitutions between the haplotypes and several unique (i.e.

private) haplotypes present in each population. One haplotype is shared between Y and SW-GVD, while EP does not share any haplotypes with either population. However, there is no reciprocal monophyly of the haplotypes associated with any of the three populations. The results of the pairwise Φ_{ST} analyses (Table 4.6) indicate that EP is significantly genetically differentiated from both SW-GVD ($P < 0.001$) and Y ($P < 0.001$), while SW-GVD and Y are not significantly differentiated ($P > 0.05$).

Table 4.6 Mitochondrial differentiation, pairwise $\Phi_{ST,}$ between the core populations of *S. psammophila*; EP = Eyre Peninsula, South Australia (*n* = 25); Y = Yellabinna Regional Reserve, South Australia (*n* = 12); SW-GVD = South-western Great Victoria Desert, Western Australia (*n* = 7).
*** Significant pairwise comparison ($P < 0.001$) after Bonferroni correction.

Φ_{ST}	EP	Y	SW-GVD
EP			
Y	0.592***		
SW-GVD	0.543***	0.209	

Mean pairwise F_{ST} and D_{est} analyses of the microsatellite loci indicated that all three populations (EP, Y and SW-GVD) contained significantly different allele frequencies (Table 4.7). STRUCTURE analysis identified three genetic clusters ($K = 3$) within *S. psammophila* corresponding to the three core populations (Figure 4.4). The single sample from Pinkawillinie CP was removed for this analysis as preliminary STRUCTURE analyses did not strongly assign this individual to any cluster. There was very little admixture between the three clusters with individuals being assigned to a particular cluster with over 90% probability (mean Q Cluster 1 = 0.99; Cluster 2 = 0.98, Cluster 3 = 0.98). The TESS analysis was concordant with the STRUCTURE analysis and strongly identified three genetic clusters representative of the three core populations.

Table 4.7 Population differentiation calculated from 16 polymorphic microsatellite loci across the three core populations of *S. psammophila*, EP = Eyre Peninsula, South Australia (*n* = 124); Y = Yellabinna Regional Reserve, South Australia (*n* = 40); SW-GVD = South-western Great Victoria Desert, Western Australia (*n* = 7). Mean pairwise F_{ST} is reported below the diagonal and D_{est} above the diagonal.
** (P < 0.01), *** (P < 0.001) significant pairwise comparison after Bonferroni correction.

	EP	Y	SW-GVD
EP		0.625**	0.554**
Y	0.166***		0.439**
SW-GVD	0.163***	0.102***	

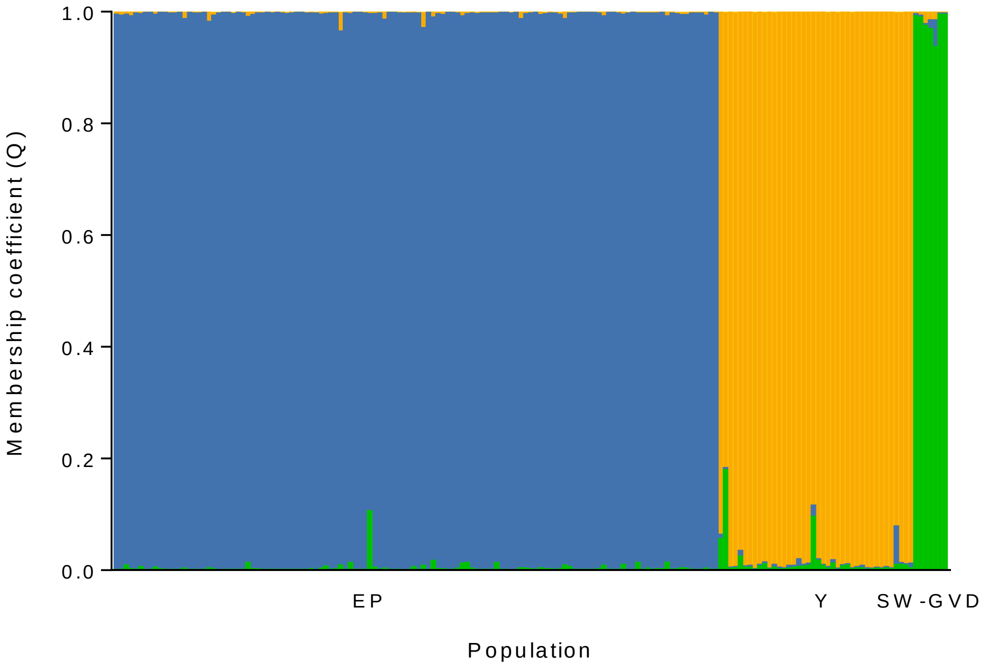

Figure 4.4 STRUCTURE plot showing the membership coefficient (Q) of each individual (vertical bar) to a particular genetic cluster when K = 3 for *S. psammophila* individuals from the three core populations; EP (blue) = Eyre Peninsula, South Australia (*n* = 124); Y (yellow) = Yellabinna Regional Reserve, South Australia (*n* = 40); SW-GVD (green) = South-western Great Victoria Desert, Western Australia (*n* = 7). Each colour represents a separate genetic cluster, which in this case corresponds to the three populations sampled.

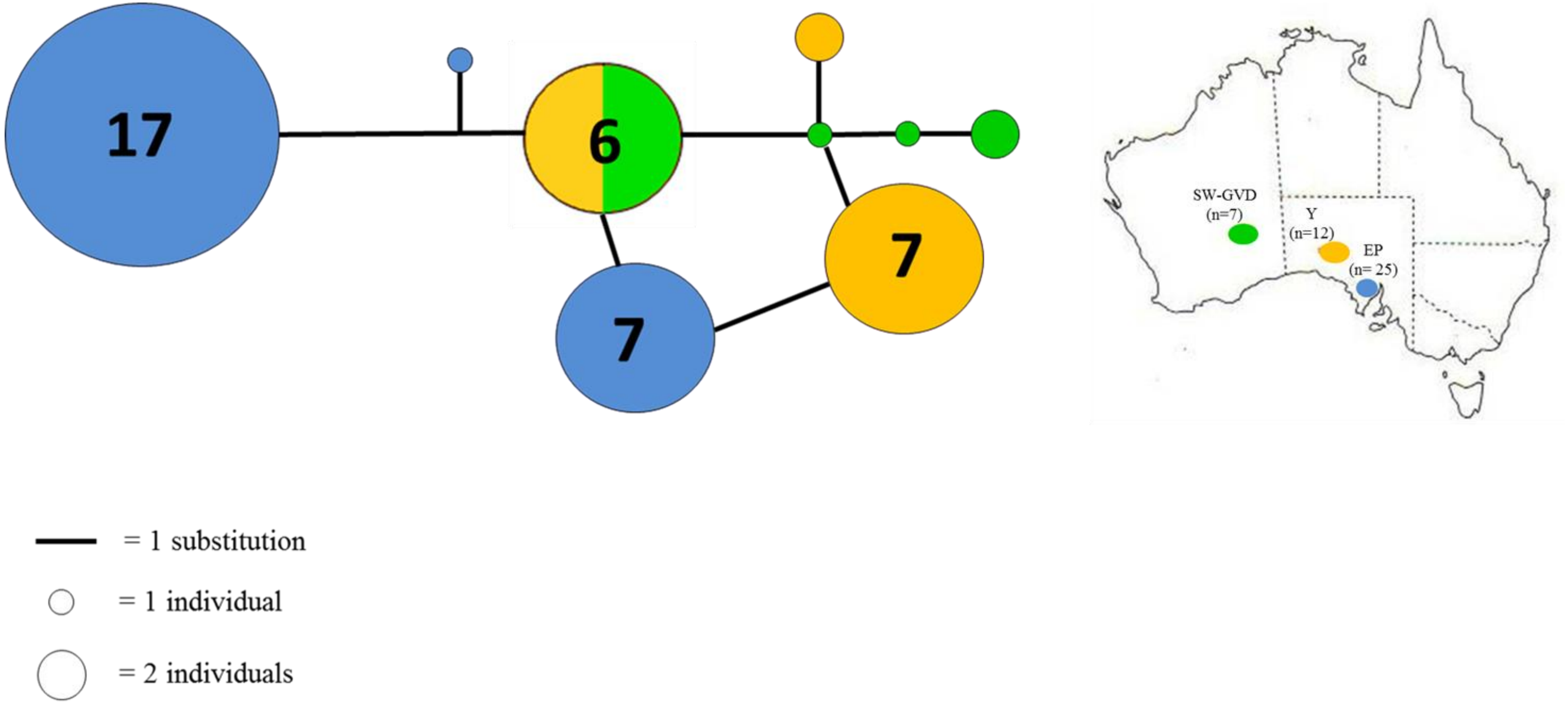

Figure 4.5 Haplotype network showing the number of *S. psammophila* individuals with each haplotype (number in circles), the number of haplotypes found in each population, the number of substitutions/sites between each haplotype and the location of each population sampled on a map of Australia. EP (blue) = Eyre Peninsula, South Australia; Y (yellow) = Yellabinna Regional Reserve, South Australia; SW-GVD (green) = South-west Great Victoria Desert, Western Australia.

4.3.3.2 Fine-scale population analyses of Middleback

Analyses of the microsatellite data revealed that the majority of genetic variation (99.38 %) within Middleback was found within sites and as such there was no significant difference in the distribution of genetic variation among sites (AMOVA, P = 0.071). Pairwise F_{ST} (range -0.014 to 0.045) and pairwise D_{est} (range -0.057 to 0.061) showed very little genetic differentiation across Middleback (Table 4.8). Pairwise F_{ST} analyses showed only one significant comparison between sites (Site 6/Site 11, P < 0.001). However, this finding was not supported by the pairwise D_{est} analysis.

Table 4.8 Population differentiation calculated from 16 polymorphic microsatellite loci across 10 *S. psammophila* sites (Site 4 was removed due to low sample size, *n* = 2) west of the Middleback Ranges (Middleback), South Australia. Mean pairwise F_{ST} is reported below the diagonal and pairwise D_{est} above the diagonal.
*** P < 0.001 significant pairwise comparison after Bonferroni correction.

	1	2	3	5	6	7	8	9	10	11
1		-0.029	-0.001	0.030	0.008	0.002	-0.029	-0.010	-0.022	0.009
2	-0.006		0.009	0.056	0.003	-0.057	0.010	-0.008	0.027	-0.009
3	0.001	0.015		0.014	0.002	0.017	-0.023	-0.013	-0.008	0.011
5	0.011	0.024	0.011		0.061	0.030	-0.015	0.024	0.056	0.048
6	0.004	0.004	-0.002	0.021		-0.007	-0.053	0.001	-0.029	0.046
7	0.000	-0.014	0.005	0.013	0.003		-0.010	-0.009	0.002	0.027
8	-0.005	0.007	-0.007	-0.014	-0.012	-0.002		-0.010	0.049	-0.033
9	-0.001	0.003	-0.003	0.009	0.001	-0.001	-0.008		-0.019	0.004
10	0.008	0.027	0.010	0.035	0.001	0.013	0.028	0.003		0.047
11	0.015	0.001	0.016	0.027	0.028***	0.013	-0.009	0.011	0.045	

STRUCTURE analysis detected only one genetic cluster across Middleback (K = 1). When higher K values were investigated STRUCTURE was unable to assign individuals strongly to any cluster. The lack of strong assignment of individuals to a cluster is shown in the STRUCTURE output of K = 2 (Figure 4.6a). The TESS analysis also was unable to assign any individuals strongly to more than one cluster when the value of K was increased, suggesting that one genetic cluster (K = 1) was optimal for Middleback (Figure 4.6b).

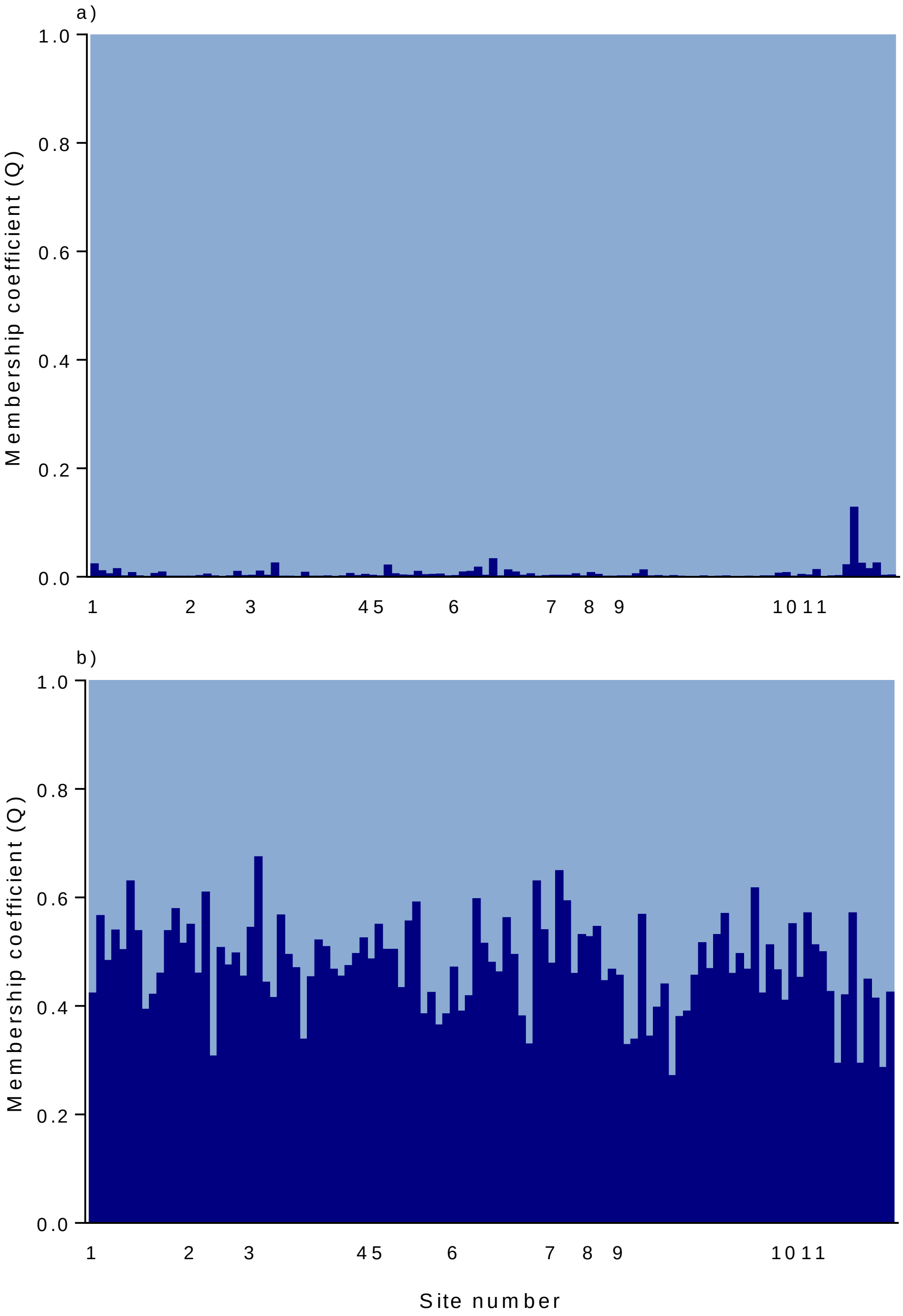

Figure 4.6 TESS (a) and STRUCTURE (b) plots showing the membership coefficient (Q) to each genetic cluster when K = 2. Each vertical bar represents one individual and the site numbers correspond to the 11 *S. psammophila* sites sampled west of the Middleback Ranges (Middleback), South Australia. Each colour represents a separate genetic cluster; however in this case, the plots suggest that there is only one genetic cluster within Middleback.

There was no significant effect of isolation by distance detected across Middleback (Mantel test; Z = -1.310, P = 0.894) and no significant effect was detected when males and females were analysed separately (Mantel test; males Z = -0.487, P = 0.644; females Z = 8.556, P = 0.628). The spatial autocorrelation analysis of all adult individuals pooled across Middleback did not identify any significant autocorrelation within the area as the heterogeneity test of the overall correlogram (Figure 4.7) did not differ significantly from zero (ω = 20.693, P = 0.042), based on the guidelines of Banks and Peakall (2012).

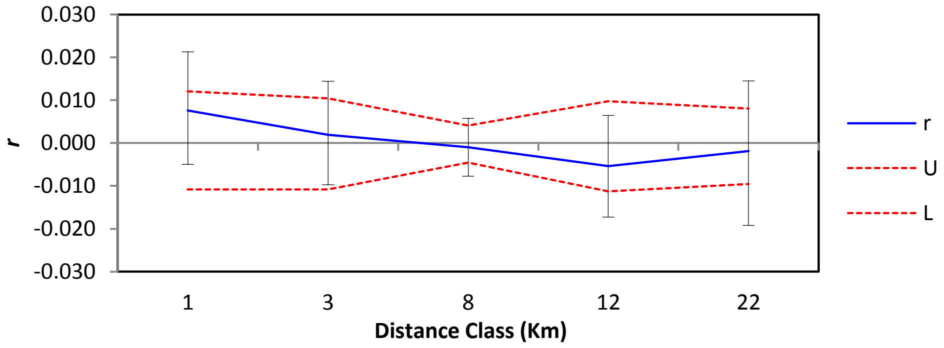

Figure 4.7 Correlogram produced by spatial autocorrelation in GenAlEx v 6.5 for all *S. psammophila* individuals caught at 11 sites west of the Middleback Ranges (Middleback), South Australia. Mean autocorrelation coefficient (*r)* with 95 % upper and lower confidence intervals (······) plotted against the distance classes.

