THE ECOLOGY OF FERAL CATS, *FELIS CATUS*, IN OPEN FOREST IN NEW SOUTH WALES: INTERACTIONS WITH FOOD RESOURCES AND FOXES

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STATEMENT OF RESPONSIBILITY

This thesis is my own original work, except where specifically acknowledged

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ABSTRACT

Despite increasing evidence for the impact of feral cats *Felis catus* on native fauna in Australia, little is known of the ecology of cats, particularly factors that limit cat abundance. The ecology of the feral cat in Australia is represented by just 15 published studies on diet, only one of which has examined diet in relation to prey availability, and one study of home range behaviour. The red fox *Vulpes vulpes* is a significant pest to agriculture and native fauna in Australia and widespread fox removals have been proposed by the Vertebrate Biocontrol Cooperative Research Centre (VBCRC). However, there is concern that feral cats may increase compensatorily when fox populations are reduced, as has occurred in Western Australia, and therefore that predation pressure may not be alleviated on native fauna following fox control programs.

This thesis is divided into two parts. First, the diet and home range size of cats is examined in relation to prey availability, and home range overlap and habitat use are determined. In the second part, several niche parameters (diet, home range and habitat use) that were potentially important resources for foxes and cats were quantified to assess the potential for competition. Avoidance and aggression between cats and foxes was examined using simultaneous radiotracking techniques and video observations. The hypothesis that foxes limit cats through interspecific competition (exploitation and interference) was then tested using a fox removal experiment. Finally, three further hypotheses were tested using a fox removal experiment to determine which factors limit feral cats at Burrendong. The four hypotheses tested were thus: i) Cats are limited independently of foxes through other factors such as food availability; ii) Foxes limit cats through interspecific competition (exploitation and / or interference); iii) Foxes limit cats through intraguild predation; iv) Cats benefit from the presence of foxes through facilitation.

The diets and spatial use of feral cats were examined on agricultural land on the eastern shore of Lake Burrendong, New South Wales (32° °
July 1994 and June 1997. The major land use for the area is water catchment under the agistment of sheep *Ovis aries* and cattle *Bos taurus*. The study area encompasses about 90 km^2 of hilly terrain with undulating slopes that extend down to a flat foreshore area that has been extensively cleared of trees for grazing. The slopes are generally well timbered and dominated by white box *Eucalyptus albens* woodlands with some yellow box *E. melliodora* associations. Stands of cyprus pines *Callitris* spp. are also common. Feral cats and red foxes are established throughout the study area, and the European rabbit *Oryctolagus cuniculus* was abundant until the arrival of Rabbit Calicivirus Disease (RCD) in June 1996.

The diet of feral cats was determined from the analysis of 499 scats. Rabbits were the staple prey of cats, with occurrence (O) in 81.6% of scats and comprising 68.4% by volume (V). Carrion (mostly eastern grey kangaroo *Macropus giganteus* and sheep) (O 21.5%, V 11.5%) was an important secondary food, particularly in winter and spring. Other mammalian prey included brushtail possums *Trichosurus vulpecula* (O 4.6%, V 2.4%), house mice *Mus domesticus* (O 6.2%, V 3.2%), black rats *Rattus rattus* (O 2.6%, V 1.4%) and a dunnart *Sminthopsis* sp. (probably *S. murina*) (O 0.2%, V 0.006%). Invertebrates (mostly Orthopterans) (O 41.5%, V 7.5%), vegetation (O 26.3%, V 3.6%), birds (O 4.2%, V 0.8%) and reptiles (O 3.4%, V 0.3%) were generally of minor importance in the diet. Few significant seasonal differences were found, although invertebrates contributed significantly less, and possums more, to the mean scat volume in winter and summer respectively.

A significant dietary response was found for changes in rabbit abundance, but not for the other prey groups. Cats continued to prey heavily on rabbits after the arrival of Rabbit Calicivirus Disease, despite the relatively low numbers of rabbits. Ten months post-RCD, house mice increased in importance in the diet. However, it was not known whether this represented prey switching *sensu stricto* or opportunistic predation on an increased mouse population, as mouse abundance was not measured during this period.

Seventy-seven cats (48 recaptures) were caught in 6762 trap nights between November 1994 and August 1996 using both cage traps and leg-hold traps. A further 18 individual cats were trapped as non-target animals by the VBCRC Fox Sterility Project and used in this study. Trapped adult cats were fitted with radio collars and their home range size, overlap and habitat use examined. Home ranges and core areas were quantified using 95% and 50% kernel utilisation distributions (KE 95 and KE 50) and minimum convex polygons (MCP 100, MCP 95, MCP 50). Four habitat types (grassland, open woodland, open forest, and mudflats) were delineated on aerial photographs and a habitat map produced using ARC/INFO. Compositional analysis was used to examine habitat preference in cats.

Home range sizes of cats (n = 15, 598 fixes) in winter 1995, prior to fox removal, were similar to those reported in the only published study of cat spatial use in Australia, but larger than those recorded elsewhere. This may have reflected more dispersed food resources in Australia, although home range size was not correlated significantly with rabbit abundance. Male ranges (MCP 95 $\bar{x}$ = 284 ha, n = 11) tended to be larger than females ($\bar{x}$ = 151ha, n = 4), but no differences were detected between young (1-3 years, $\bar{x}$ = 271ha, n = 7) and old (>3 years, $\bar{x}$ = 221ha, n = 8) cats. Cats were active both by day and night with no temporal differences being detected in range size. Both adult male and female cats tended to be solitary, although home ranges overlapped extensively. Kin groups were indicated (but not confirmed) as most inter-sexual overlap occurred between young and old cats.

Habitat composition of home ranges generally reflected the availability of habitats at the study site, although cats significantly avoided mudflats. Home ranges comprised mostly open woodland and open forest habitats with smaller areas of grassland and mudflats. However, within individual home ranges, cats used grassland and open woodland habitats most often where rabbits were more abundant. Inter-individual (sex, age) or temporal (day/night) differences in habitat use were not detected.

Comparison of resource use between cats and foxes indicated a large overlap in diet, home ranges and habitat use. Dietary breadths and overlaps between cats and foxes increased when rabbit availability declined in autumn and post-RCD. Dietary overlap was high overall (75%), although some resource partitioning was detected.

Rabbits were more important in the diet of cats than foxes, particularly in summer, when foxes ate more grasshoppers. Carrion, invertebrates and vegetation were more important for foxes than for cats overall. Home ranges of both cats and foxes comprised mostly open woodland habitats followed by grassland, open forest and mudflats, which largely reflected their relative availabilities. However, within individual home ranges, cats showed a preference for grassland habitats. In addition, cats tended to deposit scats more often than foxes at rabbit warrens and at hollow log entrances, while foxes deposited scats more often than cats on sand plots, tracks and at dams. The large overlap in resource use between cats and foxes indicated a high potential for exploitation competition.

Foxes may attempt to lessen competition by killing cats (interference competition). Three radiocollared cats were killed by foxes and aggression was observed toward cats. Home ranges overlapped extensively, but avoidance was indicated from the simultaneous radiotracking of both predators, as greater separations and lower overlaps in home ranges and core areas were recorded between species than within species. In addition, video observations suggested avoidance of carcasses by cats in the presence of foxes.

The hypothesis that foxes limit feral cats through interspecific competition was then tested using a fox removal experiment. Foxes were reduced at two of the four sites

Predator-Prey project. Resource use and abundance of cats were compared before and after fox removal and between treated and untreated sites. Although no increase in cat abundance followed the removal of foxes, significant behavioural changes by cats strongly suggested interspecific competition operating via exploitation and interference. Exploitation competition was supported by the increased consumption of carrion by cats at the treated sites after fox removal, while support for interference competition came from the increased use of grassland habitats at night after fox removal. The direction of the resource shifts to more prey-rich habitats indicated asymmetry in the relationship between the two predator species. Although the null hypothesis of no limitation of cats by foxes could not be rejected, as no increase in cat abundance was recorded after fox removal, interspecific competition was considered to be the most likely mechanism limiting feral cats at Burrendong. Intraguild predation was not indicated as no cat remains were found in any of the 343 fox scats or 255 fox stomachs that were examined. In addition, minimal evidence was found for facilitation between cats and foxes, or for food limitation.

The potential for foxes to limit cats, as shown in this study, indicates that cats need to be considered in future fox control operations. Integrated pest management, where foxes, cats and rabbits are controlled together, is strongly proposed if the objective is to safeguard native fauna in Australia. Further research is required to improve the effectiveness of current techniques for censusing cat populations, particularly in forested areas. This is essential for monitoring the effectiveness of control campaigns and quantifying factors that limit cat populations, and ultimately for effective protection of susceptible native fauna.

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CHAPTER 1

GENERAL INTRODUCTION

This thesis examines the ecology of the feral cat *Felis catus* in open forest in New South Wales and experimentally tests factors that may limit cat abundance. Feral cats have been implicated in the decline and extinction of numerous native mammal species in Australia (review in Dickman 1996). However, little is known about the ecology of feral cats, particularly factors that affect their abundance. Potential limiting factors for feral cat populations that will be investigated include the availability of food, and interactions (competition and intraguild predation) with red foxes *Vulpes vulpes*. Foxes are considered a significant pest to native fauna and to agriculture in Australia (Saunders *et al.* 1995) and populations have been targeted for broad-scale reduction using fertility control, which is being developed by the Vertebrate Biocontrol Cooperative Research Centre (VBCRC) (Tyndale-Biscoe 1994). However, there is concern that feral cat populations may increase compensatorily when foxes are removed. Possible mesopredator release (*sensu* *et al.* 1988) of cats following widespread fox removals may not alleviate predation pressure on native prey populations, and is an issue that needs to be addressed.

This first chapter reviews the history and biology of introduced species, particularly mammals, and examines factors that contribute to their success. Evidence is then presented for the impact of introduced mammalian carnivores on native species, and is followed by an examination of factors that can affect population dynamics. Evidence for interactions between mammalian predators is then examined, and in the final section I present the aims and scope of the thesis.

1.1. BIOLOGY OF INTRODUCED SPECIES

1.1.1. History of introductions

Organisms have been introduced to areas outside their native range by human agency for millennia (Pimm 1987). The most widespread accidental introduction has involved rodents, *Mus domesticus*, *Rattus rattus* and *R. norvegicus*, which are now established on all non-polar continents throughout the world (Jarman and Johnson 1977). In Australia, more than 60 vertebrate species were released after European settlement in just 20 years between 1860 and 1880 (Myers 1986). Many introductions were made privately in an attempt to turn Australia into another England (Myers

Acclimatization Societies actively introduced plants for agriculture, forestry, hedges, soil erosion control and as ornamentals (Myers 1986). Many species were also

(Michael 1972).

Although it is a commonly held belief that Australia has been particularly susceptible to species introductions (Amor and Piggin 1977), we have fewer exotic species than many other continents (Kitching 1986). For example, 8% of terrestrial mammal species are exotic compared to 92% in New Zealand and 22% in Great Britain.

in New Zealand and 14% in Great Britain (Kitching 1986). However, the magnitude of the problems associated with introduced species in Australia has received wide attention (e.g. Dickman 1996).

Do introduced species have an impact? Although introduced animals are implicated in 40% of historic extinctions of native taxa (Caughley and Gunn 1996), evidence for their impact is controversial (Elton 1958, Simberloff 1981, Herbold and Moyle 1986). Simberloff (1981) argued that introductions rarely have an impact, but many authors (e.g. Elton 1958, Herbold and Moyle 1986) refute this. While impacts of introduced animals have been often observed, they have been quantified rarely. Removal experiments, where the alien species is removed or excluded and the putatively impacted species then recovers, provide the most conclusive evidence for the impact of introduced species. However, such experiments have been carried out rarely (e.g. Kinnear *et al.* 1988) and the findings often contested (cf. Hone 1994, Kinnear *et al.* 1998).

Are introductions usually successful? Not all introductions are successful, and most introduced plant and animal species become established, and of those, 10% become pests (Williamson and Brown 1986, Williamson 1996). However, while most exotic species fail to establish, the cumulative effect of the few successful invaders on native flora and fauna may be large (Williamson 1996).

What determines the success of an introduction? The reasons why some species successfully establish and others do not, are not well understood (Newsome and Noble 1986). Some species with certain attributes become invaders, while others with the same attributes do not. Although invasive species as a group show certain attributes in common, no one species possesses all attributes and different species tend to have different combinations of attributes, which make them potentially invasive. Nevertheless, some generalisations can be made about the attributes common to most successful introduced species.

Three main phases must be completed successfully before an introduced species is established: introduction of the species, establishment of the population through reproduction, and dispersal (Arthington and Mitchell 1986). At each phase, three sets of factors interact to determine whether the invasion will be successful. These

(competitors, predators, parasites and pathogens).

Biological attributes common in invading species include flexible requirements for habitat and diet, high reproduction and survival rates, and high mobility. For example, successful invasions usually involve generalist species rather than specialists (e.g. Maran and Henttonen 1995). In Australia, introduced generalist species such as feral cats and foxes, have successfully established in a wide range of habitats, while the more specialised tropical mongoose and ferrets have died out (Myers 1986). Similarly, introduced mice and rats are widespread on the continent, while other rodents (e.g. two squirrel species) failed to establish because they were food specialists (Myers 1986). High reproductive rates also increase the chance of successful establishment (Williamson 1996). Where only a few individuals are introduced, the potential for reproduction, for finding a suitable habitat, or for resisting climatic extremes, is reduced (Swincer 1986, Di Castri 1990, Williamson 1996).

The ability to disperse is the final stage in the successful establishment of an introduced species, affecting the genetic structure of the population (Krebs 1994).

sample of a population, such that the new population may be genetically a subset of the source population. Founder effects may also limit the gene pool of the invading species such that they are not able to resist new parasites (Freeland 1983). But just as there are no set biological or eco-physiological attributes that characterise successful invaders (Newsome and Noble 1986, Roy 1990), there are also no genetic characteristics that are common to all invaders (Barrett and Richardson 1986).

Which communities are most vulnerable? Empirical observations show that some regions and ecosystems are more vulnerable to invasions than others (Di Castri 1990). For example, at a very large scale, ecosystems in the Northern Hemisphere are more resistant than those in the Southern Hemisphere (Di Castri 1990). Invasions are relatively unusual in the tropics compared to temperate areas, while oceanic islands are particularly vulnerable to invasions (Vitousek *et al.* 1997). Simberloff (1981) addressed some theoretical considerations of community response to invasions, particularly community models of island biogeography and limiting similarity, but found little support for either model in the literature. Other reviews show that invading species are often more successful in disturbed environments, through the

Anderson 1977, Kitching and Jones 1981, Fox and Fox 1986).

The disturbance hypothesis has been supported by a number of studies (Moore 1959, Fox and Fox 1986). Moore (1959) demonstrated that in the absence of grazing in Australia there were no introduced pasture species, but where grazing was present, three native grasses, previously dominant in the pasture, were lost and introduced species dominated. Similarly, prickly pear *Opuntia stricta* invades woodlands subjected to altered fire regimes, introduced grazing and clearing (Fox and Fox 1986). However, there is also evidence that animals are able to invade undisturbed communities (Fox and Fox 1986). These species are usually r-strategists or c-strategists, often with the additional advantage of freedom from pests and diseases (Arthington and Mitchell 1986). For example, the cane toad *Bufo marinus* is currently spreading through undisturbed and extensive areas of wetlands in northern Australia (Fox and Fox 1986). This conflicting evidence for the disturbance hypothesis may arise if seemingly undisturbed habitats are in fact disturbed, and the effects of the disturbance are subtle or difficult to detect (Fox and Fox 1986).

The species richness hypothesis (Fox and Fox 1986) predicts that rich communities are less susceptible to invasion because the high interconnectedness between many interacting species means that existing resources will be fully utilised. However, there is little experimental evidence to support this hypothesis, and numerous contradictory observations (e.g. Macdonald *et al.* 1986, Williamson 1996). Many species have invaded rich ecosystems, for example *Hakea* species from Australia and *Pinus* species from the Northern Hemisphere have readily invaded speciose plant communities in South Africa (Macdonald *et al.* 1986). Further, impoverished marshes or mountaintops, and this confounds the species richness hypothesis also (Williamson 1996). Similarly, the seemingly greater vulnerability to invasion of islands (Newsome and Noble 1986) that have generally simple community structures may be a statistical artifact (Williamson 1986). Fewer indigenous species are usually present and islands have been subject to greater proportional change to the landscape and a greater enthusiasm for deliberate introductions in the past. Nevertheless, impacts of introduced species have often been more pronounced on islands as the indigenous fauna often lack antipredator behaviour or the genetic diversity to resist introduced parasites and diseases (e.g. Diamond and Veitch 1981, Savidge 1984).

1.1.2. Impact of introduced mammalian predators

Throughout the world, introduced mammalian predators have caused, or still are causing, declines and extinctions of endemic fauna, particularly on Pacific Islands, New Zealand and in Australia (King 1980, Diamond and Veitch 1981, Karl and Best 1982, King 1984, Griffin *et al.* 1988). Most impacts have tended to be wrought by predation, which causes rapid population declines, rather than competition, parasite or disease transfer. Predation by introduced mammalian predators accounts for half of all known island bird extinctions (Diamond 1984). On the island of Guam, introduced mammals (feral dogs, cats and rats), reptiles (brown tree snake *Boiga* *irregularis*) and disease are implicated in the decline of entire forest avifauna toward extinction (Savidge 1984). On islands in the tropical Pacific, mongoose *Herpestes* spp. have been implicated in the collapse of native vertebrate faunas (Fagerstone *et al.* 1995). On the Galapagos archipelago, the dark-rumped petrel *Pterodroma phaeopygia* is threatened by introduced rats, cats, dogs *Canis familiaris* and pigs *Sus scrofa* which prey on eggs, nestlings and adults (Cruz and Cruz 1987). On Lord Howe Island, the endemic woodhen *Tricholimnas sylvestris* declined to very low numbers as a result of predation on chicks and eggs by the feral pig (Fullagar 1985).

In New Zealand, introduced mammalian predators were partly responsible for massive losses in the endemic avifauna (King 1984). In Australia, feral cats have been implicated in the decline and extinction of numerous native fauna species (Dickman 1993, 1996); evidence for these impacts is discussed in Chapter 2. Red foxes have been shown experimentally to affect the survival of remnant populations of black-footed rock wallabies *Petrogale lateralis* (Kinnear *et al.* 1988, 1998), malleefowl *Leipoa ocellata* (Priddel 1991), numbats *Myrmecobius fasciatus* (Friend 1990) and chuditch *Dasyurus geoffroii* (Morris 1992).

Elsewhere, red foxes have also had negative impacts (Ralls and White 1995). In California, the red fox is indigenous only to the Sierra Nevada and has greatly expanded its range since the 1890s (Lewis *et al.* 1993). Populations of some prey species are now thought to be threatened, including the California least tern *Sterna antillarum browni*, the salt marsh harvest mouse *Reithrodontomys raviventris* and the San Joaquin kit fox *Vulpes macrotis mutica* (Ralls and White 1995, Reynolds and Tapper 1996). In the British Isles, range expansion by red foxes has also threatened bird populations (Musgrave 1993). In boreal and arctic regions, arctic foxes *Alopex lagopus* were introduced to many of the Aleutian Islands in the north Pacific by Russian fur-traders during the early nineteenth century, resulting in the decimation of seabird populations (Bailey 1993). Recent attempts to eradicate the arctic fox have involved introducing sterile red foxes as biological control agents (Bailey 1992).

Conventional wisdom argues that exotic predators have stronger effects than their

birds, in particular, are thought to be more vulnerable to predation by exotic predators, compared to native predators, because they have evolved in the absence of significant predation (MacArthur 1972) and therefore lack effective antipredator adaptations. Although this hypothesis has found wide support in New Zealand and Hawaii (Atkinson 1977, 1985, King 1985), recent studies have shown no differences between endemic and introduced birds in New Zealand in vulnerability to predation by introduced mammalian predators (mustelids, rodents and feral cats) (Moors 1983). Similarly, on western Mauna Kea in Hawaii, no evidence was found that introduced mammals (feral cats, mongooses and house mice) preyed on endemic birds (Amarasekare 1994).

1.2. FACTORS LIMITING MAMMAL POPULATIONS

It has long been recognised that populations do not go on increasing without limit, but it was not until the twentieth century that attempts were made to formally analyse the factors that regulate populations (Krebs 1994). In the 1950s and 1960s controversy about regulation, and the mechanisms that bring it about, erupted (e.g. Andrewartha and Birch 1954, Lack 1954, Chitty 1955). Today debate still surrounds this topic and few examples of regulatory processes have been demonstrated unambiguously.

there is confusion and disagreement over their precise definitions (Sinclair 1989, 1991, Sinclair and Pech 1996). In this thesis, limiting factors are taken to be those that have a negative impact on population growth, while regulatory factors involve the negative impact increasing with population density. A population is therefore regulated when it undergoes density-dependent mortality (or reductions in natality) which tend to return it to an equilibrium value (Sinclair 1989, 1991). The

constant. While the operation of limitation and regulation in populations has received much theoretical support, most field studies have demonstrated only limitation, and evidence for regulation in nature is rare.

Two paradigms of population regulation. Two paradigms of population regulation were

(1911) and developed further by Nicholson (1933, 1954, and 1958) and Lack (1954). This paradigm assumes density-dependence, such that birth, death and movement

not assume density-dependence. It searches for relationships between birth, death and movement rates, and the mechanisms controlling populations, such as disease, predation, food shortage and territoriality (Krebs 1995). This paradigm arose from the work of Bodenheimer and Uvarov in the 1920s (Krebs 1995) and was developed further by Andrewartha and Birch (1954) and Chitty (1955).

The density-dependent paradigm for population regulation is widely supported today, particularly by such proponents as Hassell (1986) and Sinclair (1989). Density-dependence occurs when the per capita growth rate of a population (including mortality and reproduction) depends on its own density (Sinclair and Pech 1996). Causes of density-dependence include intra- and interspecific competition, and

mortality, which then theoretically returns it to an equilibrium value (Sinclair 1989, 1991). In contrast, the mechanistic paradigm relates birth and death rates directly to the complexity of factors that interact to set birth and death rates in natural populations (Krebs 1995).

Although examples exist in mammalian studies where rates of birth or death are clearly related to density, which supports the density-dependence paradigm (see reviews in Sinclair 1989, Wolda 1989), there are also many instances where no such relationship exists (Krebs 1994). In these situations, other factors such as measurement error or delayed-density-dependence are often proposed (Trostel *et al.* 1987). Krebs (1995) argued that the very act of explaining everything within a dichotomous paradigm is hindering progress in the science of population regulation. A density-independent relationship can explain any scatter of points and therefore results can always be explained within the density-independence paradigm. While Krebs (1994) did not question the validity of density-dependence, he believed that

the mechanisms of population regulation, i.e. the mechanistic paradigm, would be a more fruitful approach.

Population densities can be influenced by a number of factors that can be broadly described as weather, resources (food and shelter), and enemies (predators, parasites, disease, and competitors), which can often interact (Krebs 1994, 1995, Holmes 1995). The relative importance of these factors is still the subject of much debate (e.g. Tamarin 1983, Power 1992, Strong 1992). Understanding the mechanisms that regulate or limit populations is of paramount importance, particularly when species are to be conserved or introduced pests controlled.

1.2.1. Resource availability

All animal populations are limited to some extent by the availability of resources. Resources are needed for survival and reproduction, and can include food, shelter, water, nesting sites and space to set up territories. Resource availability can be defined as the direct accessibility of resources to consumers, and is usually a subset of resource abundance (Wiens 1984). Resource availability is difficult to measure and the relationship with true resource abundance is usually unknown (Wiens 1984). Resource limitation may arise when the availability of a resource is less than, or equal to, the demand of the consumer population (Wiens 1984). This can result in intraspecific competition where individuals of the same species utilise common resources that are in short supply (Birch 1957).

Food is the resource that is predicted usually to influence the abundance of predators (Hairston *et al.* 1960), although regulation of population size by food scarcity has been difficult to demonstrate (Moran 1995). If intraspecific competition for food occurs, its intensity must be density-dependent and hence regulatory rather than limiting. Lack (1954) reviewed studies of North American ungulates and concluded that food shortages play a role in both population cycles and irruptions through density-dependence. However, much of his evidence was confounded with other factors. For example, although population declines were recorded after food shortages, predation pressure had also altered. Andrewartha and Birch (1954) also proposed that food was a major limiting factor for populations, but rejected the distinction between density-dependent and density-independent factors. They argued that all factors were related to population density to some degree, even weather. Evidence for food as a regulatory factor has come from studies that have shown numerical responses of predators to fluctuating prey populations (Pech *et al.* 1992, White and Garrott 1997).

Evidence for food limitation, however, has been obtained in food removal and addition experiments (e.g. Brown and Davidson 1977, Brown *et al.* 1979, Taitt and Krebs 1981, Galindo 1986, Krebs *et al.* 1986). For example, densities of snowshoe hares and voles increased after the provision of extra food (Taitt and Krebs 1981, Krebs *et al.* 1986), and elk densities were maintained at a higher level as the result of supplementary feeding (Boyce 1989).

1.2.2. Competition

Definitions. Competition occurs when a number of animals (or other organisms) utilise a resource that is in short supply (Birch 1957). It can also occur, however, when resources are not in short supply and the individuals seeking the resource harm each other in the process. It can occur within species (intraspecific) or between species (interspecific), however, only the latter will be examined in this section.

Interspecific competition occurs when individuals of different species suffer a reduction in fecundity, survivorship or growth as a result of mutual resource exploitation or interference (Birch 1957, Begon *et al.* 1996). Although it implies harm to both species involved in the interaction, effects are often asymmetrical with one species being the weaker competitor (Lawton and Hassell 1981, Connell 1983, Schoener 1983, Dickman 1986a, Brown *et al.* 1986).

Is interspecific competition important? The importance of interspecific competition in influencing community structure has been the subject of many debates (e.g. Keddy 1989, Cooper 1993). Some authors regard competition as of utmost importance (e.g. Hutchinson 1959, Diamond 1978, Bengtsson 1989), while others suggest that it has little effect on population size or community structure (e.g. Andrewartha and Birch 1954, Wiens 1977). One of the main reasons for this controversy is the difficulty in proving that competition has occurred in field situations. Unlike in laboratory experiments, it is often difficult in nature to isolate the mechanism responsible for the regulation of populations, as it is usually a combination of different factors, such as intraspecific competition, predation, disease and environmental variability. Even where the importance of interspecific competition has been demonstrated in nature, conclusions have often been questioned on the grounds that the results were statistically indistinguishable from chance events (Schoener 1982, 1983). Field studies have also been criticised for describing aspects of the competitive process only and not indicating the causes of stable coexistence or showing conclusively that competition was responsible for the disappearance of a species (Arthur 1987).

The Competitive Exclusion Principle. The importance of competition in shaping communities was first described by theorists such as Lotka (1932), Volterra (1926) and Gause (1934). This early work led to the development of the Competitive Exclusion Principle, which states that two competing species can coexist only if there is some degree of resource separation, otherwise one species will exclude the other (Gause 1934). In this way, two different species cannot occur in identical niches. Niche is defined here as a species role in the community and includes its relationship to food and enemies (Elton 1927, Hutchinson 1958).

Numerous laboratory experiments have provided support for the principle under stable conditions with species such as *Paramecium* spp. (Gause 1934, 1935) and *Drosophila* spp. (Jones and Probert 1980, Barker 1983, Arthur and Middlecote 1984). However, relatively little conclusive evidence for competitive exclusion has been found in nature (Schoener 1983, Connell 1983). Connell (1961) demonstrated that one species of barnacle actively excluded another species in the intertidal zone in Scotland. Inouye (1978) demonstrated competitive exclusion among two species of bumble bees in Colorado. Diamond (1975) described competitive exclusion among three species of ground doves that occupied different habitats on the mainland of New Guinea compared to offshore islands where not all species were present. But the relative lack of evidence for competitive exclusion in nature (Schoener 1983, Connell 1983), coupled with the frequent observations of closely related species coexisting in seemingly identical niches (e.g. Fryer 1959, Schroder and Rosenzweig 1975), has led to the principle being heavily criticised, particularly by field ecologists (Vadas 1990, Sinclair 1991, Caughley and Sinclair 1994).

To explain this ecological paradox of frequent extinctions in closely related species in laboratory experiments but the coexistence of many similar species in nature, two main views have developed (Krebs 1994). Competition is rare in nature, thereby accounting for the lack of evidence for competitive exclusion. Alternatively, competition has occurred frequently throughout the evolutionary history of communities; the lack of current evidence for competition is then due to adaptations

Reviews of the literature by Connell (1983) and Schoener (1983), although obtaining different results, show that interspecific competition is not rare in nature. Schoener reviewed 164 studies and found that 76% of species were in competition, while Connell found that 55% of species in 72 studies competed. The reviews also indicated that interspecific competition was less common in terrestrial than marine or freshwater systems, perhaps due to the heterogeneity of food resources in terrestrial environments (Krebs 1994). Similarly, interspecific competition was considered less common in invertebrates, which may be more vulnerable to climatic changes or predation losses (Schoener 1974), compared to plants or vertebrates. These reviews were biased at the outset because competition is usually studied only when it is expected to occur, and if an experiment fails to find competition the researchers may not bother to write it up, or it may not be accepted for publication (Keddy 1989). However, both reviews reached the same conclusion that competition is not rare in nature.

The Competitive Exclusion Principle has also been criticised because it cannot be disproved: both coexistence and exclusion are consistent with the principle, and it therefore cannot be tested (Sinclair 1991). To test the principle, two niches need to be shown to be identical, which is not possible as it can always be said that some other factor that makes the niches different has been overlooked. Nevertheless, the Competitive Exclusion Principle provides a theoretical explanation for at least part of the phenomenon of ecological replacement, and underlies studies of resource partitioning among groups of coexisting species (MacArthur 1970, Schoener 1974).

Resource partitioning. The Competitive Exclusion Principle predicts that coexisting species must differ in their ecological requirements by some degree (Rosenzweig 1966). Coexisting granivorous ants partition seed resources on the basis of size, density and micro-distribution of the seeds (Davidson 1977). Similarly, three sympatric species of hermit crabs preferred different-sized gastropod shells for habitation and different habitat types (Vance 1978). MacArthur (1958) described the habitat partitioning of five species of warblers within conifer trees; they were able to coexist because their feeding positions varied in both heights in the tree and in use of inner and outer branches. However, to use the occurrence of resource partitioning as evidence for competitive exclusion is illogical. By definition two species must be genetically different and consequently differ physiologically, structurally or ecologically. More important to consider is the degree to which niches can overlap and still allow coexistence. Niche overlap is the joint use of a resource, or resources, by two or more species (Colwell and Futuyma 1971).

Niche overlap. The idea that there must be an upper limit to the degree of niche

May 1973, 1974). MacArthur and Levins (1967) predicted values of limiting similarity based on theoretical arguments about the distance between the midpoints of species distributions, but this approach has proved to be unrealistic (May and MacArthur 1972, May 1973, 1978, Turelli 1981, Chesson 1986). May and MacArthur (1972) theorised that the maximal permissible overlap should be relatively insensitive to both the number of species and environmental variability. Pianka *et al.* (1979) examined how much niches would overlap among desert lizards if resources were allocated randomly among species, and concluded that a higher frequency of species with small niche overlaps was found than would be predicted by chance. Similarly, some empirical studies have showed that assemblages of ecologically similar, coexisting species differ from each other more than would be expected by chance (Schoener 1970, 1984, Brown 1973, Brown and Bowers 1985, but see Simberloff 1984) which implies that interspecific competition can cause niche segregation.

The niche-complementarity hypothesis predicts that for coexistence to occur, high overlap in one dimension will be compensated by low overlap in another. Fuentes and Jaksic (1979) found support for this phenomenon among two fox species in

South America, *Pseudalopex culpaeus* and *P. griseus*. Where these two species had low habitat overlap, dietary overlap was high, but where habitat overlap was high, dietary overlap was low. More detailed studies of the two fox species provided further support for the niche-complementarity hypothesis, but on a finer scale (Jimenez *et al.* 1996). The larger *P. culpaeus* was shown to exclude the smaller *P. griseus* from high quality habitat patches through interference. It was found that where they are sympatric they have complete overlap in activity time, intermediate overlap in diet, but little overlap in habitat use.

Niche overlap values have often been proposed as measures of current competition and as indicators of past competition (Levins 1968, Schoener 1974). However, the existence of niche overlap between two species is not sufficient to demonstrate competition. Niche overlap may indicate a lack of competition if the considered resource is in oversupply or irrelevant to one or both species (Colwell and Futuyma 1971, Vandermeer 1972, Rathcke 1976). Alternatively, a lack of niche overlap may indicate avoidance of competition or different but independently evolved resource preferences.

The idea that niche overlap can be positively or negatively correlated with competition led Pianka (1974) to develop the *niche overlap hypothesis.* This hypothesis predicts that maximal tolerable niche overlap should be lower in intensely competitive situations, and is supported by both experiments and field studies (Schoener 1974, Diamond 1978, Sinclair *et al.* 1982, Caughley and Sinclair 1994). This hypothesis is also supported by one theory of *habitat selection* (Rosenzweig 1981), which predicts that species should contract their habitat niches when resources are limiting due to competition. For example, Pimm and Pimm (1982) showed that Hawaiian honeycreepers conformed to these predictions with habitat niche width contracting in response to declining resources. However, several other studies have shown that niche dynamics may be more complicated than originally thought (Schoener 1982, 1989, Hansson 1995), and traditional niche theory has been challenged increasingly in recent years (Freeland 1983, Arthur 1987, Vadas 1990, Hansson 1995).

Some studies have shown that niche overlap can also increase when resources are limiting (Schoener 1982, Litvaitis and Harrison 1989). Such observations support o*ptimal foraging theory,* which predicts that when resources are not limiting, species should concentrate their feeding on the best types of food or habitat and ignore poorer resources regardless of abundance (Stephens and Krebs 1986). Then when resources become limiting co-occurring species should expand their niches to use a wider range of resources and increase their overlap. In support of this, Leslie *et al.* (1984) showed that dietary overlap increased between elk and deer in winter when resources were less abundant. However, using simulation models Hansson (1995) showed that decreases and increases in overlap were equally common and varied with competition intensity. Freeland (1983) also challenged traditional niche theory, and argued that the maintenance of low levels of shared parasites is the most important factor in allowing the coexistence of similar species.

Niche overlap, therefore, is clearly not sufficient to demonstrate competition. A change in resource use after the removal of one of the potential competitors must also be shown and the mechanism underlying the individual interaction understood.

*Mechanisms of interspecific competition***.** Traditionally, two mechanisms have been described in competition theory, exploitation and interference (Begon *et al.* 1996). To avoid exploitation competition, where competing organisms utilise the same limited resource, a species will often show a change in diet (MacArthur 1972, Arthur 1987, Krebs 1989). It is mediated indirectly because the species interact through a resource or third species, and not directly. In contrast, interference competition occurs when two species cause direct physical harm to each other, for example, through toxins or aggressive encounters, and is often avoided through differential habitat use (Krebs 1978, Rosenzweig 1981, Arthur 1987, Pimm *et al.* 1995).

(1983) review, some authors argue that interference is the most widespread form of competition in nature (Case and Gilpin 1974). However, many studies are unable to distinguish between direct interference and indirect exploitation, as the mechanism of competition is often not investigated (Tilman 1987). For example, space can be used to deprive another species through exploitation but may also involve interference behaviour. Similarly, shifts in diet may be a secondary consequence of habitat change.

Other types of competition include diffuse, indirect and apparent competition. *Diffuse competition* describes the combined effects of many species upon a given species (MacArthur 1972). These effects are often difficult to measure, as any single pair of species may have very weak interactions. Diffuse competition, however, was demonstrated experimentally among harvester ants over a five year period in the Chihuahuan Desert (Davidson 1985). Despite dietary overlap between a large species and a small species of ant, the large species facilitated the small species indirectly, by suppressing populations of an intermediate-sized species.

Competition can also have indirect effects (Abrams 1987), even when resources are not limiting; these are often considered to be artifacts and can be overlooked. For example, the niches of two species may not overlap and they may not compete, but affect each other through interactions with other competing species i.e. *indirect competition* (Caughley and Sinclair 1994). Further, the two species could be alternate prey for a food-limited predator i.e. *apparent competition* (Holt 1977, 1984). Shared predation, where a generalist predator attacks two or more prey species, can easily imitate the effects of exploitation competition, such as indirect exclusion of one prey species by another. For example, rabbits have been implicated in the decline of native herbivores in Australia through either direct competition for food or by apparent competition in supporting fox populations (King *et al.* 1981).

Demonstrating interspecific competition. Of the numerous studies that have examined similar coexisting species, few have actually demonstrated that the species do compete. Much of the evidence that has been advanced merely shows large overlaps in resource use. Some studies have observed changes in the abundance of one species after the perturbation of a potentially competing species, however, this is also not enough to demonstrate the mechanism of competition. The removal of one species may allow the other species to increase if direct predation is involved (Hairston 1985). Additional information on resource use is necessary.

The strongest evidence for the existence of competition has come from field experiments that have manipulated the densities of one or more competing species and observed changes in population size, fecundity, growth or resource use of the remaining competitor. Experiments of this nature have been conducted on desert plants (Fonteyn and Mahall 1981), intertidal gastropods (Underwood 1978) salamanders (Jaeger 1971, Hairston 1986), rodents (Heske *et al.* 1994, Valone and Brown 1995), dasyurids (Dickman 1986a) and between rodents and ants (Brown *et al.* 1979). Knowledge of the mechanisms underlying a competitive interaction is important in predicting individual behaviour and resource use, and in understanding community processes (Tilman 1987).

1.2.3. Predation

Definition. Predation can be defined as the eating of all, or parts of, other live individuals and does not include the scavenging of dead material (Caughley and Sinclair 1994). It usually, but not always, involves killing the prey (Krebs 1994). In contrast to competition, predation usually involves interactions between individuals in different trophic levels, with the negative effects experienced by only one species, the prey (Caughley and Sinclair 1994). Of the four main types of predation (herbivory, parasitism, carnivory and cannibalism) (Caughley and Sinclair 1994), only carnivory, will be addressed here.

Is predation important? Mammalian predators were once thought to merely remove already-doomed individuals, such as those that were sick or weak, with little impact on prey distribution or abundance (Errington 1946, 1951). Research since that time has shown that predators can have complex effects on prey populations (see reviews in Sih *et al.* 1985, Lima and Dill 1990), and considerable field evidence has demonstrated that predation can depress rates of increase in natural populations (e.g. Bergerud 1971, Potts 1980, Sievert and Keith 1985). However, the importance of predation, relative to competition, in influencing prey populations and communities is controversial (Sih *et al.* 1985). Some studies have shown it to be of utmost importance (Paine 1971, Caswell 1978, Zaret 1980), while others indicate that it is less important than competition (Cody 1974, May 1974, Schoener 1974). Sih *et al.* (1985) reviewed the literature on predation experiments in a similar way to Connell (1983) and Schoener (1983), and concluded that both predation and interspecific competition are about equally important. Literature reviews, however, are not the best way to determine the relative importance of different factors in influencing population dynamics or community structure.

The ideal way to test the hypothesis that predators can regulate or limit prey populations is to remove predators from a system and measure the prey response. Such experiments have shown conflicting results, with limitation indicated in some situations (Caughley *et al.* 1980) but not in others (Bertram 1978, Boutin 1992). In

provided evidence that dingoes *Canis lupus dingo* suppressed both kangaroo and emu numbers (Caughley *et al.* 1980). Other studies have also shown that dingoes and foxes can suppress the growth of prey populations (e.g. rodents, rabbits, kangaroos, wallabies and pigs) (Newsome and Corbett 1975, Newsome *et al.* 1983a, Corbett and Newsome 1987, Newsome *et al.* 1989, Pech *et al.* 1992, Banks *et al.* 1998). In California, regulation by carnivores was implicated in the population cycling of meadow mice *Microtus californicus* (Pearson 1966, 1971).

In contrast, field studies have also shown that predation is not the most important factor influencing prey population dynamics (Bertram 1978, Boutin 1992). Wolves were removed in parts of North America to release predation pressure on moose in five studies, but significant increases in moose numbers were detected only in one study (Boutin 1992). Similarly, in the Serengeti Plains of eastern Africa, larger ungulates appear to be regulated by intraspecific competition for food rather than predation (see review in Sinclair 1995). These studies supported the doomed surplus hypothesis, with most prey taken being old, injured or sick. Kruuk (1972) showed that the taking of sick or injured prey was related to the ease in catching them. Hyenas in Africa take wildebeest that are in poor condition because they are otherwise difficult to catch, but take gazelles at random because they are easy to catch in good condition or poor (Kruuk 1972).

It is clear then that predation is important in influencing population dynamics in some instances but not in others. Understanding the characteristics that increase predator effectiveness is important in wildlife management and agricultural pest control. Description of the functional and numerical responses, and consequently the total response, in predator-prey interactions is essential in this process (but see Sinclair 1989).

Functional response. This describes the relationship between the prey population size and the number of prey killed per unit time by an individual predator (Abrams 1982). Three types of functional response were identified originally by Holling (1959), where the relationship between prey consumption (Y-axis) and prey density (X-axis) is described. A type I functional response shows a linear relationship, with the number of prey consumed increasing directly with prey density; this response is often indicative of filter feeders. A type II functional response shows an initial linear relationship that then levels off and has been described primarily for invertebrate predators. A type III response has a sigmoidal shaped curve as, at low prey densities, predators switch to alternative prey; this is more typical for vertebrate generalist predators.

The asymptotic curves of type II and III responses at high prey densities occur primarily because predators become satiated or cannot get access to further prey due to interference behaviour or territoriality. A type II functional response predicts that at low prey densities predators have an inversely density-dependent effect at all prey densities, but the effects are more complex when a Type III response is involved. In this situation, there is a density-dependent response by predators, while at higher prey densities the response is inversely density-dependent.

Although Holling (1959) suggested that these different functional response curves were characteristic of different types of organisms, recent studies have shown that vertebrate predators can have type II functional responses (Messier 1995), and invertebrate predators can exhibit a type III response (Hassell 1978). In addition, Abrams (1982) showed that the traditional three types of functional response were not sufficient to describe the wide range of responses exhibited by animals in the wild. Boutin (1995) also argued that few studies of predation have actually demonstrated a functional response. In most cases, the data are open to alternative explanations, and data at low and high prey densities are often lacking. Functional response curves, although useful in describing predator-prey relationships, may also not be realistic when multiple species are involved.

Numerical response. Predators can regulate prey at an individual level (i.e. functional response) and at a population level through a numerical increase as a response to an

predator density may or may not be density-dependent. At high prey densities, the numerical response predicts that more predators will survive and reproduce or immigrate, and consequently eat more prey. Because the density of predators will eventually level off, due to interference behaviour, the numerical response can have a destabilising effect at high prey densities by either causing extinctions or eruptions in prey populations (Caughley and Sinclair 1994).

Total response. To determine whether a predator can regulate a prey population, the

(Pech *et al.* 1992). The total response is the product of the functional and numerical responses, and describes the predation rate of a predator (Solomon 1949). Although each predator has a characteristic functional and numerical response, a direct relationship between the functional and numerical response need not exist (Krebs 1989). For example, where predator numbers are limited by prey abundance, the numerical response of predators will be tied closely to the functional response. Conversely, where predator abundance is determined by other factors, a functional response may arise without a numerical response.

Total response curves predict that where there is density-dependence, two stable states will occur. Firstly, predators can regulate prey over the entire range of prey densities. Alternatively, predators may not regulate prey but have a depensatory effect on prey populations that are regulated by intraspecific competition for food (Caughley and Sinclair 1994). Recent studies have shown that both stable states may operate in the same area, producing multiple stable states (Pech *et al.* 1992). Total responses of feral cats and foxes to changing rabbit densities were demonstrated experimentally in semi-arid New South Wales (Newsome *et al.* 1989, Pech *et al.* 1992). Foxes and cats were removed through persistent shooting from two areas and, as predicted from total response curves, the density of rabbits increased in both areas and remained low where predators were left untreated (Newsome *et al.* 1989). Rabbits were prevented from increasing naturally by predation and were held in a back into the treated areas, rabbit numbers failed to decline. Predators thus exerted a regulatory effect over only a limited range of prey densities. At low densities, foxes and cats switched to alternative prey, while at high densities, predation was inconsequential. Knowledge of the range of prey densities over which a predator can exert a regulatory role is important, particularly when prey populations are to be safeguarded.

Antipredator behaviour. In addition to directly killing prey (Sinclair and Pech 1996), predators can also have sublethal, indirect effects, by affecting prey behaviour,

Gresser 1996). Antipredator behaviour and animal decision-making under the risk of predation have recently been studied extensively and may play a role in population regulation (Lima and Dill 1990). For example, odours of mammalian predators can elicit behavioural changes in prey species that alter local distribution, diurnal activity, mobility and intraspecific aggressiveness, and even suppress reproduction

Few studies, however, have dealt with environments with multiple predators, preferring to describe antipredator behaviour toward a single predator (Lima 1992). The combination of different predators may, however, have a synergistic effect on decision-making in prey (Lima 1992). Prey often are unable to avoid two predators that appear simultaneously, as behavioural adaptations to avoid one predator may not be effective in avoiding a second predator; this is *predator facilitation* (Charnov *et al.* 1976, Kotler *et al.* 1992). For example, in captivity two species of gerbil avoided open microhabitats when exposed to owls and closed microhabitats when exposed to snakes, but when exposed to both predators, gerbils foraged in the open (Kotler *et al.* 1992). The gerbils received conflicting signals and were not able to simultaneously forage effectively and remain safe.

Although the effects of increased predation risk on habitat use and foraging behaviour have been demonstrated in small mammals, with resulting shifts in habitat and diet, the sublethal effects of predators have rarely been shown to have population level consequences (Hik 1995). Recently, however, the hypothesis that a trade-off occurs between the avoidance of predators and gaining sufficient food (which may lead to a decline in condition and fecundity), was tested in a controlled field experiment in the Yukon in Canada (Hik 1995). In this experiment, predator numbers (lynx and coyote) and the food supply of their prey (snowshoe hares) were manipulated (Hik 1995). Predation was shown to be important in limiting the densities of snowshoe hares, but other sublethal behavioural and physiological effects associated with increased predation risk may have also played a role (Krebs *et al.* 1995). Hik (1995) argued that hares are able to assess predation risks in different habitats and, during population declines, they restrict their activity to dense cover in order to minimise their probability of getting killed; i.e (PSF). This results in a trade-off between reproduction (which requires good quality food that is unavailable in dense cover) and survival. The PSF hypothesis therefore predicts that animals take greater risks to obtain more food when food is limiting, and consequently increase their chance of getting killed. This has gained further support from studies of wildebeest in the Serengeti (Sinclair and Arcese 1995).

Intraguild predation. Intraguild predation (IGP) is the killing and eating of individuals of other species in the same guild that are potential competitors (Polis and McCormick 1987). A guild includes all taxa in a community that use similar resources (food or space) and thus may compete, regardless of differences in tactics of resource acquisition (Polis *et al.* 1989). IGP may involve both species eating each other or just one species preying on the other (Rosenheim *et al.* 1995). IGP is therefore a combination, potentially of both competition and predation, but differs from classical predation as IGP occurs among species that are potential competitors. It also differs from classical competition as species A receives an immediate energetic gain from the consumption of species B, and need suffer minimal or zero detrimental effect. Although IGP and some types of interference competition appear to produce similar patterns (Oksanen *et al.* 1979), interference mechanisms usually result in a pattern of contiguous distribution with little spatial overlap.

IGP is proving increasingly to be important in shaping predator communities, but until recently has received little attention (Frafjord *et al.* Norrdahl 1989, review in Polis *et al.* 1989, Doncaster 1992, Mattson *et al.* 1992, Rosenheim *et al.* 1995). It is particularly prevalent among generalist predators and may also be important in regulating the abundance of certain species (Polis *et al.* 1989). However, although numerous studies have demonstrated intraguild predation (e.g. Storch *et al.* 1990), its relative importance in influencing population dynamics is speculative (Litvaitis 1992, Lindstrom *et al.* 1995) and little experimental confirmation of its effects has been found (Doncaster 1992).

1.2.4. Disease and parasites

The importance of parasites and disease in influencing the distribution and abundance of species at the population level (compared to the individual level) has only relatively recently been identified (reviews in Anderson and May 1978, 1979). Parasites, for example, can accentuate the decline of endangered species (Warner 1968). Recent experimental and theoretical studies have also shown that parasites play an important role in apparent competition (review in Hudson and Greenman 1998). One competing species may remain superior simply by harbouring and transmitting a pathogen to a more vulnerable species. For example, grey squirrels *Sciurus carolinensis* introduced to Britain carried a parapox virus that may have reduced the competitive ability of endemic red quirrels *S. vulgaris* (Hudson and Greenman 1998). Similarly, the effects of rabies, imported by domestic dogs, have reduced the competitive ability of some endangered canids, such as Ethiopian wolves *Canis simensis* and wild dogs *Lycaon pictus* (Macdonald 1993, Pain 1997).

Apparent competition has also been demonstrated when an invading pathogen reverses the outcome of exploitation competition. When mixed cultures of two flour beetle species were bred in the absence of a sporozoan parasite, one species dominated (Park 1948, Anderson and May 1986). However, when the parasite was present, the reverse occurred. This parasite reduced the competitive ability of the dominant species, which allowed the inferior competitor to persist. Similarly, meningeal worms *Parelaphostrongylus tenuis* mediated competition between moose *Alces alces* and white-tailed deer *Odocoileus virginianus* by influencing fluctuations in moose populations (Price *et al.* 1988). However, until recently, few studies of shared pathogens have distinguished between apparent competition and exploitation competition (Bonsall and Hassell 1997).

Freeland (1983) argued that parasitism can allow the coexistence of similar species and that it may be more important than competition in driving niche separation. Sympatric species that have similar body sizes and morphologies may be able to coexist because they have different parasite susceptibilities resulting from differences in diet and phylogeny. For example, differentiation of parasitic faunas has been recorded in sympatric rodents in England (Sharpe 1964) and sympatric wolves and coyotes in Alberta, Canada (Holmes and Podesta 1968).

Although the ability of macro-parasites to regulate population densities has been demonstrated experimentally for some mammal species under laboratory conditions (Keymer 1985, Singleton and Spratt 1986, Scott 1987), there is little evidence of similar effects from field manipulations of parasite loads (Singleton *et al.* 1995). For example, in one of the first replicated field experiments to examine parasite-host interactions, the parasitic nematode *Capillaria hepatica* failed to limit populations of house mice in southeastern Queensland (Singleton *et al.* 1995).

