# The Ecology of the Red Fox (*Vulpes vulpes*) in the Central Tablelands of New South Wales

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For Moya Lenore Farrell
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This thesis is my original work and has not been submitted, in whole or in part, for a degree at this or any other university. Nor does it contain, to the best of my knowledge and belief, any material published or written by another person, except as acknowledged in the text.

Mani Berghout
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# ABSTRACT

The red fox occurs across a very broad range of habitats, and displays great behavioural flexibility under different environmental conditions. In Australia, mounting concern over the impacts of foxes on livestock and native fauna has highlighted a need for more information on fox ecology under Australian conditions as a fundamental step towards developing more strategic means of managing foxes. This study explores ranging behaviour, dispersal, use of dens, activity rhythms, population dynamics and diet in the absence of management in productive agricultural land in the central tablelands of New South Wales.

The study was conducted from June 1994 to June 1997 on private property near Murringo, NSW Australia (34°15’ S, 148°30’ E). The site was primarily sheep and cattle grazing land and had a history of no fox management. Rainfall was considerably below average for much of the study.

A total of 83 foxes were trapped over 3931 trapnights, of which 50 were fitted with radio-collars (23 adult and 6 juvenile females, 12 adult and 9 juvenile males) and 26 released with eartags only (all juveniles: 10 females, 16 males). Thirty-three foxes were radio-tracked using fixed towers between March 1995 and December 1996, with between 11 and 28 foxes tracked at any time. Mean home range size was 446.1 ha ± 69.8 se using 95% Minimum Convex Polygons (MCP), and 276.4 ha ± 36.3 se using 95% kernel utilisation distributions. Male home ranges defined by MCP were significantly larger than female ranges, but no significant difference was found using 95% kernels. Core ranges were estimated to be 133.4 ha ± 23.7 se using 50% MCP and 59.8 ha ± 6.1 se using 95% kernels, with no significant difference between sexes. No significant differences were found between range sizes of adults and juveniles or between years or seasons. While most home ranges were steady for the duration of the study, some foxes were observed to shift range location and 4 foxes displayed nomadic behaviour for at least some of the study. There was a high incidence of overlapping home ranges, most commonly between females or males and females but occasionally between males, but core areas were usually separate. Fully overlapping core areas were observed in 1995 but not in 1996.

Juvenile foxes were significantly more likely to disperse than adults, and usually travelled further (juveniles 61.1 km 31.6 ± se; adults 5.9 km 1.1 ± se). Males and females were equally likely to disperse, and there was no significant difference in the distance travelled. The furthest distances were 285 km and 140 km, but mean distance of dispersal excluding these animals was 12.3 km ± 4.3 se ($n = 13$).

Thorough surveys across a 16.4 $km^2$ area located 200 dens, with 68 of these active in 1995 and 96 active in 1996. Density of breeding foxes was estimated to be 0.55 and 0.52 adult foxes/$km^2$ in 1995 and 1996 respectively based on natal den counts. Density estimates based on active den counts, which include non-breeding foxes, were 0.91and 1.30 foxes/$km^2$ in 1995 and 1996 respectively. These estimates appear lower than other studies in similar habitats but this is likely due to using a half home range boundary strip around the surveyed area in the present study. Application of mark-recapture analysis found very high ‘recapture’ rates of dens and gave a similar estimate of the total number of dens to that observed directly. Natal dens were regularly distributed across the study area, whereas active dens tended to be in clusters. There was a high turnover of which dens were used each year, but the total number of natal dens was similar across years (16 in 1995 and 17 in 1996). Natal dens were more likely to be used on repeat occasions than other dens, but not necessarily by the same vixen. Litter size based on sightings of emergent cubs was 2.8.

Foxes were predominantly nocturnal, with a major peak in activity about an hour after sunset. A new method of analysing activity rhythm data using Fourier series to mathematically describe animal movements was developed, that allowed systematic identification of the cyclical components underlying overall movement patterns. General fox behaviour could be clearly described by a 24-hour and a 12-hour cyclical component when corrected for variation in daylength. The rising and setting of the sun appeared to be a major trigger underlying movement patterns. Seasonal and sex differences were observed in patterns of activity.

The annual rate of increase of the fox population was found to vary around a mean of zero between June 1994 and June 1997. A major drop in fox numbers as estimated by spotlight counts occurred in the second half of 1995, but numbers recovered by the end of 1996. Kaplan-Meier analysis of radio-tagged foxes found annual adult survival was generally very high (0.56-0.96) with lowest survival between July and October. Causes of mortality were human-related outside the site and apparently of natural causes within the site. However foxes dying of natural causes outside the site were unlikely to be found. There was no overall movement of foxes into or out of the site. Immigration was detected following the drop in fox numbers in late 1995, but there was no evidence of immigration prior to this period although emigration occurred.

A sensitivity analysis was conducted on the effects of a small change in life history parameters on finite rate of increase using published data as well as adult mortality data from the present study. The two most influential life-history parameters were adult and juvenile survival, while changes in fecundity and age at first reproduction had much less impact on finite rate of increase. In terms of management, in which fertility control is being considered as an alternative to lethal control, this implies that a small change in fecundity may cause less change in the rate of increase of foxes than lethal control.

Foxes were culled in June 1997 on completion of the study. Estimated density using a Petersen estimate was 2.4-5.3 foxes/km$^2$ and index-manipulation-index was 1.4-3.2 foxes/km$^2$. The different methods used to cull foxes appeared to target different age groups within the population, and were generally biased in favour of younger foxes. Success at killing animals was low, leading to large standard errors in the population estimates.

Stomachs of foxes shot in the Orange district were found to contain predominantly rabbit and carrion, with invertebrates present when abundant. These findings were not strictly representative of the diet of foxes in the study area, where rabbits were scarce. Foxes scavenged heavily on lamb carcasses within the study site. The quantity of fresh lamb carrion removed from a lambing paddock in winter 1996 was estimated to support 13-24 foxes, with available fresh lamb theoretically able to support 240-440 foxes. Density based on removal of fresh carcasses was estimated to be 0.83-1.5 foxes/km$^2$.

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# CHAPTER 1

# GENERAL INTRODUCTION

This thesis investigates aspects of the ecology of the red fox in the absence of management in the central tablelands of New South Wales. The impetus for this work was provided by a large-scale field study into the effects of imposed sterility on foxes, the purpose of which being to test the concept of using fertility control to manage fox numbers. While the main focus is on fox ecology, the work has broader implications for management of foxes and their impacts.

## 1.1 ECOLOGY OF THE RED FOX

The red fox (*Vulpes vulpes*) is indigenous to the northern hemisphere, with a virtually continuous distribution from western Europe through Asia to northern America, interrupted only by the Bering Straits (Jarman 1986). The largest member of its genus, it is also the most widespread (Lloyd 1980). Its distribution encompasses habitats inclusive of tundra, deserts, mountains to 4200m, densely populated agricultural areas and urban environments (Saunders *et al.* 1995). Much of this adaptability is associated with its size and light build, and it has been argued a smaller animal would not have sufficient mobility to survive in barren conditions, but a larger animal would need larger food items and would have difficulty concealing itself from unwanted human attention (Lloyd 1980).

Numerous studies of aspects of fox ecology have been conducted in a variety of habitats in Europe, Asia and North America (Corbet and Harris 1991). Australian studies have taken place in alpine habitats, (Green and Osborne 1981; Bubela 1995), semi-arid western New South Wales (eg Newsome *et al.* 1989; Marlow 1992; Lugton 1993a) and semi-arid Western Australia (eg Marlow *et al.* 2000; Thomson *et al.* 2000), forest in eastern Australia (eg Triggs *et al.* 1984; Phillips and Catling 1991; Banks 1997), temperate agricultural land (eg Coman *et al.* 1991; Thompson and Fleming 1994) and in urban environments (eg Marks and Bloomfield 1999). Details of specific Australian studies will be presented in the introductions to the relevant chapters.

### *1.1.1 Ranging behaviour and spatial organisation*

Macdonald (1981) observed that foxes have the greatest variation in range size of any species among the Carnivora. For example, in urban England, Saunders *et al*. (1993) estimated range sizes of 30 ha, while Jones and Theberge (1982) estimated ranges of 1611 ha in tundra in British Columbia. Seasonal climatic variation, patterns of mortality and degree of food diversity are thought to contribute to home range size (Voigt and Macdonald 1984). Fox population density is also related to range size (Harris 1980). Ranging behaviour will be further reviewed in Chapter 2 of this thesis.

Fox social structure also differs under different environmental conditions (Voigt and Macdonald 1984). At one extreme, foxes form monogamous pairs for breeding (Fox 1971; Sargeant 1972; Storm *et al.* 1976), while at the other, social groups of a dominant male and female and a number of subordinate related females have been observed (Macdonald 1979; Reynolds and Tapper 1995). My interpretation is that common to both these extremes appears to be a defence of the breeding territory by its occupants against incursions by other foxes. Other studies have observed a high degree of overlap of home ranges, but found foxes had individual focal areas of activity (Ables 1969b; Harris 1980; Lloyd 1980; Niewold 1980; Voigt and Macdonald 1984; Poulle *et al.* 1994). Whether social groups will form is thought to be influenced by how heterogeneously resources are distributed in space and time, with groups forming while resources are in excess of the requirements of the dominant pair (Macdonald 1983; von Schantz 1984a). Social structure and territory overlap will be further explored in Chapter 2.

### *1.1.2 Dispersal*

As with ranging behaviour and social structure, distance of dispersal is linked to habitat. How far foxes disperse is positively correlated with home range size and negatively correlated with population density (Trewhella *et al.* 1988). It is also thought that foxes disperse further in more heterogeneous habitats (Trewhella *et al.* 1988). The proportion of foxes that disperse also differs according to habitat (Zimen 1984). Most information on dispersal of foxes comes from Europe and North America, with very little data from Australia. Dispersal of foxes is thought be the most significant factor in the spread of rabies in Europe (Bogel and Moegle 1980), and a need for better understanding of rabies transmission has promoted much study of fox dispersal in Europe and North America (Phillips *et al.* 1972; Storm *et al.* 1976; Lloyd 1980; Zimen 1984; Trewhella *et al.* 1988). How quickly foxes will recolonise an area following population reduction is also dependent on rates and distances of dispersal, which has major implications for fox management programs both in Australia and overseas. The lack of data on fox dispersal in Australian conditions needs to be addressed both for rabies contingency planning purposes and for more successful fox management. Studies of fox dispersal will be reviewed in Chapter 2.

### *1.1.3 Population density estimation*

Estimation of fox population density is difficult and often inaccurate due to their cryptic and elusive nature (Saunders *et al.* 1995). Comparisons of density between different populations may be difficult as the occurrence of foxes over such a wide variety of habitats makes it difficult to apply a common census technique (Saunders *et al.* 1995). Counts of breeding dens are regarded as being the most accurate means of estimating fox density, provided the size of family groups and social structure are known (Trewhella *et al.* 1988; Saunders *et al.* 1995). As all possible den sites within an area must be known, this method is inappropriate for use over large areas or where dens are difficult to locate (Marlow 1992). Estimation of fox abundance using breeding den counts will be further reviewed in Chapter 3, and other estimation techniques will be considered in Chapter 5.

### *1.1.4 Use of dens*

Foxes are known to utilise dens throughout the year as refuges, but den usage is at its peak in the breeding season, when dens are used for the birth and rearing of cubs (Lloyd 1977; Nakazono and Ono 1987). Foxes may dig their own dens or enlarge holes of other burrowing mammals such as rabbits (*Oryctolagus cuniculus*) (Ables 1975). In forested or rocky areas, foxes sometimes use above-ground cover such as hollows beneath buttress roots and boulders. In urban habitats they will have litters in a variety of places that provide suitable shelter, including beneath garden sheds and electricity transformers (Lloyd 1980). Further detail on den location, spacing, longevity and usage will be given in Chapter 3.

### *1.1.5 Fox activity rhythms*

Foxes in North America (Storm 1965; Ables 1969a), Europe (Maurel 1980; Blanco 1986; Saunders *et al.* 1993; Reynolds and Tapper 1995; Doncaster and Macdonald 1997) and Australia (Phillips and Catling 1991; Bubela 1995; Saunders *et al.* 1995; Banks 1997; Meek 1998) are largely nocturnal, with a tendency towards crepuscular activity. Studies of fox activity rhythms commonly present a chart showing the percentage of active fixes at differing times of day, and determine patterns of activity by visual appraisal of such charts, without formal analysis (eg Ables 1975; Maurel 1980; Blanco 1986; Reynolds and Tapper 1995; Banks 1997; Doncaster and Macdonald 1997). Activity rhythms of mammals have been observed to include cyclic components (Ashby 1972), but activity rhythms of foxes have not previously been analysed in terms of cyclic behaviour. Analysis of cyclic behaviour and its applications will be detailed in Chapter 4.

### *1.1.6 Population dynamics*

Foxes are monoestrous, with studies in Europe (Lloyd 1980) and North America (Storm *et al.* 1976) finding peak ovulation occurs in winter between January and March, with peak ovulation later at higher latitudes. In Australia ovulation is also in winter, with peak ovulation during July (McIntosh 1963b; Ryan 1976; McIlroy *et al.* in press), and some suggestion that latitudinal variation also occurs in Australia (Bubela 1995). There is much variation in findings between studies of fox reproduction. Mean litter sizes range from 2.8 (Allen 1984) in North America to 7.2 in Sweden (Englund 1970), and pregnancy rates range from 97% in Australia (McIntosh 1963b) to less than 10% in Alaska (Zabel and Taggart 1989). This variation may be due to temporal or spatial food availability in the different areas (Englund 1970; Zapata *et al.* 1998), but differences in litter sizes may also be explained in part by the technique or combination of techniques used to estimate litter size. Techniques such as counts of embryos tend to give higher estimates than counts of placental scars (Harris 1979) or the number of cubs at dens (Storm *et al.* 1976). The degree of pigmentation of placental scars indicates whether the embryo was resorbed, born alive or from a previous pregnancy (Lindstrom 1981; Lindstrom 1994), with studies not consistent as to which shades were counted (Storm *et al.* 1976; Lloyd 1980).

The lifespan of the fox is such that few foxes survive beyond four years in North America (Ables 1975; Storm *et al.* 1976), Europe (Fairley 1969; Harris 1977; Lloyd 1980) and Asia (Yoneda and Maekawa 1982). Mortality is usually human related (Storm *et al.* 1976; Harris 1978b; Reynolds and Tapper 1995), and foxes attain greater mean ages in areas where there is less fox control (Phillips 1970; Lloyd 1980; Yoneda and Maekawa 1982). Very little is known of causes of fox mortality in Australia (Saunders *et al.* 1995). Survival of foxes and other aspects of population dynamics will be further reviewed in Chapter 5.

### *1.1.7 Diet of the red fox*

The fox is predominantly carnivorous, but is an opportunistic predator and scavenger with no specialised food requirements (Jarman 1986). A review of dietary studies in Europe found the principal food items of foxes to be rodents, rabbits, hares, birds, carrion and domestic livestock (Sequeira 1980). Findings from North America are similar, listing the major food items as small rodents, rabbits, wild fruit and insects (Ables 1975). Regional and seasonal variations have been observed in dietary components, but it is generally considered that foxes take any acceptable food approximately in proportion to its availability (Ables 1975; Sequeira 1980). In Australia, comprehensive studies of diet in agricultural land in Victoria (Coman 1973a) and New South Wales (Croft and Hone 1978) indicate the most important food items to the fox in terms of its energy intake are sheep (taken as carrion), rabbits and house mice while native species contribute only a small proportion of dietary intake. However occurrence in the diet of foxes does not reflect impacts on prey species, with a rare occurrence in the diet potentially having a significant impact on some endangered species. Species that contribute the bulk of the diet may be in sufficient numbers that their populations are tolerant of predation (Saunders *et al.* 1995). Furthermore, high numbers of foxes supported by a staple food source such as rabbits can still prey opportunistically and thereby liimit alternative prey species

(Newsome *et al.* 1997). Rigorous scientific studies are required to quantify damage as a result of fox predation (Hone 1999a). Studies of fox diet in Australia will be reviewed in greater detail in Chapter 6.

The final chapter of this thesis, Chapter 7, provides a synthesis of results from the previous five chapters, thereby developing a picture of fox social structure in the central tablelands environment. Implications for management and directions for future research are discussed in the light of these findings.

### *1.1.8 Other aspects of fox ecology*

Some aspects of fox ecology were outside the scope of the present study. Diseases and parasites of foxes are two such topics, and are reviewed in Saunders *et al*. (1995).

## 1.2 MANAGEMENT

The fox is considered as a major pest species in Australia, implicated as a predator of native species and livestock. It is also a potential host for rabies, should the disease enter Australia. Management of the fox is therefore necessary to minimise its impacts. These issues are reviewed below.

