Resource use and preference of the southern ningaui, *Ningaui yvonneae* (Dasyuridae: Marsupialia), in the Middleback Ranges, South Australia.

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Abstract

This study was the first detailed investigation on the ecology of the southern ningaui (*Ningaui yvonneae*). It focused on the use of resources by this small nocturnal species, with particular reference to diet and habitat. Baseline information on *N. yvonneae*'s biology and population ecology found that *N. yvonneae* had an annual and seasonal breeding cycle which commenced after winter (early October). This was thought to be linked to the increase in prey availability and timed to maximise the opportunities for juveniles to survive the following winter (a time of stress for *N. yvonneae*). *N. yvonneae* was also recorded to have a relatively high capture rate, which was influenced by seasons. Investigation of movement behaviour found frequent but temporally spaced captures, which were thought to be indicative of large or drifting home ranges. *N. yvonneae* was also found to undertake regular large movements. There was much variation recorded within the population, with movement behaviour dependant on sex, season and location of capture. Females tended to be more sedentary than males and may establish larger home ranges. Males were more mobile, with short-term site fidelity. Seasonal differences in movement revolved around the breeding season, especially for males. In general, *N. yvonneae* was more sedentary during pre-breeding (winter) or post breeding (mature adults).

The distribution and abundance of *N. yvonneae* at the local scale were found to be influenced by *Triodia* and a combination of the cover of *Triodia* and shrub. At least some *Triodia* was required for *N. yvonneae* to be present in the landscape, while shrub was only used when *Triodia* was present. The requirement for cover was considered an indication that predation influenced *N. yvonneae* habitat selection. *Triodia* was also found to be important for foraging *N. yvonneae* during the investigation of fine-scale habitat use. However, ningauis used a wide range of habitat components, with some being more important at certain times of the year. Leaf litter was also used frequently for foraging, although ningauis tended to remain close to *Triodia*. Underground was used specifically as a refuge, mostly in cooler temperatures. Overall, habitat use by foraging ningauis was influenced by season, including a reduced use of *Triodia* during winter, possibly due to reduced predation, reduced prey (requiring more foraging time) or predators (snakes) using *Triodia* themselves as a refuge.

Examination of dietary preferences showed that *N. yvonneae* consumed a wide range of prey. Although considered a dietary generalist, ningauis showed some a distinct preference for certain taxa, including Blattodea, Orthoptera, Chilopoda, Lepidoptera and Araneae. There were noted differences in prey consumption between sexes, possibly because of different nutritional requirements or because of varying habitat preferences. The effect of predation risk on *N. yvonneae* was also investigated. Due to the nature of the habitat (in particular, the regular availability of *Triodia*), predation was thought to have only a marginal impact on behaviour at a fine scale. However, at a broader scale, it was believed that predation may have a greater effect on habitat selection and the distribution of *N. yvonneae*.

Statement of originality.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and that, to the best of my knowledge, this thesis contains no material previously published or written by another person, except where due reference is made in the text.

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Chapter 1 - The use and selection of resources.

1.1 Introduction.

Understanding what resources an animal uses, how it uses those resources, at what times it uses them and why it uses them are all integral questions to an animals ecology. Most importantly, answers to these questions can be important for the conservation management of an animal and its habitat (e.g. Taylor *et al.* 1999; Law & Anderson 2000). As such, many ecologically based studies on fauna have examined the use and selection of resources (e.g. Churchfield *et al.* 1997; Tew *et al.* 2000; Ward *et al.* 2000; Moore *et al.* 2001; Ford *et al.* 2003). The use of any resource is essentially governed by an animals' needs, the most prominent of these being reproductive fitness (Krebs 1994). To achieve this or satisfy any of its needs, an animal must have access to the necessary resources. The needs of most animals are complicated by several factors, such as the time of year or age of the animal. Consequently, obtaining an accurate assessment of the use and selection of resources by an animal can be complex (e.g. Jackson, S.M. 2001; Jackson, T.P. 2001).

Habitat is the broadest scale at which resource use and selection are examined. Being the "place where animals live", habitat is described by the biological, geographical or physiological characteristics of a landscape. The scale of habitat can vary widely, from local to landscape. Habitat is generally more than a specific food resource or shelter site, it deals with the combinations of such resources or habitat components (or micro-habitats) within a landscape. These components are used to describe and distinguish between different habitats. The selection of any habitat is in part a selection for the individual components or resources provided. For example, nesting yellow-legged gulls (*Larus cachinnans*) showed an overall preference for shrub habitat, because of the high percentage of tall vegetation cover located there (Bosch & Sohl 1998). However, many animals make decisions based on how the components of a habitat combine to satisfy their needs. For example, Lawton & Woodroffe (1991) found that water voles (*Arvicola terrestris*) selected sections of waterways that combined a high percentage of grass, steep bank angles and high layering of vegetation. This combination provided food (grass), was beneficial for burrow construction (steep bank angles) and minimised predation risk (vegetation layering).

The most common resource needs influencing habitat selection are food/water and shelter (Anderson 1991; Krebs 1994). For most animals, food and water are required on a regular basis. The amount of food required will be dependant on the biology and ecology of the species and the nature of the food. Obtaining food resources can have a significant influence on animal life and behaviour. For example, Churchfield *et al.* (1997) found that food was a major influence in the distribution of shrews (*Sorex sp.*), while Norton (1987) reported the density of *Rattus lutreolus velutinus* in different habitats was associated with food resources. The requirement of food can also influence behaviour temporally. For example, Brants' whistling rat (*Parotomys brantsii*) increased foraging activity in the afternoon to accumulate an overnight food store, allowing the rats to reduce night time exposure to colder temperatures and predation (Jackson, T.P. 2001). Similarly, Churchill (1994) suggested that an increase in food abundance during the tropical wet season contributed to an increase in dispersal and changes in roost sites of orange horseshoe-bats (*Rhinonycteris aurantius*). The abundance of food resources can also determine the timing of reproduction. Jackson, S.M. (2001) found that mahogany gliders (*Petaurus gracilis*) timed their breeding so that lactation coincided with the highest availability of invertebrates (a protein rich food source, see also Churchill 1994; Scott *et al.* 1999; Gilfillan 2001a).

Animals seek shelter primarily for the protection from unfavourable conditions (such as extreme heat or cold), to minimise the risk of predation, or a combination of the two. Some animals actively seek habitats that contain plentiful or regular shelter, often in response to predation risk. For example, Read (1987a) found that taller vegetation was important for *Planigale* species because of the enhanced protection from predators. Alternatively, some species avoid cover, having morphological or behavioural adaptations that allow them to more efficiently avoid predators in open areas (e.g. desert kangaroo rat (*Dipodomys desertii*); Kotler 1984). In this manner, an increase in cover or structural complexity can also increase the risk of predation (e.g. Schooley *et al.* 1996; Bosch & Sohl 1998; Sharpe & Van Horne 1998) either by providing cover for predators or by obstructing the animal's escape. Alternatively, some species develop a strong association with a single shelter source, which becomes the central focus for other activities, such as gathering and/or consuming food (e.g. Holmes 1991; Jackson, T.P. 2001). For other species, shelter may be more important to escape unfavourable or enhance favourable temperatures (see Kinlaw 1999). For example, Moro & Morris (2000) found Lakeland Downes short-tailed mice (*Leggadina lakedownensis*) used simple burrows as a diurnal resting spot. The burrows provided a more stable climate (in terms of temperature and humidity) that may have improved water economy (Moro & Morris 2000). Shelter can also be important in rearing young, providing an area of containment and safety or again sheltering young from climatic extremes or reducing predation risk (e.g. Messier & Virgil 1992; Cockburn & Lazenby-Cohen 1992; Kinlaw 1999).

Food and shelter are only some of the needs that determine a habitats suitability. Anderson (1991) lists a range of other factors necessary for population survival, such as solar radiation, temperature (zone of tolerance), daylight (and night light) and soil type/condition. Such factors were found to be important in site selection of the Allegheny woodrat (*Neotoma magister*), which displayed a preference for the warmer, drier micro-climates on south facing slopes (Balcom & Yahner 1996).

1.2 Making decisions regarding resource use.

Locating and obtaining a resource will often require an animal to assess different situations or conditions and make a decision regarding the use of that resource. This may mean deciding to use or avoid a resource, choosing between different resources or determining when to start or stop using a resource. For example, a granivore may make decisions on which patch of seed to feed from, how long to feed from it so to maximise energetic return, and what the risks of predation are when feeding on it (e.g. Hughes & Ward 1993; Kotler 1997). Resources may be required on a regular basis, for the ongoing survival of a species, or, for a particular event (such as nesting). In general, a decision regarding the use or selection of any resource can be influenced by a variety of factors, such as time of year or day, sex of the animal, breeding state, maturity, competition, mobility, predation or habitat/resource quality. Influencing factors may also be more specific, such as phase of the moon, the state of hunger or substrate texture (e.g. Sherman 1994; Hughes *et al.* 1995; Dill & Fraser 1997; Thorson *et al.* 1998).

Animals will and do adapt their behaviour to account for these influencing factors (Kotler 1984; Ward *et al.* 2000). These behavioural changes are well documented, and include altering movement patterns (e.g. Walther & Gosler 2001), adjusting foraging time or location (e.g. Sih *et al.* 1998; Valenzuela & Ceballos 2000; Jones *et al.* 2001) or giving greater consideration to their distance from cover (e.g. Sharpe & Van Horne 1998; Hughes & Ward 1993). One of the broadest behaviour adaptations is the level of specialisation in resource use by a species. Some species are flexible in their resource requirements, being adaptable to survive in a range of conditions or situations or make use of a variety of resources. Bell (1991) suggested that generalist species are often found in habitats where there are few competitors, either due to low resource abundance or area restrictions (e.g. on an island). One advantage of being a generalist is the flexibility of resource use. For example, Gibson (2001) found the greater bilby (*Macrotis lagotis*) to be a generalist forager and suggested this was an advantage in an environment which had spatially and temporally variable food resources. Conversely, many species display some level of selectivity when using resources. Specialisation may result from having specific needs, maximising resource use or to reduce competition with other species. For example, Downey & Dickman (1993) found certain species of desert lizard occurred almost exclusively on the crests of sand dunes and suggested strong habitat associations such as this aided in separation of species in the community.

1.2.1 Considering risk

Some of the most important factors influencing resource use are the costs or risks associated with using a resource. This often relates to the energetic cost of obtaining the resource and whether that cost (e.g. handling or search time) outweighs energetic rewards. Similarly, risk can vary with availability of a resource (Kacelnik & Bateson 1996). For example, an animal may need to decide between a resource that is available consistently at moderate quality or one that fluctuates between high and low quality (e.g. McNamara & Houston 1992; McNamara 1996; Lawes & Perrin 1995). Costs also include the potential risk of predation. Predation could be deemed the most important consideration in use of a resource, for as Lima & Dill (1990) suggest, the failure to avoid a predator is unforgiving. Sih (1993) suggests several ways in which predation risk affects resource use (foraging), including altering habitat use, increasing vigilance, increasing nutritional demands and altering diet. Indeed, predation is thought to have a significant influence on the structure of animal communities (e.g. Kotler 1984). Additionally, by avoiding one predator an animal may expose themselves to another (e.g. Jones *et al.* 2001; Kotler *et al.* 1992; Bouskila 1995*)*. Other possible costs and/or risks associated with resource use include the loss of territory, failure to locate food, loss of breeding rights, risk of injury or predation on dependant young. Given that use of most resources comes at a cost, it is necessary for many animals to make trade-offs between costs and needs. Decision making processes that balance costs and trade-offs have been widely studied, both empirically (e.g. Brown *et al.* 1992; Dill & Fraser 1997; Sih 1997; Jackson, T.P. 2001) and theoretically (e.g. Kramer & Bonenfant 1997; Ward *et al.* 2000). Often, animals are required to make these decisions under a certain amount of duress. In general, the resource that is selected will be the one that most efficiently maximises the animals fitness (that is, contributes most to reproductive ability for the lowest energetic cost or smallest amount of risk).

The concept of maximising energetic return is exemplified by the optimal foraging theory. Optimal foraging theory is based on the premise that natural selection influences animal behaviour so that animals assess their foraging strategies according to certain criteria in order to optimise foraging with regard to species fitness. In essence, an animal will search for food in a way that balances the risks (such as predation) and the rewards (energetic gain). Optimal foraging theory, or at least the principles behind it, has been used in many studies to help explain behaviour in many different taxa (e.g. Kotler *et al.* 1994; Morris 1997; Henderson & Elgar 1999; Jackson, T.P. 2001). Although widely used and discussed, optimal foraging theory has some recognised limitations and assumptions, and as such, has been subject of much debate (see Pyke 1984; Pierce & Ollason 1987; Bell 1991; Perry & Pianka 1997). Although optimisation generally refers to energetic return, certain resources can be essential despite a negative energetic return. For example, in one study, new Holland honeyeaters (*Phylidonyris novaehollandiae*) satisfied their essential protein requirements by capturing insects, despite it being energetically disadvantageous to do so (Paton 1982).

Any consideration of optimal foraging and resource use requires assessment of the distribution of resources within the landscape. Many resources are irregularly distributed within a landscape (Bell 1991), varying in presence and/or abundance. The use of any resource patch will be dependant not only on the intrinsic values of the patch (that is, its quality) but also its position within the landscape (such as, distance to other similar patches). Resources that satisfy different needs can also be patchily distributed and may require behavioural adaptation. For example, Bolam's mice (*Pseudomys bolami*) were recorded to forage in chenopod swales but seek nightly shelter in the adjacent vegetated dunes, requiring regular movement between the two habitats (Moseby & Read 1998). External factors such as predation risk while travelling to or using a resource patch, will also influence patch use. For example, Brown *et al.* (1992) recorded changes in patch use by fox squirrels (*Sciurus niger*) when the predation risk (distance from cover) and patch quality (seed abundance) were altered. The optimisation of food patch use is modelled by Charnov's (1976) marginal value theorem, which suggests that an animal should continue to forage in a patch until their harvest rate falls below the mean harvest rate of all patches within the landscape (Charnov 1976; Bell 1991; Kotler 1997). However, the marginal value theorem makes several assumptions that limit its applicability (Kotler 1997), such as a constant risk of predation. While patch use is most commonly discussed in terms of balancing foraging with predation risk (e.g. Krebs *et al.* 1974; Holmes

1984; Brown 1992; Holtcamp *et al.* 1997) or patch quality/use (e.g. Livoreil & Giraldeau 1997; Devenport *et al.* 1998), it has also been studied in relation to habitat use (e.g. Gillis & Nams 1998).

1.2.2 Accessing and obtaining resources

The manner in which animals move is a key element of both optimal foraging theory and the marginal value theorum, since they are concerned primarily with decision on when to move from one patch to another or how to move within a patch. Movement influences an animals ability to access patchily distributed resources within a landscape. The ability of animals to move to access resources is considered important in ecological studies (Anderson 1991; Szacki & Liro 1991; Ims 1995). For example, Dickman (1995) suggested that individuals from several small mammal species moved long distances (several km's) in response to localised increases in food resources triggered by rainfall (see also Predavec 1994). The distance moved by animals can vary from longer distance or migratory movements (e.g. Clark *et al.* 1988; Dickman 1995; McCorquodale 1999) to shorter distances or localised movements (e.g. Benhamou 1996; Caravanta *et al.* 2000) and can vary across ages, seasons or sex (e.g. Lunney & Leary 1989; Diffendorfer & Slade 2002) The ability to move and movement behaviour within a landscape is dependant on several factors. The most obvious is the risk of predation. Movements can take an animal away from shelter or familiar surroundings, and thus increase the risk of predation. Consequently, animals may also need to adapt their movement patterns in response to predation. For example, Walther & Gosler (2001) found tits (*Parus* sp.) regularly used clusters of hawthorn bushes, which provided protection from predators, as 'highways' when moving between food patches (see also Szacki *et al.* 1993). Likewise, Norrdahl & Korpimaki (2000) suggested that rodents may decrease their mobility in response to high predation risk. An animals ability to move also depends on the nature of the habitat and whether the habitat physically impedes movement. For example, limited vegetation cover was preferred by *Notomys alexis* because their bipedal gait was hindered by abundant vegetation (Masters 1993). The ability to move within a habitat is also important in regard to food. Indeed, some habitats are chosen not for prey abundance but because access to prey or prey capture rates are better (e.g. Edwards *et al.* 2002).

An animal's access to resources is also influenced by competition within and between species. For a landscape to be of use to an animal, it not only has to contain the necessary resources but must also allow for an appropriate level of access to those resources. As resources are generally finite or patchy in their distribution, there is often great competition for resource patches (especially those of high quality). This competition can be either 'exploitative' (the competitor consumes some of a finite resource) or 'interference' (the competitor prevents access to a resource; Sih 1993). Krebs (1994) considered that habitat suitability would decline as the density of individuals increased, with a population increasing until the habitat quality was similar to more marginal habitats. This is commonly referred to as the ideal free distribution, which suggests that at some population threshold an animal may be better to choose a sub-optimal habitat (Houston & McNamara 1997; Bosch & Sol 1998; Ward *et al.* 2000). This concept intimates that animals not only assess a habitat on its quality, but also on the access to its component resources. This phenomenon was recorded in populations of water voles (*Arvicola terrestris*), which established breeding colonies in marginal sites when population numbers were high, and returned to better quality habitats as population numbers fell (Lawton & Woodroffe 1991). Competition between different species can also influence resource use. For example, the narrow-nosed planigale (*Planigale tenuirostris*) and Giles' planigale (*Planigale gilesi*) were found to increase their use of soil cracks in response to the presence of the fat-tailed dunnart (*Sminthopsis crassicaudata*) at the soil surface (Moss & Croft 1988). Animal communities have developed several mechanisms to overcome inter-specific competition. Body size is one such mechanism (e.g. Hall 1980, Adler 1995; Churchfield *et al.* 1999), as is temporal activity (e.g. Jones *et al.* 2001).

Use of resources can vary greatly within populations, differing between sexes, age groups and status (e.g. alpha males). For example, Cowlishaw (1997) found that female Baboons used refuges more than males, most likely because they were smaller and less able to defend themselves against predators. Likewise, Valenzuela & Ceballos (2000) recorded that larger male white-nosed coati (*Nasua narica*) adopted different activity patterns than females because of their larger size. Resource use can also vary temporally, as a result of changes to the population, the environmental conditions or the nature of the resource. For example, Hall & Lee (1982) found that the preferences of floristic composition and cover for bush rat (*Rattus fuscipes*) and dusky antechinus (*Antechinus swainsonii*) changed between seasons and years, suggesting that it was a result of shifting resource abundance. Similarly, Lunney *et al.* (1989) found that the white-footed dunnart (*Sminthopsis leucopis*) preferred recently disturbed areas, with the population declining and becoming non-existent as the habitat regrew. Masters (1993) found that small mammal distributions were influenced by the successional stage of *Triodia* sp, which was influencing food densities. Reproductive status also has a significant influence on decisions about resource use. Reproduction changes the needs of an animal, such as an increase food requirements, changes in the type of food required, greater protection from predators or extreme climates or the requirement for new resources (such as nesting material). For example, Taylor *et al.* (1999) found dramatic differences in the requirements between nesting and brood-rearing Northern Bobwhites (*Colinus virginianus*).

1.3 Resource selection in dasyurids.

Dasyurids are classified as being carnivorous or insectivorous marsupials. There is little variation in body shape or form across species, with most having unspecialised legs, poorly developed pouches and dentition that is suited to biting and cutting (Strahan 1995). Dasyurids display a large range in body size, the largest being the Tasmanian devil (*Sarcophilus harrisii*) at 9 kg, with the smallest species being a *Planigale* (4 g; Strahan 1995). The family has adapted to a wide range of landscapes within Australia, including arid (e.g. *Dasycercus cristicauda*; Chen *et al.* 1998), alpine and subalpine (e.g. *Antechinus swainsonii* and *A. stuartii*; Green 1989), temperate (e.g. *Phascogale tapoatafa*; van der Ree *et al.* 2001) and tropical climates (e.g. *Antechinus leo*; Leung 1999).

The perceived risk of predation and abundance or composition of food resources are two factors commonly attributed as having an affect on the habitat selection of dasyurid species, especially smaller species. For example, Leung (1999) found the distribution of the Cape York antechinus (*Antechinus leo*) was related to sapling and vine density and suggested the improved cover of these habitat components reduced predation risk. Likewise, densely vegetated habitats were preferred by the agile antechinus (*Antechinus agilis*) because of either the reduced predation risk or increase in invertebrate activity (Sutherland & Predavec 1999). Some larger dasyurids also consider predation risk in choosing habitat, with large old trees being preferred by the brush-tailed phascogale (*Phascogale tapoatafa*) because they reduce the potential exposure to predators (van der Ree *et al.* 2001). However, not all dasyurids show a preference for complex or abundant vegetation cover. For example, Lunney *et al.* (1989) recorded the white-footed dunnart (*Sminthopsis leucopus*) to select treeless ridges and slopes with sparse ground cover. Similarly, the common dunnart (*Sminthopsis murina*) was found by Catling & Burt (1995) to select areas of low habitat complexity. However, not all *Sminthopsis* sp. display this type of habitat selection, with the distribution of the little long-tailed dunnart (*Sminthopsis dolichura*) being influenced by the composition and abundance of prey (Friend *et al.* 1997).

Although predation risk is suggested in many studies as an influencing factor in habitat selection of dasyurids, in general it has been poorly studied. Sutherland & Predavec (1999) were the first to examine this specifically, by studying changes in behaviour under varying levels of light (a presumed indicator of predation risk). They found that the agile antechinus (*Antechinus agilis*) did not alter microhabitat use under different levels of light intensity. Either the species was not influenced by predation risk or light was not an indicator of predation risk. Similarly, Haythornthwaite & Dickman (2000) examined the influence of perceived predator risk on the foraging behaviour of the lesser-hairy-footed dunnart (*Sminthopsis youngsoni*). Like Sutherland & Predavec (1999), they too found that changes in light intensity (predator risk) had little effect on foraging behaviour.

In contrast to the limited studies on predator risk, diet and foraging behaviour in dasyurids has been widely examined. Dasyurids are characterised by their carnivorous/insectivorous diets, although some species have been recorded to seasonally supplement their diet with other sources. For example, Scarf *et al.* (1998) recorded brush-tailed phascogale (*Phascogale tapoatafa*) to consume nectar (see also Statham 1982). The consumption of invertebrate or vertebrate prey is largely dependant on body size. Most smaller sized dasyurids (such as *Sminthopsis*, *Ningaui*, *Antechinus*, *Planigale*) specialise on invertebrate prey (e.g. Woolnough & Carthew 1996; Gilfillan 2001a) while larger dasyurids (such as *Dasyurus, Dasyuroides, Sarcophilus*) are known to consume vertebrate prey (e.g. Belcher 1995; Chen *et al.* 1998). While most prey are taken live, some dasyurids have been recorded to take carrion (e.g. Scarff *et al.* 1998; Jones 1998).

Most dasyurids appear to be generalists in terms of diet. However, many display some selectivity in prey consumption when compared to the availability of different prey types. For example, Fox & Archer (1984) found that although the common dunnart (*Sminthopsis murina*) and brown antechinus (*Antechinus stuartii*) were qualitatively opportunistic in their feeding (that is they feed from almost the entire range of available food), quantitatively, both species displayed prey consumption patterns that differ from the availability of prey during certain parts of the year. Fisher & Dickman (1993a) drew similar conclusions, noting that although the dasyurids in their study displayed a generalist diet, all 17 species investigated showed a preference or avoidance for some categories of prey.

The size of prey consumed by dasyurids and the associated influence of dasyurid body size on diet selection has been well studied and often considered a key determinant in dietary selection. However, Fisher & Dickman (1993b) state that there is some uncertainty as to the full effects of predator body size on prey size selection. In early studies of dasyurid predators, Dickman (1988) found that there was no specialisation on different size prey, with species tending to maximise their energy intake by feeding preferentially on larger prey. Similarly, after examining prey handling time for three sympatric dasyurid species, Calver *et al.* (1989) found that that none of the species tested should have a preferred prey size preference. In contrast to these findings, Fisher & Dickman (1993b) concluded that there was a positive correlation between predator body size and prey size. They suggest this was a result of predators attempting to maximise their energy intake and foraging in habitats containing their preferred size of prey. They concluded that dasyurids under 16 g selectively preyed on smaller prey to obtain highest energy returns, while larger dasyurids, (greater than 20 g) showed a preference for larger prey species. The suggestion that smaller dasyurids were constrained to consume smaller prey was refuted, as Fisher & Dickman (1993b) found small dasyurids were physically capable of consuming most large prey.

Despite apparent size based preferences, Dickman (1988) noted that the encounter rate of prey had a bearing on the type of prey consumed. Dickman (1988) suggested that the large number of smaller prey consumed in his study may be because there was a high proportion of small prey available. Predation may also have a bearing on prey size selection. Both Calver (*et al.* 1988) and Dickman (1988) suggested that the selection of larger prey may, in part, be related to exposure to predation, with consumption of larger prey reducing the time between foraging sallies and thus minimising exposure to predators. Inter-specific competition can also have an influence of diet. Dickman (1988) recorded that during removal experiments, the smaller predators switched to more productive foraging habitats and consumed larger prey when large insectivores were removed. Dickman (1988) considered this competition to result from interference rather than exploitation.

1.4 The genus *Ningaui*

Ningauis are one of the smallest dasyurids. They evaded scientific notice until the mid 1970's, when pit-fall trapping developed as a technique for conducting small mammal surveys. The small size of ningauis meant that they were not sampled by traditional weight-reliant live-capture traps. Baverstock & Aslin (1975), one of the first to capture members of this genus, commented that the animal seemed particularly wary of the usual trapping techniques. The genus has since been recorded across much of semi-arid and arid Australia. There are three recognised species of *Ningaui; N. ridei*, *N. timealeyi* and *N. yvonneae*. *N. yvonneae* is the most recent addition to this genus, being identified when Kitchener *et al.* (1983) revised the work of Archer (1975). This revision saw *N. ridei* divided into two species; *N. ridei*, found in central Australia, and *N. yvonneae*, found in the southerly semi-arid regions of Australia. *N. timealeyi* is found in the Hammersley plateau of Western Australia. This definition of the *Ningaui* genus was supported by Baverstock *et al* (1983) and Krajewski *et al.* (1997), with the latter describing *N. yvonneae* and *N. ridei* as sister species.

In general, there is limited information on the ecology of the genus. This is in part due to their distribution in remote areas and their cryptic nature. The distribution of all three species appears to be strongly associated with hummock grass (*Triodia sp.*). *N. ridei* and *N. timealeyi* are reported as being reliant on habitats containing *Triodia* (Johnson & Roff 1980; Dunlop & Sawle 1982; Fanning 1982; Kitchener *et al.* 1983). While *N. yvonneae* is found in a wider range of habitats (see Chapter 5 for detailed discussion), it too is most commonly found in semi-arid mallee with at least a partial cover of hummock grass (Kitchener *et al.* 1983; Kitchener *et al.* 1986). However, Coventry & Dixon (1984) report that in Victoria, *N. yvonneae* has been found in areas without *Triodia*, although in low numbers.

All three species are insectivores and although generalist in nature, do display some preference for smaller prey (Calver *et al.* 1988; Fisher & Dickman 1993a; Woolnough & Carthew 1996). Their broad diet is also known to include occasional vertebrates. Ningauis are primarily nocturnal, with some species displaying occasional daytime activity (Dunlop & Sawle 1982). Ningauis are active throughout the year, coping with winter by regularly entering short periods of torpor (Geiser & Baudinette 1988). Largely terrestrial, they are also reported as being agile climbers (Johnson & Roff 1980; Dunlop & Swale 1982). Breeding usually commences around spring, with young reaching independence in mid to late summer. However, the breeding season can be influenced by poor conditions, as has been reported for *N. timealeyi* (Dunlop & Sawle 1982; Dunlop 1995). Although polyestrus, females usually only raise one litter in the season (Kitchener *et al.* 1986). Female *N. ridei* and *N. yvonneae* have seven teats and litters of five to seven young (Kitchener *et al.* 1993; Johnson & Roff 1980; Fanning 1982), while *N. timealeyi* females have six teats and produce litters of five to six (Kitchener *et al.* 1993; Dunlop 1995). There is no evidence to support "a dramatic post-mating mortality in male ningauis" as occurs in other Dasyurids (Kitchener *et al.* 1986, p21). In fact, it is suggested that a high portion of adults of both sexes survive beyond the breeding season (Kitchener *et al.* 1986; Dunlop & Sawle 1982).

None of the species are reported as having a fixed home range, although little work has been done to study this specifically. McKenzie & Dickman (1995) reported that radio tracking showed individuals did not have a fixed home range, with some specimens having been recorded to move up to 1.5 km within three days. Carthew & Keynes (2000) also recorded larger scale movements (2 km) in a population of *N. yvonneae*. They suggested that the population may be composed of a combination of both transient and sedentary animals. Anecdotal information reported by Fanning (1982) suggested that *N. ridei* developed an advanced communication system in part because of its widely dispersed population and to overcome distances between individuals. Fanning (1982) believed that this implied a high level of mobility in the population.

1.5 The purpose of this study.

Ningaui yvonneae is an animal on which little detailed research has been undertaken, especially in terms of resource use and selection. The purpose of this study was to address questions associated with the use of resources by *N. yvonneae.* In particular, to investigate what resources were important to *N. yvonneae*, what resources they avoided or selected, how they used these resources and what behavioural adaptations they employed to allow them to use these resources.

Central to the study was the manner in which *N. yvonneae* used *Triodia irritans* (hummock grass). As mentioned in Section 1.4, there have been suggestions that *N. yvonneae* is a *Triodia* specialist, or at least, only found in those habitats that contain at least some *Triodia.* An initial consideration of the project was to quantify this relationship (see Chapter 5) and if found to exist, identify why and how *N. yvonneae* used *Triodia* (see Chapters 6 and 8*)*. Also of interest with regard to habitat use was an examination of preferences at various scales, namely the fine (trap) scale and broad (grid/landscape) scale (see Chapter 5). Movement patterns within habitat provide an insight into the use of resources (see Chapter 4), detailing how a species accesses a resource and possible restriction on that access. Food was another resource which was investigated (see Chapter 7). In particular, the aim was to determine what prey items were consumed, what prey were selected and from where the prey were captured. Factors that govern resource use were also of interest. The influence of predators on decisions to use a resource was considered a key element in the life history of *N. yvonneae*, especially with regard to foraging behaviour. Although the effects of predation are widely studied in small mammals, very few studies have examined dasyurids (see Chapter 8).

Chapter 2 - General methodology

2.1 Study site

This study was undertaken in the Middleback Ranges, which are located 40 km west of Whyalla on the Eyre Peninsula, South Australia (137°07′E 33°09′S). They extend for approximately 30 km in a north/south direction, but rarely exceed 4 km in width. The highest peak reaches 445 m above sea level, although the ranges are characterised by a discontinuous line of hogback rich in iron-ore with long foot-slopes (Johnson 1982; Johns 1985). Mean annual rainfall is approximately 250 mm, with up to 20% of annual rainfall occurring during the summer months (Schwerdtfeger 1985). The Middleback ranges contain numerous ore deposits, which are under lease by the Broken Hill Proprietary Company. Mines have been in operation since the 1930's (Johnson 1982). The only other significant land use is grazing (sheep) and cropping. Despite mining and agriculture, large sections of the ranges remain relatively undisturbed. As such, the ranges are considered an area of high conservation value, and a fauna and flora refuge within the pastoral zone of the Eyre Peninsula.

Vegetation on the ranges is influenced by the north/south orientation of the ranges, with semi-arid mallee extending to the west and Chenopod shrub lands to the east. The fauna of the ranges is considered quite unique, in part due to the ranges occurring on the ecotone between the mallee and arid land systems of Specht (1972; Johnston 1982). There is a diversity of vertebrate species, especially reptiles. Johnston (1982) reported the ranges as having 60 species of herpetofauna; two amphibians and 58 reptile. At a national level, several of the fauna species found in the ranges (such as the bardick; *Echiopsis curta* and *Ningaui yvonneae*) are only rarely seen and most have been little studied.

The trapping site was located on the western flanks of the southern section of the Middleback Ranges (the Cook Range). The vegetation was a mallee community dominated by *Eucalyptus socialis*, *E. porosa*, *E. gracilis*, and *E. oleosa*. These species formed mixed stands of varying age and structure. Understorey vegetation was dominated by hummock grass (*Triodia irritans*), which forms clumps of densely packed sharpened spines. Various other shrubs were present, the most common being *Eremophila alternifolia*, *Alyxia buxifola* and *Melaleuca lanceolata*. The most obvious difference in vegetation across the study site was the abundance of *Triodia* (Fig. 2.1).

2.2. Trap design, trapping effort and animal processing

The trapping grid was designed to record medium to long distance movements made by *N. yvonneae* as well as provide a comparison of the use of different habitats by the study species. The trapping site was composed of 13 trapping grids (Fig. 2.1). These were organised into 12 small grids, each containing nine pit-fall traps in a 3x3 arrangement, and one large central grid, composed of 49 pit-fall traps (7x7). The trapping site encompassed an area of 41 ha. Each pit-fall trap consisted of a plastic bucket (40 cm deep and 28 cm diameter) set in the ground and a permanent 6 m length of 30 cm high aluminium fly-wire netting (Morton *et al.* 1988; Friend *et al.* 1989, see also Appendix 1). The netting (drift fence) was centred on the bucket (3 m either side) and oriented to minimise habitat disturbance. Pit-fall traps were spaced 15 m apart and were closed between trapping sessions by covering with a plastic lid. Additional traps were used during September 1998 for a concurrently running project. These traps were located near the centre of the trapping grid (Fig. 2.1) and consisted of a line transect of 10 pit-fall buckets spaced 10 m apart (with one continuous length of drift-fence).

Twenty trapping sessions were undertaken between August 1996 and December 1998, with each session lasting an average of 8 days. All months of the year were sampled at least once, except January. Trap grid use and data collected differed across different stages and aspects (ie. chapters) of the study. Where relevant, these differences are detailed at the start of each chapter. Between September 1996 and August 1997, all small grids (grids A-L) were open during each field trip, with the large central grid (M) being opened when possible depending on time constraints and weather. By August 1997, sufficient data had been collected from the small grids regarding habitat preferences, so grids that rarely caught ningauis (grids B, C, G, J and K; see Table 3.4) were no longer opened (to maximise trapping efficiency). These grids were titled 'no-capture' grids, and were characterised by the absence of *Triodia irritans*. The one exception to this closure was grid K, which was opened frequently despite low captures because of its ease of access and proximity to some of the 'capture' grids. For the first trapping session (August 1996), only the capture grids were opened, with the remainder in the process of being installed.