1.2.5. Facilitation

Facilitative interactions, where at least one species benefits from an association without harming the other species, occur frequently in nature between terrestrial vertebrates but are often overlooked (Dickman 1992a). Facilitation may be commensal (+, 0) where only one species benefits, or mutualistic (+, +) where both species benefit. In addition, the relationship may be facultative, where the species benefiting is not dependent on the other species for survival, or obligatory e.g. fungi and algae that comprise lichen, where one or both of the benefiting species are dependent (Caughley and Sinclair 1994). Obligatory associations, for example, between fungi and algae, are more common in plants and invertebrates, while associations between terrestrial vertebrates are generally not permanent and may last only a few minutes. Resource overlap is generally low compared to single species associations, which presumably reduces competition (Dickman 1992a).

Benefits of mixed-species associations are diverse compared to conspecific associations and include reduced parasite loads, reduced predation risk, and increased access to food and other resources (review in Dickman 1992a). For example, food availability is enhanced through the flushing of prey by some groups of insectivorous birds (Perrins and Birkenhead 1983) and some bird species use other species to locate food (Knight and Knight 1983). Further, smaller bird species have been shown to rely on larger species to open up tough integuments of carcasses (Hewson 1981, Wallace and Temple 1987, Skagen *et al.* 1991).

Mixed species associations may result also in the creation of new habitat for smaller species. In Tanzania, elephants trample the high vegetation around lakes which provides habitat for smaller herbivores, such as buffalo, which thereby increases the number of species that can live in that habitat (Vesey-Fitzgerald 1960). Similarly, on the Isle of Rhum in Scotland, deer preferentially graze areas that have been used by cattle (Gordon 1988). The greater biomass of green grass in cattle-grazed areas increases the reproductive rate of deer.

Shelters and nest sites constructed by one species are also used frequently by other species. Rats *R. rattus* and *R. norvegicus* and house mice have benefited by human structures and occur at highest densities in urban and agricultural areas throughout the world. Similarly, foxes frequently use rabbit burrows as dens (Saunders *et al.* 1995). Species that produce resources or structures that are used subsequently by
et al. 1994, 1997).

Facilitation has often been found to be the major mechanism in communities that were previously thought to be dominated by interspecific competition (Dickman 1992a). Although coyotes have been shown to avoid wolves in some areas in North America (Fuller and Keith 1981, Carbyn 1982), they appeared to have a facilitative relationship in Manitoba in Canada (Paquet 1991). On 36 occasions, coyotes were observed following wolves directly to wolf-killed ungulates. All wolf kills examined (n = 198) were scavenged by coyotes within 24 hours of abandonment by wolves.

Although evidence for facilitation has largely been descriptive, its existence is certain. However, experiments are required to determine the importance of facilitation in shaping both population sizes of interacting species, and community structure.

1.3. INTERACTIONS BETWEEN MAMMALIAN PREDATORS

1.3.1. *Mesopredator release*

The observation that, in the absence of a dominant predator, smaller predators undergo population explosions and thereby intensify predation on prey (i.e. *sensu* *et al.* 1988) has long been recognised (Latham 1952, Emmons 1984). Mesopredator release has been recorded in a range of systems *et al.* 1988), grasslands (Vickery *et al.* 1992) and prairie wetlands (Ball *et al.* 1995, Sovada *et al.* 1995), and in a variety of mammalian *et al.* 1988, Estes 1996). In North America, populations of smaller predators (e.g. foxes *Vulpes* spp., skunks *Mephitis* spp., and domestic cats *Felis domesticus*) increased after local or near extinctions of coyotes *Canis latrans*. Their increase then led to the reduction or local extinction of some prey species such *et al.* 1988, Estes 1996). Similarly, Palomares *et al.* (1995) suggested that increased predation on rabbits in southwestern Spain was due to an increase in mongoose *Herpestes ichneumon* numbers following the removal of Iberian lynx *Felis pardina*.

Further support for the hypothesis of mesopredator release comes from studies reporting negative associations between sympatric carnivore species, although the subsequent impact on prey populations was not measured. In North America, coyote numbers increased after declines in wolf *Canis lupus* populations (Dekker 1986). Similarly, the abundance of bobcats *Felis rufus* (Litvaitis and Harrison 1989), red foxes and swift foxes *Vulpes velox* increased following coyote control (Robinson 1961, Linhart and Robinson 1972, Sargeant *et al.* 1993). In Scandinavia, densities of pine martens *Martes martes* increased rapidly following a decline in red foxes (Storch *et al.* 1990, Lindstrom *et al.* 1995). In Australia, lower densities of red foxes have been observed where dingoes are not controlled north of the Dingo Barrier Fence (Newsome 1990), and foxes are often scarce or absent in areas with high densities of dingoes (Jarman 1986, Catling and Burt 1995). These negative associations indicate that some carnivores may suppress populations of other species through interspecific competition and/or intraguild predation.

1.3.2. *Interspecific competition*

Circumstantial evidence consistent with exploitation competition can be drawn from studies that have demonstrated resource partitioning among ecologically similar species. For example, despite sharing the same staple prey, red foxes are able to coexist with coyotes by exploiting different alternative prey and habitat types (Major and Sherburne 1987, Theberge and Wedeles 1989). Dietary partitioning has also been recorded between sympatric bobcats and coyotes (Litvaitis 1981). The Island fox *Urocyon littoralis* and the island spotted skunk *Spilogale gracilis amphiala* are able to coexist on Santa Cruz Island, despite overlapping home ranges, because they differ in habitat use, diet and circadian activity (Crooks and van Vuren 1995). In sympatry, the South American gray fox *Dusicyon griseus* and culpeo fox *D. culpaeus* eat similar foods but in different proportions (Johnson and Franklin 1994). Five predator species in the Serengeti occupy similar ecological niches but coexist by consuming different sections of the same potential prey populations (Sinclair and Norton-Griffiths 1979). In India, Asiatic wild dogs *Cuon alpinus*, leopards *Panthera pardus* and tigers *Panthera tigris* coexist despite large overlaps in diet because of differences in sex and age of prey species, and in spatio-temporal use of the habitat (Venkataraman 1995). However, although resource partitioning has been documented widely, it is often unclear whether the observed differences in resource use are a result of independently evolved species-specific preferences, or the exclusion of the subordinate species from optimal habitats by the dominant competitor via interference (Dekker 1989, Johnson and Franklin 1994).

Interference competition has been inferred often from studies that have shown spatial segregation between carnivores. For example, in areas where coyotes and red foxes are sympatric, foxes tend to occupy territories on the periphery or outside of coyote territories (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant *et al.* 1987, Harrison *et al.* 1989). Interference competition has been supported by observations of coyotes killing red foxes (Sargeant and Allen 1989, Gese *et al.* 1996). Interference has also been inferred between coyotes and other fox species including swift foxes *V. velox* (Scott-Brown *et al.* 1987) and gray foxes (Cypher 1993), and coyote predation has been shown to be an important source of mortality for San Joaquin kit foxes *V. macrotis mutica* (Cypher and Scrivner 1992, Ralls and White 1995, Cypher and Spencer 1998). Similarly, wolves kill coyotes and exclude them from preferred habitat (Fuller and Keith 1981, Carbyn 1982). In addition, stronger evidence for interference competition has come from studies where two carnivore species share the same staple prey but the dominant carnivore exclusively occupies habitats where the staple prey are more abundant (Theberge and Wedeles 1989).

Frequently, both types of competition have been inferred between ecologically similar carnivore species. Exploitation competition was suggested between coyotes and San Joaquin kit foxes as they consume many of the same food items (Cypher *et al.* 1994, White *et al.* 1995, Cypher and Spencer 1998), but this may be lessened by coyotes killing kit foxes (Cypher and Scrivner 1992, Ralls and White 1995, Cypher and Spencer 1998) via interference. Cypher and Spencer (1998) suggested that kit foxes can coexist with coyotes by using different behavioural strategies, such as year-round use of dens to avoid agonistic encounters, and also resource partitioning and expanded dietary breadth. Similarly, mountain lions *Felis concolor*, bobcats *Lynx rufus* and coyotes are sympatric throughout most of western North America (Chapman and Feldhamer 1982). Resource partitioning occurs in summer with differences in the use of elevation, forest types and the density of terrain overstory (Koehler and Hornocker 1991). However, resource use in winter overlaps significantly between the three predators when snow confines prey and predators to lower elevations. During this time, mountain lions were observed killing bobcats and coyotes, while defending or usurping food caches.

1.3.3. Intraguild predation

Direct predation between carnivore species may reduce interspecific competition for resources and allow greater niche overlap (Polis *et al.* 1989). In New Zealand, cats kill and eat stoats, which may reduce exploitation competition given the large overlap in diet of the two species (Fitzgerald and Karl 1979). Similarly, in Scandinavia, intraguild predation by red foxes, rather than exploitation competition, was the most likely mechanism resulting in an increase in pine martens when foxes declined (Storch *et al.* 1990, Lindstrom *et al.* 1995). In North America, Canada lynx *Felis lynx* have been observed killing and eating red foxes, particularly when populations of their staple prey (snowshoe hare) crash (Stephenson *et al.* 1991, Donoghue *et al.* 1995). Similarly, coyotes, wolves and even lynxes *Lynx canadensis*, kill lynxes during food shortages (Donoghue *et al.* 1995).

1.3.4. *Other factors involved in carnivore interactions*

Most studies investigating negative associations between carnivores have shown that larger species usually displace smaller species (Linhart and Robinson 1972, Litvaitis and Harrison 1989, Storch *et al.* 1990, Sargeant *et al.* 1993, Lindstrom *et al.* 1995). However, the reverse can also occur when other factors are involved, such as human interference and drought (Rau *et al.* 1985). For example, the smaller and more opportunistic coyote has replaced the larger and more specialised wolf in most of North America as a consequence of increased habitat disturbance and wolf eradication programs, rather than by interspecific competition (Rau *et al.* 1985). Similarly, in Donana National Park in Spain, the smaller and more opportunistic red fox has displaced the larger lynx *Lynx pardina* (Rau *et al.* 1985). These latter authors suggest that, until recently, the lynx controlled fox numbers by interference competition and were themselves controlled by the availability of rabbits (Rau *et al.* 1985). However, a persisting low density of rabbits may have caused a decrease in lynx abundance and allowed a build up of fox numbers. When rabbits increased subsequently, recolonisation was difficult for the lynx, despite its larger size, because of competition for space with the increased density of foxes.

Litvaitis and Villafuerte (1996) argued that landscape differences, rather than intraguild predation or mesopredator release, were a more parsimonious explanation for the increase in mongoose recorded by Palomares *et al.* (1995) when the larger lynx declined in south-western Spain. As human-altered landscapes increase, top predators will become increasingly scarce and consequently, smaller predators will increase because of the elevated foraging opportunities and efficiencies in a heterogenous landscape, and not because larger predators are limiting them. However, although some smaller predators will increase as a result of habitat alteration (particularly food and habitat generalists), Palomares *et al.* (1996) argued that the overall abundance of other smaller predators that are subject to intraguild predation would also increase. In addition, mongoose did not use patches used by lynx that were in human-altered areas (Palomares *et al.* 1995, 1996).

1.4. STUDY AIMS AND SCOPE OF THESIS

The overall objective of this thesis is to describe the ecology of the feral cat in open forest in New South Wales, and to elucidate factors that limit cat abundance. Specific aims are to:

1) describe the feeding ecology of cats in relation to prey abundance;
2) describe home range size, overlap and habitat use of cats;
3) examine dietary and spatial overlap between cats and foxes;
4) examine evidence for avoidance and aggression between cats and foxes;
5) test the hypothesis that foxes limit cat populations through interspecific competition using a fox removal experiment.

In the preceding section I pointed out the damage that introduced species can cause, and highlighted the need for experimental evidence for understanding factors that contribute to the success of introduced species. I then presented a number of different mechanisms (competition, predation, disease / parasites, facilitation) that can influence mammal populations and argued that there is a paucity of evidence for population regulation in nature. In Chapter 2, I describe the biology, introduction, distribution and impacts of the feral cat in Australia. I highlight the deficiencies in current knowledge and the need for experimental studies for identifying factors that limit cat abundance. Following a description of the study area and general methods in Chapter 3, I present information on the feeding ecology of feral cats in relation to prey availability in Chapter 4. In Chapter 5, I examine the home range size, overlap and habitat use of cats. I then examine the degree of overlap between cats and foxes in diet and spatial use and examine any evidence for aggression or avoidance behaviours in Chapter 6. After identifying the fox as a potential limiting factor for cats in Chapter 6, I experimentally test the hypothesis that foxes limit cats through interspecific competition, using a fox removal experiment in Chapter 7. In the General Discussion (Chapter 8), I synthesize the results from all chapters and discuss the most important findings for the ecology of cats and for factors that limit their abundance at the study area. Finally, I suggest the most likely interaction between cats and foxes, and consider the management implications for feral cats.

CHAPTER 2

THE FERAL CAT IN AUSTRALIA

2.1. INTRODUCTION OF THE FERAL CAT TO AUSTRALIA

It is not known when cats first established in Australia, but it is generally accepted that they arrived on the east coast in 1788 with the first European settlers (Rolls 1969, Baldwin 1980). On the northwest coast, however, cats may have arrived much earlier, dispersing from Dutch shipwrecks in the seventeenth century (Burbidge *et al.*1988), or even earlier, aboard Indonesian trading vessels in the fifteenth century (Baldwin 1980). An early arrival is supported by surveys of Aboriginal people in central Australia which found that cats (a favoured food item) were regarded as having always been present, or that they arrived very early from the west (Burbidge *et al.*1988). In addition, Aboriginal people from the Kimberley region on the northwest coast regard the cat as a native species (Rolls 1969). Evidence for the early arrival of cats is currently being investigated using genetic techniques (McKay 1994). Preliminary findings suggest that feral cats in Australia are more closely related to those in Asia, than to those in Europe.

Despite the early arrival of cats in Australia their presence is not noted in reports and diaries of explorers and overlanders until the 1890s (review in Dickman 1996). This was probably because they were in low numbers or patchily distributed prior to this time (Dickman 1996). Alternatively, they may have been as difficult to detect then as they are now, at least in areas without rabbits (e.g. Mahon *et al.* 1998). Detailed fauna surveys in recent years have still failed to detect feral cats (Burbidge and McKenzie 1978, Friend *et al.* 1991), despite their presence being known from previous surveys (e.g. Miles and Burbidge 1975).

Regardless of the precise arrival date, feral cats were established successfully throughout the continent in the 1850s (Rolls 1969). In the 1880s, feral cat numbers increased in NSW as they were intentionally released to hunt rabbits in response to the *Rabbit Nuisance Bill 1883* (Mahood 1980). For example, 400 cats were transported in cages by rail to Bourke for release in 1886. Prior to release, these cats were acclimatised in pens with food gradually being diminished (Rolls 1969). During this time, quolls *Dasyurus* spp. and wedge-tailed eagles *Aquila audax* (also rabbit predators) were actively destroyed (Rolls 1969).

2.2. DISTRIBUTION AND DENSITY OF FERAL CATS

The domestic cat is the most widespread of all carnivore species, ranging from 55^0N to 55^0S (Apps 1983, Konecny 1987). In Australia, feral cats have successfully adapted to all habitat types including alpine and urban areas, deserts and the tropics (Wilson *et al.* 1992) (Fig. 2.1). In contrast to the situation in much of the Northern Hemisphere, feral cats are not forced to be commensal during winter as temperatures are not as extreme and prey are available year round (Newsome 1991). Further, they can survive without water as long as they get sufficient moisture from their prey (Lundie- Jenkins 1992) and have a high reproductive potential (Jones and Coman 1982).

Feral cats also occur on at least 40 islands off the coast of Australia (Dickman 1992b), seven off the coast of New Zealand (Veitch 1985) and around 40 elsewhere in the Pacific (King 1973, 1984). Once introduced, populations expand quickly. For example, five domestic cats were introduced to Marion Island as pets in 1949 and by 1975 an estimated 2139 feral cats were killing 450,000 burrowing petrels (Procellariidae) each year (van Aarde 1979, 1984).

Although the total population of feral cats in Australia is not known, it is estimated to be between 3.8 and 18.4 million (Cross 1990, Potter 1991). Few reliable population estimates are available, as the cryptic and nocturnal habits of cats make them difficult to detect (e.g. Mahon *et al.* 1998) and they are of little economic importance. In addition, comparisons of estimates between studies are often hampered because of differences in methodology, season when estimates were made, and state borders (see Fig. 2.1). Seasonal variation in cat abundance has been recorded in a number of studies (e.g. van Aarde 1978) with higher numbers usually recorded in summer after the recruitment of young (Jones and Coman 1982).

Nevertheless, crude estimates indicate that densities of feral cats are lower in the tropics, alpine and sub-alpine areas (Newsome and Catling 1979, Gordon 1991, Bubela 1995, review in Dickman 1996, Banks 1997), which may be related to zero or low densities of rabbits. In arid environments, numbers tend to be highly variable, presumably reflecting the influence of unpredictable environmental conditions on prey species (Dickman 1996). Cats are more often sighted around urban settlements and some temperate and semi-arid regions in eastern Australia (Wilson *et al.* 1992) (Fig. 2.1). However, observer bias in open habitats and around heavily populated areas may influence the frequency of sightings.

Density estimates range from 0.14 to 6 cats km^2 in temperate and semi-arid habitats but are generally around 1-2 km^2 or less on the mainland (review in Dickman 1996). On offshore islands where food is abundant, densities can reach 20-30 cats km^2 such as on Althorpe Island in South Australia, or up to 100 cats km^2 on North West Island in Queensland (Domm and Messersmith 1990). In general, cats are more abundant in open habitats in inland environments compared to closed forest and wet heath habitats in temperate or tropical areas (review in Dickman 1996).

No reliable technique is currently available for the estimation of cat densities as individuals are secretive and distributions are often clumped around food sources (e.g. rubbish dumps) in urban and semi-urban areas. Conversions from observed or actual numbers to estimates of real numbers are then difficult as the degree of clumping is site-specific. Methods for determining the abundance of cats remain elementary (Mahon *et al.* 1998, Molsher *et al.* 1999), and yet are critical when evaluating impacts on native fauna.

2.3. IMPACTS OF FERAL CATS

The predatory impact of feral cats on native fauna has long been recognised (Gould 1863) and more recently, their role in disease transmission (Obendorf and Munday 1990, Dickman 1993) and potential competitive effects (Cross 1990) have also been identified.

2.3.1. Predatory impacts

Cats have been implicated in the decline and extinction of numerous native mammal species in Australia on both a local and regional scale (review in Dickman 1996). On Australian offshore islands alone, cats have contributed to the local extinction of 25 mammal species and were considered the only known potential threat for 15 of these species (review in Dickman 1996). In western New South Wales, cat predation has been implicated in regional declines of both mammals and birds and in regional extinctions of up to 10 species of native mammals prior to 1857 (Dickman *et al.*

Xenicus

lyalli (*n* = about 22) in 1894 (Atkinson and Bell 1973, King 1984).

Declines and extinctions such as these have led to feral cat predation being listed as a key threatening process for native fauna in Australia under the *Endangered Species Protection Act 1992*. However, experimental evidence for the impact of cats on native fauna is lacking. This is largely because declines in prey species have been often observed but not quantified, and interactions with other factors (e.g. habitat change and other introduced animals) are often involved. Further, cats are not regarded as an agricultural pest (Coman 1978) and consequently have ranked low on the order of priorities for research funding. Nevertheless, strong inferences can be made from historical evidence, anecdotal observations, island case histories and studies of reintroduction programs.

Historical information indicates that extinctions of native fauna occurred shortly after European settlement (Dickman 1996). The feral cat was the only obvious threat to native fauna during the first half of the nineteenth century, as the pastoral industry was not yet established, and foxes and rabbits had not been introduced (Dickman 1996, Rolls 1969). Although it is not known whether cats occurred in all localities and periods that experienced declines (Dickman 1996), all mammals extinct prior to 1900 weighed ≤ 200 g, which is the preferred prey size for feral cats (review in Dickman 1996). In addition, most were ground-dwelling species that occupied open habitats (Dickman *et al.* 1993) making them more vulnerable to cat predation (Dickman 1992c).

Although cats generally kill prey only up to their own body weight (Leyhausen 1979), populations of much larger prey species are also vulnerable to cat predation when juveniles are preyed upon, e.g. the common brushtail possum (4 kg) *Trichosurus vulpecula* (Fitzgerald and Karl 1979), bridled nailtail wallaby (4.5 kg) *Onychogalea fraenata* (Horsup and Evans 1993), and the allied rock wallaby (4 kg) *Petrogale assimilis* (Spencer 1991). Where antipredator behaviours are lacking, as on some islands, larger species may also become rare or extinct e.g. various species of petrel (Fitzgerald and Veitch 1985), frigate birds *Fregata* spp., flightless cormorants *Phalacrocorax* spp., pelicans *Pelecanus* spp. (Konecny 1987) and Kakapo parrots *Strigops habroptilus* (Cresswell 1996). However, most population impacts have been on small and medium-sized mammals and birds, with impacts on reptiles, amphibians and fish being rarely recorded.

Evidence from dietary studies shows that feral cats prey on vulnerable and endangered mammals, such as the rufous hare-wallaby *Lagorchestes hirsutus* (Johnson 1991), numbat *Myrmecobius fasciatus* (Kinnear 1991) and the eastern barred bandicoot *Perameles gunnii* (Seebeck *et al.*1991).

Prey selection and individual variation in prey preference by cats (Leyhausen 1979, Konecny 1987, Gibson *et al.* 1994) may also threaten prey populations, particularly those in low numbers (Newsome 1990). For example, reintroduced rufous hare-wallabies persisted for some time in the Tanami Desert of the Northern Territory with cats before killings began (Lundie-Jenkins *et al.* 1993). Specific cats were thought responsible, as killings ceased after the removal of four individuals (Gibson *et al.* 1994). In addition, cats often select the young of a species (Jones 1977, Fitzgerald and Karl 1979, Childs 1986, Horsup and Evans 1993), which has the potential to have a major impact on isolated colonies (e.g. Spencer 1991). In tropical Queensland, one individual feral cat was known to have killed five juvenile allied rock-wallabies *Petrogale assimilis* out of a total juvenile population of 11. Wallaby numbers declined from 83 to 26 in 4 years, although drought was also implicated.

Further evidence for the impact of cats on native fauna comes from changes in island fauna after introductions and removals of cats. For example, on Little Barrier Island in New Zealand, the stitchbird *Notiomystis cincta* increased over six fold from less than 500 individuals to 3000 in just a few years following the removal of cats in the early 1980s (Griffin *et al.*1988). Similarly, cats were introduced to St Francis Island in South Australia to control the abundant brush-tailed bettong (*B. penicillata*) in the late 1800s, and by the early 1900s the bettong was extinct (Jones 1924). Although other factors may have hastened this process (e.g. clearing of vegetation), cats were considered to be the major cause.

Reintroduction programs also provide evidence for the impact of cats. In some programs, cat predation has been indicated from the analysis of radio collars from dead animals. In other programs initial failure has been turned to success after the removal of cats. These programs indicate that cats were the major cause of failure for some reintroduced species, including the golden bandicoot *Isoodon auratus* (Christensen and Burrows 1995), burrowing bettong *Bettongia lesueur* (Short and Turner 1993, Christensen and Burrows 1995) and the rufous hare-wallaby *Lagorchestes hirsutus* (Gibson *et al.* 1994). Further, cats have been implicated along with other factors (e.g. habitat change and predation by foxes, dingoes, raptors and goannas), in the failure of a number of other reintroductions including the brushtailed phascogale *Phascogale tapoatafa* (Soderquist 1995), numbat *Myrmecobius fasciatus* (Kinnear 1991) and numerous macropod species (Short *et al.* 1992). Although feral cats may not have been the cause of the local extinction in the first place, as habitat change and anti-predator behaviours may have been site-specific (Dickman 1996), they clearly can prevent the re-establishment of native fauna.

There are anomalies, however, where cats have coexisted with apparently quite stable populations. For example, while the golden bandicoot disappeared quickly after the introduction of cats to Hermite Island, the ecologically similar southern brown bandicoot *Isoodon obesulus* persisted with cats on both Francis Island and Kangaroo Island (Dickman 1996). Similarly, the reintroduced golden bandicoot persisted for a time with cats in the Gibson Desert, while the ecologically similar reintroduced burrowing bettong *Bettongia lesueur* was highly vulnerable to cat predation (Christensen and Burrows 1995). Differences in biological and behavioural traits were considered to be the most likely cause for the differences between the bandicoots and bettongs in vulnerability to cat predation (Christensen and Burrows 1995). Burrowing bettongs are gregarious, slow moving and leave the warren systems (their only refugia) at dusk each night to travel on a set route to feed. In contrast, the bandicoots are nomadic, solitary, use spinifex clumps as shelter and are never far from refugia even when in the open (Christensen and Burrows 1995). Similarly, cats are thought to have a significant impact on the endangered bridled nailtail wallaby, which is a solitary species that responds to danger by lying flat and motionless (Horsup and Evans 1993). A complete evaluation of behavioural and biological attributes (e.g. body weight, fecundity, habitat use and mobility) of endangered native fauna, and their relative susceptibility to cat predation is described in Dickman (1996). However, while behavioural differences can account for some of this variation in the persistence of native fauna, other factors such as abundant alternative prey and habitat degradation, are also clearly important.

native fauna experiences abnormally high predation after the rabbit population crashes and predators shift to alternative prey (Smith and Quin 1996). This was illustrated on Macquarie Island where the endemic ground-nesting parakeet *Cyanoramphus novaezelandiae erythrotis* coexisted with cats in quite high numbers for at least 60 years between 1810 and 1880 until the introduction of rabbits (Taylor 1979). Predation then intensified as cat numbers increased, and the parakeet rapidly disappeared between 1881 and 1890. Hyperpredation by feral cats has also been suggested as the principal cause of decline in conilurine rodents in Australia (Smith and Quin 1996).

Fragmented forest systems also increase impacts of predators when native species are restricted to remnant vegetation (e.g. Dickman 1996). In Tasmania, for example, where habitats are largely intact (and foxes and rabbits are not present), no native mammals (except the Thylacine) have gone extinct since European settlement. Similarly, native mammals have persisted with cats in tropical Australia and Kangaroo Island for at least a century with few species becoming extinct and none that appear related to cat predation. Intact habitats clearly provide important refugia for native fauna.

Despite the lack of empirical evidence for the negative impacts of cats on native fauna (Wilson *et al.* 1992), the consistency of increases in prey species after cat removals provides strong evidence for the predatory impact of feral cats. Two controlled field removal experiments that are currently underway investigating the effect of cat predation on native fauna (Risbey and Calver 1998, C. Dickman and P. Mahon unpublished data) will provide valuable and much needed information.

Although most impacts of feral cats in Australia have caused declines and extinctions of native fauna, cat predation can also affect native fauna in other ways, such as evolutionary trends (Stone *et al.* 1994). For example, wariness and smaller body size in lava lizards (*Tropidurus* spp) tends to be correlated with cat presence in the Galapagos archipelago (Grant 1975, Kramer 1984, Stone *et al.* 1994).

2.3.2. Competitive impacts

Although feral cats have a high potential to compete with native fauna, e.g. quolls, raptors and lace monitor lizards (Brooker 1977, Caughley 1980, Weavers 1989, Cross 1990), where resource requirements are similar, no conclusive competitive relationship has yet been demonstrated (Dickman and Read 1992).

Quolls (*Dasyurus* spp.) are probably the most ecologically similar native species to feral cats and consequently have the greatest potential for competition (e.g. Edgar 1983). They are sympatric in forest and woodland habitats in eastern, western and northern parts of the continent (Godsell 1982, Serena and Soderquist 1989, Serena *et al.* 1991). Cats eat similar prey to all four quoll species which are active hunters, preying on small mammals, birds, lizards, frogs, invertebrates and plant matter (Belcher 1995). The spotted-tailed quoll *D. maculatus* and western quoll *D. geoffroii* are, however, the most carnivorous (Belcher 1995, Soderquist and Serena 1994). The western quoll and eastern quoll *D. viverrinus* also have similar den and habitat requirements to feral cats (Godsell 1982, Serena and Soderquist 1989, Serena *et al.* 1991). Declines in the spotted-tailed quoll and eastern quoll were recorded on the mainland soon after the release of cats (Rolls 1969) and feral cats were suspected to be the major factor in the decline of the spotted-tailed quoll on King Island (Courtney 1963). However, human predation and habitat alteration were also implicated in these declines.

Predatory birds (e.g. owls, kites, hawks, eagles and falcons) and large lizards, (e.g. goannas) may also compete with feral cats given their similar diets (review in Dickman 1996, Weavers 1989). For example, on Marion Island, the sub-Antarctic skua *Catharacta lonnbergi* (territorial bird), declined in numbers after cats reduced their staple prey, the burrowing petrel (Procellariidae) (Hunter 1990). Further competitive interactions may occur between feral cats and other native fauna, such as possums, gliders and bats, which occupy similar shelter sites (e.g. hollow trees).

2.3.3. Disease transmission

Indirect effects of cats may occur via the transmission of disease, parasites or pathogens to native fauna. Cats are definitive (or final) hosts for two pathogens that can produce severe clinical signs and death in a wide range of native species (Dubey 1986), although their impact at the population level is not known.

The first of these is the helminth parasite *Spirometra erinacei*, which is carried by feral cats in eastern Australia (Coman *et al.* 1981) and which also infects foxes and dingoes (Coman 1973a). It can cause muscular haemorrhage, damage to soft tissues and potentially death in native animals (Munday 1988). The second pathogen is the protozoan *Toxoplasma gondii*, which causes toxoplasmosis. Cats are the only definitive host for *T. gondii*, while humans, native mammals, birds and livestock act as secondary hosts (Dubey 1986, Mahood 1980, Obendorf and Munday 1990). Symptoms include lethargy, poor coordination, blindness and sometimes death, and have been recorded in at least 20 species of native mammals (Moodie 1995). Toxoplasmosis can also cause abortions in humans (Frenkel 1973) and in sheep and goats (Callow 1984). It has been postulated that an apparent decline in native mammals prior to 1770 was due to toxoplasmosis that had been introduced by cats (McKay 1994). Although toxoplasmosis has also long been suggested as the major cause for the decline of several larger carnivorous marsupials around the turn of the century (Caughley 1980), there is no evidence that it has caused past extinctions.

Further, cats transmit sarcosporidiosis, a disease that affects sheep and consequently the meat industry (Dubey and Miller 1986, Langham and Charleston 1990). Cats can also act as important host species for rabies (Page *et al.* 1992).

2. 4. WHAT LIMITS FERAL CAT POPULATIONS?

Factors that limit feral cat populations have not been evaluated experimentally in Australia or elsewhere. However, interactions with other predators and declines in food availability have been suggested as the major limiting factors (Jones 1977, Dickman 1996). Other factors that may limit feral cat populations include high kitten mortality, lack of shelter, cannibalism, disease and parasitism.

2.4.1. Interactions with other predators

Increases in feral cat populations have been reported after the removal of foxes in a number of areas in Western Australia (Christensen and Burrows 1995, Short *et al.* 1995, Risbey and Calver 1998, P. deTores pers. comm.), and after the removal of dingoes in the Diamantina region (Pettigrew 1993) and Tanami desert (Lundie-Jenkins *et al.* 1993). At Shark Bay in WA, increases in cat numbers following fox removal were postulated to be the result of reduced predation and competition (Risbey and Calver 1998).

Foxes are known to eat cats (Coman 1973b, Brunner *et al.* 1991, Taylor and Lupica 1998, D. Risbey pers. comm., R. Paltridge pers. comm.) but they are eaten more frequently by dingoes, although in low numbers (Newsome *et al.* 1983b, Lundie-Jenkins 1992, Pettigrew 1993, Corbett 1995). Cat remains have also been recorded in the diet of other predators, including the lace monitor lizard *Varanus varius* (Weavers 1989), (presumably scavenged) and the wedge-tailed eagle *Aquila audax* (mostly juvenile cats) (Brooker and Ridpath 1980).

Feral cats and foxes may also compete when resources are limited. In Australia, these predators are sympatric over much of their range (e.g. Bayly 1978, Newsome and Catling 1979, Triggs *et al.* 1984, Catling 1988, Newsome *et al* 1989, Catling and Burt 1995) and occupy similar ecological niches. They are both opportunistic predators (Van Aarde 1980, Jones and Coman 1981, Apps 1983) and have a large overlap in diet (Triggs *et al.* 1984, Catling 1988). In addition, the abundance of feral cats tends to be correlated negatively with foxes in southern NSW (Catling and Burt 1995). However, the competitive or predatory relationship between feral cats and other introduced predators is as yet untested.

2 4.2. Food availability

A decline in food availability (particularly rabbits) has been suggested as the major limiting factor for feral cat populations in some studies (Jones 1977, Jones and Coman 1982). For example, a numerical response by cats to changing rabbit densities (3-4 month lag) was indicated in semi-arid NSW (Pech *et al.* 1992). Further, more cat deaths occurred on

Macquarie Island in winter when the availability of subadult rabbits declined, compared to other seasons (Jones 1977). Feral cats show a clear preference for subadult rabbits (Jones 1977, Fitzgerald and Karl 1979, Liberg 1984a, Catling 1988) and are not well adapted to hunting adult rabbits (Parer 1977, Gibb *et al.* 1978, Corbett 1979). In winter, when the availability of subadult rabbits is generally low (Jones 1977, Fitzgerald and Karl 1979, Catling 1988), very old, sick or juvenile cats may be unable to catch the larger adult rabbits (Jones 1977). In addition, juvenile cats have been observed starving when adult rabbits were abundant (Coman 1991).

2.4.3. Other factors

Feral cats also appear to suffer a high mortality rate (Coman 1991). Despite the high reproductive potential of cats (two litters per year, mean litter size 4.4, and sexual maturity at 12 months) (Jones and Coman 1982), feral cat populations often show a slow recovery rate when removed from an area (Coman 1991). For example, 21 cats were culled from an area in Victoria but three years later, when the same culling procedures were applied, only one cat was culled (Coman 1991). Similarly, little recruitment was recorded in cats after their experimental removal in semi-arid NSW, while the replacement of foxes was rapid in the second year (Newsome *et al.* 1989).

High kitten mortality. Disproportionately high mortality rates among subadult cats, compared to adults, have been recorded in some studies (e.g. Brothers *et al.* 1985, Mirmovitch 1995) and are thought to be the result of nutritional stress and disease (van Aarde 1984). For example, mortality rates of 42% for neonatal and pre-weaning and 37.9% for yearlings (4-12 months age) were estimated for the cat population on Marion Island (van Aarde 1984). This suggests an overall mortality rate of 79.9% in the first year of life. Similarly, less than 43% of young feral cats born on Macquarie Island survived to an age of six months (Brothers *et al.* 1985).

Subadult cats appear to be susceptible to nutritional stress more than adults (Jones 1977, Coman 1991), particularly during autumn and winter when the availability of suitable prey (e.g. juvenile rabbits, lizards and grasshoppers) is low (Jones 1977, Coman 1991). In support of this, adult cats on Macquarie Island were generally in good condition in winter, while the condition of juveniles was highly variable (Jones 1977). Further, adult cat abundance remained relatively stable in the Victorian Mallee, while large fluctuations were recorded in subadult numbers (Jones and Coman 1982).

Heavy kitten mortality from infectious diseases has also been recorded in a number of studies (Dards 1978, Oppenheimer 1980, Izawa *et al.* 1982). Upper respiratory tract infections are particularly prevalent and highly contagious in cats (Apps 1983). Symptoms include nasal congestion, running eyes, ulceration of the mouth, loss of appetite and general lethargy, which

Shelter. In urban areas, cats appear to be more dependent on the availability of shelter than food (Calhoon and Haspel 1989). However, there is no evidence that shelter is a limiting resource elsewhere. Cats often use rabbit warrens, trees, logs, rock piles for dens (Calaby 1951, Mahood 1980), which are unlikely to be in limited supply in most parts of Australia.

Cannibalism. Maternal cannibalism, and cannibalism by scavenging during periods of food shortage, have been reported in a number of studies of cat populations (Hubbs 1951, Jones 1977, Jones and Coman 1981). However, its importance as a population limiting mechanism is not known.

Parasitism. Investigation of the parasite loads of adult feral cats in Victoria and NSW indicates that parasitism is not a limiting factor for feral cat populations (Coman *et al.* 1981). No correlation was found between the degree of parasitism and body condition of cats. However, parasitism in young cats was not investigated (Coman *et al.* 1981). This lack of severe parasitism may be due to the low population densities of feral cats and to their largely solitary nature. Detailed parasitic studies of feral cats are reviewed in Moodie (1995).

CHAPTER 3

STUDY AREA AND GENERAL METHODS

3.1. DESCRIPTION OF STUDY AREA

3.1.1. Topography

Research was carried out on the eastern shore of Lake Burrendong (Fig. 3.1a), located on the Macquarie River about 32 km upstream of Wellington in central-eastern New South Wales (32° °
of sheep *Ovis aries* and cattle *Bos taurus* (Fig. 3.1b). The study area encompasses about 90 km^2 of hilly, undulating slopes extending down to a flat foreshore area which has been extensively cleared of trees for grazing.

3.1.2. Vegetation

The foreshores are dominated by perennial grasses including red grass *Bothriochloa macra*, *Danthonia* sp. and *Stipa* sp. Other species common in the pastures include burr medic *Medicago polymorpha*, small woolly burr medic *M. minima*, narrow-leaf clover *Trifolium angustifolium* and stinking and weeping love grasses *Eragrostis* spp. The rugged higher country is generally heavily timbered and dominated by white box *Eucalyptus albens* and yellow box *E. melliodora* associations, with stands of cyprus pines *Callitris* spp. also being common. The understorey comprises shrubs, herbs and coarse grasses. The most common understorey species is the Daisy-bush (*Olearia* sp.) with Nodding blue-lily *Stypandra glauca*, Western golden wattle *Acacia decora* and Hill wattle *A. buxifolia* distributed patchily throughout the area. Between the higher country and the foreshore areas are open woodland areas with scattered trees and little understorey. Ground cover in these areas is generally sparse, comprising isolated bushes and fallen timber. Weeds are prevalent and include blackberry *Rubus fruticosus*, sweet briar *Rosa rubiginosa*, tree of heaven *Ailanthus altissima* and prickly pear *Opuntia stricta*.

3.1.3. Mammal fauna

Feral cats *Felis catus* and red foxes *Vulpes vulpes* are established throughout the study area and the European rabbit *Oryctolagus cuniculus* was abundant until the arrival of Rabbit Calicivirus Disease (RCD) in June 1996 (Saunders *et al.* 1998, A. Newsome unpublished data). Other common introduced species include the pig *Sus scrofa*, house mouse *Mus domesticus* and black rat *Rattus rattus*. Native mammal species seen regularly include the eastern grey kangaroo *Macropus giganteus*, euro *Macropus robustus*, swamp wallaby *Wallabia bicolor*, and common brushtail possum *Trichosurus vulpecula*.

3.1.4. Climate

The area is characterised by mild to cool winters (2-15 ° C) and warm to hot summers (14-33 ° C) with an average annual rainfall of 614 mm. Drought conditions prevailed in the region from March 1994 to December 1995 (Fig. 3.2). During this period, the cumulative deviation of monthly rainfall was generally below the long-term monthly average (46 years) (after Foley 1957). It was considered that this period reflected suboptimal environmental conditions for the area.

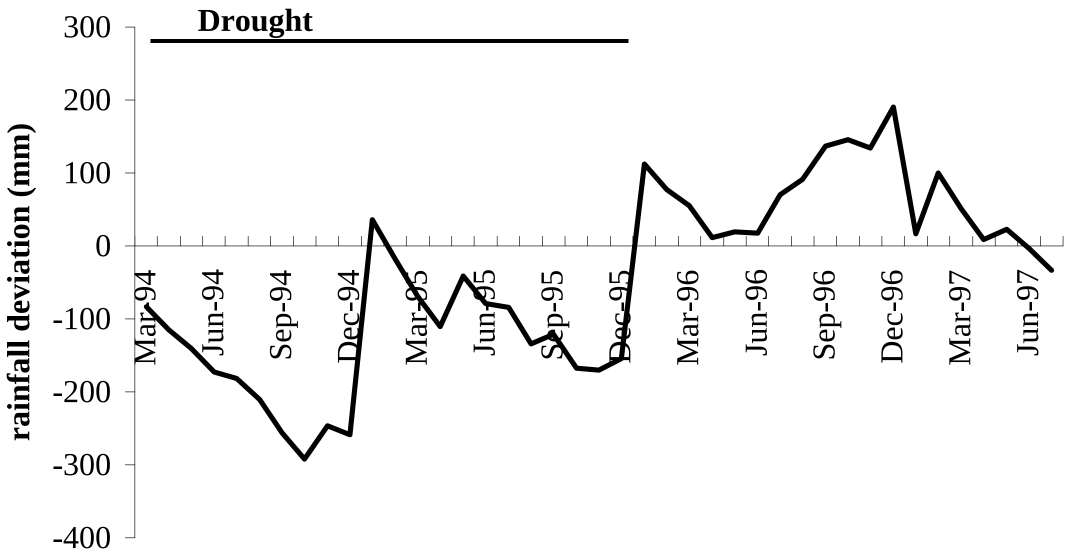

Fig. 3.2. Cumulative deviation of monthly rainfall for the Burrendong region showing "drought" conditions in 1994 and 1995.

3.2. WHY BURRENDONG WAS SELECTED FOR THE STUDY

The Lake Burrendong area was selected for this study because it contained a high density population of foxes, and feral cats were also present. In addition, the land is typical of much of the grazed country of the western slopes of the Great Dividing Range in eastern Australia, so that results should have wider relevance. Furthermore, the site was large enough to successfully carry out an experimental removal of foxes, it had numerous high points for radiotracking, and minimum interference from the public.

3.3. STUDY SITES

Four sites were established on the eastern shore of Lake Burrendong in July 1994: Dog Trap (DT); Gunnel Creek (GC); Devils Hole (DH); and Harrys Creek (HC) (Fig. 3.3). Sites ranged in size from 10 km^2 at GC to 14 km^2 at DT, 16 km^2 at DH and 19 km^2 at HC. Two sites (DT and GC) were subject to a fox removal experiment in October 1995 (Chapter 7).

3.4. GENERAL METHODS

This section describes general methods that apply to more than one chapter.

3.4.1. Scat collection and prey identification

Cat and fox scats were collected on random walks throughout the study area in most months from July 1994 to June 1997. Scats were distinguished between cat and fox by size, shape, colour, texture and odour (Triggs 1996). Scats that could not be identified positively were excluded from the analysis. Groups of scats were examined individually. Scats were air-dried and stored individually in plastic bags with location, habitat, date and scat description recorded. Fox scats were baked in an oven at 80 ^{o} C for 24 hours to kill parasites (Brunner and Wallis 1986). To separate the food items, all scats were soaked in 70% ethanol for 24 hours and rinsed through a fine sieve with hot water.

Mammalian prey remains were identified from microscopic analysis of hairs using cross section and whole mount techniques (Brunner and Coman 1974). The age of ingested rabbits was determined by measurements of claws and classified as adult or subadult by comparison to a reference collection of entire rabbits from the study area. Rabbits weighing ≤ 800 g were considered subadult; claws of these animals were < 8 mm long. If blowfly larvae were present in scats, the contents were classified as carrion. Kangaroo, sheep and cattle remains were also classified as carrion, irrespective of the presence of blowfly larvae. Carrion remains could not be aged as few identifiable skeletal parts were found in the scats. Non-mammalian food items were identified by comparison to reference collections and reference books (Cogger 1994, Zborowski and Storey 1995).

The percentage volume of each food item was estimated visually and the mean percentage volume and percentage occurrence calculated for each monthly sample of scats. Percentage volume was defined as the proportion of the total volume of a scat that was occupied by a particular food item, while percentage occurrence was defined as the proportion of scats in a sample that contained a particular food item (Reynolds and Aebischer 1991). As some scats contained more than one food type, the sum of the percentage occurrences could exceed 100%. Both methods were used to reduce the limitations imposed by each single method (Reynolds and Aebischer 1991). The accuracy of the visual estimate of percentage volume was determined by the following method. The contents of each scat (n = 10) were sorted into food groups (mammal, bird, reptile, invertebrate and vegetation) in a petri dish. A grid was placed under the dish and the numbers of squares comprising each food group were counted. The percentage volume of each food group in every scat was then estimated visually. The visual estimates and the grid method were compared using a paired t-test, where each food group was tested separately. The percentages were transformed using the arcsine transformation so that the data approximated a normal distribution (Zar 1984). Visual estimates were considered reliable as they were not significantly different from the quantitative method for assessing diet ($P > 0.05$). All prey identifications were conducted by the same person (R. Molsher) to reduce inconsistencies due to observer bias.

3.4.2. Abundance indices for foxes, cats and rabbits

Abundance estimates (animals km^{-1}) were obtained by two other VBCRC projects (A. Newsome unpublished data, J. McIlroy unpublished data) using spotlight counts. Counts were conducted before (July 1994 to September 1995) and after fox removal (October 1995 to August 1998) using a 100 W spotlight from the top of a vehicle travelling < 10 km/h. Replicate spotlight counts, over three consecutive nights, were conducted after July 1995 in each month at DT, GC, and DH. At HC, spotlight counts were conducted at three-monthly intervals for three consecutive nights over the entire period. Moonlit, windy and rainy nights were avoided to reduce weather-related variability in counts (Williams *et al.* 1995) and biases due to inactivity of the species (Kolb 1992). Transects followed the main access roads that traversed each site, with length varying from 5.6 km at DT to 5.0 km at GC, 5.3 km at HC, and 7 km at DH.

3.4.3. Capture and handling of feral cats

Detailed trapping procedures are described in Appendix 1. Feral cats were trapped using both wire mesh cage traps (40 cm by 40 cm by 60 cm) and Victor Soft Catch leg-hold traps (Nos. 1, 1.5 and 3, Woodstream, Corp., Lititz, Pa., USA) (Figs. 3. 4a and b). Leg-hold trap jaws were padded with rubber to minimise injury. Traps were set in a variety of habitats, including under bushes, beside vehicle tracks, on animal runways and at rabbit warrens. Trap sites were chosen carefully to minimise capture of non-target species. Traps were checked each morning from first light, left set and checked again in the afternoon during unfavourable weather. A total of 77 cats (48 recaptures) were caught in 6762 trap nights from November 1994 to August 1996. A further 18 individual cats were trapped as non-target animals by the VBCRC Fox Sterility Project.

Trapped cats were anaesthetised with Ketamine (22mg/kg) and Rompun (1.1mg/kg Xylazine)

The anaesthetised cat was weighed, sexed, aged and detailed body measurements recorded (Appendix 1). Adult cats were fitted with SIRTRACK and AVM two-stage radio transmitters that were encased in epoxy resin and attached to a leather collar with a 22 cm vertical whip aerial. Adult cats were

also fitted with sheep swivel eartags (34 mm by 10 mm, diameter 5 mm, weight 1.8 g). Male cats were tagged in the left ear and females in the right. Both eartags and transmitters were

daylight and by spotlight at night.

Radio transmitters were powered by AA lithium cells (40 pulses per minute with an 18 ms

The radio transmitters operated on the 216 MHz and 150-151 MHz bands with at least a 20 kHz spacing. Transmitters had an expected life of 31 months, but operational life varied greatly with few remaining functional after 15 months. Ten radio transmitters stopped functioning within one month of fitting. The average range of the transmitters was 1 km under line-of-sight conditions from elevated positions. Radiocollared animals were located with a hand-held three-element Yagi aerial and an AVM AR8000 receiver. At least 24 hours was allowed between trapping and initiation of radiotracking to avoid possible bias caused by trapping and handling.

3.4.4. Radiotracking

technique for providing data on location, movement and behaviour of mammalian species (Harris *et al.* 1990). Radiotracking data can be used for determining home range size, patterns of activity, foraging behaviour, nest sites, habitat selection and dispersal movements. The two main techniques for estimating locations of animals are 1) radio-assisted surveillance, where radiotracking is used to simply locate the animal and direct behavioural observations are then made, and 2) remote radiotelemetry, where location bearings are taken from mobile or fixed tracking stations (White and Garrott 1990). Radio-assisted surveillance yields very accurate data but is very time consuming and not appropriate when numerous fixes are to be obtained on a number of animals over a short period of time. Remote radiotelemetry, however, allows a large quantity of location fixes to be obtained which are suitable for range analysis. Fixed tracking stations give a high degree of precision and are justified in terms of expense if the study is lengthy, while hand-held receiving stations give greater mobility and flexibility to move over a large area and remain close to the animals being monitored. In this study, remote radiotelemetry from mobile tracking stations (i.e. R. Molsher) was used to obtain triangulated location bearings for range analysis of cats. Fixed tracking stations were used to obtain locations on foxes (J. McIlroy and G. Saunders, unpublished data).

Triangulation. Triangulation was used to estimate the locations of the transmitters. This involves taking two or more directional bearings from known locations that are remote from the transmitter (White and Garrott 1990). Bearings were taken from locations situated at least 200 m apart and were usually in areas that had a clear line-of-sight. All location bearings were estimated using a hand-held SILVA system sighting compass pointed in the direction of the strongest signal of the radio transmitter. At least three bearings were taken where possible to reduce errors associated with signal bounce (White and Garrott 1990). Each bearing was given a code from 1-5, which represented the confidence of the observer in the obtained bearing. A code of 1 was given when the observer was very confident of the bearing and the animal was sighted, while a code of 5 indicated that the bearing was doubtful. Locations were estimated from the bearings using Program LOCATE (Nams 1990). Bearings with a code ≥ 3 were excluded from location estimates when they distorted location estimates (determined visually), while bearings with a code < 3 were not excluded regardless of their congruence with the other bearings.

Homing-in on the animal. This method was used to locate animals to determine dens and rest sites and to confirm that they were alive. This non-triangulation method involves following the line of increasing signal strength until the focal animal is sighted. Direct observations are

technique was not used for home range determination in this study.

Fox spatial use. The home range data were obtained for foxes by the VBCRC Fox sterility project (J. McIlroy and G. Saunders, unpublished data) between June and December in both 1995 and 1996. Simultaneous bearings were taken from three to four fixed radio towers every hour for six hours beginning one hour after sunset. Six locations were obtained for each fox on each of eight nights every month. Radio towers were located at elevated positions and comprised a standard aluminium shed with a 6 m high aerial. Each tower consisted of two five element 150 MHz yagi antennae with 7 m of coaxial cable and matching baluns. Locations of foxes were estimated on LOCATE using triangulation techniques. Mean bearing error estimated from fixed transmitters (*n* = 282) was 3.56^0 ± 0.25 s. e. at a mean distance of 4.94 km.

Coordinate system. The Universal Transverse Mercator (UTM) system, which is a worldwide

advantages of this method rather than the system of longitude and latitude is that it is metric, provides a continuous Cartesian coordinate system which allows easy calculations of distances between points, and simplifies the calculations used in triangulation (White and Garrott 1990).