4.3.4 <u>Relatedness and sex-biased dispersal</u>

Spatial autocorrelation analyses did not show any significant autocorrelation for either sex over the study area. However, females had a higher ω value than males and the P-value for females approached significance (females ω = 19.404, P = 0.060; males ω = 14.563, P = 0.185) (Figure 4.8 a & b). In the 1 km distance class, which compares individuals caught within the same site, females showed a higher relatedness (*r*) than males. However, the heterogeneity test did not detect any significant difference between the overall correlograms of males and females (ω = 18.688, P = 0.075) (Figure 4.8c) or at any of the distance classes (Table 4.9).

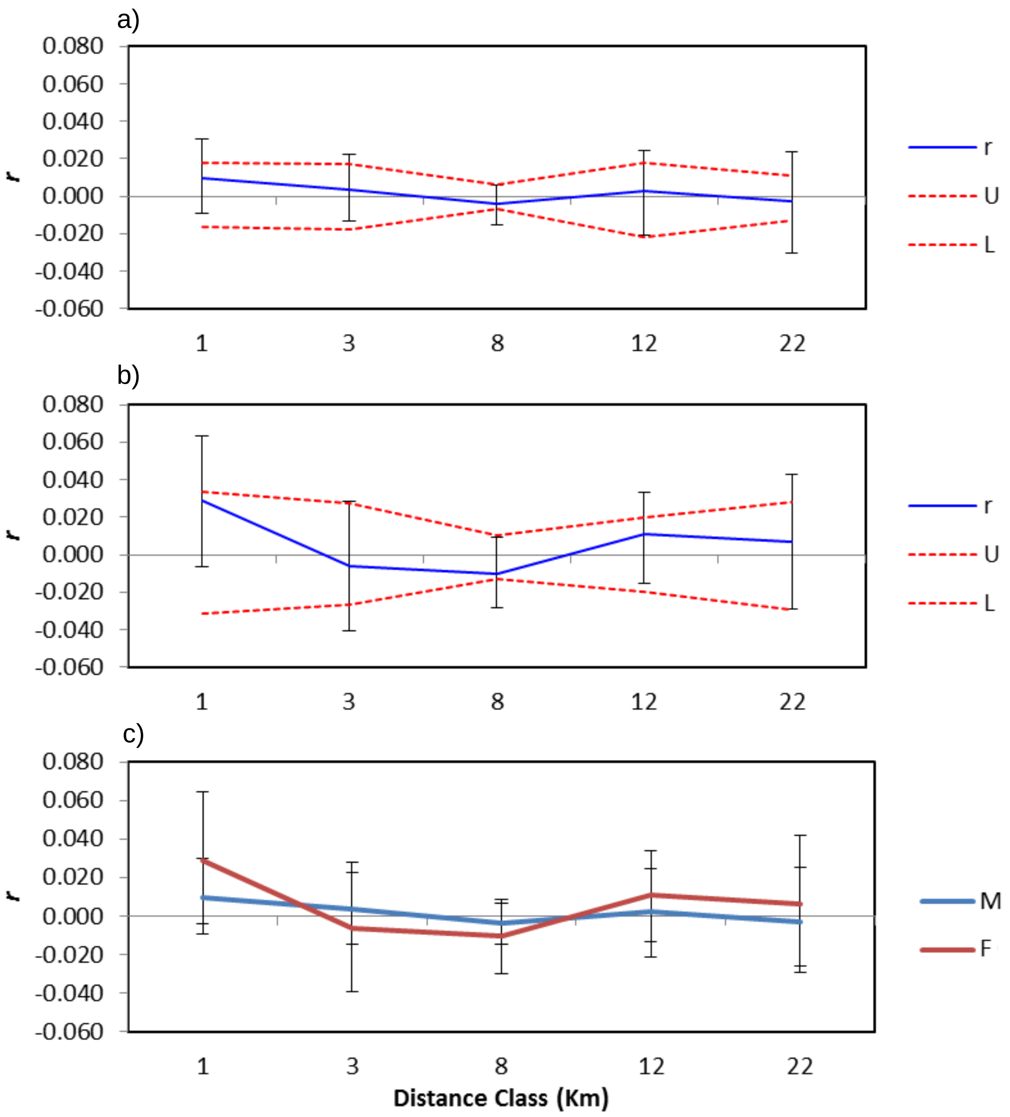

Figure 4.8 Correlograms produced by spatial autocorrelation in GenAlEx v 6.5 generated from 16 polymorphic microsatellite loci for a) adult male *S. psammophila*, b) adult female *S. psammophila* and c) adult male compared to adult female *S. psammophila* west of the Middleback Ranges (Middleback), South Australia. Mean autocorrelation coefficient (*r)* with 95 % upper and lower confidence intervals (······) plotted against the distance classes.

Table 4.9 Results of heterogeneity test between adult male and female *S. psammophila* west of the Middleback Ranges, South Australia (Middleback) showing the squared paired-sample t-test statistic (T2) for each distance class and the corresponding P-value.

Distance class (Km)	T2	P-value
1	0.543	0.480
3	0.195	0.657
8	0.128	0.775
12	0.147	0.775
22	0.097	0.763

Mean pairwise relatedness values (*Relatedness*) for males and females indicated that animals caught at the same site were generally unrelated to each other, although there was more variation in relatedness values for males than females (Figure 4.9). Mean pairwise relatedness values calculated in KINGROUP for adult males and adult females pooled over all sites also did not show any significant difference (Wilcoxon ranked sum test, W = 257211, P = 0.138) between adult males (*Relatedness* = -0.007) or adult females (*Relatedness* = 0.004).

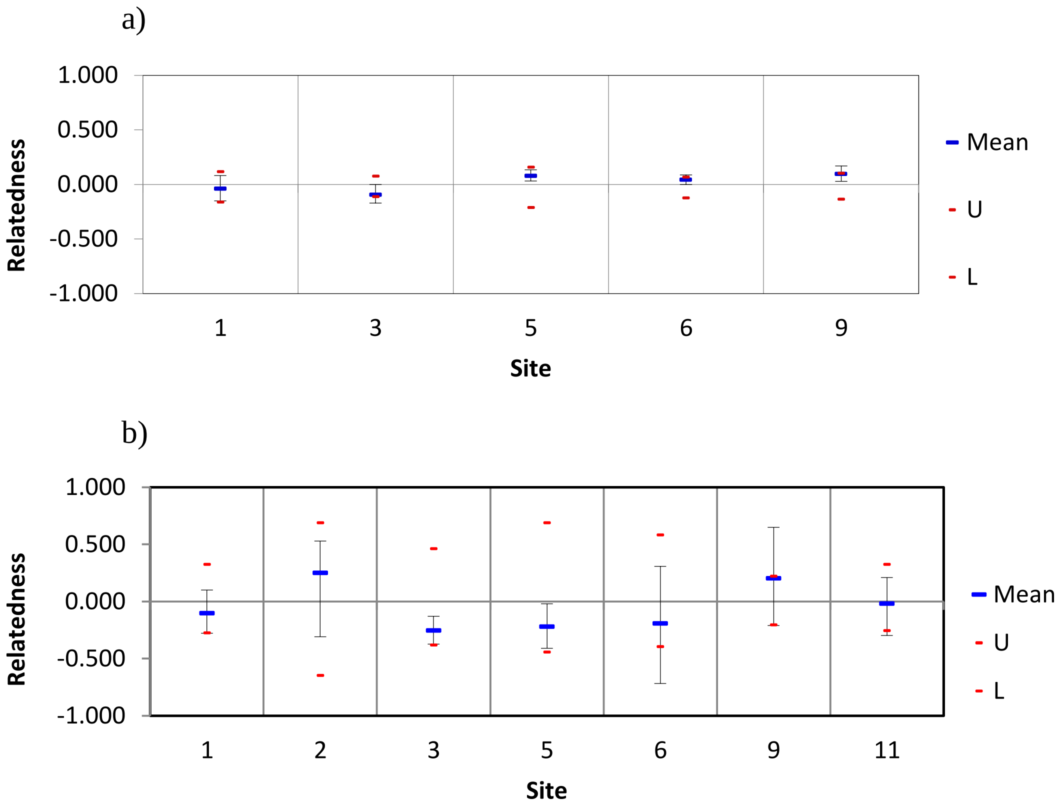

Figure 4.9 Mean pairwise relatedness values (Queller and Goodnight 1989) of *S. psammophila* a) females and b) males within sites established west of the Middleback Ranges (Middleback), South Australia. Upper and lower 95 % confidence limits (-) for the null hypothesis that there is no significant relatedness within sites based on 999 permutations. Error bars around the mean relatedness value derived from 999 bootstrap pseudosamples.

4.4 Discussion

4.4.1 Genetic structure within Middleback

Fine-scale microsatellite analyses did not show any significant genetic structure across Middleback. Additionally, no effect of isolation by distance was detected and although spatial autocorrelation tests indicated that females caught at the same site were slightly more related to each other than females caught further apart, this result was not significant. These findings suggest that the study area of 24,000 ha should be considered a single panmictic population for *S. psammophila.* A panmictic population indicates that high levels of gene flow have been maintained between the sample sites (a maximum distance of 22 km), further suggesting that animals disperse from their natal areas, potentially long distances at times, to breed with individuals from other sites within Middleback.

Effective dispersal of individuals is one of the main drivers of genetic structure in populations (Berven and Grudzien 1990) and is closely linked to the species' breeding system (Greenwood 1980). Dispersal is driven by pressures exerted on individuals, such as resource availability, kin competition avoidance and inbreeding avoidance (Handley and Perrin 2007). In semi-arid and arid environments resource availability appears to have a strong influence on dispersal and movement patterns of animals. European rabbits (*Oryctolagus cuniculus*) in Australia moved longer distances during resource poor years (Richardson *et al.* 2002), and in the semi-arid part of its range, zebra finches (*Taeniopygia guttata*) showed high mobility and no sex-biased dispersal (Zann and Runciman 1994). Unpredictable resource pulses are created by irregular rainfall events (Letnic and Dickman 2010; Morton *et al.* 2011), therefore it is advantageous for individuals to move, potentially long distances, to exploit resources when they become available (Dickman *et al.* 1995). Previous capture-mark-recapture (Letnic *et al.* 2004; Letnic and Dickman 2005; Letnic *et al.* 2005) and radio-telemetry studies (Letnic 2002; Masters 2003; Haythornthwaite and Dickman 2006b) of native Australian rodents and dasyurid marsupials in arid systems have documented long distance movements; of up to 14 km for the sandy inland mouse (*Pseudomys hermannsburgensis*) and one occurrence of 12 km for the lesser hairy-footed dunnart (*S. youngsoni*) (Dickman *et al.* 1995). Furthermore, individuals were detected moving in the direction of known rainfall, presumably to exploit the resource pulse it would bring (Dickman *et al.* 1995). Capture-mark-recapture studies have also observed a relatively high proportion of transient individuals (i.e. those caught only once during a study) such as, 100 % of trapped individuals in the dusky hopping mouse (*Notomys fuscus*) (Moseby *et al.* 2006), 57 % in the mallee ningaui (*Ningaui yvonneae*) (Bos and Carthew 2001) and 35.5 % in the brush-tailed mulgara (*Dasycercus blythi*) (Masters and Dickman 2012). In the current study, 51 % of the trapped population of *S. psammophila* were recorded as transients (Chapter 2). High proportions of transient individuals may indicate low site fidelity and suggest high mobility (e.g., Giles' planigale, *Planigale gilesi*; Read 1984 and fat-tailed dunnart, *S. crassicaudata*; Morton 1978a). Fewer studies have been conducted on semi-arid species, but studies to date suggest that like their arid counterparts, semi-arid species are also highly mobile (Morton 1978a; Read 1984; Carthew and Keynes 2000; Bos and Carthew 2001). Although there have been few genetic studies on semi-arid or arid species comparable to this study (although see banner-tail kangaroo rat, *Dipodomys spectabilis*; Waser and Elliott 1991; western grey kangaroo, *Macropus fuliginosus*; Neaves *et al.* 2009 and the northern hairy-nosed wombat, *Lasiorhinus krefftii*; Taylor *et al.* 1994), our results support previous ecological observations of high mobility in semi-arid species.

4.4.1.1 Sex-biased dispersal

The microsatellite data did not reveal any significant sex-biased dispersal in *S. psammophila* within Middleback. However, a trend of higher relatedness between females (but not males) within the 1 km distance class (within sites) was evident, suggesting that males may move further from their natal area than females. Nevertheless, relatedness between females or between males within sites was not significant, suggesting that the animals caught at each site were generally unrelated.

The lack of any significant sex-biased dispersal supports the field observations made during this study (Chapter 2) and field studies of other arid *Sminthopsis* species, which suggest that both sexes disperse from their natal areas as juveniles (Read 1984; Dickman *et al.* 1995; Friend *et al.* 1997). Furthermore, as adults, males may be more active and move longer distances than females (Chapter 2), as found in the little long-tailed dunnart (*S. dolichura*) (Friend *et al.* 1997) and the lesser hairy-footed dunnart (*S. youngsoni*) (Haythornthwaite and Dickman 2006b). Dickman *et al.* (1995) observed similar movement patterns for females, males, juveniles and non-breeding adults of three species of *Sminthopsis* and two rodent species in the Simpson Desert of Australia, and concluded that movement was not related to age, sex or reproductive condition. These findings further suggest that in arid and semi-arid systems dispersal of both sexes is largely influenced by resource availability. In contrast, dasyurids that live in temperate regions with relatively reliable and consistent resources, such as the yellow-footed antechinus (*Antechinus flavipes*) (Marchesan and Carthew 2004), agile antechinus (*Antechinus agilis*) (Banks *et al.* 2005), and the brush-tailed phascogale (*Phascogale tapoatafa*) (Soderquist and Lill 1995), exhibit strong male biased dispersal from the natal area. In these regions resources are not as limiting and so other factors such as inbreeding avoidance, may have a greater influence on dispersal.

4.4.2 *Genetic structure within* S. psammophila

Broad-scale analyses of the microsatellite data indicated that the three core populations of *S. psammophila* are significantly genetically differentiated. Separate analyses of the *CR* sequence data, which allowed assessment of phylogeographic structure within the species, showed that EP was significantly differentiated from Y and SW-GVD. However, Y and SW-GVD were not significantly differentiated and were observed to share a mtDNA haplotype, despite both populations being geographically further away from each other (815 km), than EP is to Y (508 km). This pattern of differentiation suggests that there is very little, if any, female-mediated gene flow between EP and the two populations in the GVD (Y and SW-GVD). However, the lack of reciprocal monophyly of the *CR* haplotypes from EP and Y/ SW-GVD and overall shallow phylogeographic structure, with low levels of divergence among the *CR* haplotypes, suggests that this lack of gene flow occurred relatively recently. Placing a time-frame, however, on the differentiation of the populations requires additional genetic analyses that were beyond the scope of the current study.

Physical geographical barriers may have contributed to the isolation of these populations and several barriers have been identified in previous phylogenetic studies of arid species, such as the Nullarbor Plain in various bird species; (Dolman and Joseph 2012) and the Murray River/ Lake Bungunnia (a historical lake) in the fat tailed-dunnart (*S. crassicaudata*) (Cooper *et al.* 2000). However, there are limited geographical barriers between EP, Y and SW-GVD that might explain the genetic pattern observed in *S. psammophila*. The Nullarbor Plain is too far south to be considered a barrier in *S. psammophila*, as the SW-GVD and Y occur north of the Nullarbor Plain. A potential barrier that may have influenced the differentiation of EP and Y is the Gawler Ranges, which occurs northwest of the Eyre Peninsula. However, there is a strip of relatively continuous vegetation south of the ranges, which may have supported connecting populations and encouraged gene flow between EP and Y. There does not appear to be any geographical barriers between Y and SW-GVD as both are situated in the Great Victoria Desert, which is a region of relatively continuous vegetation (Department of Environment and Heritage 1999) and has been largely untouched by European development. The *CR* sequence analyses showed a lack of genetic differentiation of Y and SW-GVD, suggesting that, until recently, the two populations were connected to some degree, potentially through additional intermediate populations. It is possible that any potential connecting populations between these core populations may have become locally extinct over time, such as during periods of increased aridity (e.g., LGM), when the species may have retreated back to multiple refugia across its range (Byrne *et al.* 2008) and populations have not recolonised these areas. However, given the logistic constraints of conducting surveys in remote areas, there may still be undiscovered populations between all three known populations. In conjunction with living in remote areas, the high mobility and natural low density of *S. psammophila* make detecting the species difficult (Chapter 2). We therefore suggest that further survey effort, in suitable habitat, is needed to verify the presence or absence of additional populations that may still be present between the known core populations.