Traps were checked after sunrise, with captured *N. yvonneae* sexed, weighed to the nearest 0.1 g, and where possible, measured (including snout vent, pes, tail, testes width and head). Breeding condition of females was assessed according to the descriptions provided by Fanning (1982). Females were identified as not breeding, pregnant, with pouch young or lactating. Testes widths of males was measured and number of pouch young recorded for females. Most animals were given an individual number using a series of small 'V' shaped ear notches before being released at the point of capture.

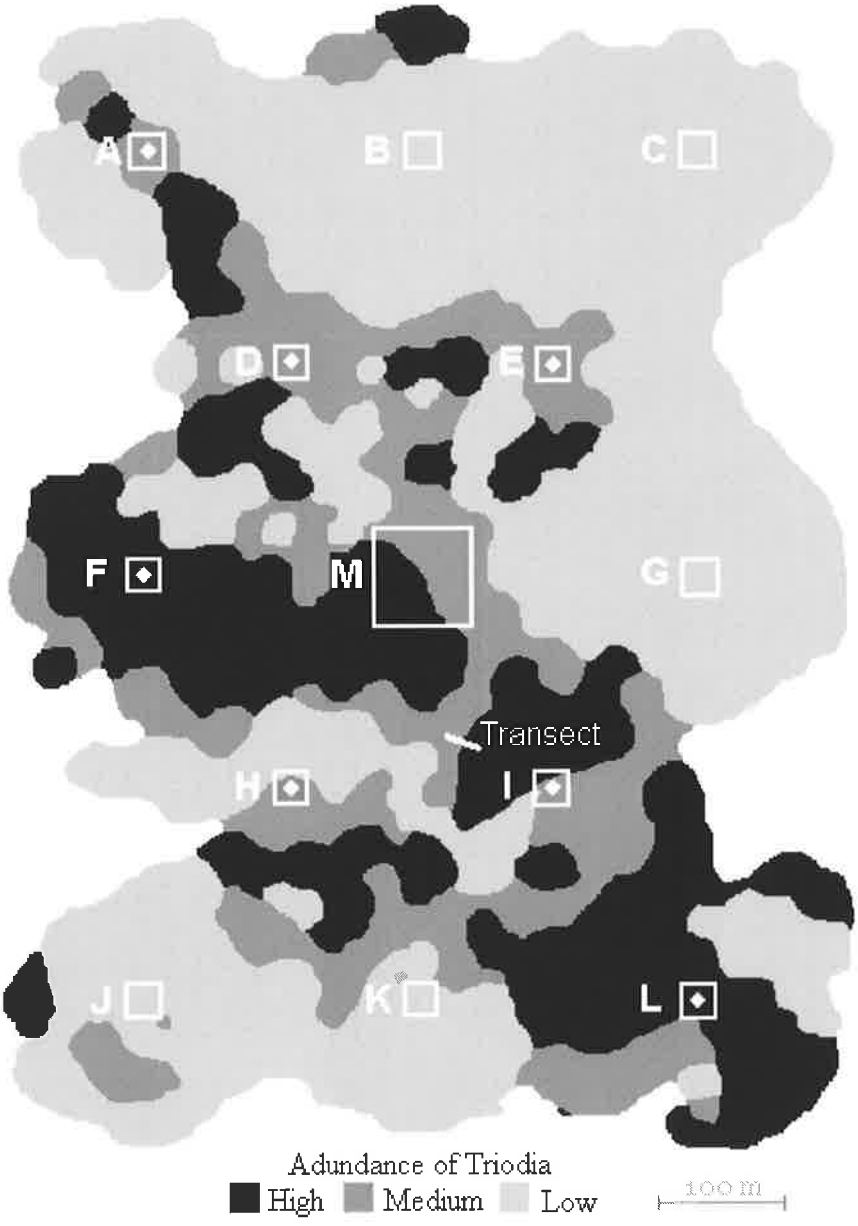

Fig. 2.1. Design of trapping grids and distribution of *Triodia irritans*. Non-capture grids (☐) are those grids that up to August 1997 rarely caught ningauis and were no longer opened (after this date) in order to maximise trapping efficiency (see Section 2.2).

2.3 Seasons

Traditional seasons (Winter [June, July, August], Spring [September, October, November], Summer [December, January, February] and Autumn [March, April, May]) were used for data analysis in Chapter 3. For Chapter 4, simplified "seasons" relating to breeding state were used, being Pre-breeding, breeding and post-breeding (see Section 4.2 for details). In the remaining chapters, four time periods were developed that were believed to better reflect the life history of *N. yvonneae*. These were: 'Growth' (February-April), 'Maturation' (May-July), 'Breeding' (August-October) and 'Nurture' (November-January). These "seasons" were based on climate conditions, population age and breeding biology (see Chapter 3). Growth encompassed the first three months of juvenile *N. yvonneae* independence, preceding the onset of winter. Maturation covered the majority of winter, when ningauis progressed from adolescence to adulthood. Breeding covered the beginning of warmer weather and the start of breeding, concluding with mating in October. Finally, Nurture covered the latter stages of ningaui adult life, and incorporated gestation, lactation and weaning by females.

The minimum and maximum temperatures were recorded daily during each field trip to allow comparison between seasons. The climate showed much variation in temperature across a year, ranging from a recorded maximum summer temperature of 48°C to a minimum recorded winter temperature of -3°C (Table 2.1). Rainfall was also recorded during field and between trapping sessions. Rain was recorded during all sessions, with total rainfall for trapping sessions ranged from 0.5 mm to 42 mm.

	Maximum Temp ^{0}C		Minimum Temp ^{0}C	
	Mean (± s.e)	Range	Mean (± s.e)	Range
Growth	28.9 (± 1.4)	18 - 48	13.2 (± 1.4)	0 - 28
Maturation	19.8 (± 0.8)	14 - 33.5	5.5 (± 1.0)	-3.5 - 1.9
Breeding	23.6 (± 1.1)	11 - 36	8.8 (± 0.8)	- 1.5 - 25
Nurture	30.0 (± 0.8)	21 - 38.5	14.1 (± 0.6)	8 - 21

Table 2.1. Mean minimum and maximum temperatures (± s.e) and range for each season.

Chapter 3 - Population ecology[1].

3.1 Introduction

Few detailed field studies have been carried out on the genus *Ningaui*, with most published works simply detailing their distribution (Baverstock & Aslin 1975; Fleming & Cockburn 1979; Johnson & Roff 1980; How *et al.* 1984; Coventry & Dixon 1984; McGreevy 1987; Tidemann 1988; Whisson 1995). Studies that have involved field based research include Carthew & Keynes (2000), who investigated community structure, Fisher & Dickman (1993a; b), who investigated dietary preferences, Dickman *et al.* (2001) who examined population dynamics of three dasyurids and Masters (1993), who investigated the influence of fire succession. However, all four papers dealt with ningauis at a community level. The only known field based research to focus specifically on ningauis is by Dunlop & Sawle (1982), in their paper on habitat and life history of *N. timealeyi*. The majority of research on ningauis is laboratory based, dealing with reproductive biology (Fanning 1982; Kitchener *et al.* 1986), prey selection, identification and handling (Huang 1986; Calver *et al.* 1988; Calver *et al.* 1991; Woolnough & Carthew 1993; Woolnough & Carthew 1996) and torpor and thermoregulation (Geiser & Baudinette 1988). Ningauis have also been discussed as part of literature summaries (e.g. Morton 1982; Menkhorst & Bennett 1990) or as one component of a larger study (e.g. Calver *et al.* 1989; Brooker & Withers 1994; Paltridge & Southgate 2001).

This chapter reports on the population dynamics, life history, population abundance and general ecology of *N. yvonneae*, expanding on the work of Carthew & Keynes (2000).

3.2 Methods

3.2.1 Trapping and data collection

Animals were trapped as per the description in Chapter 2 (see Section 2.2). To reduce bias in the sampling effort caused by trapping in areas with few ningauis in the first half of the study, the four no-capture grids (Fig. 2.1; Section 2.2) that were closed were excluded from the estimation of trapping effort (ie. trap nights). The three captures recorded in these grids (two

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[1] Chapter published as Bos, D.G. & Carthew, S.M. (2001) Population ecology of *Ningaui yvonneae* (Dasyurideae: Marsupialia) in the Middleback Ranges, Eyre Peninsula, South Australia. *Wildlife Research* **28**: 507-515.

at grid B and one at grid J) have been excluded from capture/recapture data and individuals known to be alive (KTBA), but are included for data that are independent of capture location and trap effort, such as mean weight and body size. It should be noted that while not all the small grids were opened during the first trapping session (August 1996), the collected data is comparable to other trapping sessions because the unopened grids were all no-capture grids. Additionally, data collected from grid K is treated as being from a capture grid except in Table 3.1.

3.3 Results

3.3.1 Trends in population abundance and recapture rates.

Data for this chapter derive from 144 nights of trapping, with a total trapping effort of 11,016 trap-nights (Table 3.1). Five species of native mammal were captured, *N. yvonneae* being the most prevalent with 306 captures (Table 3.2). Western pygmy possum (*Cercartetus concinnus*) was captured 223 times, little long-tailed dunnart (*Sminthopsis dolichura*) 25 times, Bolam's mouse (*Pseudomys bolami*) six times and Mitchell's hopping mouse (*Notomys mitchelli*) twice.

The 130 individually marked *N. yvonneae* were captured on 232 occasions. The remaining 74 captures consist of unmarked ningauis and have not been included in capture/recapture results unless stated. Trapping success varied during the study (Fig. 3.1a). The capture rate for the entire study was 2.1 individuals per 100 trap nights (2.8 for all captures), but ranged from 0.3 in September 1996 to 8.7 in February 1997 (Fig. 3.1a). The number of *N. yvonneae* KTBA (known to be alive) also fluctuated over time (Fig. 3.1b). More male *N. yvonneae* were usually caught than female (Table 3.2), with a mean capture rate (± s.e.) across all field trips of 1.9 (± 0.3) and 1.1 (± 0.2) individuals per 100 trap nights respectively.

Over half of the marked population (57.6%) were caught only once during the study (Fig. 3.2), giving a recapture rate of 42.3%. When all captures were considered, the recapture rate was 33.3%. For males, 60% of individuals were captured once only (recapture rate of 40%) while for females, the recapture rate was 46% (54% of individuals caught only once). Each male was captured an average of 1.7 times (range 1-5) and each female an average of 1.9 times (range 1-7).

	No-capture					Capture								
	B	C	G	J	K	A	D	E	F	H	I	L	M	Total[1]
Trap Effort	648	603	558	551	1,125	1,305	1,089	1,026	1,296	1,206	1,206	1,314	1,449	11,016
No. sessions grid open	10	9	9	9	18	20	19	18	20	20	20	20	8	
Closed after Aug. 1997	Y	Y	Y	Y	N	N	N	N	N	N	N	N	N	

Table 3.1. Trapping effort (trap nights) for each capture and no-capture grid. [1]For grids opened for the entire study only.

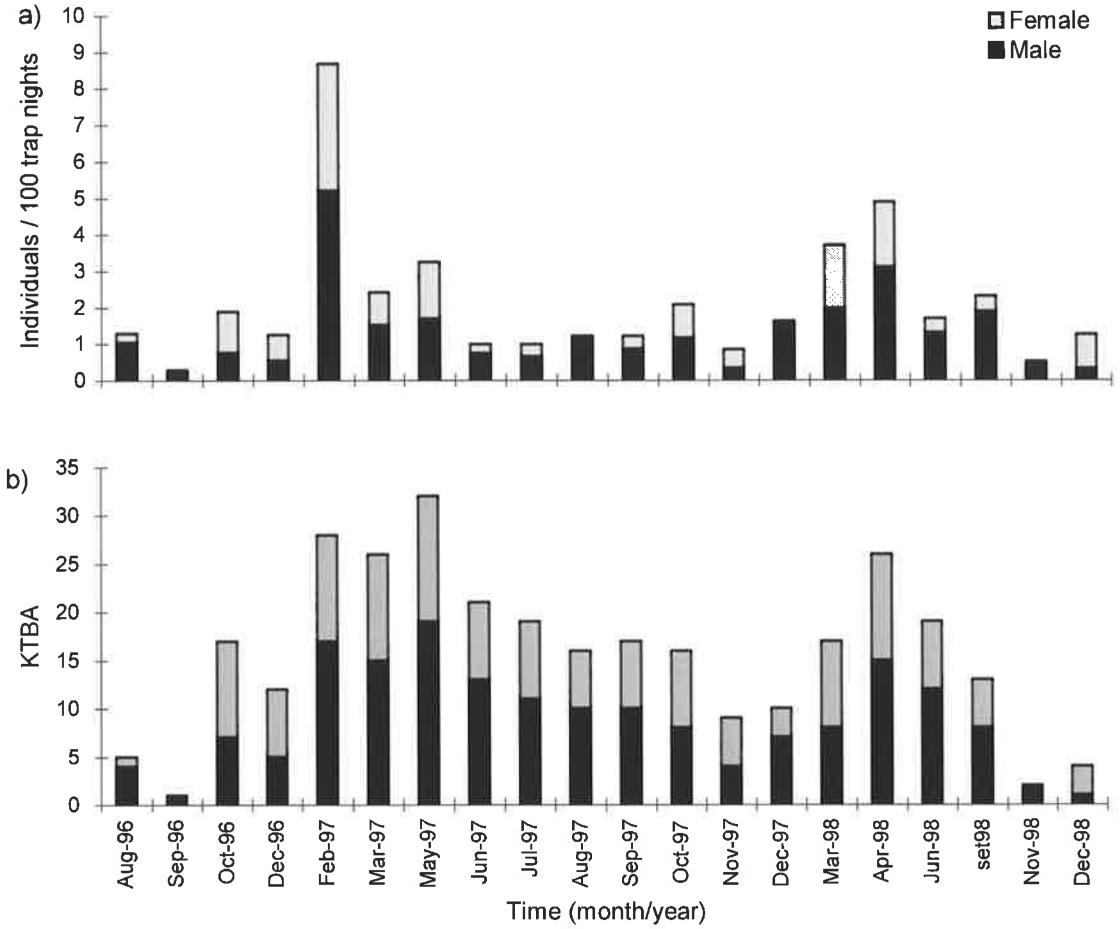

Fig. 3.1. a) Capture rates of *Ningaui yvonneae* individuals and b) individuals KTBA over time.

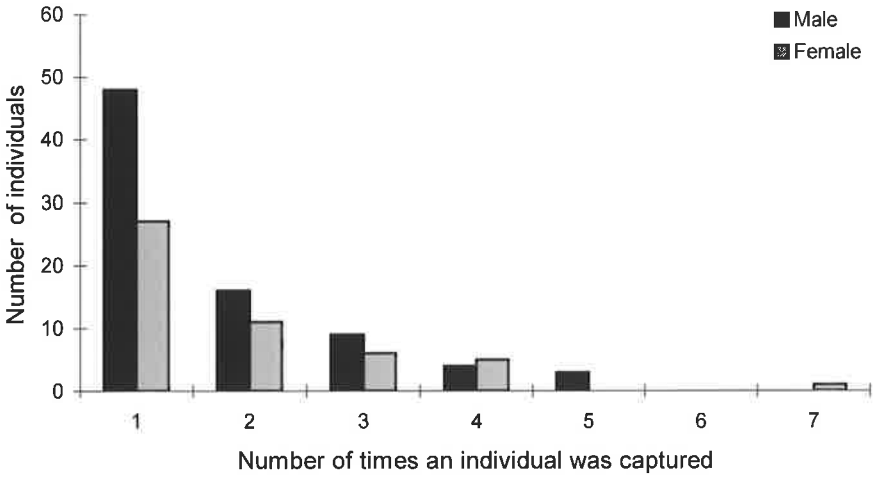

Fig. 3.2. Frequency distribution of number of times individual *Ningaui yvonneae* were captured.

Trap success varied considerably between capture grids (Table 3.3). For the small grids, Grids L and F had the highest capture rates for individuals (2.3 and 2.2 individuals per 100 trap nights respectively) while K had the lowest, at 0.5. Grid M was also successful, with a capture rate of 1.9 individuals per 100 trap nights. Trapping success also varied between seasons, with most captures in autumn and summer (Table 3.4). The higher variability in summer is largely due to large numbers of captures in February 1997 (see Fig. 3.1a). Winter was the least rewarding of seasons in terms of captures, with mean capture rate of only 1.2 individuals per 100 trap nights.

	Male	Female	Unknown	Total
Captures	181	113	12	306
Recaptures	58	44		102
Marked individuals	80	50		130
Marked individuals recaptured	32	23		55

Table 3.2. Number of male and female *Ningaui yvonneae* captured, marked and recaptured. Unknown are animals which escaped prior to sexing.

Grid	Male	Female	Total	Individuals / 100 trap nights
A	16 (25)	7 (17)	23 (43)	1.8
D	12 (15)	7 (12)	19 (28)	1.7
E	8 (18)	6 (11)	14 (29)	1.4
F	21 (33)	8 (13)	29 (48)	2.2
H	7 (15)	2 (7)	9 (22)	0.7
I	10 (12)	6 (9)	16 (23)	1.3
K	4 (6)	2 (3)	6 (10)	0.5
L	20 (37	10 (19)	30 (57)	2.3
M	11 (21)	16 (21)	27 (46)	1.9

Table 3.3. Number of individuals captured (total captures) for each successful trapping grid for male and female *Ningaui yvonneae*. Total captures include those animals that escaped prior to sexing.

3.3.2 Sex ratios

Males comprised 59.1% of captures and females 36.9% (Table 3.2). This difference was found to be significant ($\chi^2 = 16.7$, $P = 0.01$). Number of individuals caught also differed with males comprising 61.5% and females 38.5% of marked individuals. Similar male to female ratios were recorded for recapture rates (male 56.8% and female 43.2%). More male than female *N. yvonneae* were captured in all seasons and on all but four field trips. More male individuals were also captured on all trapping grids, except grid M (Table 3.3).

3.3.3 Life history and reproduction

A total of 15 female *N. yvonneae* were recorded as in breeding condition (either pregnant, with pouch young or lactating). All but three of these were caught in November or December (Table 3.5a). The time of conception for these 15 females was estimated by comparing their condition with estimates for development of young and a 17 day gestation period described by Fanning (1982) for *N. ridei*. In 1996 and 1997, most of the captured females apparently conceived in mid October (Table 3.5b). In 1998, only half of the captured females were estimated to have conceived in October, with conception also occurring in late November and early February. Most females carried between five and seven pouch young (mean 5.75 ± 0.3).

Since the breeding season of *N. yvonneae* appeared relatively focused, a common date of conception (mid October, with birth in December) was used, in conjunction with reproductive maturity (Kitchener *et al.* 1986), to place individual *N. yvonneae* into age classes. Animals captured between February and March were generally considered juveniles, from April to July as adolescent and from August till death as adult. Adults from the previous cohort were occasionally caught after February, but were easily distinguished from the new cohort by their size and body condition.

	Summer	Autumn	Winter	Spring
Total captures	84	93	55	75
No. trap nights	2352	2163	3462	3039
Mean individuals/100 trap nights (± s.e.)	2.7 (± 1.5)	3.6 (± 0.5)	1.2 (± 0.1)	1.4 (± 0.3)

Table 3.4. Seasonal variation in capture success of *N. yvonneae*.

a)

	October		November		December		April	
	N	B (%)	N	B (%)	N	B (%)	N	B (%)
1996	12	1 (8)	-	-	6	3 (50)	-	-
1997	4	1 (25)	4	4 (100)	2	2 (100)	-	-
1998	0	0	-	-	6	3 (50)	10	1 (10)
Total	16	2 (12)	4	4 (100)	14	8 (57)	10	1 (10)

b)

Month	Sept				Oct				Nov				Feb			
Week	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1996							3									
1997				1		4	2									
1998					2							1	1			

Table 3.5. a) Numbers of female *Ningaui yvonneae* captured (N) and number recorded as in breeding condition (ie. either pregnant, with pouch young or lactating) (B) over months and years; and b) estimated dates of conception. Values are numbers of females for each week/month.

	Mean (± s.e.)	Min	Max	n
Juvenile	3.7 (± 0.1)	3.2	4.7	13
Adolescent	7.1 (± 0.2)	5	9.3	27
Adult	8.9 (± 0.3)	6	14.1	37

Table 3.6. Mean width of testes (± s.e.) for three age classes of male *Ningaui yvonneae*.

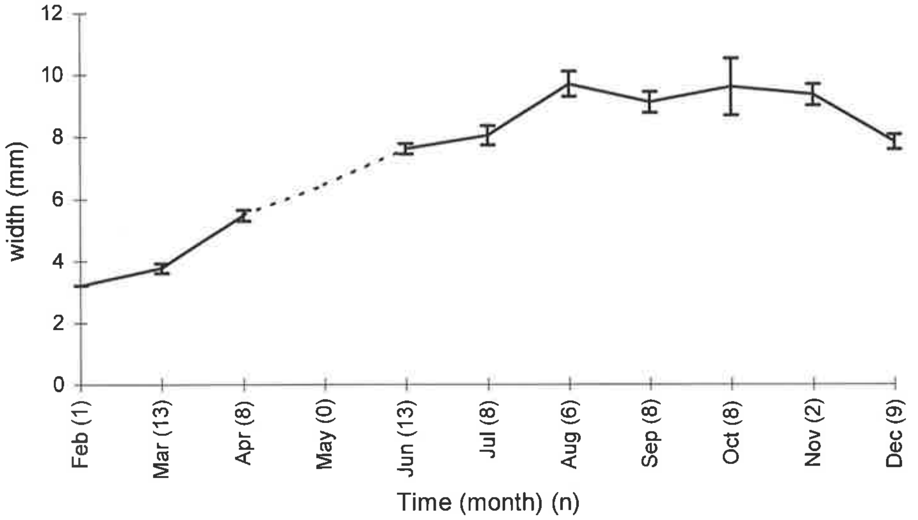

Fig. 3.3. Mean width of male *Ningaui yvonneae* testes (± s.e.) over time. Broken line represents missing data. Data from three years are pooled for each month.

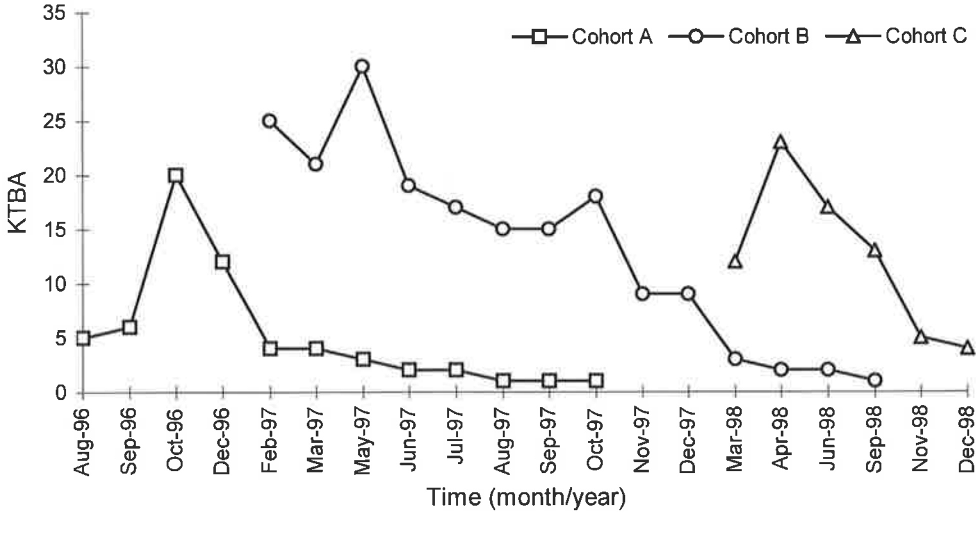

Fig. 3.4. Individual *Ningaui yvonneae* KTBA in each cohort over time.

Mean testes width of males increased steadily from February to August, with the average adult width being more than twice that of juveniles (Table 3.6). Testes widths peaked in October, during which time there was a higher variation (± 0.9 mm; Fig. 3.3). After October, mean testes width began to decline. In August/September, most males were found to have swollen and red anus'. This was interpreted as sign of the impending breeding season, as it is most likely caused by scent marking with the cloaca (Croft 1982; Fanning 1982).

Dispersing juveniles were first captured in February (1997), at which time they composed the majority (97%) of the population. In March 1998, juveniles made up 86% of the population (*n* = 15). The transition between cohorts is shown in Figure 3.4. Most of each cohort lived until February/March of the year following their birth. Using a standard birth date of December, it is anticipated that the majority of the cohort lived (from pouch to death) for approximately 14 months. Using the same birth date, the longest recorded life span was an estimated 20 and 23 months for a male and female respectively.

		Female			Male		
		Juvenile	Adolescent	Adult	Juvenile	Adolescent	Adult
Weight	Mean	5.6 (± 0.2)	6.2 (± 0.1)	8.9 (± 0.2)	5.4 (± 0.1)	6.9 (± 0.1)	10.4 (± 0.2)
	Range	3.9 - 7.6	5.2 - 8.2	7.1 - 11.3	3.6 - 6.7	5.8 - 8.8	6.9 - 13.8
	n	24	30	43	34	43	83
Pes	Mean	12.4 (±0.1)	12.8 (± 0.2)	12.6 (± 0.2)	12.3 (± 0.2)	13.4 (± 0.1)	13 (± 0.1)
	Range	11 - 13.2	11.1 - 14.0	10.7 - 13.8	10.5 - 13.0	11.7 - 14.5	11.9 - 14.4
	n	16	17	23	17	33	52
Head	Mean	20.9 (± 0.3)	21.7 (± 0.2)	22.6 (± 0.2)	20.7 (± 0.3)	22.1 (± 0.2)	23.1 (± 0.2)
	Range	18.2 - 22.4	19.6 - 23.2	20.5 - 24.4	18 - 22.4	20.0 - 23.9	20.1 - 25.0
	n	15	17	21	19	35	45
S-V	Mean	60.9 (± 0.8)	64.3 (± 1.2)	64.4 (± 1.5)	59.8 (± 1.3)	63.8 (± 1.4)	71.8 (± 1)
	Range	54.1 - 66.3	55.1 - 71.4	55.6 - 75.5	51.3 - 69.7	56.9 - 74.4	59.5 - 81.0
	n	15	14	16	17	25	31
Tail	Mean	56.0 (± 1.9)	56.9 (± 1.0)	60.1 (± 0.8)	55.3 (± 1.5)	59.5 (± 0.7)	61.9 (± 0.6)
	Range	39.1 - 67.6	46.1 - 61.3	53.7 - 68.7	41.2 - 63.3	52.3 - 65.7	54.7 - 68.5
	n	14	14	17	17	26	30

Table 3.7. Mean (± s.e.) and range of weight (g) and body measurements (mm) for male and female *Ningaui yvonneae* age classes. S-V = snout-vent.

3.3.4 Growth and development

Average weights (± s.e.; range) were 8.6 g (± 0.2 g; 3.6-13.7 g) for males and 7.2 g (± 0.2 g; 3.9-11.3 g) for females (Table 3.7). Body weights for juvenile male and female *N. yvonneae* were similar, with males becoming increasingly larger than females as they aged (Fig. 3.5, Table 3.7). As adults, males tended to weigh, on average, 1.5 g more than females. This difference was even more pronounced during the breeding season, reaching a maximum difference in means of 2.8 g in October. Weights for males and females peaked in October and September respectively, with both sexes experiencing minimal weight gain between March and June. Body measurements of adult males were only slightly greater than those of adult females (Table 3.7), except for snout-vent length, for which males had a mean 7.4 mm longer than females. There was little difference between juveniles and adults in many of the body size measurements. For example, mean pes size for juvenile and adult females were 12.4 mm (± 0.1) and 12.8 mm (± 0.2) respectively. Greater difference in body size between juveniles and adults were found in tail lengths and snout-vent length for males (Table 3.7).

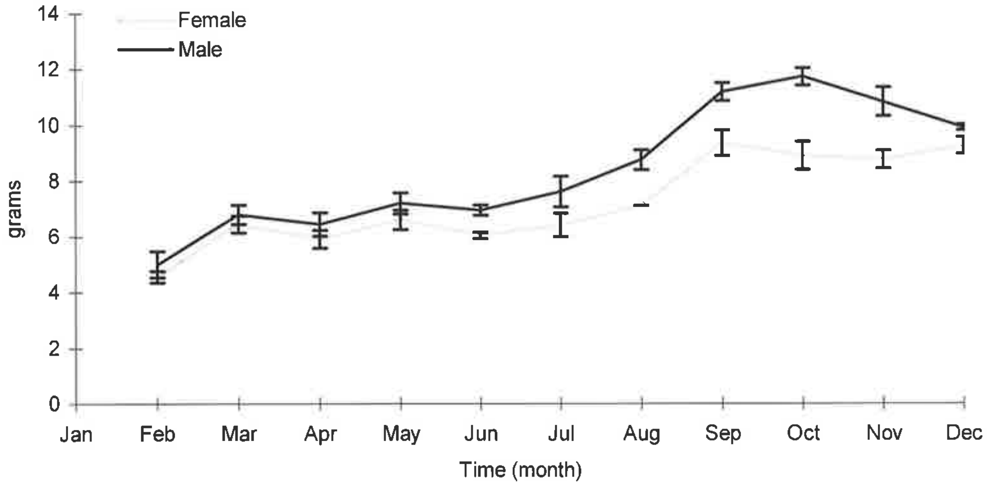

Fig. 3.5. Mean weight (g) ± s.e. for male and female *Ningaui yvonneae* over time. The zero standard error for females in July is due to $n = 1$. Data were pooled for each month, as weights were similar between years.

3.4 Discussion

The capture success rate for this study was excellent. A review of capture rates for small to medium dasyurids (Table 3.8) revealed the average capture rate for studies using pit-fall traps in arid/semi-arid regions was only 1.4%. In contrast, studies using Elliott traps (temperate or tropical regions) tended to be more successful, with an average capture rate of 3.8%. The capture rate for this study was more successful than other studies on *N. yvonneae,* undertaken in Western Victoria (Table 3.8). The only comparable result for *N. yvonneae* was the work of Carthew & Keynes (2000), who trapped in the same region. Clearly, the Middleback Ranges is an excellent location for studying *N. yvonneae*.

The recapture rate for *N. yvonneae* in this study (42.3%) was quite high compared to many arid dwelling dasyurid species. For example, Read (1984) reported recapture rates of 19% for *Sminthopsis crassicuadata*, 39% for *Planigale gilesi* and 28% for *P. tenuirostris*. Carthew & Keynes (2000) had a substantially lower recapture rate for *N. yvonneae* (5% between and 13% within sampling periods). This may, in part, be due to longer separation between sampling periods by Carthew & Keynes (2000), 14 field trips over 41 months, compared to 20 field trips over 28 months for this study. Regular field trips may be necessary when studying an animal that lives for just over one year and is possibly quite mobile (see Chapter 4).

Differences in capture success of *N. yvonneae* between seasons were also recorded by Carthew & Keynes (2000). They too had a low capture rate during winter (mean of 1.9 captures / 100 trap nights), however, their lowest capture success was in summer (mean of 1.6 captures / 100 trap nights). Dunlop & Sawle (1982) reported capture rate being lowest during winter for *N. timealeyi*. The relatively consistent numbers of ningauis known to be alive during winter months suggests that mortality was not the cause for low captures in winter. Most likely, the low capture success derives from reduced activity in the population, due to low temperatures or a change in foraging behaviour (possibly attributed to changes in food abundance), as has been reported for other species (e.g. Braithwaite 1979; Read 1988; Green 1989). The increased capture success during autumn is most likely due to the influx in the population from the new cohort, and the dispersal of juveniles (resulting in increased trapability).

Based on the original classification of life history strategies of Lee *et al.* (1982) and the work on *Ningaui sp.* (*ridei*) by Fanning (1982), Lee & Cockburn (1985) placed *Ningaui* sp. in the stage V life history category. Stage V life history animals are characterised by polyoestrous females with annual and seasonal breeding over an extended period. Stage V animals reach maturity between 8-11 months of age, meaning that individuals do not breed in their season of birth. Our results support the findings of Lee & Cockburn (1985). The occurrence of conception from mid/late September to early February suggests that *N. yvonneae* was polyoestrous. Kitchener *et al.* (1986) also reported *Ningaui* sp. as being polyoestrous. In the

Species	Capt. Success (%)	Trap nights	No. locations (sites)	Sampling Periods	Years	Region	Trap type	Source
Ningaui yvonneae	0.2	13400	1(13)	-	~3	Arid/semi-arid	P	Coventry & Dixon 1984
Ningaui yvonneae	3.0	6579	1(3)	14	3	Arid/semi-arid	P	Carthew & Keynes 2000
Ningaui yvonneae	1.3	-	1(22)	-	~2	Arid/semi-arid	P	A. Bennett pers. comm
Ningaui timealeyi	2.5[1]	6333	1(6)	-	1	Arid/semi-arid	P	Dunlop & Sawle 1982
Sminthopsis dolichura	2.4	30784	2 (4-6)	-	8	Arid/semi-arid	P	Friend *et al.* 1997
Sminthopsis crassicaudata	0.6	2135	2	-	~3	Arid/semi-arid	P	Read 1987a
Planigale gilesi	0.9	2135	2	-	~3	Arid/semi-arid	P	Read 1987a
Planigale tenuirostris	0.6	2135	2	-	~3	Arid/semi-arid	P	Read 1987a
Antechinus stuartii	3.7	5690	19	-	<1	Temperate	E	Dickman 1980
Antechinus adustus	2.3	9167	3	~30	3	Tropical	E	Watt 1997
Antechinus subtropicus + A. flavipes	4.5	3206	3	3	1	Tropical	E, S	Barry 1984
Antechinus flavipes	11.0	1050	1 (4)	1	1	Temperate	E	Goldingay & Denny 1986
Antechinus agilis	2.5	5690	19	-	<1	Temperate	E	Dickman 1980
Antechinus flavipes	4.7	22690	1(3)	~29	3	-	E, W	Smith 1984
Antechinus flavipes rubeculus	0.8	4076	1	~30	3	Tropical	E	Watt 1997
Antechinus bellus	4.5	9525	1 (3)	15	~3	Tropical	E, W	Friend 1985
Antechinus godmani	0.3	5091	2	~30	3	Tropical	E	Watt 1997
Antechinus leo	4.0	17900	-	8	2	Tropical	E	Leung 1999
Antechinus minimus	4.3	1500	1	3	<1	Temperate	E	Wainer 1976

[1] figure is for number of individuals caught only.

Table 3.8. Capture success rates for some small-medium sized dasyurids of Australia. Trap types are P, Pitfall, E, Elliott aluminium, S snap traps, W wire cages.

present study, breeding appeared to occur annually and there was little evidence to suggest individuals would breed more than once during their life time. The one indication of this was the female with young captured in April 1998. It is possible this female was raising a second complete litter or, alternatively, a new litter after the first had failed (Fanning 1982). Breeding also appeared to be seasonal, with mating always occurring after winter, particularly in early October.