3.4.5. Accuracy of radiotelemetry

Estimates of error.
error (Springer 1979). However, the accuracy of bearings may be affected by many factors including the equipment used, terrain, weather, observers, power lines and vegetation (review

not measured exactly using triangulation techniques, then the associated error must be estimated and reported. The accuracy of bearings consists of both bias and precision, which are measured by examining bearing error, where error is defined as the difference between the true bearing and that estimated using a receiver (White and Garrott 1990, review in Salz 1994). Estimates of error should be included in all radiotracking studies regardless of which method is used to estimate animal locations.

The precision of an estimated location is dependent on three factors which must be considered together to produce a reliable error measure (Salz 1994). These factors include the variance around the bearings (error arc), distance to transmitter and the intersection angle of the

of all the error arcs, was introduced (Heezen and Tester 1967) to incorporate these three factors and provide an adequate measure of triangulation error (Salz and White 1990). However, this technique does not work with more than two bearings and cannot cope with signal bounce. This is because the error estimate uses only bearing errors that were measured

of error polygons and use three bearings which produce a triangle and the area of the triangle is quantified (Nams 1990). Precision with this technique, however, does not increase with

1981a and b), overcomes most of these problems and is a more rigorous technique for estimating triangulation error (White and Garrott 1984). This technique estimates the most likely true location of an animal and its associated error estimate by considering the placement of the telemetry stations, the number of bearings and the deviation of each bearing from the estimated location (Nams 1990). In this study, locations and associated confidence ellipses (95%) were estimated with the Lenth technique of 95% confidence ellipses using Program LOCATE II (Nams 1990).

Triangulation error was evaluated using fixed transmitters placed in two different habitat types (forest and grassland) by an independent observer (Litvaitis *et al.* 1986). Estimates of the locations of these transmitters provided an estimate of the precision of the methods being used. Error was calculated from the difference between the observed signal azimuth and the real azimuth. There was no significant difference in the bearing error between forest ($7.06^0 \pm 0.55^0$ s.e.) and grassland habitats ($8.42^0 \pm 0.63^0$ s.e.) ($t = -1.51$; d. f. = 137; $P = 0.13$), so the data were pooled. Mean bearing error overall was $7.71^0 \pm 0.42^0$ (s.e.) at a mean distance of 950 m ± 50 m (s.e.). This was considered acceptable, as it was less than 10 degrees (White and Garrott 1990).

Movement error can also affect the accuracy of a location and occurs when animals move between consecutive bearings. Movement error was minimised in this study by taking consecutive bearings as close in time as possible with a maximum of twenty minutes between consecutive bearings. Signal bounce was minimised by obtaining bearings from high points where possible.

Validity of radiotracking data. If an estimated location was considered unreasonable, was not within a feasible distance of the previous location, or the rate of travel needed between the previous location and the current location was not possible (White and Garrott 1990), then that datum was excluded.

Autocorrelation of Data. Most statistical techniques for home range analysis assume

t is not influenced by its position at time t^{-1} (Cresswell and Smith 1992). Where successive locations are not independent, temporal autocorrelation may bias estimates and, in particular, may lead to underestimation of home range sizes (Swihart and Slade 1985). Although the degree of temporal autocorrelation decreases with increasing time intervals between fixes (Swihart and Slade 1985), in fixed duration studies, a trade-off occurs between sample size and sampling interval. Autocorrelated data, however, may be a better alternative for estimating home-range size, than extremely long intervals between fixes where biologically important data may be sacrificed (Reynolds and Laundre 1990, Rooney *et al.* 1998).

In this study, consecutive locations were separated by ≥ 30 minutes to avoid problems associated with autocorrelation. In many carnivore studies, 30 minutes has been found to be adequate to ensure independence between consecutive locations (e.g. Newdick 1983, Cavallini 1996). However, in this study, despite the 30 minute time interval between locations, tests to determine independence of animal-movement data (Swihart and Slade 1985) showed that some ranges remained autocorrelated. In accordance with Powell (1987) and Goodrich and Buskirk (1998), autocorrelation was disregarded because it was accepted that individual movements were likely to depend on past experience and knowledge of the location of resources within the home range. Although all fixes may not have been statistically independent (Swihart and Slade 1985) they were considered to be biologically independent (Lucherini and Lovari 1996), as a time interval of 30 minutes was sufficient to allow any radiocollared cat to traverse entirely its home range.

3.4.6. Home range analysis

Although the size and shape of the home range of an animal is frequently measured there is much disagreement over what it is and how to measure it (Anderson 1982). A home range

area where the animal normally moves are not considered part of the home range (Burt 1943).

definition is a time frame over which the home range is measured. In this study, home range is defined as that area traversed by an animal in its normal activities during a specified time period (Hansteen *et al.* 1997).

size and utilisation distribution (UD). Home range size of mammals is often inversely dependent on the availability of food (Mares *et al.* 1982) and increases with body size (Haspel and Calhoon 1989) and metabolic requirements (Grant *et al.* 1992). Home ranges are rarely

ranges can often provide a clearer picture of range use than total range area, particularly when investigating intraspecific and interspecific relations (Harris *et al.* 1990). An alternative estimate of home range size and core area is the utilisation distribution (UD), which describes

more informative than estimates of range size (Worton 1987) and can visually illustrate spatial use (Anderson 1982).

There are many different methods of range analysis, each having its own strengths and weaknesses that have been reviewed by Macdonald *et al.* (1980), Voigt and Tinline (1980), Worton (1987), Kenward (1987), Harris *et al.* (1990) and White and Garrott (1990). Range analysis can be divided into two main categories of non-statistical and statistical (or probabilistic) methods. Probabilistic methods can be further divided into parametric and non-parametric.

Non-statistical methods. Non-statistical techniques for range analysis include the use of grid cells (Siniff and Tester 1965, Voigt and Tinline 1980) and minimum convex polygons (MCP) (Mohr 1947). The grid cell approach concentrates on the grid cell in which each fix occurs but has numerous limitations as it is affected by the size of the grid cell chosen and takes very many fixes to reach sampling saturation (Kenward 1987). The MCP is the smallest convex polygon containing all the observed position locations and is the oldest and most widely used non-statistical method for estimating home range size. The advantages of the MCP are its simplicity and unambiguity for comparisons between studies. It is also less affected by a lack of independence between successive location fixes (Harris *et al.* 1990) and the home range software program used (Lawson and Rodgers 1997), compared to other estimators. The MCP also defines a limit to the area that may be visited by an animal and therefore the habitat types and neighbouring individuals it can encounter (Kenward 1992). However, it is influenced strongly by outlying fixes and small sample sizes, and may include large areas that are never actually visited by the animal (Harris *et al.* 1990). Peeled polygons attempt to overcome some of these problems by excluding a designated proportion of fixes furthest from the activity centre. For example, the 95% minimum convex polygon (MCP 95) excludes 5% of fixes furthest from the activity centre. The major limitation of the MCP is that it gives no indication of how intensively an animal uses different parts of its range (Kenward 1987).

Statistical methods. Probabilistic methods of range-analysis attempt to assess the UD of an animal and can be calculated using both parametric (e.g. circular normal and bivariate normal) and non-parametric methods (e.g. harmonic mean, Fourier transform). Parametric

about a single arithmetic activity. These methods are relatively stable with respect to sample size but are unrealistic as they assume a single activity centre that is derived from the arithmetic mean, and may thus have no biological significance (Harris *et al.* 1990). Non-parametric methods make fewer assumptions about the underlying distribution of space use, and therefore overcome many of the problems associated with parametric methods, but are more sensitive to changes in sample size.

Kernel methods. The kernel methods (Worton 1989) are a further development of probability density functions and are less biased by small sample sizes. While kernel methods include the harmonic mean approach, they contain an additional concept of using a function with a negative exponential term for fix distances. The fix densities at grid intersections are then derived using a bivariate normal kernel estimator (Worton 1989). This results in less grid-dependence than the harmonic mean function and makes the kernel contouring method more robust and reliable while also avoiding some of the problems inherent in the harmonic mean approach (Larkin and Halkin 1994, Worton 1987). For example, kernel methods are free of parametric assumptions, provide a means of smoothing data, have well-understood and consistent statistical properties, and are used widely in both univariate and multivariate probability density estimation (Worton 1989). In addition, kernel methods provide a good means of identifying areas of concentrated use (Worton 1987).

Resolution. Because each range analysis method has its own advantages and disadvantages, a multifaceted approach was used in this study to overcome the limitations of each single method (Voigt and Tinline 1980). Both statistical and non-statistical methods were used to describe the range use of feral cats: 1) the minimum convex polygon including all locations (MCP100), 2) MCP 95 including 95% of fixes closest to the harmonic mean centre, and 3) the kernel contouring method including 95% of fixes closest to the harmonic mean centre (KE 95) (Fig. 3.5). The core area was estimated using the minimum convex polygon and kernel analysis, both including 50% of locations (MCP 50 and KE 50 respectively) (Fig. 3.5). These methods were chosen to allow comparisons with past and future studies. The MCP methods were chosen for their simplicity, ease of plotting, comparability to previous studies and assumed independence of the statistical properties of the UD (Harris *et al.*1990). The kernel estimator (Worton 1987, 1989) was chosen as it is a non-parametric technique that is more robust than other techniques and allows more than one core area to be identified. Home ranges were calculated only where ≥ 20 location fixes were obtained and an asymptote was reached with increasing numbers of fixes.

Home ranges were calculated using the harmonic mean fix as the centre of activity. The harmonic mean fix is the fix where the inverse reciprocal mean distance to all the other fixes is minimal (Spencer and Barrett 1984) and is more robust than other measures (Kenward and Hodder 1996). Fixed kernel, rather than adaptive kernel, methods were used in this study because they are more appropriate for highly

clumped and large data sets (Lawson and Rodgers 1997) and do not produce unacceptable expansion of the outermost contours (Kenward and Hodder 1996). In addition, fixed kernel methods use a smoothing parameter of a fixed value over the plane, while the adaptive kernel varies the smoothing parameter so that areas with a low concentration of points have higher values and are therefore smoothed more than areas with a high concentration of points (Worton 1989).

Fix resolution, which is a boundary strip created around polygon edges, was set at zero in this study to allow comparison with other studies where boundary strips are suppressed. RANGES V (Kenward and Hodder 1996) was selected as the most appropriate software package for home range analysis as it is more suitable for large data sets and provides the widest variety of algorithms for calculating home-range estimators (Lawson and Rodgers 1997). In addition, RANGES V has the greatest number of user-selected options for calculating each estimator (Lawson and Rodgers 1997).

3.4.7. Habitat utilisation

Many studies use radiotracking data to examine habitat use and the various methods have been reviewed by Alldredge and Ratti (1986), White and Garrott (1990) and Palomares and

important aspect of animal ecology. Habitat preference occurs when a habitat type is used more than expected from its availability (i.e. non-random) and is useful when used as a

statements about habitat preference cannot be made because the proportional use of one habitat type is not independent of the remaining habitat types (Aebischer *et al.* 1993), and other factors constraining use of preferred habitats, such as competitors or predators, can be rarely removed.

Methods for determining habitat preference. The most widely used statistical technique for assessing whether habitats are used randomly by an animal or if selection exists, is a Chi-square goodness-of-fit test of whether the observed habitat use is equal to expected use (White and Garrott 1990). This method, however, does not identify which habitats are avoided or preferred. To overcome this problem Neu *et al.* (1974) constructed confidence intervals for each habitat based on the Bonferroni *z*-statistic. Although the Neu method (Neu *et al.* 1974) identifies where habitat selection occurs, it does not compare the relative importance of each habitat type with respect to another. The Johnson method (Johnson 1980) ranks both the utilisation and availability of each habitat and then uses the difference between the ranks as a measure of preference. This method, however, does not test for habitat selection for each animal but uses each animal as an observation to test for preference by the population. Compositional analysis (Aebischer *et al.* 1993), which uses log-ratios to examine proportional habitat use and allows the ranking of preferred habitats, overcomes most of the problems associated with previous methods, and was therefore used in this study. This method uses the radiocollared animal as the sampling unit and thereby avoids problems such as statistical dependence upon numbers of radio locations, non-independence among radio locations and allows separation of within-animal and between-animal variation. In addition, compositional analysis considers habitat types simultaneously, thereby reducing the likelihood of type I errors that are associated with multiple applications of the same statistical test (Aebischer and Robertson 1992). Further, compositional analysis allows powerful statistical tests, such as ANOVA-like techniques, to be used to test various hypotheses about habitat use between groups (e.g. age and sex).

In this study, compositional analysis was used to determine whether habitat use differed from random, by converting proportional habitat use and habitat availability to log-ratios, using open woodland as the denominator. The arbitrary choice of denominator does not affect the results (Aitchison 1986). The log-ratio differences between use and availability were then compared using a two-factor ANOVA, with a probability of < 0.05 indicating non-random utilisation of available habitats. Where habitat utilisation was significantly non-random, the habitat types were ranked according to utilisation by constructing a ranking matrix based on mean pair-wise differences between log-ratios (Aebischer *et al.* 1993). For easier interpretation, mean log-ratio differences were then replaced by their sign. A row of positives indicated that the particular habitat type was most preferred (highest rank), while a row of negatives indicated it was least preferred (lowest rank). Signs were tripled if significantly *t*-test. This method therefore ranked habitat types according to utilisation, from most preferred to least preferred, and indicated when different ranks represented statistically significant differences in their relative utilisation of the corresponding habitat types.

Habitat availability. Measures of habitat use are often compared with some measure of habitat availability, which is usually defined from the total study area (Aebischer *et al.* 1993). The boundaries of a study area are defined arbitrarily by the researcher and can have a large effect on the conclusions drawn (Aebischer and Robertson 1992). In this study, habitat availability was evaluated separately for each of the four study sites as marked habitat differences were apparent between sites. The site was defined as the smallest minimum convex polygon that included all home ranges of cats from that site (Quinn 1997).

Habitat map. Four broad habitat types were delineated on aerial photographs of the entire study area (scale 1: 50,000 and 1: 12,500) according to the number of trees present (Fig. 3.6). The habitat types comprised 1) mudflats, 2) grassland, 3) open woodland and 4) open forest. Mudflats were areas devoid of trees and shrubs which were between the low and high water marks of Lake Burrendong (Fig. 3.7a). These areas were inundated with water at times, while at other times were exposed with a sparse covering of grass when the dam level was low. Grassland habitats were areas with ≤ 3 trees/ha (Fig. 3.7a and b). Open woodland habitats comprised >3-10 trees/ha (Fig. 3.7b), while open forest habitats had denser cover with >10 trees/ ha (Fig. 3.7c). No distinction was possible between tree type or presence of understorey from the aerial photos. Patches less than one hectare were ignored as a hectare was beyond the resolution of the radiotracking data.

Classifications of habitat types from aerial photos were ground-truthed to verify classification and improve accuracy. A 20 km transect was established across the entire study area (on roads), with classification checks made every 500 m (n = 20 spots). Comparisons were made by an independent observer between my visual classification of the habitat types at each spot and that delineated on the habitat map. The habitat map was accepted as sufficiently accurate as 90% of visual classifications corresponded to those delineated on the map.

Habitat boundaries were digitised and polygons formed for each habitat type using a Geographic Information System (ARC/INFO). The habitat map was then converted to raster format where the cell size was 0.01, equivalent to one hectare. Radio locations were overlaid with the digitised map to obtain the proportion of habitat types utilised by individual animals, using RANGES V.

Measurement of error.

that the habitat type is assigned correctly. However, even where data are precise, the confidence ellipse of a location may overlap more than one habitat type. Methods to overcome these problems include, excluding these boundary locations or randomly assigning the location to one of the habitats (White and Garrott 1986). Neither of these methods is appropriate, however, if habitat selection is of interest and data sets are small. A third approach is to ignore the confidence ellipse of the location and record the habitat type at the estimated location. This approach is valid where the habitat type does not affect the radiotracking system. In this study, this latter approach was used to determine habitat utilisation as no effect of habitat was found on the radiotracking system (see *Accuracy of radiotelemetry*).

Errors in radiotracking can affect the detection of habitat selection by lowering the power of tests (White and Garrott 1986). When patch size is small relative to location precision, then the probability of a Type II error is increased. Type II errors occur when the researcher fails to reject the hypothesis of no habitat preference when the animal is actually selecting habitats. Therefore, statistics must be used in the same units of measurement (area) for the patch size and triangulation precision (Salz and White 1990). For this reason, habitat patches that were less than a hectare were ignored in constructing the habitat map, and the scale of the map was coarse to accommodate the coarse resolution of radiotracking data.

Levels of habitat preference. Habitat preference was examined on two levels because of the difficulties in defining availability and the different levels of choice faced by an animal (Johnson 1980, Aebischer and Robertson 1992). These stages were: 1) home range selection within an arbitrarily defined study area; and 2) habitat use within the home range. For example, a particular habitat may not be important in terms of percentage area of a home range, but it may be used more intensively than other habitats within the home range. In this study, habitat preference was expressed as the proportional use of habitat in: 1) the home range compared to availability at the study site; and 2) location fixes compared to availability in the home range.

Diurnal versus nocturnal habitat use. Many studies examining habitat preference have disregarded the time of day in which locations were obtained, and so may have underestimated foraging habitat, if the locations were obtained on inactive animals (review in Palomares and Delibes 1992). To overcome this problem, some studies have considered day and night habitat use separately, assuming that one period approximates resting time, and the other activity (e.g. Haroldson and Fritzell 1984). This approach was adopted in this study.

Home range methods and study animals. Home ranges for the habitat analyses were delineated using the 95% minimum convex polygon (MCP 95) method. The choice of MCP 95 was based on its widespread use in home range (Harris *et al.* 1990) and habitat selection studies (e.g. Aebischer *et al.* 1993). In addition, the kernel estimator is a probabilistic method and therefore suffers from problems associated with serial correlation as it assumes independence between points. As with the home range size analyses, only home ranges with ≥ 20 location fixes and that reached an asymptote with increasing numbers of fixes were included in the habitat analyses. Habitat composition (proportions of each habitat type) of the respective sites and home ranges (MCP 95) of individual cats were determined using RANGES V. Similarly, the proportion of location fixes in each habitat type was calculated for individual cats. Where a habitat was available but not used, it was assigned a value of 0.01 (Aebischer *et al.* 1993).

CHAPTER 4

FEEDING ECOLOGY AND POPULATION DYNAMICS OF THE FERAL CAT IN RELATION TO PREY AVAILABILITY

4.1. INTRODUCTION

Feral cats have been implicated in the decline of numerous species of native mammals throughout Australia (Dickman *et al.* 1993, Short and Smith 1994, Smith and Quin 1996) and dietary studies have shown that cats prey on vulnerable and endangered mammals (Seebeck *et al.* 1991, Horsup and Evans 1993). Although the introduced European rabbit is the major prey for cats where it is abundant in Australia (Jones 1977, Bayly 1978, Mahood 1980, Jones and Coman 1981, Catling 1988, Paltridge *et al.* 1997), predation on native fauna increases when rabbit numbers decline (Catling 1988, Pech *et al.* 1992). Individual variation in prey preference (Leyhausen 1979, Konecny 1987, Gibson *et al.* 1994) may also threaten native fauna when cats select a particular prey species disproportionately to their abundance. Despite increasing evidence for the impact of feral cats on native fauna (review in Dickman 1996), the feeding ecology of feral cats in Australia is restricted to 16 published studies on diet (review in Dickman 1996, Martin *et al.* 1996, Paltridge *et al.* 1997). Of these studies, only one has examined the influence of prey availability on dietary composition (Catling 1988).

Although feral cats are sometimes regarded as having a beneficial role in controlling pest species, such as rabbits, house mice and black rats (e.g. Tidemann *et al.* 1994), their ability by

numerical responses (Boutin 1995). Recent experimental evidence from semi-arid Australia has demonstrated that feral cats and foxes could together exert a regulatory role on medium-density rabbit populations (Pech *et al.* 1992). However, at high rabbit densities, predation was found to be inconsequential, and at low rabbit densities, cats shifted to a broader range of alternative prey species (Catling 1988). This ability of cats to shift between prey species as prey abundance fluctuates has invoked concern from wildlife managers that the spread of Rabbit Calicivirus Disease (RCD) may have a damaging effect on native fauna where rabbit numbers decline (Newsome *et al.* 1997).

The aim of this chapter is to examine the diet and abundance of feral cats in relation to prey availability. This chapter also provides comparative data on cat diets at one study site, before and after a large decline in rabbit abundance, which coincided with the arrival of RCD. In addition, the diet of two individual cats is investigated in detail from collections of their scats at latrines.

4.2. METHODS

General methods for scat collection, prey identification and cat and rabbit abundance indices (spotlight counts) are described in Chapter 3. This chapter presents data on cat scats collected randomly throughout the study area, and cat and rabbit abundance indices, for the period of July 1994 to June 1997.

4.2.1. Scat collection at latrines

In addition, single collections were made of scats found in two cat latrines and the data analysed separately. The latrines each occupied a maximum area of 30 cm by 15 cm and were located 5 km apart. The first latrine was among rocks, and the second in soft soil beneath a low overhanging branch. Given the usually solitary nature of feral cats (Leyhausen 1965), it was assumed that only one adult cat (cat A and cat B) visited each latrine. Cat A latrine (*n* =

early November in 1995. It was assumed that the cat defecated only in the latrine and that

n = 44 scats)

represented an estimated six weeks feeding during mid October to late November in 1996. Both cats were female, and cat B was observed with kittens at the time of scat collection. Smaller scats that were assumed to be those of kittens were excluded from the analysis.

4.2.2. Estimates of minor prey populations

Indices of prey abundance were obtained for four other potential prey groups, carrion, small mammals, reptiles and grasshoppers, at four to eight replicate sites between May 1995 and January 1997. Distances between sites ranged from one to ten km.

Carrion abundance was recorded opportunistically while driving throughout the study area in most months from August 1995 to January 1997. Approximately 50 km of tracks were traversed each month, encompassing all areas where scats were collected. All dead mammals observed were counted as carrion and the data expressed as the total number of carcasses seen per 50 km. Carrion counts were assumed to be accurate.

Small mammal abundance was determined every three months from May 1995 to December 1996 using standard Elliott trapping techniques (Catling and Burt 1997). Twenty traps were set in open woodland at each of seven sites for three consecutive nights, every three months. Trapped animals were identified, weighed, sexed, and then released. Animals were marked on the top of the head with liquid paper, which remained at least for the duration of the trapping session. The abundance of mammals was expressed as the number captured per 100 trap nights. Captured reptiles were also identified and released.

Reptile abundance was determined with active searches on foot at four sites each month from November 1995 to January 1997. Searches were conducted for one hour between 11 am and 3 pm at a time when reptiles were considered to be most active. To reduce wariness and to preserve habitat, standard transects were not established nor rocks and debris overturned. Data were expressed as the number of reptiles seen per hour of search time.

Grasshoppers were counted on standard walking transects (100 m long) at eight sites each month from December 1995 to January 1997. Grasshoppers that took off or landed one metre either side of the transect were counted. Counts were conducted on cloudless days to reduce weather effects on grasshopper activity (Mann *et al.* 1980). Abundance was expressed as the mean number per hectare.

4.2.3. Data analysis

Seasons were defined as summer (December to February), autumn (March to May), winter

to confirm that sample sizes were large enough to warrant seasonal analysis of diet. Seasonal dietary differences in the percentage volume of each prey group in the scats were examined using a general linear model. Season, treatment, site and fox removal were fitted to the model as fixed factors. Year was incorporated into the error term of the model. Each prey group was tested separately to avoid problems associated with the lack of independence between groups. Prey groups that were not often recorded in the diet were log-transformed (log (X +1)) to reduce the clumping of residuals resulting from a large number of zero counts (Zar 1984).

The dietary and numerical responses of cats to changing prey densities were examined using the Pearson product-moment correlation coefficient. Lag phases of 1-6 months were examined in order to assess delayed responses in cat abundance to changes in prey density (Pech *et al.* 1992).

A dietary response curve was fitted to the observed relationship between rabbit abundance and the proportion of scats containing rabbit by eye. Although this curve was constrained to asymptote at 100%, given the nature of percentage data, it was considered analogous to a true Holling functional response curve (Holling 1959). Despite numerous limitations being associated with measuring functional responses using dietary changes reflected in scats (Boutin 1995), percentage occurrence data were used as an index of the number of rabbits eaten/cat/day under the following two assumptions. Firstly, cats deposited only one scat per day and secondly, any rabbit hair detected in a scat represented the remains of only one rabbit. In support of these assumptions, previous studies have found that healthy cats deposit around one scat per day (Howard 1957, Fitzgerald and Karl 1979) and the remains of multiple adult rabbits were not usually detected in cat stomachs at Yathong in NSW (P. Catling, pers. comm.). Although an average-sized feral cat (4kg) consumes about 260 g of wet flesh per day (B. Green, pers. comm.), well below the weight of an adult rabbit (> 800 g), it is assumed that cats do not cache prey remains and do not kill more than one rabbit in one day. Where these assumptions are not met (e.g. partial prey consumption, multiple scats per day, or prey caching), rabbit consumption will be underestimated.

Variation in dietary composition (frequency of scats containing a particular prey group) between individual cats and a sample of scats from the cat population at Burrendong was

tested separately.

4.3. RESULTS

A total of 499 cat scats was collected throughout the study from July 1994 to June 1997 (about 20 scats/month). Most scats (35%) were found on rabbit warrens where little attempt had been made to bury them. In addition, 101 scats were collected from two cat latrines and data from these were analysed separately.

4.3.1. Overall diet

Mammalian remains occurred in all scats and comprised 87.5% by volume of the overall diet. Rabbits were the most important prey both by volume (V) (68.4%) and occurrence (O) (81.6%). They were identified in scats in all sample months, except May 1997 when only five scats were collected. Carrion, mostly eastern grey kangaroo (O 17%, V 8%) and sheep (O 4%, V 3%), was the next most important prey group by volume (11.5%) and occurred in 21.5% of scats. Cattle (O 0.6%, V 0.4%) and pigs (O 0.2%, V 0.1%), which were assumed to be carrion, were eaten infrequently. Invertebrates (mostly Orthopterans) occurred in 41.5% of scats but were a minor component by volume (7.5%). Other mammalian prey included brushtail possums (O 4.6%, V 2.4%), house mice (O 6.2%, V 3.2%), black rats (O 2.6%, V 1.4%) and a dunnart (*Sminthopsis* sp.) (O 0.2%, V 0.006%). Vegetation (mostly sweet briar fruits and grass spp.) (O 26.3%, V 3.6%), birds (O 4.2%, V 0.8%) and reptiles (O 3.4%, V 0.3%) were minor components of the diet. A complete list of food items identified is included in Appendix 2.

4.3.2. Seasonal variation in diet

A sample of 436 scats was classified as fresh (< one month old) based on appearance and smell, and included in the seasonal analyses. Older scats (n = 63) that were used in the overall dietary analyses were excluded to avoid potential confounding of the seasons.

Rabbit was the major prey in all seasons (except for the small sample in autumn 1997) (Fig. 4.1). Carrion tended to be eaten more frequently in winter and spring when it also contributed a greater amount to the mean scat volume (Fig. 4.1). Invertebrates were eaten throughout the year but the species composition varied seasonally. Those invertebrates eaten during winter and spring comprised largely beetles (Coleoptera) and cockroaches (Blattodea), while grasshoppers (Orthoptera) were eaten most often in summer and autumn.

Few significant seasonal differences in the diet of cats (% volume) were detected. However, invertebrates (F = 5.68; d. f. = 3, 33; P = 0.003) contributed less and possums (F = 3.41; d. f. = 3, 24; P = 0.034) more to the mean scat volume in winter and summer respectively (Fig. 4.2). No further seasonal comparisons were significant (P > 0.05).

4.3.3. Diet in relation to prey availability

Peaks in rabbit abundance occurred in early summer in both 1994 and 1995, while in 1996, numbers were substantially lower following the arrival of RCD in June 1996 (Fig. 4.3). Rabbit remained important in the diet even at low rabbit densities during the drought and post-RCD (Figs. 4.3 and 4.4). Correlation analyses showed a significant dietary response by cats to changes in rabbit abundance overall (r = 0.50; n = 18; P = 0.03) (Fig. 4.3). Predation on rabbits tended to be more severe when rabbits were on the decrease (r = 0.49; n = 11; P = 0.13) than when on the increase (r = 0.25; n = 7; P = 0.57) (Fig. 4.4), however, the relationship was not significant.

Of 407 occurrences of rabbit detected in scats, 36 were identified as adult (> 800 g), 31 as subadult (≤ 800 g) and the remainder were of unknown age. In winter 1995, when rabbit numbers were low during the drought, most rabbits eaten and that

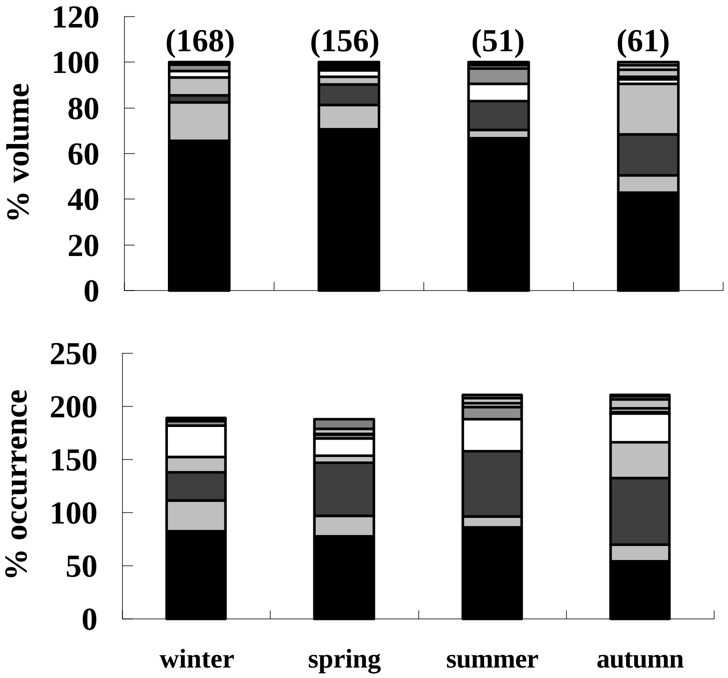

Fig. 4.2. Overall seasonal variation in the diet of cats from July 1994 to June 1997 (*n* = 436 scats). Years were pooled. Legend as for Fig. 4.1.

could be aged were adults (82%, *n* = 23 aged rabbits). In spring 1995, most rabbits eaten were subadult (100%, *n* = 11 aged rabbits) at a time when a marked increase in subadult rabbits was also observed (R. Molsher, personal observation). Insufficient sample sizes (*n* < 10 scats) of aged rabbits in other seasons precluded further comparisons.

Cats tended to eat carrion more often in late winter and early spring when carrion abundance was generally higher, but the relationship was not significant (*r* = 0.13; *n* = 12; *P* = 0.67) (Fig. 4.3). Carrion abundance declined over late spring and summer in 1995, increased in autumn 1996, and reached a peak in July 1996 (mostly rabbit carrion) with the arrival of RCD (Fig. 4.3). Carrion recorded in other months, however, comprised mostly kangaroos that had been culled.

Correlation analyses showed no significant dietary response by cats to changes in small mammal abundance (*P* > 0.05). Few small mammals were trapped over the

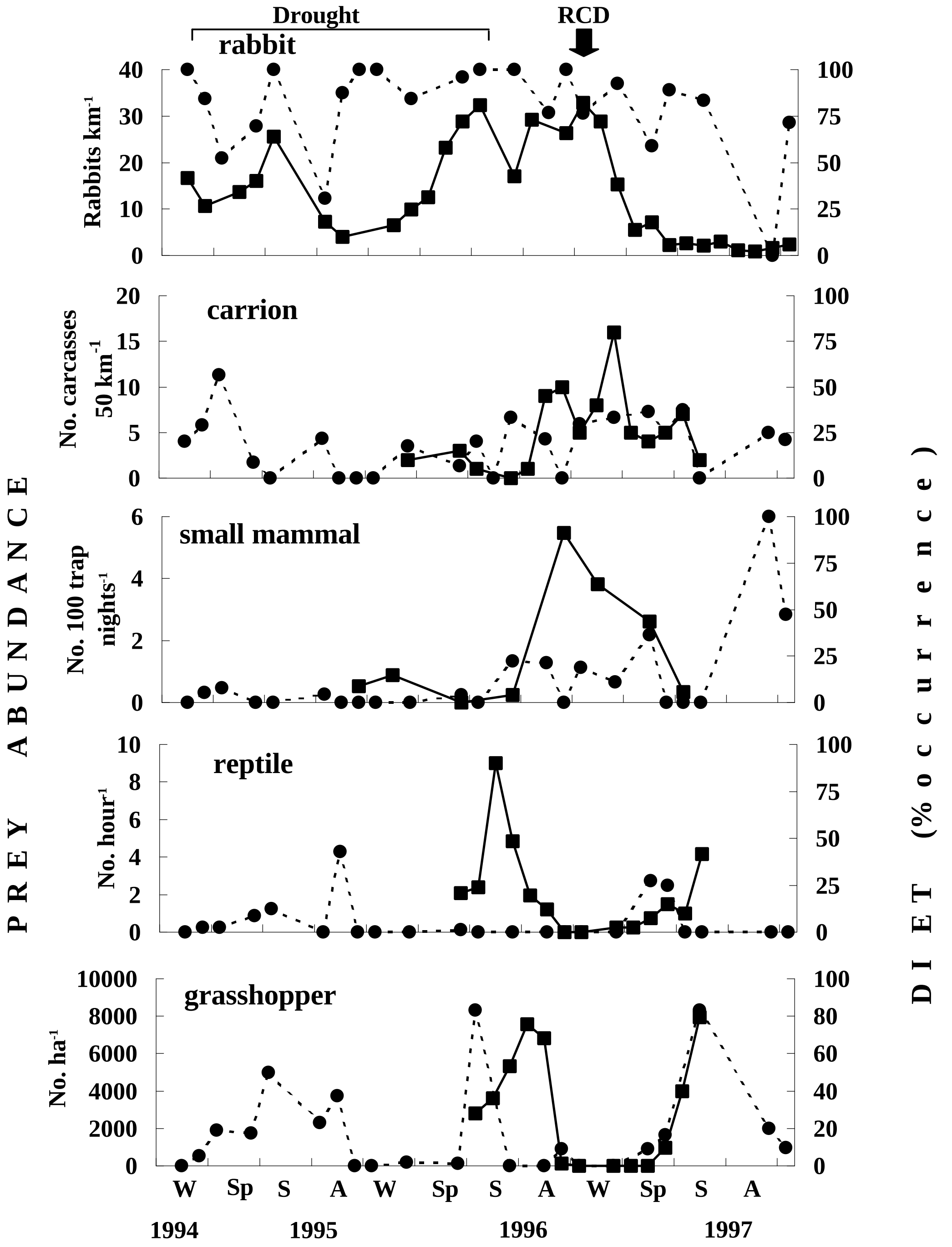

Fig. 4.3. Cat diet in relation to prey availability for five major prey groups.
--● Diet —■ Prey Availability

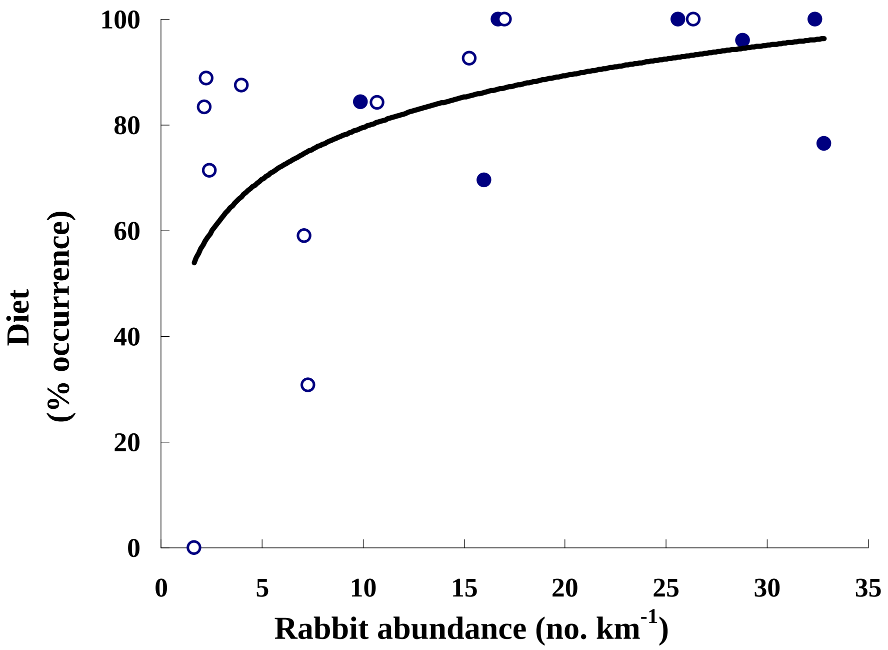

Fig. 4.4. Dietary response of cats to changing rabbit densities (n = 436 scats). Data are divided into periods when rabbit numbers were on the ● increase (r = 0.25), and ○decrease (r = 0.49). The line is a dietary response curve fitted by eye.

summer period and numbers were low following the 1995 drought (Fig. 4.3). The most common small mammal species trapped was the house mouse, followed by the common dunnart (*Sminthopsis murina*), although its distribution was less ubiquitous. Mammal species captured in low numbers included the black rat and the yellow-footed antechinus (*Antechinus flavipes*). Reptiles were captured as non-target species over spring and summer.

No significant dietary response to reptile abundance was found ($P > 0.05$). Most reptiles were eaten from late spring to autumn, while numbers of reptiles sighted were highest in midsummer in both 1996 and 1997 (Fig. 4.3). Few reptiles were observed over the colder months from May to August 1996 (Fig. 4.3). Most reptiles observed were skinks (Family Scincidae); the most common species was *Egernia striolata*.

Cats ate grasshoppers more often in summer, which tended to correspond to increases in grasshopper abundance, but the dietary response was not significant ($r = 0.42$; $n = 9$; $P = 0.27$) (Fig. 4.3). Grasshopper abundance peaked over late summer and autumn in 1996, declining rapidly to zero over winter and spring, before increasing again the following summer (Fig. 4.3).

4.3.4. Post-RCD diet

Cats continued to prey heavily on rabbits after the arrival of RCD at Burrendong in June 1996, despite a decline in rabbit abundance by over 90% (Fig. 4.3). Ten months post-RCD, an increase in house mouse consumption by cats was detected. House mice occurred in 100% of scats in autumn and 43% in winter in 1997 (Fig. 4.1). House mice had not occurred in more than 19% of scats in any month in the 2.5 years prior to this period.

4.3.5. Indices of abundance

Cat and rabbit abundance were not correlated significantly with lag phases of 0, 1, 2, 3, 4 and 5 months ($P > 0.05$) (Fig. 4.5). With a six month lag period, however, a significant negative correlation was found ($r = -0.40$, $n = 24$; $P = 0.05$), indicating that cat numbers were low six months after high rabbit numbers were recorded. Cat abundance also tended to be correlated with the abundance of carrion ($r = 0.44$; $n = 14$; $P < 0.10$), small mammals (4 month lag, $r = -0.66$; $n = 7$; $P < 0.10$), reptiles (1 month lag $r = -0.52$; $n = 13$; $P < 0.10$, 2 month lag $r = -0.61$; $n = 13$; $P < 0.05$) and grasshoppers (3 month lag $r = -0.51$; $n = 12$; $P < 0.10$).

4.3.6. Diet of individual cats

Rabbits were the main prey, both by volume (Fig. 4.6) and occurrence, for both cats A and B in spring 1995 and 1996, as for all cats. However, differences between individual cats and the population in the importance of other prey types were found. Cat A ate carrion ($G = 7.15$; d. f. = 1; $P < 0.05$), reptiles ($G = 13.36$; d. f. = 1; $P < 0.001$), invertebrates ($G = 12.35$; d. f. = 1; $P < 0.001$) and vegetation ($G = 5.60$; d. f. = 1; $P < 0.05$) significantly more often than the population of cats, in spring 1995. Similarly, cat B ate birds significantly more often ($G = 18.51$; d. f. = 1; $P < 0.001$), and carrion ($G = 6.98$; d. f. = 1; $P < 0.05$), reptiles ($G = 13.04$; d. f. = 1; $P < 0.001$), and invertebrates ($G = 7.64$; d. f. = 1; $P < 0.05$) significantly less often,

a rubber washer (Cat A) and a sugar glider, *Petaurus breviceps* (Cat B).

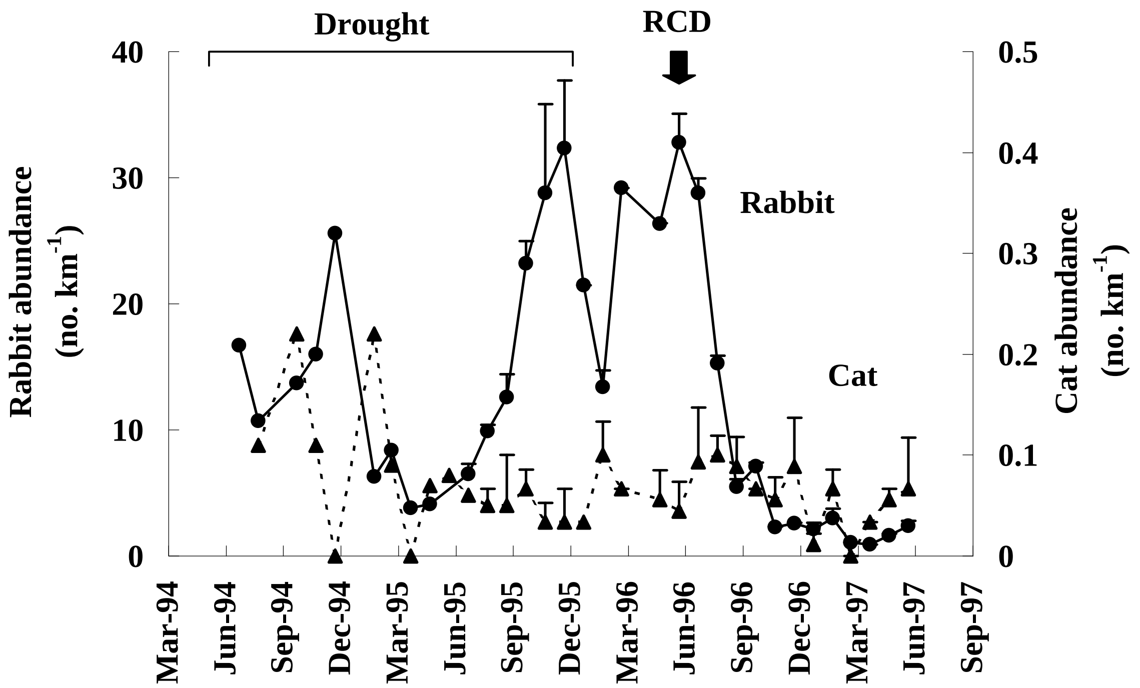

Fig. 4.5. Abundance of cats and rabbits recorded in spotlight transects from July 1994 to June 1997. Means and standard errors are shown. Data collected by the VBCRC Predator-Prey Project.

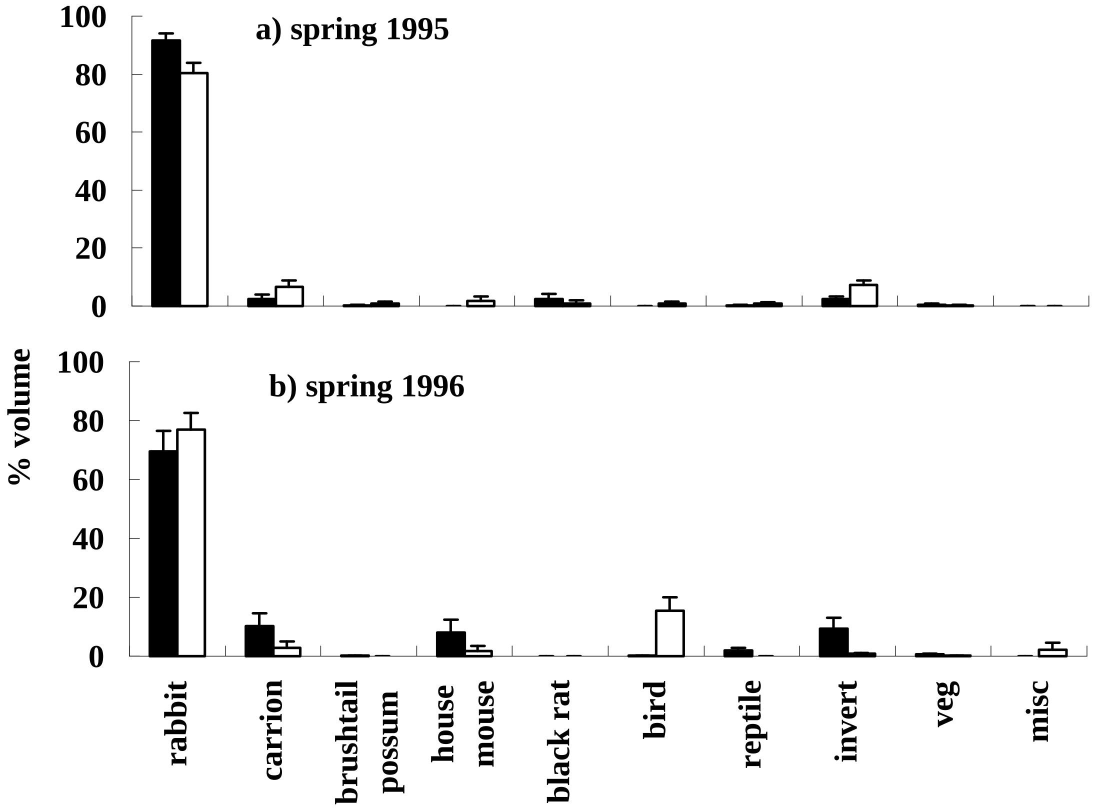

Fig.4.6. Dietary comparison between individual cats (A and B; *n* = 57 and 44 scats) and the overall diet of cats recorded at Burrendong for (a) spring 1995 (*n* = 76) and (b) 1996 (*n* = 36). Means + s.e. are shown. (■overall diet, □individual cats: A in spring 1995 and B in spring 1996).

4.4. DISCUSSION

4.4.1. Overall diet

Mammals dominated the diet of feral cats at Burrendong, occurring in all 499 scats examined. By occurrence, rabbit was the single most important food item (81.6%) and carrion an important secondary food (21.5%). Invertebrates (41.5%), vegetation (26.3%), other mammalian prey (13.6%), birds (4.2%) and reptiles (3.4%), were generally minor components of the diet. Few significant seasonal differences in diet were found; in consumption of possum and invertebrates only.

4.4.2. Diet in relation to prey availability

Rabbit was the staple prey for cats in this study, as elsewhere where rabbits are common (Bayly 1978, Mahood 1980, Jones and Coman 1981, Strong and Low 1983, Catling 1988, Paltridge *et al.* 1997). The lack of seasonal variation in rabbit consumption may be due to the generally high abundance of rabbits at Burrendong prior to RCD, or to the differences in rabbit abundance between years. Seasonal changes in rabbit consumption have been recorded in some studies where consumption was highest in spring and summer during rabbit breeding and lowest in winter (Fitzgerald and Karl 1979, Jones and Coman 1981, Catling 1988), although the data in these studies were not tested statistically.

Almost half the ingested rabbits that could be aged (n = 67) were subadult. Adult rabbits were consumed mostly at the end of the drought when environmental conditions were unfavourable and predation may have been high on sick or weak individuals. Cats are not well adapted to hunting adult rabbits (Parer 1977, Gibb *et al.* 1978, Corbett 1979) and several dietary studies elsewhere show selection for juveniles (Jones 1977, Fitzgerald and Karl 1979, Liberg 1984a, Catling 1988). Body size may be important in this respect: in pastoral areas in Western Australia, only larger male cats ate rabbits (age unknown) (Martin *et al.* 1996).

Carrion (mostly eastern grey kangaroo and sheep) was an important secondary food in this study and tended to be eaten more often in winter and spring. Increased carrion consumption over winter has been recorded in other studies when rabbit consumption has declined (Jones and Coman 1981, Catling 1988). The high incidence of carrion in the diet of cats at Burrendong (21.5%) contrasts with previous studies that have found carrion to be a minor component of the diet (Coman and Brunner 1972, Jones 1977, Jones and Coman 1981, Martin *et al.* 1996, Paltridge *et al.* 1997), or eaten only during drought (Catling 1988, G. Edwards pers. comm.). In New Zealand, cats scavenged carcasses only after the flesh had already been exposed (Langham 1990). This unusually high occurrence of carrion in the diet at Burrendong may be due to the high abundance of kangaroo carcasses from regular culling and the high density of carnivores that are able to open carcasses, such as foxes, pigs and eagles.

Brushtail possums were minor prey for cats at Burrendong with occurrence in 4.6% of scats. Possum was significantly more important in the diet during summer, which may have reflected increased predation on subadults that had become independent from their mothers. Seasonal variation in brushtail possum consumption by feral cats has also been recorded in New Zealand, with adult possums being eaten in winter as carrion, and young possums in spring when they first become independent (Fitzgerald and Karl 1979, Langham 1990).

Bird remains were in few scats (4.2%). In contrast to popular belief, birds are seldom an important prey item for feral cats (Coman and Brunner 1972, Clevenger 1995, Paltridge *et al.* 1997), presumably as they are difficult to catch (Turner and Bateson 1988). Birds become important food for cats when the abundance of mammalian prey is low or absent, such as on islands (Fitzgerald and Veitch 1985, Kirkpatrick and Rauzon 1986). Individual cats, however, may become skilled at hunting birds; this may have occurred with cat B in this study, where bird remains occurred in 41% of scats.

Reptiles were also a minor component of the diet (4.3%) which is consistent with other studies where mammalian prey were also present (Coman and Brunner 1972, Karl and Best 1982). As in other studies, reptiles were more common in the diet during the warmer months (Triggs *et al.* 1984, Catling 1988, Paltridge *et al.* 1997) when they are most accessible.

Invertebrates (mostly grasshoppers and beetles) occurred in 41.5% of scats at Burrendong but comprised a minor component by volume (7.5%). In most studies, invertebrates are a minor but consistent component of the diet of cats (Karl and Best 1982, Jones and Coman 1981), with orthopterans being the dominant group eaten when abundant (Bayly 1976, Fitzgerald and Karl 1979, Jones and Coman 1981, Fitzgerald and Veitch 1985, Tidemann *et al.* 1994, Martin *et al.* 1996, Paltridge *et al.* 1997). Seasonal declines in invertebrate consumption over winter were recorded at Burrendong and elsewhere (Catling 1988), presumably reflecting general declines in invertebrate activity and abundance over the colder months.