The Eyre Peninsula is another geographical feature that may have contributed to the genetic differentiation of EP from Y by acting as a refuge for *S. psammophila* during periods of increased aridity (e.g., LGM). The Eyre Peninsula has previously been identified as a refuge for the grey-bellied dunnart (*S. griseoventer*) and the heath mouse (*Pseudomys shortridgei*) during the Pleistocene (Kemper *et al.* 2010; Kemper *et al.* 2011). However, *P. shortridgei* is no longer present on the Eyre Peninsula, most likely due to the habitat loss and fragmentation of southern and central Eyre Peninsula that has occurred since European settlement (Kemper *et al.* 2010). The extent to which *S. psammophila* may be affected by habitat loss and fragmentation is unknown, however, current and historic records suggest that the species may have been wide- spread over central and northern Eyre Peninsula prior to European settlement. Over the past 15 years, very small numbers of *S. psammophila* have been detected in patches of remnant vegetation over central and northern Eyre Peninsula, such as Pinkawillinie Conservation Park (CP) (central-north Eyre Pen.) (J. Lee, and J. Read and K. Moseby, unpublished data), Hambridge CP (central Eyre Pen.) (Churchill 2001b), Hincks CP (central Eyre Pen.) (D. Driscoll unpublished data) and Cowell (central-east Eyre Pen.) (Churchill 2001b) (Figure 4.1). In addition to these captures, *S. psammophila* sub-fossils have been found in Venus Bay (Baynes 1987), remains of the species were identified in owl pellets from Darke Peak (1984) (Baynes 1987) and one individual was caught at Mamblin (central-north Eyre Pen.) in 1969 (Aitken 1971). Unfortunately, the Eyre Peninsula has lost approximately half (57 %) of its native vegetation since European settlement (Churchill 2001a), with slightly greater vegetation loss occurring in the southern biogeographic regions (Eyre Hills, Southern Block and Talia, 15 %, 7084 km^2, remnant vegetation remains) than the northern regions (Eyre Mallee and Eyre Hills, Northern Block 23 %, 10477 km^2, remnant vegetation remains)

(Brandle 2010). The loss of vegetation appears to have resulted in the contraction of the once wide spread, *S. psammophila,* to remnant patches in the central and northern Eyre Peninsula.

4.4.3 Conservation implications

Sminthopsis psammophila is classified as Endangered (IUCN 2013) and is potentially threatened by habitat loss, changing fire regimes, introduced predators (domestic cats, *F. catus* and red foxes, *V. vulpes*) (Churchill 2001a) and climate change. In order to conserve the species effectively, it is important to preserve the full range of genetic diversity within *S. psammophila* to provide maximum potential for the species to respond to future changes, such as climate change (Lande 1988; Frankham 2005; Hedtke *et al.* 2007). It can be useful to define populations of species as either Evolutionarily Significant Units (ESUs) or Management Units (MUs) in order to prioritise populations for conservation. Based on the criteria of Moritz (1994) each core population of *S. psammophila* should be considered, at the very least, separate MUs, as each population showed significant allele frequency differences at nuclear and mtDNA loci. Although there were fixed mtDNA haplotype differences at EP compared to Y/ SW-GVD there was no evidence for reciprocal monophyly of the mtDNA haplotypes within MB and hence under the criteria of Moritz (1994) the core populations do not represent separate ESUs. The classification of MUs suggests that gene flow is low between the core populations and that the populations may be functionally separate (Moritz 1994). However, as mentioned above, given the large geographical distances between SW-GVD, Y and EP the populations may have different allele frequencies even though they could be partially connected by undiscovered populations. In addition to genetic exchangeability, ecological exchangeability should also be considered when defining populations for management purposes (Crandall *et al.* 2000). Ecological exchangeability takes into consideration adaptive divergence of populations to different environmental conditions through genetic drift and natural selection. As Y and SW-GVD are situated in an arid climate and EP is in a semi-arid climate, there may be adaptive differences between the populations that would warrant separate management, but further research, for example, on the timing of breeding or behavioural adaptations, would be needed to determine if this is the case.

Overall, we suggest that future conservation priorities for *S. psammophila* should be to protect the known populations, use genetic methods to monitor levels of genetic diversity over time in the core populations and survey, within suitable habitat, for *S. psammophila* in localities between the three core populations. If further surveys suggest that the core populations are indeed isolated and genetic diversity is being lost over time, we may need to consider strategies to re-establish gene flow between them in order to prevent further loss of genetic diversity and adaptability (Frankham 2005, 2010b). Re-establishment of gene flow could be achieved by translocation of individuals from one population into another or by establishing new (connecting) populations between the core populations. These types of translocations have been referred to by Weeks *et al.* (2011) as 'genetic adaptation' with the aim of the translocations being to increase the genetic adaptability of the species to future threats, like climate change. However, before translocation options are considered, it is important to conduct a risk assessment of both scenarios where translocation does and does not occur (Weeks *et al.* 2011). Possible consequences of combining individuals from different populations include the development of outbreeding depression (Frankham *et al.* 2011) and a loss of local adaptability (Crandall *et al.* 2000; Weeks *et al.* 2011).

The isolated nature of remnant vegetation patches on Eyre Peninsula where *S. psammophila* has been detected, including Hambridge CP, Hinks CP and Pinkawillinie CP (Churchill 2001b, J. Read and K. Moseby unpublished data), is another area of concern. Further research is needed to determine the long-term viability of these populations and the level of connectivity (gene flow) between them. The effects of habitat fragmentation on *S. psammophila* is currently unknown, however if remnant patches are isolated, populations may become locally extinct due to environmental (e.g., wildfire), demographic and genetic stochastic events that can threaten small, isolated populations (Lande 1988). If further genetic analyses reveal that populations within the remnant vegetation patches are isolated, management strategies, such as increasing connectivity using habitat corridors or translocations, may be advisable to re-establish gene flow.

At the fine-scale, the genetic information from Middleback suggests that individual *S. psammophila* are highly mobile and can potentially move long distances to acquire sufficient food resources. By extension, this suggests that large areas of continuous habitat may be required to maintain viable populations. The location and timing of resource pulses are unpredictable in semi-arid and arid systems and may occur outside of protected areas (Dickman *et al.* 1995). This study showed that *S. psammophila* is able to maintain a panmictic population over at least 24,000 ha with gene flow occurring inside and outside of the conservation park. Therefore, to effectively protect the species, large areas of suitable continuous habitat will need to be maintained both inside and outside of conservation parks, which will require co-operation between private landholders and governments, given the extent of habitat loss and fragmentation that has already occurred on the Eyre Peninsula. In addition, further study on the habitat preferences of *S. psammophila* is needed in order to identify and protect areas of suitable habitat for the species.

4.5 Conclusion

The findings of this study indicate that the three core populations of *S. psammophila* are genetically differentiated; however, there is no evidence for long-term isolation of the populations. Based on the definition of Moritz (1994) the three populations should be considered, at the very least Management Units. Within one core population (Middleback) of *S. psammophila* we did not detect any significant population structure or sex-biased dispersal, suggesting there the study region of 24,000 ha represents a panmictic population. These findings indicate that both males and females disperse from their natal areas prior to the breeding season and may remain relatively mobile during their lifetime. The relatively high mobility in this species is most likely an adaptation to a system with variable food resources; individuals need to be mobile in order to track food pulses created by rainfall through the landscape. This study has provided insights into the dispersal patterns and maintenance of genetic diversity of a semi-arid dasyurid marsupial and has highlighted the need for large areas of continuous suitable habitat to maintain a viable population of *S. psammophila*. Further research is needed to determine the habitat preferences of *S. psammophila* in order to define and protected suitable habitat for the species.

CHAPTER 5: Location, location, location: Habitat preferences of a rare semi-arid marsupial

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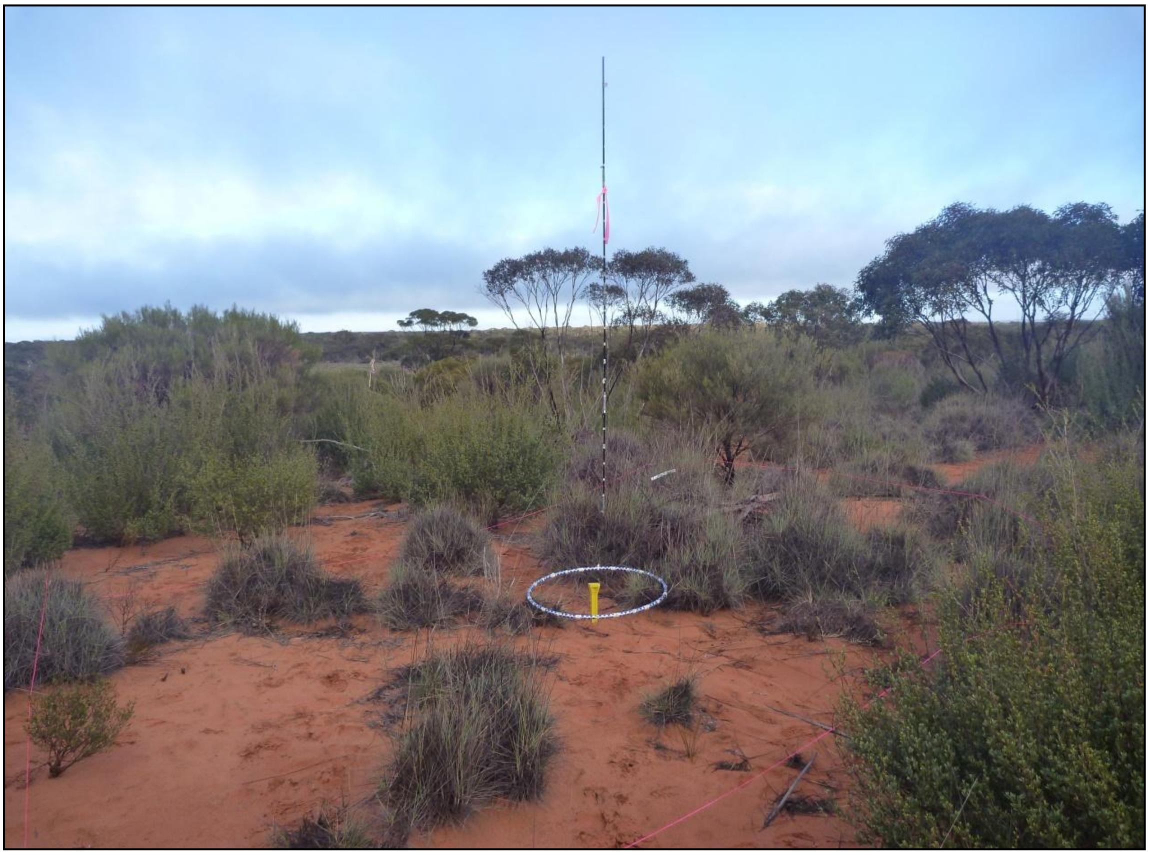

Vegetation survey set up of a 4 x 4 m quadrat at Site 3. Photo A. McLean

Statement of Authorship

Title of paper	Location, location, location: Habitat preferences of a rare and endangered semi-arid dasyurid marsupial							
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Author contributions

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate's thesis.

Name of Principle Author	Amanda L. McLean (Candidate)	
Contribution to the Paper	Designed project, collected data, preformed analyses, interpreted analyses and wrote manuscript.	
Signature		Date

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Signature		Date 25-03-2015

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Signature		Date 14/4/15

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Signature		Date 14/4/15

Abstract

Australia has one of the highest rates of mammal extinction in the world and 55 mammal species are listed as threatened. Before management plans can be developed and implemented, key aspects of a species' ecology, including habitat preferences, need to be understood. The sandhill dunnart (*Sminthopsis psammophila*) is an endangered dasyurid marsupial and, as is the case for many such species, its ecology is poorly understood. Currently the species is known from three disjointed populations in semi-arid and arid regions in South Australia and Western Australia. Knowledge of this species' habitat preferences are required in order to protect suitable habitat for the known populations, and to continue to survey for additional populations. This study aimed to define the habitat preferences of *S. psammophila* in one core population during a two year capture-mark-recapture study. In addition, we also explored the influence of time since fire and rainfall in determining habitat preferences. Our analysis revealed that the three most important habitat variables for predicting *S. psammophila* abundance were the number of logs (≥ 5 cm diameter), the average height of the *Triodia* hummocks and the overall complexity of the vegetation. We did not find a preference for a particular post-fire age of vegetation. However, there did appear to be an influence of rainfall on the abundance and habitat preferences of *S. psammophila*. This study has highlighted the importance of considering a range of habitat variables including *Triodia* presence and structure, the overall complexity of the vegetation, and possibly rainfall patterns, when identify potential *S. psammophila* habitat in the future. Future research should focus on the foraging behaviour of *S. psammophila* so that we can understand: (1) how the habitat is used, and (2) use of possible habitat refugia during low resource (e.g., low rainfall) years.

Keywords: *Sminthopsis psammophila* — Semi-arid — Dasyuridae — Marsupial —Fire — Rainfall — *Triodia* — Refugia

5.1 Introduction

The use of different habitats by individuals provides valuable information about the distribution and resource needs of various mammal species. Habitat preference or selection can be defined as the non-random use of habitats in relation to their availability (McIntyre 1997). Habitat preferences exist at multiple temporal (e.g., Sundell *et al.* 2012) and spatial (e.g., Martínez *et al.* 2003) scales and can be influenced by complex interactions between abiotic factors, such as rainfall (Dickman *et al.* 1995) and biotic factors, such as availability of food resources (Fisher 2000). Therefore, changes in habitat use can indicate the relative importance of alterative habitats over time and at different spatial scales (Brown 1988; Leblond *et al.* 2011).

The arid and semi-arid zones of Australia have suffered a major decline in mammal species due to a combination of threatening processes (Fisher *et al.* 2003; Bennett *et al.* 2006; McKenzie *et al.* 2007; Johnson and Isaac 2009). Although information on the habitat preferences for threatened species is vital for the development of effective conservation management plans (Finlayson *et al.* 2008), it is lacking for many endangered arid and semi-arid species. To date a number of studies have reported weak correlations between species abundance and vegetation structure (e.g., Letnic *et al.* 2004; Haythornthwaite and Dickman 2006a). The weak associations with vegetation structure may be a result of strong interactions between population abundance and abiotic factors (e.g., rainfall and wildfires) that influence food resources and shelter (Masters 1993; Arthur *et al.* 2012).

Various theoretical models have been proposed to explain why and how fauna species respond to the habitat heterogeneity inherent in arid systems. Letnic and Dickman (2010) reviewed three models that influence these systems: the ecological refuge model, the predator refuge model and the fire mosaic model. The ecological refuge model suggests that within a given landscape there are places with relatively dependable resources in which species can persist during drought years (drought refugia). Drought refugia may be permanent areas, such as rocky outcrops (Byrne and Hopper 2008; Millar *et al.* 2014) or temporary patches produced by localised rainfall events (Dickman *et al.* 1995). Identification of refugia has important conservation management implications, but so far there has been limited effort and success in detecting refugia for arid and semi-arid mammal species (although see Milstead *et al.* 2007; Foley *et al.* 2008; Klein *et al.* 2009; Dickman *et al.* 2011; Millar *et al.* 2014; Pavey *et al.* 2014). The predator refuge model acknowledges that predation can strongly influence the presence of species and that species will occur in areas of reduced predation, either through suppression of meso-predators by a top predator or in areas of more complex habitat that limit predator access. The fire mosaic model suggests that species exploit different habitats created by fire mosaics in the landscape and that the presence of mosaics may increase species diversity. However, the response of arid and semi-arid mammal species to fire is particularly complex and has not been well studied compared to the response of species in temperate systems. There is limited support for the notion that fire mosaics increase mammal diversity (Letnic and Dickman 2005; Kelly *et al.* 2012) and studies to date suggest that at least some mammal species do not show a strong preference for a particular age of vegetation post-fire (e.g., Letnic 2003; Letnic and Dickman 2005). Letnic and Dickman (2010) proposed a state-and-transition model for spinifex landscapes that combines aspects of these three models and suggest that rainfall, availability of food resources and predation have a greater influence on small mammal presence and abundance than vegetation structure. We employed this framework to investigate the influence of both rainfall and fire on the habitat preferences and abundance of our study species, an endangered (IUCN 2013) dasyurid marsupial, the sandhill dunnart (*Sminthopsis psammophila*).