Lee & Cockburn (1985) describe category V species as having a breeding season which is 'extended'. While *N. yvonneae* can breed over an extended time frame, it is likely that the breeding season commences in October during most years and for most individuals. Captures of females with pouch young by Carthew & Keynes (2000) also suggested conception in October or November. Breeding any later in the season may involve a greater risk to juveniles, as they would have less time before winter, which is a time of stress for *N. yvonneae* (see below). Friend *et al.* (1997) observed similar breeding behaviour in *Sminthopsis dolichura*. There was little evidence that *S. dolichura* raised a second litter in a season, despite being polyeostrous and being known to produce young in early autumn. Friend *et al.* (1997) suggested that polyeostry may be a way to increase breeding options (extended breeding when conditions are suitable) and flexibility in breeding time. This was also suggested by Dunlop & Sawle (1982) for *Ningaui timealeyi*.

At most times, the population of *N. yvonneae* was dominated by a single cohort. This was also observed in *N. yvonneae* in the mallee region of Victoria (A. Bennett pers comm.). Summer is the only time when two cohorts coexisted, at the end of the breeding season. The data indicated that the transition between cohorts was quite abrupt. However, there was no evidence of a dramatic post-breeding die off of males, which is supported by Kitchener *et al.* (1986). In fact, males tended to live beyond typical breeding times (October), with regular captures of adult males during late December. Kitchener *et al.* (1986) concluded that many ningauis live for at least 18 months. The post-mating survival of males may be a strategy used to capitalise on the polyeostrous nature of females, providing opportunity for a second litter if conditions are suitable. Most adults of both sexes have disappeared from the population after December, so it is unlikely that they breed in their second year. Similar conclusions were drawn by Dunlop & Sawle (1982) for *N. timealeyi* and A. Bennett (pers comm.) for *N. yvonneae*.

In this study, juveniles made up the majority of the population by February/March. Similar findings were recorded for *N. timealeyi* by Dunlop & Sawle (1982) and *N. yvonneae* by A. Bennett (pers comm.). The latter recorded that 89% of the population were juveniles by January/February. Between February and March in this study, juvenile *N. yvonneae* experienced a substantial increase in their weight. This pre-winter growth is probably vital to the survival of juveniles. As mentioned earlier, the low capture success during winter is considered to be as a result of cool temperatures and reduced prey availability, which may make winter a time of stress for *N. yvonneae*. The plateau of mean weight during the winter months provides further evidence of this. From March to July, there is only a slight increase in mean weights for males and no increase for females. A. Bennett (pers comm.) also found that weights of *N. yvonneae* plateaued during winter (in the mallee region of Victoria). Similar results have also been found for other dasyurids, including *Sminthopsis crassicaudata* (Morton 1978b), *S. dolichura* (Friend *et al.* 1997) and *Antechinus subtropicus* (Wood 1970; Braithwaite 1979). It is suspected that survival during winter relies heavily on obtaining suitable body mass prior to winter and possibly foraging experience (e.g. Green 1989, Green 2001). In the present study, there was a rapid rise in mean weight during spring. This is most likely due to increasing prey availability and as part of the preparation for the breeding season. Until September, male and female *N. yvonneae* showed similar patterns of weight gain. However, from September, they diverged, with males continuing to gain weight until the peak of the breeding season (October), after which they began to lose weight. It is expected that this loss is due to the stress associated with breeding. Dunlop & Sawle (1982), found similar results, with weights for male *N. timealeyi* being significantly greater than females during the breeding period.

Chapter 4 - Movement patterns and behaviour

4.1 Introduction

The ability of individuals to travel within their environment is vital to most animal populations. It enables individuals to locate resources or breeding partners, especially in patchy or unpredictable environments (e.g. Clark *et al.* 1988; Lunney & Leary 1989; Dickman *et al.* 1995). An understanding of movement behaviour and patterns of species provides valuable insight into their ecology. Clark *et al.* (1988), Szacki & Liro (1991) and Szacki *et al.* (1993) suggested that movements (including direction and routes) are particularly important for understanding aspects such as population regulation, social organisation and genetic structure within small mammal populations.

Some recent studies have drawn attention to the ability of small mammals to make long range movements (e.g. Szacki *et al.* 1993; Dickman *et al.* 1995; Bowne *et al.* 1999). Such movements had previously been overlooked because of inappropriate sampling designs, which did not reveal the true extent of movement, and the opinion that such movements were not important to the structure and dynamics of the population (Faust *et al.* 1971; Clark *et al.* 1988; Koenig *et al.* 1996). Often, individuals not seen after their initial capture were assumed to be consequences of mortality or emigration. Long range movements are now recognised as being important to the survival of populations of many small mammals (e.g. Liro & Szacki 1987; Clark *et al.* 1988; Lunney & Leary 1989; Wegner & Merriam 1990; Bowne *et al.* 1999). For example, in the Australian arid zone, Dickman *et al.* (1995) recorded long range movements towards areas of rainfall, presumably for the increase in resources. However, Szacki & Liro (1991) suggested that long range movements for many small mammals might be a normal part of their movement patterns, and not related to a specific behaviour such as dispersal.

Work on some small species of dasyurid (less than 15 g) have shown a propensity for frequent and often large movements. For example, in arid Australia, Read (1984) recorded a maximum Average Distance (AD) of 1,050 m in female *Sminthopsis crassicaudata*, and 1,300 m for female *Planigale gilesi*. Dickman *et al.* (1995), also recorded frequent movements of over 1,000 m in the arid zone for *Sminthopsis hirtipes*, *S. dolichura* and *S. youngsoni*. In a temperate climate, Lunney & Leary (1989) recorded some male *S. leucopus* to have an observed range length of over 700 m. The only published study to detail *N. yvonneae* movements reported the movements of up to 2,100 m by male *N. yvonneae* (Carthew & Keynes 2000). However, there was much variation in movements made by males, with an average of 451 ± 204 m. This chapter aimed to further document the patterns of movement and behaviour of *N. yvonneae*. Of particular interest was the frequency and distance of movements made by ningauis as well as the propensity for establishing home ranges and variation in movements across seasons and between sexes.

4.2 Methods

Details on capture methodology are described in Chapter 2. Data from all trapping grids (see Fig. 2.1) and trapping sessions were used in the analysis. Movement behaviour was recorded via two methods. The first involved monitoring the distances between successive captures of individual *N. yvonneae*. The second involved radio tracking selected individuals. Animals were fitted with single stage transmitters prior to release (Titley Electronics, Ballina NSW Aust. model LT1, 500 mg). Transmitters were attached to the shoulder hair with super glue. The location of individuals was recorded at intervals greater than 1 hour through the night and twice during the day. Each location was flagged and the habitat component recorded.

Recaptures of individual *N. yvonneae* were classified as either within trap session (0-10 days) or between trap sessions. Between-trap session data were further categorised into two time periods. The first, 17-99 days, was approximately equal in time to two trapping sessions. The twenty trapping sessions conducted for this study were separated on average by an interval of 38 days (range 17-93 days). The second interval was 100+ days.

Data for this chapter were categorised as a function of animal age and the time of year relative to the breeding season. These 'seasons' were: pre-breeding (juvenile to adolescent ningauis captured between February and September); breeding (adult ningauis captured between October and January) and post-breeding (adult ningauis from the previous cohort captured after February). When a movement was recorded across two seasons, it was assigned to the season in which the majority of the movement occurred. Distance moved was also summarised as being either a between- or within-grid movement.

Average Distance (AD) refers to the average distance moved between consecutive captures by an individual. Observed Range Length (ORL) refers to the maximum distance between any two captures of an individual recaught more than once (Read 1999). This includes recaptures from the same trap session. Due to the non-normal nature of the data, Kruskal-Wallis (H_c) and Mann-Whitney (U) tests were used to identify differences between average distances moved. For the latter, normal approximation (Z) was used for large data sets (when the smaller sample exceeded 20 and the larger 40; Zar 1999). Spearman Rank Correlations (r_s) were used to identify relationships between time separating captures and the distance moved.

4.3 Results

Captures from a total of 140 individual *N. yvonneae* were used in the analysis for this chapter (Table 4.1). This included four captures of individual *N. yvonneae* from the transect line (see Fig. 2.1), three of which were recaptures from other trapping grids. While some animals were caught during as many as five trapping sessions, the majority of the population (59%) was caught during only one trapping session, giving a recapture rate of 41%[1] (42% and 40% for females and males respectively; Table 4.1).

	Male	Female	Total
No. individuals captured	90	50	140
No. individuals recaptured	36	20	56
No. recaptures within trap session	12	17	29
No. recaptures between trap sessions	51	27	78
19-99 days	36	14	50
100 + days	15	13	28

Table 4.1. Number of male and female *Ningaui yvonneae* captured and recaptured.

The majority of recaptures (73%) occurred between trapping sessions (Table 4.1, Fig. 4.1). Of these, 70% of males and 51% of females were recaught between 19-99 days after their initial capture (Table 4.1, Fig. 4.1). This difference between sexes was also reflected in the average number of days (± s.e., range) separating recaptures; 86.7 days (± 8.9, 24-302) for males and 140.4 days (± 21.1, 23-470) for females. Females were also caught over a greater time period, with an average (± s.e.) of 7.2 months (± 1.3) separating the first and last capture. In contrast, the average time (± s.e.) for males was 4.9 months (± 0.5; Fig. 4.1).

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[1] This figure differs slightly from that reported in Chapter 3 because of differences in the data used for each chapter. Some of these differences are described above and in Sections 2.2 and 3.2.1.

4.3.2 Distance moved

Within-grid movements comprised 58% of recaptures, with 75% and 51% for within and between trap session recaptures respectively. Generally, female movements occurred within-grids, except for movements separated by more than 100 days (Fig. 4.2b). However, there was no correlation between time separating captures and distance moved ($r_{s\ 0.05\ (2),\ 44} = 0.257$, $P = 0.5$, Fig. 4.3b). In contrast, males tended to make more between-grid movements (Fig. 4.2a) and there was a significant positive correlation between time separating captures and distance moved ($r_{s\ 0.001\ (2),\ 63} = 0.55$, $P = 0.001$, Fig. 4.3a). The minimum and maximum possible distance for between-grid movements were approximately 80 and 926 m respectively. Most between-grid movements by both sexes tended to be short, with few recorded movements of over 500 m (Fig. 4.3). Only one animal was recorded to move the maximal distance (Fig. 4.3).

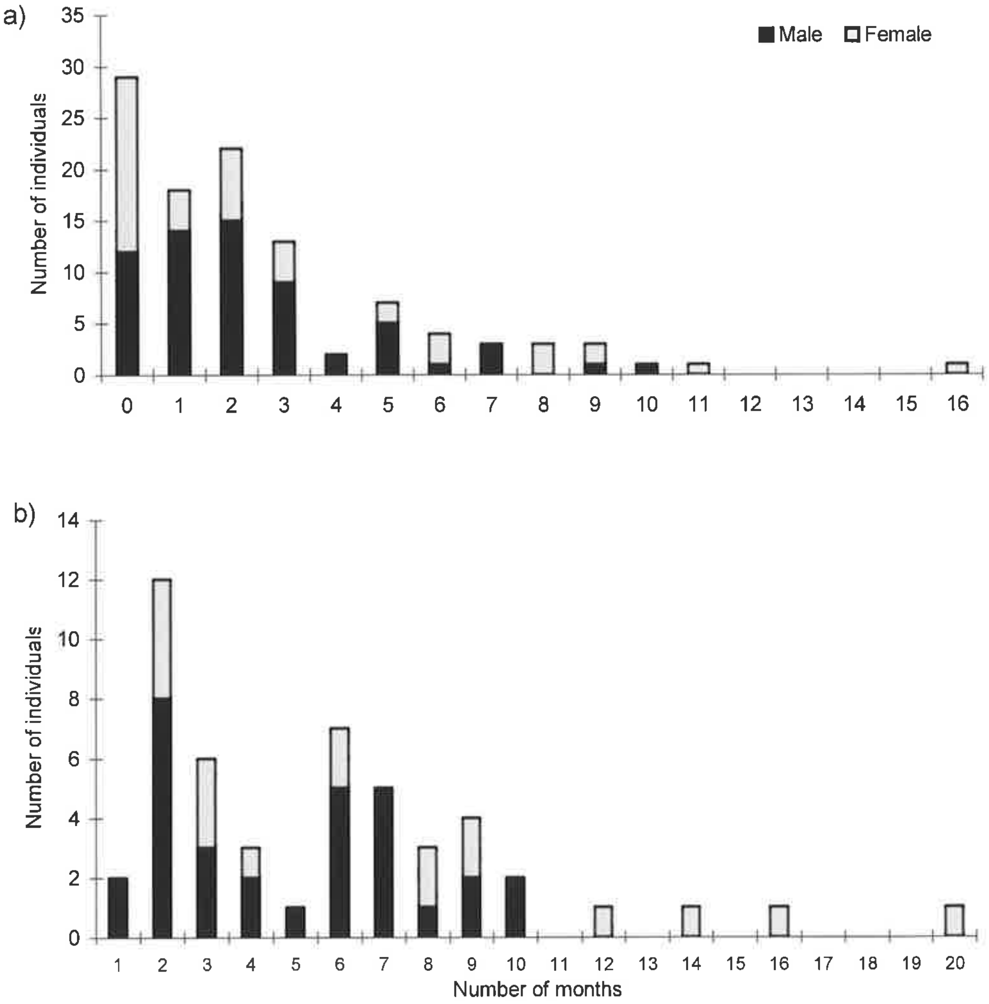

Fig. 4.1. Frequency distribution of a) months between captures for all *Ningaui yvonneae* caught (0 months represents within trap session recaptures), and b) months between first and last capture for male and female *Ningaui yvonneae* (between trap session captures only). The number of months is given as total days divided by 30.

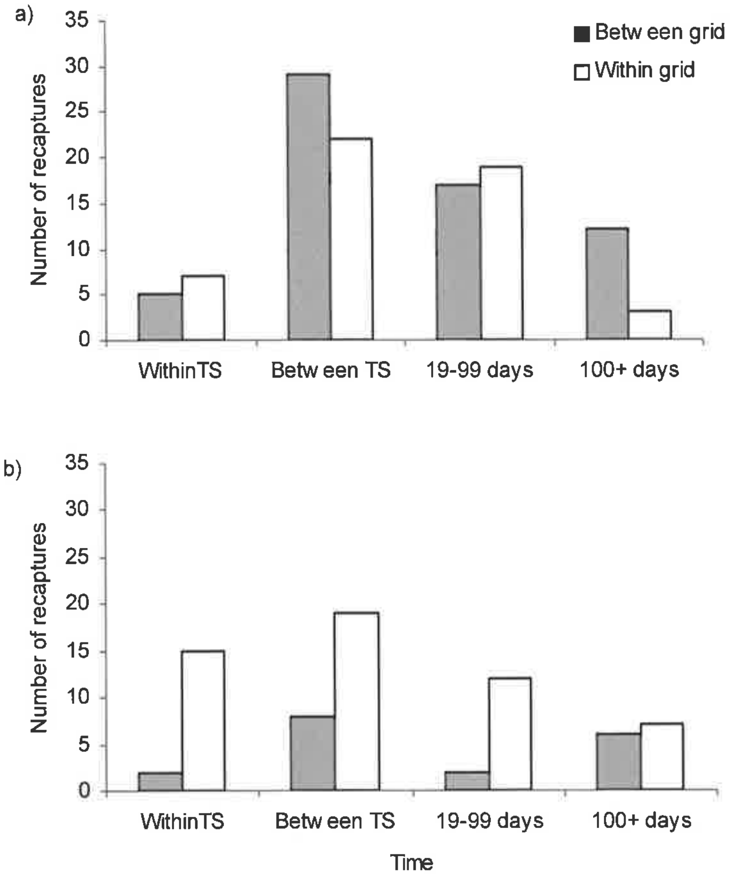

Fig. 4.2. Number of between- and within-grid movements made over different time periods for a) male and b) female *Ningaui yvonneae*. TS = trap session.

The average distance (AD) moved by *N. yvonneae* (± s.e.; range) for within- and between-trap session recaptures was 83.7 m (range of 0-398 m) and 159.9 m (± 20.8 m; 0-926.3 m) respectively (Fig. 4.4). There was no significant difference in distances moved between males and females (U = 117, P = 0.05) for within-trap session recaptures, although males and females differed significantly for between-trap session recaptures (Z = 2.2, P = 0.05; Fig. 4.4). Male and female *N. yvonneae* only recorded similar AD for recaptures separated by more than 100 days (Fig. 4.4).

There were clear differences in average distances moved by animals between seasons (Fig. 4.5). Distances moved within a trap session were generally small (less than 100 m), except during the breeding season when males tended to move considerably further (AD = 215.6 m ± 51.1; Fig. 4.5a). These movements were significantly larger than those recorded for males during pre-breeding ($U = 32$, $P = 0.05$). No within-trap session captures were recorded for post breeding *N. yvonneae*. For between-trap session recaptures, significant differences were recorded across seasons for both males ($H_c = 15.9$, d.f. = 2, $P = 0.001$) and females ($H_c = 8.6$, d.f. = 2, $P = 0.025$). For males, movements were greater in the breeding season than in pre-breeding and post breeding (Fig. 4.5b). In contrast, female *N. yvonneae* movements in pre-breeding and breeding were similar, and much smaller for post breeding. The only significant difference between sexes was recorded for between-trap sessions during pre-breeding ($U = 491$), with males having a significantly larger AD (Fig. 4.5).

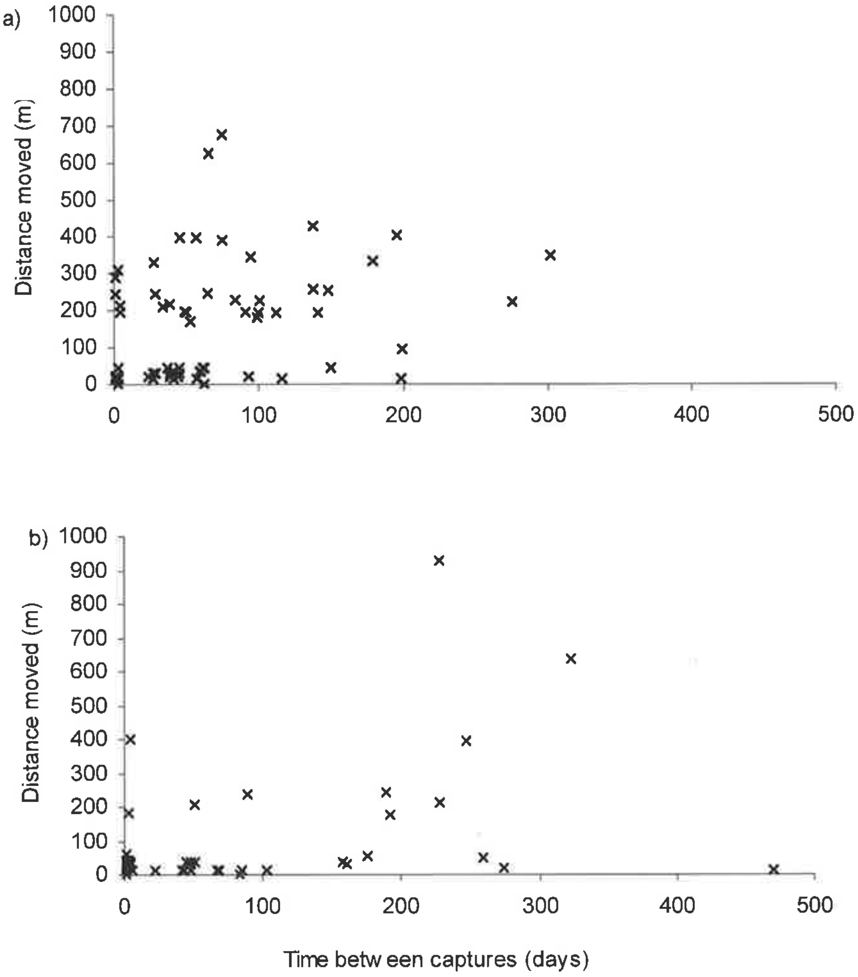

Fig. 4.3. Distance moved as a function of time between recaptures for a) male and b) female *Ningaui yvonneae*. All recorded within-grid movements were less than 52.5 m in length. The minimum and maximum possible distance for a between-grid movement was approximately 80 m and 926 m respectively.

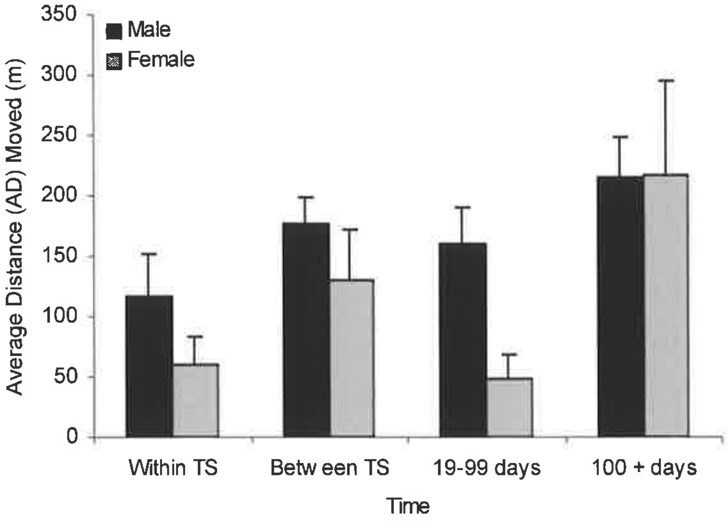

Fig. 4.4. Average Distance (AD) moved (± s.e) by *Ningaui yvonneae* over different time periods. TS = trap session.

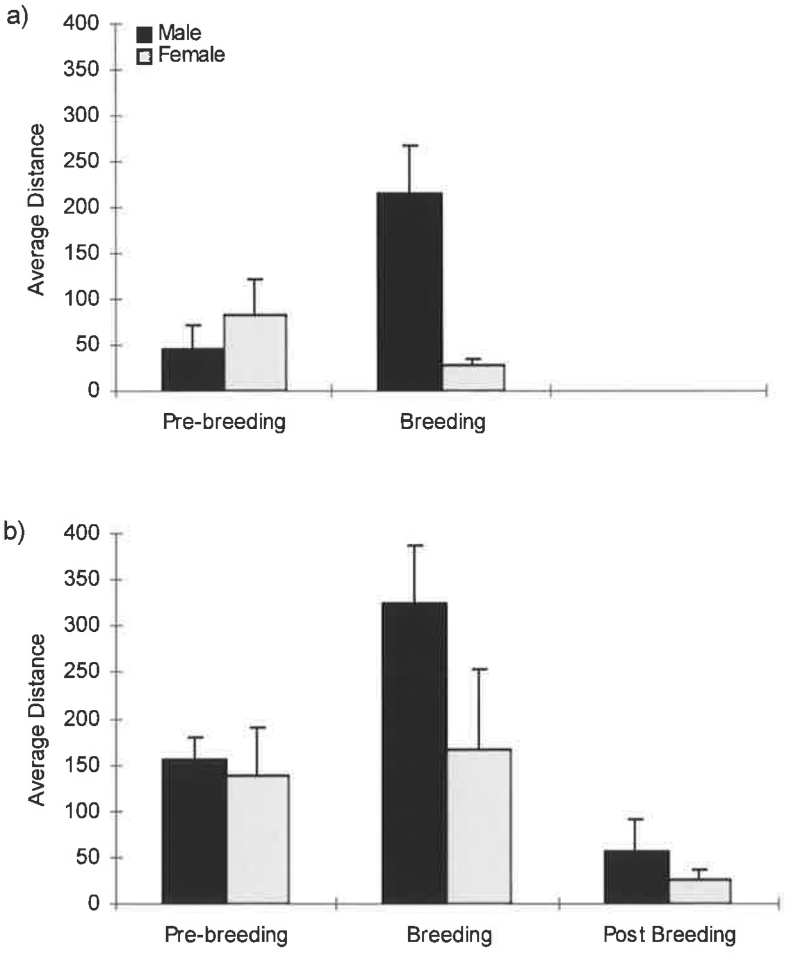

Fig. 4.5. Average Distance (AD) moved (± s.e) each season for movements by *Ningaui yvonneae* a) within a trap session and b) between trap sessions. No movements were recorded post-breeding within a trap session.

The average observed range length (ORL)(± s.e.) was 282.6 m ± 42.1 m. It was higher for males than females, being 300.6 m ± 46.2 m, and 255.6 m ± 81.5 m respectively. However, due to the low number of recaptures for most individuals, the ORL did not reach a plateau and hence was most likely underestimated (Lunney & Leary 1989).

4.3.3 Trapping grid fidelity

Most *N. yvonneae* were either recorded from only one grid for all captures (41%) or a different grid for each capture (39%; Table 4.3). Some *N. yvonneae* (14%) had consecutive captures on the one grid following or followed by a between-grid movement, while fewer returned to the same grid after visiting another (6%). Patterns of use were different for males and females, with more females (61%) being captured at only the one grid and more males (48.5%) at a different grid on all occasions. Patterns of recaptures also varied across grids (Fig. 4.6). Grid L had the highest number of within-grid movements (27%) and from this grid, 65% of animals caught made an within-grid movement. Grids F and E also recorded a large portion of known residents, with 23% and 19% respectively. In contrast, all nine animals caught in grid D were recorded to make between-grid movements (Fig. 4.6).

	Within-grid only	Between-grid only	Within-grid and between-grid^1	Between-grid, grid return^2
Male	9	16	6	2
Female	11	5	1	1
Total	20	21	7	3

Table 4.3. The pattern of between-trap session grid captures for individual male and female *Ningaui yvonneae*. [1]A within-grid movement, with a between-grid movement either preceding or following. [2]Two (or more) captures in one grid separated by a between-grid movement.

4.3.4. Radio tracking

Ten attempts were made to radio track *N. yvonneae*. Only two of these were successful (Table 4.4). The first (female #9, nine locations) was monitored over two nights, with the trial terminated due to poor transmitter reception. When the animal was trapped to remove the transmitter, the transmitter aerial had broken off. The second successful trial (female #17, 15 locations) involved four nights of monitoring, being stopped at the end of the trapping session. Most of the failed trials were a result of either a lost signal (four animals) or removal of the transmitter within the first few hours of monitoring (three animals). One animal was found dead in a burrow under a clump of *Triodia* on the following morning. One of the "lost" animals (female #19, four locations) was recaught during the trapping session following the tracking attempt. Due to the poor success of radio tracking, home range could not be calculated. Instead, the radio tracking data was used to augment trapping data (Table 4.4). Both animals displayed large movements over a short period of time, moving an estimated 14-18 m per hour of darkness.

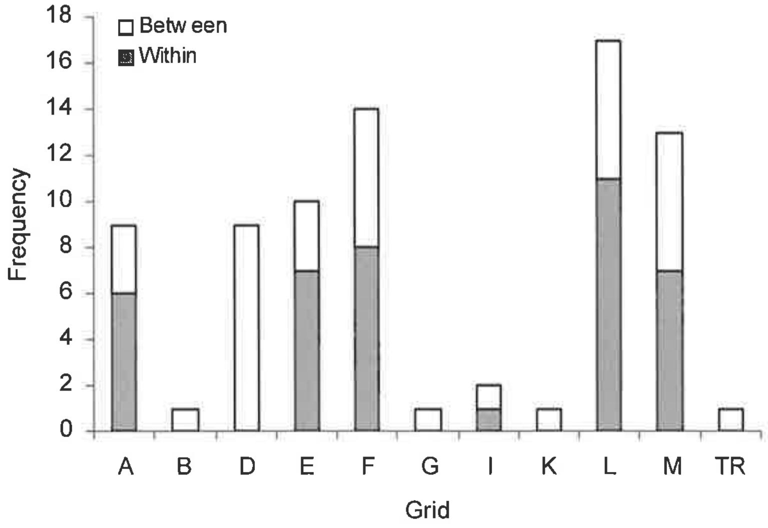

Fig. 4.6. Frequency of between- and within-grid movements by *Ningaui yvonneae* after capture in each grid. Data is for between-trap session captures only.

Female #9 was repeatedly observed/trapped on grid M, being recaught there one month after the radio tracking. This female was observed to use a burrow over two nights. The burrow was central to the nine observation points collected. Female #17 made a single diurnal movement (between 9:30 am and 3.01 pm) of four metres. This animal moved from one *Triodia* hummock to another. This individual was observed to take a rest in its nightly foraging, being located in the same location at 9:45 pm and 10:45 pm.

		Distance moved			Distance (m) / hr of Darkness
Animal	Trial length (hrs)	ORL[1]	R – L[2]	Total[3]	Total
F9	24:08	110	71.5	219.5	~18
F17	61:12	158.5	137.5	428.5	~14

Table 4.4. Distance moved (m) by radio tracked *Ningaui yvonneae*. [1]Maximum distance between locality fixes. [2]Distance from release point to last known location point. [3]Sum of distances between location points

4.4 Discussion

Recaptures rates for *N. yvonneae* in this study were high compared to data on other small dasyurids inhabiting arid areas (e.g. Read 1984; Dickman *et al.* 1995). In particular, Carthew & Keynes (2000), who undertook research at the same study site, had a substantially lower recapture rate (5% and 14% for between and within trap session respectively). In Chapter 3, it was suggested that the low recapture rates of Carthew & Keynes (2000) were a result of trapping effort, with Carthew & Keynes (2000) having fewer trapping sessions across the 14 month life cycle of *N. yvonneae*. Based on the results of this paper, an additional suggestion is the coverage by trapping grids. With frequent between-grid movements, recapture rates would be expected to increase when trapping grids encompassed a greater area. This is especially true given that movement in the study site was limited by the "corridor like" distribution of *Triodia, N. yvonneae's* primary habitat (see Fig. 2.1; Chapter 5).

While recapture rates were comparatively high in this study, a large number of individual *N. yvonneae* were captured only once. This can be indicative of the population composed of individuals continuously moving or establishing large home ranges. In a study on *Sminthopsis* and *Planigale* spp., Read (1984) considered a combination of low overall recapture rates and few between-trip recaptures as a sign that a population was mostly transient (ie. did not establish a permanent home range). However, in contrast to Read (1984), there were a large number of between trip recaptures in the present study, many separated by more than 100 days. Recaptures separated by a greater amount of time can be indicative of longer residency (McIntyre 1997). The relatively large number of individuals in this study remaining in an area over time suggests that a large or drifting home range (a temporarily established home range) might better explain the recorded observations. Davies & Houston (1984) suggested that species may avoid establishing permanent home ranges because of either poor quality or sparsely distributed resources (too large an area to maintain) or alternatively, because of high quality of resources (excessive competition). However, providing a specific explanation for movement behaviour for *N. yvonneae* as a species is difficult, because movement patterns were strongly influenced by sex, time of year and to a lesser extent, the location of capture.

The AD moved by *N. yvonneae* in this study was often greater than that recorded for many other small dasyurids (e.g. Wainer 1976; Smith 1984; Friend 1985; Lunney & Leary 1989). However, caution is necessary when making such comparisons, as unlike many other studies, the trap design for this research was designed for recording longer range movements (see Koenig *et al.* 1996). Those species whose AD's were comparable to, or greater than, *N. yvonneae* were generally other arid or semi-arid dwelling species (e.g. Read 1984; Dickman *et al.* 1995; see also Gilfillan 2001b). The high number of short, within-grid movements recorded in the study should not detract from the range of longer movements obtained. For example, Dickman *et al.* (1995) recorded species making extremely long movements (~14 km) despite the majority of individuals being caught on the same trapping grid of their initial capture.

The willingness of *N. yvonneae* to undertake longer movements seemed in part to be influenced by sex. Female *N. yvonneae* were relatively sedentary, with most movements being within-grid and most individuals remaining in the one grid for their entire capture history. This suggests that female *N. yvonneae* may establish a relatively permanent home range. The longer length of time than males between recaptures might be attributed to the establishment of large home ranges, with females returning to the trapping grid infrequently. Alternatively, females may be trap shy or wary. Both suggestions could explain why male and female recaptures were similar despite the sedentary nature of females. While females showed strong site fidelity, they did occasionally undertake longer movements (up to 926 m), although such movements were uncommon (only 12.5% of movements between trap sessions were greater than 300 m). This might result from a small portion of the population being mobile or the population becoming mobile at different stages of the life cycle (see below for discussion on seasonal influences).

In contrast to females, the majority of movements made by male *N. yvonneae* were between-grid movements. This, combined with the larger AD values recorded for males, suggests that males were more mobile than females. This may help explain the bias towards male captures recorded in Chapter 3, with males having a higher chance of capture due to greater movements (Leung 1999). Also indicative of mobility was the numerous large movements made over a short time span (for example, there were some between-grid movements recorded within trap sessions). However, males did display some site fidelity, mostly over short term periods (17-99 days). This mobility combined with short term fidelity could indicate that male *N. yvonneae* establish drifting home ranges. Drifting home ranges have been suggested for *Sminthopsis crassicaudata, Planigale gilesi* and *P. tenuirostris* (Read 1982; 1984; Morton

1978a) on the basis of patterns of recapture (time between recaptures), change in AD over time, and recapture rates.

Movements of *N. yvonneae* were also influenced by season. Brown (1966) considered seasonal movements to be common in small mammals, linking them primarily to survival (namely food). Read (1984) also found that season influenced the movement of *Planigale gilesi*. In the present study, there were substantial differences in the AD moved during the breeding and pre-breeding seasons, particularly for male *N. yvonneae*. Moreover, AD's were similar for both sexes, except during the breeding season. Similar data were recorded for male *Planigale gilesi* (Read 1982), with a substantial change in movements made by males between the breeding and non-breeding seasons. The particularly high AD for breeding season males in this study suggests that they may be seeking females (Read 1982), possibly in more established territories. The greater movement of males in breeding was highlighted by five within-trap session between-grid movements, four of which occurred during the breeding season. Less movement during pre-breeding may be due to the temporary establishment of home ranges by males. This might be an important survival strategy during winter, allowing *N. yvonneae* to become familiar with good foraging areas and refuge burrows in a time of stress (see Chapter 3). Another notable seasonal influence was a reduction in movement of mature adults after the breeding season. Few adult ningauis remain alive beyond the end of breeding season (Chapter 3). Those few older *N. yvonneae* (14+ months) may increase their chances of survival by establishing a more permanent home range during a time when competition is high (influx of juvenile *N. yvonneae;* Chapter 3) and their bodies are ageing.

This chapter provides valuable insight into the movement behaviour of *N. yvonneae* and the changing patterns over time. However, the conclusions presented here would benefit from more detailed data, which could be obtained by focusing trapping on "corridors" of preferred habitat (see Fig. 2.1). However, the use of trapping data alone can be problematic and may make the definition of movement patterns or trends difficult (for examples see Faust *et al.* 1971; Desby *et al.* 1989*;* Koenig *et al.* 1996). Ideally, trapping should be supported by radio tracking or similar techniques. Unfortunately, as experienced in this study, small species (less than 15 g) such as *N. yvonneae* can be difficult to track because of the limitations on tracking equipment (transmitter size and weight) and the behaviour of the species (e.g. ningauis propensity for moving though dense clumps of *Triodia*).