### *1.2.1 Conservation issues*

The fox is regarded as a serious threat to native fauna in Australia, and Saunders *et al.* (1995) list 23 mammal species and 7 bird species believed to be at risk from fox predation, while predation by foxes has been identified as a threatening process for native rodents in Queensland (Dickman *et al.* 2000) and Victoria (Seebeck and Menkhorst 2000). One form of evidence implicating fox predation in the decline of native species comes from predator removal studies in which prey species numbers rose following fox removal (eg Kinnear *et al.* 1988; Friend 1990; Priddel and Wheeler 1997; Kinnear *et al.* 1998; Morris *et al.* 1998; Sinclair *et al.* 1998). However Hone (1999a) notes the need for better data on some aspects and more thorough hypothesis testing before concluding predation is responsible for the decline of a species. Not all native species show a response to fox control, as found by Banks (1999), where numbers of bush rats (*Rattus fuscipes*) did not rise following control of foxes. Other evidence comes from reintroduction programs where success rates are very much higher where foxes have been managed (Short *et al.* 1992). Diet studies have found native fauna are consumed (eg Norman 1971; Coman 1973a; Croft and Hone 1978; Green and Osborne 1981; Thompson 1983; Triggs *et al.* 1984; Brown and Triggs 1990; Lunney *et al.* 1990; Brunner *et al.* 1991; Palmer 1995), with the inference that foxes could be having a major impact on such species. Circumstantial evidence such as the abundance of ground dwelling mammals in places where foxes do not occur such as Tasmania, Kangaroo Island and the wet tropics (Johnson *et al.* 1989) and major changes in the distribution of prey species in the presence of foxes (Saunders *et al.* 1995) further implicate foxes. Recent studies (Gresser 1996; Banks 1997) have found prey species to alter their foraging behaviour in the presence of foxes, indicating a cost to prey species associated with fox presence in addition to direct predation. Competition between foxes and native species may also be an issue but is poorly understood. The rise in numbers of western quolls (*Dasyurus geoffroii*) where foxes have been managed (Morris *et al.* 1998) may be due to competition rather than direct predation.

### *1.2.2 Agricultural impacts of foxes*

The fox is perceived as a serious threat to agricultural productivity, although there is an absence of conclusive data on fox damage and the costs and benefits of management (Saunders *et al.* 1995). While most studies of impacts of foxes on sheep production usually conclude foxes take only a small percentage of lambs (McFarlane 1964; Alexander *et al.* 1967; Dennis 1969; Rowley 1970; Greentree *et al.* 2000), evidence exists that foxes may be significant predators of lambs (Lugton 1993b). Other livestock affected by fox predation include poultry, commercially farmed emus and ostriches and newborn goat kids, but the level of loss is not considered to be of economic significance (Saunders *et al.* 1995).

### *1.2.3 Rabies*

The red fox is very susceptible to rabies (Macdonald 1980), and in Europe it is thought that, without the fox, rabies could not be maintained in other wild species (Lloyd 1980). Australia is presently free of rabies, and has quarantine and contingency policies in place to avoid it becoming established (O'Brien and Berry 1992; Saunders *et al.* 1995). While eradicating a rabies outbreak from domestic animals in Australia would be relatively straightforward, this would not be the case if rabies became established in Australian wildlife (O'Brien 1992). A variety of potential hosts of rabies are present in Australia, such as feral cats (*Felis catus*), flying foxes (*Pteropus* species) and brushtail possums (*Trichosurus vulpecula*), but canid species (foxes, domestic and wild dogs and dingoes) are considered the most likely vectors of the virus (Newsome and Catling 1992). Oral vaccination is a current practice for treating rabies epidemics in countries where the disease is endemic including France, Germany, Belgium, Switzerland, Luxembourg, Italy, Austria and Canada (Voigt and Johnston 1992), while other methods rely on reducing fox density by methods including poison baiting, trapping, gassing of dens and hunting (Macdonald 1980).

### *1.2.4 Positive effects of foxes*

The sole positive economic impact of foxes has been the supply of fox pelts. However overseas demand for fox pelts fluctuates widely and their value has been very low since the first half of the 1980s, resulting in a decline in harvesting for pelts in Australia (Ramsay 1994). There is no evidence that commercial harvesting of foxes for pelts significantly reduces fox impact (Saunders *et al.* 1995), although this remains untested. Given the current slump in economic returns from commercial harvesting and the apparent lack of benefit in terms of damage reduction, any threats to this industry as a result of more effective fox management are not a major economic consideration.

### *1.2.5 Methods of control*

Current fox management strategies in Australia rely on lethal control or exclusion. Methods include poisoning with sodium monofluoroacetate (1080), strychnine or cyanide, shooting, trapping, exclusion fencing and fumigation of dens using chloropicrin or phosphine gas (Saunders *et al.* 1995). Historically, bounties have been used as an incentive to manage foxes, but these were ineffective at controlling foxes (Saunders *et al.* 1995). Recreational hunting practices in addition to shooting are also used in Australia, including the English tradition of riding with hounds (Macdonald and Johnson 1996), battues (fox drives) in which unarmed beaters drive foxes into a waiting line of guns, and use of small terrier dogs to flush foxes from dens (Saunders *et al.* 1995). Trapping can be inefficient (Kay *et al.* 2000), and factors such as season and position of traps in relation to home range influence fox trappability (Bubela *et al.* 1998). Poisoning with 1080 has been reported to have a large effect on fox abundance in some studies (Banks 1997; Banks *et al.* 1998; Thomson *et al.* 2000), but elsewhere to have little effect (Molsher 1999; Greentree *et al.* 2000).

It is important that pest management techniques are humane, but this usually relies on subjective assessment (Saunders *et al.* 1995). These authors argue against the use of chloropicrin in den fumigation, the use of steel jawed traps and poisoning using strychnine, but consider shooting by skilled operators, use of treadle snare traps and poisoning using cyanide or 1080 acceptable (Saunders *et al.* 1995). Fleming *et al*. (1998, Appendix 1) recommend the use of Victor Softcatch™ leghold traps (Woodstream Corporation) over other traps as being at least as effective and more humane. Whether animals suffer from 1080 poisoning is debatable. Symptoms of poisoning such as manic running, yelping and convulsing appear distressing but, as these symptoms have been found to occur even in anaesthetised, unconscious dogs, they do not necessarily indicate suffering (Marks *et al.* 2000). Foxes are particularly sensitive to 1080 poisoning (McIlroy and King 1990), and, in Western Australia where 1080 naturally occurs in vegetation (*Gastrolobium* species), native species are relatively tolerant to it (King *et al.* 1981; Morris *et al.* 1998). The quantity of 1080 used to manage foxes has been rapidly increasing in recent years, at least in part due to increasing public perception that foxes are a serious threat to agricultural productivity (Thompson *et al.* 1991), and the view is strongly held that 1080 is the most suitable poison currently available for widespread fox management (Saunders *et al.* 1995).

As an alternative to lethal control, fertility control is being considered for the fox (Tyndale-Biscoe 1994; Newsome 1995; Bradley *et al.* 1997; McIlroy and Saunders 1998) as well as other species including white-tailed deer (*Odocoileus virginianus*) (Seagle and Close 1996; Rudolph *et al.* 2000) and other ungulates (Boone and Wiegert 1994; Hobbs *et al.* 2000), rabbits (Twigg *et al.* 2000), feral horses (*Equus caballus*) (Garrott 1991), badgers (*Meles meles*) (Swinton *et al.* 1997; White *et al.* 1997) and the house mouse (*Mus domesticus*) (Chambers *et al.* 1997; Jackson *et al.* 1998). Public perception is increasingly favouring fertility control over lethal control, largely based on the beliefs that methods currently in use are inhumane, or that killing animals is immoral (Bomford 1990).

Caughley *et al*. (1992) recommend a knowledge of the social structure and mating systems of species considered for fertility control. In the theoretical situation where the breeding of a dominant female suppresses breeding in subordinate females in her group, sterilisation of the dominant female may in fact promote breeding in subordinates unless a high proportion of these are also sterilised (Caughley *et al.* 1992). The social structure of foxes differs under different environmental conditions (Voigt and Macdonald 1984), and can take the form of a dominant vixen who suppresses breeding in subordinates (Macdonald 1979). How common such social systems are among foxes in Australia is unclear. It is generally believed foxes occur in breeding pairs in Australia (Saunders *et al.* 1995; Marlow *et al.* 2000), although social groups have been observed in subalpine areas (Bubela 1995). Marlow *et al*. (2000) comment that, in higher rainfall areas of Australia where fox densities are higher, there may be a greater incidence of more complex dominance hierarchies. It is important then that the social organisation of foxes in Australian environments be more fully investigated, given its implications for the viability of fertility control.

The effectiveness of fertility control for foxes will depend on the balance between survival rates and the productivity of the remaining fertile animals (Pech *et al.* 1997). In a modelling project to predict the effectiveness of fertility control delivered by a contraceptive bait and assuming density independent growth, Pech *et al*. (1997) were hampered by a lack of information on the effects of environmental variability on survival and fecundity, this potentially having a great influence on the outcome. Macdonald and Johnson (1996) modelled the effects on population size of differing levels of mortality and fertility, allowing for density dependent effects. Their models showed populations to be more sensitive to the effects of mortality when the proportion of fertile animals was low or when litter sizes were smaller (Macdonald and Johnson 1996). Hone (1999b) predicted 65% of foxes would need to be sterilised, harvested or killed to stop population growth following a control program, assuming no compensatory changes in the rate of increase in response to control. Any compensatory changes in survival (Nichols *et al.* 1984) would undermine the effectiveness of fertility control, so this prediction is the minimum proportion that need to be controlled (Hone 1999b). Saunders and Choquenot (1995) modelled how compensatory changes in the proportion of one year-old vixens breeding, adult survival and juvenile survival would mitigate reductions in rate of increase due to sterilisation of 60-70% of vixens. In the absence of suitable data from Australia, their models were based on North American data. Their results suggest that, while compensatory changes would reduce the effects of imposed sterility, these changes would need to be very substantial to completely negate the effects of sterility (Saunders and Choquenot 1995). To predict the effects of fertility control on fox abundance, further investigation of the potential for compensatory changes is needed.

## 1.3 ASSOCIATED PROJECTS ON FOX ECOLOGY

### *1.3.1 Vertebrate Biocontrol CRC Parent Project*

In 1992 the Vertebrate Biocontrol Cooperative Research Centre was established to investigate virally-vectored or bait-delivered fertility control as a means of reducing or eliminating pest mammals in Australia (Tyndale-Biscoe 1994b). This research is focused on the rabbit, the fox and the mouse, with subprograms on reproduction, virology, immunobiology and ecology for each species (Vertebrate Biocontrol CRC 1995). Within the ecological subprogram for the fox were the following field-based projects (Vertebrate Biocontrol CRC 1995):

1. Fox population dynamics and social structure (Western Australia)
2. Social behaviour in captive and free-ranging red foxes (New South Wales/ACT)
3. Control and ecology of the red fox (Western Australia)
4. The effect of a high level of imposed sterility on the population dynamics of foxes (New South Wales)
5. Predator-prey studies (New South Wales)

The present study is nested within the fourth of these projects, *ie* the effects of imposed sterility on fox population dynamics. Some detail on the CRC sterility project will now be given to set the present study in context. The sterility project aimed to determine whether critical differences occur in social behaviour and age-specific survival of sterile and fertile vixens that may affect the rate of increase of fox populations. Initially, the study intended to determine whether a high level of sterility of vixens was sufficient to maintain fox populations at greatly reduced densities. Analogous experiments were designed for rabbits (Williams and Twigg 1996; Twigg and Williams 1999; Twigg *et al.* 2000) and mice (Chambers *et al.* 1997; Chambers *et al.* 1999). For the fox, this was to be achieved by surgically sterilising a high proportion of the vixens in the populations, then removing other foxes from the population by selective shooting. Buffer zones around the sites were intended to prevent movement into the experimental areas. The rate at which the population recovered would then be monitored. However this proved not to be feasible, and the project was modified to determine whether critical differences occur in the survival and territorial behaviour of sterile compared to fertile vixens.

The key questions in the revised CRC project were:

- Do breeding vixens allow other breeding vixens access to the resources of their breeding-season territories?
- Do sterilised vixens maintain territories during the breeding season and, if so, do they allow breeding vixens access to the resources of these territories?
- What proportion of vixens are barren?
- What is the age-specific survival of sterilised and fertile females?

The experimental design involved four study areas, two including sterilised foxes (“Mudgee” and “Molong”) and two with intact populations (“Mumbil” and “Murringo”), aiming at minimum sample sizes of radio-collared individuals of 10 fertile vixens and 10 males at each site plus 15 sterilised vixens at the two treated sites. Radio-tracking from June until December at each site provided data for the first two questions, while the latter two relied on shot samples of foxes off-site.

The present study was conducted at the Murringo site (an experimental control site) and incorporated the necessary data collection for the CRC sterility experiment as well as additional information on the ecology of the red fox in the absence of management.

### *1.3.2 NSW Agriculture fox predation project*

A NSW Agriculture project entitled “Fox predation: impact and management on agricultural land and associated remnant habitats” was also conducted in synchrony with the present project. The predation project aimed to measure the impacts of foxes on lamb production, rabbit populations and native species, as well as develop improved guidelines for fox control that optimise economic returns to landholders. The project was a replicated experiment involving three strategies of fox control: no control, 1080 baiting annually at lambing time, and intensive control three times during the year. The two sites at which no fox control was conducted were within the Murringo site. An overview of the site, experimental treatments and results are given by Greentree *et al*. (2000).

## 1.4 AIMS OF THE THESIS

In the preceding sections of this introduction I presented a broad overview of fox ecology as understood from studies from a number of continents. I then outlined conservation and production costs associated with the red fox in Australia, and ways in which foxes have been managed. I then set the present study in the context of a large-scale field experiment into the effects of imposed sterility on free-ranging foxes, testing outcomes of managing foxes using fertility control. The next section will describe the Murringo study area, where data for this project were collected on a fox population not subject to management.

## 1.5 STUDY AREA

The study was conducted on the properties of "Templemore" and "Spring Valley" near Murringo, New South Wales (34°15' S, 148°30' E) and encompassed an area of approximately 30 $km^2$. The site is midway between the towns of Boorowa and Young, on the southwest slopes of the Great Dividing Range. Agricultural land for approximately 150 years, the area supported a dairy farming industry in the 1800s (Kevin Gruber, personal communication). Currently the main agricultural enterprises are merino wool, prime lamb and beef cattle production and winter cereal cropping. Lambing takes place annually in August on both "Spring Valley" and "Templemore", with an additional lambing period in March on "Spring Valley". During the study a large intensive piggery was constructed within the study area.

### *1.5.1 Topography*

The topography of the study site is undulating to hilly, with an elevation of 400 m in the valley floor and a maximum elevation of 680 m in surrounding hills. The main watercourse running through the valley was Top Creek, a tributary of Murringo Creek. The site sits atop a granite intrusion and soils are typically red and yellow podzolics (NSW Soil Conservation Service). A major granite outcrop, the Illunie Range, runs along the western boundary of the study area, and includes Dananbilla Nature Reserve.

### *1.5.2 Climate*

The Young district experiences a wide range of temperatures, with hot summers to a maximum of 43 ºC and cold winters to a minimum of –7 ºC. Mean January temperatures for Young range from 30.4 ºC to 13.7 ºC, while in July the mean range is 12.4 ºC to 0.7 ºC (Figure 1.1). Frosts are common from April through to October, with 75 potential frost days each year. Rainfall is slightly seasonal, with a slight winter-spring dominance, with an annual average of 654 mm at Young, the nearest weather station based on 120 years of data (Figure 1.2) (Bureau of Meteorology 1998). Rainfall patterns throughout the study are shown in Figures 1.2 and 1.3 (Bureau of Meteorology 1998).

Rainfall during the study is presented as a cumulative deficiency plot in Figure 1.3. The most significant features of the plot are the trend and the steepness of the curve, while the space between the curve and the zero line has no particular significance (Foley 1957). For example an upward trend over a number of months indicates a period of below average rainfall, the steepness indicating the rate of this rise (Foley 1957). Rainfall was considerably below average for much of the study (Figure 1.3), with the area under drought declaration over the periods 1/7/94 – 30/9/95, 1/5/96 – 31/8/96 and again from 1/5/97 – 30/9/97. Above average rainfall fell during 1995 (Figure 1.3). During periods of drought Top Creek, the main watercourse draining the valley, was reduced to a series of pools but never totally dried.