Vegetation was consumed frequently by cats in this study (26.3%) but consisted mostly of a few strands of grass which may have resulted from incidental ingestion while foraging for invertebrates. Plant matter is not a necessary component of the diet of felids as it is for canids

(Lloyd 1980) and is usually a minor component of the diet of feral cats (Bayly 1978, Triggs *et al.* 1984) or not consumed at all (Catling 1988).

4.4.3. Dietary response

A significant dietary response by cats was found for rabbits, but not for the other prey groups (carrion, small mammals, reptiles and grasshoppers). Indices of abundance for these latter prey species may not have been sufficiently sensitive to detect small fluctuations in prey abundance.

Rabbit consumption generally reflected changes in rabbit abundance. Although many assumptions were made when using % occurrence data as an index of the number of rabbits eaten per cat per day, the dietary response curve shown in this chapter was considered analogous to a true Holling Type II or III functional response curve. At low prey densities a Type II curve shows a constant or decreasing slope, while a Type III curve is sigmoidal,

switch their preference to whatever prey is most common (Begon and Mortimer 1981). Although previous studies have shown that cats shift between prey species when the primary prey declines (e.g. Catling 1988), prey switching *sensu stricto* has not been demonstrated in Australia or elsewhere as few dietary studies have simultaneously measured the abundance of multiple prey species (Fitzgerald and Karl 1979, Konecny 1987). In this study, no distinction was possible between Type II and Type III curves given the lack of dietary data at very low rabbit densities where the effect of predators has a greater impact (Boutin 1995). In addition, declines in the rates of kill as prey density decreased, as measured by occurrence in scats, may not have been detected by the dietary analysis in this study.

4.4.4. Post-RCD diet

Cats continued to prey heavily on rabbits after the arrival of RCD at Burrendong in June 1996, despite the relatively low numbers of rabbits. Ten months post-RCD, house mice increased in importance in the diet. However, it was not known whether this increase in house mouse consumption reflected prey switching *sensu stricto* or opportunistic predation on an increased mouse population, as mouse abundance was not measured during this period. Despite the ability of cats to shift between prey species, cats in this study continued to feed on rabbits for some time after numbers had declined by over 90% post-RCD. Delayed dietary shifts by cats after substantial declines in rabbit populations have also been recorded on Macquarie Island (Rush 1992) and in the Flinders Ranges in South Australia (C. Holden pers. comm.). Similarly, kit foxes (*Vulpes macrotis mutica*) in California continued to eat their preferred prey (small mammals), despite a substantial reduction in prey numbers (White *et al.*

1996). Although rabbit densities declined to relatively low levels post-RCD at Burrendong, these densities may still have been sufficiently high for cats to be efficient in catching rabbits so that shifts to alternative prey were not necessary. Alternatively, selective predation may have occurred on subadult rabbits that are unaffected by RCD (Newsome *et al.* 1997), or cats may have been sustained on sick adult rabbits that were caught readily.

4.4.5. Individual variation in diet- the latrines

The ability of individual cats to target particular prey species can threaten the persistence of these species when in low numbers (Gibson *et al.* 1994). In this study, Cat A had a much higher incidence of reptiles and invertebrates in the diet, while Cat B ate more birds than did the overall cat population for the same period. This may reflect patchiness in the distribution of these prey species or variation in prey preference. There is some evidence that hunting strategies of cats differ with age and dominance status and that individuals develop hunting skills that are targeted at particular prey species (Leyhausen 1979). For example, direct observations of the hunting behaviours of feral cats on the Galapagos Islands showed that some cats ate entire grasshoppers, while others ate only the abdomens (Konecny 1987). Similarly, on Christmas Island, male cats ate significantly more plant matter than females (Tidemann *et al.* 1994). Although latrines have not formerly been described for feral cats, they may be related to breeding in females or reflect a recent domestic history for those individuals.

4.4.6. Impact on native prey

Cats preyed on few native mammal species in this study. Native mammals occurred in 4.8% of scats and included the brushtail possum (*n* = 23), a dunnart (*n* = 1) and a sugar glider (*n* = 1). Although this low occurrence may reflect the scarcity of native mammals at Burrendong, cats may still have an impact on the persistence of these species by maintaining them at low

may seldom be found in the diet or not at all, while a prey species that occurs frequently in the diet may be sufficiently abundant to show no predatory effect (Kinnear 1991).

4.4.7. Numerical response

Cat abundance was correlated weakly and positively with carrion abundance and inversely with rabbit (six month lag), small mammal (4 month lag), reptile (1 and 2 month lag) and grasshopper (3 month lag) abundance. However, behavioural changes in habitat use, rather than true fluctuations in population size, may have accounted for these patterns. For example, increased activity by cats in open areas when scavenging carcasses would result in greater detection in the spotlight, while a higher usage of forest habitats during the warmer months, when reptiles and grasshoppers are more active, may have decreased the chance of detection. In addition, spotlighting was not considered a good index of abundance for feral cats as few cats were detected in the spotlight, despite their presence being known through radiotracking (Chapter 5) and observed numbers were highly variable between runs. Possible changes in habitat use by cats and difficulties in estimating cat abundance using spotlight techniques precluded conclusive comments on the numerical response of cats to changes in prey abundance. More research is needed to improve the effectiveness of current techniques for censusing cat populations (e.g. Mahon *et al.* 1998), particularly in forested areas.

4.5. CONCLUSION

Rabbits were the staple prey of cats, while carrion was an important secondary food. Invertebrates, other mammalian prey, vegetation, birds and reptiles were generally minor components of the diet. Few significant seasonal differences in diet were found; however, invertebrates contributed less and possums more to the diet in winter and summer, respectively. A significant dietary response was found to changes in rabbit abundance, but not for the other prey types. Cats continued to prey heavily on rabbits even after a 90% decline in rabbit abundance occurred, which coincided with RCD. House mice increased in importance in the diet ten months post-RCD. Although the abundance of cats was correlated weakly with the abundance of some prey species, behavioural changes in habitat use may have influenced the observed patterns.

CHAPTER 5

HOME RANGE, RANGE OVERLAP AND HABITAT USE OF FERAL CATS

5.1. INTRODUCTION

Knowledge of spatial and social organisation is important in understanding the ecology of a species and also has management implications. For example, information on home range size, overlap and habitat preference can be used to predict population densities, and distances over which diseases may spread (Langham and Charleston 1990). This information can also influence the feasibility of fertility control (Bomford 1990), and can be used to suggest designs for trapping and poison baiting regimes. Numerous studies describe the spatial and social organisation of urban (e.g. Page *et al.* 1992, Mirmovitch 1995) and farm cats (e.g. Panaman 1981, Turner and Mertens 1986, Kerby and Macdonald 1988), but few studies involve feral cats (summarised in Table 5.1). Only two of these have been conducted in Australia (Jones and Coman 1982, Schwarz 1995). Feral cats are defined in this Thesis as free-living cats that have minimal or no reliance on humans, and that survive and reproduce in self-perpetuating populations (Moodie 1995).

Home range size, overlap and habitat use of carnivores can be influenced by factors such as

reproductive requirements, time of day, and intra- and interspecific relations (McNab 1963, Harestad and Bunnell 1979, Macdonald 1983, Carr and Macdonald 1986, Konecny 1987, Liberg and Sandell 1988, Langham and Porter 1991, Lucherini and Lovari 1996). For example, home range size usually increases with body size or metabolic requirements (McNab 1963, Harestad and Bunnell 1979, Gittleman and Harvey 1982), and decreases when food is abundant (Kruuk 1986, Sandell 1989, du Bothma *et al.* 1997). Similarly, negative correlations have been recorded between population density (as a response to abundant food) and home range size (Liberg and Sandell 1988). Inter-sexual differences are also apparent, with the spatial distribution of females being more likely to be influenced by resource availability, while that of males is also influenced by the distribution of potential mates during the mating season (Sandell 1989).

The spatial and social organisation of cats shows great variability (see review in Liberg and

active defense of borders (Leyhausen 1965, Liberg 1980, 1984, Langham and Porter 1991), others mutual tolerance (Apps 1986). Adult females may be solitary, or live in groups, and may or may not tolerate dominant males within their territories (Liberg and Sandell 1988). Much of this variability has been attributed to differences in prey distribution and abundance (Fitzgerald and Karl 1986, Genovesi *et al.* 1995).

In general, where prey is abundant and clumped, home range sizes of cats decrease (Fitzgerald and Karl 1986) and overlap increases (Liberg 1980). Ranges of domestic cats receiving supplemental feeding in urban areas, dockyards and on farms, are generally smaller than those of feral cats (Dards 1978, Macdonald and Apps 1978, Jones and Coman 1982). Cats in such environments may also form groups with overlapping ranges (Dards 1978, Macdonald and Apps 1978, Corbett 1979, Liberg 1980, Panaman 1981, Izawa *et al.* 1982). The information on social and spatial organisation of feral cats, however, is difficult to interpret (Corbett 1979, Jones and Coman 1982, Brothers *et al.* 1985), primarily because sample sizes are small (i.e. < 10 individuals) (Table 5.1).

In this Chapter, the home range size, overlap and habitat use of feral cats is examined at Lake Burrendong during the winter of 1995, prior to fox removal. Inter-individual variation (sex/age) and the influence of rabbit abundance on home range size are also examined. Social organisation is inferred from observed patterns in spatial use.

5.2. METHODS

General methods for trapping, radiotracking, home range analysis, habitat use and rabbit abundance indices are described in Chapter 3. This section gives details of the statistical analyses used to examine the home range and habitat use of feral cats at the four sites in winter 1995 (May to August); prior to fox removal. Rabbit abundance indices were also calculated for the four sites in winter 1995 only. GENSTAT was used for the *t*-tests, ANOVAs, correlation and regression analyses.

5.2.1. Home range size

Overall. In winter 1995, 21 adult cats were radiotracked (730 location fixes) to examine ranging behaviour (home range size, core area size and habitat use). Consecutive locations were separated by at least 30 minutes to reduce dependence between locations. Four home ranges with < 20 location fixes or which did not reach an asymptote with increasing numbers of fixes (Wray *et al.* 1992) were excluded from the home range size analyses. An additional two cats were excluded from the analysis as they died during the radiotracking period and appeared to exhibit abnormal ranging behaviour (i.e. limited movement) prior to death. Home range analyses were conducted on the remaining 15 cats for which 598 fixes were obtained.

Home ranges were calculated using three methods: a) minimum convex polygon (MCP 100); b) MCP 95 including 95% of fixes closest to the harmonic mean centre; and c) kernel analysis which included 95% of all fixes (KE 95). MCP 100 estimates were calculated for comparison with other studies only. The core area of cats was estimated also using the minimum convex polygon and kernel analysis, both including 50% of locations (MCP 50 and KE 50 respectively). Matched pairs *t*-tests were used to compare the estimates obtained using the two methods for home range (MCP 95 and KE 95) and core area (MCP 50 and KE 50) size. As significant linear relationships were found between MCP 95 and KE 95 ($r^2 = 0.52$, $n = 13$; $P = 0.002$) and MCP 50 and KE 50 estimates ($r^2 = 0.79$, $n = 13$; $P < 0.001$), only the MCP 95 and MCP 50 methods were used in subsequent analyses of ranging behaviour.

The effect on MCP 95 of sex and age of individual cats, and site where cats were radiotracked, was examined using a non-orthogonal three-way ANOVA (sex by age by site). Interaction effects were also examined. Sex differences in MCP 100 estimates were examined using a *t*-test to allow comparisons with other studies. Correlation analysis was used to examine the relationship between home range size and rabbit abundance.

Influence of habitat composition. Linear regression was used to examine the relationship between home range size (dependent variable) and habitat composition (within the home range and at the fixes, see Chapter 3) and habitat richness (number of habitat types within the home range). Separate regressions were performed for each habitat type to avoid problems associated with the lack of independence between habitat types. Since home range size did not differ significantly between the sexes ($P > 0.05$), the data were pooled.

Day and night ranges. Day and night range sizes (MCP 95) were examined separately as, despite being primarily nocturnal (Langham and Porter 1991), feral cats can be active by day (Jones and Coman 1982, Artois 1985). In addition, the only other published study on cat spatial use in Australia used solely day fixes (Jones and Coman 1982). Elsewhere, studies of cats have also obtained mostly day fixes (Liberg 1980, Fitzgerald and Karl 1986, Turner and Mertens 1986) with only a few studies collecting night fixes (Corbett 1979, Warner 1985, Konecny 1987, Langham and Porter 1990). For this reason, approximately half the locations were obtained during daylight hours and half at night in this study. In winter, day was defined as that period between sunrise and sunset (0700- 1700), while night was the remaining period (1701 - 0659). Differences between day and night home range sizes (MCP 95) were examined using the matched pairs *t*-test. Twelve cats were used in this analysis, as three cats with < 10 fixes in either the day or night ranges were excluded.

5.2.2. Overlap in home ranges and core areas

Percentage overlaps for each adjacent and/or overlapping pair of home ranges (MCP 95) and core areas (MCP 50) were calculated using the RANGES V program. Adjacent ranges were those that were <500 m apart, which was smaller than the average home range span of any of the cats. Range overlap was also calculated for day and night home ranges (MCP 95) separately. A non-orthogonal two-way ANOVA (sex by age) was used to test for the influence of sex and age (young adult 1-3 years and old adult >3 years) on percentage overlap for adjacent pairs overall, and for day and night periods separately. Percentage overlaps were arcsine transformed so that the data approximated a normal distribution (Zar 1984). Three sex combinations (FF, FM and MM) and three age combinations (YY, YO, OO) were possible (where F = female, M = male, Y = young adult and O = old adult cats). Age determination of cats is described in Appendix 1.

5.2.3. Habitat utilisation

Habitat analyses were conducted on the same 15 cats that had sufficient fixes for the home range size analyses. Four habitat types were defined which included: a) mud flats; b) grassland; c) open woodland; and d) open forest (see Chapter 3). Based on these types, habitat compositions (proportions of each habitat type) in home ranges (MCP 95) of individual cats, at location fixes, and in the four sites, were determined using RANGES V.

Habitat selection was evaluated using compositional analysis (Aebischer *et al.* 1993) on both levels of habitat use: a) selection of a home range from within an arbitrarily defined study area; and b) differential use of habitat types within the home range. Habitat selection was determined using a two-way ANOVA (no blocking) with the log-ratio differences as the dependent variable, and site and habitat as factors. Where significant habitat selection was found, the habitat types were ranked according to utilisation (see Chapter 3). The influences of age and sex on habitat selection were examined using a non-orthogonal three-way ANOVA where the log-ratio difference was the response variable, and habitat, age and sex were fitted to the model as factors. Interaction effects were also examined. Differences between night

and at the fixes, were examined using a two-factor ANOVA (habitat by day/night), where the percentages were arcsine transformed prior to analysis.

5.3. RESULTS

5.3.1. Home range size

Overall. Home range sizes of cats in winter 1995 (n = 15 cats, 598 location fixes) ranged from 17 to 747 ha (MCP 100 and MCP 95) and from 25 to 575 ha (KE 95) (Table 5.2). Core areas ranged from 2.5 to 165 ha (MCP 50) and from 7 to 152 ha (KE 50) (Table 5.2). Kernel estimates were significantly larger than those estimated with the minimum convex polygon method for home range (MCP 95 and KE 95) (t = 3.84; d. f. = 14; $P < 0.001$) and core areas (MCP 50 and KE 50) (t = 2.68; d. f. = 14; P = 0.02).

Male home ranges (MCP 95 $\bar{x}$ = 284 ha, n = 11) tended to be larger than those of females ($\bar{x}$ = 151 ha, n = 4) but were not significantly so (F = 4.22; d. f. = 1, 4; P = 0.11). MCP 100 estimates were also not significantly different between males ($\bar{x}$ = 423 ha, n = 11) and females ($\bar{x}$ = 238 ha, n = 4) (t = 1.71; d. f. = 13; P = 0.11). No difference in range size was found between young adult (1-3 years, $\bar{x}$ = 271ha, n = 7) and old adult cats (>3 years, $\bar{x}$ = 221ha, n = 8) (F = 1.24; d. f. = 1, 4; P = 0.33).

Mean home range sizes (MCP 95) varied between sites, ranging from 176 ha at Gunnel Creek to 329 ha at Harrys Creek, but were not significantly different (F = 1.88; d. f. = 3, 4; P = 0.28)

(Fig. 5.1). Site differences also occurred in rabbit abundance (Fig. 5.1). Home range sizes (MCP 95) tended to be smaller at higher rabbit densities but the relationship was not significant ($r^2 = 0.063$; $P = 0.72$).

Influence of habitat composition. Home range size was not related significantly to habitat composition of the home range, proportion of fixes in each habitat, or habitat richness ($P > 0.05$).

Day and night ranges. Day range sizes ($\bar{x}$ = 211 ha) were not significantly different to night ranges ($\bar{x}$ = 193 ha) overall ($t = 0.55$; d. f. = 11; $P = 0.59$), or for sexes separately (Female $t = 0.05$; d. f. = 3; $P = 0.96$; Male $t = 0.57$; d. f. = 7; $P = 0.59$) (Table 5.3).

Table 5.2. Home range and core area size (ha) of 21 radiocollared cats in winter 1995 (730 location fixes).

Study site and					**Home range area**			**Core area**	
animal ID	**No.fixes**	**Age (yrs)**	**Sex**	**A/tote**	**MCP 100**	**MCP 95**	**KE 95**	**MCP 50**	**KE 50**
Dog Trap									
216380	54	1.5	M	Yes	240	162	224	41	19.5
216620	49	1.5	M	Yes	484	342	541	66	84
150044	65	>3	M	Yes	348	322	286	84	96
_151763_	_18_	_1.5_	_M_	_No_	_208_	_120_	_333_	_14_	_35_
Gunnel Creek									
216340	24	>3	M	Yes	18	17	25	6	7
216160	37	1.5	M	Yes	390	364	459	76	84
216320	21	>3	M	Yes	674	246	575	54	110
216420	39	1.5	F	Yes	221	75	247	17	23
_216056_	_19_	_1.5_	_M_	_No_	_680_	_639_	_1370_	_142_	_39_
_216440_	_16_	_>3_	_M_	_No_	_682_	_649_	_870_	_117_	_263_
Devils Hole									
216040	20	>3	M	Yes	372	131	488	2.5	13
216360	23	1.5	M	Yes	319	318	422	13	51
216120	46	>3	F	Yes	151	102	126	7.5	11
_*216400_	_30_	_>3_	_F_	_Yes_	_36_	_35_	_32_	_2_	_4_
_*216600_	_36_	_>3_	_M_	_Yes_	_108_	_80_	_104_	_4_	_6_
_216653_	_13_	_1.5_	_F_	_Yes_	_672_	_648_	_845_	_161_	_118_
Harrys Creek									
216060	44	>3	F	Yes	196	187	246	32	53
151147	53	1.5	M	Yes	747	406	541	165	152
151983	51	1.5	M	Yes	521	308	508	49	64
216017	34	>3	F	Yes	385	241	310	54	68
216509	38	>3	M	Yes	540	503	476	69	125
mean (n = 15)	**598**				**374**	**248**	**365**	**49**	**64**
s.e.					**50.9**	**34.9**	**43.4**	**10.8**	**11.6**

A/tote = asymptote; MCP 100 = minimum convex polygon; MCP 95 and 50 = minimum convex polygon including 95% and 50% of locations, respectively, which were closest to the harmonic centre; KE 95 and 50 = kernel analysis including 95% and 50% of locations respectively. KE 50 and MCP 50 are indices of the core area. Cats in italics (n = 6) were excluded from the home range size analyses due to insufficient fixes (< 20 fixes) or * the cat died during the radiotracking period.

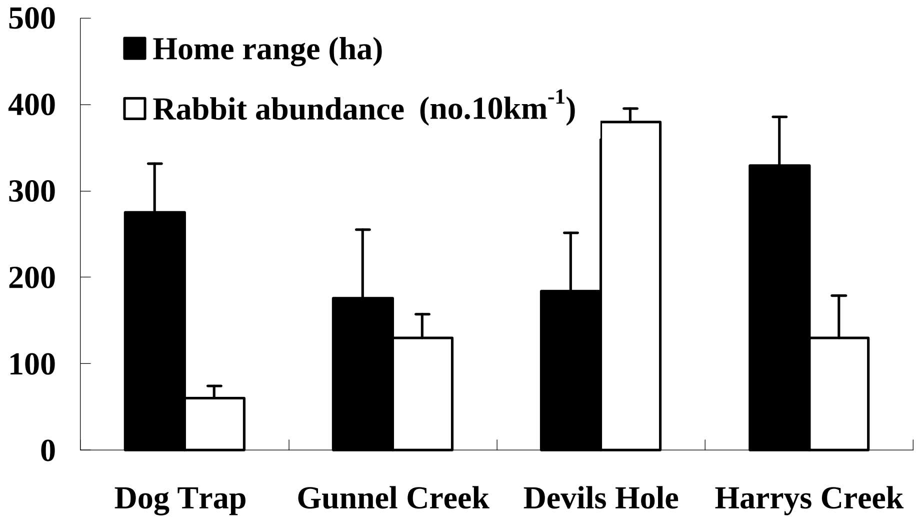

Fig. 5.1. Site differences in rabbit abundance (no.10 km^{-1}) and home range sizes (MCP 95) of cats in winter 1995. Means and standard errors are shown.

Table 5.3. Mean (± s.e.) day and night home range sizes (ha) for 12 cats in winter 1995.
* three cats were excluded where insufficient fixes (< 10) were obtained for day/night comparisons.

	Range size (MCP 95)		
	Day	**Night**	**No. fixes**
male (*n* = 8)	261 ± 30.7	236 ± 45.2	368
female (*n* =4)	110 ± 20.4	108 ± 40.6	163
Overall	**211 ± 29.9**	**193 ± 36.7**	**531**

5.3.2. Overlap in home ranges and core areas

A large degree of overlap ($\bar{x}$ ± s.e. 21% ± 3.6) in home ranges (MCP 95) was found between 28 adjacent and overlapping pairs of cats (Fig. 5.2), however, core areas (MCP 50) were further apart ($\bar{x}$ ± s.e. 7% ± 2.8) (Fig. 5.3). Percentage overlap in home ranges was influenced by age (F = 4.62; d. f. = 2, 48; P = 0.02) (Fig. 5.4), but not by sex (F = 0.33; d. f. = 2, 48; P = 0.72) and no interaction effect was detected (F = 0.53; d. f. = 3, 48; P = 0.66) (Fig. 5.2). Core area overlap also tended to be influenced by age (F = 2.10; d. f. = 2, 50; P = 0.13) (Fig. 5.4) but not by sex (F = 0.13; d. f. = 2, 50; P = 0.88) and no interaction effect was detected (F = 0.00; d. f. = 1, 50; P = 0.96) (Fig. 5.3). Adjacent pairs that comprised a young adult and an old adult cat had a greater degree of overlap in home ranges and core areas than did young-young and old-old combinations of cats (Fig. 5.4).

When day ($\bar{x}$ ± s.e. 15% ± 3.4) and night ($\bar{x}$ ± s.e. 20% ± 4.1) ranges were analysed separately, no significant differences in percentage overlap were found between the two periods (F = 0.84; d. f. = 2, 72; P = 0.44). However, age influenced the percentage overlap between adjacent pairs (F = 4.95; d. f. = 2, 72; P = 0.01) and a significant age by sex interaction was detected (F = 2.94; d. f. = 2, 72; P = 0.05) (Fig. 5.5). Combinations of cats where both individuals in the pair were young adult males had the largest degree of overlap when day and night ranges were pooled (Fig. 5.5). No overlap was found among old adult males (n = 10 pairs) or between young adult male and female combinations (n = 12 pairs) (Fig. 5.5). No interaction effects were detected between sex, age and day/night (F = 0.12; d. f. = 1, 72; P = 0.73).

5.3.3. Habitat utilisation

Habitat use. When home ranges of 15 cats were overlaid on to the four habitat types across the entire study area (Fig. 5.6), most home ranges covered at least three of the four habitat types (Table 5.4). Overall, cats used woodland and forest habitats more often than grassland and mudflats in winter 1995 (Fig. 5.7). Both levels of habitat use (proportional habitat within the home range and proportional habitat use at the location fixes) produced similar results (Fig. 5.7, Table 5.4).

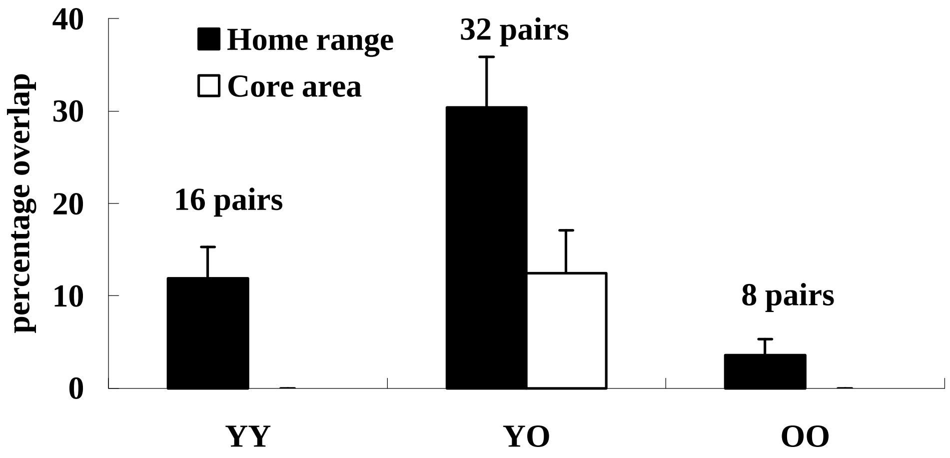

Fig. 5.4. Percentage overlap in home ranges (MCP 95) and core areas (MCP 50) between adjacent/overlapping pairs of cats for different age group combinations. Y = young (1 - 3 years); O = old (> 3 years). Means and standard errors are shown. No core area overlap occurred among YY and OO individuals.

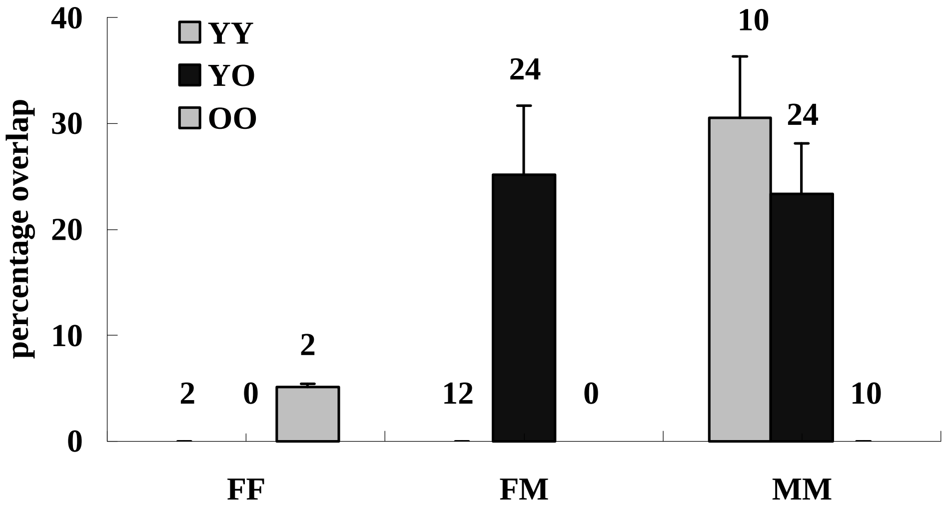

Fig. 5.5. Percentage overlap for different age and sex combinations of cats. Day and night ranges (MCP 95) were pooled. Means and standard errors are shown. Numbers of adjacent/overlapping pairs of cats are shown above the bars where Y = young (1 - 3 years); O = old (> 3 years); F = female; M = male.

Table 5.4. Percentage habitat composition for cats in winter 1995 at each study site (bold type), within each home range (MCP 95), and at the location fixes. Percentages do not always total 100 as small areas were outside the digitised habitat map.

	% home range				% location fixes			
Study site and animal ID	Grassland	Open woodland	Open forest	Mudflat	Grassland	Open woodland	Open forest	Mudflat
Dog Trap	**17.3**	**25.5**	**45.2**	**9.9**				
216380	0.4	11.2	88.5	0	3.7	16.7	79.6	0
216620	21.3	27.9	39.1	10.5	24.5	40.8	26.5	8.2
150044	9.1	27.7	63.1	0.1	1.5	27.7	70.8	0
Gunnel Creek	**4.9**	**53**	**42.1**	**0**				
216340	19.4	55.0	25.6	0	12.5	62.5	25	0
216160	4.5	45.0	50.5	0	8.1	43.2	48.7	0
216320	0.0	61.9	38.1	0	0	52.4	47.6	0
216420	2.4	53.1	44.5	0	5.1	41	53.9	0
Devils Hole	**15.1**	**52.3**	**29**	**3.2**				
216040	20.7	71.5	7.8	0	45	45	10	0
216360	2.0	98.0	0	0	0	100	0	0
216120	5.4	53.4	41.3	0	6.5	56.5	37.0	0
Harrys Creek	**23.1**	**53.2**	**12.7**	**8.6**				
216060	21.3	78.7	0	0	22.7	77.3	0	0
151147	14.2	78.3	7.5	0	15.1	81.1	3.8	0
151983	45.3	42.9	4.8	7.0	45.1	47.1	3.9	3.9
216017	38.2	37.5	5.7	15.3	52.9	38.2	2.9	2.9
216509	6.9	61.9	31.1	0	10.5	71.1	18.4	0

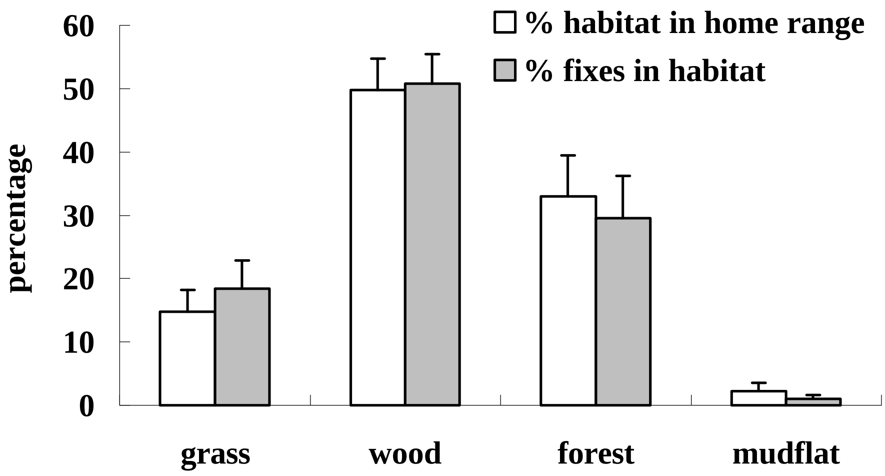

Fig. 5.7. Proportional habitat use for 15 cats in winter 1995 at two levels, a) % habitat composition of home range, and b) % fixes in each habitat type. Means and standard errors are shown.

Site differences in habitat use reflected differences in habitat availability (Fig. 5.8). For example, at Dog Trap, where forest habitat was most available, cats used it more often than at the three remaining sites, where woodland was most available and most used.

Habitat selection. Compositional analysis revealed that cats did not establish their home ranges at random within each site ($F = 8.79$; d. f. = 2, 30; $P < 0.001$). Calculation of the ranking matrix showed that mudflats were significantly under-used relative to the remaining three habitat types (Tables 5.4 and 5.5a). Overall, open woodland was the most preferred habitat (rank 3), followed by open forest (rank 2) and grassland (rank 1) (Table 5.5a). Relative to one another, however, the utilisation of these three habitat types did not differ significantly from random (Table 5.5a). Habitat preference was not influenced by age ($F = 2.32$; d. f. = 1, 30; $P = 0.138$) or sex ($F = 0.01$; d. f. = 1,30; $P = 0.916$) of individual cats and no interaction effects were detected ($F = 0.06$; d. f. = 1, 30; $P = 0.807$). In addition, no significant habitat by site interaction was found ($F = 0.44$; d. f. = 5,30; $P = 0.818$).

Habitat utilisation as described by the location fixes of each cat was also significantly different to that expected given the habitat composition of the home ranges ($F = 34.03$; d. f. = 2, 22; $P < 0.001$). Cats significantly avoided mud flats in preference for open woodland (Tables 5.5b and 5.6). Grassland was the most preferred habitat (rank 3), followed by open woodland (rank 2) and open forest (rank 1) (Table 5.5b). Relative to one another, however, again the utilisation of these habitat types did not differ significantly from random (Table 5.5b). Habitat preference was not influenced by age ($F = 0.29$; d. f. =1, 23; $P = 0.597$) or sex ($F = 0.51$; d. f. = 1, 23; $P = 0.482$) of individual cats and no interaction effects were detected ($F = 0.61$; d. f. = 1, 23; $P = 0.44$). However, a significant habitat by site interaction was detected ($F = 7.53$; d. f. = 5, 22; $P < 0.001$) indicating that cats preferred different habitats at different sites (Fig. 5.8).

Day versus night. Habitat composition of home ranges ($F = 0.02$; d. f. = 1, 120; $P = 0.895$) and at fixes ($F = 0.03$; d. f. = 1, 120; $P = 0.854$) did not differ between day and night periods (Table 5.6).

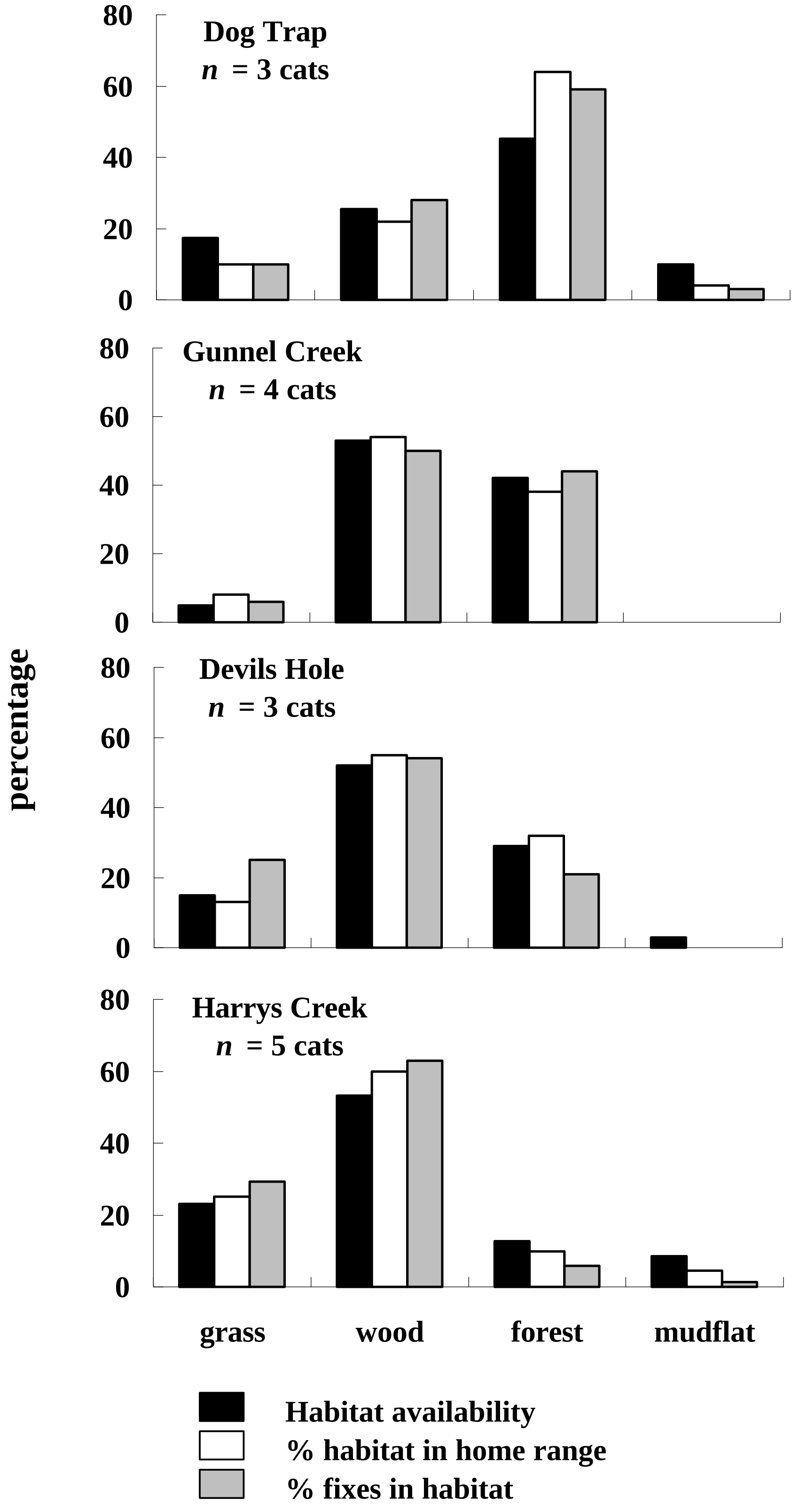

Fig. 5.8. Habitat use relative to availability for 15 cats at the four sites in winter 1995.

Table 5.5. Magnitude of mean log-ratio differences between utilised and available habitat compositions for 15 radiocollared cats in winter 1995. Each mean is replaced by its sign and tripled where the mean differs significantly from 0. The rank for each habitat type, according to use, is calculated from the number of positive values in each row where the most-used habitat type has the highest rank. The comparison of utilised with available habitat composition is assessed at two levels: (a) home-range selection within the study site; and (b) habitat utilisation within the home range.

a) Habitat composition for home ranges versus the site

	grass	wood	forest	mud	Rank
grass		-	-	+++	**1**
wood	+		+	+++	**3**
forest	+	-		+++	**2**
mud	---	---	---		**0**

b) Habitat composition derived from location fixes versus home ranges

	grass	wood	forest	mud	Rank
grass		+	+	+	**3**
wood	-		+	+	**2**
forest	-	-		+	**1**
mud	-	---	-		**0**

5.4. DISCUSSION

5.4.1. Home range size

Home range sizes of cats at Burrendong were similar to those reported in semi-arid Australia but larger than those reported elsewhere (see Table 5.1), possibly reflecting low prey density or more dispersed food resources (Macdonald 1983, Genovesi *et al.* 1995). Larger home range sizes in response to low or patchy food availability have been recorded widely in carnivores (e.g. Jones and Theberge 1982, Kruuk 1986, Sandell 1989) and felids in particular (Genovesi *et al.* 1995, Poole 1995, du Bothma *et al.* 1997, but see Breitenmoser *et al.* 1993). However, the abundance of rabbits (the staple prey for cats at Burrendong; see Chapter 4) did not influence home range size in this study. This may have been due to the lower availability of rabbit kittens in winter compared to other seasons (Catling 1988), the ubiquitous distribution of rabbits, or to the large inter-individual variation in range size. In addition, indices of rabbit abundance were recorded only using spotlight counts along one track that traversed each site which may not have been representative of the entire site in which range sizes were calculated. Some other studies of carnivores have also shown little change in home range size after declines in abundance of their staple prey (Lockie 1966, White and Ralls 1993).

Male ranges tended to be larger than those of females in this study, as has been reported elsewhere for urban (Dards 1978), farm (Macdonald and Apps 1978), and feral cats (see Table 5.1), and other felids (Corbett 1979, Johnson and Franklin 1991, du Bothma *et al.* 1997). Larger male ranges are common among carnivores, particularly when animals are polygynous (Sunquist 1981, Gosling and Baker 1989). Larger ranges increase the number of potential mates an animal encounters and may also, in part, reflect their greater energetic needs given their larger size (McNab 1963, Harested and Bunnell 1979, Haspel and Calhoon 1989, but see Konecny 1987, Reiss 1988). However, the magnitude of the intersexual difference in range size reported here (i.e. male ranges 1.8 times bigger than females) was less than the 3.5 to 10 fold difference recorded elsewhere (see reviews in Tabor 1983, Liberg and Sandell 1988), which may be related to seasonal differences. Locations of cats in this study were recorded only in winter, while many other studies have examined home range size in spring and summer. In spring and summer, pregnant and lactating females greatly reduce their range size (Jones and Coman 1982, Fitzgerald and Karl 1986, Iwamoto *et al.* unpublished data). This may have accounted for the larger intersexual differences in range size recorded in other studies.

(> 3 years) in this study was probably due to all radiotracked cats being adults. Elsewhere, smaller ranges of subadult compared to adult cats have been recorded (Corbett 1979, Liberg 1981, Fitzgerald and Karl 1986).

Temporal differences in range size were not detected in this study indicating that cats were active both by day and night, as has been recorded elsewhere (Fitzgerald and Karl 1986). However, most home-range studies of feral cats have used either day (Liberg 1980, Jones and Coman 1982, Fitzgerald and Karl 1986) or night fixes (Corbett 1979, Konecny 1987) and only one study in farmland in New Zealand has compared day and night range sizes (Langham and Porter 1991). This study found that both male and female feral cats used larger ranges at night compared to the day, and assumed this to reflect greater nocturnal activity by cats (Langham and Porter 1991). However, this New Zealand study also showed that cats occupying willow habitats (which provided cover) were active during the day. The authors suggested that cover may have allowed cats to hunt prey, such as birds, during the day which they otherwise may have been unsuccessful in capturing in more open habitats. At Burrendong, diurnal activity by cats may also have reflected abundant cover for hunting. Further, ranges were recorded in spring and summer in the New Zealand study, which may have accounted for the smaller home range sizes if activity was reduced during the warmer daytime temperatures. In winter at Burrendong temperatures were sufficiently cool to allow daytime activity. The lack of temporal differences in range size recorded here increases the comparability between studies that have used solely day or night location fixes in estimates of range size.

5.4.2. Social organisation

The home ranges of adult feral cats at Burrendong overlapped extensively ($\bar{x}$ ± s.e. 21% ± 3.6), particularly among members of the opposite sex. Higher inter-sexual compared to intra-sexual overlap has been recorded elsewhere (Schwarz 1995). This presumably reflects the solitary nature of adult male (Jones and Coman 1982, Fitzgerald and Karl 1986, Konecny 1987, Langham and Porter 1991) and female cats (Jones and Coman 1982, Fitzgerald and Karl 1986, Konecny 1987), and possibly the formation of kin groups (Macdonald and Apps 1978). At Burrendong, the home ranges of old adult males (> 3 years) were relatively exclusive, particularly among core areas. Adult female cats were also solitary, however, only four females were radiotracked and the spatial behaviour of neighbouring females was not known. Observed cats were generally solitary unless accompanied by kittens.

Felids are, with few exceptions, solitary species presumably because of their stealthy hunting (Corbett 1979, Gittleman 1989, Sandell 1989, Johnson and Franklin 1991). However, when food resources are abundant and/or clumped, female cats often form stable groups (generally kin) and males move between the groups (Macdonald and Apps 1978, Liberg 1980, 1984, Breitenmoser *et al.* 1993, Genovesi *et al.* 1995, Mirmovitch 1995); although individuals of a group usually hunt solitarily (Panaman 1981) and ranges of different groups overlap little (Izawa *et al.* 1982). Explanations as to why some Carnivora live in groups have traditionally invoked two reasons; cooperative hunting of large prey and the need for defence against predator attack (Fox 1970). While these reasons may account for the social grouping observed in wolves and lions, they do not account for those species that live in groups but hunt alone, such as feral cats, red foxes and badgers (Kruuk 1972, 1978, Dards 1978, Macdonald and Apps 1978, Kruuk and Parish 1981). Possible reasons for these groupings may include opportunities to learn from other group members, division of labour, care of the sick and alloparental care (see review in Macdonald 1983). In urban environments where food and shelter are provided, the survival rate of offspring that disperse is lower than that of

among cats may also differ between habitats. For example, cats sleeping together on a sub-Antarctic island may receive a thermoregulatory benefit (van Aarde 1978).

The high degree of inter-sexual overlap between young adult (1-3 years) and old adult (>3 years) cats at Burrendong may indicate the presence of kin groups (e.g. Macdonald and Apps 1978), although kin ties were not examined. Young males do not usually disperse from their

overlap therefore may have reflected individuals that had not yet dispersed from their natal range.

Territoriality, where more or less exclusive areas are actively defended (Davies and Houston 1984), was not examined in this study but has been recorded for feral cats elsewhere (Liberg 1980, 1984, Langham and Porter 1991). In New Zealand, adult male feral cats patrolled boundaries at night and observations were made of aggressive chases of strange males when in the vicinity of oestrous females (Langham and Porter 1991). In Sweden, female kin groups overlapped little with other female groups, and active avoidance of and aggression towards foreign females at home range borders was observed (Liberg 1984b). Communal and defended territories of female cat kin groups have also been reported elsewhere (Leyhausen 1965, Macdonald and Apps 1978). Territoriality was suggested, but not confirmed, in this study with the mutually exclusive home ranges of old adult males and the lack of burying of scats (Chapter 4), which may indicate their use as territory demarcations (Liberg 1980, Brothers *et al.* 1985).

5.4.3. Habitat utilisation

Home ranges of cats in this study comprised mostly open woodland and open forest habitats with smaller areas of grassland and mudflats. This reflected the relative availability of these habitats at the sites, as significant avoidance was recorded only for mudflats. However, within home ranges, grassland and open woodland were the most frequently used habitat types, regardless of availability.

Habitat use in felids presumably reflects the influence of prey availability and the need for protective cover from predators and from detection by prey while hunting (Johnson and Franklin 1991). In Scotland, wildcats (*Felis silvestris*) established home ranges mostly in forest-scrub associations in valleys at low altitudes where their preferred prey (rabbits) were more common, while birch forest, farmland and moorland habitats were used less often (Corbett 1979). In coastal New Zealand, feral cats used ungrazed non-dune areas more often, where prey were abundant, than grazed non-dune habitats (Alterio *et al.* 1998). In the Galapagos Islands, cats used lava/scrub habitats significantly more than grassy and sandy plain habitats (Konecny 1987). In an agricultural area in northern Italy, feral cats selected habitats providing good cover (arboreal shelter belts, reed thickets, vegetation at the end of drain channels) and hunted often in meadows but avoided cultivated fields (Genovesi *et al.* 1995). In Tasmania, feral cats favoured habitats that included at least some ground cover and avoided habitats where ground cover was absent, even where prey was abundant (Schwarz 1995). At Burrendong, rabbits are the staple prey for cats and are more abundant in grassland and open woodland habitats than the mudflats and denser open forest (R. Molsher personal observation).

Inter-individual (sex, age) or temporal (day/night) differences in habitat use were not detected in this study and have not been examined previously (Genovesi *et al.* 1995). No evidence was found for the use of wooded areas during the day for shelter and open areas (e.g. grassland) at night (Artois 1985) where rabbits are more abundant. The lack of temporal difference in home range size and habitat use is consistent with the hypothesis that cats at Burrendong hunt and rest at various times during both the day and night. Inter-sexual differences in habitat use may be expected later in spring when pregnant or lactating females, which have higher energetic needs (Scott 1976), reduce their range size (Jones and Coman 1982) and occupy more productive habitats (Konecny 1987).

5.5. CONCLUSION

The solitary habits and large home ranges of cats at Burrendong are similar to those recorded for feral cats living in other areas where humans provide no food and resources are widely dispersed (Corbett 1979, Jones and Coman 1982, Liberg and Sandell 1988). Male ranges tended to be larger than those of females but the difference was not significant. Home range sizes were not influenced by the age of adult cats or by rabbit abundance. The high degree of inter-sexual overlap between young and old adult cats indicated kin groups, although kin ties were not examined. Cats tended to use habitats in relation to availability, but significant avoidance of mudflats was detected. Home ranges of cats comprised mostly open woodland and open forest, while within ranges, grassland was the most frequently used habitat type, presumably reflecting a higher abundance of rabbits.

CHAPTER 6

OVERLAP IN RESOURCE USE AND INTERACTIONS BETWEEN FERAL CATS AND RED FOXES

6.1. INTRODUCTION

The aim of this chapter is to examine the degree of overlap in resource use between feral cats and foxes and to record any evidence of avoidance or aggressive interactions (i.e. interference behaviour). Although high overlap in resource use is not sufficient to demonstrate competition (Lawlor 1980), it can indicate a high potential for exploitation competition (Schoener 1983). Similarly, observations of aggression and spatial segregation between sympatric carnivores can indicate interference competition (e.g. Dekker 1983, Sargeant and Allen 1989). Dietary overlap between cats and native spotted-tailed quolls (*Dasyurus maculatus*) is also examined briefly as quoll scats were collected unexpectedly and opportunistically in the study area. Quolls are a potential competitor for cats at Burrendong as they have similar dietary requirements (Belcher 1995).

The niche-complementarity hypothesis predicts that for coexistence to occur among ecologically similar species, high overlap in one dimension will be compensated by low overlap in another (Schoener 1974, Fuentes and Jaksic 1979, Jimenez *et al.* 1996). Food, habitat and time are the three most important dimensions along which competitors can potentially partition resources (Schoener 1974). Much evidence exists for food and habitat segregation between sympatric mammalian predators (Fuller and Keith 1981, Litvaitis 1981, Major and Sherburne 1987, Sargeant *et al.* 1987, Harrison *et al.* 1989, Theberge and Wedeles 1989, White *et al.* 1995, Cypher and Spencer 1998), but not for time (White *et al.* 1994). Temporal differences in activity between sympatric predators may not be advantageous and do not always result in low dietary overlap (Jaksic *et al.* 1981, Jaksic 1982). For example, *et al.* 1976, Kotler *et al.* 1992, see also Appendix 3) predicts that the killing of prey at one point in time can reduce prey activity and consequently reduce foraging efficiency for subsequent predators.

Interference behaviour has been documented widely among sympatric mammalian predators in the northern hemisphere where there is high overlap in resource use (e.g. Fuller and Keith 1981, Major and Sherburne 1987, Harrison *et al.* 1989, see review in Chapter 1). However, the competitive or predatory relationship between feral cats and foxes has not been quantified in Australia or elsewhere. In Australia, red foxes and feral cats are sympatric over much of their range and have a large overlap in diet (e.g. Bayly 1978, Triggs *et al.* 1984, Catling 1988, Newsome *et al* 1989, Catling and Burt 1995). Sympatry is thought to be maintained by both predators utilizing different age groups of the same staple prey and different supplementary prey (Catling 1988). Intraguild predation has also been indicated, as cat remains are found occasionally in the diet of foxes (Coman 1973b, Brunner *et al.* 1991, Taylor and Lupica 1998, D. Risbey pers. comm., R. Paltridge pers. comm.). The home ranges and habitat use of sympatric foxes and feral cats have not been examined previously. Information on niche overlap, resource partitioning and agonistic encounters between cats and foxes will indicate the potential for competition and/or intraguild predation.