Chapter 5 - Habitat preferences[1]

5.1. Introduction.

A review on the ecology of dasyurid marsupials in the Australian arid zone by Morton (1982), suggested that dasyurids are unusual in their association with hummock grasslands (*Triodia* sp.). According to Morton (1982), the high species richness of dasyurids recorded in this habitat type is rivalled only by lizards. The association between hummock grasslands and insectivorous marsupials has been noted in several studies (e.g. Cole & Gibson 1991; Fisher & Dickman 1993a). However, few have dealt specifically with the habitat preferences of dasyurids in arid and semi-arid regions of Australia or examined why such a relationship may have evolved between hummock grass and dasyurids. Most studies simply report on the occurrence of dasyurids in habitats with a relatively abundant understorey of hummock grass (e.g. Pearson & Robinson 1990; Woolley 1991; Dickman *et al.* 1993). The small dasyurid, *Ningaui yvonneae,* is thought to be associated with *Triodia* sp. (Coventry & Dixon 1984; Bennett *et al.* 1989; Menkhorst & Bennett 1990; Fisher & Dickman 1993a). However, to date there has been no detailed habitat investigation.

Ningaui yvonneae has a broad distribution across southern Australia, where it is found in a range of habitats. In Victoria, *N. yvonneae* has been recorded in both open mallee and low heathlands (Coventry & Dixon 1984), while in Western Australia it has been recorded from sandy plains (Fisher & Dickman 1993b). In South Australia it has been found in low mallee scrub (Baverstock & Aslin 1975). A common element to most of these landscapes is an understorey of *Triodia*. *Triodia* has also been found to play an important role in the ecology of other species in the genus (Dunlop & Sawle 1982; Fisher & Dickman 1993a; Masters 1993; Dunlop 1995; McKenzie & Dickman 1995).

While some studies have suggested a positive association between *N. yvonneae* and *Triodia*, high densities of *Triodia* are apparently not required. For example, Kitchener (1995) commented that *N. yvonneae* was found in sandy habitat where *Triodia* was sparse, and Fleming & Cockburn (1979) captured the species in areas containing a sparse ground cover of *Triodia irritans*. Some questions still remain then on the importance of *Triodia* to *N.*

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[1] Chapter published as: Bos, D.G., Carthew, S.M. & Lorimer, M.F. (2002) Habitat selection by the small dasyuriod *Ningaui yvonneae* (Marsupialia: Dasyuridae) in South Australia. *Austral Ecology* **27**: 103-109.

yvonneae. This uncertainty is due in part to the absence of detailed habitat assessment for the species. Few studies have dealt specifically with the ecology of *N. yvonneae*, partly because the species was only described in 1983 and also because, as for many dasyurids, it is rather sparsely distributed. Moreover, studies that have attempted to describe *N. yvonneae's* habitat requirements (e.g. Fleming & Cockburn 1979; Coventry & Dixon 1984; Kitchener 1995) were not specific investigations on habitat selection and provide largely anecdotal information.

This chapter investigates the habitat preferences of *N. yvonneae* at the level of the trapping grid (local scale) and the trap (trap scale). In particular, the study aimed to investigate the importance and influence of *Triodia* to the distribution of *N. yvonneae*.

5.2 Methodology

5.2.1 Animal trapping

Animals were trapped as per the description in Chapter 2. Data used for this chapter were taken from the nine trapping sessions undertaken between October 1996 and November 1997. These were the only trap sessions in which all small trapping grids were opened simultaneously. These 12 trapping grids sampled the broad habitat types found within the study area. The most obvious distinction between grids was the presence or absence of *Triodia*. Seven grids contained substantial amounts of *Triodia* (grids A, D, E, F, H, I and L; see Fig. 2.1). *Triodia* was the dominant understorey in grids A, F and L. Grids K and J contained respectively, one and two small (< 10 m diameter) isolated patches of *Triodia* on their outskirts (see Fig. 2.1). The remaining grids (B, C and G) contained no *Triodia*.

5.2.2 Habitat measurements

Habitat was considered at both the trap and local scale. Data collected around traps were recorded via a point quadrat method (similar to that used by Read (1987) and Lawton & Woodroffe (1991)). Four 1.5 m long transects radiated from each trap along each primary compass direction. At three points along each transect (spaced 50 cm apart), a 60 cm pole was held vertically and the dominant habitat component touching the pole was recorded (see Moro 1991; Gonnet & Ojeda 1998; Manson & Stiles 1998). Five habitat components were defined; *Triodia*, shrub, vegetation litter, bare ground and mallee stem. The availability of these habitat components at each trap was described by the number of times, out of a possible 12, the habitat component was the dominant habitat touching the pole. These values were then defined as categorical variables, because of the large number of zeros in the data (ie. some habitat components were absent from some sites). Amount of *Triodia* was classified as either high (if there were between five and seven touches at each bucket), medium (three or four touches), low (one or two touches) and no *Triodia*. Vegetation litter and bare ground were classified as either none-low or medium-high, because there was little variation in their availability (Table 5.1). Shrub and mallee stem were classified as either present or absent because of their generally low occurrence. Local scale habitat components were derived by combining the habitat values for each trap site within a grid, to provide a total measure of habitat for the grid.

5.2.3 Statistical analysis

Separate analyses were performed at the local and trap scales. All analyses were performed in S-Plus 2000 (Mathsoft Inc.). At the local scale, a multiple linear regression (MLR) was used with the pooled trap data to determine the habitat variables that best predicted *N. yvonneae* captures. The response and each of the explanatory variables were log transformed (+1) to satisfy the assumption of constant variance. The full model fitted was:

$$\log(y_j) = \alpha + \beta_1 \log(Triodia)_j + \beta_2 \log(Shrub)_j + \beta_3 \log(Litter)_j + \beta_4 \log(Bareground)_j + R_j$$

where y = number of animals, j = 1,....12; $R_j \sim N(0,\sigma^2)$. Mallee stem was not included in this analysis as it occurred at low levels across all trap grids. The model was reduced by backward elimination.

For the trap scale data, the response was in the form of counts, so a generalised linear model (GLM) approach assuming a Poisson distribution and logarithmic link was considered to be the most appropriate way to model the data (ie. poisson regression). The maximal model for the trapping data included the main effects of the five habitat types and all their interactions. A main effect for Grid was also included to allow for variability amongst Grids. The maximal model was given by:

$$\log(\mu_{ijklmn}) = \lambda + (Grid)_i + (Triodia * Shrub * Bareground * Litter * Mallee)_{jklmn} \quad (1)$$

where, μ_{ijklm} is the expected mean number of captures in the ith Grid with *Triodia* $= j$, Shrub $= k$, Bareground $= l$, Litter $= m$ and Mallee $= n$; $I = 1,\ldots,12$; $j = 1,\ldots 4$; $k, l, m, n = 1,2$; and λ is an intercept parameter.

In order to determine the importance of these terms in describing habitat differences, terms were dropped individually from the model (highest order interactions first) and the change in residual deviance was assessed at the 5% significance level. The residual deviance is analogous to the residual sum of squares in analysis of variance, in that it is a measure of the lack of fit between the observed and fitted values. The terms having the least contribution (ie. largest P-value) on the number of captures were permanently removed from the model.

5.3 Results

A total of 7983 trap nights resulted in 228 captures of *N. yvonneae,* comprising 181 individuals. This gave a trap success rate of 2.8%. Captures were unevenly distributed across the trapping grids, with 96% of captures occurring in seven of the 12 grids (Fig. 5.1). Habitat components also varied across grids (Table 5.1), with the greatest variation being found in *Triodia*, vegetation litter and bare ground. In contrast, mallee stem had consistently low values across all grids (Table 5.1).

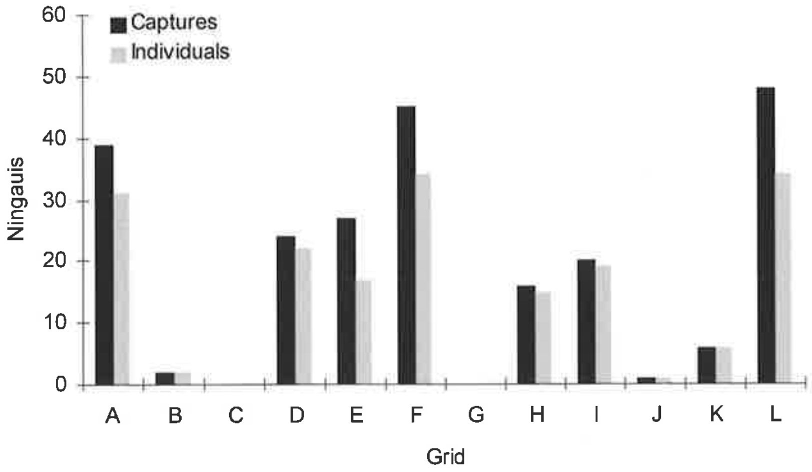

Fig. 5.1. Number of *Ningaui yvonneae* captures and individuals for each trap grid during nine field trips between October 1996 and November 1997.

5.3.1 Local scale

The multiple regression revealed that the number of contacts of *Triodia* was a highly significant ($P < 0.001$) predictor for *N. yvonneae* captures at the local scale. The abundance of shrubs was found to approach significance ($P = 0.052$), while the presence of bare ground and vegetation litter were not significant ($P = 0.756$ and $P = 0.755$ respectively). The parameter estimates and standard errors are presented in Table 5.2. Trapping grids that contained a high proportion of *Triodia* included grids A, D, F and L and a high proportion of shrub, grids B, J, H and K (Table 5.1).

Habitat component	Grid												Mean value
	A	B	C	D	E	F	G	H	I	J	K	L	
Bare ground	45.5	46	56.5	45	55.5	30	63	51	51	43	24	46	46.5 ± 3.1
Vegetation litter	23	35	37	35	27	31	32	35	35	42	60	19	34.3 ± 2.9
Triodia	24	0	0	18	11	37	1	4	9	2	2	35	11.8 ± 3.9
Shrub	6.5	19	6.5	2	5.5	1	2	10	4	13	14	0	6.8 ±1.6
Mallee stem	1	0	0	0	1	1	2	0	1	0	0	0	0.5 ± 0.1

Table 5.1. Availability of measured habitat components within each trapping grid. Habitat values are expressed as the number of contacts on the measuring pole per 100 contacts. Means are ± standard errors.

	Estimate	s.e.	t-value
Constant	-1.003	0.662	-1.52
Log(Shrub + 1)	0.506	0.226	2.24
Log(Triodia + 1)	1.240	0.154	8.04

Table 5.2. Parameter estimates and standard errors (s.e.) obtained from the multiple linear regression.

5.3.2 Trap scale

The residual deviance obtained from the maximal model was 107.11 on 74 degrees of freedom. The dispersion parameter, ϕ (the ratio of the residual deviance to the degrees of freedom) was 1.45, suggesting that the model was fitted adequately (McCullagh & Nelder 1989). To determine whether any of the interaction terms were significant, each interaction was removed separately from the full model and its importance assessed by calculating the change in deviance. The only significant interaction at the 5% level was between *Triodia* and shrub ($P = 0.01$). The main effects for bare ground, mallee stem and litter were all removed from the model as all were found to be non-significant ($P = 0.42$). The main effect for Grid was highly significant ($P < 0.001$). The final model was therefore given by:

$$\log(\mu_{ijk}) = \lambda + (Grid)_i + (Triodia)_j + (Shrub)_k + (Triodia.Shrub)_{jk} \qquad (2)$$

By substituting the parameter estimates (Table 5.3) into the final model equation, the expected mean number of captures for each trap within each grid (Table 5.4) and for the interaction between *Triodia* and *Shrub* (Table 5.5) were calculated.

	Value	s.e.	t-value
(Intercept)	1.459	0.236	6.19
Grid B	-2.388	0.751	-3.18
Grid C	-9.9	15.3	-0.64
Grid D	-0.314	0.27	-1.17
Grid E	-0.066	0.269	-0.25
Grid F	0.173	0.236	0.74
Grid G	-10.0	15.5	-0.65
Grid H	-0.834	0.327	-2.55
Grid I	-0.496	0.296	-1.68
Grid J	-3.37	1.02	-3.30
Grid K	-1.332	0.472	-2.82
Grid L	0.234	0.248	0.94
Triodia (Low)	-0.315	0.313	-1.01
Triodia (Medium)	-0.003	0.258	-0.01
Triodia (High)	-0.051	0.257	-0.20
Shrub (Present)	-0.677	0.286	-2.37
Triodia (Low):Shrub (Present)	1.355	0.475	2.85
Triodia (Medium):Shrub (Present)	0.923	0.448	2.06
Triodia (High):Shrub (Present)	NA	NA	NA

Table 5.3. Parameter estimates and standard errors (s.e.) from the final model (Model 2) for trapping data. *NA* represents combinations of habitat components that did not occur in the study area.

Grid	Predicted captures	Observed captures
L	5.31 ± 0.77	5.33 ± 1.35
F	4.96 ± 0.79	5.00 ± 1.18
A	3.92 ± 0.68	4.33 ± 0.69
E	3.35 ± 0.70	3.00 ± 0.80
D	2.61 ± 0.56	2.67 ± 0.55
I	2.26 ± 0.53	2.22 ± 0.72
H	1.58 ± 0.43	1.78 ± 0.55
K	0.90 ± 0.39	0.67 ± 0.33
B	0.32 ± 0.23	0.22 ± 0.15
J	0.12 ± 0.12	0.11 ± 0.11
C	0	0
G	0	0

Table 5.4. Predicted mean capture rate per trap (± standard error) derived from Poisson regression and observed mean capture rate per trap (± standard error) of *Ningaui yvonneae* for each grid.

	Shrub	
Triodia	Absent	Present
None	1.76 ± 0.33	0.89 ± 0.19
N	27	36
Low	1.65 ± 0.41	4.21 ± 1.04
N	10	5
Medium	4.09 ± 0.54	6 ± 1.73
n	15	2
High	4.19 ± 0.57	*NA*
n	13	

Table 5.5. Mean predicted captures of *Ningaui yvonneae* ± approximate standard error at the trap level for interactions between *Triodia* and shrub as derived from Poisson regression. *NA* represents combinations of habitat components that did not occur in the study area. *n* is the number of traps with that habitat combination.

There was considerable variation in the mean predicted capture rates per trap bucket between grids, with values ranging from 0 to 5.3 ningauis (Table 5.4). Captures appeared to be dependant on the presence of *Triodia* (Table 5.5), with fewest predicted captures when *Triodia* was absent. Predicted captures rates were also relatively low when the abundance of *Triodia* was low, except when shrubs were present. Predicted values indicated that most ningauis should be caught when the abundance of *Triodia* was medium or high, with shrubs being either present or absent.

5.4 Discussion

This investigation on the habitat requirements of *N. yvonneae* revealed that the distribution of *N. yvonneae* at the local and trap scales was influenced by the density of *Triodia* and a combination of *Triodia* and shrubs respectively. Predicted capture rates at the trap scale suggested that the abundance of *N. yvonneae* was influenced by the cover provided by shrubs and *Triodia*. Higher capture rates were expected when cover was present (as either shrub or *Triodia*). The only exception to this was when *Triodia* was absent and shrub was present. These conditions generated the lowest predicted capture rate. This implies some *Triodia* was required by *N. yvonneae* as a component of the vegetation cover in the habitat. This pattern of habitat selection explains the preferences shown at the local scale. While *Triodia* was a highly significant predictor of *N. yvonneae* presence at this scale, shrub only approached significance. Despite its provision of cover, shrub appeared to be used only when *Triodia* was present.

The importance of cover in determining habitat selection suggests that protection from predators is a chief concern for *N. yvonneae*. The influence that predation risk can have on resource selection by animal populations is well recognised (e.g. Bowyer *et al.* 1998; Gray *et al.* 1998). Fisher & Dickman (1993a) suggested that small dasyurids such as *N. yvonneae* may avoid open habitats because of an increased risk of predation. It is interesting then, that shrubs alone did not provide adequate cover for ningauis in the present study. Shrub habitats have been recorded as important for many animals because of the cover they provide (e.g. Kotler *et al.* 1991; Hughes & Ward 1993; Sutherland & Predavec 1999). However, under certain conditions, shrub cover can increase predation risk (e.g. Kotler *et al.* 1992; Bouskila 1995; Schooley *et al.* 1996). Shrubs therefore, may not provide the most effective refuge for *N. yvonneae*. Furthermore, shrubs in the study site varied greatly in form (e.g. height and stem density) and distribution. They were relatively patchy, occurring in dense clumps in some areas, and sparsely in others. This contrasts to the relatively evenly distributed and generally dense nature of *Triodia* hummocks.

The specific importance of *Triodia* as a form of protection because of its dense and spiny nature has also been recorded for other taxa (Pianka 1981; Lundie-Jenkins 1993). Several authors have suggested that *Triodia* may harbour an abundance of potential prey items for animals, thus providing food as well as cover. For example, Morton (1982) suggested that the preference for hummock grasslands by dasyurids occurs because *Triodia* provides permanent cover, which in turn, gives a more stable population of invertebrates. Similarly, Pianka (1981) believed that the strong association between Australian reptiles and *Triodia* arose because it provides protection from predators and the elements, and a rich and diverse supply of invertebrate food. Morton & James (1988) later argued that species richness in hummock grasslands is more a result of the food web working within *Triodia*, than its structure. Fisher & Dickman (1993a) suggested that both *N. yvonneae* and *N. ridei* preferred to forage in habitats such as shrubs and *Triodia* that contained small prey items. However, without detailed knowledge on foraging behaviour, it is difficult to identify a relationship between prey availability and habitat preference.

Given the apparent association between *N. yvonneae* and *Triodia,* why have ningauis been reported in areas with a low cover of *Triodia*? While most ningauis in this study were caught in areas that contained high amounts of *Triodia*, some were caught where there was little *Triodia* (Grids J, B and K; see Fig. 2.1). Masters (1993) also caught *N. ridei* occasionally in locations with less than 10% *Triodia* cover. These findings demonstrate that *N. yvonneae* is able to survive, if only temporarily, away from *Triodia*. These results could derive from the high mobility of the species (see Chapter 4), combined with the patchy nature of the habitat. *N. yvonneae* may be captured in less favoured sites as they pass through them (Stephenson 1995). Several trapping grids with little or no *Triodia* were on the edge of *Triodia* habitat (J and K; Fig. 2.1). Captures in these grids may arise from ningauis moving between patches of *Triodia* habitat. Szacki & Liro (1991) found that small mammals can make deliberate long range movements through different (including unfavourable) habitats.

This chapter confirms the suggestions of other studies that *Triodia* is a key resource of *N. yvonneae*. The provision of refuge for predators is the most likely benefit of *Triodia* to *N. yvonneae*, given the species propensity for habitats that provide cover. *Triodia* could provide either specific protection or particular food resources. However, a more detailed examination of *N. yvonneae* ecology, or specific studies investigating the influence of predation and foraging on habitat selection, such as that performed by Haythornthwaite & Dickman (2000) on *Sminthopsis youngsoni,* are required.

Chapter 6 - Foraging behaviour and habitat selection [1]

6.1 Introduction

An understanding of how animals use habitat is important if populations are to be managed and conserved. Habitat use and selection are some of the most commonly studied aspects of fauna populations, and are the focal point for many studies (Thomas *et al.* 1992; Millspaugh *et al.* 1998). Habitat is defined as an area of landscape that satisfies an animal's living requirements for food, shelter and reproduction (Anderson 1991). The use of habitat by an individual at any point in time is driven by the satisfaction of one or more of these needs (Hall *et al.* 1997). For example, the use of a burrow by a desert dwelling mammal may satisfy the requirement for sleep, temperature regulation and/or protection from predators. Understanding an animal's needs is important, as they play a significant role in the decisions regarding habitat suitability or selection.

Many studies examining habitat selection have neglected to consider how an animal's living requirements influence the selection of habitat or how the use of a habitat might satisfy a need. An examination of 50 published papers that purported to assess habitat selection in small to medium sized terrestrial mammals showed that most (86%) gave only general information on species habitat selection (such as type of habitat, floristics and structure). A number of studies (26%) examined temporal variation in habitat use, as advocated by Schooley (1994). Fewer papers (10%) detailed differences between age classes or sex. Seven papers (14%) considered animal behaviour. However, these tended to be specific, focusing on a single behaviour such as refuge selection or predation risk. In general, the importance of a habitat in satisfying a particular need was only examined in the discussion, as an explanation for the animal's use of a habitat.

There are two main reasons why the relationship between habitat and an animal's specific requirements are often neglected in the literature. First, identifying the needs being satisfied can be difficult. The simplest approach is to interpret requirements via behaviour or activity (e.g. a sleeping animal is satisfying the need for rest, a foraging animal the need for food).

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[1] Chapter published as: Bos, D.G. & Carthew, S.M. (in press) The influence of behaviour and season on habitat selection by a small dasyurid marsupial in southern Australia. *Ecography*.

Second, techniques used to record habitat selection data do not typically record needs. Two methods are commonly used to investigate habitat use or selection by small-medium terrestrial mammals. The first involves capturing or detecting individuals as they move through the habitat and comparing the numbers observed/caught at different locations with the habitat at those locations. The second involves documenting the animal's movement through its environment (either by direct observation or some indirect form of tracking), and then comparing the habitat in contact with the animal's trajectory with the overall habitat (e.g. Aebischer *et al.* 1993). While there are strengths and weaknesses with both approaches, the latter method will provide more detailed information on habitat use (e.g. McShea & Giles 1992; Aebischer *et al.* 1993; Schulte-Hostedde & Brooks 1997; Tew *et al.* 2000). The most widely used technique employed to record animal movements through the landscape is radio-tracking (Millspaugh *et al.* 1998). However, detailed information on the animal's trajectory can be difficult to obtain, as sample points must be sufficiently spaced to maintain independence. Also, radio tracking often uses triangulation to locate animals, meaning activity or habitat use is difficult to record or data less reliable. This is particularly true for studies on small ground dwelling mammals, which are often hard to observe directly. Spool-and-line tracking and fluorescent powder tracking can provide more detailed data and allow documentation of precise movement pathways. However, again actual behaviours are difficult to obtain. The most appropriate manner to record both habitat and behaviour is via observation, either directly or remotely.

In this chapter, habitat use in *N. yvonneae* is investigated via direct observation, with the aid of red lights and luminescent tags, of free foraging animals. In particular, habitats most important to *N. yvonneae* while undertaking various behaviours were examined. Particular reference was given to the relationship between *N. yvonneae* and *Triodia*, the latter being a habitat component ningauis are often associated with (Chapter 5).

6.2 Methods

6.2.1 Habitat use

Animals were captured as per the description in Chapter 2. Individual *N. yvonneae* were retained during the day for release and observation at night. While in captivity, animals were provided with mealworms (*Tenebrio* spp.) and/or wild caught invertebrates (e.g. grasshoppers and spiders). Data on habitat use by *N. yvonneae* were collected by directly observing free foraging ningauis. Animals were fitted with luminescent tags ('Starlight SL-5' mini-chemical lights, ∅ 3 x 23 mm, 0.05 g) which were easily viewed at night. Tags were attached to ningauis using a small amount of 'Selleys' supa-glue, which was applied to one end of the tag and placed on the animals rump. In this position the tag was easily seen (as the ningaui's rump usually faced the observer during trials), was protected from obstructions as ningauis moved through vegetation, and did not hinder the animal's movement. Observations were made using red light, from a distance of approximately 3 m (range 0-10 m).

Observation trials commenced 20-30 mins after sunset. Each animal was released (with tag) into the clump of *Triodia* nearest to their capture point. Preliminary trials showed that tagged animals commenced foraging almost immediately after release. However, to ensure only natural behaviour was recorded, trials commenced after at least 5 minutes of activity, or if more than 5 minutes had elapsed without movement, then when the animal left the release *Triodia*.

Data were recorded at 1 minute intervals, and at each time, the habitat component the animal occupied and the activity being performed were recorded. Habitat components included leaf litter, bare ground, woody debris, *Triodia*, *Triodia* edge, mallee trunk, shrub and underground (see Table 6.1 for definitions). Emphasis was placed on *Triodia* because of its importance in determining *N. yvonneae* distribution (Menkhorst & Bennett 1990; Fisher & Dickman 1993a; see also Chapter 5). Activities recorded were: paused, stopped, running, walking, attacking prey, consuming prey, grooming, climbing, digging and furrowing (Table 6.1). Anecdotal information was also recorded during each trial on the use of burrows, prey killing techniques and search behaviour. The length of observation trials was usually between 1-2 hours (60-120 observation points per animal). It was thought that numerous shorter trials would provide more accurate information for the population. The minimum time for a trial to be included in data was 10 minutes (10 observation points).

One concern about direct observation is the influence of human presence. Utmost caution was used when observing animals, with usually only one observer used during trials. As a rule, the observer would move only when the animal moved, would always walk and would miss data points rather than disturb an animal due to poor visibility. In general, *N. yvonneae* seemed to show little concern about the observer, and on several occasions, foraged around the observers feet. On those few occasions when an animal did appear to be influenced by an observer, no data were recorded.

If *N. yvonneae* entered a burrow and did not return to the surface within 30-40 minutes, the trial was terminated. Since animals could not be observed during this time underground, they were assumed to be resting and the activity (for the 30-40 minutes) was recorded as "stop". On occasion, animals entered spider burrows in search of food. This involved removing the spider before killing and eating, and so on these occasions behaviour for non-visible time (which was usually less than 2 minutes) was estimated (e.g. attacking). Behaviour was not estimated for any other habitat component.

Habitat component	Code	
Leaf litter	Ll	in a clump of vegetation litter or debris.
Bare ground	B	in an area with little or no vegetation litter or debris.
Woody debris	Wd	on dead trunks, branches and/or roots with a diameter > 5 cm.
Triodia	T	within a clump of *T. irritans*.
Triodia Edge	Te	in the margins of the *T. irritans* hummock fringed with numerous outward facing spines (Pianka 1969).
Mallee stem	Ms	on the stem of a mallee eucalypt.
Shrub	S	under or climbing in a shrub to a height < 60 cm.
Under ground	U	in a burrow or hole.
Activities		
Paused		temporary stop in activity, lasting < 3 seconds. Often used before a change in direction, reconnaissance or 'air sniffing' (see Appendix 2).
Stopped		a cease in activity for ≥ 3 seconds.
Digging		using front feet to move soil
Furrowing		placing snout in soil/leaf litter and moving
Running		quadrupedal bounding gait (see Andrew & Settle 1982)
Walking		slow walk
Grooming		licking fur or using forepaws to groom.
Consuming prey		in the process of eating prey
Attacking prey		in the process of subduing prey
Climbing		ascending vegetation and/or moving above the ground

Table 6.1. Description and definition of habitat components used and activities performed by *Ningaui yvonneae*.

The importance of *Triodia* for *N. yvonneae* during foraging was examined by measuring the average distance from a foraging ningaui to the nearest clump of *Triodia*. Prior to the trial, 10 random observation points were selected from the first 60 observation points. When one of these selected points was encountered, the location of the ningaui (if not in *Triodia*) was noted and marked with a survey pin. The following day, the distance from the survey pin to the nearest *Triodia* clump was recorded.

6.2.2 Habitat measurements

Habitat availability was recorded at 200 randomly located plots within the trapping area. Each plot consisted of four 1.5 m long transects radiating out from the centre of the sample plot along each primary compass direction. On each transect, 3 sample points were positioned (50 cm apart), providing a total of 2400 sample points. A 60 cm high pole was held at each point, and the habitat component with the most contacts on the pole recorded (see Moro 1991; Manson & Stiles 1998). A height of 60 cm was used because animals rarely foraged above this height. The habitat components measured were the same as those used for animal observations. The distance from the centre of each plot to the nearest clump of *Triodia* was also recorded to allow comparison with the distance to *Triodia* data recorded during observation trials.

6.2.3 Data analysis

Niche breadth was measured to gauge the level of selectivity in habitat use by *N. yvonneae*. The choice of technique for determining niche breadth depends largely on the desired emphasis in the analysis (Smith 1982; Krebs 1999). Smith's Measure (Smith 1982) was chosen to measure niche breadth of the overall population and provide an absolute value of habitat selectivity. This measure is apparently not influenced by the rarity of habitats (Smith 1982; Krebs 1999), and is given by;

$$FT = \sum_{i=1}^{n} (\sqrt{p_i a_i})$$

where FT is the niche breadth, p_i is proportional use of habitat i, a_i is proportional availability of habitat i, and n is the total number of habitats. A value of 1 indicates use of a habitat in proportion to its availability (random use). A value of 0 indicates no overlap between resource use and availability, so that resource use is selective. Preliminary examination of the data obtained in this study showed that changes in habitat use between sexes and over seasons was most notable in rarer habitat components. Hurlbert's measure (Hurlbert 1978) was used to compare between these sub-groups, as this measure is sensitive to a population's use of rare resources (Smith 1982; Krebs 1999). Hurlbert's measure is given by;

$$B' = \frac{1}{\sum (p_i^2 / a_i)}$$

where p_i is proportional use of habitat i and a_i is proportional availability of habitat i. B' was then standardised to a scale of 0-1 by the equation;

$$B'_A = \frac{B' - a_{\min}}{1 - a_{\min}}$$

where a_{min} is the lowest observed proportion of all habitat. A value of one indicates maximal overlap (random use of resources) and zero minimal overlap (selective use of resources).

Compositional analysis was then used to provide a relative ranking of preference for each habitat component. Compositional analysis is considered one of the better techniques for determining resource selection (Aebischer *et al.* 1993; Alldredge *et al.* 1998; Pendelton *et al.* 1998; Leban 1999), as it addresses some of the key problems involved with other methods (see Aebischer *et al.* 1993). It also uses data from individuals (important for consideration of individual behaviour), is suitable for comparison between population sub-groups (such a seasons or sex) and can be calculated with readily available software (Leban 1999). In addition, compositional analysis avoids making absolute statements about habitat selection. Some techniques assign a score to each habitat, using this value to measure absolute differences in the level of habitat selection. For example, they may state that the selection for habitat X is twice that of habitat Y. Such statements can be misleading (Johnson 1980; Lechowicz 1982; Aebischer *et al.* 1993). Aebischer *et al.* (1993) suggested that compositional analysis requires a minimum sample size of 10 individuals, but recommended more than 30. In this data set, the minimum sample size was 10 individuals, with a minimum of 25 observations per individual. The exception to this was the comparison of behaviour categories, where the minimum number of points per individual was 1. This was necessary because of the infrequent performance of some activities during a trial, especially eating (i.e. no animal was observed to eat more than 25 observation times during a single trial).

Log-Likelihood ratio (*G*) analysis for contingency tables (Zar 1999) was used to identify significant differences within sexes and seasons for habitat use and behaviour. Zero values were substituted with 0.001. Differences in activity budget between males and females across seasons were examined using a generalised linear model (McCullagh & Nelder 1989). A Poisson distribution was assumed and the maximal model used was defined as (Season*Sex)/Individual + Season*Sex*Activity.

6.3 Results

In all, 59 successful observation trials were conducted, totalling 2,764 minutes of observation (mean ± s.e. of 46.8 ± 2.7 minutes) and 2,657 data observation points. The 59 trials were conducted using 52 individual *N. yvonneae*, with seven individuals trialed twice. Of these, 22 were female and 30 male, with total observation points being 987 and 1670 respectively. Sixteen trials were conducted in the 'Growth' season, 17 in 'Maturation', 14 in 'Breeding' and 12 in 'Nurture'. Of the seven individuals trialed twice, those that occurred in the same season (three), were combined and used as a single record for all analyses. The four individuals with trials recorded during different seasons were treated as independent data for all analysis.

6.3.1 Habitat availability

Availability varied considerably amongst habitat components (Fig. 6.1). Leaf litter and bare ground were the most abundant habitat components, making up 39% and 37.1% of the available habitat respectively. In contrast, mallee stem and woody debris were the least available habitat components (0.5% and 0.6% respectively). Underground was recorded as not available, as no burrow entrances made contact with the sampling pole (or at least, it was never the dominant habitat component touching the pole). To estimate burrow abundance, a visual search for burrows was undertaken in 121 of the habitat availability plots. Twenty-three (19%) of the plots contained burrows of a type known to be used by *N. yvonneae*. However, these data were difficult to quantify and were not comparable with the availability data collected by contacts with the sample pole. For the category 'underground' to be used in the data analysis, an arbitrary percentage of 0.1% availability was allocated from leaf litter (where most burrows were found) to underground. The percentage of 0.1% was lower than the availability of the lowest recorded habitat component (mallee stem with 0.5%).

6.3.2 Habitat use

N. yvonneae were recorded in all eight habitat components during tracking trials. However, only one individual was recorded to use all eight habitat components during a single trial. On average, individual *N. yvonneae* were recorded to use 5.1 ± 0.2 (mean ± s.e.) habitat components during observations. Smith's measure of niche breadth indicated that *N. yvonneae* used habitat components in a similar proportion to their availability (FT = 0.85). However, in most habitat components there were clear differences between the number of times an animal was recorded in the habitat and its availability (Fig. 6.2). Compositional analysis indicated that the use of habitats by *N. yvonneae* was non-random ($\chi^2 = 58.71$, d.f. = 7, $P < 0.0001$; Table 6.2). *Triodia, Triodia* edge and leaf litter were the most preferred habitat components, while woody debris, bare ground and mallee stem were the least preferred (Table 6.2).

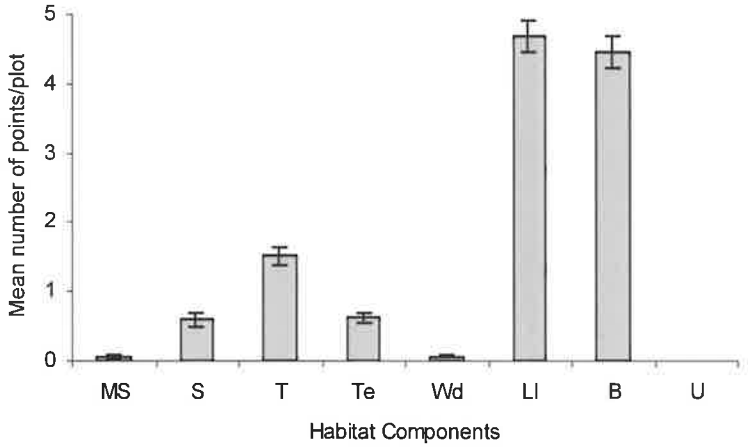

Fig. 6.1. Mean number of sample points per plot (± s.e.) for each habitat component. Data are taken from 200 random plots. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

While male and female *N. yvonneae* used some habitat components in similar proportion (e.g. shrub, *Triodia* edge; Fig. 6.2a, b), a significant difference between sexes was recorded (G = 51.42, d.f. = 7, $P < 0.001$). The most notable differences were for *Triodia*, which was used more often by females (44.5% and 31% of observation points for females and males respectively) and leaf litter, which was used more by males (28.1% and 21.3% for males and females respectively; Fig. 6.2a, b). Despite these differences, Hurlbert's measure produced a similar value for male and females, 0.18 and 0.19 respectively and compositional analysis identified similar ranks of habitat selection (Table 6.2).