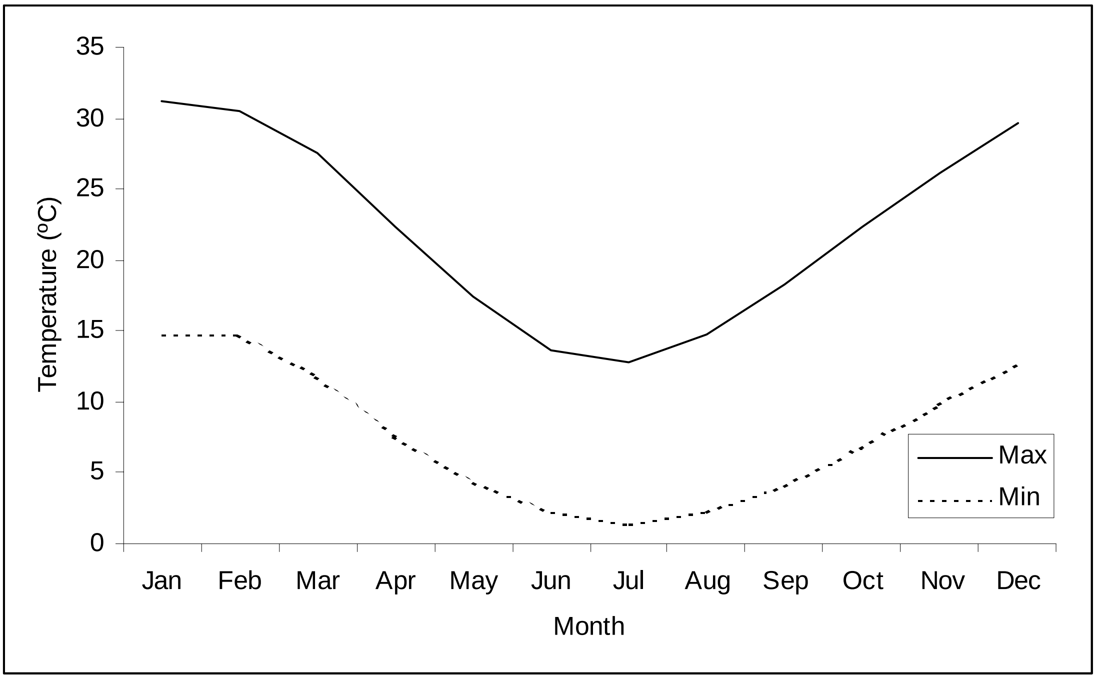


Figure 1.1. Mean daily maximum and minimum temperatures (°C). Data shown are Bureau of Meteorology temperature records for Young, 1871 – 1991.

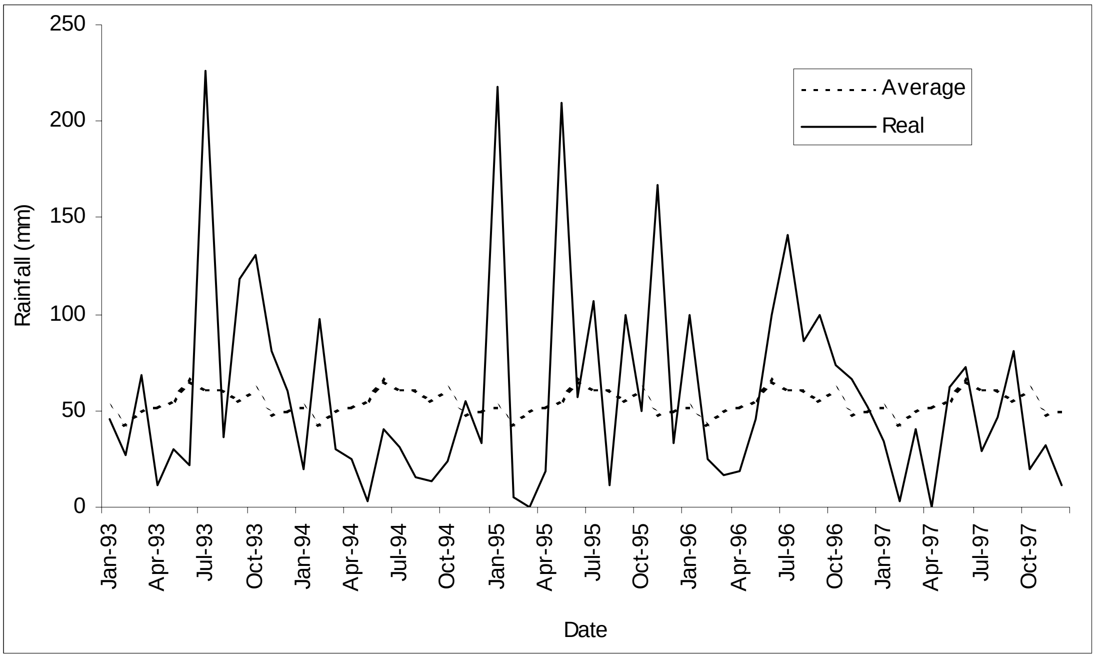


Figure 1.2. Average monthly rainfall and observed monthly rainfall prior to and during the study. Data are from the Bureau of Meteorology weather station at Young, with monthly averages based on records from 1871 – 1991.

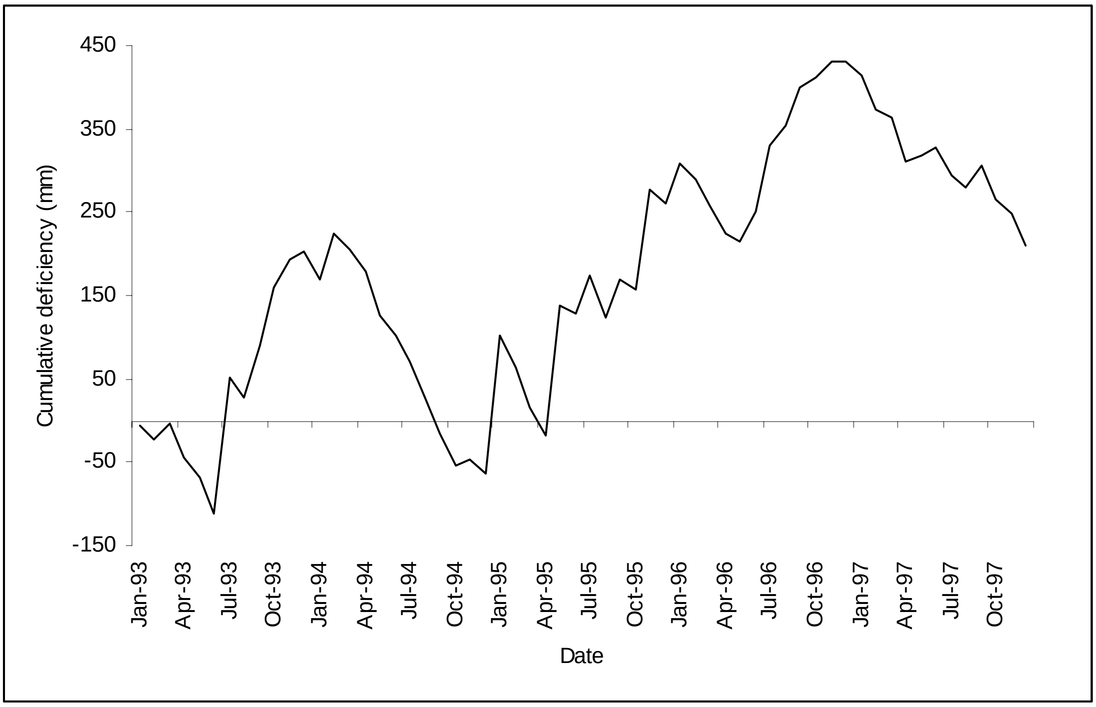


Figure 1.3. Cumulative rainfall deficiency plot (Foley 1957) for rainfall from January 1993 until completion of the study. Periods of above average rainfall are depicted by a decreasing curve, and below average by a rising curve. Data are from the Bureau of Meteorology weather station at Young.

### *1.5.3 Vegetation*

The area is largely cleared of native vegetation, and pastures are improved with legume and *Phalaris* species. Scattered remnant trees remaining in paddocks include Blakely's red gum (*Eucalyptus blakelyi*), yellow box (*Eucalyptus melliodora*) and grey box (*Eucalyptus microcarpa*). Tree cover on the Illunie Range (Dananbilla Nature Reserve) along the west of the site is predominantly white cypress (*Callitris glauca*), grey box (*Eucalyptus microcarpa*), the occasional ironbark (*Eucalyptus sideroxylon*) and *Acacia* species. On the valley floor the creeks are sandy and lined with red gums (*Eucalyptus blakelyi*) and the occasional introduced willow (*Salix* spp.).

### *1.5.4 Mammalian fauna*

Native mammal species common in the area are the eastern grey kangaroo (*Macropus giganteus*), swamp wallaby (*Wallabia bicolor*) and common brushtail possum. Occasionally sighted are the sugar glider (*Petaurus breviceps*), short-beaked echidna (*Tachyglossus aculeatus*) and brown antechinus (*Antechinus stuartii*), while records exist of the common wallaroo (*Macropus robustus*) and common wombat (*Vombatus ursinus*).

Rabbits occur in scattered patches at low density throughout the area. Hares (*Lepus capensis*), feral cats and mice are common, and there are reports of feral goat (*Capra hircus*) and feral pig (*Sus scrofa*) presence in Dananbilla Nature Reserve to the west of the site.

### *1.5.5 Why the site was selected*

The site was selected because of a history of no fox management, and property owners who were willing to continue withholding from shooting or poisoning for the duration of the study. Rabbits are uncommon in the area, so rabbit management was also rare. The site was also selected to take advantage of a concurrent study into the impacts of fox predation on lambing at that site. Fieldwork was carried out between June 1994 and August 1997.

# CHAPTER 2

# HOME RANGE AND MOVEMENTS

## 2.1 INTRODUCTION

The red fox is one of the most widely distributed wild canid species in the world, occurring on four of the six continents (Henry 1986). Ranging behaviour of the red fox has been studied in a wide variety of habitats from tundra to desert to urban, with range sizes varying from 30-1600 ha (Saunders *et al*. 1995), the greatest variation in range size among the Carnivora (Macdonald 1981). Even within relatively similar habitats there is considerable variation. In general, foxes have larger home ranges in more variable environments compared to stable ones, and in habitats of low food diversity compared with species-rich habitats (Voigt and Macdonald 1984). Similarly, fox ranges tend to be smaller at high population densities than at lower densities (Harris 1980). This trend of smaller range sizes at higher population densities is not restricted to foxes, with pigs, for example, also exhibiting this relationship (Saunders and McLeod 1999).

Studies of fox ranging behaviour are limited in Australia. Sizes of home ranges vary from 10.1 km$^2$ in alpine NSW (Bubela 1995) to 0.4-0.9 km$^2$ in urban fringe in Victoria (Coman *et al.* 1991). The most similar habitat to the present study was agricultural land in central Victoria, where range size was estimated to be 3.7-6.1 km$^2$ (Coman *et al.* 1991). Some difficulty exists in directly comparing results of home range studies as methods and assumptions used in defining home ranges vary widely, affecting the estimated size (Harris *et al.* 1990). However these results do indicate great variation in ranging behaviour of foxes in Australia.

### *2.1.1 Defining a home range*

A commonly accepted definition of home range is “that area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt 1943). It is important when describing the home range of an animal, that “normal” movements be distinguished from other movements. Radio-telemetry is the most widely used sampling technique for collecting locations of an animal within its home range, with sampling regimes dependent on the objectives of the study (Worton 1995a). The function describing the probability of finding the animal at a particular location is known as the utilisation distribution, and contours can be drawn around this to show degree of usage by the individual (Anderson 1982). Normal movements can then be defined objectively, albeit arbitrarily, as those within a specified contour (eg 95%) (Anderson 1982; White and Garrott 1990; Worton 1995b). The home range of an animal can shift during its lifetime, so studies of home range need to specify the timeframe over which the range is being defined. Within this time period, the data collected need to be representative of the animal's movements.

If locations of the animal are collected too close together in time they may not be statistically independent (autocorrelated), as the animal may not have had sufficient time to move to any other point within its range. A considerable debate has emerged over the issue of independence of observations. Methods for establishing time to independence have been proposed (eg Dunn and Gipson 1977; Swihart and Slade 1985; Legendre 1993), but often such methods involve discarding locations until spatial independence is attained, thereby losing expensive and potentially significant information. Evidence has been published that autocorrelated data do not necessarily bias estimates of home range of mobile species, particularly if collected sequentially at short intervals, and that time to independence can overestimate the sampling interval for highly mobile species (Andersen and Rongstad 1989; Reynolds and Laundre 1990). One estimate of the time to independence using the methods of Swihart and Slade (1985) for urban foxes in Bristol was 120 minutes (Harris *et al.* 1990). However operating at such a large sampling interval is both impractical in many cases, and can also overlook biologically relevant movements in the intervening periods such as interactions between individuals, distance travelled or activity patterns. Reynolds and Tapper (1995) argue that if data are aiming to delineate territory rather than study habitat use, independence between successive fixes is not important. De Solla *et al.* (1999) found accuracy and precision of home range estimates improved at shorter time intervals despite the increase in autocorrelation.

### *2.1.2 Area estimation*

A number of estimators are available for calculating home range, each with its own assumptions, advantages and disadvantages. Boulanger and White (1990) evaluated five of the most widely used home range estimators using Monte-Carlo simulations. These were minimum convex polygon (MCP) (Mohr 1947), harmonic mean method (Dixon and Chapman 1980), Fourier series (Anderson 1982), bivariate normal model 95% ellipse estimator (Jennrich and Turner 1969), and modified bivariate normal model 95% ellipse estimator (Koeppl *et al.* 1975). They concluded that, of these, the harmonic mean method performed best. This evaluation was later extended to include 95% contour kernel methods, with the finding that this method gave less biased home range size estimations than the harmonic mean method (Worton 1995b). In this study minimum convex polygon and kernel methods are used, the former because it is the most commonly used estimator and for its simplicity of calculation, and the latter as it is the least biased of the readily available estimators.

Minimum Convex Polygon (MCP) is defined by connecting the outermost locations and measuring the area contained within. In its favour, this method is easily calculated and is unambiguous as to the area enclosed. Being non-parametric there is no requirement for the underlying data to be normally distributed, nor is autocorrelation of data an issue if all data points are included. A major disadvantage is that MCP estimates the total area utilised, not just the area used in normal movements. Moreover the size of the home range estimate increases indefinitely as sample size increases (Jennrich and Turner 1969; Anderson 1982), which requires studies to have similar sample sizes to be directly comparable. The method is strongly biased at small sample sizes, and, being based on the outermost points of the utilisation distribution, it is very sensitive to outliers (Worton 1995a). A further limitation of MCP is that the shape of the home range is constrained to being a convex polygon, which is unlikely to be a reasonable assumption.

To avoid inflation of MCP estimates by outliers, it is common to exclude the outermost fixes by generating a convex polygon inclusive of the 95% innermost fixes. The analysis can be extended to reflect areas of higher usage by drawing concentric polygons at different percentile bands (Worton 1995a). Independence of data points is assumed for this approach (Worton 1995a), and it assumes a single centre of activity.

Kernel density estimation is non-parametric, makes no assumptions such as convexity about the shape of the home range and can show multiple centres of activity (Worton 1989). This method smooths data points to create the utilisation distribution, generating contours linking areas of equal usage. The key to this method is selecting the appropriate smoothing constant, as over-smoothing will result in a loss of detail but under-smoothing gives a fragmented outcome (Worton 1989; Wray *et al.* 1992). This smoothing parameter is best chosen objectively using least-squares cross-validation (Silverman 1986; Worton 1989; Seaman *et al.* 1999). Minor changes to the smoothing parameter can have a large effect on the estimated range size, and it has been suggested the approach is more suited to analysis of range use rather than estimation of range size (Harris *et al.* 1990). It has been found that kernel densities do not require serial independence of observations when estimating home range (De Solla *et al.* 1999). Seaman *et al.* (1999) recommend a minimum of 30 and preferably 50 or more observations per animal. Lack of data points at the tails of the utilisation distribution means it is difficult to predict the precise form of the utilisation distribution, and a small error in estimation of the utilisation distribution will cause a great change in the area enclosed by the outermost contours (Anderson 1982). Estimations at lower percentages such as 50% are much more accurate (Anderson 1982; Worton 1989).

A number of methods of home range analysis have been used to estimate fox ranges in Australia. One study of fox home range in Australia used two methods to estimate home range, firstly the 100% Minimum Convex Polygon, and secondly the Fourier transform method (Anderson 1982) arbitrarily set at the 90% utilisation contour (Coman *et al.* 1991). No attempt was made to measure core ranges at the 50% level given the short sampling period (Coman *et al.* 1991). Fourier transform was also used by Marlow (1992), with 95% contours defining the home range and 50% contours for core areas. Bubela (1995) used kernel analysis, with ranges delineated by the 95% utilisation contour and core areas by the 50% contour, as well as an alternative estimation using 100% MCP. Likewise, Banks (1997) used both 95% utilisation contours (kernel method) and 100% MCP to estimate home ranges but did not define core ranges.