The general objective of this chapter is to investigate the potential of foxes to limit the abundance of cats via overlap in resource use or direct interactions (e.g. interference, predation). The specific aims of this chapter are to examine:

1) the degree of overlap in diet, home range and habitat use between cats and foxes;
2) the numerical relationship between cats and foxes;
3) the dietary and numerical responses of cats and foxes to fluctuating rabbit abundances;
4) the dietary overlap between cats and quolls;
5) the habitat types in which cats and foxes deposit scats;
6) whether foxes kill and/or eat cats;
7) any evidence for aggression or avoidance (temporal and spatial) between cats and foxes.

All work described was carried out at the Burrendong study area described in Chapter 3.

6.2. METHODS

General methods for radiotracking, habitat use, abundance indices for foxes, cats and rabbits (spotlight counts), and scat analyses are described in Chapter 3. This section gives details of the statistical analyses (Pearson product-moment correlation coefficient, ANOVAs, Tukey tests, *G*-tests and *t*-tests), that were employed using GENSTAT and SYSTAT computer programs. Spatial data for cats and foxes in this chapter were collected in the untreated area (no fox removal) in winter 1995 and 1996. Fox spatial data were collected by the VBCRC Fox Sterility Project (Chapter 3). Abundance indices for cats, foxes and rabbits (VBCRC Predator Prey Project) are presented for only the two untreated sites (Devils Hole and Harrys Creek) from July 1994 to June 1997. Cat and fox scats for dietary analysis were collected over the entire study area including from experimental (removal) areas. In addition, spotted-tailed quoll scats were collected opportunistically and the diet of this species compared with that of cats.

6.2.1. Numerical response

Predator-predator. The numerical relationship between cat and fox abundance indices, as estimated from spotlight counts, was evaluated using the Pearson product-moment correlation coefficient. Because of the lack of temporal independence in successive estimates of predator abundance, correlations were used in a descriptive rather than hypothesis-testing sense.

Predator-prey. The numerical response of cats and foxes to changing rabbit densities was also evaluated descriptively, using the Pearson product-moment correlation coefficient. Lag phases of 1, 2, 3, 4, 6, 8, and 12 months were examined in order to assess any delayed responses in predator abundance to changes in prey density (Pech *et al.* 1992).

6.2.2. Dietary comparison between cats and foxes

Overall diet. A non-orthogonal three-way ANOVA was used to compare percentage volumes of prey groups in scats between predators, seasons and years (predator by season by year). Only the main effects and the predator interactions were fitted to the model. The season by year, and predator by season by year interactions, were used as the residual in this analysis. The percentage volumes were arcsine transformed to approximate a normal distribution (Zar 1984), with each prey group tested separately to avoid problems associated with the lack of independence between prey groups. In addition, a dietary comparison was made between cats and foxes in the occurrence of each prey group using the *G*-test (Sokal and Rohlf 1994). Each prey group was tested separately.

Seasonal variation. Seasons were defined as summer (December to February), autumn

(1973) method was used to confirm that sample sizes were large enough to warrant seasonal analysis of diet. Seasonal variation in the percentage volumes of prey groups in scats between cats and foxes was examined using a non-orthogonal three-way ANOVA as described above (predator by season by year). Only fresh scats (< one month old) were used in seasonal analyses to avoid confounding of seasons. Age was judged by appearance and smell and with comparison to a reference sample of scats that had been left exposed.

Rabbit consumption relative to availability. The dietary response of cats and foxes (% occurrence of rabbits in the diets) to changing rabbit densities was examined using the Pearson product-moment correlation coefficient.

Dietary breadth and overlap. Dietary (niche) breadth of both predators was evaluated using

$$B = 1 / \Sigma p_j^2$$

where p_j

was also standardised on a scale of 0 to 1.0 (Hurlbert 1978) to facilitate comparisons with other studies and calculated as:

$$B_A = B - 1/ n- 1$$

where n

appropriate method for examination of dietary breadth as it is used widely in ecological studies and allows comparisons with other studies. This index is minimal when the population is specialised in using only one food item and maximal when the population uses all resources in equal proportions (Krebs 1989). Dietary breadth estimates were considered significant if B or B_A values differed by >10% (Dickman 1986b).

Dietary (niche) overlap between cats and foxes was evaluated using two methods: Percentage Overlap (P_{jk}

and the measures of specific and general overlap (SO, GO) of Petraitis (1979, 1985). Percentage overlap (P_{jk}) was calculated as:

$$P_{jk} = [\ \Sigma^n \text{ (minimum } p_{ij}; P_{ik}) \ ] \text{ x } 100$$

where p_{ij}; P_{ik} = the proportion that resource i is of the total resources used by species j and k, and n = the total number of resource states. This index ranges from 0 (no similarity) to 100 (complete similarity). The advantages of this method are its wide use, which allows comparisons to be made with other studies, and its ability to measure the actual overlap of the resource utilisation curves of two species. In addition, this method is not sensitive to the way in which the resource states are divided by the observer (Krebs 1989). However, it does not give any indication as to whether the overlap obtained is significant statistically. To overcome this problem, Petraitis (1979, 1985) introduced measures of specific overlap (SO) and general overlap (GO).

Specific overlap (SO) calculates the probability that the utilisation curve (proportional usage of each resource) of one species is drawn from the utilisation curve of another species. Petraitis derived the equation by examining whether or not an observed species utilisation of resource states could have been drawn randomly from the environmental resource spectrum. Specific overlap was computed as:

$$SO_{i,k} = e^{\,\mathrm{E}ikj}$$

where e is the exponential, $E_{ik} = \Sigma^{r}_{k}\,(p_{1k} \ln p_{2k}) - \Sigma^{r}_{k}\,(p_{1k} \ln p_{1k})$ and r = the number of resource states. To determine whether SO is significant the (U) test statistic was calculated as:

$$U_{i,k} = -2N_i \ln (SO_{i,k})$$

where N_i = number of scats, and $U_{i,k}$ is distributed as Chi-square with r - 1 degrees of freedom.

General overlap (GO) calculates the probability that the resource utilisation curve of two or

is computed as a weighted average of species utilisation curves as follows:

$$GO = e^{E}$$

where e is the exponential, $E = \Sigma^{s}_{i}\,\Sigma^{r}_{j}\,[\, n_{ij}\,(\ln c_j - \ln p_{ij})\,] \,/\, T$ and T = total number of scats. To determine whether GO is significant the test statistic (V) was calculated as:

$$V = -2T \ln GO$$

where V is distributed as Chi- squared with (S - 1) (r - 1) degrees of freedom, and S = the number of species. The null hypothesis underlying both measures of overlap was that the two

Dietary breadth and overlap measures were determined for each season, Post-RCD (June 1996 to June 1997), and overall.

Scat deposition. Habitat types in which scats were found were defined broadly as macro- (*Callitris*, grassland, woodland) and microhabitat types (rabbit warren, on sand-plots, on tracks, at dams, hollow log entrances, at carcasses, under bushes, on rocks or bare ground) and recorded at the time of collection (see Chapter 3). Differences between cats and foxes in the proportional frequency of deposition in macro- and microhabitat types were evaluated using the *G*-test.

6.2.3. Direct predation of cats by foxes

The possibility of direct predation of cats by foxes was determined from the analysis of fox scats, using techniques for identification of hair remains as outlined in Chapter 3.

6.2.4. Dietary comparison between cats and quolls

Dietary differences between cats and spotted-tailed quolls in the percentage occurrence of each prey group were evaluated using the *G*-test (Sokal and Rohlf 1994). Each prey category was tested separately to avoid problems associated with the lack of independence between prey groups.

6.2.5. Spatial use comparison between cats and foxes

Home range and core area size. Differences between cats and foxes in the size of home ranges (MCP 95) and core areas (MCP 50) were examined using *t*-tests for both winter 1995 and 1996.

Overlap in home ranges and core areas. The degree of overlap in adjacent ranges (< 500 m) was quantified using RANGES V, which produces a matrix of the percentage overlap for each pair of overlapping ranges. Differences in the percentage overlap of home ranges (MCP 95) and core areas (MCP 50) between cats and foxes, and between conspecifics, were evaluated using a one-way ANOVA. Multiple comparisons were then made between the three groups using the Tukey test. Percentages were arcsine transformed (Zar 1984).

Trap locations of cats in relation to fox ranges. Trap locations of cats in winter 1996 were overlaid on to the core areas (MCP 50) of cats and foxes to examine their proximity.

Overlap in habitat utilisation. Both levels of habitat use were examined: a) habitat composition within the home range; and b) proportional habitat at the location fixes. A two-way ANOVA was used to compare proportional habitat use between cats and foxes (predator by habitat type).

Habitat selection was evaluated using compositional analysis (Aebischer *et al.* 1993) on both levels of habitat use: a) selection of a home range within the study site; and b) differential use of habitat types within the home range. Habitat selection was evaluated using a one-way ANOVA with the log-ratio differences between use and availability as the dependent variable, and habitat type as the factor. Separate ANOVAs were performed for each predator (cat, fox), each level of habitat use (home range, location fixes) and each year (1995, 1996). Where significant habitat selection was found, the habitat types were ranked according to utilisation (see Chapter 3). Differences in habitat selection (log-ratios) between cats and foxes were evaluated using a two-way ANOVA (predator by habitat type).

6.2.6. Direct interactions

6.2.6.1. Simultaneous radiotracking

To evaluate possible avoidance interaction in more detail, four cats and six foxes were radiotracked simultaneously at Spring Creek (Fig. 3.3) in an untreated area in October 1996. Fixes were obtained every hour for six hours on each night for 11 nights, between 1800 and 2400 h. Consecutive bearings were taken within a 20-minute period. Size differences in home ranges (MCP 95) and core areas (MCP 50) between cats (n = 232 fixes) and foxes (n = 331 fixes) were evaluated using the t-test.

Relationships between the movements of different animals were investigated at two levels, using static interaction and dynamic (temporal) interaction analysis (Macdonald *et al.* 1980). Static interaction is determined from the spatial overlap of two home ranges and the congruence of their utilisation distributions, while dynamic interaction is the dependency in the movements of two individuals within the known limits of their home range (Doncaster 1990).

Static interaction. The percentage overlap of two home ranges provides a first approximation of static interaction (Macdonald *et al.* 1980). If A_1 and A_2 represent the home ranges of animals 1 and 2 respectively, and $A_{1,2}$ is the area of overlap, then static interaction (S) is

$$S_{1,2}= A_{1,2}/A_{1;} \qquad \text{and } S_{2,1}= A_{1,2}/A_2$$

where $S_{1,2}$ $_{2,1}$ is the

$_1$ = A_2 then $S_{1,2}$ would

not equal $S_{2,1}$ (Macdonald *et al.* 1980). Percentage overlap between overlapping or adjacent (< 500 m) ranges was calculated using RANGES V. Differences in percentage overlap of home ranges (MCP 95) and core areas (MCP 50) were evaluated between cats and foxes, and between conspecifics, using a one-way ANOVA. Multiple comparisons were made between the three groups using the Tukey test. Percentages were transformed prior to analysis using the arcsine transformation (Zar 1984).

Dynamic interaction (*temporal overlap*). Dynamic interaction is an improvement on static interaction; it takes into account the possibility that, although two ranges may overlap, the animals may not occur in the same place at the same time. Dynamic interaction determines the dependency in the simultaneous movements of a pair of individuals and is a more subtle measure of the relationship between two animals than static interaction (Macdonald 1980, Doncaster 1990). This technique, which incorporates the time series of the locational data, has not been used widely in predator studies. It requires that the animals be monitored simultaneously with a constant sampling interval within each data collection period. The

(Jacobs 1974) which was calculated using RANGES V. This analysis produces a single

(Kenward and Hodder 1996). A value of 0 indicates that the observed and possible distances compared to reduce the influence of distant locations (Kenward *et al.* 1993).

Distances between individuals. Mean geometric distances between cats and foxes, and between conspecifics, were compared using a one-way ANOVA. Multiple comparisons were made between the three groups using the Tukey test.

Habitat use. Differences between cats and foxes in the proportional use of each habitat type were evaluated using the *t*-test. Each habitat type was tested separately to avoid problems associated with the lack of independence between habitat types. Percentages were not log or arcsine transformed as variation between values was small (Zar 1984). Both methods of habitat composition, home range and fixes, were examined.

6.2.6.2. Video observations

To examine potential avoidance and aggressive behaviours between cats and foxes, carcasses were staked out and videotaped for 140 hours over a two-month period in spring 1996. A feeding area was established where carcasses (mostly kangaroo carcasses and sheep stomachs) were regularly deposited. Red light, rather than white light, illuminated the feeding area, in order to reduce wariness as has been found in captive foxes (Newsome 1995). Animals entering the feeding area were videotaped between the hours of 1800 and 0600. The video camera was housed in a canvas hide and placed approximately 30 m from the carcasses. The ratio of possible visits to actual visits was calculated from the numbers of radiocollared cats and foxes known to be in the area (possible), and the numbers of individuals observed on the video tape (actual).

6.2.6.3. Causes of mortality for radiocollared cats

Carcasses of dead radiocollared cats were examined for possible causes of death. Teeth-marks on radio collars were examined under a stereo-dissecting microscope and compared with reference skulls of cats and foxes. Examination of the kill site also provided clues as to the cause of death.

6.2.6.4. Anecdotal observations of direct interactions

Observations of interactions between cats and foxes were recorded, including those from co-workers and landholders in the area. An interaction was defined as any encounter where a cat and fox were ≤ 100 m apart. Outcomes of interactions were classified as tolerance, aggression or displacement (after Gese *et al.* 1996). Tolerance was scored when both predators appeared to ignore each other, while displacement occurred when one predator approached or chased the other predator, causing the latter to move away from the immediate area. Aggression was defined as agonistic behaviour, such as fighting or back-arching.

6.3. RESULTS

6.3.1. Numerical response

Predator-predator. Cat and fox abundance estimates were not correlated significantly (r = 0.28, n = 27; $P > 0.05$). Overall, foxes ($\bar{x}$ ± s.e.: 0.64 km^{-1} ± 0.065) were 10.6 times more numerous than cats (0.06 km^{-1} ± 0.010) at the untreated sites (Fig. 6.1). Fox counts ranged from 0 to 1.3 km^{-1}, while those for cats ranged from 0 to 0.2 km^{-1}**.**

Predator-prey. A significant negative relationship was found between the abundance of foxes and rabbits (r = -0.44, n = 27; $P < 0.05$), but not for cats and rabbits (r = -0.29, n = 27; $P > 0.05$). However, using a four month lag period, both fox (r = -0.47, n = 20; $P < 0.05$) and cat abundance (r = -0.43, n = 20; $P < 0.05$) were correlated significantly and negatively with rabbit abundance. No significant relationships were found for lag phases of 1, 2, 3, 6, 8 and 12 months ($P > 0.05$). Rabbit abundance ranged from 0.4 to 51.9 km^{-1} ($\bar{x}$ ± s.e.: 15.5 km^{-1} ± 2.8) with numbers declining dramatically post-RCD (Fig. 6.1).

6.3.2. Dietary comparison between cats and foxes

Overall diet. Totals of 499 cat scats and 343 fox scats were collected randomly throughout the study area in most months from July 1994 to June 1997. Mammals occurred in all cat scats and 92.7% by percentage occurrence (O) in fox scats, comprising 87.5% and 49.4% by volume (V), respectively, of the overall diet of cats and foxes (Table 6.1). Cats ate primarily rabbit (O: 81.6%, V: 69%) and carrion
(O: 21.5%, V: 11.5%), while vegetation (O: 64.1%, V: 28.1%), rabbit (O: 52.2%, V: 27.9%), invertebrate (O: 61.8%, V: 21%) and carrion (O: 51%, V: 17%) were important foods for foxes (Table 6.1, Fig. 6.2). Data for % occurrence and % volume showed similar trends (Fig. 6.2).

Rabbit comprised significantly more by volume of the diet of cats than of foxes (F = 21.98; d. f. = 1, 11; $P < 0.001$), while invertebrates (F = 4.71; d. f. = 1, 11; P = 0.053) and vegetation (F = 20.27; d. f. = 1, 11; $P < 0.001$) were more important in the diet of foxes (Fig. 6.2). Carrion was eaten in similar quantities by both predators (F = 2.85; d. f. = 1, 11; P = 0.120). Similarly, by occurrence, rabbit was eaten significantly more often by cats than by foxes (G =

82.36; d. f. = 1; $P < 0.001$), while carrion (mostly eastern grey kangaroo) ($G = 77.06$; d. f. = 1; $P < 0.001$), invertebrates ($G = 33.78$; d. f. = 1; $P < 0.001$) and vegetation ($G = 121.42$; d. f. = 1; $P < 0.001$) were eaten significantly more often by foxes (Fig. 6.2). Among the minor prey items, house mice and birds tended to be eaten more often by foxes than by cats, while cats tended to eat possum and reptiles more often than foxes, but the differences were not significant ($P > 0.05$) (Table 6.1; Fig. 6.2).

Seasonal variation. Totals of 436 cat scats and 321 fox scats were classified as fresh (< one month old) based on appearance and smell, and included in the seasonal analyses. A marginally significant predator by season interaction was found in the percentage volume of invertebrates ($F = 3.87$; d. f. = 3, 11; $P = 0.041$) and rabbits ($F = 2.78$; d. f. = 3, 11; $P = 0.091$) in the diet. Invertebrates were more important in summer for foxes, and in autumn for cats, compared to other seasons (Fig. 6.3). Rabbits tended to be less important in the diet for foxes in summer than in other seasons, while no marked seasonal variation was evident for cats (Fig. 6.3). No clear seasonal differences in diet between cats and foxes were found for the other prey groups ($P > 0.05$) (Fig. 6.3).

Rabbit consumption relative to availability. Positive, almost significant correlations, were recorded between the occurrence of rabbit in the diet and rabbit abundance recorded at the untreated sites for both cats ($r = 0.44$, $n = 16$; $P = 0.08$) and foxes ($r = 0.42$, $n = 17$; $P = 0.09$) (Fig. 6.4). Post-RCD, cats and foxes continued to feed on rabbits despite a dramatic decline in rabbit abundance (Fig. 6.4). Rabbit was more important in the diet of cats than foxes in most months of the study and reached 100% occurrence in cat scats on seven occasions compared to only one occasion for foxes (Fig. 6.4).

Dietary breadth and overlap. Foxes consumed a greater range of food items than cats; significantly greater dietary breadth was recorded for foxes than for cats overall, and in most seasons, except autumn (Table 6.2). In autumn, dietary breadth indices were higher for cats than in other seasons prior to RCD ($B = 4.32$, $B_A = 0.37$), at which time dietary breadth did not differ significantly between the two predators (Table 6.2). Dietary breadth for foxes was highest in winter compared to other seasons ($B = 5.29$, $B_A = 0.48$) (Table 6.2). Both predators tended to consume a wider range of prey types post-RCD than in most other periods pre-RCD (Table 6.2).

Measures of dietary overlap (P_{jk}) were high between cats and foxes overall (75%) and ranged from 73% in spring and summer to 78% in autumn (Table 6.2). Specific overlaps (SO) for each period and overall were significant ($P < 0.05$) and the null hypothesis of complete overlap was rejected. In autumn, when general overlap was higher (GO = 0.97) than in other periods, the null hypothesis was rejected (V = 19.25; d. f. = 7; $P < 0.01$). General overlap during the other periods was also high, with the null hypothesis of complete overlap being rejected in all comparisons ($P < 0.05$).

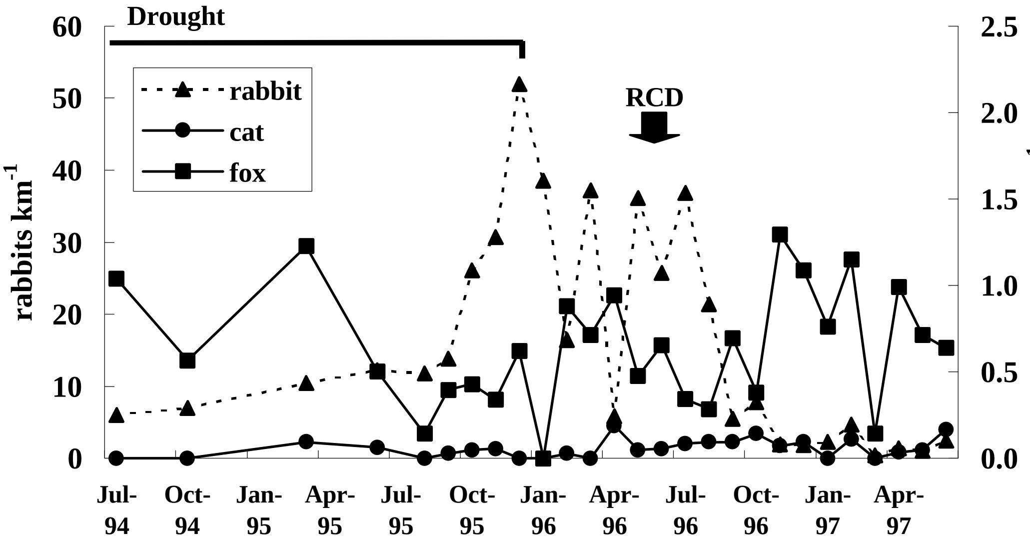

Fig. 6.1. Abundance indices (no. km^{-1}) for cats, foxes and rabbits recorded in spotlight counts at the untreated sites (DH and HC) from July 1994 to June 1997. Data collected by other VBCRC projects.

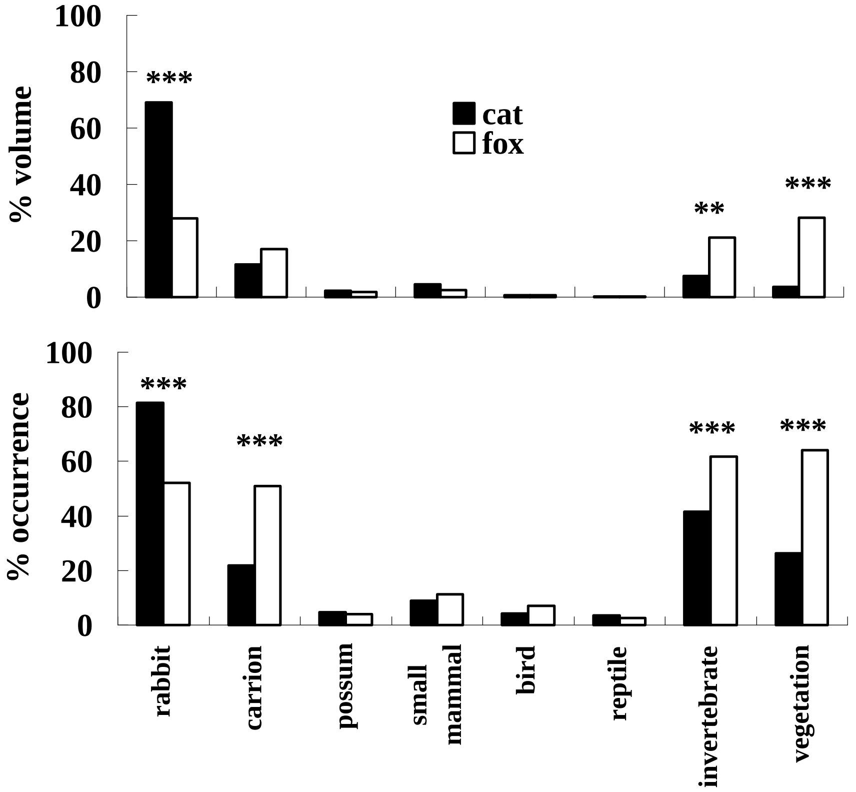

Fig. 6.2. Dietary comparison of the major prey groups for cats (*n* = 499 scats) and foxes (*n* = 343 scats). ** significant at $P < 0.05$, *** $P < 0.001$

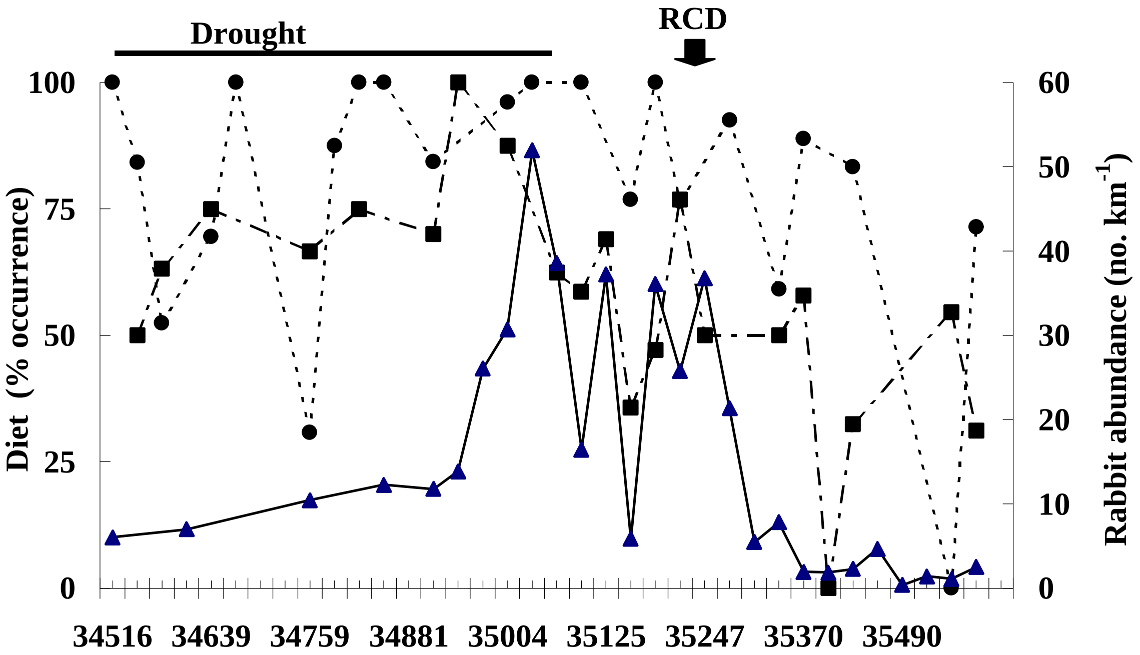

Fig. 6.4. Rabbit consumption by cats (*n* = 436 scats) and foxes (*n* = 321 scats) relative to rabbit abundance recorded in spotlight counts at the two untreated sites.

- ● **cat diet**
- ■ **fox diet**
- ▲ **rabbit abundance**

Table 6.2. Dietary breadth and overlap indices for cats (*n* = 436 scats) and foxes (*n* = 321 scats).

Where B = Levins' measure of dietary breadth, B_A = standardised Levins' measure, and P_{jk} = percentage overlap, SO = specific overlap, GO = general overlap and post-RCD = June 1996 to June 1997. * denotes values differing by 10% or more.

	Dietary breadth				**Dietary overlap**			
	(*B*)		**(*B*$_A$)**					
	cat	**fox**	**cat**	**fox**	**P_{jk}**	***SO*$_{1,2}$**	***SO*$_{2,1}$**	***GO***
winter	3.56	5.29 *	0.28	0.48 *	74%	0.81	0.82	0.95
spring	3.49	4.45 *	0.28	0.38*	73%	0.81	0.81	0.95
summer	3.63	4.36 *	0.29	0.37*	73%	0.80	0.79	0.95
autumn	4.32	4.46	0.37	0.38	78%	0.87	0.86	0.97
post-RCD	4.54	5.26 *	0.39	0.47*	75%	0.82	0.81	0.95
overall	3.75	4.83 *	0.31	0.42*	75%	0.85	0.86	0.96

Scat deposition. More scats were collected from both predators in grassland compared to *Callitris* and woodland habitats (Fig. 6.5a). However, cats and foxes deposited scats differently in the macrohabitat (G = 12.75; d. f. = 2; P = 0.002) and microhabitat types (G = 113.99; d. f. = 5; P < 0.001). Foxes deposited scats more often in grassland habitats than cats, while cats deposited scats more often in *Callitris* and woodland habitats (Fig. 6.5a). Similarly, cats deposited scats more often on rabbit warrens and at hollow log entrances than foxes, while foxes deposited scats more often on sand plots, tracks and at dams (Fig. 6.5b). Cats and foxes deposited scats in similar frequency at carcasses.

6.3.3. Direct predation of cats by foxes

No cat remains were found in any of the fox scats (n = 343 scats).

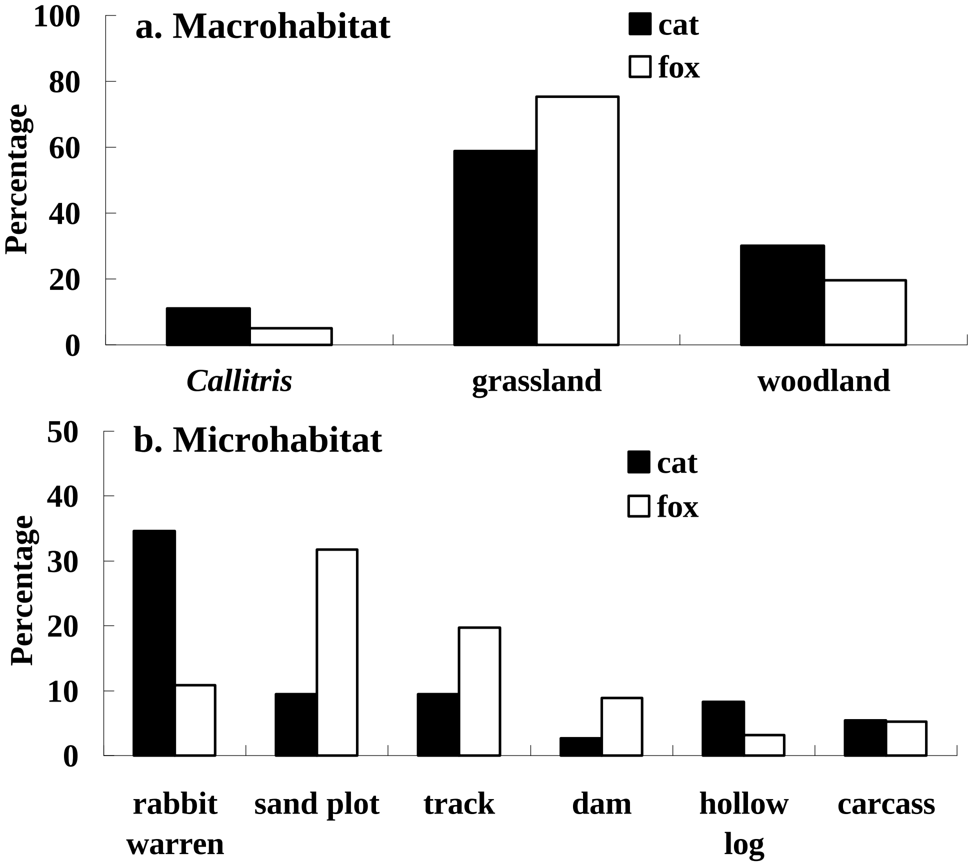

Fig. 6.5. Comparison between cats and foxes in the (a) macro- and (b) microhabitats in which scats were collected.

6.3.4. Dietary comparison between cats and quolls

Rabbits were the main prey for both cats and quolls (Fig. 6.6). Invertebrates were next most important in terms of frequency in the diet for both cats and quolls, occurring in 41.5% and 33.3% of scats respectively. Vegetation was eaten significantly less often by quolls (0%) than by cats (26.3%) (G = 6.81; d. f. = 1; P < 0.05). Reptile remains were not found in quoll scats. No significant differences were found for the other major prey types (P > 0.05, G-tests).

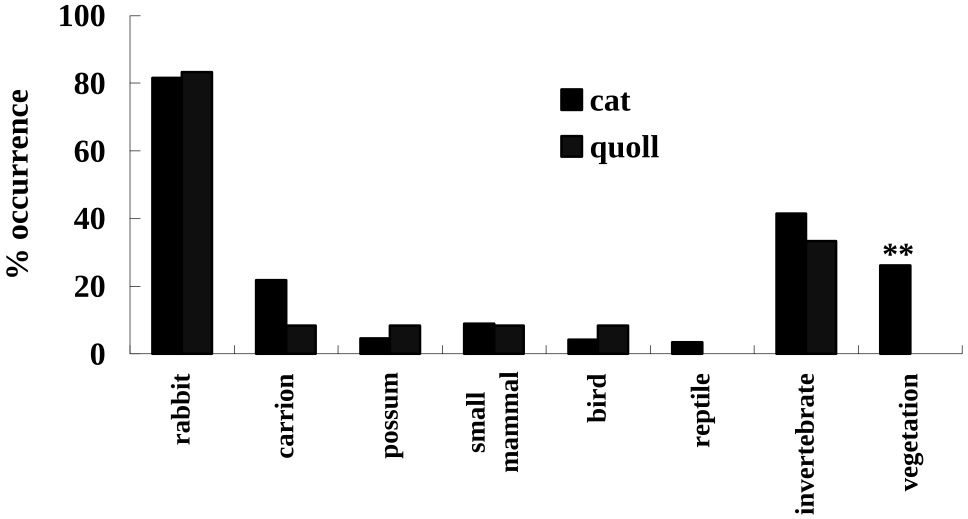

Fig. 6.6. Dietary comparison between cats (n = 499 scats) and spotted-tailed quolls (n = 12 scats) at Burrendong. ** significant at P < 0.05, G-test.

6.3.5. Spatial use comparison between cats and foxes

Home range size. Cats tended to occupy smaller home ranges (MCP 95) than foxes in winter in both 1995 and 1996 but the differences were not significant (1995: t = -0.10; d. f. = 14; P = 0.92; 1996: t = -0.68; d. f. = 19; P = 0.50) (Table 6.3). Core areas of cats and foxes were of similar size in both 1995 (t = 0.10; d. f. = 14; P = 0.92) and 1996 (t = 0.99; d. f. = 19; P = 0.34) (Table 6.3).

Table 6.3. Home range (MCP 95) and core area (MCP 50) sizes for cats and foxes in winter 1995 and 1996. Means and standard errors are shown.

		Range area		
		Home range (ha)	**Core area (ha)**	**No. locations**
Winter 1995	**cat** (*n* = 8)	275 ± 48.5	49 ± 18.6	309
	fox (*n* = 8)	285 ± 92.2	46 ± 11.2	489
Winter 1996	**cat** (*n* = 8)	309 ± 57.8	93 ± 25.5	410
	fox (*n* = 13)	396 ± 115.4	64 ± 14.9	1677
	Total			*2885*

Overlap in home ranges and core areas. A large degree of overlap occurred between the home ranges of cats and foxes, whereas little overlap was detected in core areas in both winter 1995 (Fig. 6.7) and 1996 (Fig. 6.8). In winter 1995, mean % overlap (± s. e.) of home ranges did not differ significantly between the three groups: cats and foxes (27.1% ± 3.7); cats and cats (25.8% ± 5.3); and foxes and foxes (19.5 ± 7.2) (F = 0.37; d. f. = 2, 81; P = 0.692) (Fig. 6.9). However, core areas did vary significantly (F = 3.17; d. f. = 2, 81; P = 0.047) (Fig. 6.9). The amount of overlap in core areas between cats and cats (7.7% ± 4.1) was greater than the zero overlap recorded between cats and foxes (Tukey P = 0.060). In winter 1996, mean % overlap did not differ significantly between the three groups for both home ranges (F = 1.77; d. f. = 2, 149; P = 0.174) and core areas (F = 1.56; d. f. = 2, 149; P = 0.213) (Figs. 6.8 and 6.9).

Trap locations of cats in relation to fox and cat core areas. Most cats (n = 6) were trapped in close proximity to their core areas, with only two cats trapped in fox core areas (Fig. 6.8).

Overlap in habitat utilisation. Both cats and foxes used open woodland most often and mudflats less often than other habitat types in both 1995 and 1996 (Fig. 6.10). No significant differences were found between cats and foxes in their relative use of the four habitat types at both levels of habitat composition: home range within the study site and at the location fixes within the home range (P > 0.05, Table 6.4).

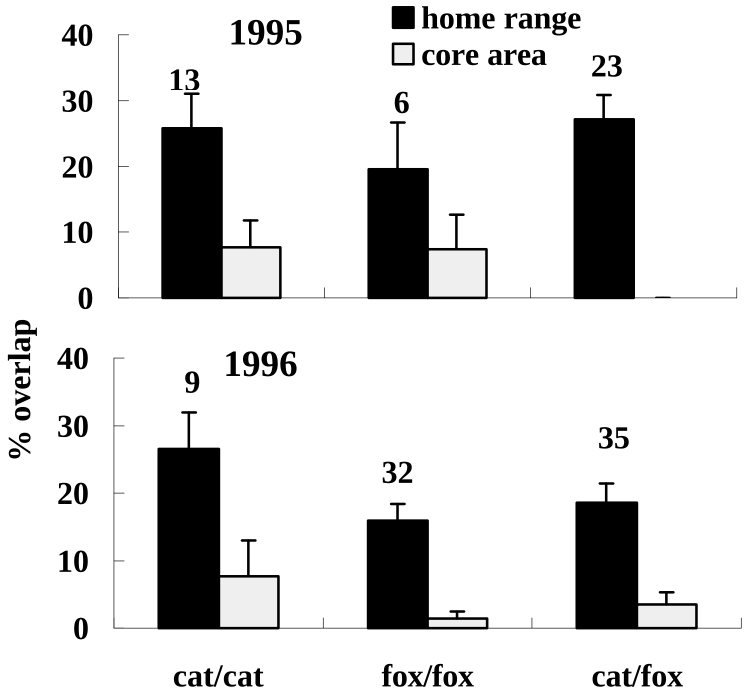

Fig. 6.9. Percentage overlap in home ranges and core areas between cats and foxes and between conspecifics in winter 1995 and 1996. Means and standard errors are shown. Values above bars represent the number of overlapping pairs.

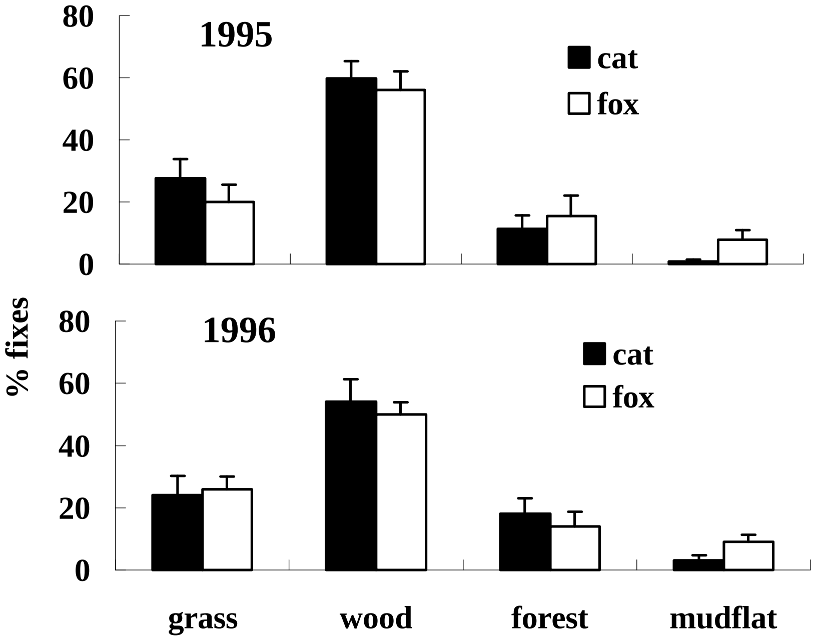

Fig. 6.10. Habitat use (% fixes in each habitat type) of cats and foxes in winter 1995 (798 fixes) and 1996 (2087 fixes). Means and standard errors are shown.

Table 6.4. Outcome of a two-way ANOVA for evaluating differences in habitat use between cats and foxes in winter 1995 and 1996. Habitat composition was determined at two levels: a) within study site, and b) within home ranges. Values represent the cat/fox by habitat interaction.

		F	***d. f .***	**P**
Winter 1995	*a) within study site*	*0.54*	*3, 56*	*0.66*
	b) within ranges	*0.89*	*3, 56*	*0.45*
Winter 1996	*a) within study site*	*0.49*	*3, 76*	*0.68*
	b) within ranges	*0.62*	*3, 76*	*0.60*

Habitat selection. Habitat selection, at the level of habitat composition within the home range compared to availability at the site, did not differ between cats and foxes in both 1995 and 1996 ($P > 0.05$). However, at the level of habitat composition at the location fixes relative to availability in the home range, habitat selection differed strongly between cats and foxes in both 1995 ($F = 6.69$; d. f. = 2, 31; $P = 0.004$) and 1996 ($F = 4.58$; d. f. = 2, 51; $P = 0.015$). In 1995, cats (mean log ratio = 0.278) used grassland more often than foxes (mean log ratio = -0.383) in relation to availability in their home ranges ($t = 2.97$; d. f. = 12; $P = 0.01$). In 1996, cats (mean log ratio = -1.39) tended to use mudflats less often than foxes (mean log ratio = 1.33) in relation to availability ($t = -1.90$; d. f. = 5; $P = 0.11$).

Compositional analysis revealed that cats did not establish their home ranges at random within the two untreated sites in either 1995 ($F = 4.81$; d. f. = 2,21; $P = 0.019$) or 1996 ($F = 3.55$; d. f. = 2,21; $P = 0.047$). Calculation of the ranking matrix showed that mudflats were significantly under-used relative to the three remaining habitat types in 1995, and relative to open woodland in 1996. Foxes did, however, establish their home ranges at random with respect to habitat in both years (1995: $F = 0.31$; d. f. = 2,18; $P = 0.739$; 1996: $F = 1.30$; d. f. = 2, 33; $P = 0.287$).

Habitat utilisation by cats based on location fixes was also significantly different to that expected from the habitat composition of the home ranges in 1995 ($F = 16.55$; d. f. = 2, 15; $P < 0.001$), but not in 1996 ($F = 3.52$; d. f. = 2, 16; $P = 0.054$). In 1995, cats avoided mudflats in preference to grassland and open woodland. Foxes selected habitats in proportion to availability in both years (1995 $F = 0.66$; d. f. = 2, 18; $P = 0.529$; 1996 $F = 1.86$; d. f. = 2, 33; $P = 0.172$).

6.3.6. Direct interactions between cats and foxes

6.3.6.1. Simultaneous radiotracking

Sizes of home ranges (MCP 95) and core areas (MCP 50) of four cats and six foxes are summarised in Table 6.5. No significant difference was found in the size of home ranges between cats ($\bar{x}$ ± s.e.: 386 ha ± 187.7) and foxes (258 ha ± 94) in October 1996 (t = 0.67; d. f. = 8; P = 0.52). Similarly, core areas were not significantly different in size between cats and foxes (t = 1.21; d. f. = 8; P = 0.26).

Table 6.5. Home range (MCP 95) and core area (MCP 50) sizes (ha) of four cats (232 fixes) and six foxes (331 fixes) at Spring Creek in October 1996.

	Radio Tag Frequency	ID	Sex	No. fixes	Range size (ha) MCP 95	Range size (ha) MCP 50
cat	216696	C2	M	50	199.5	29.7
	216934	C3	F	55	84.1	18.9
	216874	C1	M	48	331.5	67.2
	151983	C4	M	79	928	345
	mean				***386***	***115***
	s.e.				***187.7***	***77.3***
fox	150320	F2	F	58	306	134
	151320	F1	F	69	125	33
	150900	F4	F	70	57	12
	151740	F3	F	67	115	11
	150800	F5	F	33	687	16
	150580	F6	F	34	259	7
	mean				***258***	***36***
	s.e.				***94***	***20***

Static interaction. A large degree of home range (MCP 95) overlap was found between cats and foxes ($\bar{x}$ ± s.e.: 20% ± 4.8), cats and cats (34% ± 7.2), and foxes and foxes (22% ± 7.3), with no significant difference between the groups (F = 0.29; d. f. = 2, 52; P = 0.743) (Fig. 6.11a). However, core areas (MCP 50) were further apart, with minimal overlap recorded between cats and foxes (3.5% ± 3.03) and foxes and foxes (0.04% ± 0.03), and considerable overlap recorded between cats and cats (59% ±

10.80) (Fig. 6.11b). The difference in the amount of overlap between the three groups was significant ($F = 19.58$; d. f. = 2, 52; $P < 0.001$). Overlap between cats and cats was significantly greater than that recorded between cats and foxes ($P < 0.001$, Tukey) and between foxes and foxes ($P < 0.001$, Tukey). No difference in the amount of overlap was found between cats and foxes, and foxes and foxes ($P > 0.05$, Tukey).

Dynamic interaction.

adjacent ranges (Table 6.6) indicating attraction in spatial movements, while indices were mostly negative or close to zero between cats and foxes, indicating weak avoidance behaviour

foxes overall was 0.0007 ($n = 12$), indicating that cat movements were not influenced by fox

were 0.178 ($n = 3$) and between foxes and foxes 0.03 ($n = 4$).

Table 6.6. Jacobs' index describing the nature of the interaction between cats (C1-4) and foxes (F1-6) and between conspecifics in Spring Creek in October 1996. Where 0 = no interaction, -1 = avoidance and +1 = attraction. Values are shown for individuals with adjacent/overlapping home ranges

		Animal ID							
		C2	**C3**	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**
		216696	**216934**	**151320**	**150320**	**151740**	**150900**	**150800**	**150580**
C1	**216874**	0.34	0.23	-0.04	0.19			0.16	-0.20
C2	**216696**		-0.03		-0.09	0.02		-0.04	0.01
C3	**216934**				0.01				-0.01
C4	**151983**				-0.01		0.01		
F1	**151320**					-0.03		0.16	-0.06
F2	**150320**								
F5	**150800**								0.04

Distances maintained between individuals. Significant differences were found in the mean geometric distances between cats and foxes and between conspecifics ($F = 3.64$; d. f. = 2, 15; $P = 0.051$). Cats kept significantly further away from foxes ($\bar{x}$ ± s.e.: 1426 m ± 150.8) than they did from other cats (663 m ± 61.5) ($P = 0.045$, Tukey) (Fig. 6.12). Similarly, foxes tended to keep further away from cats than they did from each other (1134 m ± 183.2), but the difference was not significant ($P = 0.511$, Tukey) (Fig. 6.12). No significant difference was found in the distances between cats and cats, and foxes and foxes ($P = 0.368$, Tukey) (Fig. 6.12).

Habitat use. Both levels of habitat use (proportional habitat within the home range and proportional habitat use at the location fixes) produced similar results (Fig. 6.13). Open woodland was the most used habitat type by both cats and foxes while mudflats were used less often at Spring Creek in October 1996. Cats tended to use open woodland habitats more often and grassland less often than foxes, but the differences were not significant at the level of either home range or at the fixes ($P > 0.05$) (Fig. 6.13).

6.3.6.2. Video observations

In 140 hours of video observations, over 100 fox/fox interactions were recorded but only one cat/fox interaction. On this occasion, the cat remained at the carcass and the fox (a sub-adult) ran off. Cats visited the carcasses on only two occasions and only when foxes were not in the immediate vicinity. This area was known to be visited by at least three radiocollared cats and three radiocollared foxes, but only one individual cat visited the carcasses compared to at least 15 individual foxes. The ratio of possible visits to actual visits was 1:3 for foxes and 1: 0.3 for cats.

6.3.6.3. Causes of mortality for radiocollared cats

Of 17 confirmed cat deaths, decomposition was too advanced in nine cases for the cause of death to be determined. Where a cause of death was determined from carcass examination ($n = 8$), three were attributed to fox attack, three to trap injury, one was sick when trapped, and one was inadvertently shot. Fox attack was determined from the analysis of teethmarks on radio collars and puncture wounds detected in some bones. Teethmarks on the three radio collars were consistent with fox teeth marks (Fig. 6.14a). In addition, the leather collars were ripped, while collars of cats that died from other causes were generally intact (Fig. 6.14b).

6.3.6.4. Anecdotal observations of direct interactions

Eleven observations of interactions (i.e. ≤ 100 m) between cats and foxes are described in Table 6.7. Cats and foxes generally ignored each other (tolerance) at distances ≥ 50 m apart, while aggressive or displacement interactions were often observed when < 50 m apart (nos. 6, 8, 9 and 10, Table 6.7). On incident 6, a fox was sighted in the spotlight at the top of a dam levee. On sighting, the fox moved off and a cat appeared on the levee within 5 minutes. On

9, a cat was observed in a tree, while a fox was located 20m away. On incident 10, a fox was end as it circled the cat. The fox then chased the cat out of sight, a fox yelp was heard, and the cat was seen running off.

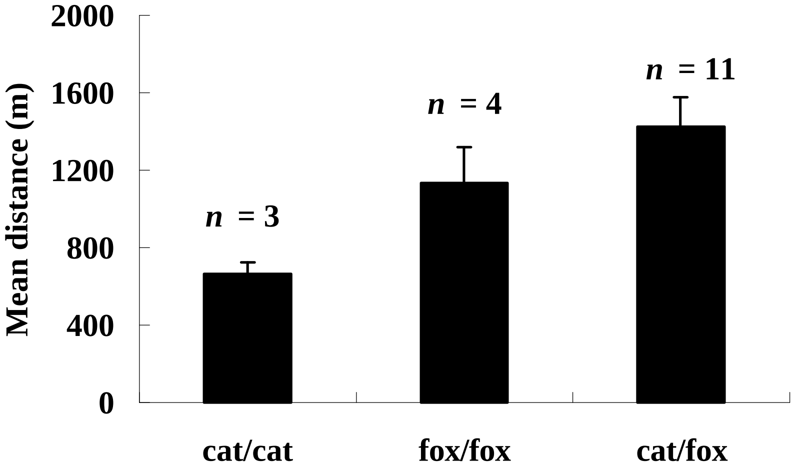

Fig. 6.12. Geometric distances recorded between cats (*n* = 4) and foxes (*n* = 6) and between conspecifics at Spring Creek in October 1996. Means and standard errors are shown. Values above bars represent the number of adjacent/overlapping pairs.