There were significant differences in the use of habitat components between seasons ($G = 442.41$, d.f. = 21, $P < 0.001$). For example, *Triodia* was used substantially less during Maturation than other times, underground almost exclusively during Growth and Maturation and mallee stem more during Maturation. Hurlbert's measure of niche breadth also rated the four seasons differently. During Growth and Maturation, animals showed greater selectivity in habitat use ($B'_A = 0.12$ and 0.05 respectively) than during Breeding and Nurture ($B'_A = 0.39$ and 0.35 respectively). Seasonal differences were also reflected in the relative selection of habitat components identified by compositional analysis (Table 6.2). In particular, the relative importance of *Triodia*, shrub and *Triodia* edge varied. Male and female *N. yvonneae* also differed in use of habitat components across seasons. Females tended to use *Triodia* more often than males during Breeding and Nurture, and shrub more often during Maturation. In addition, the use of underground was largely restricted to males during Maturation and females during Growth.

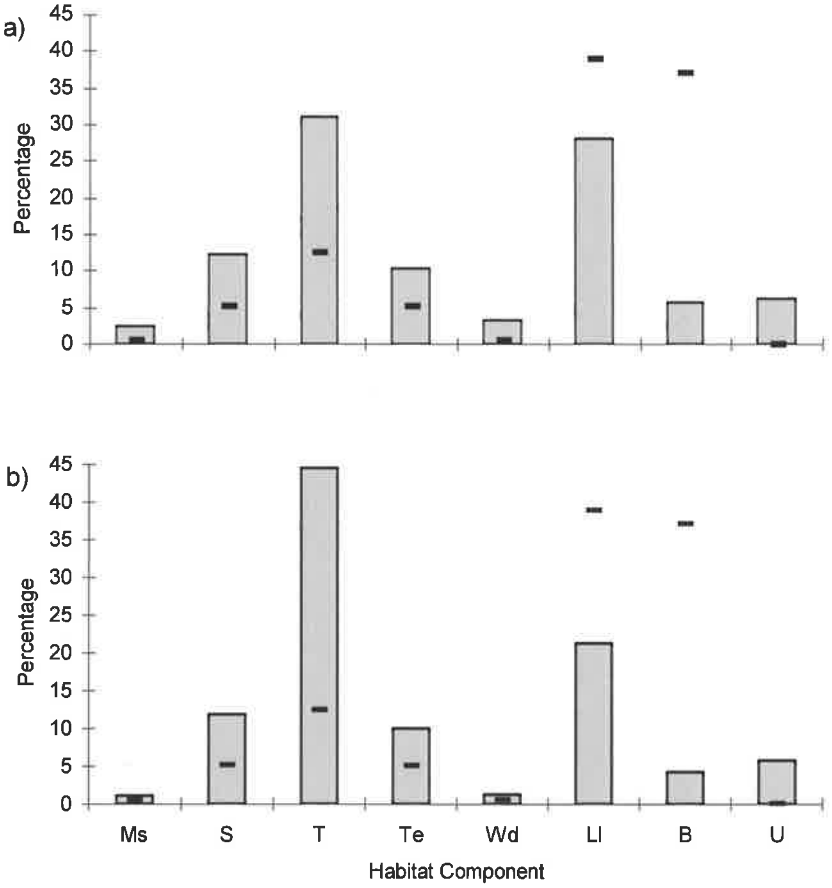

Fig. 6.2. Percentage of observation points recorded for a) male and b) female *Ningaui yvonneae* in a particular habitat component (bars) and the percentage availability for each component (dashes). Number of observation points for male use was 1670 and female use was 987. See text for explanation on the availability of underground. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

6.3.3 Behaviour and use of habitat

N. yvonneae engaged in all 10 designated activities during observation trials (Table 6.3). Digging and furrowing were combined for the analysis because of their similarity and low occurrence during trials, and were pooled as 'soil search'. Activities were divided into three behaviour categories, 'rest' (groom and stop), 'eat' (attack and consume) and 'active' (pause, walk, run, climb, soil search). Pause was included in 'active' because it formed part of typical active behaviour (see Table 6.1). Of the 10 activities recorded, six were recorded for less than 6% of the time. However, the frequency with which these activities were performed was often high. For example, although *N. yvonneae* spent little actual time climbing (5.9%), climbing was recorded in 43 trials (76%; Table 6.3). Such activities were considered to constitute part of the 'typical' ningaui foraging behaviour. Differences were recorded in behaviour between sex and season. For example, females spent proportionally more time than males climbing and walking and during the season Maturation, ningauis spent proportionally less time walking and more time soil searching (Table 6.3).

Differences in activity budget between male and females across seasons were examined by a generalised linear model. This gave a value of $p = 0.0541$ (d.f. = 408), which was marginally significant. This suggests that a combination of season and sex had some influence on activity patterns. For example, Maturation was the season males spent more time at rest. In contrast, Maturation was the most active season for females. However, other factors may also be important, as the variance in the model was high ($\varnothing = 2.96$).

Habitat	Rank								*N*	*n*	χ^2	*P*
	1	2	3	4	5	6	7	8				
Sex												
Male	T	Te	Ll	S	U^a	Wd^a	B^a	Ms^a	29	1626	32.83	***
Female	T	Te	Ll	U	S	Wd	Ms	B	19	910	46.53	***
Season												
Growth	T	Te	Ll	U^a	S^a	Wd	B	Ms	13	718	65.67	***
Maturation	Te	Ll	T^a	U^a	Ms^a	S^a	B^b	Wd^b	11	682	17.11	*
Breeding	T	S	Ll	Te	U	Ms	B^a	Wd^a	13	656	36.65	***
Nurture	T	Te	Ll	Wd^a	U^a	S^a	Ms^a	B^a	11	480	28.78	**
Total	T	Te^a	Ll^a	S^b	U^b	Wd	Ms^c	B^c	48	2536	58.71	***

Table 6.2. Rank of habitat components derived from compositional analysis for trials with ≥ 25 observation points. Ranks range from 1 (most preferred) to 8 (least preferred). Habitat components with like superscripts do not differ significantly in rank. *N* = number of individuals, *n* = number of observation points. T = *Triodia*, Te = *Triodia* edge, Ll = leaf litter , S = shrub, U = underground, Wd = woody debris, B = bare ground, Ms = mallee stem. For *P* values, * = 0.05, ** = 0.001 and *** = 0.0001.

	Active						**Eat**			**Rest**		
	Walk	Pause	Run	Climb	Soil Srch	**Total**	Consume	Attack	**Total**	Stop	Groom	**Total**
Sex												
Male	39.8	5.2	5.9	4.7	4.3	**59.9**	10.7	1.3	**12**	25.6	2.7	**28.3**
Female	43	6.4	5.4	8	2.4	**65.2**	9.3	1.9	**11.2**	21.7	1.9	**23.6**
Season												
Growth	42.5	6.9	5.9	4.7	3.8	**63.8**	8.9	2	**10.9**	22.7	2.6	**25.3**
Maturation	36	3.7	5.9	6.4	4.4	**56.4**	13	0.9	**13.9**	27	2.7	**29.7**
Breed	43.2	6	4.5	7.6	3.4	**64.7**	7	0.9	**7.9**	25.6	1.8	**27.4**
Nurture	43	6.3	6.7	4.9	2.2	**63.1**	12	2.4	**14.4**	19.9	2.6	**22.5**
Total	40.9	5.6	5.7	5.9	3.6	**61.7**	10.2	1.5	**11.7**	24.1	2.4	**26.5**
N	56	47	44	43	37	**56**	44	22	**46**	53	32	**53**

Table 6.3. Activity budget for male and female *Ningaui yvonneae* and over seasons. Values are the percentage of observation points for each activity. *N* is the number of trials (out of a total of 56) in which an activity was performed at least once.

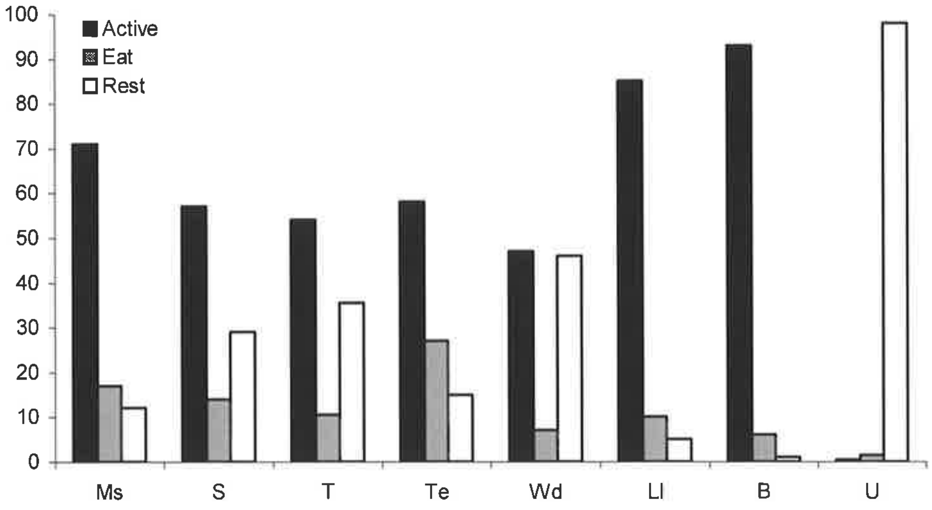

Fig. 6.3. Percentage of *Ningaui yvonneae* observation points recorded as active (pause, walk, run, climb and soil search), at rest (groom and stop) or eating (attack and eat) for each habitat component. Ms (mallee stem), S (shrub), T (*Triodia*), Te (*Triodia* edge), Wd (woody debris), Ll (leaf litter) B (bare ground) and U (underground).

	Foraging *N. yvonneae*						Random
	Woody debris	Leaf litter	Under shrub	Bare ground	Eucalypt stem	Total	
Mean distance	2.3	0.6	2.8	0.6	0.2	1.3	2.0
s.e.	-	0.13	0.74	0.19	0.09	0.28	0.26
n	1	40	24	4	3	72	179

Table 6.4. Mean distance (m) to the nearest *Triodia* clump from foraging *Ningaui yvonneae* in various habitats and from random points within the study area.

Activity Type	Rank 1	2	3	4	5	6	7	8	*N*	*n*	χ^2	*P*
Active	T^a	Ll^a	Te	S	Wd	U	B^b	Ms^b	56	1639	109.31	***
Eat	Te	T	U	Ll	Ms	Wd^a	S^a	B	46	313	65.78	***
Rest	T	U	S	Te	D	Ms	Ll	B	53	683	131.73	***

Table 6.5. Rank of habitats derived from compositional analysis for each activity type, ranging from 1 (most preferred) to 8 (least preferred). Habitats with like superscripts do not differ significantly in rank. *N* = total number of individuals, *n* = total number of observation points. T = *Triodia*, Te = *Triodia* edge, Ll = leaf litter , S = shrub, U = underground, Wd = woody debris, B = bare ground and Ms = mallee stem. For *P* values, * = 0.05, ** = 0.001 and *** = 0.0001.

Activities performed also varied as a function of habitat (Fig. 6.3). Time spent in mallee stem, leaf litter and bare ground was mostly classed as active. In contrast, time in the underground habitat component was almost exclusively rest, while time in *Triodia*, shrub and woody debris was more evenly split between active and rest. Compared with other habitat components, a substantial percentage of observations (27%) in *Triodia* edge were classed as eat (of which 93% was the behaviour 'consume'). Of the active time spent on bare ground, the majority was running (60%). This contrasts with leaf litter, for which 71% of the active behaviour was walking. For shrub, 95.5% of observations were of *N. yvonneae* under the shrub (as opposed to climbing in it).

The mean distance (± s.e.) between foraging ningauis and *Triodia* was recorded on 72 occasions (Table 6.4). The average of 1.3 m (± 0.28) was lower than the mean distance (± s.e.) from a random point to the nearest clump of *Triodia* (2.0 m ± 0.26) indicating that *N. yvonneae* stayed closer to this form of cover than expected from its distribution. The distance between *Triodia* and a foraging ningaui differed between habitat components. For example, in leaf litter, the mean distance was 0.6 m (± 0.13), while for the habitat component shrub, *N. yvonneae* was on average 2.8 m (± 0.74) away from the nearest *Triodia* (Table 6.4).

Compositional analysis identified differences in the ranking of habitat components between behaviour categories ('active', 'eat' and 'rest'), particularly for the habitat components leaf litter, *Triodia* edge, underground, shrub and mallee stem (Table 6.5). Although some habitats had few observations for any of the activities (e.g. mallee stem; Fig. 6.4), the frequency with which these habitat components were recorded in trials was high. For example, the use of mallee stem by an active ningaui was recorded in 37 trials (66%) despite a proportional use of only 2.5%. Likewise, the use of *Triodia* edge by active ningauis occurred only 10.3% of the time, but was recorded in 43 (76.7%) trials. Similar patterns were also recorded for shrub and bare ground.

Variation in the selection of habitat components across different activities was also observed for sex (Fig. 6.4) and season (Fig. 6.5). Significant differences between males and females were found for active ($G = 64.0$, d.f. = 7, $P < 0.001$), eating ($G = 22.4$, d.f. = 7, $P < 0.005$) and resting ningauis ($G = 25.9$, d.f. = 7, $P < 0.001$). Active females tended to use *Triodia* more and leaf litter less than active males (Fig. 6.4). In contrast, eating females used leaf litter more than males and more time was spent in *Triodia* edge by eating males (Fig. 6.4). When resting, males spent less time in *Triodia* and *Triodia* edge and more time in shrub woody debris and leaf litter than females. Despite such differences, compositional analysis showed similar habitat component rankings for animals at rest or active. No compositional analysis was performed for eating because of small sample sizes.

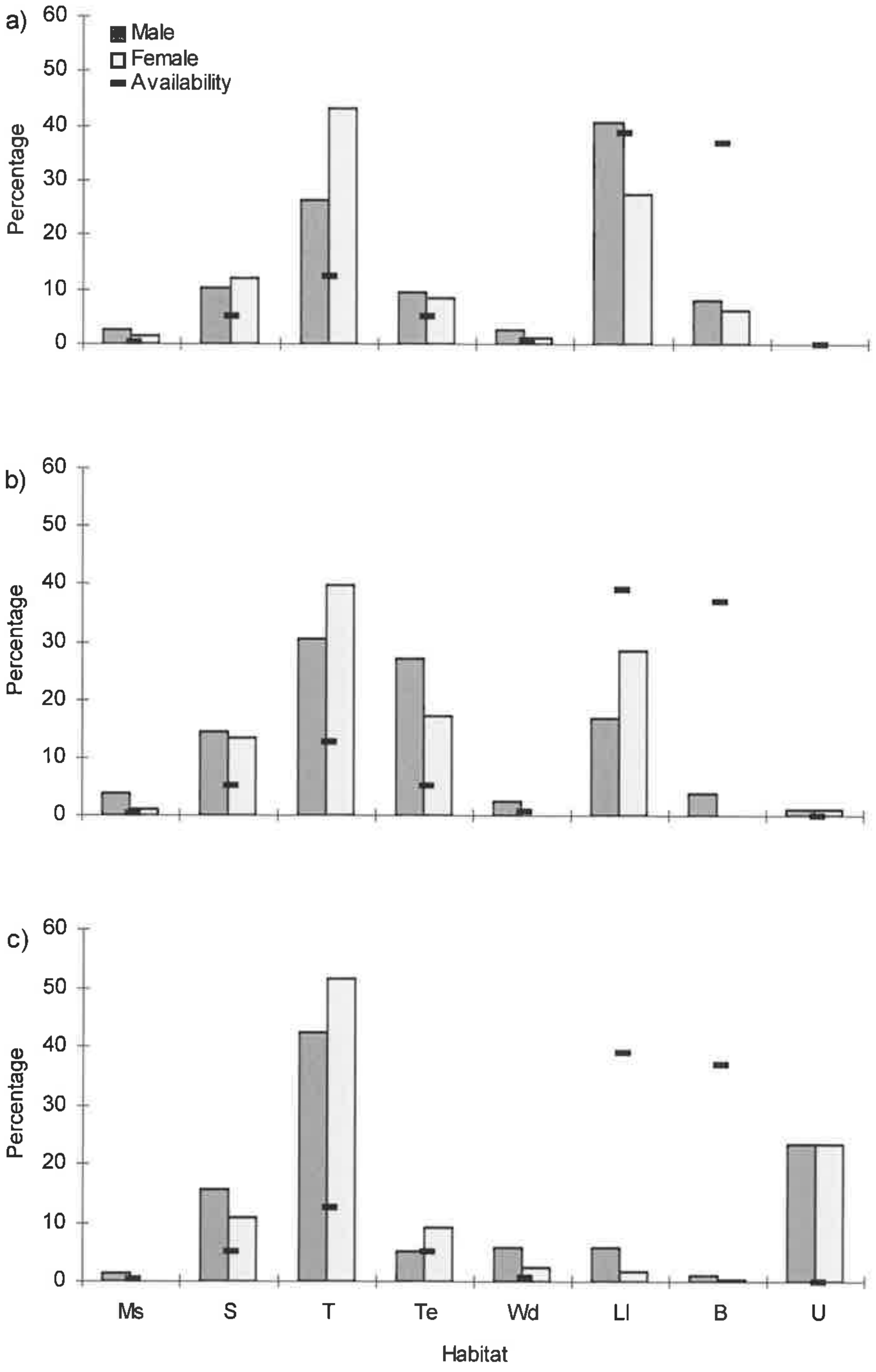

Fig. 6.4. Percentage of male and female *Ningaui yvonneae* observation points recorded in each habitat component and percentage availability for each component when animals were a) active, b) eating and c) resting. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

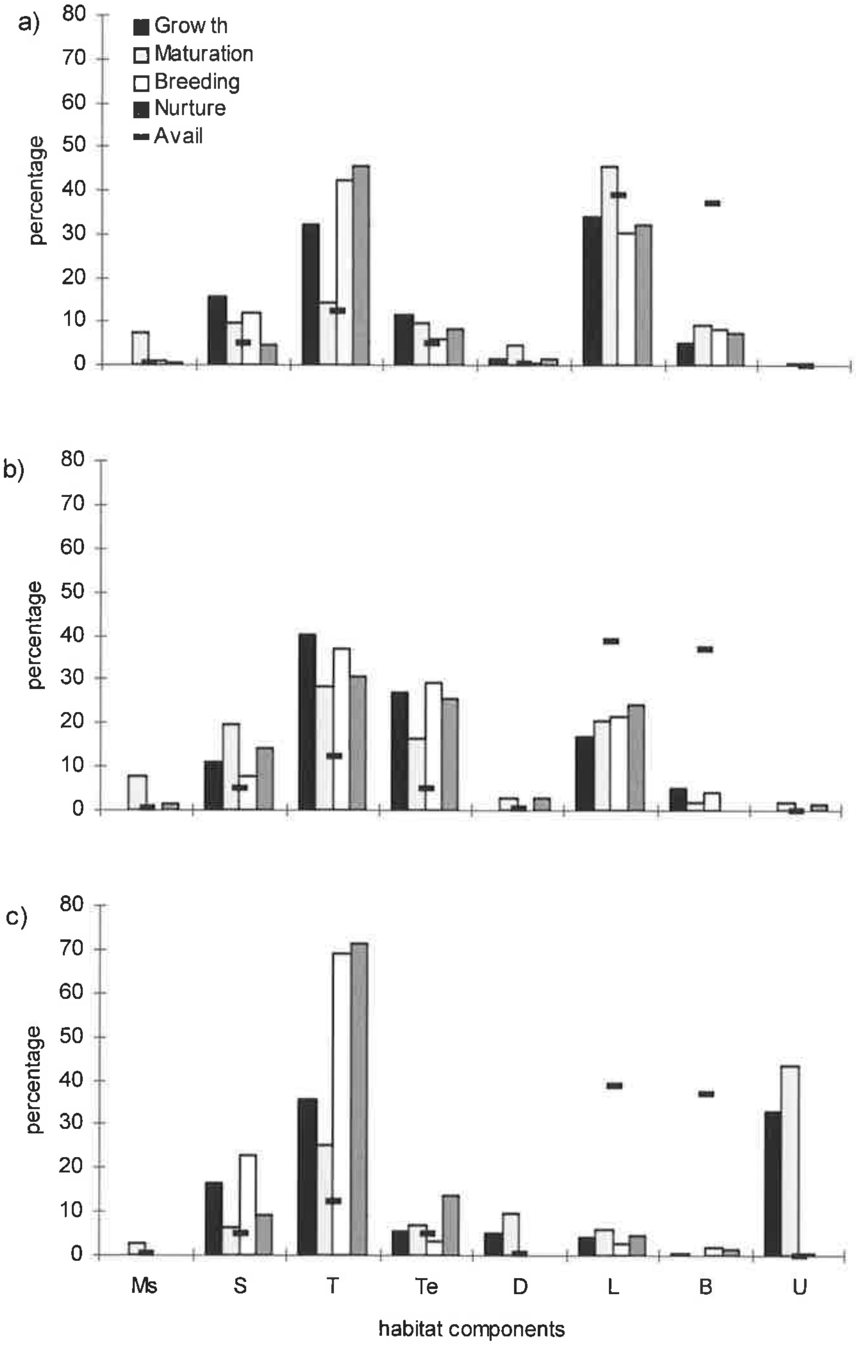

Fig. 6.5. Percentage of *Ningaui yvonneae* observation points recorded in each habitat component and percentage availability for each component for each season when a) active, b) eating and c) resting. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

When season was considered, there were significant differences in the use of habitat components for active (G =211.3, d.f. = 21, $P < 0.001$) and resting (G = 301.4, d.f. = 21, $P < 0.001$) ningauis, but not for eating (G = 40.2, d.f. = 7, $P > 0.005$). Due to the small sample sizes, compositional analysis was not performed on these groupings. However, Fig. 6.5 highlights some obvious differences between seasons. Active *N. yvonneae* used mallee stem and leaf litter more and *Triodia* less in Maturation than any other season. The use of *Triodia* also differed between seasons for resting ningauis, being used more often during Breeding and Nurture. In Growth and Maturation, most resting took place in underground.

6.4 Discussion

This is the first investigation of fine-scale habitat selection for this species. During the study, *N. yvonneae* was found to use a wide range of habitat components while foraging. The importance of multiple resources in habitat selection is well documented (e.g. Porter & Church 1987; Downes & Shine 1998). Indeed, in Chapter 5 a combination of *Triodia* and shrubs was found to be important in the distribution of *N. yvonneae*. However, the labelling of *N. yvonneae* as a generalist is simplistic, and obscures the fact that there were distinct selections for certain habitat components in this study. Such disparity may be a result of any habitat specialisation being offset by the diversity of habitat components used while foraging. Alternatively, *N. yvonneae* may favour different habitat components at distinct times or for certain needs. The latter suggestion in particular was supported by the data.

Overall, *Triodia* was found to be the preferred habitat component of *N. yvonneae*. This is a significant result, supporting suggestions from other studies that *Triodia* provides a key habitat for *N. yvonneae* (Menkhorst & Bennett 1990; see also Chapter 5). The suggested benefits of *Triodia* are its provision of near impenetrable cover which acts as a refuge and/or a stable population of invertebrate prey (see Pianka 1981; Morton 1982; Morton & James 1988; Lundie-Jenkins 1993). Our results show that *Triodia* was one of the preferred habitat components when *N. yvonneae* was active (foraging) and most preferred when at rest. *Triodia* also ranked highly when ningauis were eating. The value of *Triodia* to this species might be its multi-functional nature, being used for a variety of needs or activities.

The use of and selection for *Triodia* was influenced by season, with a decline in use during Maturation. Two possible reasons for this are proposed, both of which derive from the cooler temperatures experienced during this season. Firstly, in Chapter 5, it was suggested that

Triodia may be an important refuge from elapid snakes, which are common in the study area. In particular, *Triodia* was considered safer than shrubs, which have been recorded to increase the risk of predation from snakes in some other studies (e.g. Kotler *et al.* 1992; 1993; Schooley *et al.* 1996; see also Sharpe & Van Horne 1998). The absence of active snakes during Maturation may reduce the need for *N. yvonneae* to use *Triodia* during foraging bouts. Alternatively, snakes may themselves use *Triodia* as a refuge during the cooler months. Secondly, there are likely to be fewer invertebrates active during the cooler months (see Gibson 2001), requiring *N. yvonneae* to spend more time in habitat components that provide prey at this time (primarily leaf litter; pers. obs.). Changes in predation risk and the availability of food have been suggested in many studies as the cause for switches in habitat selection across seasons (e.g. Unsworth *et al.* 1998; Todd *et al.* 2000). A further example of seasonal change in habitat use in the present study was the habitat component underground, which was used equally or more than *Triodia* by resting *N. yvonneae* during the seasons Growth and Maturation.

Changes in the risk of predation may also explain the differences between sexes in the use of *Triodia.* For example, in Nurture when snake predation risk is relatively high, females may have sought the protection offered by *Triodia* when active because their agility (and ability to flee predators) may be restricted by the presence of pouch young. Alternatively, male *N. yvonneae* may have used *Triodia* less than females because they are more mobile (particularly during the Breeding season) and tend to undertake greater movements than females (Carthew & Keynes 2000). The increased use of *Triodia* edge by males for eating may also reflect predation risk. As males spent more time in leaf litter than females, it is reasonable to assume they sought protection from predators in the *Triodia* edge (see below) more often than females.

The avoidance of both leaf litter and bare ground by resting ningauis was likely a result of increased predation risk in these 'open' habitats. Change in perception of predation risk between different habitat components has been documented by several authors (e.g. Sharpe & Van Horne 1998; Tew *et al.* 2000), with open habitats generally considered a higher risk. While ningauis at rest avoided both leaf litter and bare ground, when active, they favoured leaf litter but still avoided bare ground. This distinction was most likely due to varying availability of prey between the two habitat components. Active time spent in the leaf litter was mostly walking, which was equated with foraging. Indeed the majority of observed prey captures occurred in leaf litter (see Chapter 7). Leaf litter may also offer slightly greater protection from predators (Dickman 1995) than bare ground. However, while leaf litter was favoured over bare ground, it was still perceived as a risky environment, with animals choosing to stay close to *Triodia* when in this habitat component.

Why was leaf litter favoured for foraging, given that it was considered risky in terms of predation and *Triodia* provided foraging opportunities? Other studies have reported that *N. yvonneae* show a preference for smaller prey (Fisher & Dickman 1993a; Woolnough & Carthew 1996). Leaf litter may offer the best opportunities for such prey. However, Fisher & Dickman (1993a) reported that in arid areas larger prey items were located in the open areas between shrubs and *Triodia*. Moreover, Diaz (1998) also reported that the invertebrates in *Triodia* hummocks were mostly small. The accessibility of prey items may influence the decision about where to forage. For example, Odderskaer *et al.* (1997) found that some birds choose habitats with less food, because that food was more accessible due to the simplistic structure of that habitat. Similar conclusions were also noted by Christensen & Persson (1993) for ambush predators. In this environment, the dense structure of *Triodia* may make searching and capturing prey costly in terms of energy-efficiency. Put simply, the risks of foraging in leaf litter (close to *Triodia* margins) may be outweighed by the energetic rewards associated with foraging in this structurally simple habitat component.

Ningaui yvonneae attempted to minimise the risk of foraging by remaining in close proximity to *Triodia* when in leaf litter. Moreover, *Triodia* edge was the favoured habitat component of eating ningauis. The location of eating behaviour does not always reflect the location of prey captures. It is suspected that animals chose to avoid more open habitats when consuming prey, preferring the relative safety of the *Triodia's* margins. This has been observed for *N. yvonneae,* other dasyurid species and other taxa, particularly when consuming larger prey items (e.g. Andrew & Settle 1982; Jackson, T.P. 2001; Appendix 2). *Triodia* edge may have been chosen over other habitat components for prey consumption as it was one of the more available habitats (in terms of distribution), it was easily accessed (compared to *Triodia* proper) and provided suitable temporary protection from predators.

Underground was used primarily by resting ningauis. The thermoregulatory benefits of burrows may be one reason for their use (Ellison 1993; Kinlaw 1999; Moro & Morris 2000). In particular, the increased warmth of burrows may explain their use by foraging *N. yvonneae* during the low minimum temperatures of Maturation. Burrows can also provide cooler conditions than ambient temperatures, yet they were not used widely during Nurture (which had the highest recorded mean minimum and maximum temperatures). This may in part be attributed to the time the animals were observed (at night), which was when daily temperatures were near their lowest. It is possible that *N. yvonneae* only uses burrows during Nurture to escape maximum temperatures occurring during the day. Additionally, the use of underground may be linked to predation by snakes. Burrows may offer poor refuge from snakes and so may be avoided by *N. yvonneae* when snakes were most active at night during warmer seasons.

This chapter highlights the level of complexity often involved in identifying habitat preferences for small mammals. While superficially *Triodia* appeared to be the habitat component most preferred by *N. yvonneae,* several other habitat components (such as leaf litter) were valued for specific purposes. Such results were explained by the behavioural patterns displayed in each habitat component, with different habitat components often fulfilling different or specific needs. Documenting behaviour clearly increases the understanding of habitat selection and most importantly, the specific values of critical resources.

Chapter 7 - Prey consumption and dietary selection.

7.1 Introduction

Ningaui yvonneae is one of smallest endothermic terrestrial carnivores in Australia. As discussed in previous chapters, it has a short life cycle, is active all year round, is highly mobile and lives under variable climatic conditions. As such, *N. yvonneae* has high energy demands, requiring regular and large amounts of food. Calver *et al.* (1991) recorded the daily food consumption of ningauis and other small mammals. They found that under laboratory conditions, *Ningaui* spp (combined results for *N. ridei* and *N. yvonneae*) consumed approximately 28% of their body weight per day. This is quite high when compared to several of the other dasyurids tested. For example, *Sminthopsis crassicaudata* consumed 17% and *Sminthopsis hirtipes* 18.5%. Moreover, Calver *et al.* (1991) suggest that these daily results are approximately a third of the expected food consumption rate in the field. It could be expected that ningauis need to consume the near equivalent of their body weight in prey each day. Thus, the ability of *N. yvonneae* to maintain regular food uptake is vital to its survival. Several factors influence this ability, including the range of prey sizes that can/are taken and the habitats that can be utilised.

Several studies have considered the dietary ecology of *N. yvonneae.* However, most of these have dealt largely with preferences based on prey size or type or prey handling (Calver *et al.* 1988; Fisher & Dickman 1993a; Fisher & Dickman 1993b; Woolnough & Carthew 1996). The prey preference trials undertaken by Fisher & Dickman (1993b) showed that *N. yvonneae* (and *N. ridei*) preferred smaller prey of up to 5 mm in length. Woolnough & Carthew (1996) found a similar result for *N. yvonneae* when individuals were offered a choice of two sizes of prey. McKenzie & Dickman (1995) found a preference for invertebrates less than 10 mm in length in *N. ridei.* Only Fisher & Dickman (1993b) and Woolnough & Carthew (1996) identified the range of invertebrate taxa consumed by *N. yvonneae,* with only the latter examining prey taxa preferences.

The purpose of this chapter was to further investigate the diet of *N. yvonneae*, building on the studies discussed above. Of particular interest was the type and size of prey chosen and the location (habitat components) from which prey were collected. Comparison of different techniques for sampling prey consumption was also considered.

7.2 Methods

7.2.1 Prey consumption

Prey consumption data were collected via three methods. First, scats were collected from animals held captive for use in other trials (such as radio tracking, behavioural experiments and habitat selection). *N. yvonneae* were captured in pit-fall traps during regular sampling periods (see Chapter 2). Fine sand used as a substrate in holding containers (16 x 10 x 7 cm) was sieved to remove scats deposited while ningauis were held in captivity. Although some individuals were provided with food while in captivity, only scats deposited prior to feeding were collected for analysis. Scats were also collected from calico bags used to transport individuals between the trap site and field base. All scats were stored separately in 70% ethanol, and the sex, time and location of animal recorded. Different scat pellets collected from an individual *N. yvonneae* at one time were pooled and treated as a single scat. Scats were teased apart under a dissecting microscope with most prey remains identified to Order, except for Classes Diplopoda and Chilopoda. Identification was aided by comparison with reference specimens collected for prey availability data (see Section 7.2.2). The contents of scats were also monitored for the quantity of sand particles and fur.

Captures of prey were recorded during observation trials in which free living animals were directly observed in their nightly activity (see Section 6.2 for details). During these trials, the type and approximate size of any captured prey items were recorded. Invertebrates were visually assessed to the level of Order (except for Classes Diplopoda and Chilopoda). Size categories were recorded as small (< 15 mm in length), medium (16-30 mm) and large (> 30 mm). The time (from start of trial) and location (habitat component) of each successful capture was also recorded. Stomach contents were also obtained from deceased animals (trap deaths). The animals' stomach and intestines were stored in 70% ethanol and the remains of invertebrates identified to Order where possible. Percentage of soil and vegetation material were also noted.

7.2.2 Sampling prey availability

To sample potential prey items, the 6.5 ha study site was divided into 32 individual 45 m^2 quadrats. Three quadrats were selected at random during each sampling period. In each of these three quadrats an area containing a representative sample of each of the habitat components (bare ground, *Triodia*, *Triodia* edge, shrub, leaf litter, woody debris and mallee stem) within a 10 m radius was selected. Three small pit-fall traps comprising 14 x 25 mm test tubes were placed in the ground in each habitat component, in line and approximately 1 m apart (giving a total of 21 pit-falls per quadrat). The exception was mallee stem, where each test tube was taped to an upright trunk of a mallee tree. Each test tube was part filled (3 cm) with 70% ethanol and left for two nights. This methodology was used during three field trips towards the latter part of 1997. However, because no record was kept on sampling dates, this data is not used in comparison of prey availability between seasons.

The prey sampling methodology was modified in 1998 to improve capture rates and overcome difficulties in establishing test tube pit-falls in sandy soils. Mallee stem was no longer sampled. Individual test-tubes were inserted into permanently installed plastic sheaths made of electrical conduit. The plastic sheaths were installed flush with the soil surface and allowed easy insertion and removal of test tubes. The sheaths were closed off with a cork between sampling periods. A larger pit-fall trap was introduced to increase the diversity of captures, especially larger invertebrates. The large pit-fall, made of a plastic cup (top ∅ 60 mm, height 90 mm, bottom ∅ 45 mm), was positioned in line, 1 m from the nearest test tube pit-fall. The pit-fall traps were used in the same three quadrats over five field trips during 1998 (March, April, July, September and November). At least two of these sites were sampled simultaneously during a field trip, for between two and three nights.