### *2.1.3 Ranging and social behaviour of foxes*

Most studies of space use by foxes assume that they have a home range, and that they are territorial (Voigt and Macdonald 1984; Newsome 1995). However studies have also identified the presence of dispersers and itinerants (Ables 1969b; Macdonald 1980; Zabel and Taggart 1989; Marlow 1992). Foxes are considered to be solitary animals that form monogamous pairs for breeding (Fox 1971; Sargeant 1972; Storm *et al.* 1976; Lloyd 1980; Voigt and Macdonald 1984; Saunders *et al.* 1995), although other social groups of foxes have been described (eg Macdonald 1979; von Schantz 1981; Lindstrom 1986; Bubela 1995). These ranges are thought to be steady, with well-defined borders that do not overlap with neighbouring family groups (Storm 1965; Ables 1969b; Sargeant 1972; Pils and Martin 1978; Voigt and Macdonald 1984). Evidence from studies of movements, encounters between individuals and scent marking suggest that home ranges are in fact territories, that is, they are actively defended (Henry 1979; Macdonald 1979).

Where and why spatial groups arise rather than breeding pairs has been the subject of some attention. Spatial group formation is not essential for reproductive success of the red fox (von Schantz 1984a), and a number of hypotheses have been proposed to explain this phenomenon. Two hypotheses, the Resource Dispersion Hypothesis (Macdonald 1983) and the Constant Territory Size Hypothesis (von Schantz 1984a), relate to how heterogeneously resources are distributed in space and time. The Resource Dispersion Hypothesis (RDH) states that ‘spatial groups may develop when food resources are dispersed such that the smallest economically defensible territory for a pair can also sustain additional individuals’. The Constant Territory Size Hypothesis fits within the RDH, predicting that if food supply fluctuates between years with a shorter period than an average individual’s lifespan, then that individual will maintain a territory of constant size adapted to the point of lowest resource availability. For both hypotheses, while resources in excess of the requirements of the dominant pair are available, spatial groups will form. When resources become scarce, subordinate individuals are evicted. A further hypothesis, the Territory Inheritance

Hypothesis (Lindstrom 1986), proposes dominant pairs allow offspring to remain at home, thereby ensuring the territory is inherited by carriers of their genes. A female offspring's decision to stay or disperse is based on the relative probability of gaining breeding status in the natal versus an unoccupied territory.

### *2.1.4 Dispersal*

Dispersal is usually defined as the process in which an animal moves from its birthplace to another locality (Storm *et al.* 1976). Dispersal has a role in regulating population size and distribution, avoiding inbreeding and disrupting local adaptation (Greenwood 1980). Greenwood (1980) observed that in mammals, males tended to be the dispersing sex, whereas in birds the converse applied. He proposed this related to the animals mating system, with monogamy, the predominant mating system of birds, favouring female dispersal and polygyny, the predominant mating system of mammals, favouring male dispersal. This hypothesis is supported by empirical evidence collated by Johnson and Gaines (1990). In terms of age at which dispersal occurs, it has been proposed that dispersal in mammals is most likely to occur when animals are very young and very old (Morris 1982). This argument proposes that adults may gain benefits, in addition to any benefits the offspring could themselves gain, by forcing the offspring to disperse. However when parents became too old, they benefited, through the gain in inclusive fitness, by dispersing and leaving their range to their offspring. In a review of causal factors of dispersal in birds and mammals it was concluded that dispersal should be a common phenomenon even in stable habitats and even if the survival of dispersers is low (Johnson and Gaines 1990). Temporal and spatial variability in the environment play a major role in determining the optimal dispersal rate, with temporal variation tending to result in increased dispersal and spatial variation in decreased dispersal (Johnson and Gaines 1990).

Dispersal of foxes has been widely studied in Europe and North America, primarily motivated by the role of this behaviour in spreading rabies (Phillips *et al.* 1972; Storm *et al.* 1976; Lloyd 1980; Zimen 1984; Trewhella *et al.* 1988). Dispersal distance has been found to be positively correlated with home range size, and negatively correlated with population density, and it is assumed that in more heterogeneous habitats individuals move greater distances seeking out vacant sites (Trewhella *et al.* 1988).

In a study investigating the major factors influencing cub dispersal, Trewhella and Harris (1988) found the cubs most likely to disperse were small males from large litters, especially those born in sub-optimal areas of low fox density.

Dispersal tends to take place in autumn, and it is widely considered that juvenile males are more likely to disperse than females, and disperse earlier and further (Ables 1975; Storm *et al.* 1976; Lloyd 1980; Saunders *et al.* 1995). However other studies have found no difference between the sexes in dispersal rate or distance (Englund 1980b; Zimen 1984). The trend for males to disperse and females to be philopatric is common to many small-bodied canids including kit foxes (*Vulpes macrotis*), arctic foxes (*Alopex lagopus*), bat-eared foxes (*Otocyon megalotis*) and crab-eating foxes (*Cerdocyon thous*) (Koopman *et al.* 2000). Dispersal distances are usually small, ranging from straight line distances of 2.8-43.5 km for males and 1.8-38.6 km for females (Trewhella *et al.* 1988), although exceptional distances of up to 394 km have been recorded (Ables 1965).

Dispersal studies usually rely upon the recovery of tagged individuals (eg Storm *et al.* 1976; Pils and Martin 1978; Trewhella *et al.* 1988). Such studies record the straight-line distance from point of tagging to place of recovery, usually the point of death. In some cases animals are fitted with radio-transmitters, which allows monitoring of the animals while still alive (eg Storm *et al.* 1976; Zimen 1984; Koopman *et al.* 2000). However all such studies are biased towards recovering animals nearer the point of capture. As dispersing animals move further from their point of capture, the area over which they may be found drastically increases and the probability of location is decreased. A further bias towards recovering animals nearer the point of capture is that they may be recovered before completing their dispersal movement (Ables 1975). This possibility can only be eliminated if movements of the individual can be monitored at its point of recovery (Trewhella *et al.* 1988). Studies of dispersal of red foxes generally only consider movements of animals marked before 6 months of age to avoid the risk that dispersal has already occurred (eg Storm *et al.* 1976; Englund 1980b; Lloyd 1980; Trewhella *et al.* 1988; Coman *et al.* 1991).

Dispersal has been poorly studied in Australia, with one study involving 137 tagged cubs in Victoria (Coman *et al.* 1991), and another involving 6 cubs in semi-arid NSW

(Marlow 1992). As well as its role in disease transmission, an understanding of how many and how far animals are likely to disperse has implications for predicting reinvasion of areas where control programs have been carried out.

This study aimed to establish average range size and spatial arrangement of an unmanipulated fox population, particularly whether differences occurred in ranging behaviour between seasons and sexes, and whether itinerant foxes were present. The study also aimed to estimate the proportion of animals dispersing and the mean distance travelled.

## 2.2 METHODS

### *2.2.1 Animal capture*

Foxes were caught in Victor Softcatch™ leghold traps (Woodstream Corporation) between June 1994 and March 1996 following the method outlined in Kay *et al.* (2000). Animal ethics approval for this project was given by NSW Agriculture (permit no. ORA 93/009). Traps were set at locations bearing evidence of fox presence such as scats, tracks or strong fox odour. A variety of baits were used, including fresh lamb, beef, pork and day old chicks. Traps were also set at popholes in fences and around any carcasses found in paddocks. In some instances scent lures such as urine and synthetic fermented egg were sprayed near the trap. Initially an animal carcass was dragged behind a vehicle past each trap every day, but this was abandoned when trapping success was not noticeably improved by the practice.

Traps were checked at first light each day. Captured animals were subdued using a blanket, then placed in a hessian bag for transport back to the field base. Animals were then anaesthetised with a mixture of ketamine hydrochloride (0.2 mL per 5 kg) and xylazine hydrochloride (0.1 mL per 5 kg) (Pond and O'Gara 1994). Age was estimated according to tooth wear (Harris 1978a), and categorised as <1 year old (“juvenile”), >1 year old (“adult”) and >>1 year old (“old”). Physical dimensions (head-body, pes, tibia, tail, brachium lengths and neck circumference) and weight were recorded, body condition was assessed visually (good, moderate or poor) and any evidence of mange or injury noted. Females were also examined for evidence of pregnancy, lactation or enlarged nipples indicating previous lactation.

All captured animals were fitted with numbered plastic eartags bearing a contact address and phone number in the event of recovery by a member of the public. Fully-grown foxes were fitted with radio-transmitters. Animals were released at point of capture immediately after processing and monitored from a nearby vantage point until they fully recovered from the anaesthetic.

### *2.2.2 Radio-telemetry*

The radio-transmitters were manufactured by Sirtrack™ Ltd and consisted of a two stage transmitter and lithium battery sealed in epoxy resin and attached to a synthetic collar which was fixed around the animal’s neck using bolts. Transmitters had a 15cm plastic coated whip antenna impregnated with chilli powder to deter chewing of the antenna. The signal pulsed 60 times per second on the 151 MHz band (also used by Coman *et al.* 1991; Marlow 1992; Bubela 1995; Banks 1997), with a battery life expectancy of 60 months and a range of approximately 10 km line-of-sight at ground level. The entire radio-collar weighed approximately 140g, and was less than 5% of total body mass of foxes collared. A Telonics Inc. TR-4 receiver was used to detect signals.

Foxes were tracked on foot using a folding 3-element Yagi antenna at least monthly to visually establish state of health. Between July and November this effort was intensified, particularly for female animals, to establish locations of breeding dens and numbers of offspring. Periodically the area surrounding the study area was thoroughly searched for signals of animals that had vanished from the study site. Up to a 10 km radius around the site was searched by listening for signals from any accessible high points. Any detected signals were approached on foot to establish exact whereabouts and whether the fox was still living. Aerial tracking was attempted once following completion of the study, but was unsuccessful at locating any missing animals due to severe radio-interference with signals.

### *2.2.3 Fixed tower telemetry*

Radio-telemetry masts were set up within the site to enable remote tracking of foxes. Remote tracking has the advantages of not disturbing the animal and allowing rapid collection of large numbers of fixes on multiple animals. Paired seven-element Yagi antennas attached to a 6m mast fitted with a compass rose were erected on three hilltops surrounding the study area in a triangular formation (mean distance between towers 4.55 km). For the first tracking session in March 1995 three towers were used, but after this a fourth tower was erected on a lower hill in the centre of the site to improve accuracy of fixes (mean distance from perimeter towers to centre tower 2.66 km). To test alignment of towers, 10 transmitters were located across the study site and bearings from each tower to each transmitter calculated theoretically. Transmitters were located from each tower five times each by three different observers. Observed bearings were subtracted from true bearings for each tower, and mean deflection and standard error of each tower were calculated. Towers were then fine-tuned by the appropriate number of degrees to render a mean of zero, this indicating no bias in reception (White and Garrott 1990). Telemetry sessions were carried out at monthly intervals from June through to December during 1995 and 1996, and aimed to track at least 10 each of males and females.

Telemetry sessions during 1995 relied on taking a bearing in the direction of the strongest signal. This was done by rotating the mast of the antenna to establish the bearings at which the signal faded out. This angle was bisected to give the direction of the animal. In 1996 a null-peak system was adopted. Under this system a null occurs directly towards the animal, with loud signal immediately to either side. This system was found to give a more consistent result, particularly when operators of the towers were inexperienced.

Tracking sessions commenced during the hour before sunset and ran for 6 hours. In Australia, foxes have been reported to be most active during the night (Bubela 1995; Saunders *et al.* 1995; Banks 1997), so foxes were most likely to cover the majority of their ranges during this period. Fixes were taken at hourly intervals for each animal on the list, but when only a limited number of animals had audible signals, fixes were taken at 45 minute or 30 minute intervals. Similar intervals between fixes for foxes have been used by Reynolds and Tapper (1995). Additional tracking sessions during which data was collected around-the-clock for 4 days were carried out during March, July and October 1995, and February and May 1996 to establish fox movements at other times of the day and in other seasons. These seasons aimed to correspond with key phases of fox breeding biology, with spring covering birth and lactation, summer weaning, autumn dispersal and winter mating and gestation (Meia and Weber 1995; Saunders *et al.* 1995; White *et al.* 1995).

To monitor accuracy of individuals and alignment of tracking towers, at least two “dummy” transmitters were located within the area. “Dummy” transmitters were attached to a bottle of saline solution to mimic signal attenuation caused by proximity to the animal’s body (Samuel and Fuller 1994). Identity and locations of these were not revealed to the trackers, and they were usually relocated from day-to-day. Incorporating an anonymous “dummy” transmitter is a common means of testing observer and equipment accuracy (eg Mills and Knowlton 1989; Marlow 1992; Dexter 1995).

### *2.2.4 Analysis of fixed tower data*

The actual bearing to each “dummy” was calculated theoretically, and mean deflection from the correct bearing calculated for each tower for all “dummy” transmitters tracked during each tracking period. This mean indicated magnitude and direction of misalignment of the tower (White and Garrott 1990), and all data collected from each tower were then adjusted within an Excel spreadsheet by the appropriate correction factor. The standard deviation of this calculation showed how consistent readings were. A high standard deviation implied either faulty equipment or user error (White and Garrott 1990), and, where this was unacceptably high (SD>4), data were rejected.

Corrected data were sorted so simultaneous records for each animal were grouped, then loaded into Locate II (Nams 1990). In this program, simultaneous bearings were triangulated and an estimate of the location of each fox calculated using the Maximum Likelihood Estimator procedure, under which all bearings are weighted equally. This procedure works by first estimating the most likely location of the animal, then estimating the deviation of each bearing from the estimated location. An error ellipse (95% confidence area) is then generated based on the bearing standard deviation, the placement of telemetry towers and the number of bearings used. At least three bearings are required for this calculation. Where this was unacceptably large (>500 ha), the fix was discarded. Both fox and “dummy” locations were run through this program.

Fixes on each fox were then loaded into Ranges V (Kenward and Hodder 1996) for home range calculation, with fix resolution entered as the average distance in metres of estimated “dummy” collar locations from their true locations. Fixes collected by tracking on foot were also included. Data for each animal were investigated, and any clear forays (ie a sequence of points in rapid succession on a once-off movement from the regular area) were removed from the data set. To avoid bias by non-independent fixes, if a fox rested in one place for several fixes only the first fix was used (Meia and Weber 1995). This provided the final data set from which home range calculations could be made. The process also highlighted if and when any sudden shifts in the animal’s ranging behaviour occurred. Home range areas were calculated based on 95% Minimum Convex Polygon (MCP) and 95% kernel methods. Core range areas were calculated using 50% MCP and 50% kernels.

Animals were excluded from home range analysis if less than 30 fixes were collected or if they were tracked for less than 3 months. Ranges defined by 95% MCP were then examined using the incremental area analysis option in Ranges V. In this process range size was repeatedly calculated with sequential additions of data points, with the outermost 5% of points from the arithmetic centre excluded in each calculation. A plot of 95% MCP range size against number of points used for calculation was then examined and accepted if range size had ceased to increase with further additions of points. Ranges in which size was still continuing to increase with additional data points were rejected. Seaman *et al*. (1999) recommend a minimum of 30, and preferably 50, fixes in kernel analysis. On this basis kernel range calculations were performed on all data sets with 50 or more fixes, although in winter 1996 ranges were accepted with data sets of 40 or more fixes.

The mean of total fox home range size over the duration of the study was calculated using all data on foxes for which there were sufficient fixes to define a range. Means of total male and female range sizes were also calculated and compared using Students *t*-test. The data set was then divided into three seasons (winter, spring and summer/autumn) for 1995 and 1996 and ranges calculated for each season in each year. A three-way factorial analysis of variance was conducted using SPSS, comparing factors of year, sex and season and their interactions. As there was some negative skew in the data sets, data were transformed to logarithms to base 10 and the same tests repeated. Ranges of subadults from March (time of capture) until November of the same year (when animals were assumed to have reached one year of age) were compared to ranges of mature foxes over the same periods using a Students *t*-test. As larger numbers of fixes tend to result in larger MCP range estimates, regression analyses of MCP area against number of fixes were conducted to test for a relationship.

Range outlines and core area outlines as estimated by the MCP method for each season in 1995 and 1996 were plotted on a map and examined for presence of overlap. Where overlapping individuals were observed in a season, their spatial arrangements in successive seasons were also followed to assess whether overlap was temporary or on an ongoing basis.

### *2.2.5 Dispersal*

Mean distance of dispersal from point of capture was measured by retrieval of tagged animals found dead or killed outside the site. On a smaller scale, where a radio-collared animal shifted home range or the distance from point of capture to eventual home range was more than the average maximum length (span) of a home range, this was also defined as dispersal on the basis that animals would be likely to move up to this distance in regular movements (Storm *et al.* 1976; Englund 1980b; Coman *et al.* 1991). The arithmetic centre (mean of *x* and *y* coordinates of fixes) of the animal’s home range was used to calculate distances.

## 2.3 RESULTS

### 2.3.1 Animal capture and radio-collaring

A total of 83 foxes (41 females, 42 males) were trapped over 3931 trapnights. Of these, 36 were adults (24 females, 12 males), and 47 were juveniles (17 females, 30 males) (Table 2.1). Only one trapped animal, a vixen, was classified as “old” (>>1 year) based on tooth wear. Severe trap injuries resulted in 7 animals being euthanased (2 females, 5 males). As 5 of those euthanased were unweaned cubs, traps ceased to be set where cubs were likely to be caught to avoid unnecessary injuries. Juveniles less than 5 months of age were too small to radio-collar, so were released with eartags only. This was the case for 23 juveniles. Fifty foxes were radio-collared (29 females, 21 males).