Sminthopsis psammophila is presently known from three disjunct populations in arid and semi-arid southern Australia (Eyre Peninsula, South Australia; Yellabinna Regional Reserve, South Australia and south-west Great Victoria Desert, Western Australia) (Churchill 2001b). *S. psammophila* has previously been caught in or near sandy areas or sand dunes ranging from 5 m to 30 m high with the vegetation consisting of mallee (e.g., *Eucalytpus oleosa* and *E. socialis*), a range of shrubs (e.g., *Acacia* spp., *Hakea* spp.) and an understory of *Triodia* spp. (spinifex grass) covering 10 % to 70 % of the ground (Churchill 2001b). Churchill (2001b) suggested that *S. psammophila* has a strong affinity with large *Triodia* hummocks and nests in hummocks that have begun to die off in the middle, which would provide protection from predators and variations in extreme temperatures. However, other components of the vegetation may also be important for *S. psammophila* persistence, such as the presence of shrubs in areas with low *Triodia* cover (Philp 2011). Specific habitat preferences of *S. psammophila* have yet to be determined and it may be that preferences vary between arid and semi-arid zones. Both fire and rainfall have a strong influence on *Triodia* structure, as fire can remove the majority of *Triodia* in an area, while the amount of rainfall can influence the rate of germination and growth of *Triodia* after a fire event. Variation in rainfall, between regions and over time, may change the growth rate of *Triodia,* which could influence the length of time it takes for vegetation to become suitable for *S. psammophila* post fire. Previous studies have noted that as time since fire increases, the structure of *Triodia* hummocks break down (Haslem *et al.* 2011). Churchill (2001b) suggested that as the *Triodia* hummock breaks down it will become unsuitable for *S. psammophila* after ~30 years post-fire. At the other extreme, *S. psammophila* has not been caught in areas younger than eight years post-fire, possibly because prior to eight years the vegetation has not regrown enough to provide suitable habitat. However, to date this has not been examined in detail, and no preference for vegetation of a specific time since fire has been determined for *S. psammophila.*

The focus of this study was a core *S. psammophila* population on Eyre Peninsula, South Australia. Both rainfall and fire are important drivers in the system (Morton *et al.* 2011), but the influence of either on the habitat preferences of *S. psammophila* is unknown. In addition to assessing correlations between *S. psammophila* abundance and vegetation structure, we explored the response of *S. psammophila* to time since fire by including sites in four different age categories post-fire. We also considered the influence rainfall may have on *S. psammophila* abundance and habitat preference by comparing capture rates (density) and the number of resident females at each site as a proxy for high quality habitat (Mosser *et al.* 2009) during a high rainfall (high resource) year and a low rainfall (low resource) year. We predict that understorey components of the vegetation, such as *Triodia* and shrubs will be important habitat components for *S. psammophila* as they provide cover for individuals moving through the landscape and *Triodia* hummocks offer nesting opportunities (Churchill 2001b). Since *S. psammophila* appears to be influenced by rainfall (Chapter 2), it is likely that individuals contract back to high quality habitat when food resources are low, as per the state-and-transition model for spinifex landscapes.

5.2 Methods

5.2.1 Study site

The study site is located west of the Middleback Ranges on the Eyre Peninsula, South Australia (33°09′S, 137°07′E) (Figure 5.1). The region has a semi-arid climate, with relatively hot dry summers and cold winters. Mean rainfall is ~ 250 mm per year and although most rainfall generally occurs during winter, up to 20 % occurs during summer

(Schwerdtfeger 1985). The western side of the Middleback Ranges is characterised by parallel sand dunes ranging from 10 to 20 meters high. The main plant species include mallee species (*Eucalyptus socialis, E. gracilis, E. incrassata, E. oleosa, E. brachycalyx*), with an understorey dominated by *Triodia irritans* and other shrubs (*Alyxia buxifolia, Eremophila scoparia, Senna artemissioides, Hakea francisiana Melaleuca lanceolata, Dodonaea viscosa)* (Bos and Carthew 2001). The study area is a mosaic of four different fire age classes, seven years post-fire, 20 years post-fire, 39 years post-fire and 60+ years post-fire. Exact timing of the last fire in sites 60+ years post-fire is unknown as the fire maps suggest the area has not been burnt since fire mapping commenced during 1931 (Department of Environment Water and Natural Resources 2013), however local knowledge from land owners indicates that the last fire was approximately 60 years ago (pers. comm. L. Jacobs).

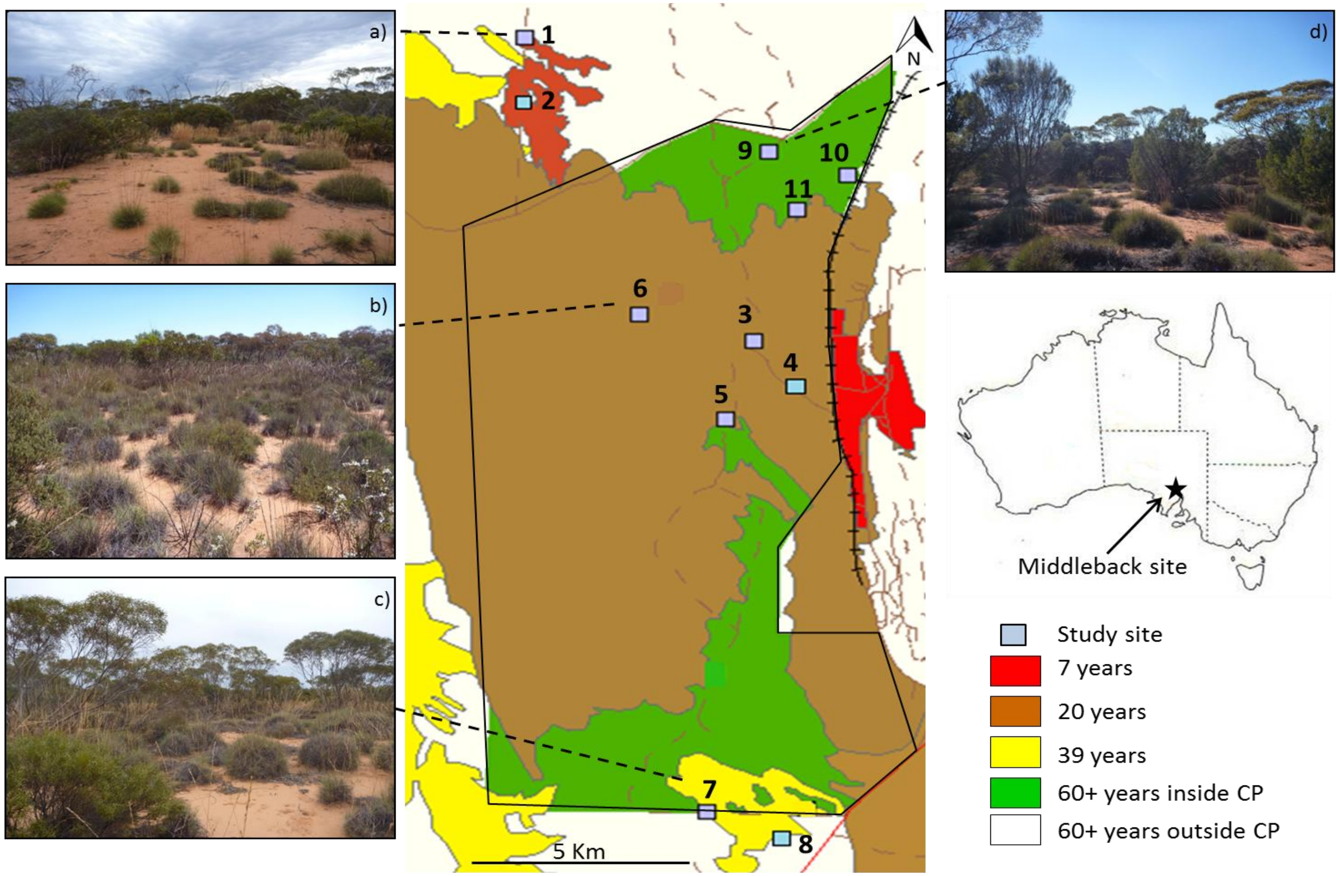

Figure 5.1 Location of the Middleback study site, west of the Middleback Ranges, Eyre Peninsula, South Australia and fire map of the study site showing the location of the 11 *S. psammophila* sites and the four fire ages of the vegetation a) 7 years post-fire, b) 20 years post-fire, c) 39 years post-fire and d) 60+ years post-fire present at the commencement of the study. Photos show the general structure and composition of plants in each fire age class. The black line represents the boarder of Ironstone Hill Conservation Park (Department of Environment Water and Natural Resources 2013).

5.2.2 <u>Trapping protocol</u>

Eleven sites were established within Ironstone Hill Conservation Park and surrounding private property (Pine Hill and Cooyerdoo Station). All sites were trapped seasonally (summer, autumn, winter, spring) during a two year period (eight trapping sessions per site). Twelve additional trapping sessions also occurred at a subset of sites (*n* = 6) to track the breeding season of *S. psammophila* (Chapter 2) and were included in the modelling analyses here. All sites were at least 1.5 km apart and established on sand dunes or in sandy areas where *Triodia irritans* was present, as past surveys have found that *S. psammophila* has a close affinity with this plant (Churchill 2001b). Sites consisted of four transects of alternating Elliott (type A; 24 in total) and deep pitfall traps (600 mm deep, 230 mm diameter; 12 in total) and spanned an area of approximately 10,800 m^2. Each trapping session lasted for six nights at each site with Elliott traps closed every alternate night to reduce the chance of recaptures. All capture mammals were identified to species level and released with minimal handling. *S. psammophila* were measured (left pes length, tail length, head length), weighed, sexed and microchipped for individual identification (for additional information on trapping protocol refer to Chapter 2).

5.2.3 <u>Habitat assessment</u>

Vegetation was assessed once at each site during May 2013. A total of 16 quadrats (4 m x 4 m) per site were used with four quadrats along each transect of the trapping grid. Quadrats were located by assigning a randomly generated number between zero and 200 to each quadrat, representing the number of meters from the start of the transect (0 m) to the end of the transect (200 m). Quadrats were placed 5 m to the side of the trapping transect to reduce the impact of vegetation disturbance caused by trap placement and trapping sessions. Within each quadrat 15 pole touches were taken at random distances (0 - 400 cm) from the centre point of the quadrat and at random bearings (0 - 360°) using randomly generated numbers. Pole touches were taken at ground level and vertical heights of 10 cm, 20 cm, 30 cm, 40 cm, 50 cm, 100 cm, 150 cm, 200 cm, 250 cm, 300 cm and > 300 cm. At each height interval the number of touches of each plant was counted up to a maximum of 10 touches. Plant categories were *Triodia*, shrub and mallee. In addition to the pole touches several measurements were taken within each quadrat, including number of shrubs, number of *Triodia* plants, number of plant species, number of logs and the number of mallee stems. The three closest *Triodia* plants to the centre of the quadrat were also measured (height, width, length and distance to nearest *Triodia*) as per Ward (2009), as *S. psammophila* is known to nest in large *Triodia* spp. hummocks (Churchill 2001b). Volume was calculated as the volume of a cube (length x height x width), with the value for Stage 4 and 5 plants divided by 2 to give an indication of the volume lost due to the hole in the middle of the plant (Figure 5.2).

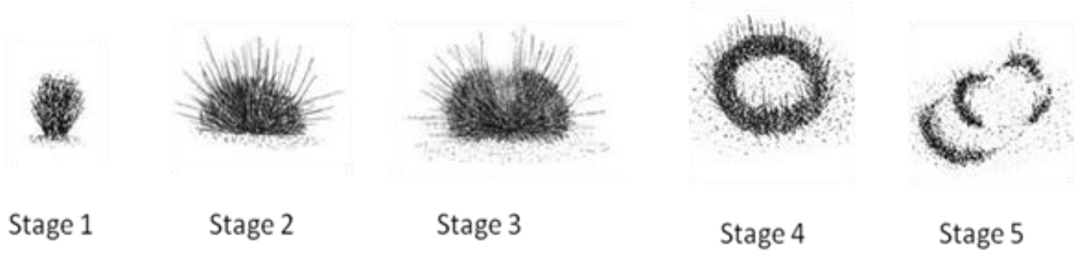

Figure 5.2 Life stages of *Triodia* spp. as per Churchill (2001b). As the *Triodia* plant grows outwards, it begins to die off in the middle (Stage 3), at Stage 4 only the outside ring remains and by Stage 5 the ring has broken down into segments.

5.2.4 Data analysis

5.2.4.1 Defining key habitat variables

Habitat data were pooled across quadrats for each transect for analyses. Data were checked for outliers using Cleveland dot plots in the R package `lattice` (Sarkar 2008) and outliers were removed. The full range of habitat variables measured (Appendix 2) was investigated during initial data exploration using principal component analysis (PCA) performed in the R package `vegan` (Oksanen *et al.* 2013). PCA was used to visually assess how the vegetation structure differed between sites and which habitat variables may be important in order to reduce the number of habitat variables prior to further analyses. The first axis of the PCA explained 28.74 % of the variation and the second axis explained 25.79 % of the variation, giving a total of 54.53 % variation explained within the first two axes. The PCA revealed that measurements of the same habitat type (e.g., *Triodia* at various height classes) grouped together, and in general the summary measurement of either understorey or upperstorey (e.g., *Triodia*.understorey) was the strongest variable. PCA also showed that although there was some variation between transects at the same site, generally, transects from a site grouped together (Figure 5.3).

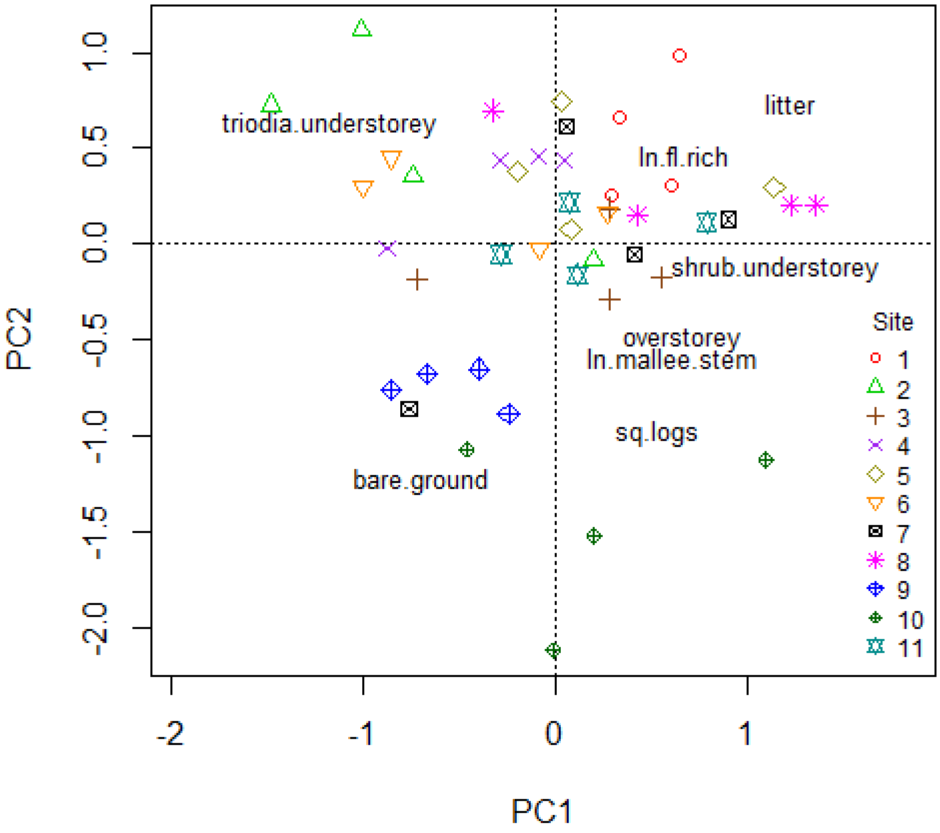

Figure 5.3 PCA scaling ordination plot of eight retained habitat variables measured at four transects per each of the 11 *S. psammophila* sites sampled during the two year study west of the Middleback Ranges, Eyre Peninsula, South Australia. Each symbol/ colour combination represents a different site and although there was some variation between transects within the same site, generally transects from each site grouped together.

Based on the initial PCA, eight variables were selected to represent the structure (e.g., ground cover, understorey, upperstorey and density (number of mallee stems and number of logs)) and different components (e.g., leaf litter, logs, shrubs, *Triodia* and mallee) of the vegetation that may be important for *S. psammophila*. In addition to the eight variables selected, we included two variables that we considered important for determining suitable *S. psammophila* habitat. The first was the average height of *Triodia* hummocks (meters). *S. psammophila* have been documented nesting in large *Triodia* hummocks (Churchill 2001b) and large hummocks were favoured by individuals moving through the vegetation (Philp 2011), therefore *Triodia* height and may be a good indicator of suitable *S. psammophila* habitat. The second was an index of overall vertical habitat complexity, which was derived from the pole touch data (e.g., Albanese and Ojeda 2012) using the Shannon-Wiener index (MacArthur and MacArthur 1961). Increased habitat complexity has been correlated to an increase in invertebrates (e.g., Gardner *et al.* 1995; Lassau *et al.* 2005; Barrow *et al.* 2007), which form the main part of *S. psammophila's* diet (Churchill 2001b), and also provide protection from predators (aerial and terrestrial) (Stokes *et al.* 2004). Table 5.1 provides a summary of the final 10 habitat variables used in further analyses.

Retained habitat variables were checked for collinearity using Pearsons correlation coefficient in the R script `Highstats` (Zuur *et al.* 2009). Variables with correlation coefficients of 0.6 or higher were not used together in the same model. Variables that were correlated with each other included shrub.understorey/ triodia.understorey (-0.73) and litter/ bare ground (-0.81). .