All captured invertebrates were stored in vials containing 70% ethanol. For each pit-fall, the presence (as opposed to abundance) and size (< 1 mm, 1-5 mm, 5-10 mm and > 10 mm) of invertebrates. Invertebrates were identified to the level of Order, except for Classes Diplopoda and Chilopoda, and are hereafter referred to as "taxa". Each taxon was counted only once per pit-fall and allocated a size class according to the average size of individuals within the taxon.

7.2.3 Statistical analysis and definitions

For invertebrate availability data, "captures" is defined as the number of taxa caught in a trap as opposed to the number of individual invertebrates present in the trap. For example, six captures refers to a pit-fall trap capturing six different Orders. Captures are then expressed as percentage of traps (or frequency occurrence), being the number of pitfalls to record a taxon divided by the total number of pit-falls examined. Observed capture data are also represented as a frequency occurrence, although only captures for which the type of prey could be identified or the location of capture recorded (habitat component) were used for statistical analysis or graphical representation. Likewise, frequency occurrence data for scats use only scats from which an invertebrate sample was recorded.

Log-Likelihood ratio (*G*) for contingency tables (Zar 1999) was used to identify significant differences within sexes and season for observed prey captures and size of prey consumed. Zero values were substituted with 0.001. Niche breadth was calculated by Smith's Measure (Smith 1982; Krebs 1999; see Chapter 6 for more detailed explanation). For comparison with studies by Fisher & Dickman (1993b), values of Proportional Similarity (*PS*) were calculated, with *PS* given by;

$$PS = 1 - 0.5\sum_i |p_i - q_i|$$

where *PS* is the Proportional Similarity index, p_i is the proportional use of prey taxon *i* and q_i is the proportional availability of prey taxa *i*. A value of one indicates the animal is a complete generalist. A value of *min* q_i indicates an animal is highly selective. Due to the nature of the data (e.g. lack of information on individual ningauis, see Aebischer *et al.* 1993 and Chapter 6), Manly's alpha index was chosen to provide a relative ranking of preference for each prey taxa (Krebs 1999). Manly's α is given by;

$$\alpha = \frac{r_i}{n_i} \frac{1}{\sum (r_j / n_j)}$$

where α_i is the preference index for prey taxa *i*, r_i and r_j are the proportion of prey taxa *i* or *j* in the diet and n_i and n_j are the proportional availability of prey taxa *i* or *j*. A value greater than $1/m$ (where *m* is the number of prey taxa available) indicates that a prey type is preferred. A value less than $1/m$ indicates that the prey taxa is avoided. Where α_i is equal to $1/m$, selective feeding does not occur (Krebs 1999).

7.3 Results

7.3.1 Prey availability

Sampling effort for methodologies one and two were 378 and 576 trap nights respectively, giving a total of 954 trap nights. In total, 22 invertebrate taxa were identified from 591 captures, with an average of three taxa recorded per pit-fall (range of 1-8). The majority of these were recorded infrequently (< 5%), with captures being dominated by Hymenoptera and

Collembola (Fig. 7.1). The majority of captures were small invertebrates, with the two types of pit-fall traps and habitat components all recording similar proportions of invertebrate sizes. Of the 591 captures, 446 (75%) were < 5 mm, 91 (15%) between 5-10 mm, 47 (8%) between 10-30 mm and 7 (1%) > 30 mm. Different capture rates were recorded across seasons (see Chapter 2, Section 2.3 for definitions), with Nurture having a higher trap success (56%) than Growth (49%), Breeding (35%) or Maturation (30%). Although the total number of taxa did not differ substantially between seasons (Nurture 15, Growth 18, and Breeding and Maturation 12), there were variations in individual taxa. For example, the trap success for Araneae was 15% and 18% for Nurture and Growth respectively, compared to 6% and 7% for Breeding and Maturation respectively. Excluding mallee stem (which had a trap success of 3.7% and recorded only three types of taxa), there was little variation in the trap success (mean ± s.e. of 42.4% ± 2.6; Fig. 7.2) or the diversity of taxa (mean ± s.e. of 14.8 ± 0.5) between habitat components.

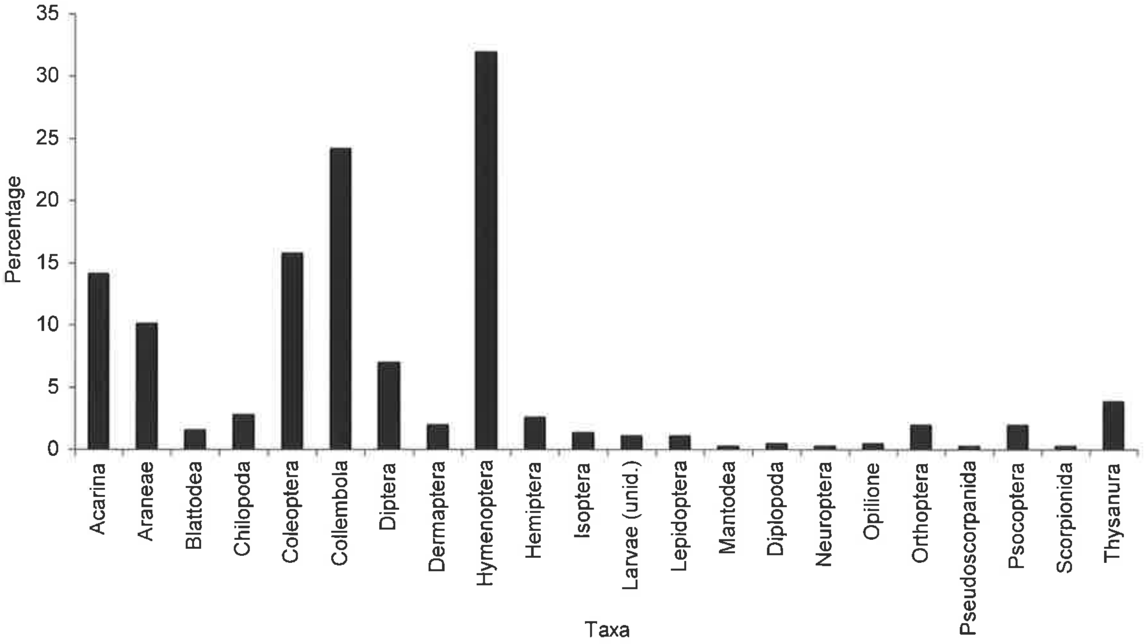

Fig. 7.1: Percentage of traps containing various invertebrate taxa. Invertebrates are classified by Order except for Diplopoda and Chilopoda (Class).

7.3.2 Observed prey consumption

From 59 observation trials, 197 prey capture events were recorded. In 140 (71%) of these, the type of prey could not be identified, with captures being consumed too quickly (usually smaller prey) or away from the observer (for example, within *Triodia*). In the remainder, twelve different types of prey were identified, with most of these being invertebrates (from 9 Orders, 1 Class and 1 unknown; Fig. 7.3). Of the prey identified, most were Araneae (18%), Blattodea (16%) or Orthoptera (12%; Fig. 7.3). Most Hymenoptera were of the Family

Formicidae, and all Hemiptera were of the Superfamily Coccoidae. Male and female *N. yvonneae* showed significant differences in the type of prey consumed ($G = 27.62$, d.f. = 11, $P < 0.01$; Fig. 7.3). In particular, significant differences were found between prey available and consumed for invertebrate grubs ($\chi^2 = 5.0$, d.f. = 1, $P < 0.05$), Blattodea ($\chi^2 = 5.4$, d.f. = 1, $P < 0.05$) and Isoptera ($\chi^2 = 5.0$, d.f. = 1, $P < 0.05$; Fig. 7.3). Notably, males had a more diverse diet, being observed consuming 11 types of prey, compared to seven for females. Significant differences were also recorded across seasons ($G = 61.99$, d.f. = 33, $P < 0.005$; Fig. 7.4). For example, Hymenoptera were only observed being consumed during the season Breeding while Araneae were mostly consumed during maturation (Fig. 7.4).

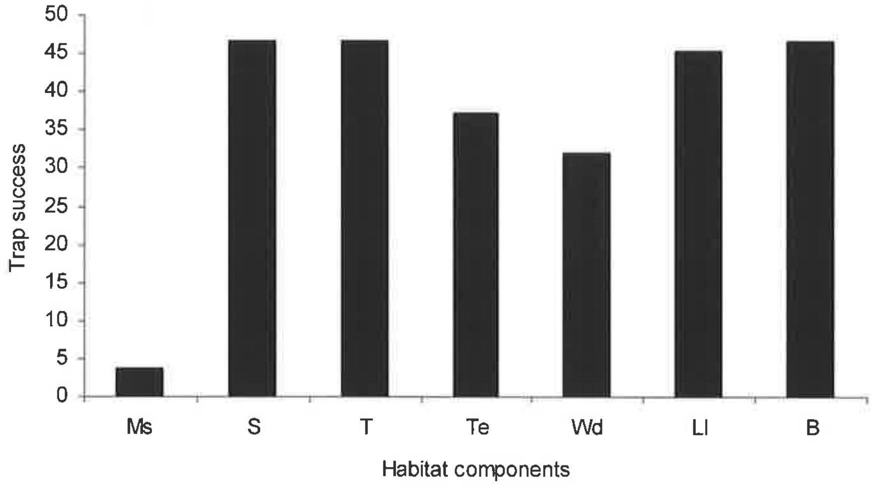

Fig. 7.2: Percentage invertebrate trap success for each habitat component. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground.

The habitat component in which prey were captured was recorded for most (96%) observed prey capture events. Almost half of captures (45%; Fig. 7.5) were observed in leaf litter, with 22% in *Triodia*. There was no significant difference between male and female *N. yvonneae* in the number of captures in different habitat components ($G = 12.14$, d.f. = 7, $P > 0.05$). However, differences between seasons were significant ($G = 42.2$, d.f. = 21, $P < 0.05$). Notably, captures were recorded in eight habitat components during Maturation, compared with five during Growth and Breeding (Fig. 7.6). However, leaf litter remained the most often used habitat component in all four seasons (Fig. 7.6).

Size of prey was recorded in 121 of observed prey captures. Animals were recorded to take prey up to 10 cm in length (Appendix 2). However, most (58%) were classed as small (< 15 mm). Although females were observed to consume fewer small prey (Fig. 7.7), the differences between sexes was not significant ($G = 2.47$, d.f. = 2, $P > 0.05$). Likewise, there were no significant differences recorded between seasons ($G = 8.76$, d.f. = 6, $P > 0.05$).

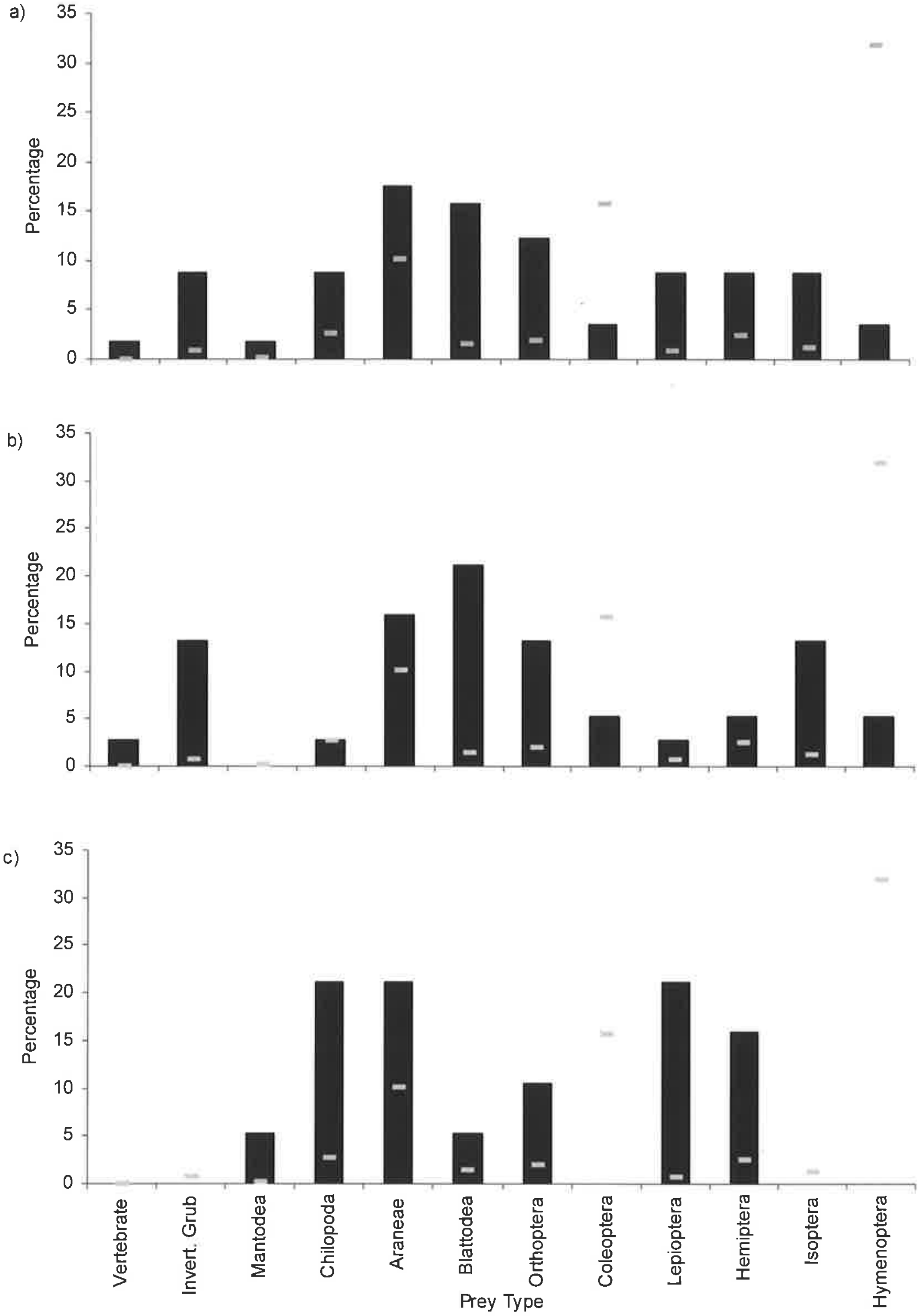

Fig. 7.3: Percentage of observed captures by *Ningaui yvonneae* of prey types (bars) and availability of prey (dashes) for a) all (n = 57), b) male (n = 38) and c) female (n = 19) *N. yvonneae*.

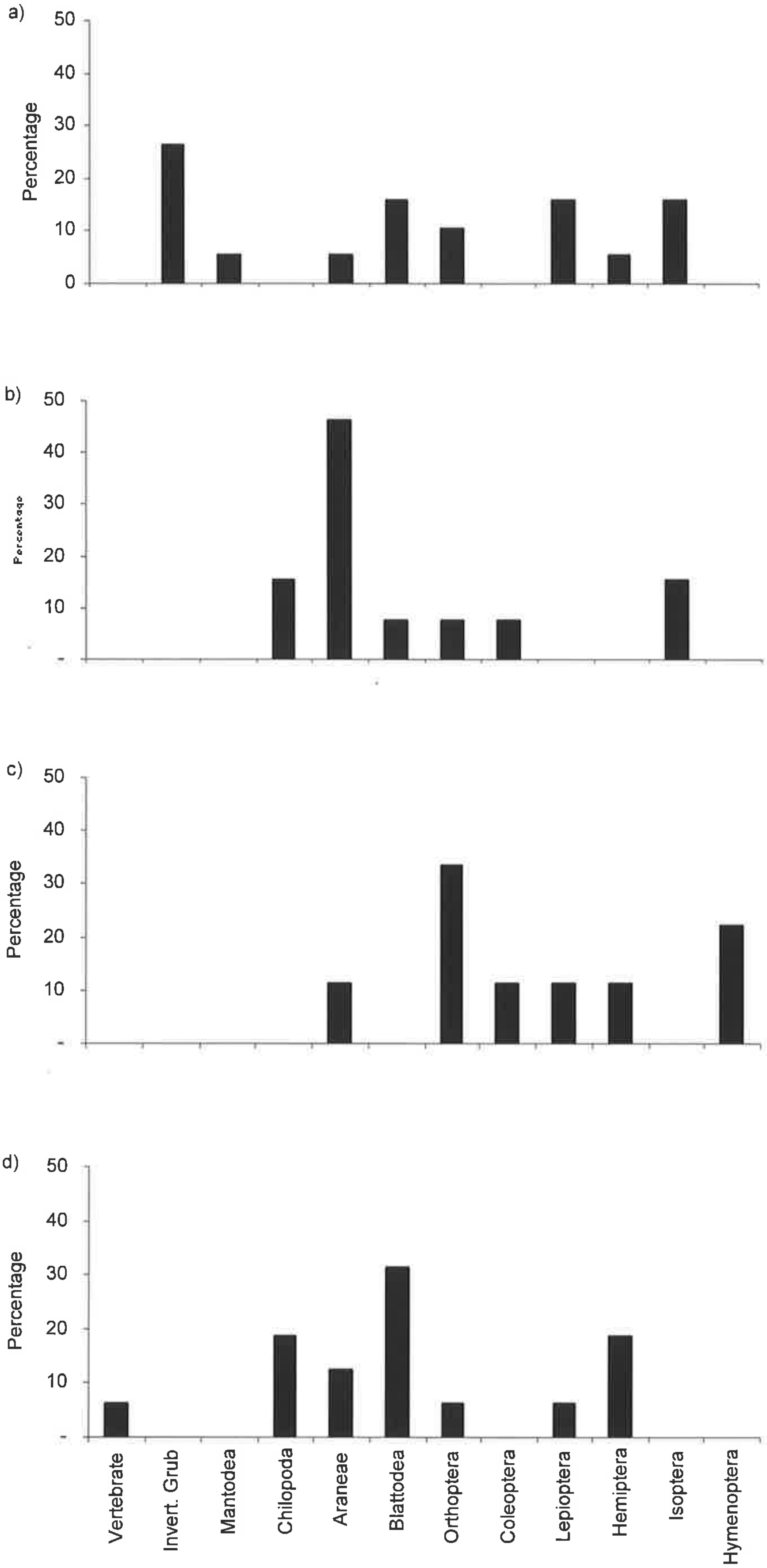

Fig. 7.4: Percentage of observed captures by *Ningaui yvonneae* of different prey types during a) Growth (n = 48), b) Maturation (n = 64), c) Breeding (n = 44) and d) Nurture (n = 32).

7.3.3 Faecal and stomach contents

Scats were collected from 60 individuals between February 1996 and February 2000. Invertebrate fragments were identified in 48 of these. The remaining 12 were composed of either soil material mixed with organic matter or "furballs", or unidentifiable invertebrate fragments. Most scats revealed only one type of prey (range 1-3). The cumulative number of prey taxa recorded in scats began to plateau after six scats (individual animals; Fig. 7.8), suggesting that the 48 scats sufficiently sampled the diversity of prey consumed by *N. yvonneae*.

Of the eight taxa recorded in scats, Hymenoptera and Araneae were the most common (Fig. 7.9). As noted for the observed captures, the majority of Hymenoptera found in the scats were of the Family Formicidae. Smith's Measure (using scat data) was 0.78, suggesting *N. yvonneae* was a generalist forager. Manly's alpha recorded Blattodea (0.37), Orthoptera (0.18), Chilopoda (0.15), Lepidoptera (0.13) and Araneae (0.09) as the Orders preferred by *N. yvonneae* (where m = 0.05). The frequency of the Orders Araneae, Hymenoptera and Orthoptera recorded in scats differed substantially between males and females. However, this difference was not significant ($G = 11.91$, d.f. = 7, $P > 0.05$; Fig. 7.9). The absence of Hymenoptera and Chilopoda and increase in Araneae during Nurture was the most notable difference between seasons (Fig. 7.10). However, differences between seasons were not significant ($G = 18.31$, d.f. = 21, $P > 0.05$).

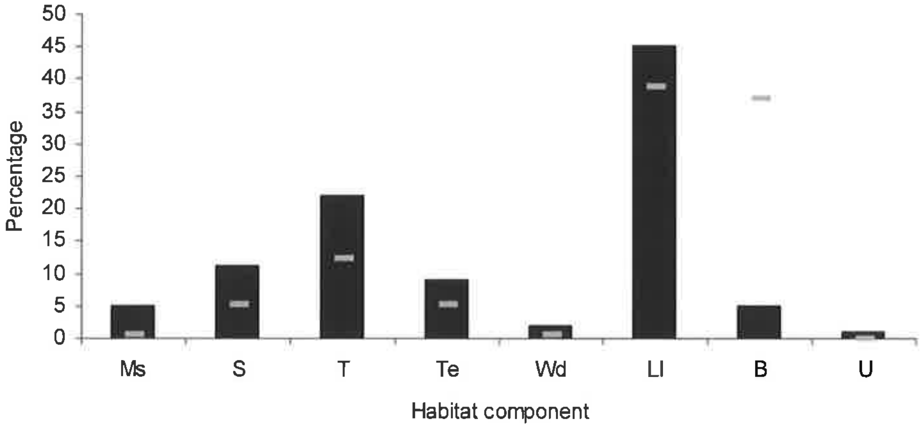

Fig. 7.5. Percentage of observed captures of prey by *Ningaui yvonneae* in different habitat components (bars) and availability of habitat components (dashes). Location of capture was recorded for 190 capture events. Availability of habitat components is taken from Chapter 6. Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

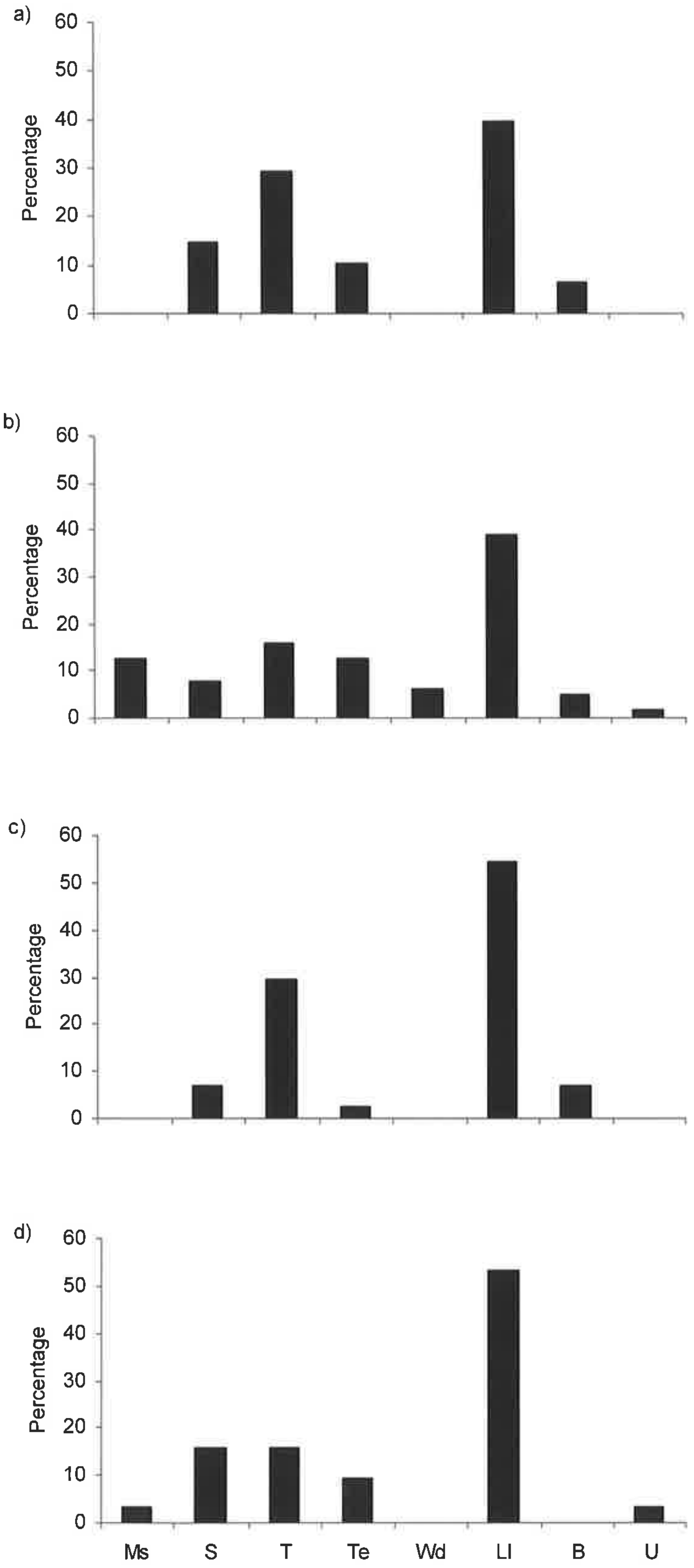

Fig. 7.6: Percentage of observed prey captures by *Ningaui yvonneae* in different habitat components for a) Growth (n = 48), b) Maturation (n = 64), c) Breeding (n = 44) and d) Nurture (n = 32). Ms = mallee stem, S = shrub, T = *Triodia*, Te = *Triodia* edge, Wd = woody debris, Ll = leaf litter, B = bare ground, U = underground.

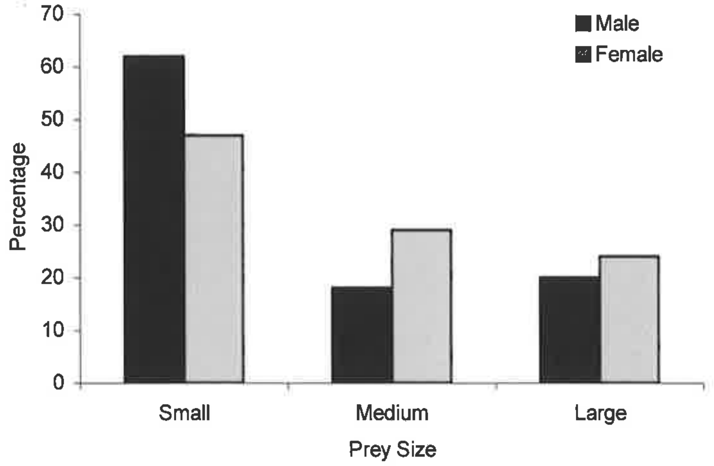

Fig. 7.7: Percentage of small (≤15 mm), medium (16-30 mm) and large (≥30 mm) prey observed captured by foraging male and female *Ningaui yvonneae*.

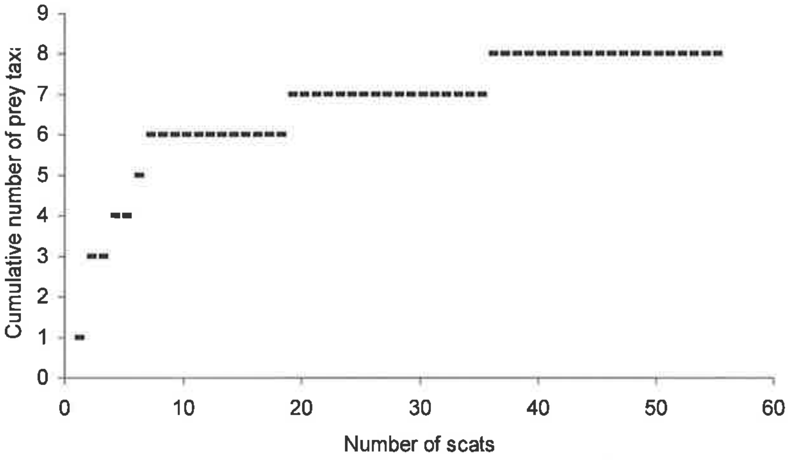

Fig. 7.8. Cumulative number of different types of prey taxa recorded in scats of *Ningaui yvonneae*.

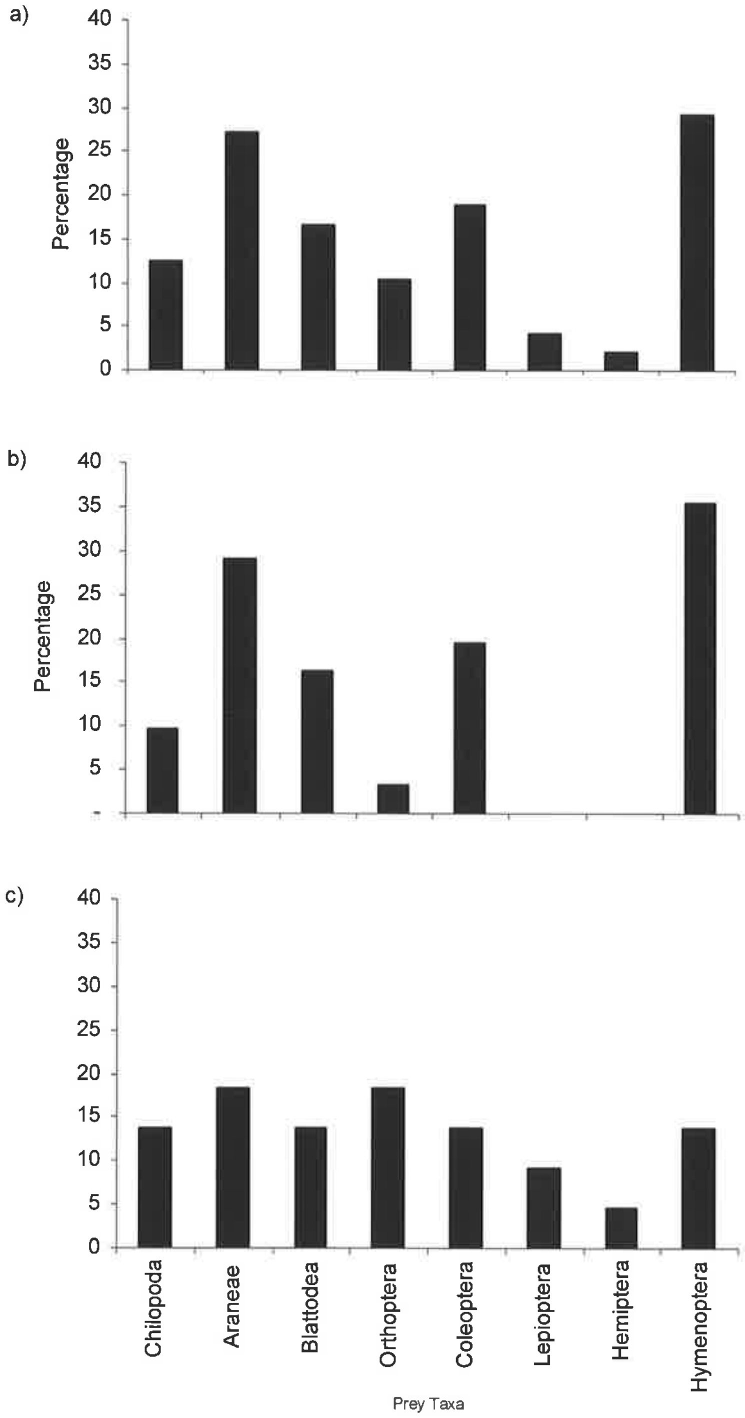

Fig. 7.9: Percentage of scats containing each prey taxon for a) all, b) male and c) female *Ningaui yvonneae*.

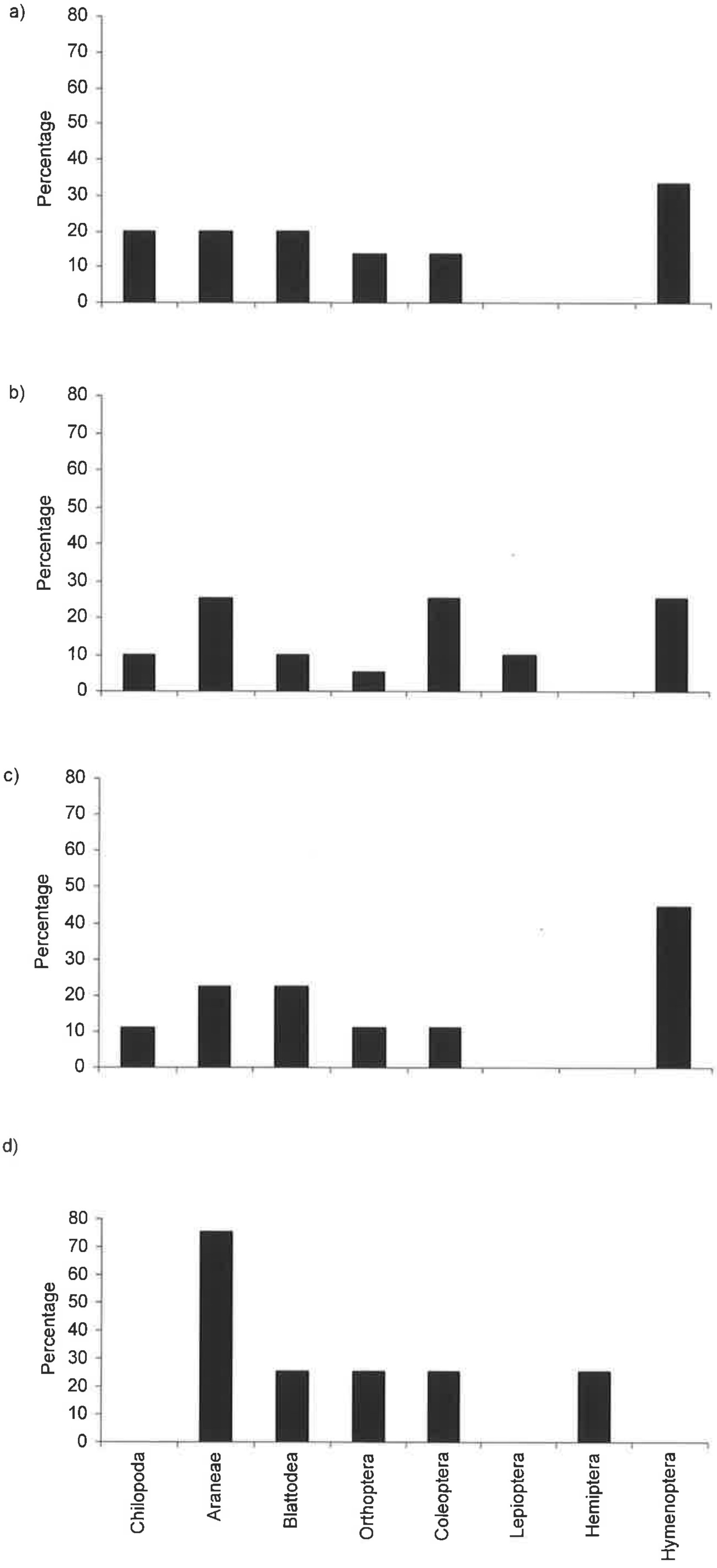

Fig. 7.10: Percentage of *Ningaui yvonneae* scats to contain each prey taxon during a) Growth, b) Maturation, c) Breeding and d) Nurture.