Table 2.1. Animals trapped and radio-collared between June 1994 and March 1996 at Murringo. ‘Juvenile’ indicates <1 year old, ‘adult’ indicates >1 year old. One vixen estimated to be ‘old’ (>>1 year old) is included with adults.

| | **Females** | **Males** | **Total** |
|---|---|---|---|
| **Juveniles** | 17 | 30 | 47 |
| **Adults** | 24 | 12 | 36 |
| **Total** | 41 | 42 | 83 |
| **Radio-collared** | 29 (23 adult; 6 juv) | 21 (12 adult; 9 juv) | 50 (35 adult; 15 juv) |
| **Eartag only** | 10 (all juv) | 16 (all juv) | 26 (all juv) |
| **Euthanased** | 2 (1 adult, 1 juv) | 5 (all juv) | 7 (1 adult, 1 juv) |

### 2.3.2 Recaptures

A total of 12 foxes were recaptured, one of these twice. All but 4 of the recaptures were estimated to be 5 months or less of age (2 females, 6 males). Of the adults, 3 were vixens and one was a dog-fox.

### 2.3.3 Morphometrics

Measurements of weight, head length, head-body length and brachium length of adult foxes (12 months or greater in age) are presented in Table 2.2. Head length was significantly larger in males than females ($t$ = 5.01, df = 31, $p<0.0001$), as was brachium ($t$ = 2.79, df = 21, $p<0.05$). There were no significant differences between males and females in measurements of weight (*t* = 2.02, df = 19, p =0.06) or head-body length (*t* = 1.25, df = 19, p = 0.22).

Table 2.2. Weight, head length, combined head-body length and brachium length of foxes captured at 12 months of age or greater. Means and standard errors are shown.

| | **Females (n=24)** | **Males (n=12)** | **Total (n=36)** |
|---|---|---|---|
| **Weight (kg)** | 4.9 ± 0.1 | 5.4 ± 0.2 | 5.1 ± 0.1 |
| **Head (mm)** | 163 ± 1 | 174 ± 2 | 167 ± 1 |
| **Head-body (mm)** | 656 ± 9 | 679 ± 16 | 664 ± 8 |
| **Brachium (mm)** | 376 ± 3 | 392 ± 5 | 381.9 ± 2.8 |

### *2.3.4 Radio-telemetry*

The number of animals tracked during fixed tower tracking sessions ranged from 11 foxes in March 1995 to 28 foxes in May 1996. The number of males tracked in each session ranged from 5 (March 1995) to 13 (May 1996) and number of females ranged from 6 (March 95) to 17 (July 1995). Insufficient data eliminated 17 foxes from further evaluation from the original 50 animals fitted with radio-collars. Of these, 5 died shortly after capture and the signals were lost of a further 12 animals either through emigration from the site or signal failure.

Fix resolution was set at 187 m in Ranges V, this being the average displacement of estimated “dummy” collar locations from their true locations (*n* = 809). Ranges V incorporated a boundary strip of half this value into polygon edges and areas.

Areas of 95% Minimum Convex Polygon (MCP) home ranges were initially examined with incremental additions of fixes to establish whether a maximum size had been reached. Of the 33 animals for which more than 30 fixes were collected over at least a three month period, all reached a plateau in home range size when all fixes were included. Mean and standard error of total range size using 95% MCP was 446.1 ± 69.8 ha, with a mean span of 3179 ± 261m (Table 2.3). Mean core area size, defined by 50% MCP, was found to be 133.4 ± 23.7 ha. The number of fixes used to generate each range varied from 49 to 454, averaging 189, and all animals were tracked for at least 5 months up to a maximum of 36 months. Using the same data set, total mean home range size and standard error defined by 95% kernels was 276.4 ± 36.3 ha, and core area defined by 50% kernels was 59.8 ± 6.1 ha (Table 2.3).

Mean and standard error of total male home range size using 95% MCP was 650.6 ± 148.8 ha, spanning 4045 ± 486 m. Using 95% kernels, male range size was 368.9 ± 77.9 ha (Table 2.3). Core male range size was 189.3 ± 54.2 ha using 50% MCP and 75.3 ± 12.0 ha using 50% kernels. Total female range size was 313.2 ± 45.6 ha with a span of 2617 ± 224 m using 95% MCP and 216.4 ± 26.4 ha using 95% kernels. Core range size for females was 97.0 ± 13.5 ha using 50% MCP and 49.7 ± 5.5 ha using 50% kernels. Total male ranges were significantly larger than female ranges when defined by 95% MCP ($t$ = 2.17, df = 14, $p<0.05$), but no significant differences were found for 95% kernel ranges ($t$ = 1.85, df = 15, p= 0.08). No significant differences were observed between core ranges either using 50% MCP ($t$ = 1.65, df = 14, p= 0.12) or 50% kernels ($t$ = 1.94, df = 17, p= 0.07). Range span was significantly larger for males than females ($t$ = 2.67, df = 17, $p<0.05$) (Table 2.3).

Table 2.3. Mean and standard error of total range sizes (95% MCP and kernel), core range sizes (50% MCP and kernel) (ha) and 95% MCP range span (m) for all foxes, males and females tracked between July 1994 and July 1997. Also shown are the mean and standard errors of the number of months over which animals were tracked and the number of usable fixes collected. Minimum and maximum number of months tracked and fixes collected are shown in brackets.

| | **All foxes (n=33)** | **Males (n=13)** | **Females (n=20)** |
|---|---|---|---|
| **95% MCP (ha)** | 446.1 ± 69.8 | 650.6 ± 148.8 | 313.2 ± 45.6 |
| **95% Kernel (ha)** | 276.4 ± 36.3 | 368.9 ± 77.9 | 216.4 ± 26.4 |
| **50% MCP (ha)** | 133.4 ± 23.7 | 189.3 ± 54.2 | 97.0 ± 13.5 |
| **50% Kernel (ha)** | 59.8 ± 6.1 | 75.3 ± 12.0 | 49.7 ± 5.5 |
| **95% MCP range span** | 3179 ± 261 | 4045 ± 486 | 2617 ± 224 |
| **Months tracked** | 16 ± 1 (5-36) | 16 ± 1 (5-33) | 17 ± 3 (6-36) |
| **Fixes** | 189 ± 19 (49-454) | 186 ± 32 (49-454) | 192 ± 23 (61-395) |

There was considerable disparity in total range sizes, with the smallest measuring 71 ha (90 fixes) and the largest 1927 ha (159 fixes). A frequency distribution of 95% MCP range sizes shows most ranges to fall between 100-600 ha, with the greatest number falling between 200-300 ha (Figure 2.1). Range size was negatively skewed, with six outliers (2 female, 4 male) very much larger than the rest (Figure 2.1). A regression of 95% MCP area against number of fixes used was not significant ($r^2$ = 0.010, p=0.58), indicating range size was not driven by the number of fixes used to define it. The majority of ranges based on 95% kernel estimates fell between 100-400 ha, with two ranges smaller than this (both females) and six above this zone. There was only one extreme outlier (male) (Figure 2.2).

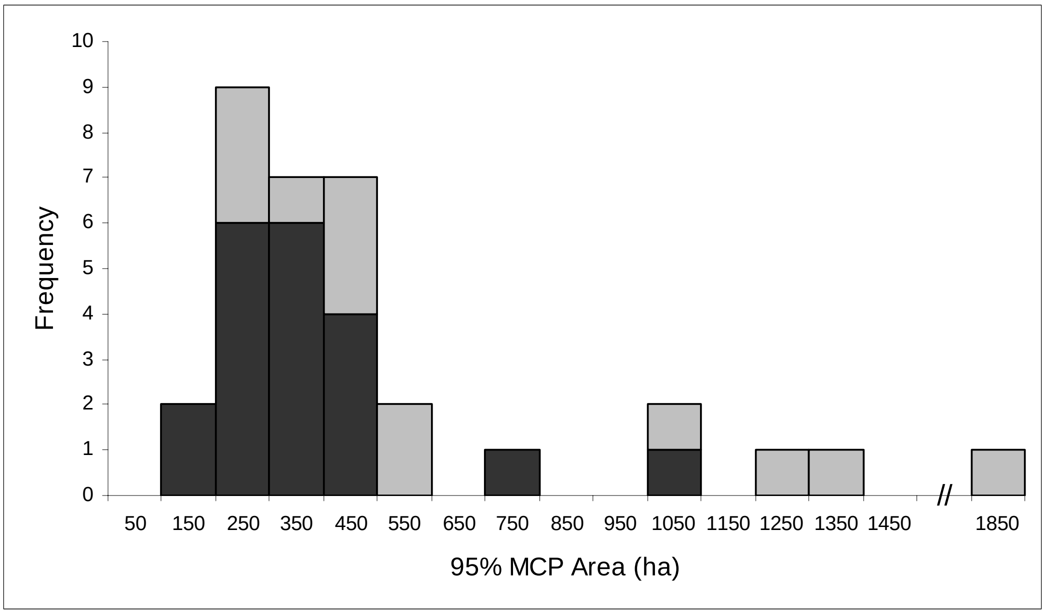


Figure 2.1. Frequency distribution of 95% MCP home range areas (ha) of foxes tracked between July 1994 to July 1997.□ = males, ■ = females. Range sizes shown are the midpoints of each division.

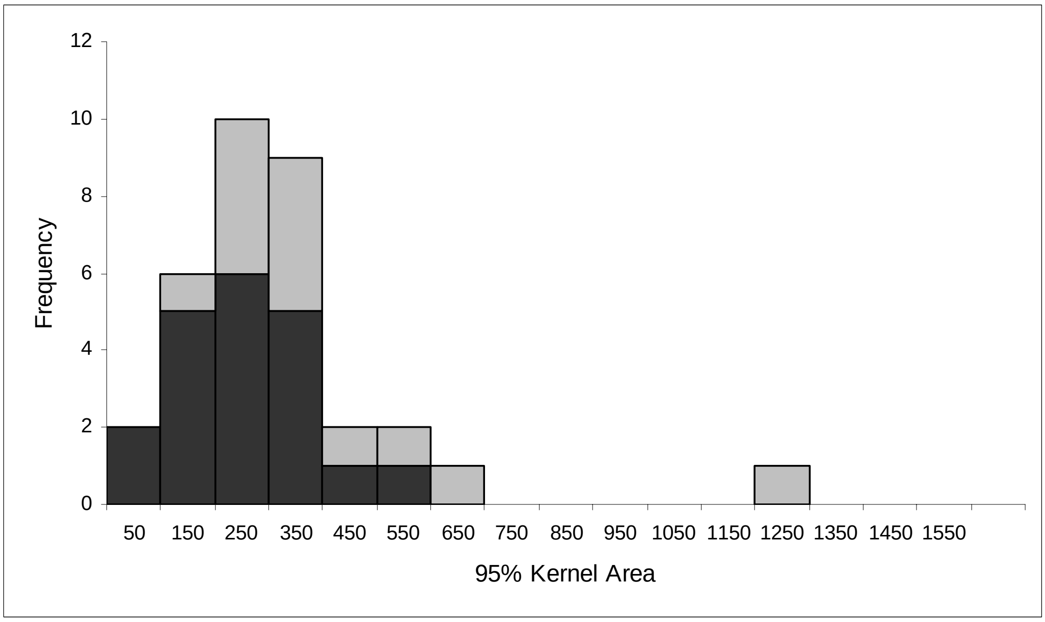


Figure 2.2. Frequency distribution of 95% kernel home range areas (ha) of foxes tracked between July 1994 to July 1997.□ = males, ■ = females. Range sizes shown are the midpoints of each division.

To test for any differences in range size between juveniles and adults, ranges of juveniles from March (when captured) until November of the same year (when assumed to have reached one year of age) were compared with ranges of foxes greater than one year of age over the same period (Table 2.4). No significant differences were detected in home range size using 95% MCP ($t$ = 0.81, df = 3, p= 0.48) or 95% kernels ($t$ = 0.64, df = 5, p= 0.55). Likewise there was no significant difference in core range size either by 50% MCP ($t$ = 1.29, df = 3, p= 0.29) or 50% kernels ($t$ = 0.81, df = 5, p= 0.45). Only a limited number of data sets for juvenile foxes contained sufficient fixes for the range to have stabilised. Adult foxes are more likely to remain in the study area and occupy a steady home range than juveniles ($\chi^2$=7.9, df=1, p<0.05).

Table 2.4. Home range and core range sizes of juvenile and adult foxes tracked from March to November in 1995 and 1996. *n* = number of ranges, fixes = mean and standard error of the number of fixes used to generate ranges.

| **Method** | **Juvenile Foxes** | ***n*** | **Fixes** | **Adult Foxes** | ***n*** | **Fixes** |
|---|---|---|---|---|---|---|
| **95%MCP** | 656.2 ± 348.1 | 4 | 115 ± 24 | 368.8 ± 70.6 | 32 | 113 ± 8 |
| **95%Kernel** | 241.1 ± 54.4 | 5 | 108 ± 20 | 204.8 ± 17.2 | 31 | 117 ± 7 |
| **50%MCP** | 238.3 ± 104.4 | 4 | 115 ± 24 | 101.0 ± 19.3 | 32 | 113 ± 8 |
| **50%Kernel** | 56.3 ± 14.7 | 5 | 108 ± 20 | 44.9 ± 3.4 | 31 | 117 ± 7 |

Home range and core range size estimates for all foxes combined, males and females in summer/autumn, winter and spring in 1995 and 1996 are presented in Table 2.5. Minimum Convex Polygon estimates were only conducted on data sets with sufficient fixes that the MCP area had reached a plateau. Kernel estimates were conducted on data sets with >50 fixes except in winter 1996 when data sets with >40 fixes that showed a plateauing in incremental analysis of 95% MCP were accepted for kernel analysis. Frequency distributions of seasonal 95% MCP home range sizes and 95% kernel range sizes are shown in Figures 2.3 and 2.4 respectively.

Table 2.5. Mean and standard error of home range and core range size estimates (ha) using Minimum convex polygon (MCP) and kernel estimators during combined summer/autumn, winter and spring in 1995 and 1996. *n* = number of ranges in each seasonal sample, fixes = mean and standard error of the number of fixes used to generate ranges.