Table 5.1 Final 10 habitat variables used in generalized additive models (GAMs) to describe the relationship between *S. psammophila* abundance and its habitat. Variable refers to the abbreviation of the habitat variable used throughout the chapter. Description refers to the vegetation characteristic that was measured. Measurement of variable describes how the variable was measured. Habitat variables were used per transect for further analyses (e.g., GAMs), therefore habitat variables measured at the quadrat level were added across the four quadrats on each transect to give a total per transect. Likewise the number of pole touches for each habitat variable measured with poles was first added across all poles on the transect and then divided by the total number of touches (of all poles on the transect), within the respective height categories, to calculate a proportion of touches per transect.
* Foliage height diversity (MacArthur and MacArthur 1961)

Variable	Description	Measurement of variable
bare.ground	Sand	Proportion of poles with sand ground cover
litter	Leaf litter	Proportion of poles with leaf litter ground cover
logs	Logs (≥ 5cm diameter) on ground	Sum of logs (≥ 5 cm diam.) per quadrat
triodia.understorey	Live *Triodia*	Proportion of *Triodia* pole touches 0 - 50 cm
shrub.understorey	Shrub (e.g. *Grevillea* spp., *Daviesia benthanii*)	Proportion of shrub pole touches 0 - 50 cm
overstorey	Mallee spp. (e.g. *E. socialis*, *E. oleosa*) & shrub spp. (e.g. *Hakea* spp., *Melaleuca* spp., *Acacia* spp.)	Proportion of combined mallee and shrub pole touches 51 - 300 cm
mallee.stems	Mallee stems	Sum of mallee stems per quadrat
floristic.richness	Live plants	Sum of plant species per quadrat
ave.triodia.height	*Triodia* height (m)	Average *Triodia* height per quadrat
habitat.complexity	Vertical vegetation structure	Shannon–Wiener index, Foliage height diversity* (pole touch data)

5.2.4.2 Habitat preferences of S. psammophila

Relationships between the selected habitat variables and total number of *S. psammophila* captures per transect (excluding same session recaptures) were investigated using generalized additive models (GAMs) in the R package `mgcv` (Wood 2011). Differences in the number of trap nights for transects were accounted for by including log(trap nights) as a covariate in each model. Site was added as a random factor in the models to account for correlated capture counts between transects measured at the same site. A set of 44 candidate models was examined; the model set was made up of single variable models and additive pair-wise combinations of all habitat variables (excluding the cases where the variables were strongly correlated as described above). We did not examine more complicated models to avoid over-fitting given the constraints of the available data.

The Poisson distribution was used initially to represent the variance in the counts of *S. psammophila* captures. However, all candidate models exhibited over-dispersion, and so a negative binomial distribution was used for all subsequent analysis. Candidate models were ranked using Akaike's Information Criterion corrected for small sample size (AIC_c) (Johnson and Omland 2004). AIC_c uses information on both the fit and complexity of each model (number of parameters) to rank the candidate models from 'best' (lowest AIC_c score) to 'worst' (Burnham and Anderson 2002; Johnson and Omland 2004). The following were calculated for each candidate model with considerable support ($\Delta AIC_c < 4$) (Burnham and Anderson 2002); AIC_c difference (ΔAIC_c) (difference between the AICc of the model with lowest AIC_c score and the particular model in question), Akaike weight (*wi*) (relative support of a particular model based on the candidate models provided) (Burnham and Anderson 2002) and percentage of null deviance explained by the model (% Dev) (Zuur *et al.* 2009) The relative importance (Σwi) of each habitat variable, the sum of Akaike weights of all models that include the habitat variable in question, was also reported.

5.2.4.3 Influence of fire age class on habitat characteristics and S. psammophila

To investigate the influence of time since fire on *S. psammophila* abundance, sites were established in the four fire age classes within the study region. The number of replicates in each fire age class was constrained by the size of each fire scar and our requirement that each site be at least 1.5 km apart to ensure sites were independent of each other. Therefore we had two sites within the seven years post-fire age class, four sites within the 20 years post-fire age class, two sites in the 39 years post-fire age class and three sites in the long unburnt (60+) years post-fire age class (Figure 5.1).

We used a descriptive approach to investigate the influence of fire age class on *S. psammophila* abundance due to the inherent variability of sites caused by the nature of fire (e.g., patchy burning) which reduced our ability to use a formal test. In addition, fire age class is a categorical grouping of the 11 sites sampled and would therefore compete with the more flexible random site variation if used in a model. The conditional means of the random effect of site generated from the null model (generalised additive model containing *S. psammophila* captures, log(trap nights) and the random effect of site) were extracted, plotted against each site and coloured according to fire age class (Appendix 4). These show the variation in *S. psammophila* captures due to site, and if fire age class had a strong influence on the capture rate we would expect sites of the same fire age class to group together (i.e. sites of the same fire age class would have similar capture rates).

We also examined the effect of fire age on individual habitat variables used in the GAMs. Firstly, a PCA was performed using the R package `vegan` (Oksanen *et al.* 2013) to visually assess if sites within the same fire age class had similar habitat characteristics and therefore grouped together. Secondly, for each habitat variable two single variable GAMs were generated, one with fire age as a categorical variable (GAM_{FIRE}) and the second without fire age ($GAM_{NO\ FIRE}$). The distribution used in each set of GAMs was dependent on the distribution of the habitat variable in question and site was included as a random factor in all models. The two models were ranked using AIC_c (as described above in section 5.2.4.2) to determine whether habitat characteristics differed among fire age classes.

5.2.4.4 Influence of rainfall on habitat preferences and S. psammophila

Rainfall was used as a predictor of resource availability, as rainfall is known to stimulate increases in primary resources in arid and semi-arid systems (Dickman *et al.* 2001; Dickman *et al.* 2011; Morton *et al.* 2011). Rainfall data were obtained from the Bureau of Meteorology using the closest weather station to the field site, approximately 15 km away (Whyalla; Moola, station number 018117; Figure 5.4). During the first year (2011) the region experienced an above average annual rainfall (2011 annual rainfall = 377.6 mm) and large summer and autumn rains that did not occur during the following year (2012; annual rainfall = 188.0) (Bureau of Meteorology 2012a).

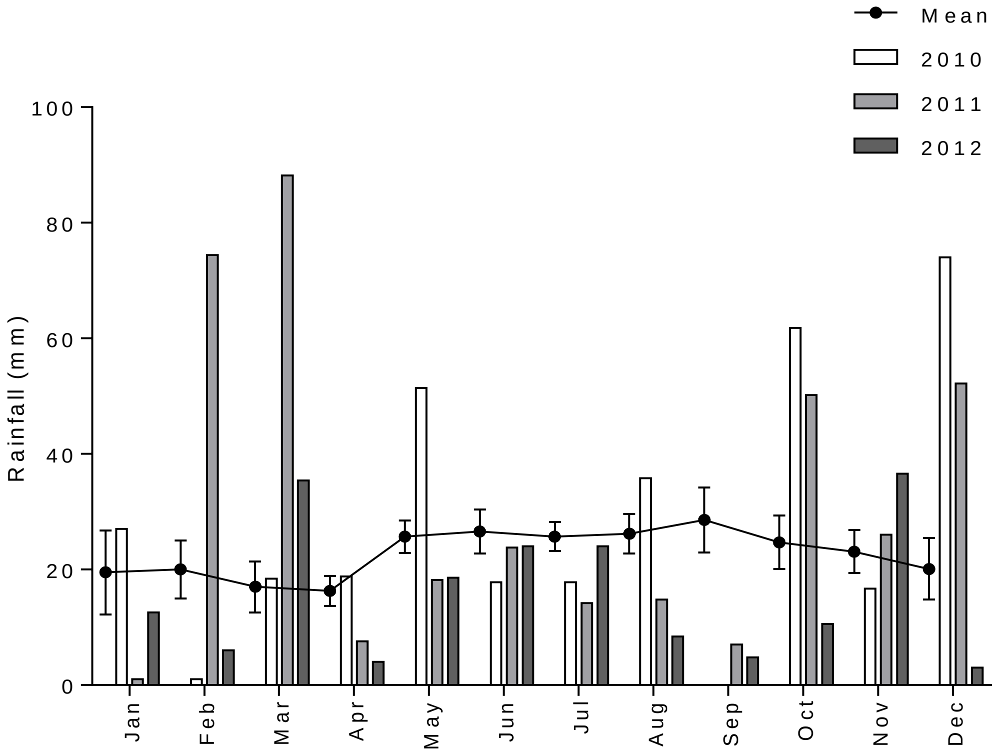

Figure 5.4 Monthly rainfall recorded during 2010, 2011 and 2012 (bars) and mean monthly rainfall (± S.E.) recorded from 1958 to 2012 at the closest weather station to the Middleback Ranges study site, Whyalla (Moola), weather station number 018117 (33.11°S 137.17°E) (Bureau of Meteorology 2012a).

To explore whether any sites acted as potential refugia for *S. psammophila* during low rainfall years, the number of adult male and female residents and suspected transients were recorded at each site for each year. A 'resident' was defined as an individual caught at the same site during more than one trapping session, ignoring same session recaptures as per Marchesan and Carthew (2004) and Masters and Dickman (2012). A 'transient' was defined as an individual that was caught only once at a given site. Only adults (defined here as an animal caught from April onwards in a given year) were included in the analysis as dispersing juveniles may not be caught in habitat that is representative of high quality *S. psammophila* habitat. However if a juvenile was recaptured as an adult later in the year it was included. Only seasonal trapping sessions were used to define residents to ensure that the time period between trapping sessions (three months) was consistent between sites. Various population demographic measures, such as total abundance of the study species (e.g., Martin *et al.* 2010), number of breeding females and/ or number of offspring (e.g., Mosser *et al.* 2009) and number of resident females (e.g., Marchesan and Carthew 2004) have been used previously as indicators of habitat quality. In this study the following population demographics were recorded for each site and each year: the number of adult male and female individuals caught, the total number of adult individuals caught and standardised to 100 trap nights (TN) and the proportion of adult females that were considered residents. In addition, the number of pouch young litters caught during 2011 (high rainfall year) was included as a further indication of high quality habitat, however, no breeding animals were caught during 2012 (low rainfall year) to verify the habitat quality the following year. Our hypothesis was that if a site was consistently of higher habitat quality (e.g., had greater food resources/ shelter compared to other sites) it would be able to support resident adult females during both high and low rainfall (and therefore low resource) years, and may therefore represent habitat refugia or core habitat. In addition, differences in the top habitat variables, identified from the models, between ‘high habitat quality’ sites and other sites were investigated using a Wilcoxon ranked sum test.

GAMs with a negative binomial distribution and a log function were used to investigate differences in habitat preference between years with the R package `mgcv` (Wood 2011). Capture data were split between years (2011 and 2012) and a set of 44 candidate GAMs were produced for each year using the same 10 habitat variables defined in section 5.2.4.1 and GAM parameters defined in section 5.2.4.2. Differences in the number of trap nights per transect were accounted for including log(trap nights) for each year and site was included as a random factor in all models. The majority of *S. psammophila* capture data came from 2011 (high rainfall year) and therefore the model fits for 2012 (low rainfall year) were very poor. Given these considerations we did not include this analysis in our results.

5.3 Results

5.3.1 Capture statistics

A total of 241 captures of 107 individual *S. psammophila* (61 males and 46 females) was obtained during 23,529 trap nights (pitfall and Elliott traps combined) over 2011 and 2012. The overall capture rate of *S. psammophila* was 1.0 captures/ 100 trap nights (TN). *S. psammophila* individuals were caught at all 11 sites during the study, however, captures varied between sites and years (range = 0.0 – 6.3 captures/ 100 TN).

5.3.2 Habitat preferences of S. psammophila

The most important variables for predicting *S. psammophila* abundance were a positive association with the number of logs (≥ 5 cm diameter), a negative association with the average *Triodia* height and a positive association with habitat complexity (Shannon-Weiner index) (Figure 5.5 & Table 5.2 & Table 5.3). The top three models ($\Delta AIC_c < 2.0$, Table 5.1; Burnham and Anderson 2002) contained different combinations of these three covariates and had very similar deviances ranging from 75.5 % to 75.1 %. There was also a significant effect of site and trap effort (number of trap nights) within all candidate models.

Table 5.2 Model selection summary statistics of the generalized additive models describing the relationship between *S. psammophila* abundance (captures) and candidate habitat variables. *S. psammophila* captures (same session recaptures excluded) were modelled using a negative binomial distribution with a log function. Site was added as a random effect to account for correlated capture counts between transects measured at the same site. Differences in trap effort between transects were accounted for by including log(trap nights per transect) as a covariate. AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = difference in AIC_c from minimum AIC_c model, w*i* = Akaike weight of model and % Dev = percentage of deviance explained by model. Models with strong support ($\Delta AIC_c < 2.0$) are highlighted in bold and models with considerable support ($\Delta AIC_c <4.0$) are shown (Burnham and Anderson 2002).

Rank	Model	*df*	AIC_c	ΔAIC_c	*wi*	% Dev
1	**habitat.complexity + ave.triodia.height**	**12**	**216.22**	**0.00**	**0.152**	**75.5**
2	**sq.logs + ave.triodia.height**	**12**	**216.30**	**0.08**	**0.146**	**75.1**
3	**sq.logs**	**11**	**216.56**	**0.34**	**0.128**	**75.1**
4	sq.logs + ln.mallee.stems	11	218.31	2.09	0.053	71.7
5	ave.triodia.height	12	218.63	2.41	0.045	74.2
6	ln.mallee.stems	10	218.96	2.74	0.039	68.8
7	ave.triodia.height + litter	12	219.13	2.91	0.035	73.7
8	ave.triodia.height + ln.mallee.stems	13	219.24	3.02	0.034	75.8
9	sq.logs + triodia.understorey	12	219.24	3.02	0.033	71.8
10	sq.logs + litter	12	219.45	3.23	0.030	71.5
11	sq.logs + bare.ground	12	219.55	3.33	0.029	71.4
12	sq.logs + shrub.understorey	12	219.71	3.49	0.026	71.6
13	sq.logs + habitat.complexity	12	219.99	3.77	0.023	71.5
14	sq.logs + overstorey	12	220.10	3.88	0.022	71.5

Table 5.3 Parameter estimates (estimate and 95 % lower and upper confidence interval) of generalized additive models (GAMs) with strong support ($\Delta AIC_c < 2.0$) describing the association between *S. psammophila* abundance (captures) and candidate habitat variables. *S. psammophila* captures (same session recaptures excluded) were modelled using a negative binomial distribution with a log function. Site was added as a random effect to account for correlated capture counts between transects measured at the same site. Differences in trap effort between transects were accounted for by including log(trap nights per transect) as a covariate.

Rank	Model	Variable	Est.	Lwr CI	Upr CI
1	habitat.complexity + ave.triodia.height	habitat.complexity	1.307	0.217	2.141
		ave.triodia.height	-6.711	-10.697	-3.577
2	sq.logs + ave.triodia.height	sq.logs	0.194	0.062	0.356
		ave.triodia.height	-4.509	-8.392	-1.330
3	sq.logs	sq.logs	0.225	0.043	0.408

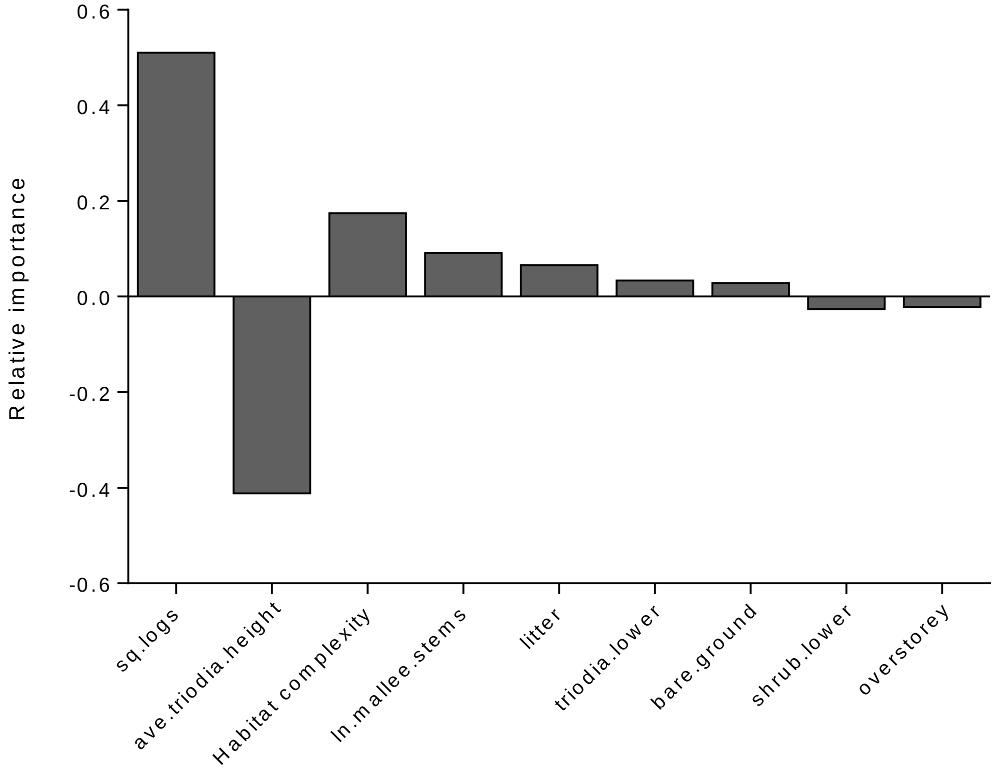

Figure 5.5 Relative importance of each explanatory variable for *S. psammophila* abundance (captures), calculated as the sum of Akaike weights of all generalized additive models (GAMs), used to describe the association between *S. psammophila* abundance (captures) and candidate habitat variables, containing each explanatory variable (Σwi) with $\Delta AIC_c < 4.0$. Direction of weight indicates the positive or negative association with *S. psammophila* abundance based on GAM results.