Soil was commonly recorded in the scats of *N. yvonneae*, with 15 (25%) scats containing at least one pellet composed of at least 50% stones/dirt. Soil material was recorded in scats in similar amount for three of the seasons (Growth, Mature & Breeding), but not at all in Nurture. From the 13 stomach samples collected, positive identification of invertebrates could only be obtained from five contents. These included two records of Hymenoptera and single records of Araneae, Orthoptera and Coleoptera. One stomach was recorded to contain a type of Nematode, four contained unidentifiable invertebrate contents and three were empty.

7.4 Discussion

Ningaui yvonneae was found to include a range of prey types in its diet, with 11 invertebrate taxa recorded from scat analysis, stomach contents and direct observation. Woolnough & Carthew (1996) recorded similar diversity from their scat analysis of *N. yvonneae* in the same study area, with seven Orders identified (Hymenoptera, Coleoptera, Chilopoda, Araneae, Orthoptera, Scorpionida and Diplopoda). Statistical comparisons of the taxa consumed with the availability of those taxa suggests that like many dasyurids (e.g. Fisher & Dickman 1993b; Scarff *et al.* 1998; Gilfillan 2001a; Lunney *et al.* 2001), *N. yvonneae* tends towards being a dietary generalist. This is based on a qualitative interpretation of the term generalist (see Fox & Archer 1984 for detailed discussion). A generalist diet is also implied when the proportional use of each habitat component is compared to the percentage of prey captured in each habitat component. It appears that *N. yvonneae* captures prey as it encounters them whilst moving within or through a habitat component. Such behaviour was recorded in shrews (*Sorex* sp.) by Churchfield *et al.* (1999), who commented that dietary selection may be influenced by the encounter rate of different taxa. The only exception to this in the present study was bare ground, where proportionally fewer prey were captured than was available.

Although considered a dietary generalist, Fisher & Dickman (1993b) found that of the six dasyurid species they studied, *N. yvonneae* was the most specialised of all, with a Proportional Similarity (*PS*) value of 0.28. The *PS* value for *N. ridei* was also low, being 0.39. Fisher & Dickman (1993b) suggested that these results were due to the ningauis preference for spiders and beetles and general avoidance of ants. However, Fisher & Dickman (1993b) did not consider *N. yvonneae* as an extreme specialist. The results from the present study also show *N. yvonneae* to be selective for certain taxa, with preferences for Blattodea, Orthoptera, Chilopoda, Lepidoptera and Araneae. Araneae also figured highly in the results of *Ningaui* spp. studied by Calver *et al.* (1988). Fisher & Dickman (1993b) also recorded a strong preference for Araneae ($\alpha = 0.66$, where $1/m = 0.33$) and a marginal preference for 'Others' which included Blattodea and Lepidoptera ($\alpha = 0.35$, where $1/m = 0.33$). The *PS* value for *N. yvonneae* in the present study (*PS* = 0.46) was higher than that recorded by Fisher & Dickman (1993b), further suggesting that *N. yvonneae* was only a partial or occasional specialist. The lower *PS* value recorded by Fisher & Dickman (1993b) could be attributed to the presence of other dasyurids at their study site, which may compete for prey resources and necessitate greater specialisation by *N. yvonneae*.

The preference for Chilopoda in this study is a contrast to the suggestion of Fisher & Dickman (1993b) that small dasyurids avoid Chilopoda because of their difficulty of handling and immobilisation (see also Read 1987b). Observations of foraging *N. yvonneae* in this study confirm that this species is able and willing to capture larger specimens of Chilopoda (see Appendix 2). However, the preference for Chilopoda in this study may be over rated, as Chilopoda can be under-sampled by pit-fall trapping (Fisher & Dickman 1993b). Although the scat analysis recorded a high percentage of Hymenoptera, this taxon was found to be avoided relative to their abundance. Fisher & Dickman (1993b) found similar results for all species in their study, as did Fox & Archer (1984) for *Antechinus stuartii* and *Sminthopsis murina.* Fisher & Dickman (1993b) suggest that because of the extremely high availability of Hymenoptera in arid areas (for example, in this study, Hymenoptera were recorded in 80% of traps), few predator species will statistically appear to show a preference for Hymenoptera. Fox & Archer (1984) suggested that this phenomenon may result from using pit-fall trapping to sample Hymenoptera, as the technique may favour the sampling of ants. However, in the present study, observation trials recorded *N. yvonneae* deliberately avoiding ants on several occasions.

There were notable differences in the prey consumption between male and female *N. yvonneae*, including diversity of taxa and amount of each taxon. Lunney *et al.* (2001) suggested that differences in diet between male and female agile antechinus (*Antechinus agilis*) meant either they were foraging in different areas or with different behaviours. It is unlikely that the differences observed between sexes in the present study result solely from differences in habitat use, as the location of prey captures did not differ significantly between males and females (see also Chapter 6 for habitat preference data). However, some of the variation in prey selection between sexes may be explained by specific habitat preferences. For example, female *N. yvonneae* tend to use *Triodia* more than males (see Chapter 6).

Behavioural differences may also contribute to differences in diet between sexes. For example, males are more mobile than females (see Chapter 4) and thus may encounter a different range of prey. Lunney *et al.* (2001) suggest that the different nutritional requirements of certain prey items may influence selection between sexes. They provide the example that prey with higher energy contents (such as insect larvae) may be selected by males nearing the breeding season. It is plausible that the conditions of different seasons in this study place varying demands on the nutritional or energetic requirements of *N. yvonneae*. Such demands were alluded to in Chapter 3.

Changes in predator diet between seasons is not uncommon (e.g. Fox & Archer 1984; Green 1989; Murray & Dickman 1994; Chen *et al.* 1998; Gilfillan 2001a), often being attributed to variation in the abundance or activity of prey. For example, Read (1987b), Green (1989), Gilfillan (2001a) and Paltridge & Southgate (2001) all recorded a reduction in invertebrate prey numbers during winter, while Gibson (2001) found greater invertebrate activity during summer. Seasonal variation in food resources can have a significant influence on the population dynamics and life histories of a species (Jackson, S.M. 2001). In Chapter 3 it was suggested that Winter (Maturation) was a time of stress for ningauis, due to cooler temperatures and the assumption that there was a reduction in prey availability or activity (see also Ward 2000). This is now supported by the data on prey availability in this chapter, which was at its lowest during Maturation. Lunney *et al.* (2001) commented that many invertebrates during winter remain inactive or undergo diapause under bark, in logs, or in the soil. This may explain the increase in soil searching behaviour during Maturation recorded in Chapter 6. It is also likely that the breeding behaviour of *N. yvonneae* was influenced by season, being timed to coincide with food availability (or avoid times of stress and low food). Prey activity was highest during Nurture, a time when females are gestating, lactating and weaning. Prey activity was also high in Growth, giving juvenile *N. yvonneae* the opportunity to maximise weight gain. In Chapter 3, this dramatic increase in weight (and condition) is suggested as being vital for juvenile survival during the cooler temperatures of Winter (Maturation).

The differences between seasons in observed consumption of specific prey types could also be attributed to the recorded changes in prey activity. For example, Blattodea were not consumed or available in Breeding. Such results may be expected if the predator species is considered a generalist forager. However, it is of interest to note that although Araneae were most active during Growth, the highest observed consumption of this taxa occurred during Maturity. This is further evidence that there is some selectivity in the diet of *N. yvonneae*. Although the data from scats did not register significant variation between seasons there were still some notable differences. The most obvious was a greater consumption of Araneae in Nurture, which contradicts the results from the observation data.

Chen *et al.* (1998) suggested that seasonal changes in diet may also result from alteration to predator behaviour and/or habitat use. Variation in habitat use across seasons was recorded in Chapter 6. Results from the present chapter show that the five most preferred taxa of *N. yvonneae* were generally recorded across all habitat components. For example, Blattodea were recorded in four habitat components, while Orthoptera were recorded in five and Chilopoda six. The observed captures also correlate with the availability of habitat components. It is possible that as a generalist feeder, *N. yvonneae* consumes the more common or accessible taxa in the habitat components it prefers to use, with changes in habitat being reflected in changes to diet. An alternative explanation is that the distribution of prey influences *N. yvonneae's* habitat selection. The distribution of *N. yvonneae*'s preferred prey across all habitat components may be the reason ningauis appear to be generalist habitat selectors, as discussed in Chapter 6. The suggestion that diet influences habitat selection has been raised by other studies. For example, prey abundance was found to be an important factor in affecting habitat occurrence of shrews in the study by Churchfield *et al.* (1997). Likewise, Ford *et al.* (2003) found smoky mice (*Pseudomys fumeus*) altered habitats in spring and summer in response to changes in diet. The data in this chapter are insufficient to identify the full relationship between habitat and diet selection, although as discussed by Dickman (1995) the two are most likely closely associated.

The majority of prey consumed by *N. yvonneae* were small. This is consistent with the findings of both Woolnough & Carthew (1996) and Fisher & Dickman (1993b) who found *N. yvonneae* preferentially chose smaller prey. In this study most of the invertebrates recorded as available were also small, suggesting that *N. yvonneae* is relatively opportunistic in terms of prey size. Green (1989) reported similar findings, with the size of prey consumed by *Antechinus agilis* and *A. swainsonii* being determined by the size of available taxa (they did not specifically select prey items based on size). Likewise, Dickman (1988) suggested that smaller prey were included in the diet of the *Antechinus*, *Sminthopsis* and *Parantechinus* species studied because they were more abundant than larger prey in the field. Although most prey consumed in this study were small, *N. yvonneae* was observed to consume larger prey on occasion, including larger Chilopoda and vertebrates (see also Woolnough & Carthew 1996;

Appendix 2). This is not surprising, as Fisher & Dickman (1993a) found that small dasyurids were not physically constrained to eating smaller prey.

Data from both observation and scat/stomach analysis had limitations. Some of the problems associated with direct observations of animals are addressed in Chapter 6. Specifically for dietary studies, there is a general bias towards harder bodied or larger prey (often slower to consume and thus more likely to be identified); identification is influenced by the location of prey capture or consumption (only those prey caught or consumed in the open or in more visible habitat components could be identified) and there is a reliance on visual identification (may result in subjective classification of taxa). The problems associated with using scats and stomach samples to identify prey are well documented (see Dickman & Huang 1988 for detailed discussion). In summary, they include a bias towards hard bodied invertebrates; invertebrates that can be identified from individual body components or smaller prey items (see Fox & Archer 1984; Green 1989; Dickman 1995; Scott *et al.* 1999; Lunney *et al.* 2001). The incorporation of observation data assisted in overcoming some of these problems (such as the identification of soft bodied prey). The inclusion of both techniques may therefore allow for a better overall picture of an insectivores diet, detailing not only what is eaten but also where and how often prey are consumed. Moreover, the two techniques may complement each other, despite apparent discrepancies. For example, one apparent discrepancy relates to consumption of Araneae. Most Araneae were consumed during Maturation and Nurture for observation and scat data respectively. It is possible that different sized species of Araneae were captured in Nurture and Maturation, and that the smaller prey missed by observation were recorded by scat sampling. Subsequently, a more accurate understanding of the diet is provided.

Chapter 8 - Influence of predation on behaviour and habitat preference.

8.1 Introduction

As outlined in Chapters 5 and 6, many studies have examined the influence on behaviour and habitat selection of foraging animals by the presence or absence of predators. Many species adjust aspects of their behaviour to accommodate the risk of predation. For example, Jones *et al.* (2001) found that two species of spiny mice (*Acomys* spp) increased their use of open habitats in summer in reaction to increased predator activity in covered (not open) habitats. The compulsion or requirement to avoid predators can be very strong. For example, Jones *et al.* (2001) recorded that predator avoidance overrode the desire to minimise metabolic cost and water loss. Similarly, Walther & Gosler (2001) found that great tits (*Parus major*) avoided the richest patches of food because they were located away from protective cover.

Studies investigating predation risk and anti-predatory behaviour often do so via the manipulation of conditions to test hypothesis experimentally. Such tests are performed using different techniques. Some studies, such as Jonsson *et al.* (2000), use large outdoor enclosures composed of simulated habitat, in this case to examine spacing behaviour in rodents. Other studies, such as Pierce *et al.* (1992), have undertaken indoor laboratory experiments, in this case to investigate species specific reactions to snake predation. In contrast, some studies, such as Kotler (1984) or Jones *et al.* (2001), have used free living animals in natural settings, where often the availability of food is manipulated to test animal behaviour. The experimental design for this study on *N. yvonneae* was developed in 1998. At that time there were no known predation experiments on dasyurids. Since then, both Sutherland & Predavec (1999) and Haythornthwaite & Dickman (2000) have examined dasyurid responses to manipulated light and/or food availability.

In previous chapters, habitat selection by *N. yvonneae* was thought to be strongly influenced by predation risk. The general supposition was that *N. yvonneae* chose habitats partly because they offered greater protection from predators. In the Middleback Ranges, *N. yvonneae* are likely to be subjected to predation from both elapid snakes and owls (see Morton 1982; Heywood & Pavey 2002), both of which have been frequently recorded in and near the trapping site throughout the entire study. Although the general preference for *Triodia* by *N.*

yvonneae was attributed to its provision of both food and protection, *Triodia* was thought to be favoured over other refuge sites (such as shrubs or burrows) because of its protection from snakes in particular. The aim of this chapter was to test this hypothesis experimentally. Of interest was the extent to which predation risk influenced the use and selection of habitat components (namely when foraging); the type of habitat components considered to be safest by *N. yvonneae* (the most preferred); and whether different predators had differing effects on the selection of habitat components.

8.2 Methods and results

Two types of experiment were used to test the effects of predation on habitat selection and foraging behaviour of *N. yvonneae*. They were giving up density (GUD) and behavioural trials. Although both types of experiments have been widely used to investigate the foraging behaviours of small terrestrial mammals (see Sections 8.2.1 and 8.2.2 below for examples) most studies have been concerned with granivorous rodents. As a result, their adaptation to *N. yvonneae* was complicated and a variety of problems were encountered during these trials. This resulted in a lack of data.

8.2.1 Giving up density

GUD is a commonly used method for assessing an animals perceived risk of predation and the difference in this perception between habitats. This is achieved by comparing the consumption of food from artificial food "patches" under different levels of predation risk across different habitats. Traditionally, GUD has been used for studies on rodents (e.g. Brown 1988; Vasquez 1996; Kotler *et al.* 1998). More recently, GUD has been used with insectivorous marsupials in central Australia (Haythornthwaite & Dickman 2000). Typically, the amount of food consumed within each habitat under different conditions (usually the level of light) is compared and interpreted as the willingness of an animal to remain in each habitat under those conditions. It can be expected that more food will be consumed (a lower GUD) when an animal feels "safe". In this study, GUD was used to determine whether *N. yvonneae* had different perceptions of predation risk between open habitats such as bare ground or leaf litter and cover providing habitats such as *Triodia* and shrub.

Two attempts were made at collecting GUD data for *N. yvonneae*, with each attempt employing slightly different techniques. The first used plastic "kitty litter" trays (approximately 40 x 25 x 4 cm) as food patches. A 3 cm layer of compacted sand was placed in each tray. On this were placed five meal worms (*Tenebrio* spp.) which were then covered with a thin layer of fine leaf litter. The sand substrate and leaf litter were designed to mimic the natural foraging substrate of *N. yvonneae*. The sand was compacted to minimise the chance of meal worms burrowing into the soil. Trays were initially divided into five pairs, with each pair consisting of one tray in an "open" habitat (at least 2-3 m from nearest cover) and one in or adjacent to "cover" (*Triodia* or shrub). If successful, an additional 10 pairs of trays would have been used. Trays were sunk into the ground to sit flush with the soil surface. GUD was to be compared between different natural lighting conditions (phases of the moon). This technique was trialed over four nights in December 1998. None of these trials were successful, as many meal worms either escaped from the "patch" (63% of meal worms were observed crawling along ground) or were consumed by ants (20% of trays were infested with ants).

The second technique attempted to reduce ant predation and prevent meal worms from escaping. It was trialed in July 1999. Food patches were made from a 25 mm thick section of timber (30 x 20 cm), into which was drilled 150 (10 x 15) holes (∅ 10 mm, depth of 19 mm). Small meal worms or pieces of meal worm were placed in 15 randomly selected holes. The intention was that worms could not escape and would be less obvious to ants. The holes replicated the need for animals to search for food amongst leaf litter. One advantage of this technique was the requirement for ningauis to place their head in the hole to retrieve the food. This was tested with captured specimens. By having to cover their eyes entirely and ears partly, the trade-offs between predation risk and foraging (the basic principles of GUD) were amplified. To further reduce ant predation of mealworm pieces, double-sided tape was placed around the vertical edge of the timber. However, this was discontinued as litter and sand was easily blown onto the tape, rendering it ineffective. Furthermore, ants appeared to be able to walk over the tape. This technique was trialed over two nights, with nine sites each containing a food patch in *Triodia*, bare ground and shrub. It is estimated that almost 70% of trays were subject to ant predation (that is, ants were present in the morning when patches were checked). The failure of both these techniques meant that no data was collected on GUD.

8.2.2 Behavioural trials

The aims of the behavioural experiments were to test whether *N. yvonneae* distinguished between different predators, the specific preference for habitat components, and their preference for habitat components when threatened by different predators. Laboratory based experiments on predation and foraging are widely reported (e.g. Pierce *et al.* 1992; Kotler *et al.* 1993; Eilam *et al.* 1999; Jonsson *et al.* 2000). They allow for more specific testing of hypothesis and potentially more accurate conclusions.

Several trials were attempted in a variety of locations and conditions. The first was undertaken at the study site (Middleback Ranges) using wild caught animals held in short term captivity (two-three nights). Field based experiments with wild animals were preferred to retain the animal's natural behaviour and mimic the natural environmental conditions. For this, individual ningauis were placed into an enclosure (4 x 4 m) and offered a choice of four habitats (shrub, *Triodia*, woody debris and underground) as refuge, with the remaining space being bare ground. A source of food (5-6 mealworms placed in a petri dish) was positioned in the centre of the pen. The trial commenced by placing the ningaui in the underground habitat component. They were then left to explore the entire enclosure and to become familiar with each habitat component. When the animal commenced eating, it was scared by "swooping" it with a model owl (other predators were to be trialed later) and the habitat chosen as the refuge site was recorded. Different lighting conditions were used to represent different levels of predation risk. This first round of trials were attempted on several field trips in late 1997 to early 1998. During this time, minor variations of the trial were attempted. These included changing the methods of scaring animals, the starting position for the trial animal or the introduction of food after the enclosure had been explored.

All outdoor trials were unsuccessful, because many animals spent most of their time attempting to escape from the enclosure, either walking along the enclosure's wall or by attempting to jump over walls. Other animals never attempted to explore the enclosure (e.g. they remained in the underground indefinitely) or did not explore the enclosure fully before finding the food (biasing the result). The problems were linked to the presence of an observer and overly bright lighting conditions necessary to observe the animals. Also, the large size of the enclosure meant that it could take a long time for ningauis to explore the entire pen. The proposed solution was to simplify the whole experiment, by using a smaller enclosure, fewer habitat components and a simpler experiment design.

The second attempt at a behaviour trial involved bringing wild caught *N. yvonneae* into permanent captivity. *N. yvonneae* were collected on two occasions, eight in December 1998 and 10 in March 1999 (Appendix 3). Animals were returned to the University (the

Roseworthy Campus Small Animal House), where they were housed under reverse lighting conditions (approximately 14 hr day and 10 hr night). Experiments were conducted in a glass tank (1500 x 50 x 45 mm) which was located in the same room as the captive ningauis. A range of experiments were considered, including preference of habitats when scared, behavioural changes under different lighting conditions (levels of predation risk) or for different predators and the animals willingness to consume food in "open" habitat components (similar to GUD). To minimise disturbance, observations would take place from a designated observation booth.

As with the first attempt, these behavioural trials were subject to a range of problems that rendered them ineffective. The most dramatic was the death of all the ningauis from the second collection (see Appendix 3 for details). This left an insufficiently sized sample population that would bias any result (six mature males). However, the ningauis in the first collection were used for trialing the experimental design. Again, several problems were identified. These included difficulty in observing ningauis from the observation booth under low light conditions (the booth was designed for observation of larger or diurnal animals), a distinct behavioural change when an observer was present in the experiment room, unsettled behaviour (eg. trying to jump out of the tank) and difficulty in having ningauis distinguish between predators (for example, ningauis showed a total disregard for the scent of snakes). The proposed solution was to undertake behavioural trials at the field study site, but using the same sized tank and a video camera to observe animals.

The third and final attempt at behavioural experiments was conducted in April 2000 and involved holding captured *N. yvonneae* for short periods (three-four days) at the study site. Experiments were conducted in the same tank used in the previous trial, with behaviour observed on a television monitor linked to a video camera situated above the tank. This allowed the observer to sit relatively unnoticed 4-5 m away from the experimental tank. The experiment was kept simple. Two habitat components were used in the tank, with one at either end (with the end for each being alternated between trials). The preference for habitat components were compared via two treatments, *Triodia* versus woody debris and *Triodia* versus shrub. The comparison between shrub and woody debris was not complete due to time restrictions and limits on the number of experimental animals obtained. A food source (meal worms) was located central to these habitat components. Individual *N. yvonneae* were introduced into the centre of the tank and the first habitat component chosen was recorded.

When the ningaui was observed to be feeding, they were scared (by making a loud noise) and the habitat they retreated to recorded. The area of tank explored prior to eating was noted, and only those trials in which the animal had explored both habitat components were included in the results. The general goal was to identify what type of cover they selected when avoiding predation.

Again several difficulties were encountered with this behavioural trial. A number of the ningauis (41%) died in captivity; several animals exhibited flighty behaviour (constantly trying to escape from tank) and some animals remained completely inactive. Additionally, capture rates of *N. yvonneae* were generally low at this time, reducing the number of individuals trialed. In addition, 44% of ningauis in the tank were difficult to scare. Indeed, on numerous occasions, the ningaui was only scared when the observer attempted to catch it by hand.

Despite these complications, 25 trials (using 15 individuals) were successfully completed, being composed of 15 *Triodia* vs. shrub and 10 *Triodia* vs. woody debris treatments. On release, the majority of animals in Treatment one (*Triodia* vs. shrub) preferred *Triodia* (Fig. 8.1a). In contrast, animals were more likely to retreat to shrub after a simulated predation attack (Fig. 8.1b). Results from Treatment two (*Triodia* vs. woody debris) were different, with more animals preferring to retreat to *Triodia* (Fig. 7.2b). None of these results were significant at $P = 0.05$.

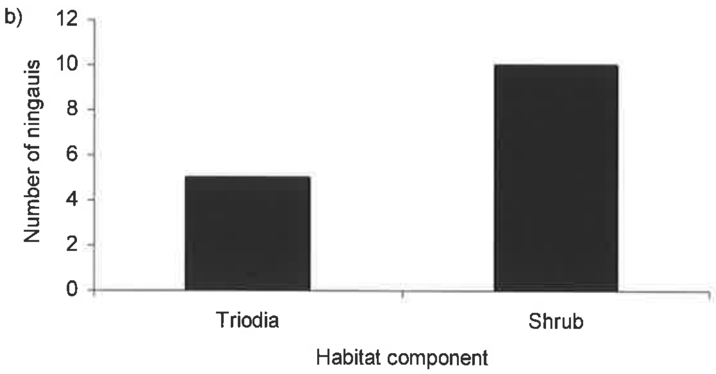

Fig. 8.1: Number of *Ningaui yvonneae* (n = 15) to move to either *Triodia* or shrub when a) first released into the holding tank or b) after the simulation of predation.

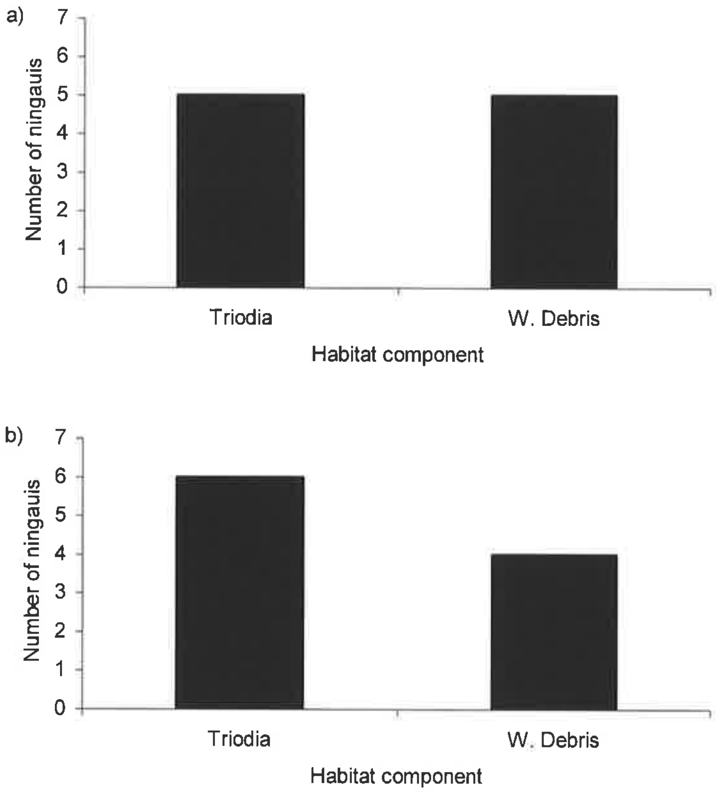

Fig. 8.2: Number of *Ningaui yvonneae* (n = 10) to move to either *Triodia* or woody debris (W. Debris) when a) first released into the holding tank or b) after the simulation of predation.

8.4 Discussion

Wild caught dasyurids and *Ningaui* spp. have been successfully kept in short and long term captivity and participated effectively in both laboratory and field based experiments during other studies (e.g. Wood 1970; Fanning 1982; Huang 1986; Woolley 1988; Geiser & Baudinette 1988; Woolnough & Carthew 1996). Why difficulties were encountered during this study is uncertain. It is possible that the experimental trials for this study were too complicated compared to these other studies (for example, expecting ningauis to find a central source of food only after exploring all four habitats available to them) or expectations too high (for example, expecting ningauis to react to snake scent). Many of the other studies that have successfully used dasyurids were comparatively simple, such as diet selection. For example, Woolnough & Carthew (1996) tested for prey preference by observing the choice made by *N. yvonneae* when offered two sizes of prey. The only trial in the present study to provide a result was the final behaviour trial, which was a simplified version of early trials. It is possible that given more time and additional field trips, this trial could have provided more conclusive information. The deaths encountered during the trials were unexpected, given previous success of holding the species in captivity. The reasons for the deaths occurring during long term captivity are explored in Appendix 3. The explanation for the deaths during short term captivity (during the final behavioural trials) is unknown.

The lack of other studies on predation risk in dasyurids also makes it difficult to compare and then identify an explanation for the problems encountered. Sutherland & Predavec (1999) recorded little response by the agile antechinus (*Antechinus agilis*) to variation in light levels. This they attributed either to illumination not acting as a cue for either predation risk or prey availability, or because *Antechinus agilis* used denser, more protective habitat components regardless of light intensity. Sutherland & Predavec (1999) suggested the latter may be an evolved fixed behaviour in response to predation risk, with *A. agilis* always acting as if there is a risk of predation. After completion of the field work for this study, Haythornthwaite & Dickman (2000) published details of a GUD experiment with the lesser hairy-footed dunnart (*Sminthopsis youngsoni*). They considered their experimental design as successful, recording 75 foraging events at their GUD feeding stations. They do discuss several possible faults with the experimental design, however dismiss these as inconsequential. Haythornthwaite & Dickman (2000) make no mention of controlling the movement of mealworms or predation by ants. These issues were either not encountered or were insignificant and did not impact their results.

The failure of the GUD trials here makes it difficult to draw conclusions about whether predation influences *N. yvonneae* foraging behaviour, which was one of the intentions of this chapter. Haythornthwaite & Dickman (2000) found a lack of any consistent foraging pattern by *Sminthopsis youngsoni* in their GUD trials. They suggested that this was due to predation risk being relatively low but constant across their study site. They attributed a lower predation risk partly to low numbers of predators (that is, predators showed favour to rodents species) and the regular proximity of cover (in particular *Triodia*) which allowed for a rapid escape. Haythornthwaite & Dickman (2000) also claimed that the of ability of *Sminthopsis youngsoni* to travel long distances and their lack of site fidelity is indicative of an environment with lower predation risk. A low predation risk may also apply to *N. yvonneae*, which also has ready access to cover (Chapter 5), limited site fidelity and an ability to make longer range movements (Chapter 4; Carthew & Keynes 2000). However, unlike the habitat recorded for the *Sminthopsis youngsoni* study (Haythornthwaite & Dickman 2000), there is no significant or constant rodent population at the study site in the Middleback Ranges (see Carthew & Keynes 2000). If *N. yvonneae* at this study site was subject to a low risk of predation, then it was most likely a result of the habitat, with the regular distribution of *Triodia* providing for easy access to cover. If predation was low due to limited number of predators or preference of predators for other taxa (such as rodents), then it would be reasonable to expect ningauis to use habitats that did not provide as prolific cover (for example, trapping grids B and C, Table 5.1). However, use of sites with limited cover was uncommon in this study (see Chapter 5). A low risk of predation would not mean that predation has no influence on animal behaviour, as the low risk would occur only in areas of abundant *Triodia*. Away from *Triodia, N. yvonneae* would be exposed to a higher risk of predation. *N. yvonneae*'s choice of habitat (*Triodia*) is governed (in part) by predation risk. This is demonstrated by the results of habitat preferences at the local and trap scale in Chapter 5, with *Triodia* having greater significance at the local scale.

A low threat of predation may also explain the difficulty encountered when "scaring" ningauis during behaviour trails. The proximity of the cover (refuge) in the tank may have reflected *N. yvonneae*'s natural habitat, meaning their reactions were natural and that they needed to flee only when directly threatened. This may be especially true given that food was present (during the trial) in high abundance (that is, they had a low GUD), with *N. yvonneae* willing to place themselves at risk if high energetic rewards exist (see Chapter 6). Similar observations were made in the field experiments during direct observations of foraging *N. yvonneae* (Chapter 6). On one occasion, the observer was able to physically remove a prey item (a type of cocoon) that was being attacked by a ningaui. Alternatively, ningauis may be wary of predation risk that originates from specific sources. For example, they may be more attuned to threats close to the ground (for example, snake predation), meaning the threats posed during experiments and foraging observations would have been unrealistic or of no concern.

Chapter 9 - Discussion and conclusion

This study is the first detailed investigation into the ecology of the southern ningaui (*Ningaui yvonneae*). As such, it provides a significant advance in the knowledge on the species, including clarification of habitat preferences and diet and new insights into movement patterns and behaviour, breeding biology and foraging behaviour.

During this study (in particular Chapters 6 and 7) the question was raised as to whether habitat selection was a function of resource availability or alternatively, whether resource availability determined the habitat selected. That is, are the habitats chosen by *N. yvonneae* a result of the food resources they contain or do the food resources consumed simply reflect the habitats *N. yvonneae* prefers/requires, especially in terms of predation risk? The data collected during the study may not be sufficient to determine this with certainty. However, I offer three models of behaviour that could describe the relationships between prey, habitat and predation in *N. yvonneae*. First, the risk of predation could be the most significant factor influencing *N. yvonneae* and will govern the use of habitat or behaviour adopted (e.g. remaining close to cover while foraging). In this model, the type of prey consumed is determined by their availability within "safe" habitats. Alternatively, habitat use and behaviour in *N. yvonneae* could be influenced primarily by their preferred diet. Predation risk would still be an important consideration in obtaining the preferred diet, with ningauis choosing habitats that offer a compromise or balance between preferred prey and predation risk. Lastly, it is possible that *N. yvonneae* does not react to predation risk (or it is treated as being constant) providing there is some cover (i.e. *Triodia*) available locally. Prey, either preferred or not, are then consumed where they are most available or accessible, providing this does not distance them from cover. I suspect it is the latter model that best describes the relationship between *N. yvonneae* and its prey and habitat, as the species appears to forage with or show little concern for predation while it is near *Triodia*. However, the interaction between prey, habitat and predation is not easily explained. As mentioned in previous chapters, habitat selection can be governed by many factors, many of which change over time and across needs (see Section 1.2). Indeed, it has been suggested that there is relatively little known about the factors that determine the density and habitat selection of dasyurids (Gilfillan 2001b).

In several aspects of this study *Triodia* was found to be the most preferred or important habitat component. In particular, *N. yvonneae* was recorded primarily in areas containing at least some cover of *Triodia* (Chapter 5) and *Triodia* was the most preferred habitat component during nightly foraging activity (Chapter 6). As such, it is reasonable to suggest that *Triodia* is the key habitat of *N. yvonneae*. This supports suggestions from other studies (see Coventry & Dixon 1984; Bennett *et al.* 1989; Menkhorst & Bennett 1990; Fisher & Dickman 1993a). Most likely, the strong association between *N. yvonneae* and *Triodia* occurs because the latter provides a regularly spaced and available form of cover. Cover was found to be an important factor in the distribution and abundance of *N. yvonneae* at the local scale (Chapter 5). However, not all types of cover were valued equally. For example, shrub cover alone was not widely used by *N. yvonneae*. The regular network of cover provided by *Triodia* grants *N. yvonneae* reliable escape opportunities from predators. An easily accessed refuge was also used to explain why *N. yvonneae* displayed a limited response to predation threat in Chapter 8. The activity patterns of *N. yvonneae* provided additional evidence that *Triodia* was important for cover, with most resting *N. yvonneae* selecting *Triodia*. Indeed, *Triodia* was frequently rated by compositional analysis as the most preferred habitat component across different seasons, activities and sex.

If *Triodia* was important for reasons other than protection from predators, it might be reasonable to record ningauis in areas without *Triodia. N. yvonneae* was an adaptable forager, capturing a wide range of taxa of differing sizes and from various habitat components. The species also displayed a range of different killing techniques and was observed to be an agile and efficient predator (see Appendix 2; Woolnough & Carthew 1993). Dietary adaptability has been found to be important to other dasyurids species (e.g. Fisher & Dickman 1993b; Chen *et al.* 1998). It is not unreasonable to expect ningauis to be capable of foraging successfully in areas without *Triodia*. Indeed, 69% of prey was caught in a habitat component other than *Triodia*. Why then did ningauis not forage away from *Triodia* if not for the protection it provided? It is possible that *Triodia* contained a type of taxa that was important/preferred or *Triodia* was positively associated with leaf litter, the main foraging habitat component for *N. yvonneae*. However, the five preferred taxa of *N. yvonneae* were recorded in a range of other habitat components (73% of captures of preferred taxa were for habitat components other than *Triodia*) and on average, non-*Triodia* (non-capture grids; see Section 2.2 and Chapter 5) contained a higher percentage of leaf litter (40%) than *Triodia* (capture) grids (25%). It might appear that diet did not have a significant impact on habitat selection by *N. yvonneae*, as has been recorded for several other dasyurids. For example, Lunney *et al.* (1989) found that food was not a consideration in selection of habitat by *Sminthopsis leucopus*. Similarly, Masters (1993) reported that dasyurid diversity was unaffected by a reduction in invertebrate biomass and diversity, but was significantly reduced after the simplification of micro-habitat. Areas without *Triodia* may be avoided despite apparent foraging opportunities because they do not provided the same level of protection. It may be that refuges within these habitats are less reliable or common, making the habitat less suitable for *N. yvonneae*.