| | **Method** | **1995** | ***n*** | **Fixes** | **1996** | ***n*** | **Fixes** |
|---|---|---|---|---|---|---|---|
| **Summer/ Autumn** All foxes | 95%MCP | 218.4 ± 42.5 | 7 | 46 ± 5 | 210.1 ± 22.1 | 8 | 54 ± 3 |
| | 95%Kernel | 228.9 ± 46.8 | 5 | 56 ± 2 | 165.7 ± 20.4 | 9 | 61 ± 2 |
| | 50%MCP | 81.2 ± 12.5 | 7 | 46 ± 5 | 70.9 ± 8.5 | 8 | 54 ± 3 |
| | 50%Kernel | 61.3 ± 11.7 | 5 | 56 ± 2 | 41.5 ± 6.2 | 9 | 61 ± 2 |
| Males | 95%MCP | 360.4 ± 79.5 | 2 | 56 ± 4 | 224.7 ± 91.4 | 2 | 43 ± 11 |
| | 95%Kernel | 267.2 ± 73.9 | 3 | 57 ± 3 | 141.9 ± 23.5 | 3 | 61 ± 4 |
| | 50%MCP | 124.4 ± 24.3 | 2 | 56 ± 4 | 41.0 ± 2.8 | 2 | 43 ± 11 |
| | 50%Kernel | 71.0 ± 18.3 | 3 | 57 ± 3 | 31.4 ± 11.0 | 3 | 61 ± 4 |
| Females | 95%MCP | 161.6 ± 18.5 | 5 | 42 ± 6 | 205.2 ± 18.3 | 6 | 57 ± 6 |
| | 95%Kernel | 171.4 ± 5.5 | 2 | 55 ± 3 | 177.6 ± 28.4 | 6 | 62 ± 3 |
| | 50%MCP | 64.5 ± 3.9 | 5 | 42 ± 6 | 80.9 ± 7.3 | 6 | 57 ± 6 |
| | 50%Kernel | 46.7 ± 1.8 | 2 | 55 ± 3 | 46.5 ± 7.2 | 6 | 62 ± 3 |
| **Winter** All foxes | 95%MCP | 257.7 ± 42.1 | 18 | 68 ± 3 | 163.5 ± 14.9 | 15 | 38 ± 1 |
| | 95%Kernel | 136.8 ± 17.7 | 16 | 72 ± 2 | 148.9 ± 28.3 | 7 | 43 ± 1 |
| | 50%MCP | 64.8 ± 7.7 | 18 | 68 ± 3 | 54.9 ± 5.5 | 15 | 38 ± 1 |
| | 50%Kernel | 31.2 ± 5.1 | 16 | 72 ± 2 | 34.2 ± 6.4 | 7 | 43 ± 1 |
| Males | 95%MCP | 385.9 ± 106.9 | 6 | 59 ± 9 | 192.0 ± 27.2 | 5 | 35 ± 3 |
| | 95%Kernel | 174.2 ± 35.1 | 4 | 72 ± 4 | 226.1 ± 21.4 | 2 | 43 ± 1 |
| | 50%MCP | 80.2 ± 17.8 | 6 | 59 ± 9 | 69.8 ± 10.7 | 5 | 35 ± 3 |
| | 50%Kernel | 37.2 ± 13.4 | 4 | 72 ± 4 | 53.7 ± 11.0 | 2 | 43 ± 1 |
| Females | 95%MCP | 193.7 ± 19.5 | 12 | 72 ± 2 | 149.3 ± 17.0 | 10 | 40 ± 1 |
| | 95%Kernel | 124.4 ± 20.1 | 12 | 72 ± 4 | 118.0 ± 28.3 | 5 | 43 ± 1 |
| | 50%MCP | 57.1 ± 7.1 | 12 | 72 ± 2 | 47.4 ± 5.2 | 10 | 40 ± 1 |
| | 50%Kernel | 29.3 ± 5.4 | 12 | 72 ± 4 | 26.4 ± 4.6 | 5 | 43 ± 1 |
| **Spring** All foxes | 95%MCP | 342.5 ± 126.0 | 14 | 89 ± 7 | 185.0 ± 31.8 | 16 | 61 ± 3 |
| | 95%Kernel | 203.9 ± 43.0 | 14 | 85 ± 5 | 153.4 ± 24.8 | 15 | 63 ± 2 |
| | 50%MCP | 103.1 ± 33.3 | 14 | 89 ± 7 | 62.6 ± 5.4 | 16 | 61 ± 3 |
| | 50%Kernel | 45.9 ± 9.0 | 14 | 85 ± 5 | 35.7 ± 4.0 | 15 | 63 ± 2 |
| Males | 95%MCP | 472.4 ± 290.2 | 6 | 84 ± 9 | 246.3 ± 75.2 | 6 | 69 ± 4 |
| | 95%Kernel | 193.9 ± 79.9 | 6 | 84 ± 9 | 185.6 ± 59.9 | 6 | 69 ± 4 |
| | 50%MCP | 136.3 ± 77.3 | 6 | 84 ± 9 | 72.5 ± 6.5 | 6 | 69 ± 4 |
| | 50%Kernel | 39.6 ± 15.9 | 6 | 84 ± 9 | 37.4 ± 8.0 | 6 | 69 ± 4 |
| Females | 95%MCP | 245.1 ± 57.6 | 8 | 79 ± 11 | 148.1 ± 20.2 | 10 | 56 ± 4 |
| | 95%Kernel | 211.4 ± 50.7 | 8 | 86 ± 7 | 132.0 ± 12.6 | 9 | 59 ± 3 |
| | 50%MCP | 78.2 ± 14.2 | 8 | 79 ± 11 | 56.6 ± 7.3 | 10 | 56 ± 4 |
| | 50%Kernel | 50.6 ± 11.1 | 8 | 86 ± 7 | 34.5 ± 4.4 | 9 | 59 ± 3 |

A three-way factorial analysis of variance was conducted to examine differences in range size defined by 95% MCP due to year, sex and season and their interactions (Table 2.6). Ranges of male foxes were significantly larger than those of female foxes but there were no significant differences between years or seasons. No significant interactions were detected between season, sex or year. The data set contained a number of outliers, predominantly males in 1995, causing a degree of negative skew to the data set. A log transformation of the data set reversed this skew but did not alter significance of the outcome, indicating any influence of these outliers was relatively weak.

Table 2.6. Results of 3-factor analysis of variance for home range areas defined by 95% MCP in seasons summer/autumn, winter and spring, sexes males and females and years 1995 and 1996.

| Source of Variation | Sum of Squares | DF | Mean Square | F | Sig of F |
|---|---|---|---|---|---|
| SEASON | 35426.374 | 2 | 17713.187 | .344 | .710 |
| SEX | 244932.210 | 1 | 244932.210 | 4.755 | .033 |
| YEAR | 172441.134 | 1 | 172441.134 | 3.348 | .072 |
| SEASON SEX | 9709.955 | 2 | 4854.978 | .094 | .910 |
| SEASON YEAR | 28025.729 | 2 | 14012.864 | .272 | .763 |
| SEX YEAR | 84735.884 | 1 | 84735.884 | 1.645 | .204 |
| SEASON SEX YEAR | 1342.912 | 2 | 671.456 | .013 | .987 |
| Residual | 3399616.594 | 66 | 51509.342 | | |
| Total | 4117366.298 | 77 | 53472.290 | | |

Core ranges defined by 50% MCP were also examined by three-way factorial analysis of variance for differences due to year, sex and season. No significant differences were found between years, sexes or seasons and no interactions of these factors were detected (Table 2.7)

Table 2.7. Results of 3-factor analysis of variance for core range areas defined by 50% MCP in seasons summer/autumn, winter and spring, sexes males and females and years 1995 and 1996.

| Source of Variation | Sum of Squares | DF | Mean Square | F | Sig of F |
|---|---|---|---|---|---|
| SEASON | 7277.887 | 2 | 3638.943 | 1.089 | .343 |
| SEX | 7852.390 | 1 | 7852.390 | 2.349 | .130 |
| YEAR | 12018.626 | 1 | 12018.626 | 3.596 | .062 |
| SEASON SEX | 1690.886 | 2 | 845.443 | .253 | .777 |
| SEASON YEAR | 3976.960 | 2 | 1988.480 | .595 | .555 |
| SEX YEAR | 8234.712 | 1 | 8234.712 | 2.464 | .121 |
| SEASON SEX YEAR | 5297.033 | 2 | 2648.516 | .792 | .457 |
| Residual | 220604.978 | 66 | 3342.500 | | |
| Total | 265375.365 | 77 | 3446.433 | | |

When the results of ranges defined by 95% kernels were examined by three-way factorial analysis of variance, no significant differences or interactions were found for year, sex or season (Table 2.8). Likewise no differences or interactions were detected between year, sex or season for core ranges defined by 50% kernels (Table 2.9).

Table 2.8. Results of 3-factor analysis of variance for home range areas defined by 95% kernels in seasons summer/autumn, winter and spring, sexes males and females and years 1995 and 1996.

| Source of Variation | Sum of Squares | DF | Mean Square | F | Sig of F |
|---|---|---|---|---|---|
| SEASON | 5070.689 | 2 | 2535.344 | .245 | .784 |
| SEX | 26358.234 | 1 | 26358.234 | 2.543 | .116 |
| YEAR | 11415.881 | 1 | 11415.881 | 1.102 | .298 |
| SEASON SEX | 13773.613 | 2 | 6886.807 | .665 | .518 |
| SEASON YEAR | 12629.386 | 2 | 6314.693 | .609 | .547 |
| SEX YEAR | 105.532 | 1 | 105.532 | .010 | .920 |
| SEASON SEX YEAR | 22375.153 | 2 | 11187.577 | 1.080 | .346 |
| Residual | 611418.757 | 59 | 10363.030 | | |
| Total | 731299.883 | 70 | 10447.141 | | |

Table 2.9. Results of 3-factor analysis of variance for core range areas defined by 50% kernels in seasons summer/autumn, winter and spring, sexes males and females and years 1995 and 1996.

| Source of Variation | Sum of Squares | DF | Mean Square | F | Sig of F |
|---|---|---|---|---|---|
| SEASON | 854.180 | 2 | 427.090 | .821 | .445 |
| SEX | 505.433 | 1 | 505.433 | .971 | .328 |
| YEAR | 740.862 | 1 | 740.862 | 1.424 | .238 |
| SEASON SEX | 1346.817 | 2 | 673.408 | 1.294 | .282 |
| SEASON YEAR | 1311.669 | 2 | 655.834 | 1.260 | .291 |
| SEX YEAR | 63.202 | 1 | 63.202 | .121 | .729 |
| SEASON SEX YEAR | 1653.219 | 2 | 826.610 | 1.588 | .213 |
| Residual | 30704.564 | 59 | 520.418 | | |
| Total | 38103.786 | 70 | 544.340 | | |

### 2.3.5 *Outliers and animals for which ranges could not be defined*

There were a number of individuals for which MCP home ranges showed no signs of plateauing despite in excess of 40 fixes, and sometimes over 100 fixes. Fixes on these individuals were examined visually to see what features of their movements led them not to qualify for home range estimation. Movements of individuals whose range sizes were outliers in overall (Figures 2.1 and 2.2) and seasonal analyses (Figures 2.3 and 2.4) were also examined.

No individuals were excluded from overall home range analysis, as all ranges reached a plateau in size. However six outliers were detected in the overall 95% MCP range analysis (Figure 2.1). Five of the six outliers were animals showing a shift in ranging area, with one juvenile male occupying three different areas of activity before reaching one year of age. Two of these animals were females (both adult) and four were males (2 adult, 2 juvenile when first collared) (Table 2.10). There was no apparent pattern as to when shifts occurred, with shifts in all seasons (Table 2.10). The individual for which no range shift could be detected was an adult male who frequently moved out of range of the tracking towers and made many extended forays which would not all have been removed in the 5% of fixes excluded in 95% MCP analysis. Home ranges defined by 95% kernel analysis had fewer outliers, but the same individuals that were outliers using MCP had the largest home ranges using kernel analysis. Likewise, the individuals with the smallest ranges using kernel analysis also had the smallest ranges using MCP.

Table 2.10. Sex and age of individuals at the time of range shifts

| Tag | Sex | Age | When Shifted |
|---|---|---|---|
| 82 | Female | > 1 year | December 1994 |
| 262 | Female | > 1 year | August 1996 |
| 93 | Male | < 1 year | August 1995 |
| 439 | Male | < 1 year | March 1996 |
| 439 | Male | < 1 year | October 1996 |
| 263 | Male | > 1 year | November 1995 |

In seasonal analyses, of animals rejected from analyses, only the 5 individuals with more than 40 fixes were closely examined, as insufficient data was available for other individuals. Five outliers were also examined. Observations on rejected and outlying foxes are summarised in Table 2.11, as well as the sex and age of these foxes and number of fixes collected. Three general patterns of behaviour were found to underly outliers and individuals rejected from seasonal analyses. These were a range shift during the seasonal period (3 individuals, all outliers), a range with multiple centres of activity (4 individuals, 2 outliers, 2 rejected) or high mobility with many forays (3 individuals, all rejected). Two of the individuals classed as having range shifts were foxes that appeared to settle into a range for the first time during the seasonal period, while the third shifted from one definable range to another. All three were male, two of which were less than one year of age, and range shifts took place in winter or spring (Table 2.11). Individuals with multiple centres of activity were of both sexes, all mature, and this pattern was observed in spring and summer/autumn ranges (Table 2.11). Individuals displaying a high degree of mobility were all mature males, and all occurred in summer/autumn ranges (Table 2.11).

Table 2.11. Sex, age and observations on outliers and foxes rejected from seasonal analyses for which more than 40 fixes were collected.

| **Tag** | **Sex** | **Age** | **Season, Year** | **Rejected/ Outlier** | **Fixes** | **Observations** |
|---|---|---|---|---|---|---|
| 72 | Male | >1 year | summer/ autumn 1995 | rejected | 59 | very mobile |
| 85 | Male | >1 year | summer/ autumn 1995 | outlier | 60 | bimodal range |
| 93 | Male | <1 year | winter 1995 | outlier | 43 | nomadic until Aug 95 |
| 82 | Female | >1 year | spring 1995 | rejected | 78 | bimodal range Nov 95 |
| 262 | Female | >1 year | spring 1995 | outlier | 108 | bimodal range spring 95, poss nomadic |
| 263 | Male | >1 year | spring 1995 | outlier | 88 | nomadic until Nov 95 |
| 90 | Male | >1 year | summer/ autumn 1996 | rejected | 60 | very mobile during Feb 96 |
| 252 | Female | >1 year | summer/ autumn 1996 | rejected | 57 | multiple centres of activity |
| 263 | Male | >1 year | summer/ autumn 1996 | rejected | 69 | many extended forays |
| 439 | Male | <1 year | spring 1996 | outlier | 62 | range shift Oct 96, nomadic. |

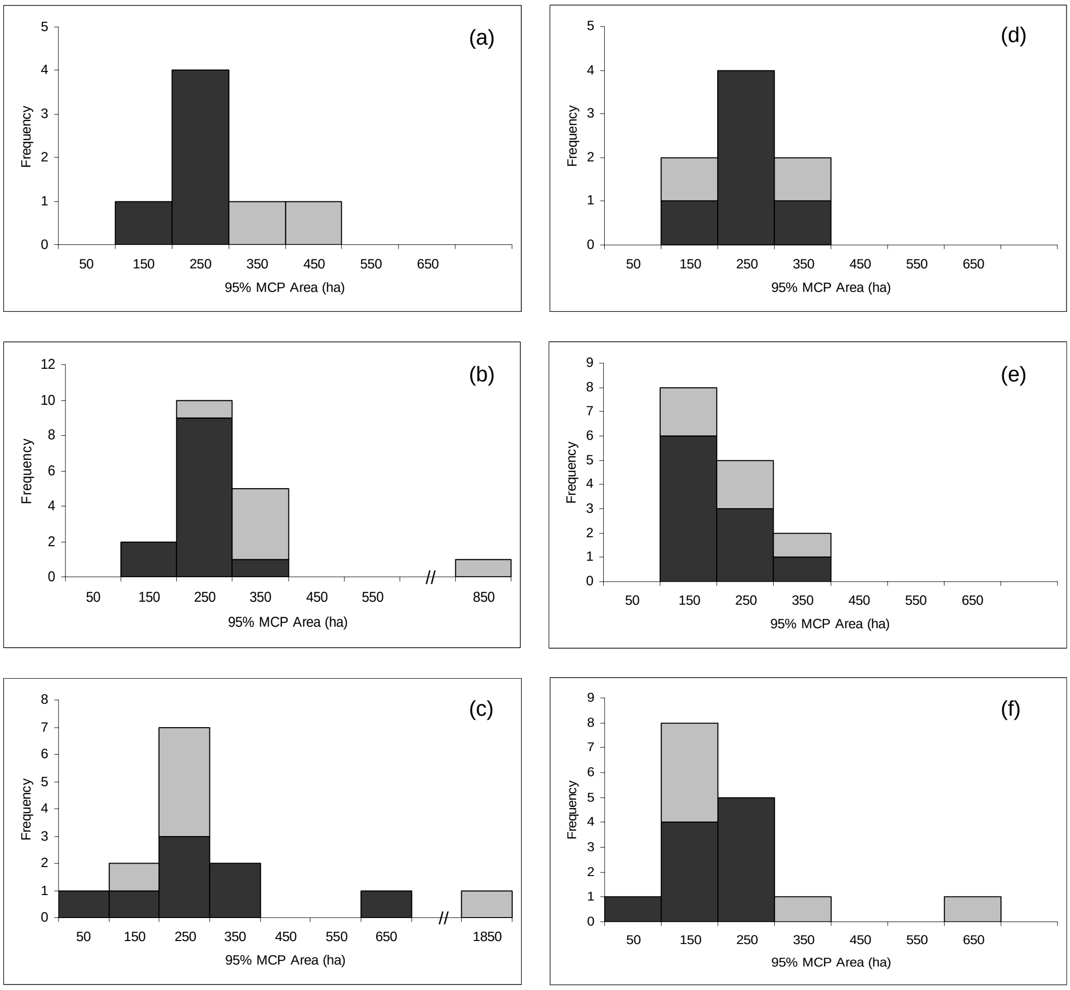


Figure 2.3. Frequency distributions of areas of 95% MCPs for (a) summer/autumn 1995, (b) winter 1995, (c) spring 1995, (d) summer/autumn 1996, (e) winter 1996 and (f) spring 1996 (☐ = males, ■= females). Range sizes shown are the midpoints of each division.