5.3.3 Influence of fire age class on habitat characteristics and S. psammophila

PCA of the habitat variables revealed two groupings of the sites, those within the seven year post-fire age class grouped separately from the other fire age classes (20, 39 and 60+ years post-fire), indicating that habitat characteristics differed between sites seven year post-fire and the other fire age categories (Appendix 3). The GAM_{FIRE} and GAM_{NOFIRE} of the habitat variables were not distinguishable from each other, which suggests that we did not detect a strong effect of fire age class on the other habitat characteristics measured (Table 5.4). Overall, fire age class did not appear to be a good classification of the habitat characteristics at a particular site, as habitat characteristics varied between sites within the same fire age class.

In addition, we did not detect an effect of fire age class on *S. psammophila* abundance (captures). The plot of the conditional means (extracted from the null model) against site did not show any groupings of sites based on fire age class (Appendix 4), indicating that we did not detect an influence of fire age class on the capture rate of *S. psammophila*.

Table 5.4 Model selection summary statistics of generalized additive models (GAMs) used to assess the influence of fire age class on individual habitat characteristics (response variables) used in GAMs previously to describe the association between *S. psammophila* abundance and habitat characteristics. For each habitat characteristic two single variable GAMs were generated, one with fire age class as a categorical variable (+) and the second without fire age class (-). Models were then ranked from best to worst using Akaike's Information Criterion corrected for small sample size (AIC_c), ΔAIC_c and Akaike weight (*wi*) of each model. Habitat characteristics were ranked from most important to least important for determining *S. psammophila* abundance as per the relative importance (Σwi) previously calculated from GAMs with $\Delta AIC_c < 4.0$ for determining habitat preferences of *S. psammophila*.

Response variable	Fire age class	*df*	AIC_c	ΔAIC_c	*wi*
Number of logs	+	7	263.324	0.000	0.706
	-	8	265.076	1.752	0.294
Ave Triodia height	-	8	-130.452	0.000	0.656
	+	9	-129.164	1.288	0.344
habitat complexity	-	2	-20.700	0.000	0.956
	+	5	-14.500	6.170	0.044
Number of mallee stems	-	10	360.100	0.000	0.604
	+	10	360.945	0.845	0.396
Leaf litter	-	1	60.032	0.000	0.554
	+	4	60.468	0.435	0.446
Triodia understorey	-	1	52.749	0.000	0.935
	+	4	58.079	5.330	0.065
Bare ground	+	4	52.057	0.000	0.808
	-	1	54.928	2.871	0.192
Shrub understorey	-	1	11.288	0.000	0.970
	+	4	18.220	6.932	0.030
Overstorey	-	1	14.073	0.000	0.970
	+	4	21.026	6.953	0.030
Floristic richness	+	7	256.264	0.000	0.814
	-	8	259.215	2.951	0.186

5.3.4 Influence of rainfall on habitat preferences and S. psammophila

Sminthopsis psammophila captures across the study area were significantly lower during 2012 (0.4 captures/ 100 TN) than 2011 (1.9 captures/ 100 TN) (Wilcoxon ranked sum test, W = 246.5, P < 0.001). There was also a decline in the proportion of resident individuals and an increase in transients, representing a considerable decrease in the population of *S. psammophila* during the low rainfall of 2012 (Chapter 2). Captures of *S. psammophila* at individual sites were not consistent between years. For example, Site 9 had a high capture rate during 2011 (12 individuals) and one of the lowest capture rates (1 individual) during 2012 (Table 5.5). Interestingly, three sites (Site 3, 6 and 9) had females with pouch young during 2011, and two of these (Sites 3 and 6) were the only ones where resident females were detected during both years. Based on this, Sites 3 and 6 were identified as possible refugia during the low rainfall year, and were assessed for their potential to provide higher quality habitat than other sites. Little difference in average *Triodia* height, logs and complexity of vegetation was evident between the potential high quality habitat sites (Site 3 and 6) and the other sites (Table 5.6). *Triodia* understorey was higher in the high quality sites (mean = 72 % cover) compared to other sites (mean = 60 % cover), although this difference was not significant (Wilcoxon ranked sum test, *W* = 90.00, P = 0.104) (Table 5.6).

Table 5.5 Population demographic measures of *S. psammophila* during a two year field study west of the Middleback Ranges, South Australia. Total number of adult male and female *S. psammophila* individuals, total number of adult individuals standardised to 100 trap nights (TN), proportion (*n* = sample size) of adult resident females caught at each site during 2011 and 2012 and the number of litters per site during 2011. Only seasonal trapping data (summer, autumn, winter, spring) were included to ensure that the time period between trapping sessions was consistent (3 months) between sites. Sites highlighted indicate potential high quality habitat (resident females both years and pouch young during 2011).

		2011						2012				
Site	Fire age	TN	No. of males	No. of females	Individuals /100 TN	Proportion female residents	No. of litters	TN	No. of males	No. of females	Individuals /100 TN	Proportion female residents
1	7	300	3	1	1.3	0 (*n* = 0)	0	468	4	3	0.9	0 (*n* = 0)
2	7	300	3	0	1.0	NA	0	528	0	0	0.0	NA
3	20	342	3	4	2.0	0.5 (*n* = 2)	2	468	1	2	0.2	0.5 (*n* = 1)
4	20	420	0	0	0.0	NA	0	468	0	0	0.0	NA
5	20	528	1	1	0.4	0 (*n* = 0)	0	492	0	0	0.0	NA
6	20	480	3	5	1.7	0.4 (*n* = 2)	2	468	1	1	0.2	1 (*n* = 1)
7	39	414	0	0	0.0	NA	0	444	1	0	0.2	NA
8	39	486	1	2	0.6	0 (*n* = 0)	0	468	0	0	0.0	NA
9	60	552	9	3	2.2	0.7 (*n* = 2)	1	540	1	0	0.2	NA
10	60	408	0	1	0.2	1 (*n* = 1)	0	480	0	0	0.0	NA
11	60	402	3	1	1.0	1 (*n* = 1)	0	564	2	1	0.4	0 (*n* = 0)

Table 5.6 Wilcoxon ranked sum test (*W*) and P-value were used to determine significant differences in the top three habitat characteristics for describing the association between *S. psammophila* abundance and habitat characteristics (number of logs, habitat complexity and average *Triodia* height) and *Triodia* understorey between the two high quality habitat sites (Site 3 and 6) and other nine sites. Differences in mean (± S. E.) *Triodia* understorey, habitat complexity (Shannon-Weiner index), number of logs ≥ 5 cm diameter and average *Triodia* height between the two potential high quality habitat sites and the other nine sites are reported along with the results of the Wilcoxon ranked sum test.

Habitat variable	High quality sites (Mean ± S. E.)	Other sites (Mean ± S. E.)	*W*	P-value
Triodia.understorey	0.72 ± 0.05	0.60 ± 0.03	90.00	0.104
Habitat complexity	2.28 ± 0.08	2.32 ± 0.03	152.00	0.823
Number of logs	7.38 ± 2.46	7.36 ± 1.14	146.50	0.951
Ave triodia height (m)	0.38 ± 0.02	0.36 ± 0.01	113.50	0.361

5.4 Discussion

This study investigated the habitat preferences of the endangered *S. psammophila* (IUCN 2013) in a semi-arid system, and the influence of fire and rainfall on these preferences. Previous studies and surveys have identified *Triodia* as the main habitat component associated with this threatened mammal (Churchill 2001b; Ward 2009; Philp 2011; Moseby *et al.* in review). Our research across 11 sites in a 10,800 m^2 area found the three most important habitat variables for predicting *S. psammophila* abundance were the number of logs (≥ 5 cm diameter), the average height of *Triodia* hummocks and the overall complexity of the vegetation. Interestingly, *Triodia* height was a negative predictor for *S. psammophila*. We also did not detect a preference for any successional stage of vegetation post-fire. However, there did appear to be an influence of rainfall on the habitat preferences and abundance of *S. psammophila*. This study has highlighted the importance of considering other habitat characteristics in addition to *Triodia* presence, such as the overall complexity of the vegetation, and combining these with climatic variables such as rainfall, when identifying potential *S. psammophila* habitat.

5.4.1 Influence of vegetation structure

Animals use habitat for a number of different reasons, such as protection from predators (e.g., Sundell *et al.* 2012), shelter (nest sites) (e.g., Morrant and Petit 2011) and foraging for food (e.g., Benoit-Bird *et al.* 2013). Here, the abundance of *S. psammophila* was positively associated with logs and habitat complexity, both of which likely reflect enhanced shelter and/or foraging opportunities. Logs have been reported as daytime refuges for a range of nocturnal ground dwelling mammals, including several dunnart species such as male *S. psammophila* (Churchill 2001b), common dunnart (*S. murina*) (Paull 2013) and fat-tailed dunnart (*S. crassicaudata*) (Michael *et al.* 2004; Paull 2013). As individuals move through the landscape, logs and a complex vertical vegetation structure may protect them from aerial and terrestrial predators, such as has been suggested for the yellow-footed antechinus (*Antechinus flavipes*) (Lada *et al.* 2008) and common dunnart (*S. murina*) (Stokes *et al.* 2004). A fine-scale study of habitat use by *S. psammophila* in the same region as the present study reported their avoidance of bare ground and preference for logs, shrubs and *Triodia* when moving through vegetation (Philp 2011). Increased habitat complexity associated with dense vegetation (including *Triodia* and shrubs), logs and leaf litter has also been correlated with increased abundance of some terrestrial invertebrates (e.g., Gardner *et al.* 1995; Lassau *et al.* 2005; Barrow *et al.* 2007), and thus potentially provide increased foraging opportunities for *S. psammophila*. Studies of habitat use in other dasyurid species have reported individuals foraging in leaf litter (e.g., mallee ningaui, *Ningaui yvonneae;* Bos and Carthew 2003) or in open areas (e.g., lesser hairy-footed dunnart, *S. youngsoni*; Haythornthwaite 2005) in close proximity to *Triodia* and retreating back to the protection of *Triodia* to consume their prey. For *S. psammophila*, limited observations showed prey to be most commonly consumed/ attacked on either bare ground or at the edge of cover (e.g., shrubs, *Triodia* or mallee stems) (Philp 2011). These results suggest *S. psammophila* may be more likely to hunt prey in the open, but will retreat back to protective cover to consume prey. Additional studies on the foraging behaviour of *S. psammophila* would help to confirm these assumptions of how *S. psammophila* may use logs and increased habitat complexity.

Triodia has previously been identified as an important habitat component for *S. psammophila* (Churchill 2001b; Ward 2009; Philp 2011; Moseby *et al.* in review) and several other small mammal species (e.g., mallee ningaui, *Ningaui yvonneae*; Bos *et al.* 2002; Kelly *et al.* 2013, wongai ningaui, *Ningaui ridei*; Masters 1993, lesser hairy-footed dunnart, *S youngsoni*; Dickman *et al.* 2001). Our finding of a negative association between *S. psammophila* and average *Triodia* height is seemingly contradictory to the only three other studies of *S. psammophila.* Churchill (2001b) found that the nine individuals radio-tracked on Eyre Peninsula used large *Triodia* hummocks for nest sites on 62 occasions, representing 51 % of nest sites. Philp (2011) observed *S. psammophila* favouring larger *Triodia* hummocks for protection during 24 tracking trials of 16 individuals. Moseby *et al.* (in review) reported that both *Triodia* cover (> 25 %) and the 90th percentile *Triodia* height (> 0.4 m), used as an indicator of tall hummocks that may be used for nesting, were important for determining *S. psammophila* presence. The negative association of *S. psammophila* to *Triodia* height may reflect a preference of *S. psammophila* for smaller, but potentially denser and relatively intact *Triodia* hummocks. These hummocks would likely provide better protection, a cooler micro-climate (Churchill 2001b) and possibly an increased abundance of invertebrates (Diaz 1998) than the taller hummocks. As the *Triodia* hummock begins to die off in the middle (Churchill 2001b), it may become taller, but less dense, and its ability to provide protection for *S. psammophila* would likely be reduced. In a semi-arid system (NSW) Noble and Vines (1993) found that tall and wide *Triodia* hummocks had a greater proportion of dead shoots and a lower proportion of live shoots than smaller hummocks, which would presumably decrease the protective ability of large/wide hummocks. However, additional research into how *S. psammophila* uses *Triodia* of different sizes and structures is needed to further our understanding of the association between *S. psammophila* and *Triodia*.

5.4.2 Influence of fire age class

Despite an expectation that fire may be an important driver in the system, we did not detect any effect of time since fire on *S. psammophila* presence or abundance. Studies on other semi-arid and arid species have also failed to detect a preference for a particular fire age, including the sandy inland mouse (*Pseudomys hermannsburgensis*) (Letnic and Dickman 2005), western pygmy possum (*Cercartetus concinnus*) and common dunnart (*S. murina*) (Kelly *et al.* 2011). This lack of preference for a particular fire age may reflect the stronger influence that rainfall, and the localised resource pulses it brings, has on semi-arid and arid species that are often capable of moving long distances to access resources (Letnic 2003; Letnic and Dickman 2005).

Previous studies on semi-arid and arid dasyurid marsupials have recorded differences in the time it takes species to recolonise an area after it has been burnt. In the Simpson Desert, the lesser hairy-footed dunnart (*S. youngsoni*) and the hairy-footed dunnart (*S. hirtipes*) used vegetation one to five years post-fire inconsistently during a three year study (Letnic and Dickman 2005). While Masters (1993) reported *S. hirtipes* favouring younger sites (one to four years post-fire), *S. youngsoni,* wongai ningaui (*N. ridei)* and brush-tailed mulgara (*Dasycercus blythi*) preferred older vegetation (11 to 14 years post-fire) in Uluru National Park, Northern Territory. In a semi-arid system Kelly *et al.* (2011) observed the common dunnart (*S. murina*) using habitats between one to 70 years post-fire and the mallee ningaui (*N. yvonneae*) favouring older habitats (+20 years post-fire). The length of time taken for *S. psammophila* to recolonise an area after a fire is unknown, although individuals have previously been caught in areas eight years post-fire (Churchill 2001b). The youngest fire age class in our study was seven years post-fire and *S. psammophila* was caught relatively frequently in these sites, suggesting that the vegetation had regenerated enough to provide sufficient habitat. Moseby *et al.* (in review) suggested that there may be a lower limit of vegetation post-fire at which *S. psammophila* can utilise vegetation (approximately 10 years post-fire), but not necessarily an upper limit as *Triodia* is still present in long-unburnt sites (Haslem *et al.* 2011). Seven years post-fire is the youngest fire age vegetation that *S. psammophila* has been recorded in, although we do not know if individuals are able to live permanently in this age class or if they exploit these areas for foraging only. In a semi-arid zone the common dunnart (*S. murina*) was documented using sites from one to 105 years post-fire and Kelly *et al.* (2011) suggested that the lack of preference may be due to *S. murina* utilising different fire age classes for different reasons, such as foraging and nesting. The sandy inland mouse (*P. hermannsburgensis*) and spinifex hopping mouse (*Notomys alexis*) have been documented foraging in younger vegetation, but nesting in adjacent long-unburnt vegetation (Letnic 2002). Our sites seven years post-fire were adjacent to areas of long-unburnt vegetation (39 and 60+ years post-fire), which may have provided nesting opportunities. However, further studies on where individuals forage and nest needs to be conducted to confirm this assumption.

We did not detect a significant influence of time since fire on the habitat characteristics used in our analyses. In fact, the PCA showed only two groupings of sites based on differences in vegetation structure; sites 20, 39 and 60+ post-fire exhibited a similar structure and formed one group, while sites from seven years post-fire had a different vegetation structure and formed the second group. The lack of differentiation between the fire age classes could indicate that most of the changes in vegetation structure occur before 20 years post-fire (Haslem *et al.* 2011), which may be part of the reason why we did not detect an influence of time since fire. In addition, we did not detect a significant effect of time since fire on any of the individual habitat variables used in our analyses. However, the lack of an influence of time since fire on habitat variables may be due to the inherent variability in the system caused by fire and rainfall events (e.g., Noble and Vines 1993). This variability was evident by the variation in habitat characteristics between transects within the same site. In contrast to our study, a comprehensive fire study in a semi-arid *Triodia*/ mallee system incorporating 549 sites across a 110 year post-fire chronosequence found a significant effect of time since fire in nearly every habitat characteristic measured, including the percentage cover of *Triodia scariosa*, low cover (plant matter < 0.5 m), mid cover (plant matter 0.5 – 2 m), canopy cover (plant matter > 2 m), depth of leaf litter and density of logs/ ha (Haslem *et al.* 2011). Future studies investigating the influence of fire should include younger fire age classes (< 7 years) and classes between seven and 20 years post-fire and increase the number of replicates within each fire age class (if possible) in order to account for some of the inherent variability in the system.