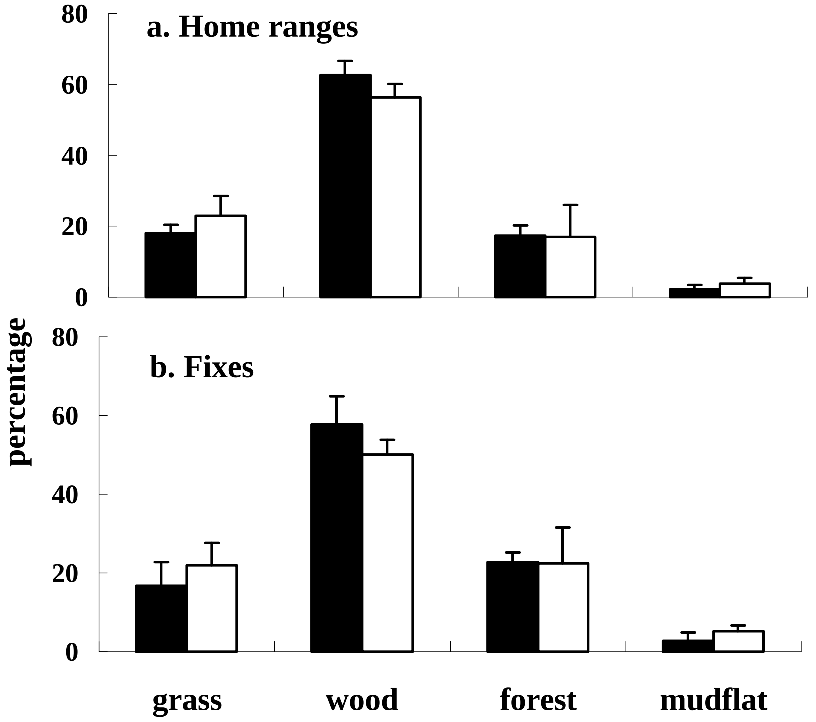

Fig. 6.13. Habitat composition of a) home ranges and b) at fixes for ■ cats (*n* = 4) and □ foxes (*n* = 6) at Spring Creek in October 1996. Means and standard errors are shown.

6.4. DISCUSSION

Cats and foxes at Burrendong had a large overlap in diet, home ranges and habitat use, indicating a high potential for exploitation competition. Some resource partitioning was detected, and avoidance and aggression were observed.

6.4.1. Overlap in diet: cats and foxes

Both predators preyed mainly on mammals and to a lesser extent birds, reptiles, invertebrates and vegetation. Although dietary overlap was high (75%), cats and foxes used many of the same prey types in different proportions. Rabbits were more important in the diet of cats than foxes, particularly in summer, when invertebrates were a significant dietary component for foxes. In contrast, carrion, invertebrates and vegetation were significantly more important in the diet of foxes than cats, overall. These interspecific differences in diet are consistent with those reported for sympatric cats and foxes elsewhere (Bayly 1978, Triggs *et al.* 1984, Catling 1988, Brunner *et al.* 1991, Wallis *et al.* 1996).

6.4.2. Overlap in diet: cats and quolls

The similarity in diet between cats and spotted-tailed quolls at Burrendong also indicated potential for exploitation competition, although few quoll scats (n = 12) were collected. Rabbits were the main prey for both predators and invertebrates second in importance. Carrion, reptiles and vegetation were eaten more often by cats than by quolls, while possums and birds tended to be eaten more often by quolls. The diet of the spotted-tailed quoll at Burrendong was similar to that recorded in open forest-woodland in Victoria (Belcher 1995), which is the only other study that has examined diet in this species.

6.4.3. Overlap in habitat use

Differences in habitat use between felids and canids were expected given their morphological and behavioural differences (Eisenberg 1986, Kruuk 1986). Felids often hunt using concealment, stalking and sudden attack, which require cover, while canids typically use open-area pursuit techniques to exhaust large prey, while at close range they pounce on small prey (Kruuk and Turner 1967, Kleiman and Eisenberg 1973, Eisenberg 1986, Henry 1986, Koehler and Hornocker 1991). Dense cover for felids allows concealment from prey but can also provide cover from potential agonistic encounters with other predators (e.g. Litvaitis and Harrison 1989). In contrast, canids do not usually use vegetation for concealment and tend to have increased hunting success in open habitats (Wells and Bekoff 1982, but see Murray *et al.* 1995). Differences in hunting behaviour between canids and felids suggest that the two groups should hunt in different habitat types, even when they share the same staple prey.

However, considerable overlap in both diet and habitat use were observed in this study and in studies of sympatric canids and felids elsewhere (e.g. Artois 1985, Major and Sherburne 1987, Litvaitis and Harrison 1989, Koehler and Hornocker 1991). For example, sympatric wild cats (*Felis silvestris*) and red foxes had similar dietary requirements in an agricultural region in France, and both predators rested in wooded cover during the day and were active at night in open areas (Artois 1985). Partitioning of habitats on a finer scale, however, may elucidate greater habitat segregation (e.g. Artois 1985).

Home ranges of both cats and foxes at Burrendong comprised mostly open woodland followed by grassland, open forest and mudflat habitats, which largely reflected the availability of these habitats. Scats from both predators were also deposited in similar macrohabitats; grassland was the most common habitat type followed by *Callitris* and woodland. However, some interspecific differences were detected in habitat preference and the microhabitats in which scats were deposited. While foxes established home ranges in habitats relative to availability, cats avoided mudflats. In addition, within individual home ranges, cats showed a preference for grassland habitats and again avoided mudflat areas, while no habitat preference was detected for foxes. Further, cats deposited scats more often than foxes at rabbit warrens and at log entrances, while foxes deposited scats more often than cats on sand plots, tracks and at dams.

The avoidance of mudflats by cats presumably reflected the paucity of prey in these areas and the lack of available shelter. Similarly, the preference for grassland habitats by cats presumably reflected the greater abundance of rabbits in these areas (personal observation) and the greater reliance on rabbits as prey, compared to foxes. The influence of prey availability on habitat preference has been documented widely in mammalian carnivores (e.g. Litvaitis *et al.* 1985, Phillips and Catling 1991). For example, bobcats were most abundant in dense understories in eastern Maine, where snowshoe hares were most abundant (Litvaitis *et al.* 1985). Similarly, foxes in coastal south-eastern Australia frequently used dry sclerophyll forest habitats, where small and medium-sized mammals were most abundant, while heathland and beach habitats were used rarely (Phillips and Catling 1991).

The interspecific differences recorded in the microhabitats in which scats were deposited were consistent with the locations of cats and foxes observed at Burrendong. Cats often used rabbit warrens and hollow logs for shelter, while foxes were observed frequently on or near tracks. In Western Australia, the higher deposition of scats by foxes than by cats at sand plots (which contained buried meat baits) was consistent with cats being reluctant to dig up baits (Risbey *et al.* 1997).

6.4.4. Home range size

Cats at Burrendong tended to occupy smaller home ranges than foxes, which is consistent with studies of these predators elsewhere in Australia (e.g. Jones and Coman 1982, Coman *et al.* 1991, Phillips and Catling 1991). However, the simultaneous locations, which were obtained only at night, showed that cats tended to occupy larger home ranges than did foxes in October. This discrepancy may be due to the small sample size (four cats and six foxes) and the short time span (one month) over which simultaneous locations were obtained. Alternatively, it may have reflected a sex bias as all foxes used in this study were females. Although red fox home range sizes do not usually differ between the sexes (e.g. Cavallini and Lovari 1994), vixens may have been denning in October, at which time activity is usually reduced and mostly diurnal (Phillips and Catling 1991). In addition, three of the four cats on which simultaneous locations were obtained were males which generally occupy larger home ranges than females (see Chapter 5).

6.4.5. Avoidance

Spatial segregation between cats and foxes at Burrendong indicated mutual avoidance with most evidence suggesting that cats avoided foxes, rather than the converse. Although all known cats and foxes in the study area were not radiocollared, as uncollared animals were frequently observed, overlap within species was greater than between species. Similarly, little interspecific overlap in core areas was observed. Most cats ($n = 6$) were trapped within or in close proximity to their core areas, while only two cats were trapped in fox core areas. In addition, the actual distances maintained between simultaneously radiotracked cats and foxes were greater than those maintained between conspecifics. Video observations (140 hours) indicated avoidance of carcasses by cats in the presence of foxes. Although carrion was an important supplementary prey for both predators and no interspecific differences were detected in the frequency of scat deposition at carcasses, cats visited the carcasses on only two occasions compared to over 100 visits by foxes. Cats visited the carcasses only when foxes were not in the immediate vicinity although the video area was located within the home ranges of three radiocollared cats and three radiocollared foxes. However, during the day when the video camera was turned off cats may have fed at the carcasses. It was not possible to distinguish diurnal scavenging by birds and cats. The video observation of avoidance of a cat by a fox probably reflected the subadult status of the fox.

Although no significant temporal avoidance was detected between simultaneously radiotracked cats and foxes (i.e. movements of both predators were random with respect to each other); they may have avoided each other in more subtle ways that were beyond the resolution of radiotracking data. This is supported by observations of no apparent interaction between cats and foxes at distances greater than 50 m. In addition, more subtle interactions could occur if one predator followed another and took approximately the same foraging route without maintaining direct contact (Doncaster and Macdonald 1997). Simultaneous locations of sympatric bobcats and coyotes in Maine also indicated a lack of attraction or avoidance between neighbouring heterospecifics, despite a large overlap in diet and spatial use and a negative correlation in abundance between the two predators (Major and Sherburne 1987, Litvaitis and Harrison 1989). Alternatively, cats may have avoided foxes in more overt ways such as by being diurnally more active. Thus video observations and simultaneous radiotracking at night may have underestimated the real amount of temporal segregation.

Avoidance of the dominant predator by a subordinate predator has been recorded widely in carnivores (e.g. Voigt and Earle 1983, Major and Sherburne 1987). For example, coyotes exclude red foxes from their core areas and foxes occupy territories on the periphery or outside of coyote territories (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant *et al.* 1987, Harrison *et al.* 1989). Although coyotes are aggressive and sometimes kill foxes, particularly when carcasses are present, at other times coyotes tolerate foxes (Fuller and Keith 1981).

6.4.6. Aggression

Aggression by foxes toward cats was indicated with the evident killing of three radiocollared cats by foxes. It was not known whether foxes subsequently ate the three cats as decomposition was too advanced. No cat remains were detected in any of the 343 fox scats (or 255 fox stomachs, Appendix 3) that were collected from Burrendong, although elsewhere cat remains have been found in the diet of foxes (Coman 1973b, Brunner *et al.* 1991, Taylor and Lupica 1998, D. Risbey pers. comm., R. Paltridge pers. comm.).

Anecdotal observations further indicated aggression toward cats. Although foxes tolerated cats at distances greater than 50 m, they were aggressive or displaced cats at distances less than 50 m. Similarly, neighbouring groups of red foxes in Bristol avoided direct encounters with each other at close distances (<50 m), presumably through sight or scent (White and Harris 1994).

6.4.7. Niche overlap theory

Traditional niche theory predicts that overlap should be lower when resources are scarce (e.g. Pianka 1974, Schoener 1982, Caughley and Sinclair 1994), but this has been challenged increasingly in recent years (Freeland 1983, Arthur 1987, Vadas 1990, Hansson 1995).

Overlap can also increase when resources are scarce (e.g. Schoener 1982, Litvaitis and Harrison 1989), since coexisting species may expand their niches to exploit suboptimal resources. Examination of dietary breadth and overlap between cats and foxes at Burrendong supports this interpretation. Cats increased their dietary breadth in autumn to include a greater range of prey types when the availability of young rabbits was low (c. f. Catling 1988), and dietary overlap with foxes increased to 78%. Cats were also more trappable in autumn, which provided further support that rabbits were scarce (see Appendix 1). In addition, when rabbit numbers declined dramatically post-RCD, the dietary breadth of both predators increased and overlap was high. Increased overlap between sympatric felids and canids during lean periods has been recorded elsewhere (Litvaitis *et al.* 1986, Litvaitis and Harrison 1989, Koehler and Hornocker 1991). In eastern Maine, bobcats overlapped more with coyotes in winter and spring when prey were less abundant and bobcats were in poor physical condition (Litvaitis *et al.* 1986, Litvaitis and Harrison 1989). Similarly, overlap among mountain lions, bobcats and coyotes increased during winter when resources were limited in central Idaho (Koehler and Hornocker 1991).

6.5. CONCLUSION

Intraguild predation was not indicated in this study as no cat remains were found in any of the fox scats. However, cats and foxes had a large overlap in diet, home ranges and habitat use, thus indicating a high potential for exploitation competition, particularly if resources were limited. Foxes may attempt to lessen competition by killing cats (interference competition). Mutual avoidance of the two species was indicated by the greater distances and lower overlap in home ranges and core areas recorded between species compared to conspecifics. Video observations suggested that cats avoided carcasses when foxes were in the vicinity. Some resource partitioning was detected in both diet and habitat use. Further resource partitioning may have occurred if prey items and habitat types had been examined on a finer scale. In addition, temporal differences in activity, although not examined here, may facilitate coexistence between cats and foxes (e.g. Das 1993, Artois 1985). However, to effectively test the hypotheses that foxes limit cat abundance through interspecific competition or intraguild predation, an experimental removal of foxes is clearly required. Such an experiment is presented in Chapter 7.

CHAPTER 7

EFFECTS OF FOX REMOVAL ON ABUNDANCE, DIET AND USE OF SPACE BY CATS

7.1. INTRODUCTION

Reported increases in feral cat abundance following fox removals in Australia (Short *et al.* 1995, Christensen and Burrows 1995, Risbey and Calver 1998, P. de Tores pers. comm.) suggest that foxes may limit cat populations, possibly through predation but more likely via interspecific competition (exploitation and/or interference). The large degree of overlap in diet, home range and habitat use recorded between feral cats and foxes in Chapter 6 indicated a high potential for exploitation competition, particularly if resources were limited. In addition, observations of avoidance and aggression between the two predators indicated possible interference competition. The aim of this chapter is to further investigate the ecological interaction between feral cats and foxes using a fox removal experiment, and to test the hypothesis that foxes limit cat populations through interspecific competition.

Studies of the role of competition in limiting carnivore species are rare in Australia and elsewhere, and experimental field tests are generally lacking. Much of the evidence suggesting competition among coexisting mammalian carnivores is based on large overlaps in resource use (e.g. White *et al.* 1995, Koehler and Hornocker 1991). Where increases in the abundance of one predator after the removal of the other have been recorded (e.g. Litvaitis and Harrison 1989, Lindstrom *et al.* 1995), other factors may have been implicated such as intraguild predation (Polis *et al.* 1989) or increases in prey availability (Hairston 1985). Although some field studies have provided strong evidence for competition by manipulating densities of one competitor and observing changes in population size and resource use of the remaining competitor (e.g. Underwood 1978, Fonteyn and Mahall 1981, Dickman 1986a, Hairston 1986, Valone and Brown 1995), none has involved mammalian carnivores.

In this chapter, the possibility that foxes limit feral cat populations through interspecific competition is examined using a fox removal experiment. To test the hypothesis of competition, four parameters (cat abundance, home range size, habitat use and diet) were examined at treated and untreated sites and before and after fox removal. Examination of these parameters allowed testing of two further hypotheses, intraguild predation and facilitation. The directions of predicted resource shifts for all hypotheses are summarised in Table 8.1, and the hypotheses tested in this chapter are described as follows:

H_0: Foxes do not limit cat populations.

According to this null hypothesis, foxes do not limit cat populations. Cats are limited independently instead through other factors such as food availability. This hypothesis will be supported if, after a reduction in foxes, there is no increase in the abundance of cats, nor change in diet, home range size, or habitat use. Food limitation will be supported if cats show a numerical response to changes in prey density (Chapters 4 and 6).

H_1: Foxes do limit cat populations, when prey densities are low, through interspecific competition (exploitation and / or interference).

a) Exploitation competition. This hypothesis predicts that, if the home ranges of foxes and cats overlap significantly, the diet of the two species will be significantly different. This hypothesis will be supported if, after fox removal, cats increase in abundance and there is a dietary change toward prey eaten previously by foxes. In addition, home range size should decrease, as cats now have access to more prey within their foraging ranges.

b) Interference competition. This hypothesis predicts that, if the home ranges of foxes and cats do not overlap significantly, the diet of the two species will not differ. Interference competition will be demonstrated if, after fox removal, cats increase in abundance and change their habitat use. Home range size may also increase after fox removal as cats become free to use areas previously occupied by foxes. Alternatively, home range size may not change if new cats move into the area and the abundance of cats increases. A dietary change would not be expected, unless a shift to previously unused habitats allowed access to new prey that occurred there. In general, shifts in resource use are expected to occur much more quickly, e.g. on a moment to moment basis, under interference competition than under exploitation, where resource shifts may take place over weeks or months.

7.2. METHODS

General methods for scat collection and for calculation of abundance indices for cats, foxes and rabbits are outlined in Chapter 3. Data were collected for four sites: Dog Trap (DT) (100% fox removal); Gunnel Creek (GC) (50-80% fox removal); Harrys Creek (HC) (untreated site); and Devils Hole (DH) (untreated site). An additional fifth site was included for the dietary analysis that included all scats collected outside the two untreated sites but which were within the untreated study area. Cat dietary data were collected between July 1994 and June 1997, while spatial data were collected for three seasons: winter 1995 (May to

August); summer 1995/96 (November to March) and winter 1996 (May to August). The VBCRC Predator-Prey Project conducted the spotlight counts and the fox baiting program. All statistical analyses in this chapter were performed using GENSTAT (ANOVA, analysis of deviance, regression, general linear modelling) and Excel (*t*-test, *G*-test, correlation analyses).

7.2.1. Fox removal experiment

The fox removal and reduction treatments were implemented from October 1995 at the two removal sites, Dog Trap (100% removal) and Gunnel Creek (50-80% removal) (A. Newsome

baiting and spotlight shooting, with control continuing to the present. Baits were

also shot when seen at the removal sites with a low velocity 0.222-calibre rifle. Although the two treated sites were not subjected to the same intensity of fox removal (i.e. 100% and 50-80%), the heavy reduction of foxes in both sites provided a suitable experimental treatment. Fox densities were not manipulated at the two untreated control sites (DH and HC). A BACI design (Underwood 1994) was therefore established with two treated (DT and GC) and two untreated sites (DH and HC).

At the 100% fox removal site (DT), 86 baits were buried at a depth of 5 cm. Baits were placed at 200 m intervals along the edges of the main access roads throughout the site. Baits were checked at the beginning of each month and replaced where necessary. All baits were then replaced at the end of each month and when rainfall exceeded 25 mm. At the partial fox removal site (GC), 27 baits were placed at 400 m intervals on the edge of the main access roads throughout the site. Baits were exposed for 10 days every three months.

7.2.2. Abundance indices for cats, foxes and rabbits

Spotlight counts were conducted by existing VBCRC projects (Chapter 3) and used to monitor the success of the fox removal program and the influence of fox removal on feral cat and rabbit numbers (A. Newsome unpublished data, J. McIlroy unpublished data). Data are expressed as sightings per km (+ standard errors) for each season, and before (July 1994 to September 1995) and after (October 1995 to August 1998) fox removal. To determine the influence of fox removal on abundance indices, indices were converted to ratios (mean before/mean after) and a *t*-test used to examine differences in the mean ratios between treated and untreated sites.

7.2.3. Cat diet

By occurrence. Effects of fox removal on the numbers of scats in which each prey group occurred were tested using an analysis of deviance with binomial error and logit link. Treatment (treated vs. untreated sites), fox removal (before vs. after) and site (1 to 5) were fitted to the model as factors. Five prey groups considered important to cats (rabbit, carrion, house mouse, possum and invertebrates) were included in the analysis. Each prey group was tested separately to avoid problems associated with the lack of independence between prey groups.

By volume. Effects of fox removal on the % volume of each of the five prey groups in the diet of cats were examined using a general linear model, where treatment (treated vs. untreated sites), fox removal (before vs. after) and site (1-5) were fitted to the model as factors. Each prey group was tested separately (as above), with those groups that were recorded infrequently in the diet being log-transformed (log X +1) to reduce the clumping of residuals.

Scat deposition. As described in Chapter 6, the macro- (grassland, *Callitris*, and woodland) and microhabitats (rabbit warren, on sand-plots, on tracks, at dams, hollow log entrances, at carcasses, under bushes, on rocks or on bare ground) in which scats were found, were generally recorded at the time of collection. However, because these were not always recorded, sample sizes for macro- and microhabitat analyses were reduced to 226 and 320 scats respectively. Fox removal effects on the numbers of cat scats in each macro- and microhabitat type were tested using analysis of deviance with binomial error and logit link. The response variable was the number of scats in each habitat type, and treatment (treated vs. untreated sites), fox removal (before vs. after) and site (1 to 5) were fitted to the model as factors. Each habitat type was tested separately. Surveys for scats were of similar intensity in the different sites before and after fox removal.

7.2.4. Cat home range size

All analyses were conducted on the MCP 95 estimate of home range size only because MCP 95 and KE 95 were significantly and positively related ($r^2 = 0.78$; $n = 41$; $P < 0.001$). Similarly, the MCP 95 and MCP 100 estimates were significantly related ($r^2 = 0.68$; $n = 41$; $P < 0.001$). Only those home ranges with ≥ 20 location fixes and which reached an asymptote with increasing numbers of fixes, were included in the analyses. In addition, two cats that died during the radiotracking period in winter 1995 were excluded (Chapter 5). Sample sizes of cats, therefore, were as follows: winter 1995, $n = 15$ (before fox removal); summer 1995/96, $n = 11$ (after fox removal); and winter 1996, $n = 17$ (after fox removal).

Fox removal effects. Effects of fox removal on the home range sizes of cats were tested using general linear regression where MCP 95 was the response variable, and sites, treatment, and fox removal were fitted to the model as factors. In addition, season (winter 1995, summer 1995/96 and winter 1996), sex and age (young vs. old) were fitted to the model as factors to examine their influences on home range size. To avoid possible confounding of seasonal effects, this analysis was repeated after excluding the summer 1995/96 period. In addition, a general linear regression (as outlined above) was used to examine the effect of fox removal on home range size of only those seven cats whose home ranges were estimated for all three seasons.

Effects of fox removal on day and night home range sizes (MCP 95) of cats were examined using general linear regression. Home range size was the response variable, and site, treatment, time of day (day vs. night), fox removal, sex and age were fitted to the model as factors. Cats with fewer than 10 location fixes in either day or night ranges were excluded from the analysis. Sample sizes for day/night range analyses were as follows: winter 1995, $n = 12$; summer 1995/96, $n = 9$; and winter 1996, $n = 15$. This analysis was conducted for cats for all three seasons, and then repeated with summer 1995/96 excluded. This analysis was not conducted on the seven cats that survived all three seasons as three of the cats had insufficient fixes (< 10) in either day or night ranges.

Day vs. night range size. Differences between day and night home range sizes overall were tested with a matched pairs *t*-test for each season separately.

Influence of rabbit abundance. The relationship between home range size of cats and rabbit abundance at the four sites was evaluated using regression analysis.

7.2.5. Cat habitat use

All analyses were conducted on the proportion of fixes in each habitat type within the home range. This was considered a more sensitive measure of habitat use than the habitat composition of the home range. Each habitat was tested separately to overcome problems associated with the lack of independence in proportional use between habitat types.

Fox removal effects. The effect of fox removal on the overall habitat use of cats was examined using general linear regression where the response variable was the proportion of location fixes in each habitat type, and treatment and fox removal were fitted to the model as factors. Sex and age were also fitted to the model to examine interaction effects. Summer habitat use was excluded from the examination of fox removal effects to avoid possible confounding of seasonal effects.

Fox removal effects on habitat use were also examined on a finer temporal scale using general linear regression, where day and night location fixes were examined separately. The proportion of location fixes in each habitat type was used as the response variable, and treatment (treated vs. untreated sites), fox removal (before vs. after) and time of day (day vs. night) were fitted to the model as factors. Sex and age were fitted to the model to examine interaction effects. Cats with fewer than 10 location fixes in day and night ranges were excluded from the analysis in both winter 1995 (n = 3 cats) and winter 1996 (n = 2 cats). This analysis was repeated with the two periods, before fox removal (winter 1995) and after fox removal (winter 1996), examined separately (treatment by time of day).

Season, sex and age variation. Variation in habitat use between seasons, sexes and ages of cats for all three seasons (winter 1995, summer 1995/96, winter 1996) was examined using general linear regression. The proportion of fixes in each habitat type was used as the response variable and season, sex, age and site were fitted to the model as factors.

Day vs. night. General linear regression was used to examine differences between day and night habitat use overall with all three seasons included in the analysis. The proportion of fixes in each habitat type was used as the response variable, and season, time of day, and site were fitted to the model as factors.

Diet of cats in winter 1995 and 1996 only. Fox removal effects on the numbers of scats containing each prey group were also examined for the period when habitat use was recorded (winters in 1995 and 1996). Each prey group was tested separately using the G-test.

7.3. RESULTS

7.3.1. Abundance indices for cats, foxes and rabbits

Effectiveness of the fox removal. Fox abundance indices did not differ significantly after fox removal at the treated sites relative to the untreated sites (t = 1.81; d. f. = 2; P = 0.212). However, fox reductions were considered reasonably effective as fox numbers declined after fox baiting began in October 1995 at the 100% fox removal site (DT) and remained stable but low at the 50-80% reduction site (GC), while at the

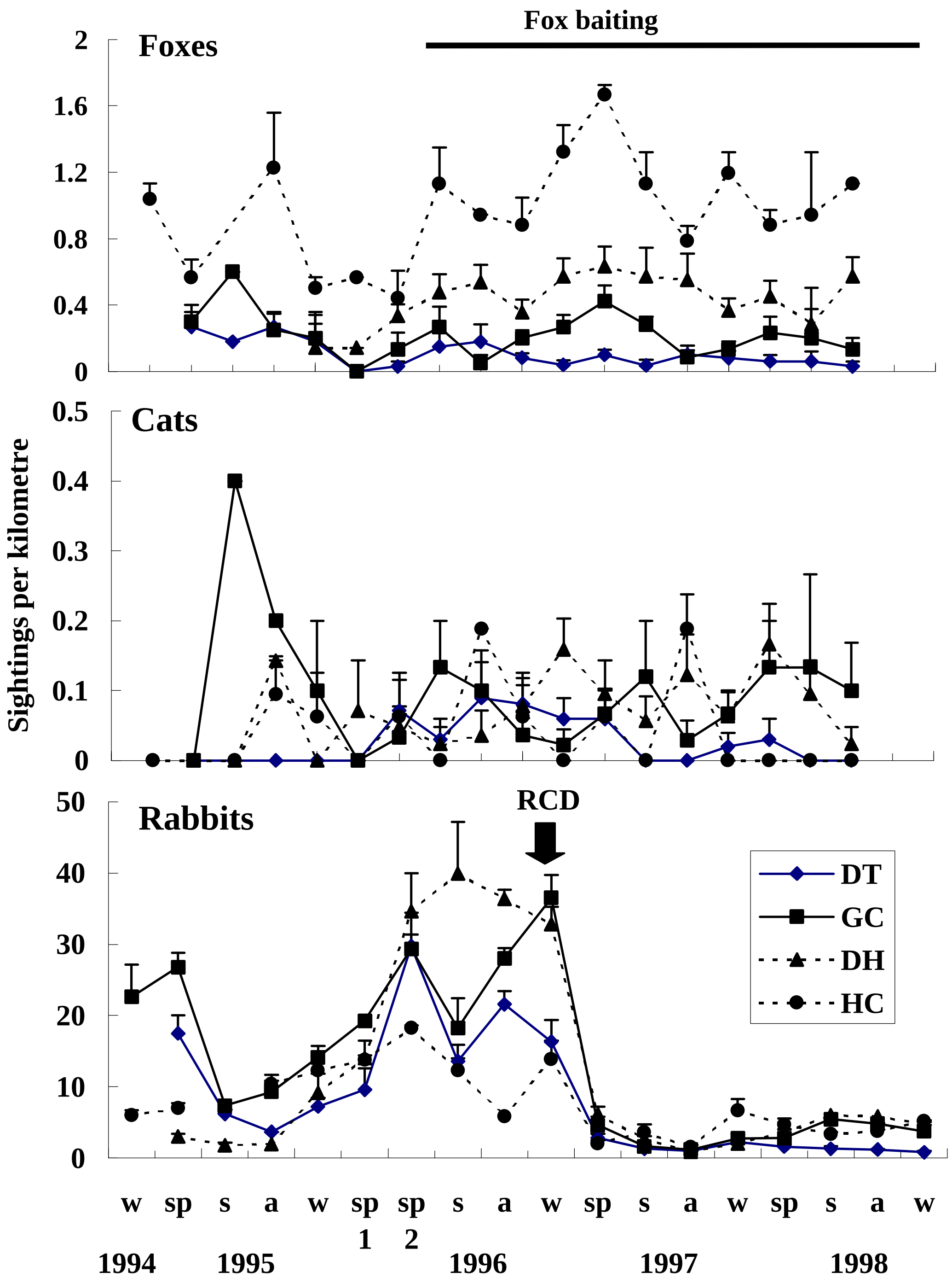

Fig. 7.1. Indices of abundance for foxes, cats and rabbits recorded in spotlight counts at treated (DT and GC) and untreated sites (DH and HC) from July 1994 to August 1998. Data collected by existing VBCRC projects. Fox baiting began in October 1995 at the two treated sites. Means and standard errors are shown. w = winter, sp = spring, s = summer and a = autumn; site names are described in full in the text.

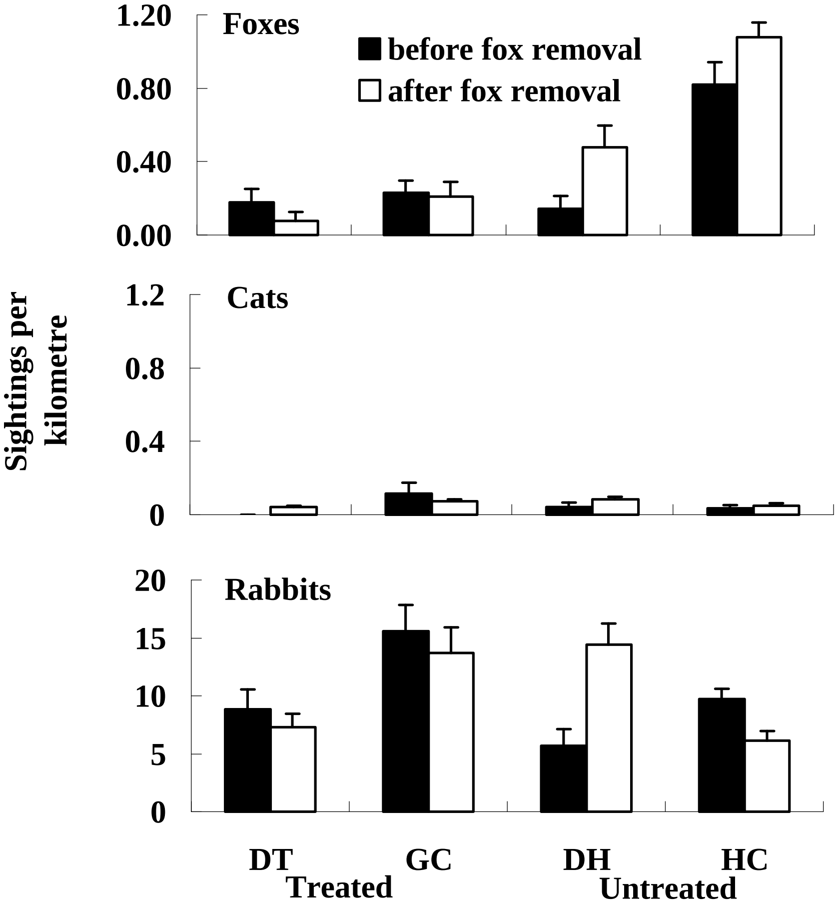

Fig. 7.2. Abundance indices for foxes, cats and rabbits recorded in spotlight counts at treated (DT and GC) and untreated sites (DH and HC), before (July 1994 to September 1995) and after (October 1995 to August 1998) fox removal. Means, calculated over all sessional samples, and standard errors are shown.

untreated sites (DH and HC) fox numbers increased (Figs. 7.1 and 7.2). In particular, following implementation of control measures, fox abundance in the two removal sites was lower than in the two non-removal sites over the next 10 seasons. Fox numbers ranged from 0 km^{-1} in spring 1995 at DT, to 1.6 km^{-1} at HC in summer 1996/97 (Fig. 7.1). Seasonal increases in fox numbers were found each year in summer and autumn at most sites (Fig. 7.1).

Cat abundance. No change in cat abundance was detected after fox removal at the treated sites relative to the untreated sites (t = 0.25; d. f. = 2; P = 0.824) (Figs. 7.1 and 7.2). Numbers of cats detected in the spotlight were low at all sites and remained relatively stable throughout the study, ranging from 0 km^{-1} at DT in spring 1994 and 1995, to 0.40 km^{-1} at GC in summer 1994/95. No clear seasonal peaks in abundance were detected (Fig. 7.1).

Rabbit abundance. Rabbit numbers did not increase after fox removal at the treated sites relative to untreated sites (t = 0.31; d. f. = 2; P = 0.784) (Figs. 7.1 and 7.2). Numbers collapsed at all sites in 1997 following the arrival of Rabbit Calicivirus Disease (RCD) in June 1996 (A. Newsome unpublished data). At DH, rabbit numbers ranged from 1.8 km^{-1} during the drought in summer 1994/95, to 39.3 km^{-1} in summer 1995/96, before declining to 2.8 km^{-1} in spring 1996 immediately post-RCD. Seasonal peaks in rabbit abundance occurred in spring at most sites in other years (Fig. 7.1).

7.3.2. Cat diet

By occurrence. Although remaining below 20%, the frequency of carrion consumption by cats increased significantly at the treated sites relative to the untreated sites after the removal of foxes (F = 21.39; d. f. = 1, 3; P < 0.05) (Fig. 7.3.). No significant differences were found for any of the other prey types tested (P > 0.05).

By volume. Invertebrates decreased significantly in the diet of cats by volume at the untreated sites relative to the treated sites (F = 4.28; d. f. = 1, 33; P = 0.046) (Fig. 7.4). This was not related to seasonal effects (treatment by removal by season interaction;

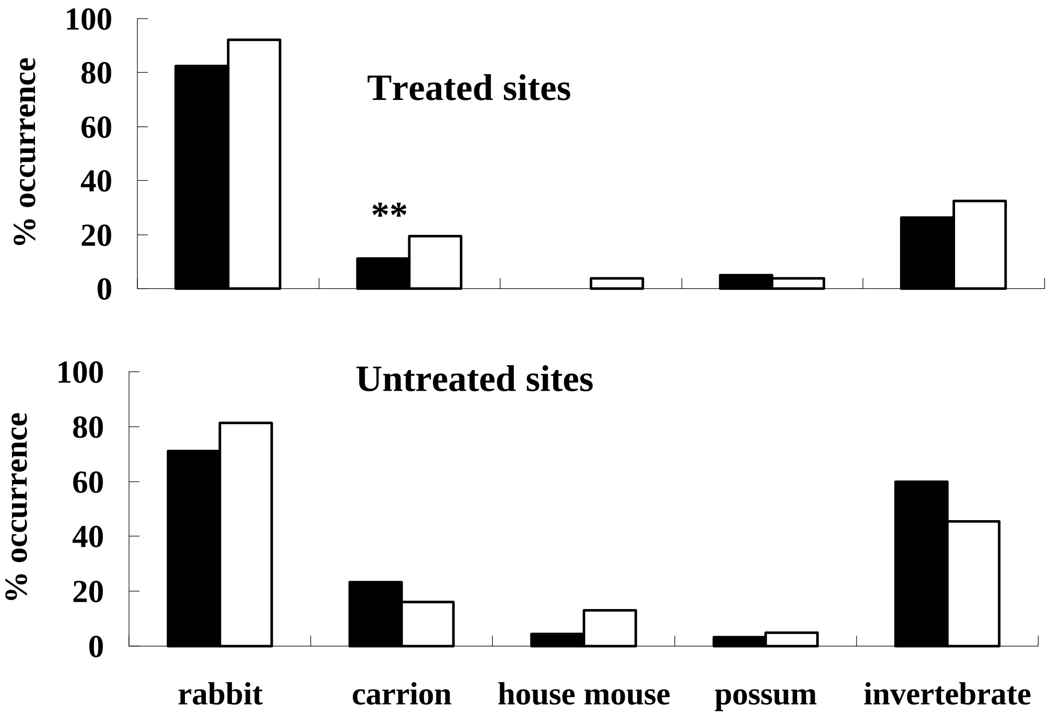

Fig. 7.3. Fox removal effects on the importance (% occurrence) of five major prey groups in the diet of cats (*n* = 408 scats). ** significant at *P* < 0.05

■ Before fox removal (July 1994 to September 1995)

□ After fox removal (October 1995 to June 1997)

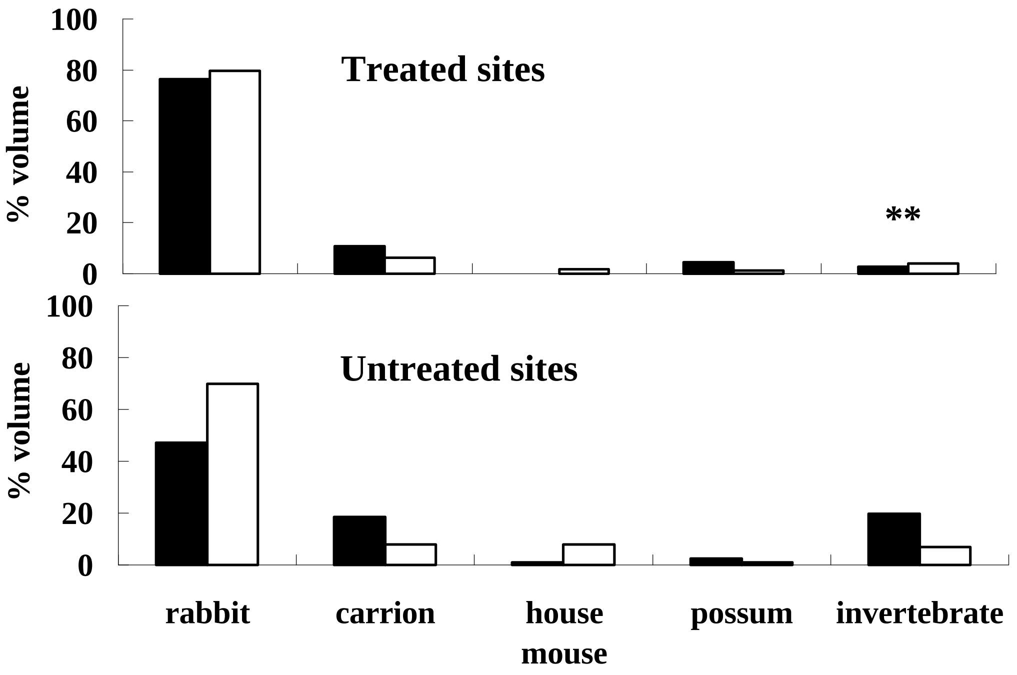

Fig. 7.4. Fox removal effects on the importance (% volume) of five major prey groups in the diet of cats (*n* = 408 scats). ** significant at *P* < 0.05

■ Before fox removal (July 1994 to September 1995)

☐ After fox removal (October 1995 to June 1997)

F = 1.94; d. f. = 3, 24; *P* = 0.149). No significant differences were found for the other prey types tested (*P* > 0.05).

Scat deposition. Numbers of scats found in both the macro- and microhabitat types did not differ significantly after fox removal at the treated sites relative to the untreated sites (*P* > 0.05) (Fig. 7.5). However, fewer cat scats tended to be found in the grassland habitats and more in the woodland habitats at the treated sites after fox removal, while scat deposition remained similar in each macrohabitat at the untreated sites (Fig. 7.5a). Similarly, more cat scats tended to be found at rabbit warrens at the treated sites after fox removal, and fewer elsewhere (Fig. 7.5b). At the untreated sites, similar numbers of scats were found at rabbit warrens after fox removal, and more scats were found on tracks, and fewer at hollow log entrances and carcasses compared to before fox removal (Fig. 7.5b).

7.3.3. Cat home range size

Fox removal effects. Overall, there were no changes in home range size (MCP 95) of cats after fox removal between treated and untreated sites when all three seasons were included in the analysis ($F = 0.01$; d. f. = 1, 39; $P = 0.908$; Fig. 7.6). However, weakly significant interaction effects were found with age ($F = 3.85$; d. f. = 1, 31; $P = 0.059$), but not with sex ($F = 1.64$; d. f. = 1, 31; $P = 0.210$). Home range sizes of old cats (> 3 years) increased after fox removal at the treated sites relative to the untreated sites where they did not change (Fig. 7.7). Home range sizes varied between the four sites but were not significantly different overall ($F = 1.77$; d. f. = 1, 39; $P = 0.170$), or between treated and untreated sites ($F = 1.95$; d. f. = 1, 39; $P = 0.170$) (Fig. 7.6).

When the summer 1995/96 season was excluded from the analysis, again no fox removal effects were detected on home range size ($F = 0.00$; d. f. = 1, 28; $P = 0.965$). However, when only those seven cats whose ranges were estimated for all three seasons were included in the analysis, home range size decreased significantly at the treated sites after fox removal, relative to the untreated sites where range sizes increased ($F = 6.87$; d. f. = 1, 12; $P = 0.022$) (Fig. 7.8). This response was less pronounced when summer 1995/96 was excluded from the analysis ($F = 4.25$; d. f. = 1, 5; $P = 0.094$). Home range sizes were smaller for the seven cats at the treated sites compared to the untreated sites overall ($F = 7.50$; d. f. = 1, 17; $P = 0.014$) (Fig. 7.8).

When day and night ranges were analysed separately no fox removal effects on home range size were found ($F = 1.24$; d. f. = 1, 64; $P = 0.270$). In addition, no significant interactions with sex ($F = 0.05$; d. f. = 1, 56; $P = 0.832$) or age ($F = 0.53$; d. f. = 1, 48; $P = 0.470$) were detected. Similar results were found when summer was excluded from the analysis ($F = 0.74$; d. f. = 1, 40; $P = 0.396$), with no interactions with sex ($F = 0.02$; d. f. = 1, 40; $P = 0.894$) or age ($F = 0.41$; d. f. = 1, 32; $P = 0.526$) being found.

Day vs. night range size. Day and night range sizes did not differ significantly in both winter 1995 ($t = 0.56$; d. f. = 11; $P = 0.58$) and 1996 ($t = 0.29$; d. f. = 14; $P = 0.77$) (Fig. 7.9). However, in summer 1995/96, day ranges ($\bar{x}$ ± s. e.: 232 ha ± 43) were

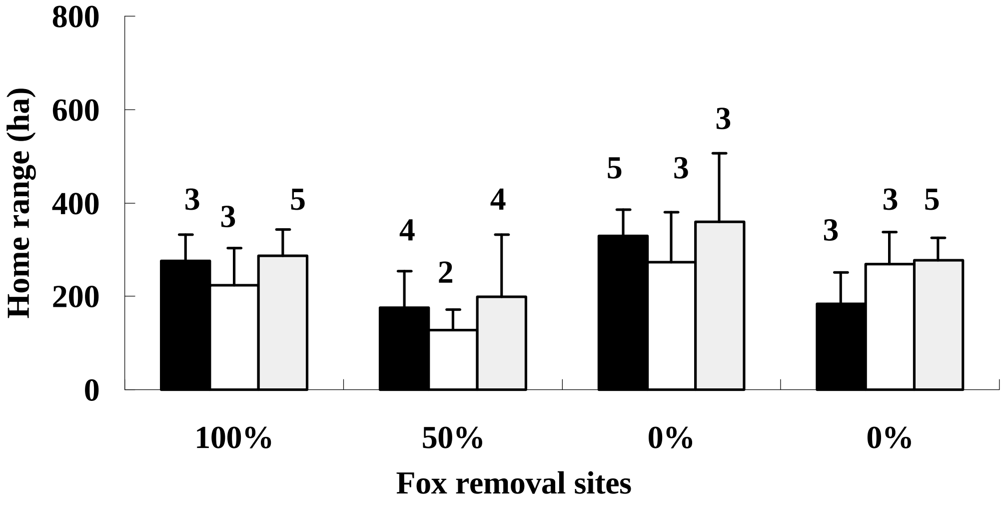

Fig. 7.6. Fox removal effects on the home range size (MCP 95) of cats for three periods. Means and standard errors are shown. Numbers of cats are above the bars.

■ Before fox removal (winter 1995) *n* = 15 cats
□ After fox removal (summer 1995/96) *n* = 11 cats
▨ After fox removal (winter 1996) *n* = 17 cats

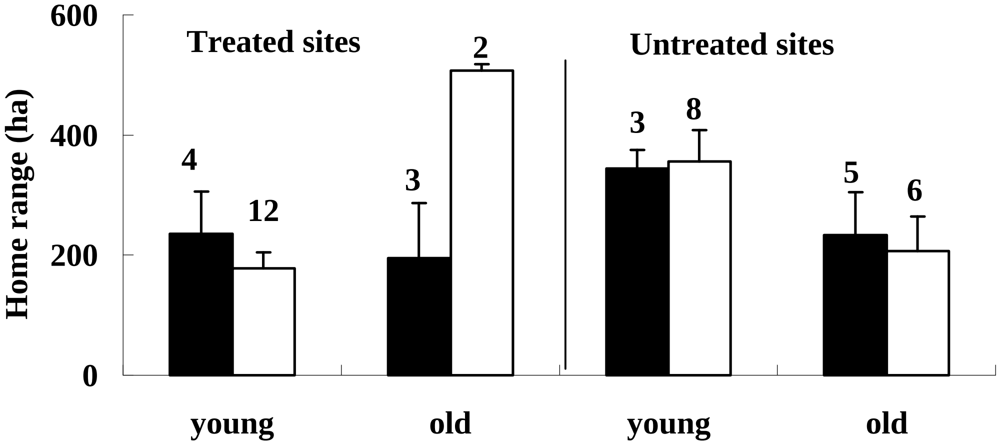

Fig. 7.7. Home range size (MCP 95) of young (1-3 years, *n* = 27) and old (>3 years, *n* = 16) cats, ■ before (winter 1995) and □ after fox removal (summer 1995/96 and winter 1996) at treated and untreated sites. Means and standard errors are shown. Numbers of cats are above the bars.

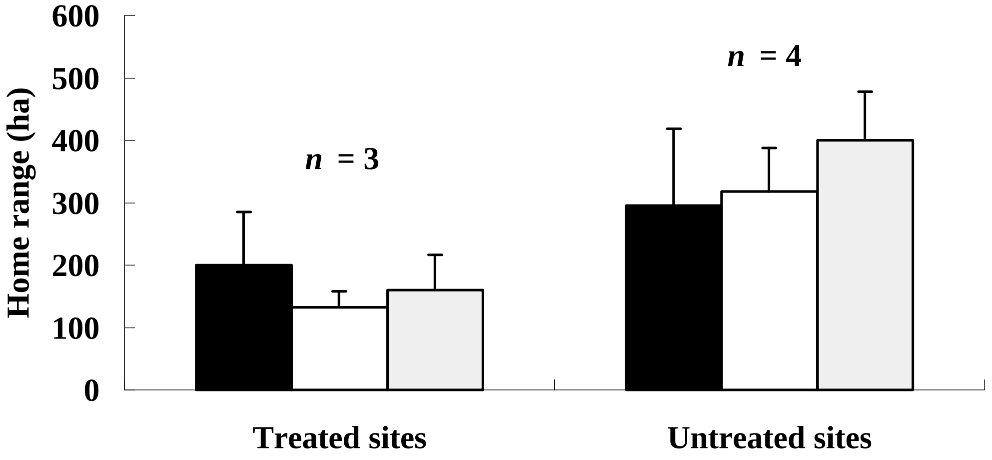

Fig. 7.8. Fox removal effects on the home range size (MCP95) of seven cats that survived all three seasons. Means and standard errors are shown.

■ Before fox removal (winter 1995)
□ After fox removal (summer 1995/96)
▨ After fox removal (winter 1996)

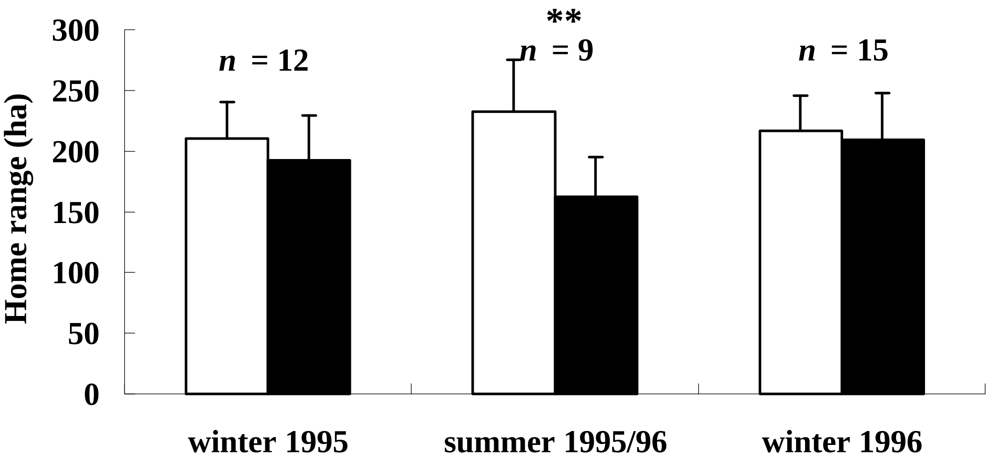

Fig. 7.9. Seasonal variation in the □ day and ■ night home range size (MCP 95) of cats. ** significant at *P* < 0.05. Means and standard errors are shown. Numbers of cats are above the bars.

significantly larger than night ranges ($\bar{x}$ ± s. e.: 162 ha ± 33) (t = 3.15; d. f. = 8; P = 0.014) (Fig. 7.9).

Seasonal variation. A decline in home range size was found at most sites in summer, with home ranges increasing again the following winter in 1996 (Fig. 7.6). However, this change was not significant overall (F = 0.30; d. f. = 2, 31; P = 0.745) or for the seven surviving cats (F = 0.91; d. f. = 2, 15; P = 0.425) (Fig. 7.8). In addition, no significant season by site interactions were detected for all cats (F = 0.15; d. f. = 6, 31; P = 0.987) or for the seven surviving cats (F = 1.51; d. f. = 2, 15; P = 0.253).

Sex and age differences. Overall, male cats (n = 33, $\bar{x}$ ± s. e.: 292 ha ± 24.7) had significantly larger home ranges than female cats (n = 10, $\bar{x}$ ± s. e.: 132 ha ± 23.7) (F = 18.17; d. f. = 1, 31; $P < 0.001$). However, no differences were found between young (1-3 years) (n = 27, $\bar{x}$ ± s. e.: 258 ha ± 26.5) and old cats (> 3 years) (n = 16, $\bar{x}$ ± s. e.: 250 ha ± 40.9) (F = 0.68; d. f. = 1, 31; P = 0.416).

Influence of rabbit abundance. No relationship was found between home range size and rabbit abundance at the four sites when all data were pooled over the three seasons (r^2 = 0.00, n = 44; P = 0.65).

Site fidelity. Cats tended to remain within the same area for extended periods of time. All home ranges of the seven cats that were monitored for all three seasons were in the same area.