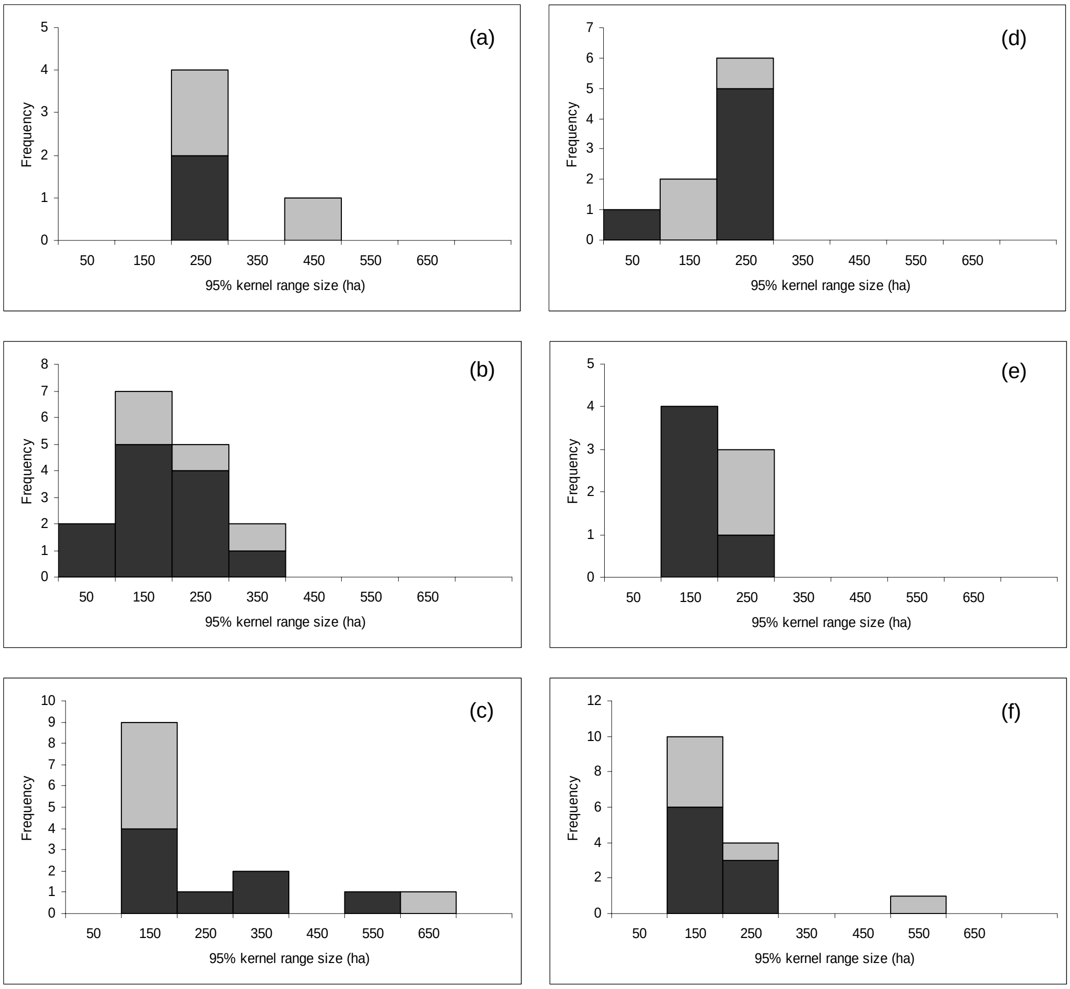


Figure 2.4. Frequency distributions of 95% kernel home range areas for (a) summer/autumn 1995, (b) winter 1995, (c) spring 1995, (d) summer/autumn 1996, (e) winter 1996 and (f) spring 1996 (□ = males, ■ = females). Range sizes shown are the midpoints of each division.

### *2.3.6 Comparison of minimum convex polygon and kernel range estimates*

Home range estimates using kernel methods were almost always smaller than those defined by MCP. In the estimates of total range size (Table 2.3), adult and juvenile range size (Table 2.4) and seasonal range size (Table 2.5), 95% kernel estimates were on average 73% of the size estimated using 95% MCP (n=23), ranging from 37% – 118%, although these differences in size were not necessarily significant. Estimates using 95% kernels were only significantly smaller than 95% MCP estimates for all foxes, all females, adult foxes, all foxes in winter 1995 and female foxes in winter 1995. Core ranges using 50% kernels were on average 54% of the size of ranges using 50% MCP in these same data sets (n=23), ranging from 24% – 77%. Core ranges estimated using kernel methods were significantly smaller than 50% MCP estimates for all but juvenile foxes, male foxes in summer/autumn 1996 and male foxes in winter 1996. Overall home ranges defined by kernel analysis had fewer outliers, but the same individuals with the largest home ranges using MCP had the largest home ranges using kernel analysis in the overall analysis (Figures 2.1 and 2.2). Likewise, the individuals with the smallest overall ranges using kernel analysis also had the smallest ranges using MCP (Figures 2.1 and 2.2).

In seasonal estimates, order of individuals in increasing magnitude of range size was not strictly preserved between kernel and MCP estimates. However, no individuals estimated as outliers under one method were not at a similar end of the spectrum by the other method, with the single exception of one individual in summer/autumn 1996 who was estimated as having an intermediate sized range using MCP but a much smaller range than other foxes using kernels. As with the overall range estimates, there were generally fewer major outliers in seasonal range estimates using kernel methods rather than 95% MCPs (Figures 2.3 and 2.4).

Assessing shapes of the 33 overall 95% kernel ranges, 16 were generally convex with one centre of activity (48%). Thirteen foxes had two core areas (39%) giving ranges a concave shape. These included the 5 individuals who shifted range during the study. A further 4 individuals (12%) were highly fragmented, with 3 core areas and a concave shape. There was a significant relationship between number of centres of activity and the ratio of 95% kernel areas: 95% MCP areas ($r^2$ =0.158, df = 32,

$p<0.05$) and a highly significant relationship between the number of centres of activity and the ratio of 50% kernel areas: 50% MCP areas ($r^2 = 0.332$, df = 32, $p<0.001$).

An example of a fox with two centres of activity and an elongate range is depicted in Figure 2.5. In this instance the range size using 95% kernels was slightly larger than that using 95% MCP (95% kernel 129.8 ha, 95% MCP 119.9 ha), but the core area was much smaller using 50% kernel analysis (50% kernel 29.8 ha, 50% MCP 59.5 ha). The area selected as the centre of activity using MCP was depicted as a corridor between two centres of activity using kernel analysis, with the arithmetic centre falling approximately 500m northeast of the centre of activity using kernel analysis. The core area depicted using 50% MCP contained neither of the two focal points of activity shown by kernel methods (Figure 2.5).

Smoothing constants selected by least-squares cross-validation generally resulted in a unified home range showing some internal detail. However a small proportion of data sets were highly fragmented, indicating under-smoothing, and, similarly, a small proportion were featureless ellipses, indicating oversmoothing. Figure 2.6 shows examples of ranges resulting from oversmoothing (smoothing constant too large) and undersmoothing (smoothing constant too small).

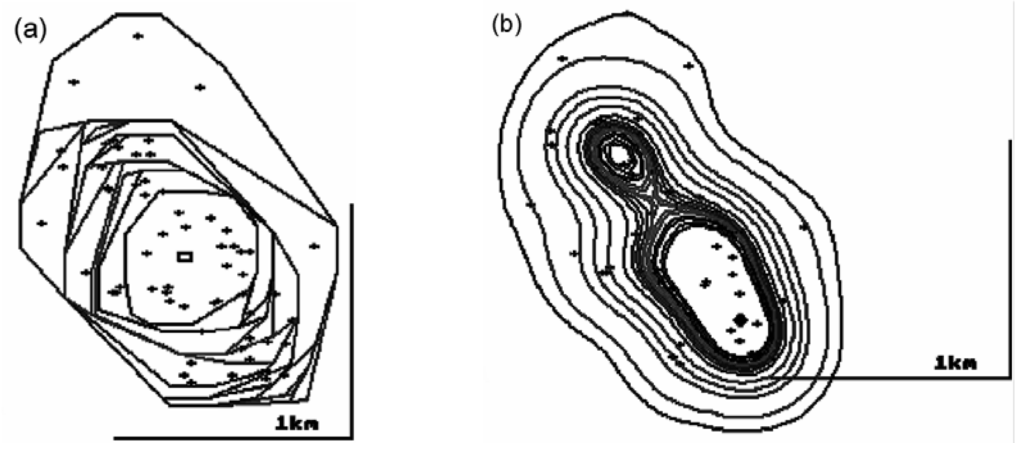


Figure 2.5. Home range of the same individual (tag 432) in spring 1996 using (a) MCP at 5% intervals (95% MCP area = 119.9 ha, 50% MCP area = 59.5 ha) and (b) kernels at 5% intervals (95% kernel area = 129.8 ha, 50% kernel area = 29.8 ha).

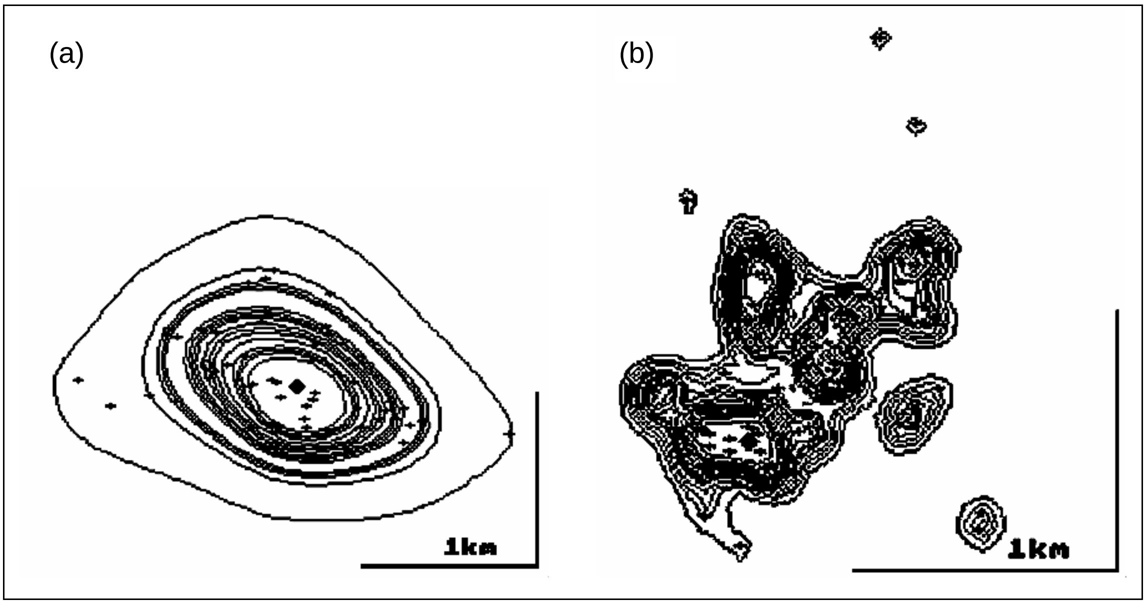


Figure 2.6. Home ranges depicted by kernels at 5% intervals showing (a) oversmoothing of data leading to a featureless ellipse (tag 252, winter 1995, 62 fixes) and (b) undersmoothing of data leading to fragmentation (tag 100, winter 1995, 75 fixes).

### *2.3.7 Overlap of ranges*

Ranges were examined visually for degree of overlap of 95% MCP home ranges and 50% core ranges in summer/autumn, winter and spring of 1995 and 1996 (Figures 2.7 to 2.12). Overlap using kernel defined ranges and core areas was not examined as some ranges were fragmented making interpretation difficult.

In summer/ autumn of 1995 a cluster of two dog foxes and one vixen was observed, with a high degree of overlap of home and core ranges (Figure 2.7). Ranges of two other vixens partially overlapped, but core ranges were distinct. The range of one dog fox largely encompassed the ranges of these two vixens plus a third vixen, but essentially no overlap of core ranges was observed for these individuals (Figure 2.7).

In winter 1995, the cluster of two dogs and a vixen from the previous season now consisted of 5 radio-collared vixens and the two dog foxes (Figure 2.8). Core ranges of the dog foxes and two vixens overlapped fully whereas the remaining three vixens had distinct core ranges within the cluster. To the west of the cluster, another pair of vixens with previously overlapping ranges but distinct cores were now seen to share both home and core ranges. Their shared range tightly abutted ranges of two other vixens but without overlap. Similarly, the home ranges of three dog foxes in the same vicinity tightly abutted each other but did not overlap. One of these males ranged over a very wide area, apparently lacking a steady range. The dog fox whose range had encompassed those of three vixens in summer/autumn 1995 now only overlapped one of the three vixens.

In spring 1995 the main cluster of foxes was still present (Figure 2.9), although one of the vixens with a fully overlapping core had died in the interim. The ranges and cores of the dog foxes still completely overlapped. Core ranges of vixens in the cluster were separate, although the core range of one vixen coincided with the core range of the dog foxes. A juvenile male fox was seen to range across a very large area, including all of the ranges of the main cluster, apparently yet to settle in a steady range. To the west, one of the two vixens with completely overlapping ranges in the previous season died at the start of the season, with the other following suit later in the season. The dog fox and vixen further west still had overlapping ranges, but overlap of core ranges was now very minimal.

There was a high degree of overlap of dog foxes and vixens, both at home range and core levels, in summer/autumn 1996 (Figure 2.10). All previously collared vixens in the main cluster were dead, but the same two males still had overlapping ranges, although overlap of core ranges was less complete. The ranges of two newly collared dog foxes neatly abutted the ranges of the overlapping males, and the unsettled juvenile male from the previous season appeared to be focusing its activity between the core range of one of the new males and the main cluster. A newly collared juvenile male now ranged across much of the east of the site, overlapping the ranges of 5 dog foxes and 5 vixens. While there was much overlap of vixen home ranges, there was only one incidence of overlapping cores, with a juvenile vixen now nested within the range of an established vixen. To the west, some overlap remained between the dog fox and vixen, but core ranges were distinct.

By winter 1996 the original cluster was gone (Figure 2.11), with one of the original two overlapping males now dead. The young male that appeared to be settling near the cluster was now also dead, leaving no collared males with overlapping ranges on the eastern side of the site. The unsettled juvenile male from summer/autumn 1996 had retracted north, and now heavily overlapped both core and range with a mature vixen, also apparently unsettled. Considerable overlap of ranges of four vixens to the south was observed, but core ranges were distinct. The sole collared male overlapping these vixens also had a separate core range. Two dog foxes with overlapping ranges and core areas were observed to the west, one of whom was a juvenile who disappeared soon after. The mature dog had previously overlapped ranges with a vixen, but now no overlap was observed.

A high degree of overlap of the southern group of vixens was still seen in spring 1996, and core ranges remained distinct but abutting (Figure 2.12). No overlap of collared dog foxes was seen, with the single exception of the juvenile nomad who was now focusing his movements further south than in winter. The dog and vixen to the west were once again overlapping, with some degree of core overlap. Essentially no other overlapping cores were observed.

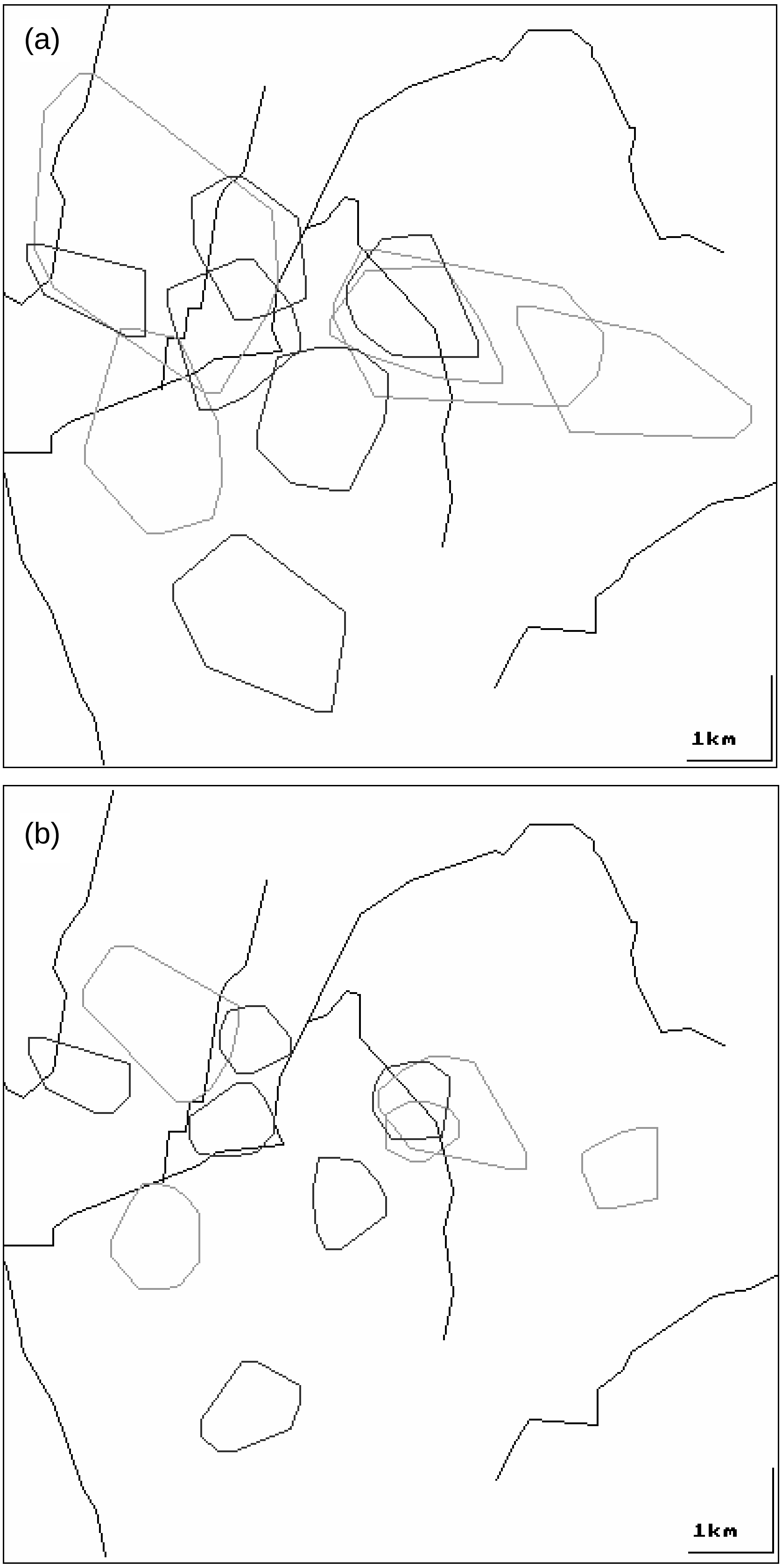


Figure 2.7. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in summer/autumn 1995. Males light grey, females dark grey, backdrop map of roads in study area.