The ability of *N. yvonneae* to use *Triodia* successfully as a refuge may provide one explanation for their being the dominant small terrestrial mammal in this landscape (Carthew & Keynes 2000). While the association between small mammals and habitats containing hummock grasses (*Triodia* spp.) is well documented (e.g. Morton 1982; Cole & Gibson 1991; Fisher & Dickman 1993a; Haythornthwaite & Dickman 2000), there appears to be little reference to or description of small terrestrial mammals moving within the hummocks (as opposed to its margins). It is possible that larger sized mammals may not fully capitalise on the protection *Triodia* offers because they are physically constrained by its dense nature. Observation of foraging animals (see Chapters 6 and 7) revealed that despite their small size, ningauis often struggled to enter *Triodia* hummocks. Indeed, gaining access to the interior of the hummock often resulted in the removal of luminescent tags or radio transmitters (by 'squeezing' between *Triodia* spines). The ability of reptiles to exploit the dense nature of *Triodia* hummocks is one reason provided for the particularly high diversity of arid zone reptiles in Australia (e.g. Morton & James 1988; Pianka 1989). Indeed, anecdotal observations during this study showed a strong propensity for fleeing diurnal reptiles to use *Triodia*, especially *Ctenotus* spp.

However, to suggest the dominance of *N. yvonneae* at this study site is due to their ability to use *Triodia* as a refuge implies that there is a greater risk of predation at this study site than other localities within Australia that contain *Triodia*, since ningauis are recorded elsewhere to live in symaptry with other small mammals (e.g. Calver *et al.* 1988; Masters 1993; Whisson 1995). Furthermore, this suggestion may not explain the low abundance of burrow dwelling mammals such as Mitchell's hopping mice (*Notomys mitchellii*), that use burrows as a major form of predator avoidance. That is, unless rodent abundance at this site was a result of other factors (such as limited food resources). The absence of a significant rodent population at the study site is likely to increase predation pressure on other species. For example, Smith & Cole (1989) suggested that rodents were the primary prey of barn owls (*Tyto alba*) because they were the most abundant small mammal (relative to dasyurids; see also Heywood & Pavey 2002). The lower diversity of small mammals at the study site and its resulting increase in predation pressure on *N. yvonneae* means that there may have been a stronger requirement for adequate cover.

If *Triodia* is a critical habitat of *N. yvonneae*, it is possible that other habitat components are used incidentally as ningauis move between patches or hummocks of *Triodia*. Walther &

Gosler (2001) reported that great tits (*Parvus* sp) used areas of protective cover like "highways", using them to move between feeding patches and thus minimising predation risk. Although abundant, *Triodia* had a patchy distribution. Moving between two distant points required animals to regularly leave *Triodia*. In Chapter 7 it was suggested that *N. yvonneae* may have been a generalist forager, with the frequency of prey captures in habitats correlating to the availability of those habitats. However, the differences in behaviour between bare ground and leaf litter suggest that leaf litter is of particular value to *N. yvonneae*. Indeed, in Chapter 6 ningauis spent most of their active time in leaf litter (presumably searching for food), while in Chapter 7 ningauis were recorded to obtain most of their prey from leaf litter. The preference for foraging in leaf litter during this study contradicts Fisher & Dickman (1993a), who suggested that both *N. yvonneae* and *N. ridei* preferred to forage in habitats such as shrubs and *Triodia*, where prey were generally small. However, in this study, there was little variation between habitat components in the sizes of available prey. The preference for leaf litter over bare ground recorded in Chapter 6 for foraging ningauis was thought to be due to the greater abundance of prey. However, it was later shown (Chapter 7) that bare ground and leaf litter had similar prey abundance (Fig. 7.2). Leaf litter may be important at this study site for four reasons: it contains specific taxa; it offers a greater prey abundance than other habitats; it contains more easily accessible prey or it is a habitat component readily available close to *Triodia*. It is mostly likely a result of the latter two suggestions, for several reasons. First, *N. yvonneae*'s preferred prey were recorded in a range of habitat components. Second, it is probable that prey within *Triodia* were not as easily accessible (because of its dense structure) than other habitat components. Third, prey availability was consistent across most habitat components. Finally, ningauis tended to remain close to *Triodia* when they were in leaf litter (Chapter 6). The strong preferences shown for leaf litter and its importance for prey captures suggests that the foraging requirements of *N. yvonneae* were likely to play an important role in the habitat use and behaviour. However, the risk of predation still played a role in foraging decisions, with ningauis remaining close to *Triodia*.

Seasonal variations in climatic conditions were a significant factor in the ecology of *N. yvonneae*. This is not surprising given that local seasonal conditions can play a significant role in the arid zone in determining faunal abundance and species richness (e.g. Paltridge & Southgate 2001). Changes in seasons had a strong influence on habitat selection and behaviour in this study. One of the most notable changes was the increased use of burrows during periods of rest in Maturity. This was at the expense of *Triodia* and was presumably for the thermoregulation benefits provided by burrows (increased warmth). Survival of small mammals such as *N. yvonneae* is complicated by their size and subsequent high energetic demands. For example, Read (1987a) believed that *Planigale* spp. were too small to exploit habitats without soil cracks, as soil cracks offered a habitat with less extreme temperatures. The ability to maintain body warmth under extreme conditions (low temperature and low prey abundance) are key issues for species such as *N. yvonneae*. Indeed, Geiser & Baudinette (1988) suggested that *N. yvonneae*'s pronounced use of torpor was a result of low nightly temperatures and variable prey availability. It is possible that *Triodia* was used partly for its thermal benefits. Morton & James (1988) and Pianka (1989) suggested that a benefit to reptiles using *Triodia* is the relatively more stable climatic conditions within the hummock. Indeed, Drury (1995) recorded more stable soil surface temperatures under *Triodia* hummocks than in open areas. The data from this study suggested that *Triodia* was not used to minimise heat loss, with *Triodia* used less often by active ningauis and there being no discernable increase in prey captures from *Triodia* during Maturation. However, it is possible that *Triodia* hummocks provide cooler temperatures or stable humidity during hotter weather. The increased use of *Triodia* during the warmer seasons (Breeding and Nurture) was thought to result from an increase in predation risk during these seasons. It is also possible that *Triodia* offered more stable climatic conditions during these seasons. However, this is difficult to confirm without further investigation.

Other factors were also influenced by seasons. For example, reproduction was timed to coincide with the higher prey availability of Nurture, as well as avoid the harsher conditions of Maturity (cooler temperature and lower prey abundance). The plateau of weight gain during Maturation is testimony to the stress of this season, being caused by reduced foraging opportunities and increased energetic demand in maintaining warmth. Indeed, Geiser & Baudinette (1988) suggest that the energetic constraints of *N. yvonneae*'s small size (body mass) resulted in more pronounced use of torpor. The changes over time (such as season or animal age) are indicative of the complexity of describing animal behaviour and ecology and determining resource use and preferences (see Section 1.2). In this study, changes in resource use between sex and season were frequently noted, as were changes according to needs (Fig. 9.1). For example, breeding biology (Chapter 3) was tied to changes in prey abundance (Chapter 7). Most importantly, these changes indicated that while *Triodia* was the most important resource for *N. yvonneae*, at certain times and for certain needs, other resources were of equal or greater significance. For example, although used relatively infrequently, the habitat component underground may be vital for surviving winter. It is therefore important to give consideration to all aspects of a species ecology in order to obtain a more accurate and true interpretation of the use of resources by that species.

Growth
(Feb - Apr)

Ningauis 3 to 5 months old, newly independent.

- Highest average capture rate (Table 3.5).
- Average distance moved is similar across males and females. Adult ningauis mostly sedentary (Fig. 4.5).
- 33% of 'resting' time spent underground and 35% in *Triodia.* 32% of 'active' time spent in Triodia (Fig. 6.5).
- 29% of observed prey captures occur in *Triodia* and 40% in leaf litter (Fig. 7.6).
- Invertebrate grubs observed to be most frequently consumed taxa (Fig 7.4). Hymenoptera the most abundant taxa in scats (Fig. 7.10).

Maturation
(May - Jul)

Ningauis 6 to 8 months old. Mean lowest night temperatures.

- Lowest average capture rate (Table 3.5).
- 43% of 'resting' time spent underground and 25% in *Triodia.* 14% of 'active' time spent in *Triodia* (Fig. 6.5).
- 16% of observed prey captures occur in *Triodia* and 39% in leaf litter (Fig. 7.6). Araneae the most frequently consumed taxa (Fig. 7.4).
- Araneae observed to be most frequently consumed taxa (Fig 7.4).
- Ningauis spend least amount of time active (Table 6.3)

Breeding
(Aug - Oct)

Ningauis 9 to 11 months old.

- Average distance moved greater in males than females (Fig. 4.5)
- 1% of 'resting' time spent underground and 69% in *Triodia.* 43% of 'active' time spent in *Triodia* (Fig. 6.5)
- 29% of observed prey captures occur in *Triodia* and 54% in leaf litter (Fig. 7.6)
- Orthoptera observed to be most frequently consumed taxa (Fig. 7.4). Hymenoptera the most abundant taxa in scats (Fig. 7.10).
- Ningauis spend least amount of time eating (Table 6.3)

Nurture
(Nov - Jan)

Ningauis 12-14 months old. Mean warmest night temperatures. Female ningauis with dependant young (0 to 2 months old).

- 0% of 'resting' time spent underground and 71% in *Triodia.* 45% of 'active' time spent in *Triodia* (Fig. 6.5).
- 16% of observed prey captures occur in *Triodia* and 53% in leaf litter (Fig. 7.6).
- Blattodea observed to be most frequently consumed taxa (Fig. 7.4). Araneae the most abundant taxa in scats (Fig. 7.10).

Fig. 9.1. Time line showing major changes in behaviour across seasons during the life of a typical *Ningaui yvonneae.*

As the first detailed examination on *N. yvonneae*, this study has provided valuable insight into the ecology of this species. However, there are several areas in which further investigation would be beneficial. In particular, it would be of value to perform experiments that allow habitat and diet preferences to be identified separately, to determine if habitat selection is a result of dietary preference or prey consumption a result of habitat preferences (as referred to in Dickman 1995). Such testing could also be linked to changing levels or perceptions in predation risk and their influence on habitat selection and prey consumption. For example, an investigation that manipulates food resources or light levels (as undertaken by Sutherland & Predavec (1999) and Haythornthwaite & Dickman (2000)) may help reveal how the level of predation risk or changes in food abundance influences *N. yvonneae* behaviour. Additional information on movement behaviour would be also be beneficial, especially the use of radio tracking technology to further explore home range and movement patterns, in particular the establishment of drifting home ranges.

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Appendix 1 - Observations of the response to pit-fall drift fences[1].

Since the adoption of pit-fall traps as a common technique for trapping Australian vertebrate fauna, there has been much discussion regarding the most effective design of the trap, especially in terms of the drift fence size and placement (e.g. Friend 1984; How *et al.* 1984; Read 1985; Hobbs *et al.* 1994). However, there has been little recorded on the actual responses by animals to encounters with drift fences. During a larger project involving the observation of free foraging *Ningaui yvonneae* (southern ningaui), I had the opportunity to observe the response of this species to permanently established pit-fall drift fences.

The project was undertaken in the Middleback Ranges, located on the Eyre Peninsula of South Australia (137°07′E 33°09′S). The trapping site was situated in a semi-arid mallee community, which had a dominant understorey of *Triodia irritans*. *N. yvonneae* is a small (10 g) nocturnal marsupial that feeds predominantly on invertebrates (Kitchener 1995; Woolnough & Carthew 1996). They have short lives (12-18 months) and although agile climbers, they are mostly terrestrial (pers obs.). Individuals were captured in 25 litre pit-fall buckets (40 cm deep, ∅28cm), over which was placed a six metre length of aluminium fly wire netting (approximately three metres either side of the pit) which was 30 cm high and dug 3-4 cm into the soil. The fences were installed permanently, and had a small gap cut into them over the bucket, to allow an animal to move through the fence while the traps were closed (Friend *et al.* 1989). Traps were arranged into 13 grids, 12 of which contained 9 traps (3 x 3) and 1, 49 traps (7 x 7). The 12 small grids were arranged in two concentric rings around the large grid. All traps in a grid were spaced 15 m apart. Captured animals were kept until night, when they were used to investigate foraging behaviour. This involved attaching a small vial of chemiluminescent liquid (Starlite SL-5 mini chemical light) to the animals rump. The chemical light allowed easy observation, with the aid of red light, of the animals movement and behaviour. Observations were usually made at a distance of 3-5 m. Most *N. yvonneae* displayed no obvious signs of apprehension in the presence of a human observer. On occasion, animals would move and even forage beneath my feet. Trials involving animals displaying

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anxious or nervous behaviour were aborted (< 5% of trials). During each trial, any contacts with a drift fence were recorded and the animals response noted, including: whether the animal followed the fence or retreated from it, how long it followed for, changes in direction while following and if the animal was captured.

A total of 27 encounters with a pit-fall trap were observed between December 1996 and November 1998 (Fig. A1.1). Of these, five *N. yvonneae* fell directly into the pit without contacting the drift fence, while 22 had some contact with the drift fence. Of the 22 animals to make contact with the drift fence, three retreated away from the fence, two climbed over the fence, and 17 followed the fence. Of those 17, only five were captured in the pit, 11 subsequently retreated from the fence and one 'escaped' through a small section with no fence near the pit's rim (formed by the gap in the fence cut above the pit).

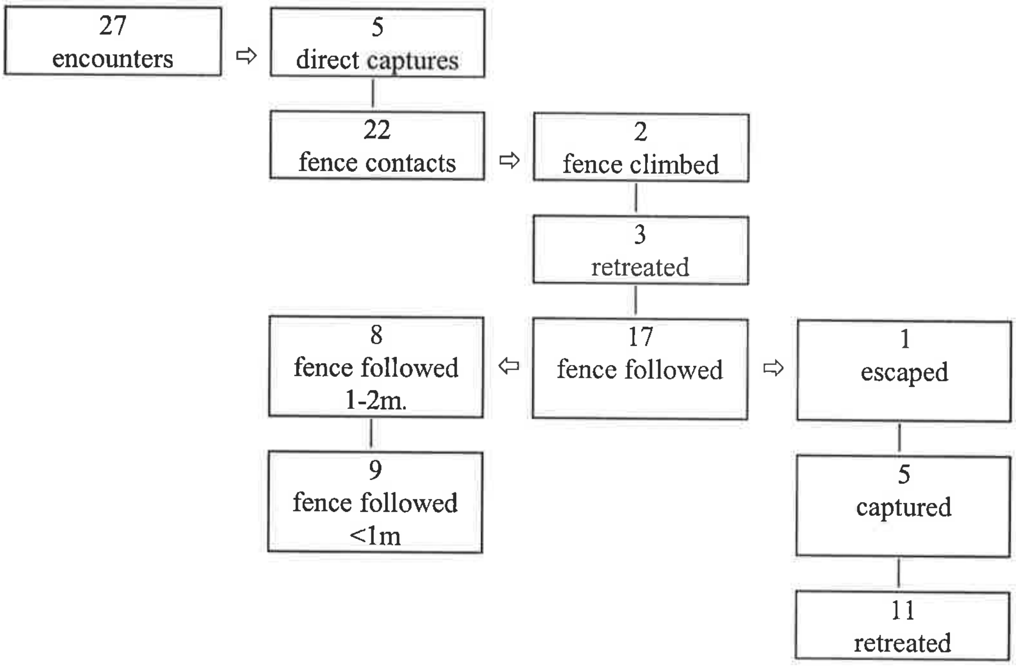

Fig. A1.1. Responses of *Ningaui yvonneae* to pit-fall drift fences.

Most *N. yvonneae* that followed the fence did so at a quick pace, although there were often short pauses in their movement. The distance followed along the drift fence was generally small. No *N. yvonneae* followed the fence for more than 2 m. Of the 17 to follow the fence, 8 (47%) did for a distance between 1 and 2 m and 9 (53%) followed for less than 1 m. Distances here do not necessarily refer to straight line distances, as changes in direction were common while following the drift fence. Therefore, an animal recorded as moving 1.5 m along the fence, may have only travelled along a 1m section of the fence. Three animals which followed the fence for 1-2 m changed direction, while only one animal changed direction in the less than 1 m category.

Most animals appeared to treat the fence as a curiosity. After contact, the majority of animals paused to examine the fence, which often included a sniffing-like behaviour. Additionally, the regular changes in direction observed at the fence were not noticed at other natural barriers (such as logs). Despite this, animals were still encouraged to travel along the fence, with only five of the 22 animals to make contact with the fence failing to follow it. The drift fence is obviously successful in guiding animal movements, yet it does not guarantee a capture, with only 30% of animals to follow the fence being caught. One of the main causes for this was the direction of travel, with animals that moved away from the bucket easily avoiding capture. Also, frequent changes in direction meant that the actual length of fence followed was reduced and therefore, so was the likelihood of the animal approaching the bucket. Unfortunately, no data were recorded on the influence of direction changes on capture success. Finally, some of the animals that followed the drift fence did not remain close to it as they moved. Instead, after contact, animals would move 20-30 cm out from the fence and follow it on a parallel course. After a short distance (anything from 20-100 cm) they would approach the fence again. This 'bouncing' effect could result in lowered capture success if the animal 'bounces' around a bucket. Overcoming the above problems is difficult. An animals inclination to change direction may be overcome by making the drift fence appear more 'natural'. Indeed, Friend *et al.* (1989) suggest that certain taxa may be attracted to the accumulated litter around the permanent fences, as foraging habitat. However, not one *N. yvonneae* was observed foraging in the litter beside drift fences. Larger sized pit-fall buckets may help overcome the 'bouncing' effect by making it harder for the animal to miss the bucket if it is travelling on a parallel course to the fence. Indeed, larger buckets have been found to improve trap success in several studies (for example, Morton *et al.* 1988; Friend *et al.* 1989).

The benefits of drift fences may be questionable, given that 50% of all captures observed during these trials were direct captures. In four of the five direct captures, animals approached the pit at a quick pace, seeming to aim deliberately for the bucket (that is, the gap in the fence). It is possible that these direct captures were a result of the familiarity of the animals with the trap, and their expectation to pass through the fence to the other side (as they might do when the traps were closed). This familiarity would not have occurred if fences were not permanently present. It is possible that direct captures were an indirect result of having permanent drift fences.

The distance travelled by *N. yvonneae* along drift fences seems to have little bearing on capture success, with 22% and 38% of animals following the fence being captured for the less than a metre and the one to two metre categories respectively. Since no *N. yvonneae* followed the fence for more than two metres, shorter drift fences may be adequate, and potentially more efficient in terms of time and expense. Moreover, the importance of fence maintenance is highlighted by the one "escape" through a very small gap in the drift fence. This escape also indicates the impact of animal responses to drift fences on capture success. This incident was one of the few occasions that a *N. yvonneae* did not move quickly along the fence, allowing the animal to locate a weakness in the drift fence. This tends to contradict the suggestion by Friend *et a.l* (1989) that foraging along the drift fence should be encouraged. Such slow movement might enable the target species to either find a weakness with the fence or to observe and thus avoid the bucket.

Appendix 2 - Observations on foraging behaviour[1].

The southern ningaui (*Ningaui yvonneae*) is a small dasyurid inhabiting semi-arid regions of southern Australia. It is a nocturnal predator, feeding mainly on small invertebrates (Woolnough & Carthew 1996; Fisher & Dickman 1993b). During a larger research project examining population dynamics, habitat selection and diet, I observed and documented aspects of the foraging behaviour of *N. yvonneae*. These observations, which are difficult to quantify, provide insight into the ecology of this poorly studied species.

Pitfall trapping was undertaken in a semi-arid mallee community, located in the Middleback Ranges, Eyre Peninsula, South Australia (137°07′E 33°09′S). The understorey vegetation was dominated by hummock grass (*Triodia irritans*). Captured *N. yvonneae* were held during the day for release 1-2 hours after dusk. On release, individuals were observed from a distance of 3-5 m with the aid of red light and chemiluminescent tags attached to the animals rump (see Bos 1999 for details). Information on foraging behaviour was collected during 59 field trials conducted between October 1996 and December 1998. Where noted, information recorded while individual *N. yvonneae* were held in captivity is also presented.

Ningaui yvonneae was an adaptable predator, catching prey in a range of habitats (from soil to under bark) and via an array of methods (such as digging or pouncing). *Ningaui yvonneae* foraged actively, with most prey found whilst moving at walking pace. While foraging, animals frequently investigated the substrate and regularly paused to 'scan' their surroundings (possibly for prey or predators). This typical behaviour was termed 'foraging walk'. Captive animals were heard to issue an 'investigatory twitter' (Fanning 1982) during this type of movement. Unlike Woolnough & Carthew (1996), *N. yvonneae* in this study was never observed to adopt sit-and-wait foraging behaviour, nor the ambush behaviour described by Andrew & Settle (1982) for *Planigale* sp.

Ningaui yvonneae displayed excellent climbing ability, and climbed many substrates, including hummock grass (*Triodia irritans*), shrubs and the stems of mallee Eucalypts. On two occasions, *N. yvonneae* was observed climbing on the underside of a near horizontal

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mallee stem. After one of these climbs the individual jumped into a clump of *Triodia*, a fall of approximately one metre. Such agility was often used to capture prey. For example, three *N. yvonneae* were observed jumping from the ground into a clump of *Triodia* to attack prey. Similar behaviour was recorded for *Planigale gilesi* (Andrew & Settle 1982). Two of these leaping attacks by *Ningaui yvonneae* were to capture moths, the other a grasshopper. Both prey types are mobile and have effective defensive/escape mechanisms (flight and jump). The speed and urgency of the attack on these three occasions may indicate prey recognition ability by *N. yvonneae*. The ability to recognise the type of prey from a distance would allow *N. yvonneae* to adopt appropriate attack techniques.

Ningaui yvonneae appeared to use olfaction, vision and hearing to locate and capture prey. Sniffing was regularly observed. Individual *N. yvonneae* would often pause from foraging, raise their heads and sniff the air, sometimes adopting a bipedal stance, as observed in *Planigale* sp. (Andrew & Settle 1982). Air sniffing occasionally involved the animal climbing the seed stems of *Triodia irritans*. In leaf litter, individual *N. yvonneae* would often submerge their noses beneath the litter, sometimes continuing to move with a 'furrowing' type motion. Animals were often observed locating prey from deep within leaf litter, consuming them only after extensive digging. Huang (1986) found olfaction to be the single most important sense for prey detection by *N. ridei* and *Sminthopsis griseoventer*. However, Huang (1986) also stated that a combination of senses provided the most successful hunting in these species. Woolnough & Carthew (1996) came to a similar conclusion for *N. yvonneae*, suggesting that a combination of olfaction and vision were the most common methods for detecting prey. In particular, they considered vision important for the detection of movement. I made similar observations, with captive animals often ignoring stationary prey. The same behaviour was recorded for *Planigale* sp. and *Dasycercus byrnei* (Aslin 1974; Andrew & Settle 1982). The importance of each sense in the detection or capture of prey is difficult to determine from these observations only. For example, while *N. yvonneae* used their noses in a furrowing motion in leaf litter, it is possible that hearing was also used, detecting the high frequency sounds made by invertebrates (Andrew & Settle 1982). However, I suspect that different senses were used at different stages of the prey capture sequence or for particular situations. For example, in leaf litter, hearing might have been used to identify any prey in the immediate area and smell used to pinpoint and capture prey.

Two styles of foraging were observed during field trials. The first was an 'intensive' search, involving continuous use of the 'foraging walk' and thorough investigation of a habitat patch.

For example, one individual spent over 30 minutes within two adjoining clumps of *Triodia*, approximately 2 metres wide. In this time, it captured four items of prey. The second foraging mode was an 'extensive' foraging style, during which the 'foraging walk' was used for brief periods, interspersed by rapid movement through the habitat (jog or run). Both styles appear to involve regular captures of prey. The choice of either strategy may be based on the productivity of a particular habitat patch, the amount or frequency of prey catches or the influence of predation (e.g. McNair 1982; Bell 1991; Benhamou 1992; Kotler 1997). Abiotic factors such as weather or moon phase may also influence the decision. However, in two successive trials on one night, two individual *N. yvonneae* displayed both types of foraging styles. Additionally, numerous animals were observed to switch between the two styles within the one trial. I suspect that extensive foraging is adopted when the animal has a set destination, and foraging is a secondary concern. For example, extensive foraging may take place on route to a refuge site.

As recorded by Woolnough & Carthew (1996), prey captured during these foraging observations were almost always killed by bites to the anterior, then consumed head first. Forepaws were used extensively to manipulate prey into position, as found by Cuttle (1982) and Woolnough & Carthew 1996 for *Phascogale tapoatafa* and *N. yvonneae* respectively. Most prey caught were invertebrates approximately 10-15 mm in length. On only one occasion was a vertebrate observed to be caught (*Ctenotus atlas*), although the remains of small reptiles were often found in pit-fall traps containing *N. yvonneae*. Not all invertebrates were available for consumption by *N. yvonneae*. On one occasion, a large black beetle was attacked, but after three attempts to subdue the prey, the ningaui retreated. I suspect the shell of the beetle was too hard for the animal to penetrate (Fisher & Dickman 1993b). Carrion was consumed by *N. yvonneae*, including one large praying mantis and dead flies in captive holding cages. After consumption of prey, animals would often self groom, especially the head with the aid of licked forepaws, as described for *Planigale* sp. (Andrew & Settle 1982).

Some prey types involved specific techniques of capture or consumption. For example, on two occasions the internal body organs of grasshoppers were removed and discarded. This was done by consuming the grasshoppers head and then using the mouth to pull the organ sack from the body cavity whilst anchoring the exoskeleton with the forepaws. After discarding the offal, the remainder of the body and legs were consumed. One of these observations was of a captive *N. yvonneae*, with the offal remaining uneaten overnight. A quick and agile style of attack was used by *N. yvonneae* for capturing large (and more dangerous) prey. Two animals were observed to capture trap-door spiders (body size of approximately 10-15 mm) from within the spider's burrow. On both occasions, the spider was dragged out of the burrow by a rapid series of 'bite - pull - release' movements. Once outside the burrow, the spider was subdued with bites to the spider's anterior, although these attacks were cautious, in a 'lunge-bite-retreat' manoeuvre. After disabling the spiders, killing bites were administered to the spiders anterior. The 'lunge-bite-retreat' attack was also observed on two other occasions, when *N. yvonneae* were observed attacking large centipedes. The first centipede was six cm in length. It was attacked (lunge-bite-retreat) from the rear, with most bites directed to its posterior and occasionally to the mid section. This appeared to be a disabling manoeuvre. With the centipede disabled, the ningaui initiated killing bites to centipede's anterior. The second centipede was approximately 10 cm in length. It was the largest living prey observed to be taken by the species. Again, the lunge-bite-retreat method was used, however this time the initial attacks focussed on the head. Disabling bites were then directed to the midsection followed by the final killing bites to the head.

Large prey items captured in open habitats such as leaf litter, would often be carried to and consumed in a habitat offering greater cover. The most frequently used habitat for prey consumption were the margins of *Triodia* hummocks, although woody debris, inner *Triodia* and shrubs were also used. For example, the larger centipede described above was consumed in *Triodia* margins after being captured on bare ground. Similar behaviours were observed for *Planigale* sp. (Andrew & Settle 1982).

Burrows were regularly used as rest sites during foraging bouts, especially during winter. Time spent in burrows resting varied from a few minutes to over an hour (this was the maximum time spent waiting for animals to exit). The most commonly used burrows for refuge were those made by moths (Hepialidae). Animals always entered and emerged from burrows head first. Observations of *N. yvonneae* in human made burrows revealed their ability to turn around without aid of a wider burrow chamber. Individuals were observed to rest with their head facing upwards, with forepaws pointing up and resting at either side of the head. The ease and speed at which *N. yvonneae* located burrows (which are visually difficult to detect) suggests that some individuals had intimate knowledge of their surrounding habitat. For example, on three occasions, animals were observed to move directly towards a burrow, often running, with little deviation in path. One of these observations occurred after the ningaui had eaten two large sized prey in succession. This burrow was covered over with leaf litter and was difficult to locate visually.

Appendix 3 - The introduction of ningauis to the laboratory[1].

The use of wild caught animals for laboratory based experiments is a relatively common technique in ecology (e.g. Wood 1970; Huang 1986; Woolley 1988; Brillhart & Kaufman 1991; Woolnough & Carthew 1996). The decision to do so is a significant one. However, if no breeding colony exists, it is often the only means of obtaining certain types of information regarding the species ecology and biology. Use of wild caught animals may also provide more accurate/reliable data.

While there has been much published on the maintenance (such as housing, feeding and breeding) of captive populations (e.g. Evans 1982), there seems to be few published articles that outline a suitable protocol for the introduction of wild caught animals to a laboratory environment. Indeed, very few authors actually describe the process they used to introduce animals to the laboratory or the survival rate of captured animals. Presented below is a short commentary on experiences in introducing wild caught *Ningaui yvonneae* to captivity.

Ningaui yvonneae is a small insectivorous marsupial that lives for up to 12-18 months. Its conservation status is common, being found across much of southern Australia. Captive specimens from the Eyre Peninsula (South Australia) were to be used in the investigation of the foraging behaviour of the species. Permission was obtained to capture and house up to 20 *N. yvonneae* for these experiments. Animals were housed in Nally tubs (65 x 40 x 30cm), in which was placed a layer of sterilised sand (1-2cm deep), a small nesting box (containing sand, leaf litter and 10cm section of PVC pipe) and one or two small leafy branches (approx. 20cm long each). Ningauis were fed daily on "Wombaroo" small carnivore food (1-2 teaspoons) supplemented by 3-4 mealworms/beetles or cockroaches (depending on availability). Live insect prey were placed under the leafy branch to encourage animals to forage. Water was provided *ad libitum*. Animals were housed under reverse lighting conditions (approximately 14 hr day and 10 hr night).

A total of 18 *N. yvonneae* were caught on two occasions. Eight and ten individuals were captured during the periods 2-17th December 1998 and 8-9th March 1999, respectively. The

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December collection consisted entirely of mature, post breeding males (aged approximately 14 months). The March collection was composed of two female and eight male ningauis, all of whom were juveniles (aged approximately five months). The survival rate of the two collections differed markedly. Most animals from the December collection survived for four to five months (Table A3.1). This was considered to be successful given their age at the time of collection. In the wild, most of these animals would have died by February see Chapter 3). Two of the specimens from the December collection survived until June 1999. The March collection was considered unsuccessful, since most specimens (80%) had died within eight days of collection (Table A3.1). All animals ate well while in captivity and showed no obvious signs of disease. The cause of death was discussed with a veterinarian and was attributed to a delayed stress reaction. I suspect the contrast in death rates of the two collections was due to different levels of stress resulting from the different protocols used to introduce each collection to the laboratory. These differences, which were unintentional, are listed below.

1) Time between capture and transportation to the laboratory. The majority of specimens in the December collection were retained at the study site for four to five days prior to transport to the University. In comparison, five ningauis from collection two were transported on the day of capture and five after one night in captivity only.

2) Time between entry into the laboratory and introduction to the reverse lighting room. The March collection was introduced into the reverse lighting room immediately upon arrival at the University. Ningauis from the December collection were introduced two to three weeks after their arrival, because the room was initially unavailable.

3) Difference between field and laboratory temperatures. Both collections occurred when maximum daily temperatures ranged between 34-37^{0}C. The small animal house is normally kept at a constant temperature of 22^{0}C. However, for both collections, the thermostat controls were temporarily faulty. For the December collection, laboratory temperatures were higher than normal, around 26-27^{0}C. In contrast, laboratory temperatures for the March collection were well below normal, at 15-17^{0}C.

While there is no direct evidence that the different introduction procedures influenced the survival of specimens, the explanation is credible. In my experience *N. yvonneae* is not a particularly difficult species to house in captivity. It has a high survival rate during short-term field-based captivity and reacts well to handling and investigatory research techniques (pers obs.). Wild caught *N. yvonneae* specimens have also been used by various other authors (e.g. Baverstock & Aslin 1978; Geiser & Baudinette 1988; Calver *et al.* 1989; Calver *et al.* 1991) and have been housed previously at Adelaide University (Roseworthy) (Woolnough & Carthew 1996). In this instance, most animals (collected in March/April1992) survived throughout the year, and a number even survived several years. These specimens had also been collected from the Middleback Ranges, although the precise collection procedure is unknown.

December collection				March collection			
Date collected	No. collected	Date of death	Alive *	Date collected	No. collected	Date of death	Alive *
12-17 Dec 1998	8 male	22-2-99	2	8-9 Mar 1999	2 female	15-3-99	0
		23-3-99			8 male	15-3-99	
		4-4-99				17-3-99	
		6-4-99				17-3-99	
		9-4-99				17-3-99	
		13-2-99**				17-3-99	
						17-3-99	
						17-3-99	
						21-3-99	
						23-3-99	

Table A3.1: Dates of deaths of individual *N. yvonneae* from the December and March collections. * Alive at the time of submission. ** Animal escaped due to a loose fitting lid.

When considered separately, it is unlikely that any one of the above mentioned factors would have impacted on the survival rate of the ningauis. However, in combination, their influence is potentially much greater. The slower introduction to new environments (e.g. Nally tubs and laboratory) and laboratory conditions (constant temperature and reverse lighting) of the December collection may have given animals more time to adjust, thus minimising stress. The different ages of the animals may have also contributed to the different survival rates of the two collections. It is possible that the younger animals of the March collection were more sensitive to capture stress and/or disease. However, I would expect the older specimens to be more susceptible. It is common for Dasyurids of older age to be captured in poor condition (e.g. worn teeth, poor condition of coat, loose fur) especially post-breeding males (e.g. Leung 1999).

I believe that it is important to give due consideration to the capture, transport and introduction protocol of wild animals to a laboratory situation. In particular, animals should be introduced slowly into the laboratory when conditions differ significantly to those in the wild.

Ideally, laboratory conditions at the time of entry should closely mimic those of the field. I also encourage researchers to describe briefly in-paper, techniques used to acclimatise animals and survival rates of animals in hope reducing mortality rates.