7.3.4. Cat habitat use

Fox removal effects. After fox removal, no change in habitat use was detected overall at the treated sites relative to the untreated sites for any of the habitat types ($P > 0.05$) (Fig 7.10, Table 7.1). Changes that occurred after fox removal were in the same direction at both the treated and untreated sites (Fig. 7.10). No significant age or sex interactions were detected ($P > 0.05$).

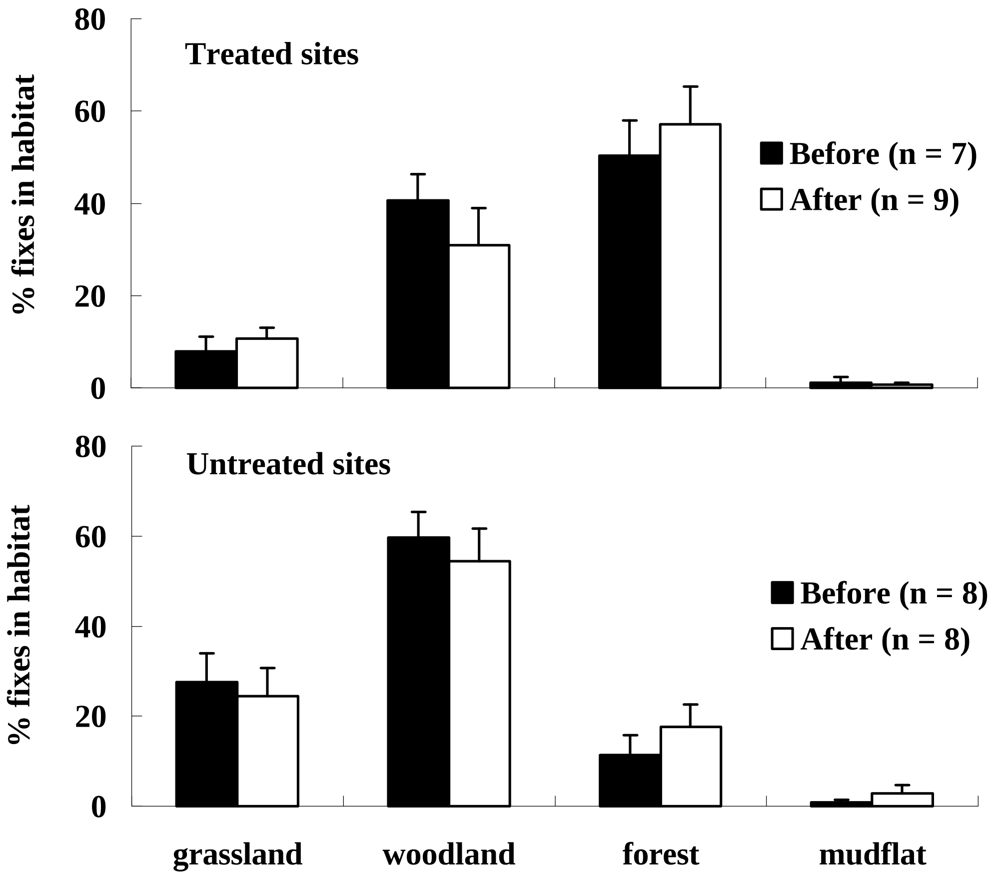

Fig. 7.10. Fox removal effects on the overall habitat use of feral cats at treated and untreated sites, before (winter 1995) and after (winter 1996) fox removal. Means and standard errors are shown. No significant differences were found.

Table 7.1. The effect of fox removal on the use of four different habitat types by cats overall.

Values given in the summary table are *F*-ratios and *P* values, which represent the fox removal (before vs. after) by treatment (treated vs. untreated sites) interactions.

	$F_{(1, 28)}$	*P*
grassland	0.37	0.55
woodland	0.10	0.75
forest	0.00	0.96
mudflat	1.23	0.28

When day and night periods were examined separately, there were no temporal differences in habitat use before fox removal (winter 1995) at both the treated and untreated sites for any of the habitat types (*P* > 0.05) (Fig. 7.11a, Table 7.2a). However, after fox removal (winter 1996), cats increased significantly their use of grassland habitats at night at the treated sites, with the opposite trend at the untreated sites (*P* < 0.05) (Fig. 7.11b, Table 7.2b). Similarly, open forest habitat tended to be used more often during the day at the treated sites with the opposite trend at the untreated sites, but this difference was not significant (Table 7.2b, Fig. 7.11b). When both periods (winter 1995 and winter 1996) were included in the analysis, the differences between day and night habitat use after fox removal were not significant (*P* > 0.05, Table 7.2c).

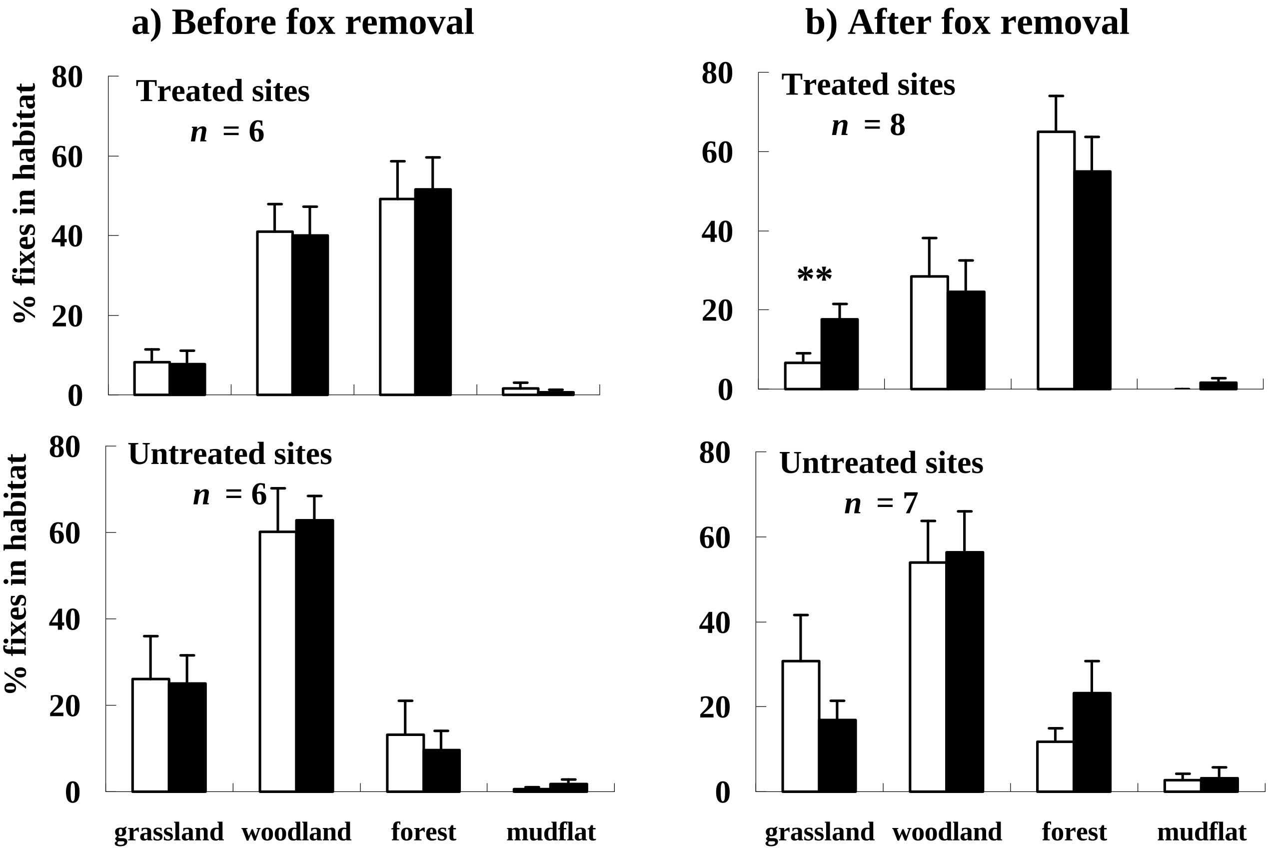

Fig. 7.11. Differences in ☐ day and ■ night habitat use a) before (winter 1995, *n* = 12 cats) and b) after (winter 1996, *n* = 15 cats) fox removal at treated and untreated sites. Means and standard errors are shown. ** significant at *P* < 0.05.

Table 7.2. The effect of fox removal on the use of four different habitat types by cats with day and night ranges analysed separately.
Values given in the summary table are *F*-ratios and *P* values (** *P*< 0.05), which represent interactions of (a and b) treatment by time (day vs. night), and (c) treatment by time by fox removal.

	a) before fox removal		b) after fox removal		c) before and after fox removal	
	$F_{(1, 20)}$	*P*	$F_{(1, 26)}$	*P*	$F_{(1, 46)}$	*P*
grassland	0.00	0.98	4.23	0.05**	1.87	0.18
woodland	0.06	0.81	0.11	0.74	0.01	0.92
forest	0.16	0.69	1.93	0.18	1.55	0.22
mudflat	0.91	0.35	0.17	0.68	0.75	0.39

Season, sex and age variation. Overall, there were no consistent seasonal differences in habitat use across the four sites (*P* > 0.05) (Table 7.3a, Fig. 7.12). For example, cats at Gunnel Creek increased their use of grassland in summer compared to winter, while the reverse occurred at Dog Trap (Fig. 7.12). Overall, sex and age did not influence the habitat use of cats when all three seasons were combined (*P* > 0.05) (Table 7.3b and c).

Table 7.3. Influence of season, sex and age on the habitat use (% fixes in each habitat) of cats.
Values given in the summary table are *F*-ratios and *P* values. Data for all three seasons (winter 1995, summer 1995/96 and winter 1996) are pooled.

	a) Season		**b) Sex**		**c) Age**	
	$F_{(2, 23)}$	***P***	$F_{(1, 23)}$	*P*	$F_{(1, 23)}$	*P*
grassland	0.25	0.78	0.52	0.48	1.79	0.19
woodland	1.48	0.25	0.07	0.79	0.02	0.88
forest	1.47	0.25	1.37	0.26	2.84	0.11
mudflat	0.19	0.83	0.76	0.39	1.25	0.28

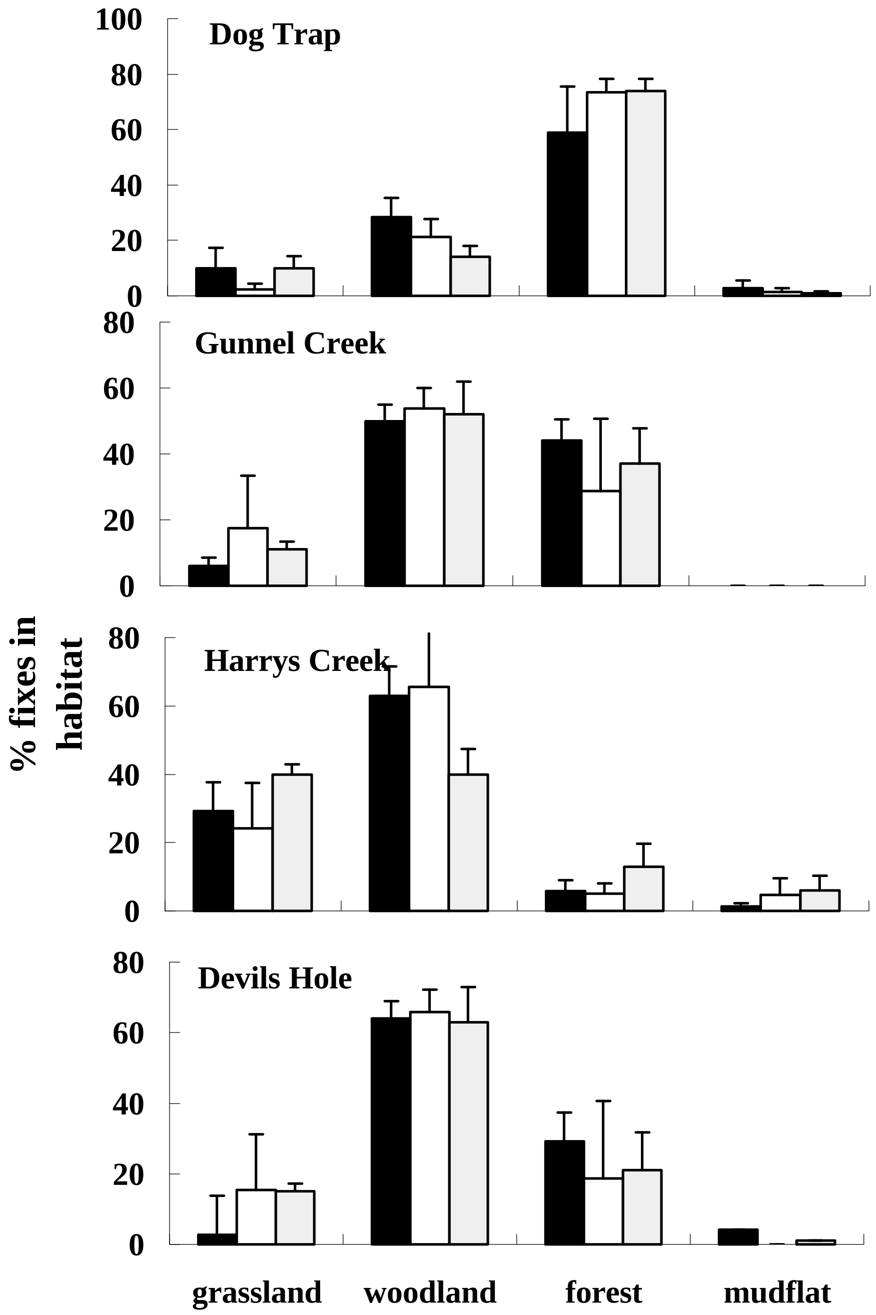

Fig. 7.12. Similarities in cat habitat use between seasons at the four sites. Means and standard errors are shown.

■ winter 1995 *n* = 15 cats
□ summer 1995/96 *n* = 11 cats
▨ winter 1996 *n* = 17 cats

Day versus night. When all four sites were pooled there were no significant differences between day and night habitat use for each habitat type ($P > 0.05$) and no significant season by day/night interactions ($P > 0.05$) (Table 7.4).

Table 7.4. Similarities in habitat use between day and night periods for each habitat type and for all three seasons.
Values given in the summary table are *F*-ratios and *P* values, which represent day vs. night differences and the season by day/night interactions.

	Day vs. night		**Season by day/night**	
	$F_{(1, 52)}$	P	$F_{(2, 52)}$	P
grassland	0.01	0.94	0.03	0.97
woodland	0.09	0.76	0.18	0.84
forest	0.20	0.65	0.25	0.78
mudflat	0.06	0.81	0.44	0.65

Diet in winter 1995 and 1996 only. When dietary data were examined for the same period as habitat use (winter 1995 and 1996 only), a significant increase in the frequency of carrion consumption occurred for cats at the treated sites after fox removal ($G = 5.15$; d. f. = 1; $P = 0.023$) (Fig. 7.13).

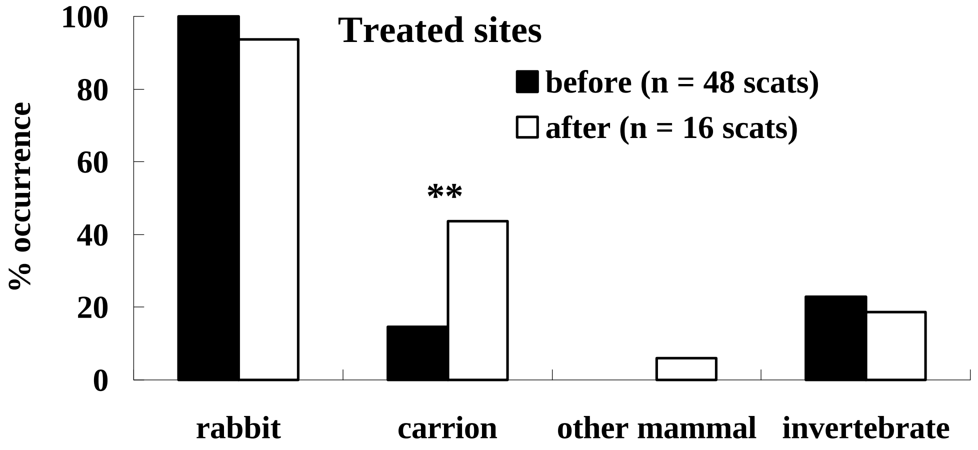

Fig. 7.13. Diet of cats before (winter 1995) and after (winter 1996) fox removal at the treated sites. ** significant at $P < 0.05$.

7.4. DISCUSSION

7.4.1. General ecology of cats

Spatial use described for cats overall in this chapter (i.e. three seasons and all sites) was consistent with that recorded for cats in the winter 1995 period at the untreated sites (Chapter 5). Males occupied larger home ranges than females. Home range size was not influenced by age, season or rabbit abundance. However, in summer, range sizes of cats were significantly larger during the day than at night. This was probably due to increased foraging on diurnal prey such as reptiles and grasshoppers during the warmer months (Chapter 4, Catling 1988). Habitat use was not influenced by sex or age and no seasonal or temporal differences were detected.

Fox densities at Burrendong ranged from 0 to 1.6 km^{-1} and cat densities ranged from 0 to 0.4 km^{-1}. These densities were similar to those recorded for foxes (e.g. Newsome and Catling 1992, Marlow 1992, review in Saunders *et al.* 1995) and cats (e.g. Ridpath 1990, Short *et al.* 1995, review in Dickman 1996) elsewhere in Australia.

7.4.2. Fox removal experiment

Effectiveness of the fox removal treatment

Despite the lack of a significant removal effect on foxes, the fox treatment was considered reasonably effective as both treated sites were subjected to the removal of some foxes and relative reductions of fox density were achieved in both. In addition, fox numbers were always lower in the two removal sites than in the two untreated sites for the entire period of the experiment. Although 100% fox removal was not achieved at DT, foxes were reduced to very low numbers and this resulted in the two treated sites being relatively similar.

Exploitation and interference competition

Despite no increase in cat abundance after fox removal, significant changes in resource use by cats at the treated sites suggested that foxes limit cat populations through interspecific competition. After fox removal, cats ate significantly more carrion and used open habitats more often at night. In addition, a reduction in range size was recorded at the treated sites after fox removal when only those seven cats that were radiotracked for all three seasons were included in the analysis; but the sample size was small.

Although carrion was not a staple prey for cats at Burrendong or elsewhere (e.g. Jones and Coman 1981, Catling 1988, Martin *et al.* 1996, Paltridge *et al.* 1997), the increase in carrion consumption (indicative of exploitation) suggests that foxes may have previously limited their access to carcasses (through interference). Although no direct evidence was obtained, video observations reported in Chapter 6 indicated that cats avoided carcasses when foxes were in the vicinity. Further, the higher nocturnal use of grassland habitats by cats after fox removal may indicate that in the absence of interference from foxes, cats were free to make use of the more open areas where carcasses were more abundant. Several hundred kangaroos were shot during a cull in winter 1996, and probably more frequently in grassland habitats where visibility for shooters was high. Personal observations suggested no apparent difference in carrion availability between treated and untreated sites.

The abundance of rabbits (staple prey for cats) was also higher in the grassland habitats (personal observation) compared to the other habitats, which may have facilitated a habitat shift to these areas after fox removal (Litvaitis *et al.* 1985). Although no increase in rabbit consumption by cats was detected, a larger number of cat scats tended to occur at rabbit warrens after fox removal at the treated sites relative to the untreated sites.

The tendency for cats to use forest habitats more often during the day after fox removal may indicate a need for cover from other predators such as wedge-tailed eagles. Alternatively, the occasional fox in the treated areas may have been sufficient for cats to continue to seek cover from potential agonistic encounters with them (Litvaitis and Harrison 1989). Felids typically prefer mixed associations that include open areas and trees for cover (e.g. Witmer and de Calesta 1986, but see Murray *et al.* 1994). In France, wild cats rested in wooded cover during the day and were active at night in open areas (Artois 1985). The continued need for cover by cats in the fox removal area may also have reflected the permanence of a previously adaptive behaviour (with either a genetic or a cultural basis) (Cavallini and Lovari 1994). In Italy, red foxes continued to select habitats with densest cover for resting despite not being hunted for ten years (Cavallini and Lovari 1994).

The seven cats that were radiotracked for all three seasons significantly reduced their range size after fox removal which was consistent with exploitation competition, although no change in home range size was detected for cats overall. The exploitation competition hypothesis predicts that the removal of the dominant competitor would allow the remaining competitor access to more prey (if there is already habitat overlap), and consequently reduce their range size (Macdonald 1983, Stephens and Krebs 1986). Significant dietary partitioning between sympatric cats and foxes (Chapter 6) provides further support for exploitation competition.

Why no increase in cat abundance?

Despite the significant behavioural shifts in resource use, cat abundance did not increase in the two and a half years following the removal of foxes. This may have been due to a number of factors. For example, spotlighting was not considered a good index of abundance for feral cats (see Chapter 4). The time lag may have been too short to allow a numerical response to be detected (e.g. Munger and Brown 1981). The dramatic decline in rabbit abundance, after the arrival of RCD eight months after fox removal, may also have reduced the potential for compensatory breeding and/or immigration. Alternatively, compensatory breeding by feral cats may have occurred, but kittens were prey for alternative predators such as goannas (Weavers 1989) or wedge-tailed eagles (Brooker and Ridpath 1980).

Interaction between cats and foxes was weaker at Burrendong than in WA?

The lack of increase in cat abundance at Burrendong contrasts with the findings in two Western Australian (WA) studies where cat numbers increased within 12 months of fox removal; at Heirisson Prong (HP) (Short *et al.* 1995) and the Gibson Desert Nature Reserve (GDNR) (Christensen and Burrows 1995). This suggests that the interaction between cats and foxes was weaker at Burrendong than in the WA studies. Three possible reasons are suggested as to why this may be.

Firstly, the method and scale of fox removal differed. At HP, a fox-free area was established using a predator-proof fence, which would have greatly reduced the potential for incursions by foxes, compared to using poison baits as at Burrendong. In addition, fox removals were conducted over much larger areas in WA compared to at Burrendong (Burrendong: 9 km^2; HP: 200 km^2 of buffer zone and 12 km^2 of core area; GDNR: 20 km radius), which should also have reduced potential incursions. As total fox removal was not achieved at Burrendong, the continual presence of a few foxes over a small area may have been sufficient to inhibit compensatory responses by cats to fox removal.

Secondly, interference competition may have been weaker at Burrendong where habitat structure is more complex than in the WA studies (Oksanen *et al.* 1979). Interference behaviour involves aggression and fighting and is usually only cost effective if the dominant competitor subsequently gains access and control of a shared resource, which is more difficult in complex habitats (Oksanen *et al.* 1979). In open habitats, subordinate species are readily seen and easier to evict, while complex habitats allow them to hide and escape aggression. Avoidance of aggressive encounters in complex habitats, such as forest and scrub environments, has been demonstrated in other mammalian communities (Hoffmeyer 1973, Hall and Lee 1982, Dickman 1991), but not in more open habitats. In the more complex woodland and forest habitats at Burrendong the cost of interference may simply outweigh the benefit of gaining access to a shared limited resource, in contrast to HP (heath) and GDNR (open arid area). Abundant trees at Burrendong would allow cats to avoid aggression from foxes. Anecdotal observations suggest that cats have also increased over large areas in forest habitats after fox removal in southwestern WA (P. de Tores pers. comm.), but over relatively long periods of time.

Thirdly, rabbit densities pre-RCD at Burrendong were much higher (max. 40 rabbits km^{-1}) than those recorded at HP (max. 7 rabbits km^{-1}), and this may have allowed coexistence of cats and foxes for much of the time with interference being necessary only during limited periods of low rabbit abundance.

Were increases in cat population densities in WA real?

The reported increases in cat densities after fox removals in the two WA studies may have reflected factors other than release from competition or predation by foxes, as control sites were not established. For example, increased prey densities can allow imitation of the effects of competitive release (Hairston 1985). At HP, increases in cat abundance after fox removal coincided with an increase in rabbit abundance. Similarly, at GDNR increases in cat abundance coincided with increased rainfall (and presumably increased prey populations) and with reduced densities of both foxes and dingoes. In contrast, no increase in rabbit densities occurred at Burrendong at the treated sites relative to the untreated sites after fox removal. Rabbit densities decreased at all sites following the arrival of RCD, eight months after fox baiting began.

Further, increases in cat abundance in the WA studies may have reflected behavioural changes in habitat use, rather than true population increases. A shift to more open habitats after fox removal at HP, as occurred at Burrendong, may have increased their detection in the spotlight. Similarly, a habitat shift by cats at GDNR may have increased their encounter rate with bait stations (index used to estimate density) which were placed on roads. In support of this, Dickman (1991) recorded an increased apparent density of insectivorous mammals within an hour of removal of a dominant species, clearly indicating a behavioural response.

7.5. CONCLUSION

Significant resource shifts by cats after fox removal strongly suggested interspecific competition, mediated by both exploitation and interference interactions. However, because cats did not increase in abundance after fox removal, the null hypothesis of no limitation by foxes could not be rejected. Further experimental evidence is required to test this hypothesis. Fox removal treatments should be conducted over as large an area as possible to maximise responses of the remaining species, and over a period of several years. Ideally, reinvasion would also be allowed at a later stage and resource shifts again quantified. Replication of this experiment in a range of habitat types (simple vs. complex) would allow the interaction with habitat structure to be examined. In addition to calculating indices of abundance, examination of resource use before and after fox removal between replicated treated and untreated sites is essential.

CHAPTER 8

GENERAL DISCUSSION

In this chapter, I first describe the major results arising from the examination of cat ecology in previous chapters and then discuss factors that influence the cat population at Burrendong. In the final section, I outline areas for further research and then discuss the implications of this study for the management of vertebrate pests.

8.1. ECOLOGY OF FERAL CATS

8.1.1. Diet

From an examination of diet in relation to prey availability, several conclusions can be drawn regarding the feeding ecology of feral cats at Burrendong.

(i) Rabbits were the staple prey of cats, as elsewhere in Australia where rabbits are common. Contrary to findings in previous studies, carrion was an important secondary food, particularly in winter and spring, which presumably reflected the high abundance of kangaroo carcasses from regular culling in the study area. Invertebrates, vegetation, other small to medium-sized mammalian prey, birds and reptiles were generally of minor importance, and appeared to be taken opportunistically.

(ii) Cats showed a significant dietary response to fluctuations in rabbit abundance, but not for the other prey groups (carrion, small mammals, reptiles and grasshoppers). Rabbits tended to be eaten relative to availability, but remained important in the diet even when rabbit abundance declined dramatically post-RCD. Ten months post-RCD, house mice increased in importance in the diet. However, it was not known whether this represented prey switching *sensu stricto* or opportunistic predation on an increased mouse population, as mouse

considered analogous to a true type II or III functional response curve. Insufficient data points at low prey densities precluded a definitive distinction between type II and III curves.
(iii) Two latrines found at Burrendong may have reflected a recent domestic history for the individuals using them, or perhaps were related to breeding dens. Both individual cats using the latrines were females, and one was known to be rearing kittens. Results from the examination of their scats highlighted the ability of individual cats to target particular prey groups.

8.1.2. Home range size, overlap and habitat use

Several conclusions regarding the spatial and social organisation of feral cats at Burrendong were drawn from an examination of home range size, range overlap and habitat use.

(i) Home ranges of cats were similar in size to those reported in the only other published study of spatial use by cats in Australia (Jones and Coman 1982), but larger than those recorded elsewhere (e.g. Langham and Porter 1991, Genovesi *et al.* 1995). This presumably reflected low prey density or more dispersed food resources (Macdonald 1983). Male ranges were larger than those of females, but no sexual differences were found in habitat use. Similarly, no differences were found between young (1-3 years) and old (> 3 years) cats in home range size or habitat use, although all cats radiotracked were adults. The lack of temporal (day/night) differences in home range size and habitat use at Burrendong is consistent with the hypothesis that cats hunt and rest at various times during both the day and night (Fitzgerald and Karl 1986).

(ii) Both male and female cats tended to be solitary, despite extensive overlap in home ranges. The high degree of inter-sexual overlap recorded between young (1-3 years) and old (> 3 years) cats may indicate the presence of kin groups (e.g. Macdonald and Apps 1978), although kin ties were not examined. Young males do not usually disperse from their

Territoriality was indicated by the mutually exclusive home ranges of old adult males and the presence of unburied scats, which may have been used as territory markers (Liberg 1980, Brothers *et al.* 1985).

(iii) Habitat composition of home ranges generally reflected the availability of habitats at the site, but cats significantly avoided mudflats. Home ranges overlapped mostly with open woodland and open forest habitats with smaller areas of grassland and mudflats. However, within individual home ranges, cats used grassland and open woodland habitats most often. Rabbits were more abundant there than in other habitats, indicating a preference by cats for prey-rich patches for foraging. Cat habitat use was consistent with studies of other felids where habitats that are prey-rich and provide cover from predators are preferred (Witmer and de Calesta 1986).

8.2. WHAT LIMITS CAT POPULATIONS AT BURRENDONG?

To determine what factors limit cat populations at Burrendong, I tested four hypotheses using a fox removal experiment. A number of parameters for cats were examined before and after fox removal at treated and untreated sites. These included cat abundance, home range size, habitat use, and diet (Chapter 7). Acceptance of a hypothesis should come when all predictions are satisfied, not just one. Multiple outcomes are possible for each hypothesis as more than one mechanism can operate at once. The hypotheses are summarised in Table 8.1. and are described as follows:

Hypothesis 1: Cat populations are limited by factors such as food availability, and not by foxes, independent of resource overlap.
Hypothesis 2: Foxes limit cat populations at low prey densities through interspecific competition (exploitation and/or interference).
Hypothesis 3: Foxes limit cat populations through intraguild predation.
Hypothesis 4: Cats benefit from the presence of foxes through facilitation.

8.2.1. Hypothesis 1: Food availability

Although food availability is likely to be a major limiting factor for predators (Hairston *et al.* 1960), this hypothesis received minimal support for cats at Burrendong. Cats did not show a numerical response to changes in the abundance of their staple prey (Chapter 4). However, the main index of abundance, spotlighting, proved not to be a reliable index of cat abundance as few cats were detected in the spotlight, despite their presence being known through trapping and

radiotracking. Moreover, observed correlations in cat and prey abundance indices probably reflected changes in cat habitat use rather than fluctuations in population size. For example, the positive correlation between indices of cat and carrion abundance likely reflected increased activity by cats in open areas when scavenging at carcasses and consequently, greater detection in the spotlight. Similarly, negative correlations between the abundance of cats and reptiles (one and two month lags) or grasshoppers (three month lag) may have reflected a higher usage of forest habitats by cats during the warmer months when these prey are more active. This may have decreased the chance of detection of cats in the spotlight.

In contrast, fluctuations in rabbit abundance have been suggested as a major limiting factor for feral cats on Macquarie Island (Jones 1977). In winter there, when rabbit abundance (particularly subadults) declined, cats were observed to be starving (Jones 1977). Effects were predicted to be greater on old, debilitated and young cats that were unable to catch the larger adult rabbits. Similarly, a numerical response to rabbits was recorded in semi-arid NSW where cat densities increased 3-4 months after rabbit densities increased (Catling 1988, Pech *et al.* 1992). The lack of a numerical response by cats to fluctuating rabbit densities at Burrendong may also have been due to cats being already satiated at the high rabbit densities that occurred prior to RCD. Further, abundant alternative prey, such as reptiles and invertebrates may have allowed dietary shifts when young rabbits were less available (Chapter 4, Catling 1988).

8.2.2. Hypothesis 2: Interspecific competition with foxes

Although no increase in cat abundance was detected after fox removal, significant shifts in resource use by cats indicated that interspecific competition was an important limiting factor for feral cats at Burrendong (Chapter 7, Table 8.1). Exploitation competition was indicated by the large overlap in diet, home range and habitat use between cats and foxes (Chapter 6) and was supported by the increased consumption of carrion by cats at the treated sites after fox removal (Chapter 7), and by resource partitioning (Chapter 6). Interference competition was indicated by aggressive and avoidance behaviours between foxes and cats (Chapter 6), and supported by the increased use of grassland habitats by cats at night after fox removal (Chapter 7).

The potential for interference competition between two coexisting species is high where there is a large overlap in resource use, and when the benefits of controlling a resource are high relative to the cost (Case and Gilpin 1974). The lack of increase in cat abundance in the two and a half years following fox removal at Burrendong contrasts with that reported in two published studies in WA where marked increases in cat densities followed fox removal

(Christensen and Burrows 1995, Short *et al.* 1995). This suggests that the interaction between cats and foxes at Burrendong may have been weaker than in the WA studies. A number of possible reasons for that are discussed in Chapter 7. Interference may not be cost effective for foxes at Burrendong, where habitats are more structurally complex than in the WA studies, as cats are able to avoid aggression from foxes (Oksanen *et al.* 1979). In addition, foxes were removed over much larger areas in the WA studies compared to at Burrendong, which may have reduced the influence of fox incursions.

Interspecific competition is usually asymmetrical, with one species being dominant over the other (Lawton and Hassell 1981). At Burrendong, foxes affected several aspects of resource use by cats. Foxes were clearly the dominant species given their dominance in aggressive interactions, the killing of three radiocollared cats and the avoidance behaviour shown by cats (Chapter 6). In addition, dietary niches were considerably wider for foxes than for cats, which preyed mostly on rabbits. Generalist species often have a competitive advantage when their broad niche overlaps the narrow niche of a more specialised species (Dibello *et al.* 1990, but see Theberge and Wedeles 1989, Johnson and Franklin 1994, Cypher and Spencer 1998). Further, foxes were around 10 times more numerous than cats at the untreated sites, although behavioural differences may have influenced abundance indices. Asymmetry often results when two species differ dramatically in density (Brown and Munger 1985) due to frequency-dependent effects. A species at high densities, even if competitively inferior, can eliminate competitors simply by its high numbers, particularly if the species is a generalist (Crowell and Pimm 1976, Rau *et al.* 1985, Crooks and Van Vuren 1995). Although a cat removal experiment is required to confirm asymmetry and to test for reciprocal effects, the clear dominance of foxes over cats is suggestive of an asymmetrical effect typical in two-species competitive interactions.

Coexistence between cats and foxes at Burrendong may be possible through diet and habitat partitioning and by the avoidance of foxes by cats. Cats may tolerate interference by foxes because the benefits of gaining access to resource-rich microhabitats outweigh the small cost of vigilance and flight to nearby refugia. This interpretation is supported by the mosaic nature of vegetation in the Burrendong study area, compared with the relatively homogenous open desert or scrub habitat in fox removal studies in WA (Christensen and Burrows 1995, Short *et al.* 1995).

8.2.3. Hypothesis 3: Intraguild predation by foxes

Intraguild predation (which involves the killing and eating of a prey) was not considered a major limiting factor for cats at Burrendong as no cat remains were found in any of the fox scats or stomachs that were examined (Table 8.1, Chapter 6, Appendix 3). However, previous studies have occasionally recorded cat remains in fox scats or stomachs (Coman 1973b, Brunner *et al.* 1991, Taylor and Lupica 1998, D. Risbey pers. comm., R. Paltridge pers. comm.). Although fox predation on cats may occur rarely it could still be sufficient to

1990). Nevertheless, the intraguild predation hypothesis received only minimal support at Burrendong. Observed aggression between cats and foxes was interpreted as interference as there was no evidence that foxes actually ate adult cats or kittens.

8.2.4. Hypothesis 4: Facilitation

Although the presence of foxes may facilitate cats, such as through the opening of the tough integument of carcasses, the facilitation hypothesis was not supported in this study (Table 8.1). After fox removal, cats did not decrease in abundance and their behavioural shifts indicated a negative interaction with foxes, as resource shifts were toward more prey-rich habitats. Cat and fox densities were also not correlated positively (Chapter 6) indicating that cats did not trail foxes in search of food (Carbyn 1982, Paquet 1991). In the Northern Hemisphere, although coyotes usually avoid wolves (Fuller and Keith 1981), they sometimes trail them at a safe distance apparently in search of food (i.e. wolf kills) (Carbyn 1982).

The presence of other scavengers at Burrendong such as wedge-tailed eagles and feral pigs that are also able to open carcasses, may have dampened any negative effects experienced by cats in the absence of foxes. In addition, carrion was not a staple prey for cats at Burrendong and consequently, even if a facilitative relationship did occur, the removal of foxes should have had little impact on the survival of cats.

8.2.5. Other factors

Disease and parasites. Although parasites of cats and foxes were not examined in this study, no indication was found for limitation by cat-specific parasites or by foxes through shared parasites. Cat abundance did not change after fox removal, and aggression and avoidance behaviours (Chapter 6), and habitat and dietary shifts by cats were not consistent with the shared parasite hypothesis.

High kitten mortality. Disproportionately high mortality rates among subadult cats have been recorded in a number of studies (e.g. Brothers *et al.* 1985, Mirmovitch 1995), presumably due to nutritional stress and disease (Jones 1977, Dards 1978, Oppenheimer 1980, Izawa *et al.* 1982, Apps 1983, van Aarde 1984, Coman 1991). At Burrendong, observations of decreases in litter size over time provided some support for this hypothesis, although only two observations were made. Litter sizes of two individual cats declined from five kittens to two, and from two kittens to one, within a two-week period. Whenever a den was located, the mother moved the kittens within 24 hours, usually 50 to 300 m away. Although the cause of the missing kittens was not known, predation by foxes, goannas or wedge-tailed eagles may have been implicated, particularly during the move to alternative dens.

8.3. FURTHER RESEARCH

Information on factors causing mortality in kittens would provide useful data in examining factors that limit feral cat populations. In addition, further research is required to improve the effectiveness of current techniques for estimating the abundance of cat populations, particularly in forested areas (Mahon *et al.* 1998). This is essential for monitoring the effectiveness of control campaigns and determining interactions with other introduced species and predation impact on native prey populations. Without a reliable estimate of cat abundance, it will be difficult to precisely identify factors that limit cat abundance.

To further elucidate the interaction between cats and foxes, fine scale examination of temporal and spatial patterns is required. Temporal separation in activity patterns may limit competition by allowing exploitation of different resources (Schoener 1974), although behavioural resource depression effects may hinder this (Charnov *et al.* 1976). Temporal separation may also reduce interference competition by decreasing the frequency of direct encounters (Case and Gilpin 1974). Evidence for differences in activity patterns between sympatric cats and foxes has been indicated in some studies, where cats were more diurnally active than foxes (Das 1993, Artois 1985). Fine-scale temporal segregation of activity in the two species is likely to come only from intensive radiotracking studies, or possibly from direct observations in large enclosures.

Examination of habitat use on a finer scale may also reveal further habitat partitioning between cats and foxes, which would facilitate coexistence. In addition, the hypothesis that foxes limit cats through interspecific competition should be tested over large areas and in a range of habitat types (simple vs. complex). In addition to deriving indices of abundance, examination of resource use before and after fox removal between replicated treated and untreated sites, as occurred in this study, is essential. Reinvasions of foxes should then be allowed after a sufficient period to test for reciprocal effects. Cat removal experiments would provide information on whether foxes are adversely affected by the presence of cats, and thus the magnitude of asymmetry in the cat-fox interaction.

Furthermore, given the long time over which numerical effects are likely to become manifest, removal experiments should ideally be carried out over periods of several years to reduce risks of committing type II errors. As argued cogently by Caughley and Gunn (1996), such errors should be avoided particularly in conservation and management-related studies, because of the deleterious consequences for threatened species or other management targets.

8.4. IMPLICATIONS FOR MANAGEMENT OF VERTEBRATE PESTS

Although cats did not increase in abundance after fox removal at Burrendong, significant shifts in resource use by cats provided some evidence for interspecific competition. Widespread fox removals, using immunocontraception, have been proposed by the Vertebrate Biocontrol Cooperative Research Centre (VBCRC) (Tyndale-Biscoe 1994). Subsequent increases in cat populations, however, may not alleviate predation pressure on native fauna and may even be more harmful than if no fox removal had occurred (Risbey and Calver 1998). At Heirisson Prong (HP) in WA, cats did increase in abundance after fox removal, and densities of small mammals declined to levels lower than those recorded prior to fox control (Risbey and Calver 1998).

Populations of rabbits, the staple prey for cats where abundant (Chapter 4, Catling 1988), are also likely to increase following fox removals (Newsome *et al.* 1989, Short *et al.* 1995, Banks *et al.* 1998). The ability of foxes to suppress medium density rabbit populations has been demonstrated experimentally in Australia (Newsome *et al.* 1989, Banks *et al.* 1998). Increased rabbit densities have the potential to facilitate increases in cat densities (Pech *et al.* 1992) and intensify competitive effects with native fauna (Williams *et al.* 1995). High rabbit densities would also increase the likelihood that remaining foxes could increase their numbers to pre-predator control levels very quickly (Pech *et al.* 1992). Furthermore, if foxes and rabbits are controlled without cats, then cats may switch to alternative prey such as isolated populations of native mammals and reptiles (Newsome *et al.* 1997).

Integrated pest management (Bottrell 1979, Allen *et al.* 1997) is therefore strongly proposed where populations of cats, foxes and rabbits are controlled together. Without the effective control or removal of all three species, compensatory responses by the remaining species may not alleviate impacts on native fauna.

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APPENDICES

Appendix 1: TRAPPABILITY OF FERAL CATS[1]

INTRODUCTION

Feral cats *Felis catus* are notoriously difficult to trap. They do not take baits readily (Risbey *et al.* 1997) and bait visitation and ingestion rates are variable and usually low (Paton 1994, Christensen and Burrows 1995, Short *et al.* 1997). Live trapping is essential, however, where animals are to be radio-collared for studies on spatial movements, habitat use or social organisation. It is also one of the main methods used in the control and eradication of feral cats, particularly in areas where domestic cats are present, or if populations have already been reduced and individual cats need to be targeted (e.g. Berruti 1986, Bloomer and Bester 1992). While some studies have used different types of traps for catching feral cats, none have reported their relative effectiveness (e.g. Veitch 1985, Bloomer and Bester 1992, Lee 1994) or evaluated factors that influence trap success. The aim of this study is to evaluate two different types of traps and 51 different bait and lure combinations for trapping feral cats. Factors influencing trap success, including season and rabbit abundance, are also examined.

METHODS

Trap types. Feral cats were trapped using both wire mesh cage traps (40cm by 40cm by 60cm) and Victor Soft Catch leg-hold traps (Nos. 1, 1.5 and 3, Woodstream, Corp., Lititz, Pa., USA). Leg-hold trap jaws were padded with rubber to minimise injury. Trapping was conducted in most months of the study in the first year (November 1994 to August 1995), but primarily in autumn and winter in the second year (November 1995 to August 1996). Relative success of the two trap types was compared using the *G*
correction, Sokal and Rohlf 1994). Trap success was defined as the number of cats trapped per 100 trap nights, while a trap night was the exposure of one trap for one night.

Trap sites were chosen carefully to minimise capture of non-target species and included a variety of habitats such as under bushes, beside vehicle tracks, on animal runways and at rabbit warrens. Cage traps were set according to the method outlined in Veitch (1985) where traps are set squarely on the ground and the doors of traps are bent upwards to increase the openness of the space. Traps were checked each morning from first light, left set and checked again in the afternoon. Traps were set approximately 200 m apart and both cage and leg-hold traps were usually operated simultaneously.

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[1] paper in preparation to be submitted to *Wildlife Research* for publication

Bait types. A variety of baits and lures (olfactory and visual) was used in the first year of the study. Baits included rabbit, chicken, beef, lamb, kangaroo, ham, bacon, house mouse, goanna, fish, mussels, dried shrimp and squid, tinned cat food, dry whiskettes, tinned sardines, rotten eggs and commercially-produced PUSSON baits. All baits were dead when used. About a handful of bait was deposited in each trap. Baits were only deposited inside the trap while olfactory lures were sometimes sprayed outside the trap. Olfactory lures included synthetic fermented egg (SFE), catnip (dried and spray) and tuna oil. Visual lures included aluminium tags attached to string, pink flagging tape, bicycle flashing lights and toy windmills on sticks. Baits were not always used in conjunction with lures. Multiple bait types were generally used within each trapping period, but only a single bait type was deposited in each trap. However, in the second year of the study freshly killed rabbit was the only bait used. Where the rabbit bait had dried out after several days of exposure, SFE was added to increase its olfactory attractiveness.

Demography. Trapped adult cats were anaesthetised and then radiocollared (Chapter 3). Measurements were obtained for all cats which included weight, body length, sex, age, and general condition. Recaptured cats were sometimes re-weighed if it was possible to do so without undue stress to the animal. Body length measurements included head length (nose to occipital condyle), maximum skull width, body length (occipital condyle to anus), tail length and neck circumference (Fig. 1a). Three age classes were determined from body weight: juveniles, subadults and adults (Brothers *et al.* 1985). Juveniles were not fully-grown (females < 1900g, males < 2200g); subadults were fully-grown but had not bred (females 1900-2500g, males 2200-3400 g); adults were fully grown and usually had bred (females > 2500 g, males > 3400 g). The approximate ages of juvenile and subadult cats were estimated from body size. Adult cats were further divided into young (1-3 years) and old (> 3

years) from the examination of toothwear (personal observation). Young adult cats had white, sharp, pointy teeth, while old cats had yellowing teeth that were mostly missing or worn to the gum (Fig. 1b). Adult females were classified as lactating or not lactating. Anecdotal observations, while radiotracking, of cats accompanied by kittens were also recorded.

Rabbit abundance. Indices of rabbit abundance were derived from monthly spotlight counts (Chapter 3). The relationship between rabbit abundance and trap success across sampling sessions was evaluated using the Pearson product-moment correlation coefficient.

RESULTS

Trap success. A total of 77 cats (48 recaptures) was trapped in 6762 trap nights using both cage (Table 1) and leg-hold traps (Table 2). A further 18 individual cats were trapped in leg-hold traps as non-target animals by the VBCRC Fox Sterility Project (McIlroy and Saunders unpublished data). No significant difference was found in the relative trap success between cage and leg-hold traps in 1995 ($G = 1.42$, d. f. = 1, $P > 0.05$) or 1996 ($G = 1.19$, d. f. = 1, $P > 0.05$) (Table 3). Trap success overall was 1.1 cats per 100 trap nights.

Most cats were trapped in late autumn and early winter, especially in June 1995, when 5.7 cats were trapped in cages per 100 trap nights (Table 1). The high trap success in June 1995 coincided with low rabbit numbers during the drought (Fig. 2), however, no relationship was detected overall ($r = 0.14$, $n = 13$, $P = 0.63$).

Demography. Of the 47 individual cats trapped, 32 were male and 15 were female. At the time of first capture, most cats were adults ($n = 35$), with 19 classified as young (5 female, 14 male) and 16 as old (6 female, 10 male). Four cats were juvenile (2 female, 2 male) and eight were subadult (2 female, 6 male). Mean (± s. e.) body weight for adult female and male cats was 3.34 ± 0.06 kg and 4.37 ± 0.14 kg, respectively**.** Mean (± s. e.) body length for adult female and male cats was 46.5 ± 0.75 cm and 49.2 ± 0.70 cm, respectively. The maximum weight recorded was for a male weighing 5.68 kg. Most cats trapped were black ($n = 22$), while the remainder were brown tabbies ($n = 18$), grey tabbies ($n = 5$) or orange ($n = 2$).

Table 1. Numbers of animals caught in cage traps from November 1994 to August 1996. ( ) indicates recaptures.

		Cat	Brushtail possum	Rabbit	Black rat	Bird	Lace monitor lizard	Blue tongue lizard	Bearded dragon	*No. trap nights*
1994	**Nov**	2 (1)	2	0	1	2	16	7	0	***530***
	Dec	2 (2)	0	0	0	0	6	1	0	***164***
1995	**Jan**	0	0	0	0	0	1	0	0	***64***
	Feb	2 (1)	0	0	0	0	10	1	0	***296***
	Mar	4(1)	0	0	0	2	6	1	2	***515***
	April	2	0	1	1	0	0	0	0	***406***
	May	6 (4)	1	1	0	2	0	0	0	***556***
	June	26 (16)	3	0	0	4	0	0	0	***453***
	July	4 (3)	0	0	0	0	0	0	0	***354***
	Aug	2 (2)	0	0	0	0	0	0	0	***166***
	Nov	0	0	2	0	0	0	0	0	***13***
1996	**Jan**	0	0	0	0	0	4	0	0	***54***
	Feb	0	0	0	0	0	1	0	0	***51***
	Mar	0	0	0	1	0	5	0	0	***198***
	April	0	2	1	4	1	5	0	0	***295***
	May	8 (4)	0	0	5	4	0	0	0	***280***
	June	6 (4)	1	0	3	6	0	0	0	***259***
	July	0	0	0	0	0	0	0	0	***76***
	Aug	1 (1)	1	1	0	0	0	0	0	***230***
Total		**65 (39)**	**4**	**4**	**13**	**21**	**54**	**10**	**2**	***5614***

Table 2. Numbers of animals caught in leg-hold traps from December 1994 to July 1996. ( ) indicates recaptures.

		Cat	**Fox**	**Brushtailpossum**	**Rabbit**	**Bird**	**Lace monitor**	***No. trap nights***
1994	**Dec**	0	0	0	0	0	0	***44***
1995	**Feb**	0	0	0	0	1	1	***110***
	March	0	0	0	0	1	1	***86***
	April	0	0	2	0	0	0	***113***
	May	5(5)	1	0	1	0	0	***226***
	June	1	0	0	0	2	0	***107***
	July	0	0	0	0	0	0	***86***
1996	**March**	0	0	0	0	0	0	***69***
	April	1 (1)	0	0	0	0	0	***76***
	May	0	0	0	0	0	0	***74***
	June	5 (3)	0	0	0	2	0	***142***
	July	0	0	0	0	2	0	***15***
Total		**12 (9)**	**1**	**2**	**1**	**8**	**2**	***1148***

Table 3. Relative trap success (no. per 100 trap nights) of cage and leg-hold traps for trapping feral cats from November 1994 to August 1996. ( ) indicates recaptures.