5.4.3 Influence of rainfall and identification of potential refugia

In the present study we showed that site had a significant effect in all models, suggesting that site to site variability had a strong influence on the presence and abundance of *S. psammophila*. During the first year (2011) the region experienced above average annual rainfall and large summer and autumn rains, which did not occur during the following year (2012). During the low rainfall year the capture rate of *S. psammophila* was significantly lower and the proportion of resident individuals caught was much reduced compared to the high rainfall year (Chapter 2 and this Chapter). In semi-arid and arid systems variable rainfall produces resource pulses, which results in marked temporal and spatial variability in food resources (Holmgren *et al.* 2006; Dickman *et al.* 2011; Morton *et al.* 2011). The variability observed in capture rates between the sites and years in this study may be due to animals responding to the temporary food resource pulses (ephemeral refugia). The state-and-transition model for spinifex landscapes proposes that animals will leave ‘resource poor’ sites in favour of ‘resource rich’ sites (Letnic and Dickman 2010). The fine-scale population genetic study of *S. psammophila* revealed that gene flow was maintained over relatively large distances (Chapter 4) and Chapter 2 speculated that individual *S. psammophila* were capable of travelling relatively long distances to find resource patches when they become available. Arid rodents (e.g., long-haired rat, *Rattus villosissimus*) and dasyurids (e.g., the lesser hairy-footed dunnart, *S. youngsoni*) have been observed tracking rainfall events, presumably to exploit the food resources they bring (Dickman *et al.* 1995; Letnic 2002; Greenville *et al.* 2013). In Chapter 2, we detected an increase in the proportion of transients and a decrease in the time residents spent at a site during the low rainfall year, which suggests that individuals can change/ increase their movement patterns when resources are low. However, additional research on changes in the presence/ abundance of *S. psammophila* and foraging behaviour at sites during periods of high and low rainfall is needed to investigate the potential use of ephemeral refugia by *S. psammophila*.

The ecological refuge model and state-and-transition model for spinifex landscapes suggest that some species may contract back to areas of higher quality habitat (termed drought refugia in the ecological refuge model) during drought years and then expand from these regions when conditions are favourable (Morton 1990; Letnic and Dickman 2010). In Chile, drought refugia for two native rodents, the long-tailed rice rat (*Oligoryzomys longicaudatus*) and the long-haired grass mouse (*Abrothrix longipilis*) have been identified and populations have been observed to contract back to fog forests and riverine shrublands (refugia) during low rainfall years and then expand into neighbouring thorn shrub during high rainfall years (Milstead *et al.* 2007). The presence of pouch young during the high rainfall year and the continued presence of resident female *S. psammophila* at two sites during this study, may suggest that these sites are of particularly high habitat quality or are able to retain their habitat quality between years, and possibly act as refugia. However, no substantial difference was detected between the key habitat characteristics in these two sites compared to the other sites, except for a trend of increased *Triodia* cover at the higher quality sites. Studies that have attempted to find drought refugia for arid mammals have had various levels of success (e.g., Paltridge and Southgate 2001; Haythornthwaite and Dickman 2006a; Milstead *et al.* 2007; Southgate *et al.* 2007; Foley *et al.* 2008; Dickman *et al.* 2011; Pavey *et al.* 2014). However, to the best of our knowledge, no drought refugia have been detected for dasyurid marsupials.

Areas that have previously been identified as drought refugia have been habitat types, such as cracking clay for plains rats (*Pseudomys australis*) (Brandle *et al.* 1999; Pavey *et al.* 2014) and creek line mulga for various Australian arid bird species (Craig and Chapman 2003), rather than discrete patches within a habitat. However, in our study site there does not appear to be a particular type of vegetation that may act as refugia for *S. psammophila*. Based on the broad-scale genetic analyses, it is possible that the whole study area is an evolutionary refugium (Byrne *et al.* 2008) and *S. psammophila* has been able to exist in the region at generally low numbers during previous drought periods (Chapter 4). During our study *S. psammophila* appeared to increase its nomadic behaviour during the low rainfall year, with the proportion of transient individuals increasing and the time residents spent at sites decreasing (this Chapter and Chapter 2). In a previous study, the behaviour of the spinifex hopping mouse (*N. alexis)* appeared similar to that of *S. psammophil*a, with individuals becoming more nomadic during dry years, possibly to utilise microsites under trees and shrubs that harboured food resources (Dickman *et al.* 2011). *S. psammophila* may utilise similar microsites within *Triodia* habitats, such as accumulations of leaf litter under mallee trees or *Triodia* hummocks. Alternatively, *S. psammophila* may exist in very low densities during dry periods and become very difficult to detect using trapping methods, such as for the brush-tailed mulgara (*Dasycercus blythi*) (Dickman *et al.* 2011). Further long-term studies will be needed to track the presence and abundance of *S. psammophila* at different sites and fine-scale habitat use during both high and low rainfall years to determine how *S. psammophila* uses the habitat and how populations persist during droughts.

5.5 Conclusion

In this study we have shown that *S. psammophila* abundance was positively associated with the number of logs (≥ 5 cm diameter) and the overall vertical complexity of the vegetation and negatively associated with the average height of *Triodia* hummocks. There was no significant influence of fire age class detected on either the habitat characteristics used to define habitat preference of *S. psammophila* or abundance of *S. psammophila*. However, we did detect an influence of rainfall on the habitat preferences and abundance of *S. psammophila*. During the high rainfall year *S. psammophila* was abundant and widespread, but during the low rainfall year population size of *S. psammophila* was reduced and resident individuals were confined to only a few sites. These observations may suggest a contraction of individuals back to sites of higher quality habitat during low rainfall years and highlights the need to define critical habitat for *S. psammophila*, particularly during low rainfall years. Identification and protection of critical/ refuge habitat and a greater understanding of how *S. psammophila* persists during low rainfall years will be needed to effectively manage this endangered species.

CHAPTER 6: General Discussion

Sunset from the top of a dune, Middleback Ranges, South Australia. Photo A. McLean

6.1 Overview

This final discussion chapter highlights and brings together the main findings of the thesis and discusses the implications of this work for the conservation management of the sandhill dunnart (*Sminthopsis psammophila*). This research has contributed new information to the fields of ecology and population genetics of arid and semi-arid zone species, and, more specifically, the findings will assist with the management of this endangered (IUCN 2013) species.

Prior to the commencement of this study only a handful of *S. psammophila* individuals were known from three regions across a broad geographical range and, additionally, mining activities had increased within the species' known distribution. Concern about this situation resulted in the formation of the Sandhill Dunnart Recovery Team by the Department of Environment, Water and Natural Resources (DEWNR) in South Australia to bring together people who were currently involved in survey and research work on *S. psammophila*. This development occurred at the commencement of field work for my study, and I was invited to be a part of the team. Prior to joining the recovery team I had already identified significant gaps in our knowledge of the ecology, phylogenetics and population genetics of *S. psammophila* and was in the process of designing my project to increase our knowledge in several of these areas. The recovery team agreed that the findings of my study would be highly valuable for developing a conservation management plan for *S. psammophila* and the members helped to focus the study design (e.g., trapping grid design) and contributed tissue samples for the molecular work. All findings from this study have been shared with the Recovery Team and used in the development of the National Recovery Plan for the Sandhill Dunnart that will direct future research priorities for *S. psammophila*.

Findings detailed in this thesis also make a significant contribution to our understanding of how dasyurids persist in an environment with variable food resources. In particular, the results of the fine-scale genetic analyses of *S. psammophila* add to the findings of relatively high mobility in semi-arid and arid mammals based on capture-mark-recapture studies, and reveal dispersal patterns that maintain genetic diversity in *S. psammophila*, which are possibly applicable to other semi-arid/ arid mammals. Methodologically, the study highlights the advantages of combining molecular approaches with capture-mark-recapture data to provide a more comprehensive picture of movement patterns in a rare species. In the following sections, I provide an overview of my findings on the biology of *S. psammophila* and how these findings relate to the persistence of *S. psammophila* in a semi-arid system. I then use the knowledge from the thesis to provide recommendations for the management of *S. psammophila* at both national and regional scales. Finally, I discuss areas for future research that I anticipate will be important to further our understanding of *S. psammophila* and improve our ability to conserve this species effectively.

6.2 Biology of *S. psammophila* in a semi-arid environment

6.2.1 Movement patterns in S. psammophila

In a system where food resources can vary greatly within and between years, it would be advantageous for both sexes to disperse from their natal areas and remain relatively mobile during their lives. In accordance with this hypothesis, no sex-biased dispersal was detected in *S. psammophila* using either capture-mark-recapture (Chapter 2) or genetic (Chapter 4) methods. However, both techniques suggest that males are slightly more mobile than females, a trend that has been observed in other dunnarts, such as the little long-tailed dunnart (*S. dolichura*) (Friend *et al.* 1997) and lesser hairy-footed dunnart (*S. youngsoni*) (Haythornthwaite and Dickman 2006b). Dispersal of individuals is important for maintaining genetic diversity in populations and it is the main driver of genetic structure (Berven and Grudzien 1990). The lack of sex-biased dispersal and natal site fidelity, especially in females, suggests that both sexes disperse from their natal areas prior to breeding. This behaviour promotes a high level of genetic ‘mixing’ within the population that is reflected in the lack of any significant genetic structure identified within the (24,000 ha) Middleback study site (Chapter 4). Very few fine-scale genetic studies have been conducted on arid or semi-arid species, and to the best of my knowledge, this study is the first on a semi-arid dasyurid. However, previous mark-recapture (Letnic *et al.* 2004; Letnic and Dickman 2005; Letnic *et al.* 2005) and radio tracking (Letnic 2002; Masters 2003; Haythornthwaite and Dickman 2006b) studies of arid species (rodents and dasyurid marsupials) also indicate that Australian arid and semi-arid species are highly mobile despite their small size.

Rainfall, which I used as a proxy for food resources, was found to affect mobility in *S. psammophila*. During the low rainfall year, as well as observing a decrease in population size, individuals appeared more mobile (increased proportion of transients and decreased time spent at sites by residents) than during the high rainfall year. An increase in the movement of individuals during low rainfall years (at least in part because they presumably needed to travel further to find resources) would assist with the maintenance of gene flow and genetic diversity within the population, despite a reduction in population size. A study of the arid banner-tailed kangaroo rat (*Dipodomys spectabilis*) found that the proportion of dispersers increased when population numbers were low during low rainfall years and this facilitated gene flow between subpopulations (Waser and Elliott 1991; Waser *et al.* 2006). Only a few individuals needed to successfully disperse between the *D. spectabilis* subpopulations to remove any signature of a genetic bottleneck (Busch *et al.* 2007), and a similar scenario may exist in *S. psammophila*.

A high proportion (51 %) of the marked population was transient (captured only once during the study) and this may indicate that individuals travel relatively long distances when foraging to find food resources. This behaviour is consistent with other species, such as the lesser hairy-footed dunnart (*S. youngsoni*), which has been recorded travelling 2.5 km in one night (Haythornthwaite and Dickman 2006b). A preliminary radio-tracking study of *S. psammophila* at Middleback Ranges by Churchill (2001b) also provided some evidence that during foraging, both males (maximum of 1960 m in two hours, average ± S.E. = 379.5 ± 34.1 m, n = 3 individuals) and females (maximum of 950 m in one hour, average ± S.E. = 277.7 ± 58.2 m, n = 2 individuals) are able to travel long distances relatively quickly. In addition, the study found that males and females remained in an average area of approximately 11.2 ha (n = 3) and 5.8 ha (n =3) respectively, during a two to 10 day period. The study also recorded one instance of a female *S. psammophila* moving her home range 400 m west during two separate tracking sessions eight months apart. Based on these results, Churchill (2001b) suggested that *S. psammophila* may have a moderately stable home range. During my study, individuals of both sexes were regularly re-trapped at the same site across months and seasons (females up to 12 months and males up to 14 months between first and last captures) (Chapter 2), suggesting that at least some individuals may remain in an area and establish a home range. However, this was affected by rainfall (see Chapter 2 and section 6.1.2.2 for further discussion), once again supporting the notion that *S. psammophila* is highly responsive to food resource availability (dictated by rainfall), and has the ability to adjust its ranging patterns in accordance to this. Such flexibility is likely to be a requirement of survival in Australian semi-arid zones, although further research on fine-scale movement patterns would help to confirm this.

6.2.2 *Factors influencing the presence and abundance of* S. psammophila

6.2.2.1 Vegetation structure and time since fire

The presence and abundance of *S. psammophila* across my study area was positively associated with the number of logs (≥ 5 cm diameter) and the overall vertical complexity of the vegetation (Chapter 5). These habitat characteristics may provide protection from predators (aerial and terrestrial) as individuals move through the vegetation (Stokes *et al.* 2004) and a source of food resources (invertebrates) (e.g., Gardner *et al.* 1995; Lassau *et al.* 2005; Barrow *et al.* 2007). The preference of *S. psammophila* for areas of increased habitat complexity is interesting given its ability to move quickly and easily across open areas (Philp 2011) and probably reflects a trade-off between ease of movement and perceived predation risk.

Previous studies and surveys have suggested that *Triodia* cover is an important habitat component for the persistence of *S. psammophila* (Churchill 2001b; Ward 2008; Ward 2009; Philp 2011; Moseby *et al.* in review) and Churchill (2001b) documented individuals (*n* = 9) nesting in large *Triodia* hummocks. In my study, there was a negative correlation between *S. psammophila* abundance and average *Triodia* height. This result was surprising, but may indicate that individuals favour areas with smaller, potentially denser, intact hummocks that have not begun to break down in the centre (Stage 2) with these *Triodia* likely to provide greater protection from predators and extreme temperatures (Churchill 2001b). The findings of my study suggest that the height and structure of the hummock may be important in determining suitable *S. psammophila* habitat; however, research on the fine-scale habitat use of *S. psammophila* (incorporating hummock structure) is needed to investigate this further.

Time since fire has a strong influence on the occurrence and structure of *Triodia* (Haslem *et al.* 2011), however, my analyses did not detect a preference of *S. psammophila* for vegetation of a particular age related to time since fire (Chapter 5). There are two possible explanations for this. Firstly, the apparent lack of preference may be an indication that rainfall, and the resource pulses it brings, has a greater influence on *S. psammophila* presence than the vegetation structure related to time since fire (Letnic 2003; Letnic and

Dickman 2005). Alternatively, the absence of very young fire age classes, less than seven years post-fire, within my broad study site precluded the full breadth of age classes from being tested. Although large hummocks for nesting have not re-grown by seven years post-fire, these sites could still provide foraging opportunities, with adjacent older sites possibly providing nest sites (as observed in the spinifex hopping mouse, *N. alexis*; Letnic 2002). Further research incorporating sites younger than seven years post-fire should be incorporated into future studies (if possible) to determine at what age post-fire habitats become hospitable for, and are recolonised by *S. psammophila*.

6.2.2.2 Variation in rainfall

As mentioned above, rainfall had a strong influence on the presence and abundance of *S. psammophila* (Chapter 2 and 5). Reduced rainfall during 2012 produced a rapid and negative response in the *S. psammophila* population with significantly lower capture rates, survival rates of second year females and post-dispersal juveniles and proportion of resident individuals recorded (Chapter 2). In addition, there also appeared to be a delay in the timing of mating or a reduction in the number of individuals that bred during the low rainfall year (Chapter 2).

Field data from this study confirmed that *S. psammophila* exhibits a Strategy V life history (Lee *et al.* 1982; Lambert *et al.* 2011), with a seasonal but extended breeding period (late-July to November) (Chapter 2). Due to its relatively fixed life history, the timing and total quantity of rainfall may be important in determining the reproductive response of *S. psammophila* in a given year. During the low rainfall year (2012) the region received just over half of its average annual rainfall. However, perhaps more importantly, there was a lack of large summer/autumn rain events that year, which had occurred during the high rainfall year (2011). The above average summer/autumn rains in 2011 may have stimulated food resources for second year females recovering from the high stress of lactation and post-dispersal juveniles, which together enabled a larger proportion of the population to survive. The rainfall in the region varies year to year, as in all semi-arid systems, and in the last 23 years the region has experienced four years of significantly above average rainfall (>100 mm above the annual average) and four years of significantly below average rainfall (< 100 mm below the annual average) (Bureau of Meteorology 2012a). Generally, low and high rainfall years last for one to two consecutive years, with extreme low or high years (average annual rainfall ± 100 mm) lasting only a year. However, the cumulative effect of consecutive below average rainfall years may be of concern for the long-term persistence of *S. psammophila*, given the species' negative response to low rainfall, particularly when combined with other threatening processes (e.g., predation).

Rainfall appeared to influence not only the size of the population, but also the locations or the likelihood of capturing *S. psammophila* at particular sites. Capture rates and the number of resident individuals differed between both sites and years, suggesting that the habitats at these sites were not of equal quality, and/ or the quality of the sites may change over time (Chapter 5). For example, capture rates at Site 9 were high during the high rainfall year (2012), but very low the following year although structurally the vegetation remained relatively constant. The state-and-transition model for spinifex landscapes proposed by Letnic and Dickman (2010) incorporates aspects of the ecological refuge model (Morton 1990), and suggests that there are areas of high quality habitat (referred to as drought refugia in the ecological refuge model) that populations retreat back to during low resource years and then expand from during high resource years. Drought refugia have been detected for several Australian arid rodent species (e.g., use of cracking clay by plains rats, *Pseudomys australis;* Brandle *et al.* 1999; Pavey *et al.* 2014), but not yet for arid or semi-arid dasyurids (although there has been very little focus on this to date). Within this study area I was able to identify two sites that consistently recorded resident females during both high and low rainfall (resource) years. These sites may represent areas of high quality habitat that could act as refugia for *S. psammophila*, however, they were not identified as such by the habitat models (Chapter 5). Letnic and Dickman (2010) suggested that ecological refugia would most likely be a type of habitat, rather than a specific area within a habitat. However, within my study site there does not appear to be a different, identifiable habitat type that could act as refugia for *S. psammophila*. Indeed, I found an increase in the nomadic behaviour of *S. psammophila* during the low rainfall year (higher proportion of transients and less long-term site fidelity), suggesting that animals were not confined to particular sites. Similarly, the spinifex hopping mouse (*N. alexis*) has been shown to increase its nomadic behaviour during low resource years and individuals were thought perhaps to utilise "microsites"; accumulations of litter under trees that harbour food resources (invertebrates and seeds) (Dickman *et al.* 2010; Dickman *et al.* 2011). *S. psammophila* may also utilise microsites within *Triodia* habitats, however, a longer term study incorporating multiple high and low rainfall events, and a fine-scale assessment of habitat use, is needed to further investigate the potential use of drought refugia in *S. psammophila* and help explain how this species persists during drought years.