		No. cats	Trap nights	Trap success	Trap nights per cat	Trap nights per new cat
November 1994	**Cage**	50 (30)	3958	1.2	79	198
to August 1995	Leg-hold	6 (5)	772	0.8	129	772
	Total	**56 (35)**	**4730**	**1.2**	**85**	**225**
November 1995	Cage	15 (9)	1656	0.9	110	276
to August 1996	Leg-hold	6 (4)	376	1.5	63	188
	Total	**21 (13)**	**2032**	**1.0**	**97**	**254**

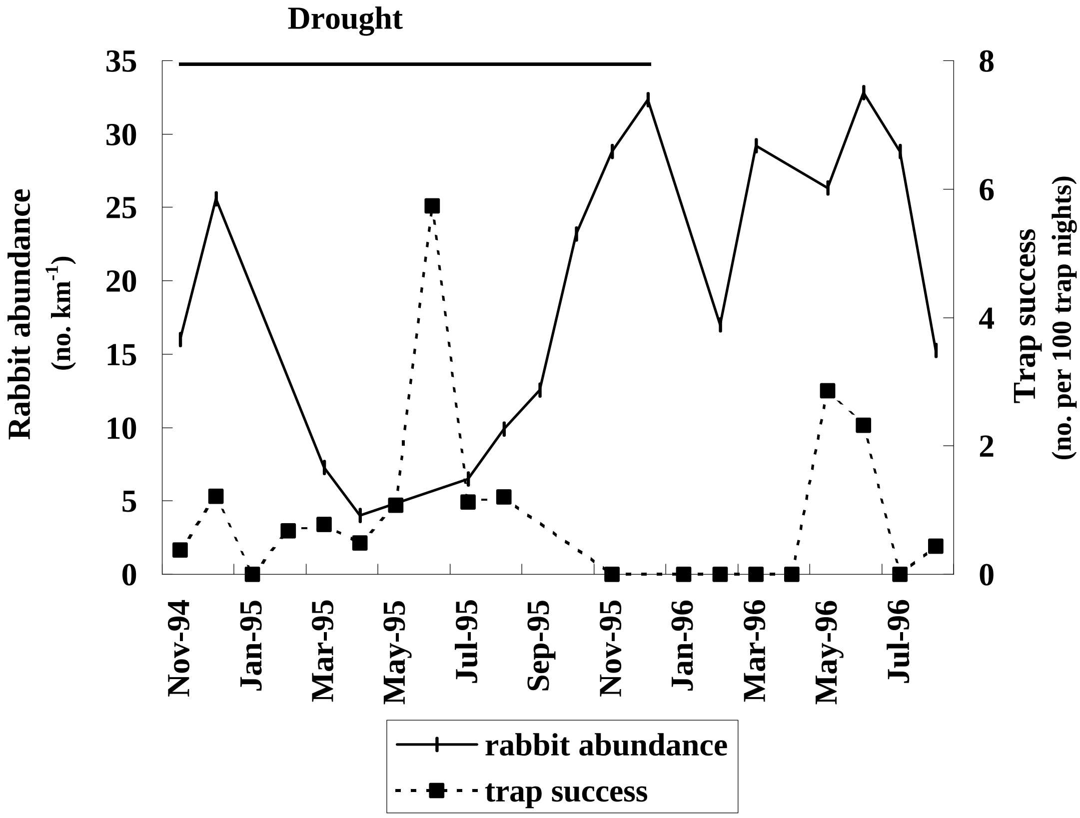

Fig. 2. Relationship between trap success of cats and rabbit abundance between November 1994 and August 1996. Indices of rabbit abundance were derived from spotlight counts conducted by the VBCRC Predator-Prey Project.

Non-target species. A total of 122 non-target animals was trapped in both cage and leg-hold traps in 6762 trap nights (1.8 animals per 100 trap nights) (Tables 1 and 2). These included the red fox (*Vulpes vulpes*), common brushtail possum (*Trichosurus vulpecula*), European rabbit (*Oryctolagus cuniculus*), black rat (*Rattus rattus*), birds and lizards. Lace monitors (*Varanus varius*) (n = 56 captures) were the most common non-target species trapped, particularly during the warmer months (November to March) in cage traps. Birds, mostly corvids, were also trapped frequently (n = 29), particularly in autumn and early winter. Non-target animals were generally released unhurt.

Bait types. A variety of baits and lures (51 combinations) was used in the first year of the study, but only 5 different bait and lure combinations were successful in catching cats (Table 4). Rabbit was the most successful bait (1.6 cats per 100 trap nights) and was therefore used more extensively than the other baits. Lures (visual and olfactory) added to rabbit did not increase trap success (1.2 cats per 100 trap nights).

Table 4. Variation in trap success (no. cats per 100 trap nights) of five bait types that were successful in catching cats (*n* = 50) in cage traps from December 1994 to November 1995.

Bait type	**No. cats**	**Trap nights**	**Trap success**
Rabbit	36	2164	1.6
Chicken	4	269	1.5
Rabbit & lure	7	572	1.2
Whiskettes & lure	1	82	1.2
Fish	2	371	0.5

Cat breeding. All litters were born between September and March with no breeding observed at other times. This was based on estimated birth dates of trapped juvenile and subadult cats (n = 12), on sightings of kittens (n = 3), on observations of lactation in trapped cats (n = 2), and on litters born to radiocollared cats (n = 3). Litters were located in the base of hollow tree trunks (dead and living) (Fig. 3a) and among boulders. Litter sizes ranged from 2-5 kittens (n = 6) (Fig. 3b). Mortality of kittens appeared to be high as subsequent locations of litters indicated reductions from initial litter sizes.

Trap-related injuries and multiple recaptures. There were fewer serious injuries associated with cage traps compared to leg-hold traps. Injuries suffered in cage traps were generally minor and involved self-inflicted abrasions to the face. Two animals (one fox and one cat) caught in leg-hold traps died or were killed through trap-related injuries. The fox broke its leg in a leg-hold trap and was immediately euthanased, while the cat was repeatedly captured in leg-hold traps within a relatively short time period (6 times in one month, 10 times in total) and later

was found dead two months later: death was possibly trap-related.

By comparison, cats that were trapped repeatedly in cages did not appear to suffer any serious injuries. One cat was re-trapped 13 times in an eight-month period and remained in good condition. Two other cats were re-trapped six times (primarily in cages) and did not suffer trap-related injuries. Twenty-three individual cats were never re-trapped, while the remaining 21 cats were re-trapped twice.

DISCUSSION

Overall trap success (no. per 100 trap nights) of feral cats at Burrendong was 1.1 and ranged from 0 in January 1995 and other months to 5.7 in June 1995. Trap success was lower than that reported on islands (7.3; Berruti 1986) and in areas associated with human settlement (9.2; Liberg 1980, 21; Page and Bennett 1994). Numerous factors can influence trap success between regions including cat density, trap type, season, and proximity to human settlement. For example, cats are much harder to trap at low densities (Rauzon 1985), and easier to trap around human settlements, particularly around rubbish dumps and camping grounds (Lee 1994) than in unsettled areas. No published data were available from rural areas to allow comparisons with this study.

Although the relative effectiveness of different trap types has not previously been evaluated, some studies have indicated that leg-hold traps are more effective in catching cats than cages (Lee 1994). In this study no significant difference in trap success was found between the two trap types. Cage traps were preferred, however, over leg-holds as they were less labour intensive to set and resulted in fewer serious hold traps resulted in only two serious injuries in this study, which is consistent with other studies where no or minimal injuries were sustained by cats (Meek *et al.* 1995, Fleming *et al.* 1998). Leg-hold traps may be more effective than cage traps for feral cats that have had minimal exposure to humans. In contrast, the relative success of cage traps at Burrendong may have been due to the continual human presence and the associated stock fences and vehicles, such that a wire cage trap and human odour may not have been too unfamiliar to the cat.

Trap success varied seasonally, being better in late autumn and early winter, which probably reflected a period of low food availability for cats. Although rabbit abundance remained high during autumn and winter in the second year of this study, the relative availability of subadult and kitten rabbits was low (Catling 1988, personal observation). As cats prefer subadult rabbits to adults (Catling 1988) and the availability of alternative prey (e.g. reptiles and grasshoppers) was low, this may have reflected a period of low food availability for cats. Feral cats elsewhere have been shown to take significantly more baits when rabbit abundance is lower (Short *et al.* 1997). In Scotland, increased trap success was recorded for wildcats (*Felis silvestris*) in autumn and winter (Corbett 1979), and was associated with declines in food availability and bad weather. Alternatively, increased trap success in autumn and winter may have reflected greater energetic needs during the colder months or increased dispersal by young adult cats (1-3 years), thereby increasing their

range when they are 1-3 years old (Dards 1978, 1983, Liberg 1980).

Cats at Burrendong showed a preference for rabbit as bait, their staple prey (Chapter 4), and were not attracted to novel baits. Despite the importance of sight in the visual detection of prey by cats (Turner and Meister 1988), visual lures did not increase trap success in this study, or bait visitation rates in other studies (Edwards *et al.* 1997, Short *et al.* 1997). Once the bait is detected, olfactory senses may be more important. In support of this, Risbey *et al.* (1997) found that cats frequently approached baits but rarely ate them.

A male bias in the sex ratio of trapped cats has also been reported in other studies (van Aarde 1978, Konecny 1987, Calhoon and Haspel 1989, Edwards *et al.* 1997), which is probably due to sex differences in behaviour, rather than sex-specific mortality (van Aarde 1978). For example, male cats occupy larger home ranges than females (Chapter 5) which would increase their encounter rate with traps. Furthermore, during the breeding season (September to March) when males are in search of females, encounter rates with traps may be higher than for females.

Litters at Burrendong were born between September and March, which is consistent with studies of feral cats elsewhere (e.g. van Aarde 1978, Jones and Coman 1982). Although litters were only found in hollow trunks and among boulders, they also may have occurred in rabbit warrens but were undetectable. Cats share warrens with rabbits (Calaby 1951, personal observation) quite amicably (Rolls 1969).

RECOMMENDATIONS FOR TRAPPING OF FERAL CATS

It is recommended that trapping be restricted to late autumn and early winter when food availability is generally low, particularly in high rabbit density areas. Trapping during this period would also reduce the capture of non-target reptiles. Baits used

may not be necessary if the trap is clearly visible or the bait has a strong odour. Cage traps should be set squarely on the ground and the doors of traps bent upwards to increase the openness of the space. In addition, the trap should be clear of vegetation so that the cat can walk completely around the trap before entering.

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Appendix 2: Taxa identified in cat scats

Class, Order, species		Common name
Mammalia		
	Oryctolagus cuniculus	Rabbit
	Macropus giganteus	Eastern Grey Kangaroo
	Mus domesticus	House Mouse
	Ovis aries	Sheep
	Rattus rattus	Black Rat
	Bos taurus	European cattle
	Sus scrofa	Pig
	Trichosurus vulpecula	Common Brushtail Possum
	Sminthopsis sp.	Dunnart
	Petaurus breviceps	Sugar glider
Reptilia		
	Varanus sp.*(* probably *varius)*	Monitor Lizard
	Ctenotus sp.*(* probably *robustus)*	
	Ramphotyphlops sp.	Blind snake
		Unidentified skink
		Unidentied dragon
		Unidentified Elapid
Amphibia		
	Litoria latopalmata	
	Litoria peronii	
Invertebrata		
Orthoptera		Grasshoppers and crickets
Coleoptera		Beetles
Lepidoptera		Moths and butterflies
Blattoidea		Cockroaches
Odonata		Dragonflies
Arachnida		Spiders
Chilopoda		Centipedes
Diptera		Flies
Hymenoptera		Ants
Vegetation		
		Grass sp.
	Rosa rubiginosa	Sweet Briar
	Rubus fruticosus	Blackberry
	Brachychiton populneum	Kurrajong
	Schinus areira	Peppercorn

Appendix 3:

Temporal synchrony and the influence of moonlight on the diet of red foxes (*Vulpes vulpes)* in central-eastern New South Wales[1]

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Abstract

This study describes temporal, spatial and individual variation in the diet of red foxes (*Vulpes vulpes*) (*n* = 255 stomachs) on agricultural land in central-eastern New South Wales from July 1994 to November 1996. Rabbits (*Oryctolagus cuniculus*), sheep (*Ovis aries*), eastern grey kangaroos (*Macropus giganteus*) and invertebrates were the most important food items overall. Foxes continued to eat rabbits after the arrival of Rabbit Calicivirus Disease in the region. Significant seasonal variations, and sex and age differences between foxes were found in the consumption of some food types. Temporal synchrony was also detected, with several individual foxes eating similar foods on the same night, which may have been related to environmental cues. On full moon nights, foxes ate rabbits and small mammals significantly less often than on other moon phases. These findings were consistent with behavioural resource depression. The implications of moonlight effects and individual variation in dietary composition are discussed.

Introduction

The red fox (*Vulpes vulpes*) was successfully introduced into Australia in the 1870s (Rolls 1969) and is now regarded as a significant pest to agriculture (lambs) (Saunders *et al.* 1995) and native fauna (Kinnear *et al.* 1988, Dickman *et al.* 1993, Priddel and Wheeler 1994). Results from 26 dietary studies in Australia confirm that the red fox is an opportunistic predator and scavenger with a diverse diet (see reviews in Banks 1997 and Newsome *et al.* 1997). Regional and seasonal variation in fox diet has been documented widely in Australia (Croft and Hone 1978, Green and Osborne

Running Head: Temporal synchrony and moonlight effects on fox diet

[1] paper submitted for publication in *Wildlife Research*

1981, Triggs *et al.* 1984, Lunney *et al.* 1996) and elsewhere (Cavallini and Lovari 1991). Few studies, however, have examined variation within fox populations on a fine local scale, such as between classes of individuals (e.g. age, sex) (Catling 1988, Lugton 1993, Palmer 1995, Cavallini and Volpi 1996) and none has examined diet on a fine temporal scale.

It is not known whether individual foxes vary in their prey consumption on the same night, or whether foraging behaviour is synchronised (temporal synchrony), perhaps as a response to environmental variables that affect prey activity. Climatic factors are important in influencing the diet of foxes (Calisti *et al.* 1990, Cavallini and Lovari 1991, Lovari *et al.* 1994, Palmer 1995). In central Italy, temperature and photoperiod were correlated significantly with insects and fruits in the diet (Calisti *et al.* 1990, Cavallini and Lovari 1991, Lovari *et al.* 1994), while in Queensland, Australia, rainfall directly influenced invertebrate consumption (Palmer 1995). Although the consumption of mammalian prey was not influenced by these abiotic factors, the role of moonlight on the prey taken by foxes, or other predators, has not been investigated previously.

Moonlight has been shown to influence the activity patterns and habitat use of various nocturnal mammal species, such as lagomorphs (Gilbert and Boutin 1991), opossums (Julien-Laferriere 1997), badgers (Cresswell and Harris 1988) and rodents (Dickman 1992). On moonlit nights, these species reduce their activity levels or use of open areas and increase their use of closed habitats. These behavioural adaptations have been interpreted as anti-predator responses to increased predation risk (Clarke 1983, Kotler *et al.* 1988). Reduced activity levels of prey on moonlit nights may influence the foraging behaviour of an opportunistic predator.

In this study we describe the diet of the red fox in agricultural land in central- eastern New South Wales and address four main questions:

1) Does dietary composition vary with season?
2) Does dietary composition differ between age and/or sex classes?
3) Do foxes show synchronisation in foraging behaviour?
4) Does moonlight affect the prey types taken by foxes?

Methods

Study area

This study was conducted within a 50 km radius of the foreshores of Lake Burrendong (32^{0} ^{0}

July 1994 to November 1996. Foxes were collected from the immediate foreshore area in

1994 and from 24 rural properties adjacent to the foreshores in 1995 and 1996. Distances between sites ranged from 2 to 95 km. Grazing by sheep (*Ovis aries*) and cattle (*Bos taurus*) was the major land use for the entire area. Sheep on the foreshores, however, were mostly wethers, while ewes were more common on the rural properties. Lambing on the rural properties was observed in spring in both 1995 and 1996. The foreshore site also differed from the neighbouring rural properties in that rabbits (*Oryctolagus cuniculus*) were more abundant, and the regular shooting (culling) of eastern grey kangaroos (*Macropus giganteus*) provided abundant carrion.

The climate is characterised by mild to cool winters (2-15^0 C) and warm to hot summers (14-33^{0}C) with an average annual rainfall of 614 mm. Both 1994 and 1995 were considered drought years as the cumulative deviation of monthly rainfall was generally below the long-term monthly average (46 years) (after Foley 1957). In 1996, conditions improved with above average rainfall recorded throughout the year (Bureau of Meteorology).

Stomach collection

Foxes were collected by cyanide baiting in 1995, and shooting from a vehicle (0.222-calibre rifle) with the aid of a spotlight in 1994 and 1996. Shooting began approximately 1.5 hours after sunset and continued for up to six hours per night. Both cyanide baiting and shooting took place on or near roads and tracks. Consecutive foxes were generally shot at least 500 m apart. Each fox was aged by sectioning teeth and counting annuli (Harris 1978), except for nine foxes whose teeth were damaged during collection. Foxes were separated into

(Catling 1988).

Prey identification

Prey remains in stomachs were sorted macroscopically into food groups. Mammalian prey remains were identified to species from microscopic analysis of hairs using cross section and whole mount techniques (Brunner and Coman 1974). The approximate age of ingested rabbits was determined by comparing sizes of recovered body parts (e.g. ears and feet) to a reference collection of entire known-age rabbits taken from the study area. Rabbits < 500 g (< 50 days) were classified as small kittens, 500 ≤ 800 g (50 ≤ 80days) as large kittens, and > 800 g (> 80 days) as adults (after Catling 1988, I. Parer, personal communication). Adult and subadult status for ingested common brushtail possums (*Trichosurus vulpecula*) and house mice (*Mus domesticus*) were estimated by comparing body part sizes to known-age reference specimens. Possums with a tibial length < 100 mm (Tyndale-Biscoe 1955) and house mice < 72 mm head-body length (Newsome 1969) were considered subadult. The presence of blowfly larvae in a stomach was used to classify the contents as carrion. Eastern grey kangaroos, sheep, cattle, pigs (*Sus scrofa*) and goats (*Capra hircus*) were also classified as carrion, given their large size, despite the absence of blowfly larvae. Carrion remains were not aged because identifiable body parts were generally not found. Non-mammalian food items were identified to species level, where possible, by comparison to reference books (Simpson and Day 1989, Cogger 1994, Zborowski and Storey 1995) and reference collections.

Data analysis

The percentage volume of each food item per stomach was estimated visually (Croft and Hone 1978), and the mean percentage volume and percentage occurrence calculated for each monthly sample of stomachs. Percentage volume was defined as the proportion of the total volume of a stomach that was occupied by a particular food item, while percentage occurrence was defined as the proportion of stomachs in a sample that contained a particular food item (Reynolds and Aebischer 1991). As some stomachs contained more than one item, the sum of percentage occurrences could exceed 100%. The visual estimate of percentage volume was considered reliable, as it did not differ significantly from other more laborious quantitative methods for assessing diet (Molsher *et al.* 1999). Both percentage volume and occurrence methods were used in assessing diet to reduce the limitations imposed by each single method (Reynolds and Aebischer 1991). All prey identifications were conducted by the same person (R. Molsher) to reduce inconsistencies between observers.

Sampling was conducted over three seasons; summer (December to February), winter (June to August) and spring (September to November). No samples were collected in autumn. Seasonal variation in the percentage volume of each prey group was examined using a non-orthogonal two-way ANOVA (season by year). Summer was excluded from the analysis because of the low sample size (n = 9). The percentage volumes were arcsine-transformed for normality (Zar 1984), and each prey group tested separately to avoid problems associated with the lack of independence between prey groups.

Age and sex differences between foxes in the percentage volume of each prey group were evaluated using a non-orthogonal two-way ANOVA (sex by age). The percentage volumes were arcsine-transformed and each prey group was tested separately. Age and sex differences in dietary composition were examined for winter and spring separately to distinguish possible interactions with season that may have been related to breeding. In addition, age and sex differences between foxes in the frequency of sheep consumption were period, and for winter and spring separately.

To examine moonlight effects on dietary composition, stomachs were allocated to one of four moon phases (full moon, last quarter, new moon, first quarter), according to the closest phase to collection date. These phases were assumed to represent different light conditions. Moonlight effects on the diet of foxes may have been underestimated, as cloud cover was not examined. Stomachs collected in 1994 from the foreshore sites were excluded from the moonlight analyses, as they were considered unrepresentative of the entire sample. Rabbits at this site were not controlled and in very high numbers, compared to those on the rural properties, and may have obscured predator responses to changes in prey activity. In addition, only one stomach was collected on a full moon night in 1994. G-tests were used to evaluate differences between the four moon phases in the frequency of each prey group in the diet. Each prey group was tested separately. Analyses were conducted for the entire period (1995 to 1996) and for winter and spring separately. In addition, variation in the percentage volume of each prey group between moon phases was evaluated using a non-orthogonal two-way ANOVA (season by moon phase). The percentage volumes were arcsine-transformed and each prey group was tested separately.

Results

Overall Diet

A total of 263 foxes (134 females and 129 males) were collected from July 1994 to November 1996. The stomachs from two foxes were damaged during collection and six were empty. In 255 fox stomachs examined, 10 species of mammal, 11 species of bird, 8 species of reptile, 2 species of amphibian, 25 species of invertebrate and 3 plant species were identified (Appendix 1).

Mammals were the most important food group for foxes by volume (63.5%), but were not found in all stomachs (93%) (Table 1). Carrion, mostly eastern grey kangaroo and sheep, was the most important food group both by volume (38.2%) and occurrence (73.8%). Invertebrates, rabbits and vegetation were next most important by volume, whereas small

comprised fish, frogs, a tortoise and an octopus (presumably scavenged from domestic

Specific food items

Eastern grey kangaroos were the major type of carrion eaten at the foreshore site, while sheep were more important subsequently for foxes collected from rural properties (Fig. 1). Peaks in sheep consumption were detected in early spring in 1995 and 1996, but not in

when goats dominated in the diet (Fig. 1).

Rabbits were more important in the diet at the foreshore site in 1994, compared to the rural properties in 1995 and 1996 (Fig. 2). Of the 41 stomachs where rabbit remains were aged, most were adults (66%), while large and small kittens both occurred in 17% of stomachs. Foxes continued to eat rabbits after the arrival of Rabbit Calicivirus Disease (RCD) in June 1996 (Saunders *et al.* 1999).

Invertebrates were important in the diet by both occurrence (72.9%) and volume (21.1%) (Table 1) and occurred in stomachs in all sample months (Fig. 2). Vegetation was eaten frequently (68.2%), but was not a major component of the diet by volume (9.6%) (Table 1). Small mammals (house mice, black rats *Rattus rattus,* and a dunnart *Sminthopsis* sp.) were minor components of the diet, occurring in 15.2% of stomachs and comprising 5.1% of the diet by volume. House mice were the most common small mammal species eaten (n = 33 stomachs), while black rats were next most common (n = 5) (Table 1). Of the 12 stomachs where house mice were aged, 10 contained subadult mice with up to three whole subadult mice occurring in individual stomachs. Common brushtail possums were a minor component of the diet with occurrence in only 5 stomachs (Table 1). One possum was classified as adult, one subadult, and three of unknown age. Possums were eaten only in three months of the year throughout the study: August, September and October. Birds comprised a minor component of the diet by volume (3.4%) (Table 1) with the common starling (*Sturnus vulgaris*) the most frequently eaten species.

Few foxes ate reptiles (Table 1) but a single stomach often contained a variety of species. For example, a stomach collected in October 1995 contained the remains of eight legless skinks (*Anomalopus leuckartii*), one blind snake (*Ramphotyphlops proximus*) and one dragon (Agamidae). *A. leuckartii* (n = 11 stomachs) and *R. proximus* (n = 5 stomachs) were the most common species eaten. Most reptiles (87.5%) were detected in stomachs collected in October and November, while *A. leuckartii* was eaten only during these months. *A. leuckartii* were eaten mostly by vixens (82%), and by young adults (9 months - 2 years, 55%), rather than by cubs (<9 months, 9%) or old adult foxes (> 2 years, 36%).

Table 1. Food items in fox stomachs collected from central-eastern NSW from July 1994 to November 1996 (*n* = 255)

* classified as carrion

Food item	**number of occurrences**	**% occurrence**	**% volume**
Mammal			
* Eastern Grey Kangaroo	96	37.6	16.4
European Rabbit	87	34.1	19.7
* Sheep	78	30.6	18.6
House Mouse	33	12.9	3.7
* Indeterminate carrion	6	2.4	1.3
Common Brushtail Possum	5	2.0	0.5
Black Rat	5	2.0	1.0
* Goat	4	1.6	1.1
* European cattle	2	0.8	0.3
* Pig	2	0.8	0.5
Dunnart sp.	1	0.3	0.4
Total mammal	*319*	*93.0*	*63.5*
Bird	41	16.1	3.4
Reptile	24	9.4	2.0
Invertebrate	186	72.9	21.1
Vegetation	174	68.2	9.6
Aquatic	8	3.1	0.5
Miscellaneous	5	2.0	0.7

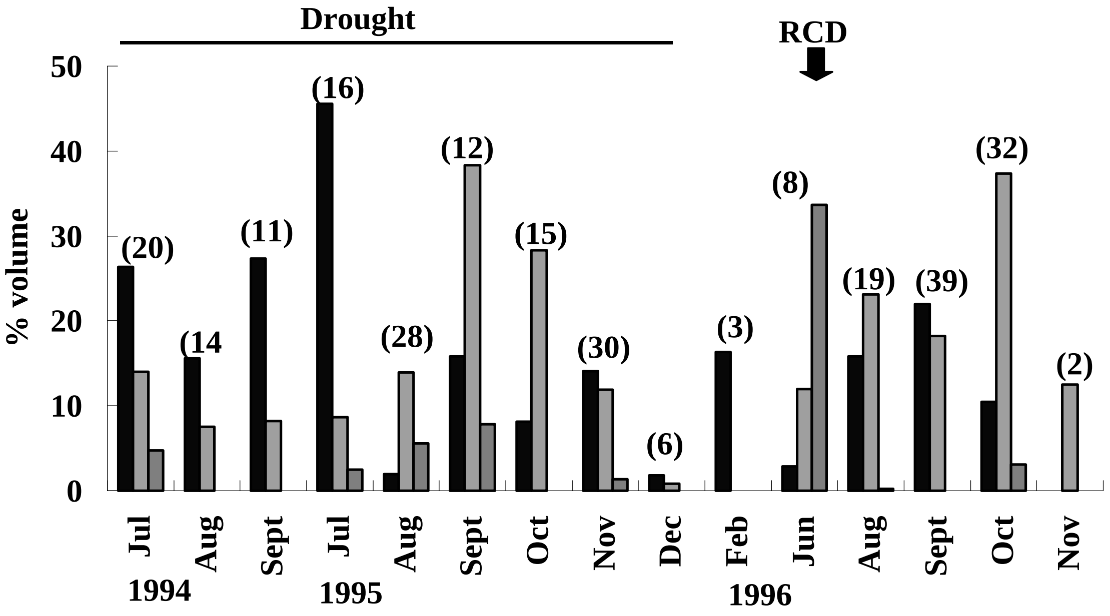

Fig. 1. Relative importance (% volume) of different types of carrion in the diet of foxes (*n* = 255). Where RCD = Rabbit Calicivirus Disease and ( ) indicates number of stomachs. Stomachs were collected from the foreshore site in 1994 and adjacent rural properties in 1995 and 1996

■	kangaroo
▨	sheep
▩	other carrion

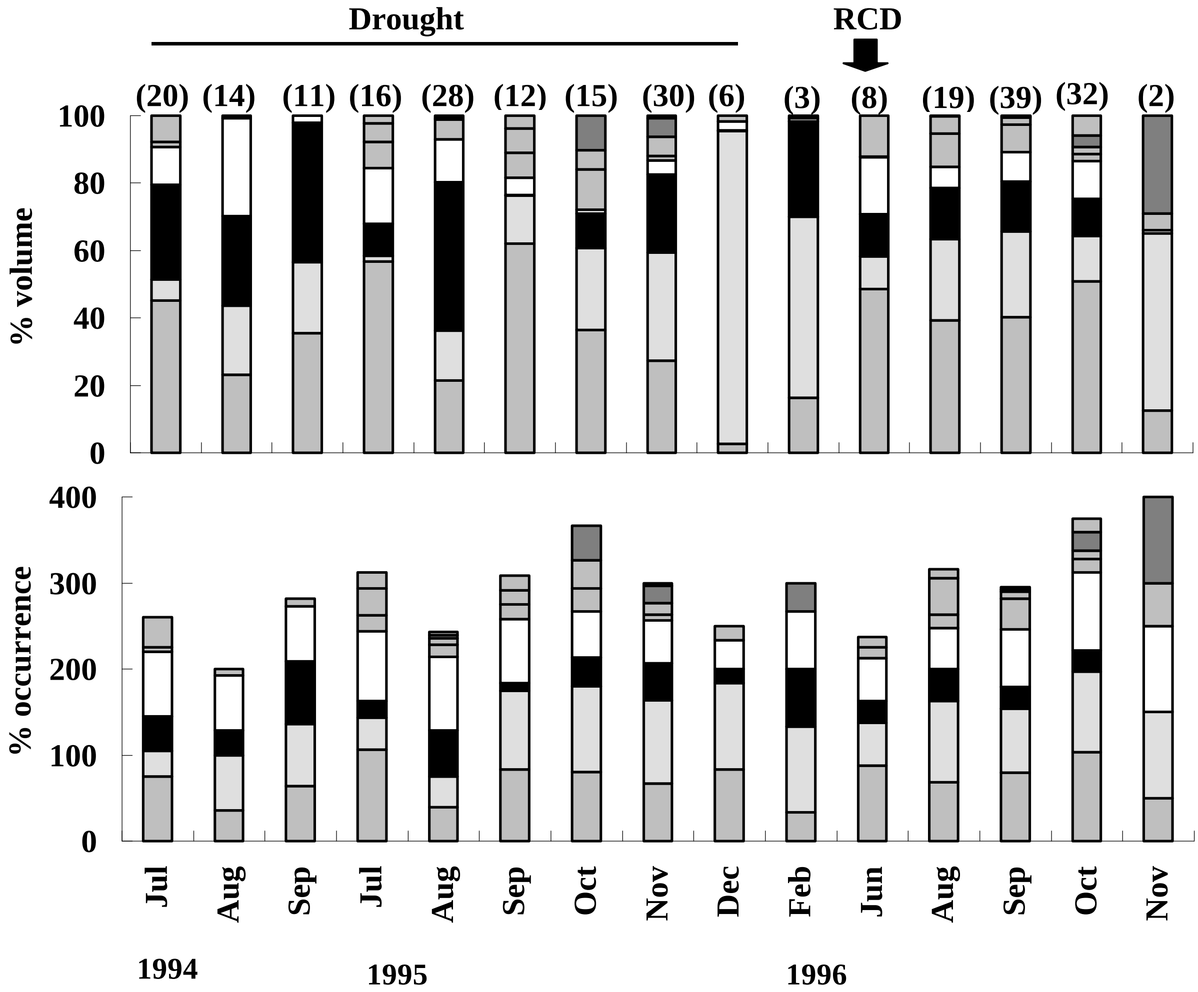

Fig. 2. Monthly variation in fox diet (*n* = 255 stomachs). Where RCD = Rabbit Calicivirus Disease and ( ) indicates number of stomachs. Stomachs were collected from the foreshore site in 1994 and adjacent rural properties in 1995 and 1996

▒ carrion
░ invertebrate
■ rabbit
□ vegetation
▒ small mammal
▒ bird
▓ reptile
▓ miscellaneous

Seasonal variation

In winter, rabbits ($F = 5.37$, d. f. = 1, 240, $P = 0.021$) and vegetation ($F = 10.11$, d. f. = 1, 240, $P = 0.002$) were more important in the diet by volume, than in spring. In spring, invertebrates ($F = 7.22$, d. f. = 1, 240, $P = 0.008$) and reptiles ($F = 9.50$, d. f. = 1, 240, $P = 0.002$) were more important in the diet than in winter. In summer, foxes tended to feed mostly on invertebrates and no small mammals or birds were detected in the diet, but this sample was small. No significant difference was found between years in the consumption of any of the prey groups and no season by year interactions were detected ($P > 0.05$).

Invertebrate taxa tended to vary seasonally, with grasshoppers and Christmas beetles the main taxa eaten in summer, and beetles, centipedes, armyworms and cockroaches in spring. Few invertebrates, mostly armyworms, were eaten in winter. In most months, vegetation comprised just a few strands of grass, except in winter, when sweet briar (*Rosa rubiginosa*) and kurrajong (*Brachychiton populneum*) seeds were an important dietary component. During this time, up to 273 sweet briar and 104 kurrajong seeds were recorded in individual stomachs.

Sex and age differences in diet

Carrion was more important by volume for male foxes compared to vixens in winter ($F = 5.29$, d. f. = 1, 96, $P = 0.024$) but not in spring ($P > 0.05$) when vixens ate more invertebrates than males ($F = 4.54$, d. f. = 1, 133, $P = 0.035$). By occurrence, sheep were eaten significantly more often by male foxes (38%) than by vixens (25%) overall ($G = 4.72$, d. f. = 1, $P < 0.05$) but no differences were found when the seasons were tested separately ($P > 0.05$).

Young adult foxes (9 months-2 years) ate more carrion by volume than old adults (> 2 years) in winter ($F = 7.55$, d. f. = 1, 96, $P = 0.007$). No cubs (< 9 months) were present in winter. In spring, cubs ate more reptiles ($F = 5.83$, d. f. = 2, 133, $P = 0.004$) and less carrion ($F = 2.60$, d. f. = 2, 133, $P = 0.07$) than the other age groups, while young adults ate less rabbits ($F = 3.11$, d. f. = 2, 133, $P = 0.048$) (Fig. 3). Cubs also tended to eat more invertebrates than the other age groups in spring but the difference was not significant ($P > 0.05$) (Fig. 3). All known age rabbits eaten by cubs were kittens. The frequency of sheep consumption did not differ between age groups ($P > 0.05$).

Significant sex by age interactions was also detected. Reptiles were more important in the diet by volume of male cubs and old adult females in spring ($F = 5.78$, d. f. = 2, 133, P

= 0.004) compared to the other age-sex combinations. In winter, carrion was more important in the diet of young adult males (F = 4.07, d. f. = 1, 96, P = 0.046).

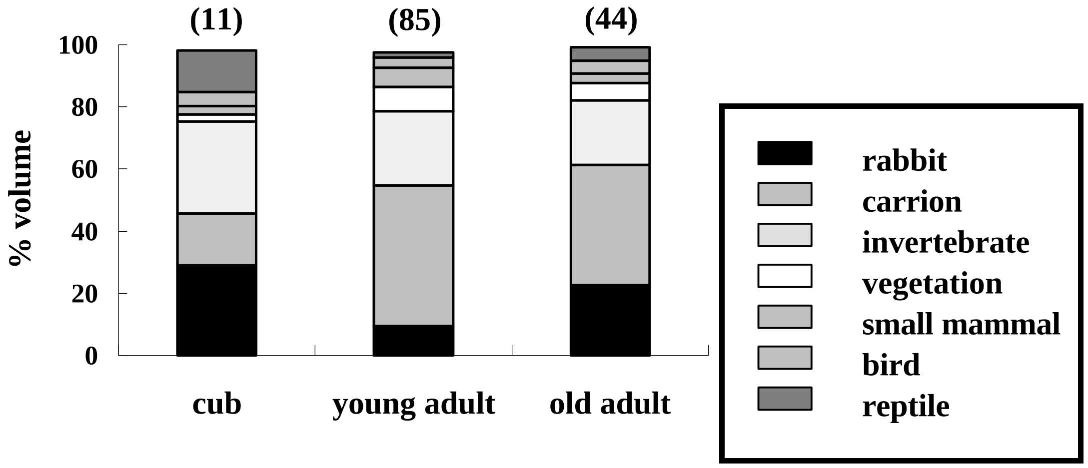

Fig. 3. Age differences in the dietary composition of foxes in spring from 1994 to 1996 (n = 140 stomachs). Where cub = less than 9 mths, young adult = 9 mths to 2 years, and old adult = more than 2 years, and ( ) indicates number of stomachs.

Temporal synchrony

Individual foxes tended to eat similar foods on the same night (Fig. 4). On 61% of nights (excluding nights where < 3 foxes collected), over half the foxes ate the same dominant food group (25 nights, 113 foxes). For example, eastern grey kangaroos were the main food group by volume for 60% of foxes on July 5, 1995 and 80% of foxes on September 5, 1996 (Figs. 4a and f). Similarly, rabbits were the major food for 64% of foxes on August 4, 1995 and 80% of foxes on 24 November 1995 (Figs. 4b and d). Invertebrates were the most important food source on 30 August 1995 (80%), 6 December 1995 (100%) and 18 September, 1996 (67%) (Figs. 4c, e and g).

Species eaten within each food group were also similar between individual foxes on the same night. For example, centipedes and armyworms were the two main invertebrate taxa eaten by all foxes on August 30, 1995 and September 18, 1996 (Figs. 4c and g). Similarly, beetles and cockroaches were the main taxa eaten on November 24, 1995 and beetles and grasshoppers on 6 December 1995 (Fig. 4d and e). In addition, the age of mammalian prey that were eaten tended to be similar among foxes collected on the same night. For example, all rabbits eaten on 24 November 1995 were small kittens (Fig. 4d).

Influence of moonlight on diet

Overall, rabbits (G = 7.36, d. f. = 3, $P < 0.10$) and small mammals (G = 8.10, d. f. = 3, $P < 0.05$) were eaten less often on full moon nights than on the other moon phases (Fig. 5). By volume, carrion was less common in the diet on new moon nights (F = 4.22, d. f. = 3, 190, P = 0.006). No significant moonlight effects were found for the consumption of the remaining food groups ($P > 0.05$).

In spring, foxes tended to eat rabbits (G = 7.49, d. f. = 3, $P < 0.10$) more often on new moon nights and invertebrates (G = 15.96, d. f. = 3, $P < 0.05$) less often on full moon nights, than on the other moon phases. Small mammals also tended to be eaten less often on full moon nights in spring (G = 4.81, d. f. = 3, $P > 0.05$). No moonlight effects were detected for any of the prey groups in winter ($P > 0.05$).

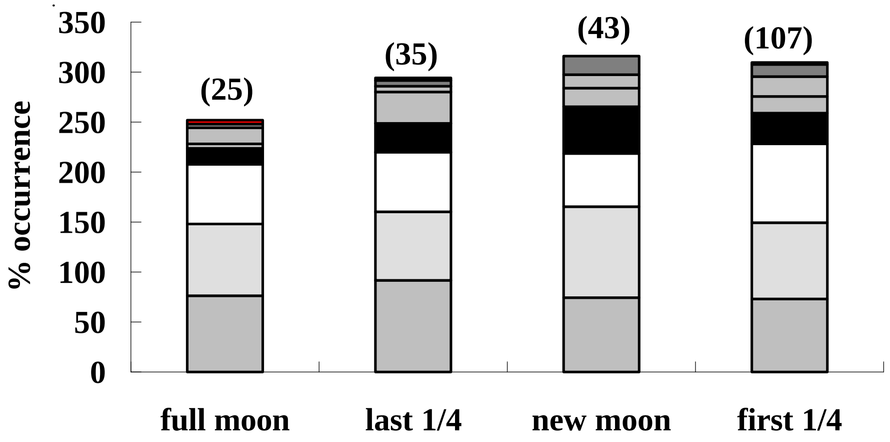

Fig.5. Fox diet in relation to moon phase at the rural properties from July 1995 to November 1996 (n = 210 stomachs). Where ( ) indicates number of stomachs

Discussion

Overall diet

The diet of foxes in central-eastern New South Wales was dominated by mammals, particularly carrion and rabbits. This concurs with previous studies that have found mammals to be the major prey where abundant in Australia (Brunner *et al.* 1976, Triggs *et al.* 1984, Woolley *et al.* 1985, Wallis and Brunner 1987, Baker and Degabriele 1987, Brown and Triggs 1990, Brunner *et al.* 1991), as elsewhere (Lindstrom 1994). Invertebrates were important supplementary prey, while birds, reptiles and vegetation were generally minor components of the diet.

Specific food items

Carrion (mostly eastern grey kangaroos and sheep) was the most important food group (occurrence 73.8%, volume 38.2%) for foxes in this study, which presumably reflected its high availability. Other carrion (cattle, pigs and goats) was of minor importance, except in June 1996, when goats dominated the diet of four foxes. These foxes were collected from near a paddock where farmed feral goats were kidding (E. Gifford personal observation).

As in previous studies, eastern grey kangaroo remains were assumed to be carrion (Martensz 1971, Coman 1973, Ryan and Croft 1974, Bayly 1978, Croft and Hone 1978, Catling 1988, Lunney *et al.* 1990, Lugton 1993, Palmer 1995), because of their large size, but predation on juveniles may have also occurred. Foxes are known to be significant predators of smaller adult macropods (e.g. Kinnear *et al.* 1988) and there is increasing evidence to suggest that predation on the juveniles of larger macropods is also prevalent (Hornsby 1982, Robertshaw and Harden 1989, Arnold *et al.* 1991, Banks 1997). Consequently, the importance of carrion in the diet may have been overestimated in this study as the prevalence of predation on juvenile large mammals was not known. Even when the age of mammalian remains was known, the limitations inherent in dietary studies precluded any distinction between scavenging and predation. For example, the presence of juvenile flesh in the stomach does not necessarily indicate that the animal was killed by that fox, while the presence of blowfly larvae does not necessarily indicate scavenging, as the animal may have been cached prior to eating.

Seasonal peaks in sheep consumption in spring during lambing may also have reflected predation on lambs, rather than scavenging at carcasses. Elsewhere, increases in sheep consumption by foxes have also coincided with greatest lambing activity (McIntosh 1963, Croft and Hone 1978). However, while foxes are known to kill lambs (Lugton 1993), fresh lamb is found infrequently in fox stomachs (McIntosh 1963, Coman 1973, Croft and Hone 1978, Lugton 1993), and the importance of fox predation on lambs is unclear. It is not common among mature males (Lugton 1993). While male foxes ate sheep significantly more often than females overall in this study, no sex differences were detected in spring during lambing.

Rabbits were the single most important mammalian prey species for foxes overall (occurrence 34.1%, volume 19.7%). They were particularly prevalent in the diet at the foreshore site, which probably reflected their greater availability. After the arrival of RCD, foxes continued to feed on rabbits despite a decline of over 90% in numbers (Saunders *et al.* 1999). This lack of diet shift in the four months post-RCD may be because rabbit abundance remained sufficiently high for foxes to be efficient in catching them. Consequently, shifts to alternative prey would not have been necessary.

Seasonal and individual variation

Seasonal variation in diet was large as is found in most other dietary studies of the fox (see review in Newsome *et al.* 1997, Cavallini and Volpi 1996), and has been shown to reflect changes in food availability (Green and Osborne 1981, Catling 1988). In this study, invertebrates and reptiles were more important in the diet in spring, than in winter, when their availability was higher (Molsher *et al.* 1999). In summer, the diet comprised mostly invertebrates, which also reflected their increased availability during this time (Molsher *et al.* 1999). In winter, foxes ate significantly more rabbits and vegetation as the abundance of reptiles and grasshoppers declined and sweet briar and kurrajong fruits increased (Molsher *et al.* 1999, R. Molsher unpublished data).

While seasonal variation in diet is often assumed to be related purely to fluctuations in prey abundance, individual variation (e.g. age and sex) is also clearly important in dietary composition. In this study, vixens ate significantly more invertebrates than males in spring, while male foxes ate more carrion than vixens in winter. Given the small sexual size dimorphism in red foxes, these season by sex differences may be related to breeding (Cavallini and Volpi 1996). Winter is the main breeding season for foxes in Australia, and most cubs are born during August and September (Saunders *et al.* 1995). The high protein content of invertebrates (McIlroy 1993) may be required for vixens during lactation and growth of young in spring, especially if alternative prey is not readily available. Similarly, male foxes are more likely to be transient in winter when they leave their territories in search of mating opportunities (Saunders *et al.* 1995). The higher consumption of carrion by males during this time may indicate that they are less adept at catching other prey, such as rabbits, which may require local knowledge. Similarly, the greater consumption of carrion by young adult males in winter may reflect reduced foraging success in unfamiliar territories.

Cubs (< 9 months) ate significantly more reptiles and less carrion than young adult (9 months-2 years) or old adult foxes (> 2 years) in this study in spring. Previous studies have not found age-related differences in reptile consumption but seasons were not distinguished (Catling 1988, Lugton 1993) and spring not examined specifically (Palmer 1995, Banks 1997), when predation on reptiles was highest. This greater consumption of reptiles by cubs probably reflects their easier catchability and inexperience in catching alternative prey, such as adult rabbits (Macdonald 1989, Dickman 1988). Similarly, the higher incidence of rabbit kittens compared to adults in the diet of cubs may reflect their easier catchability. Foxes frequently use rabbit warrens as dens for the birth and caring of cubs (Saunders *et al.* 1995) and rabbit kittens (particularly nestlings) may provide an important food source for cubs during the rabbit breeding season in spring (Gilbert *et al.* 1987).

A similar lower consumption of carrion by cubs, compared to adults, has been

predicts that larger prey are brought back for young in the den by a single-prey loader, while smaller prey are consumed on the spot (Schoener 1979, Orians and Pearson 1979). Although this has found support for red foxes in the Northern Hemisphere (Lindstrom 1994), cubs in this study ate smaller prey than did adults. This may be because large prey in the Northern Hemisphere includes rabbit-sized prey while in this study, large prey were kangaroo and sheep carcasses that would be difficult to carry back to the den. Although the sex and age-related differences in diet reported here are consistent with other studies (Catling 1988, Lugton 1993, Cavallini and Volpi 1996), individual variation in diet between seasons has not been examined previously.

Temporal synchrony and the influence of moonlight

Temporal synchrony within the population was detected with individual foxes eating similar foods on the same night. This is unlikely to reflect group feeding at carcasses as consecutive foxes were shot at least 500m from each other. Synchronisation in the foraging behaviour of foxes has not been examined previously but may reflect a generalised response to environmental cues that influence prey activity. The importance of invertebrates and vegetation in the diet of foxes has previously been correlated with rainfall, photoperiod and temperature (Calisti *et al.* 1990, Cavallini and Lovari 1991, Lovari *et al.* 1994, Palmer 1995). In this study, moonlight was correlated significantly with the consumption of mammalian prey.

The reduced consumption of rabbits and small mammals on moonlit nights in this

causes prey to reduce activity in risky areas, thereby making them more difficult to capture (Charnov *et al.* 1976, Kotler *et al.* 1992). On moonlit nights, hunting success of a range of predators may increase (Clarke 1983, Kotler *et al.* 1988) and prey activity is reduced (e.g. Gilbert and Boutin 1991). Reduced activity in rabbits and small mammals on moonlit nights may then result in increased consumption of alternative prey that are less influenced by illumination levels, such as invertebrates and carrion.

Although prey may be more active on darker nights, individual predation risk is reduced, as they are less detectable to visual predators. When food is limited, however, the advantages of foraging on moonlit nights may outweigh the disadvantages of increased predation risk (Lockard and Owings 1974, Wolfe and Summmerlin 1989). This may account for the lack of moonlight effects on dietary composition recorded in winter in this study.

Resource depression, however, predicts that prey selection on a fine temporal scale should be asynchronous, as prey reduce their activity when disturbed thereby reducing capture efficiency for subsequent predators. The lack of asynchrony recorded in this study may reflect the large area over which foxes were collected such that the hunting of a predator in one area would not be expected to influence the behaviour of prey elsewhere. Similarly, territoriality in foxes (Voigt and Macdonald 1984, Doncaster and Macdonald 1991) may also reduce resource depression effects.

Further experimentation is required to test the hypothesis that synchronisation in foraging by foxes is due to moonlight effects on prey activity. These studies need to show that moonlight affects activity levels of the prey species, and that predators from different sites have access to a similar range of prey.

Implications for future studies

The diet of foxes was significantly influenced by many sources of variation (season, sex, age, moonlight) in this study, and this may have management implications. Poison baiting is one of the main methods used in the control of foxes in Australia (Saunders *et al.* 1995). Future fertility control techniques will also depend upon baits for delivery of contraceptive vaccines (Bradley *et al.* 1998). Variation in the consumption of prey, however, may influence bait uptake rates and result in an age-sex bias in the population. For example, while baiting in winter, prior to the birth of cubs, has cost and animal welfare advantages, our results suggest that baiting only during this time may target young adult males. In addition, baiting may be more effective on moonlit nights when foxes are more likely to eat carrion, and predation on rabbits and small mammals is reduced.

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New South Wales.)

Appendix. Species identified in fox stomachs (*n* = 255) collected from central-eastern NSW from July 1994 to November 1996.

Class, Order, species		Common name
Mammalia		
	Macropus giganteus	Eastern Grey Kangaroo
	Trichosurus vulpecula	Common Brushtail Possum
	Sminthopsis sp.	Dunnart
	Bos taurus	European Cattle
	Sus scrofa	Pig
	Ovis aries	Sheep
	Capra hircus	Goat
	Oryctolagus cuniculus	Rabbit
	Rattus rattus	Black Rat
	Mus domesticus	House Mouse
Aves		
	Anas sp.	Duck or teal
	Corcorax melanorhamphos	White-winged Chough
	Coturnix australis	Brown Quail
	Malurus cyaneus	Superb Fairy-wren
	Megalurus gramineus	Little Grassbird
	Petroica goodenovii	Red-capped Robin
	Platycercus eximius	Eastern Rosella
	Podargus strigoides	Tawny Frogmouth
	Smicrornis brevirostris	Weebill
	Strepera graculina	Pied Currawong
	Sturnus vulgaris	Common Starling
Reptilia		
	Anomalopus leuckartii	
	Ctenotus robustus	Striped skink
	Ctenotus sp.	
	Egernia striolata	Tree skink
	Underwoodisaurus milii	Thick- Tailed Gecko
	Agamidae indet.	
	Ramphotyphlops proximus	Blind snake
	Ramphotyphlops sp.	
	Chelodina longicollis	Long-Necked Tortoise

Amphibia			
		Limnodynastes tasmaniensis	
Arachnida			
	Araneida		Spider
Chilopoda			
	Scolopendromorpha		Centipede
Insecta			
	Blattodea	probably *Calolampra irrorata*	Cockroach
	Coleoptera		Christmas beetle, ground beetle, scarab beetle, dung beetle
		Adelium angulicolle	Darkling beetle
		Chauliognathus lugubris	Plague soldier beetle
	Dermaptera	*Labidura truncata*	Common brown earwig
	Diptera		Flies
	Hemiptera		Grass bug
		Dysdercus sp.	Cotton stainer
	Hymenoptera		Ants
	Lepidoptera		Armyworm, cutworm, moth
	Neuroptera		Green lacewing
	Odonata		Dragonfly
	Orthoptera	*Acrida conica*	Grasshopper
		Chortoicetes terminifera	Australian plague locust
		Oedaleus australis	Grasshopper
		Oecanthus sp.	Tree cricket
		Phaulacridium vittatum	"Wingless" grasshopper
		Tettigoniidae	Katydid
Vegetation			
			Grass sp.
		Brachychiton populneum	Kurrajong tree
		Rosa rubiginosa	Sweet Briar