6.3 Implications for conservation management of *S. psammophila*

Sminthopsis psammophila is classified as Endangered (IUCN 2013) and is potentially threatened by habitat loss and fragmentation, changing fire regimes, introduced predators (domestic cat, *Felis catus*, and red fox, *Vulpes vulpes*), increased mining activities (Churchill 2001a) and climate change. In order to conserve the species effectively, it is important to protect and manage the known populations of *S. psammophila* to ensure each population retains adequate habitat and resources (food and shelter) for the future. Management techniques such as protecting suitable habitat and preserving the full range of genetic diversity within *S. psammophila* will provide the species with the maximum potential to respond to future challenges (Lande 1988; Frankham 2005; Hedtke *et al.* 2007).

6.3.1 National-scale management

The results of this study led to the conclusion that the three known core *S. psammophila* populations were connected historically but are now genetically differentiated (Chapter 4). However, there was no evidence of long-term isolation of the populations. From these findings and the criteria of Moritz (1994), each core population of *S. psammophila* should be considered, at least, as separate Management Units (MUs) rather than Evolutionarily Significant Units (ESUs), as each population showed significant allele frequency differences at nuclear and mtDNA loci. The classification of MUs suggests that gene flow is low between the core populations and the populations are functionally separate (Moritz 1994). However, given the large geographical distances (508 km to 1,323 km) between the three core populations, south-west Great Victoria Desert (SW-GVD), Yellabinna Regional Reserve area (Y) and Eyre Peninsula (EP), the difficulty of accessing these areas and the relatively intact vegetation in the north, the core populations may still possibly be connected through ‘stepping stone’ populations that have not yet been detected. I therefore recommend that surveys be conducted in suitable *S. psammophila* habitat between the three known populations to detect any additional populations. There appears to be relatively intact and suitable vegetation (spinifex – mallee community) in the Great Victoria Desert between SW-GVD and Y, northern EP and south of the Gawler Ranges between Middleback Ranges and Y. Genetic samples should be taken from any new *S. psammophila* localities detected to map the gene flow across the species' range. I recommend that the levels of genetic diversity in each core population (and any additional locality that may be detected) be monitored in the future to ensure that any loss does not go undetected.

If a loss of genetic diversity is detected within one or more of the core populations, strategies to re-establish gene flow between the populations in order to prevent loss of genetic diversity and adaptive potential may need to be considered (Frankham 2005, 2010b). Re-establishment of gene flow between the known populations could be achieved by translocation of individuals from one population into another or by establishing new (connecting) populations if none are detected through surveys (Weeks *et al.* 2011). These types of translocations have been referred to by Weeks *et al.* (2011) as 'genetic adaptation' with the aim of increasing the genetic adaptability of the species and enabling it to cope with future threats, like climate change. This approach is being increasingly considered in conservation biology to restore genetic diversity to small, isolated populations (e.g., Mitrovski *et al.* 2008). Although translocations can be a valuable conservation tool, prior to implementing this approach, ecological exchangeability should be considered in conjunction with genetic information (Crandall *et al.* 2000). Ecological exchangeability takes into consideration the adaptive divergence of populations to different environmental conditions through genetic drift and natural selection. For example, Y and SW-GVD are situated in an arid climate, but EP populations are in a semi-arid climate. Therefore, there may be adaptive differences between the populations (Y/ SW-GVD and EP) that would warrant separate management. Further research into variability of life history traits such as timing of breeding and differences in behaviour would assist with this. However, given the relatively large regions the core populations currently occupy and the high probability of additional populations existing, there is no current need for translocation to be considered.

6.3.2 Regional-scale management

The relative high mobility of *S. psammophila* (Chapter 2 and 4) and variability of food resources in the semi-arid system it resides in suggests that large areas of continuous suitable habitat will need to be protected to maintain viable populations (e.g., Dickman *et al.* 1995). The results of Chapter 4 suggest that the entire study area of 24,000 ha is a single panmictic population and therefore the area that presently consists of both private and government land should be managed as a whole. A large continuous area with complex vegetation structure will be needed to ensure that even during low rainfall years there are adequate food resources to maintain the *S. psammophila* population. The development of access tracks for mining exploration and roads should be minimised to limit access of introduced predators (domestic cats, *F. catus* and red foxes, *V. vulpes*) and prevent degradation of suitable habitat. The maintenance of large areas of continuous suitable vegetation will ideally lessen the initial negative effect of wildfires by allowing animals to find refuge in unburnt areas. Although this study did not look specifically at the effects of predation, an important future direction would be to explore the interactions between predation, fire and rainfall on *S. psammophila* persistence.

The preference of *S. psammophila* for complex vegetation structure, including logs and *Triodia* cover, suggests that individuals may not use very recently burnt vegetation (< 7 years post-fire) and that frequent burning of the vegetation may negatively affect the species. Based on current evidence, climate change is predicted to result in increased temperatures, lower rainfall and greater variability of climatic conditions worldwide (IPCC 2013). Climatic data from the Simpson Desert has shown that the average temperature and rainfall variability have increased over the past 100 years (Greenville *et al.* 2012). An increase in the frequency of large rainfall events may in turn increase plant biomass and create more frequent and intense wild fires (Greenville *et al.* 2012). Increased fire frequency may be detrimental to *S. psammophila* and I recommend retaining older habitat in the landscape.

6.4 Future research

This study, as well as providing new knowledge on a rare species, has also indicated priorities for future research. A key area for future research will be to gain a better understanding of the habitat preferences of *S. psammophila*. In this study I was constrained by the number and size of previous fires in the landscape and ideally would have included sites of younger fire age classes (< 1 – 7 years post-fire) and a larger number of replicates within each fire age class. Future studies could aim to determine when *S. psammophila* re-colonises sites after fire and, importantly, whether and how *S. psammophila* uses recently burnt vegetation. Understanding these interactions will increase our limited knowledge on the preferences of arid and semi-arid dasyurid marsupials for vegetation of a particular successional stage post-fire and help to develop an appropriate ecological burning regime for *S. psammophila*.

The interpretation of findings from the habitat preference component of this study (Chapter 5) was limited by our current knowledge on how *S. psammophila* uses its habitat. Future research on the fine-scale habitat use of *S. psammophila*, such as understanding where individuals forage, will aid in determining suitable habitat that should be protected for the species. In addition, knowledge about how habitat use changes due to changes in seasonal fluctuations of invertebrates and the life cycle of *S. psammophila* (breeding vs non-breeding) and between years of variable rainfall, will help to define areas of critical or refuge habitat that may be important during drought years. Due to the complex interactions that occur in arid and semi-arid zones the same sites should be monitored over multiple years and during multiple periods of high and low rainfall. Information on how the population survives during droughts will not only aid in protecting *S. psammophila*, but also provide valuable insights into how other arid and semi-arid dasyurid marsupials persist in these variable environments.

During this study I observed a significant decline in capture rates during the low rainfall year. I attributed this decline to a low survival rate of second year animals and post-dispersal juveniles caused by a reduction in food resources (Chapter 2). However, a longer-term study focused specifically on the influence of rainfall on a number of reproductive parameters (i.e., the timing of mating, reproductive output (number of breeding females and number of litters) and juvenile survival and recruitment into the breeding population) in *S. psammophila* is needed to confirm the observations from this study. I suggest surveys once a month during the breeding season (between at least September and October) each year at the same sites to obtain this information.

It is currently assumed that predation is a threat to *S. psammophila*, however, the actual effect of introduced predators is unknown and currently the core populations are surviving in the presence of both domestic cats (*F. catus*) and red foxes (*V. vulpes*). A study looking at the effects of predation on *S. psammophila* and interactions between rainfall, *S. psammophila* abundance and predator abundance, although complex, would be valuable in assessing when predation may be most detrimental to *S. psammophila* and when management actions, such as baiting, may be most beneficial.

Further study is also warranted on the seemingly isolated reserves on the Eyre Peninsula where *S. psammophila* has previously been detected (Hambridge Conservation Park (CP), Hinks CP and Pinkawilline CP) (Churchill 2001b, J. Read and K. Moseby unpublished data). Research should focus on determining how widespread the species is in these reserves and whether the reserves are large enough to sustain viable populations. Survey work should also incorporate the collection of tissue samples for genetic analyses to assess genetic composition and diversity, level of connectivity both within and between reserves and the effect of habitat fragmentation on the species. For isolated reserves, management strategies, such as increasing connectivity using habitat corridors or translocations could be considered to reduce the impact of environmental (e.g., wildfire), demographic and genetic stochastic effects (Lande 1988) on the populations residing in the reserves.

6.5 Conclusion

This thesis has provided valuable insights into aspects of the ecology and population genetics of *S. psammophila* that will ultimately assist in its conservation and management. The combination of ecological and genetic data shows that *S. psammophila* is highly mobile and maintains high levels of gene flow across large areas (24,000 ha). The fine-scale genetic analyses revealed that both males and females disperse from their natal areas prior to breeding. The dispersal patterns detected in this study provide insights into how arid and semi-arid mammals maintain connectivity and genetic diversity in a variable environment. The ecological data gathered on *S. psammophila* has added to the growing body of literature on the influence of rainfall in semi-arid systems and how species that reside in these areas cope with variable food resources. In addition, this study has also provided some insights into the use of different fire age classes by *S. psammophila* and highlighted important areas for future research. This thesis has answered some important questions regarding the biology of *S. psammophila*, which will contribute to determining suitable management options for the species, both nationally and regionally.

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Appendices

Triodia hummock west of the Middleback Ranges, South Australia. Photo A. McLean

Appendix 1

Pouch development in female *S. psammophila* classified into Stages 0 – 6 based on the visible changes in the pouch from descriptions by Woolley (1990a) and Godfrey (1969) for the strip-faced dunnart (*S. macroura*) and Smith (1984) for the yellow-footed antechinus (*A. flavipes*) and timing of life events in the life cycle of *S. psammophila*.

Stage	Pouch description	Life stage (Months)	Photo
0	Pouch small (hard to find in first year females), clean, no middle or edge ridge visable, pale. Teats small and pale (first year female, button shape; second year female, elongated).	Undeveloped (Jan-Mar)	
1	Pouch small, clean and edge ridge just visible. Teats pale pink and slightly larger than Stage 0.	Developing (Apr-Jul)	
2	Pouch small to medium, clean, middle and edge ridges starting to develop. Teats pale/dark pink and becoming more visible.	Mating (Aug-Sep)	
3	Pouch large, middle and edge ridges are fully developed, pouch is clean. Teats large, elongated and red/dark pink.	Pregnant (?) (Sep-Oct?)	
4	Pouch young present, pouch fully developed. Teats large, elongated and red.	Pouch young (Sep-Oct)	
5	Pouch fully developed, no pouch young, stain in pouch and around teats, lactating. Teats large, elongated and red.	Nest young (Nov-Dec?)	
6	Pouch regressing after young are weaned, similar to Stage 2, possible stain around teats.	Regressing (Dec-Feb?)	

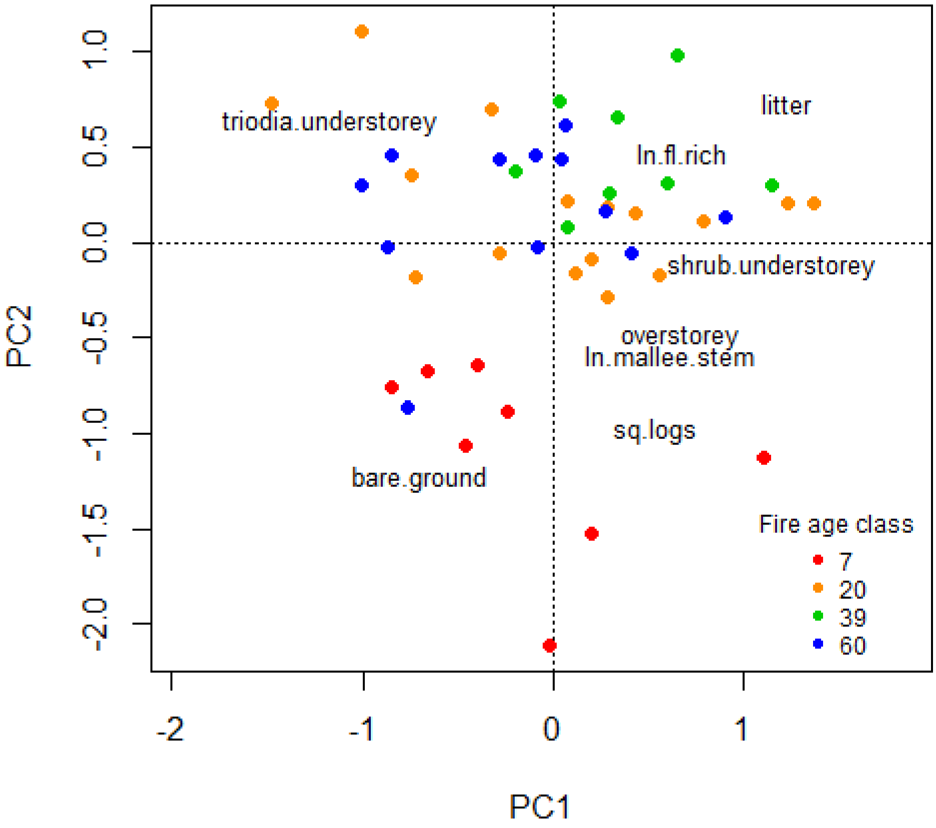
Appendix 2

The full range of habitat characteristics considered during initial data exploration using a principal components analysis (PCA). A combination of number of poles, proportion of touches of each habitat characteristic at each height class and quadrat measurements were used to capture variation in vegetation structure between the 11 *S. psammophila* sites sampled west of the Middleback Ranges, Eyre Peninsula, South Australia.

Type of measurement	Structural height	Habitat characteristic
Number of poles	Ground cover	Proportion of ground cover leaf litter
		Proportion of ground cover *Triodia*
		Proportion of ground cover bare ground
		Total cover (sum of all plant cover)
Pole touches	0 - 10 cm	Proportion of touches shrubs
		Proportion of touches *Triodia*
	11 - 20 cm	Proportion of touches shrubs
		Proportion of touches *Triodia*
	21 - 30 cm	Proportion of touches shrubs
		Proportion of touches *Triodia*
	31 - 40 cm	Proportion of touches shrubs
		Proportion of touches *Triodia*
	41 - 50 cm	Proportion of touches shrubs
		Proportion of touches *Triodia*
	Understorey (0 - 50 cm)	Proportion of touches shrubs
		Proportion of touches *Triodia*
	51 - 100 cm	Proportion of touches shrubs
		Proportion of touches mallee
		Proportion of touches *Triodia*
	101 - 150 cm	Proportion of touches shrubs
		Proportion of touches mallee
	151 - 200 cm	Proportion of touches shrubs
		Proportion of touches mallee
	201 - 300 cm	Proportion of touches shrubs
		Proportion of touches mallee
	300+ cm	Proportion of touches shrubs
		Proportion of touches mallee
	Overstorey (51- 300 cm)	Proportion of touches shrubs
		Proportion of touches mallee
Quadrat		Ave. *Triodia* height
		Ave. Triodia length
		Ave. *Triodia* width
		Ave. *Triodia* volume
		Number of *Triodia* hummocks
		Number of shrubs
		Number of logs ≥ 5 cm diameter
		Number of mallee stems
		Floristic richness

Appendix 3

PCA scaling ordination plot of the eight retained habitat variables measured at four transects per each of the 11 sites where *S. psammophila* was captured during the two year study west of the Middleback Ranges, Eyre Peninsula, South Australia. Transects are coloured based on the fire age class for each site. There was strong evidence that the habitat characteristics of sites 7 (red) years post-fire were different than the habitat characteristics of sites from the remaining fire age class, 20 (orange), 39 (green) and 60+ (blue) years post-fire.



Appendix 4

Conditional means of the random effect of site (± S.E.) were extracted from the null model of *S. psammophila* abundance (captures), plotted against site and coloured by fire age class, 7 (red), 20 (green), 39 (blue), 60+ (purple) years post-fire, to investigate the influence of fire age class on *S. psammophila* across the 11 *S. psammophila* sites sampled west of the Middleback Ranges, Eyre Peninsula, South Australia. *S. psammophila* captures (same session recaptures excluded) were modelled using a negative binomial distribution with a log function. Site was added as a random effect to account for correlated capture counts between transects measured at the same site. Differences in trap effort between transects were accounted for by including log(trap nights per transect) as a covariate. The plot does not show any strong grouping of the 11 sites based on fire age class and therefore suggests that no effect of fire age class on *S. psammophila* abundance (captures) was detected.