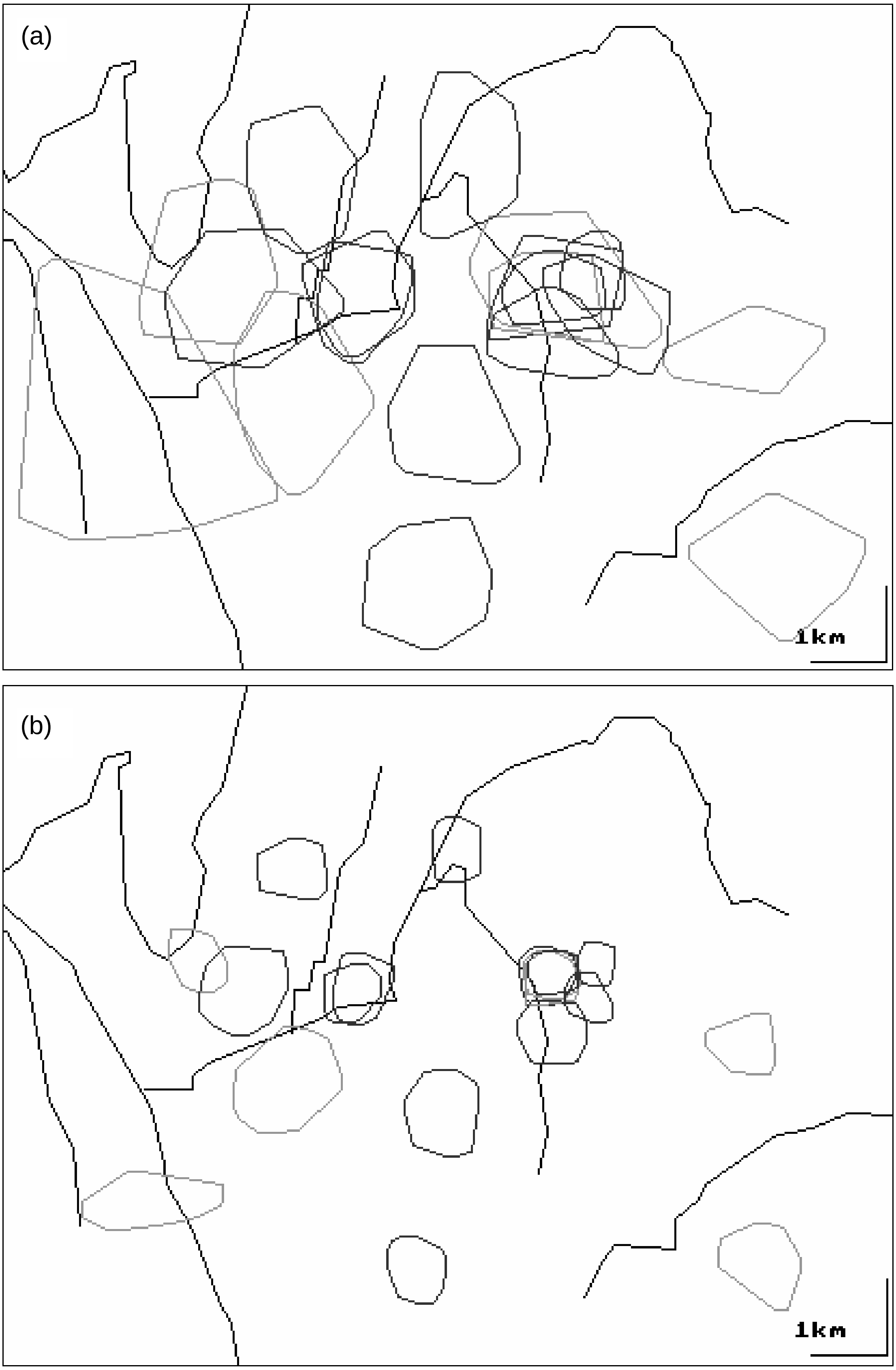


Figure 2.8. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in winter 1995. Males light grey, females dark grey, backdrop map of roads in study area.

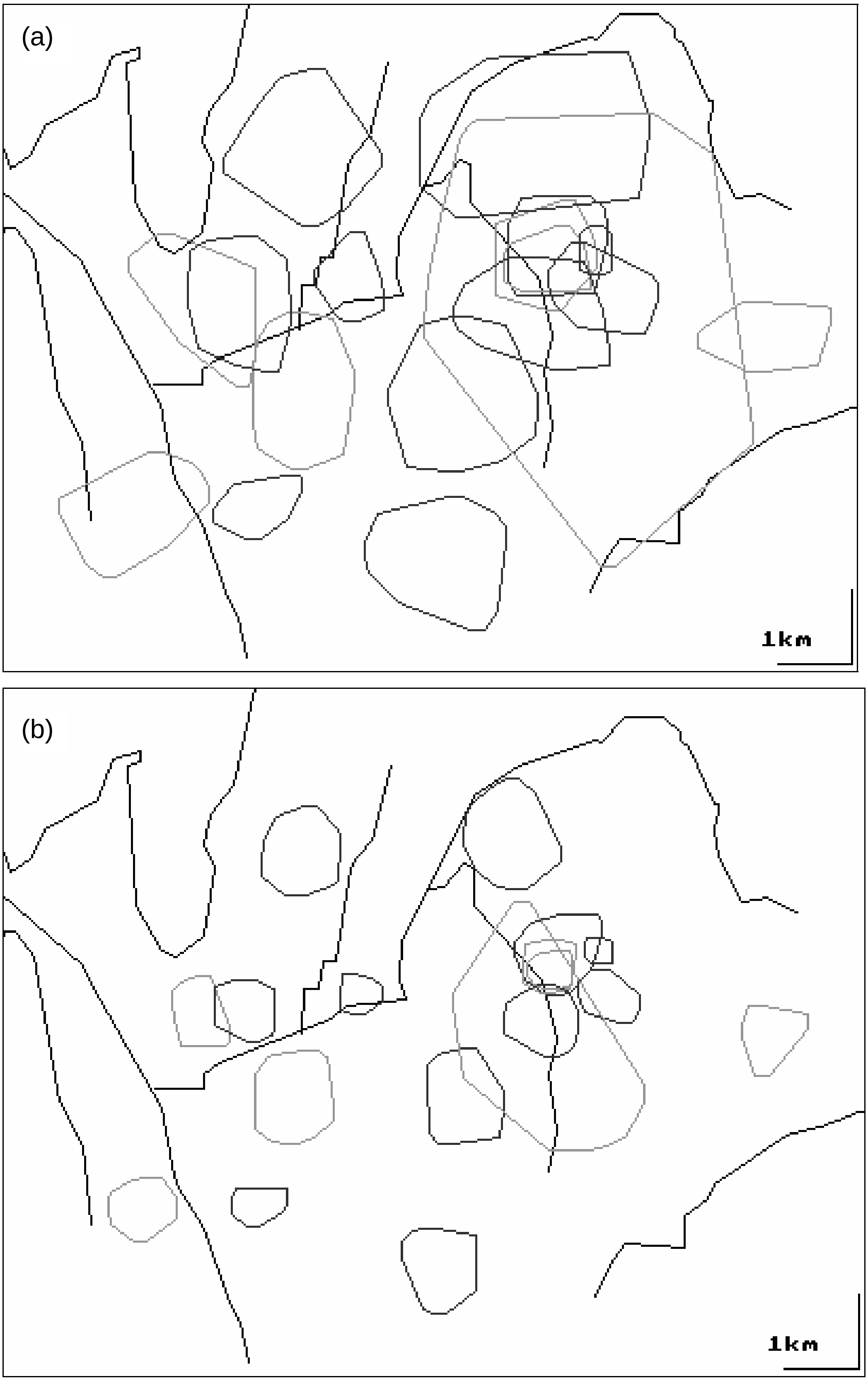


Figure 2.9. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in spring 1995. Males light grey, females dark grey, backdrop map of roads in study area.

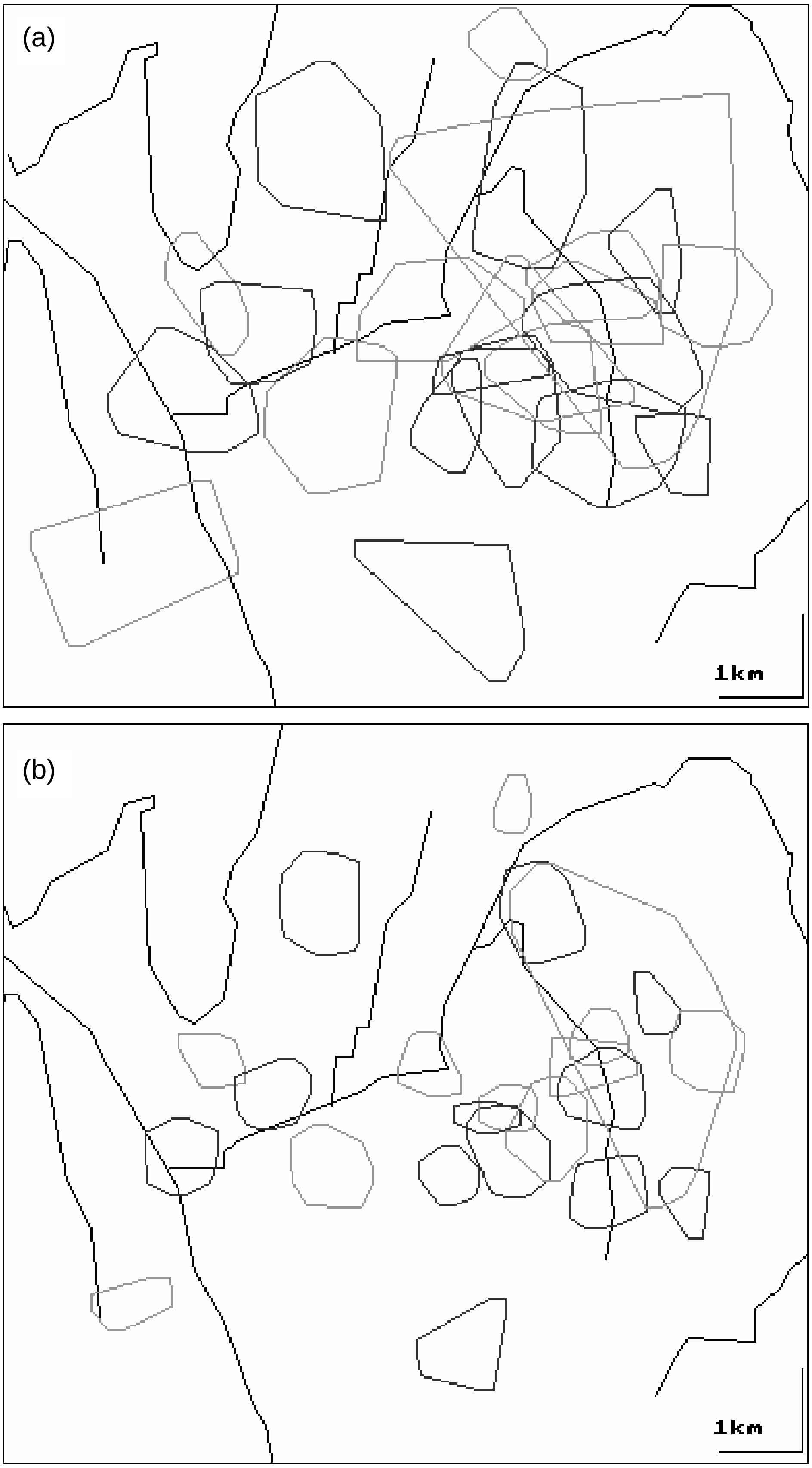


Figure 2.10. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in summer/autumn 1996. Males light grey, females dark grey, backdrop map of roads in study area.

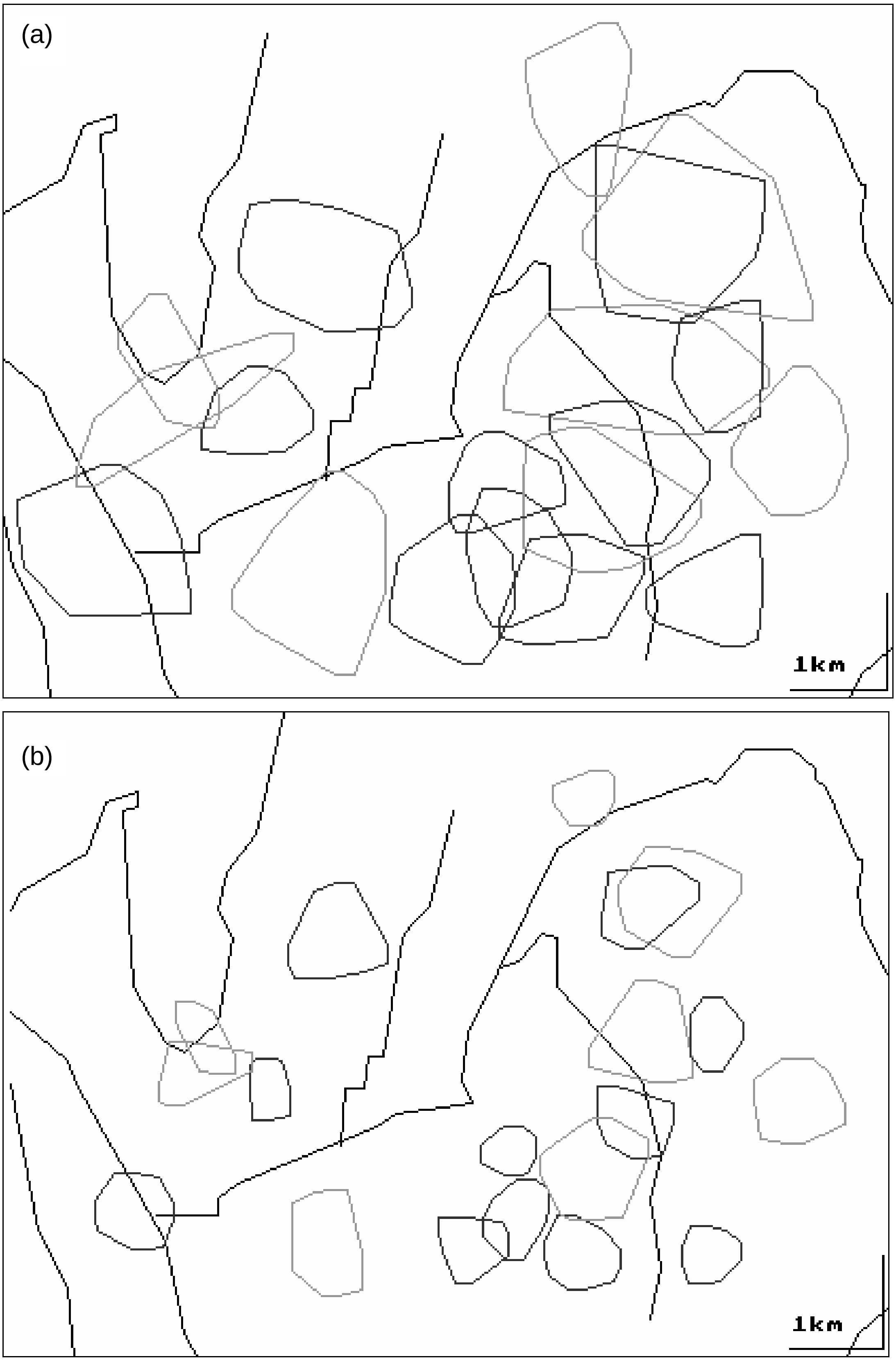


Figure 2.11. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in winter 1996. Males light grey, females dark grey, backdrop map of roads in study area.

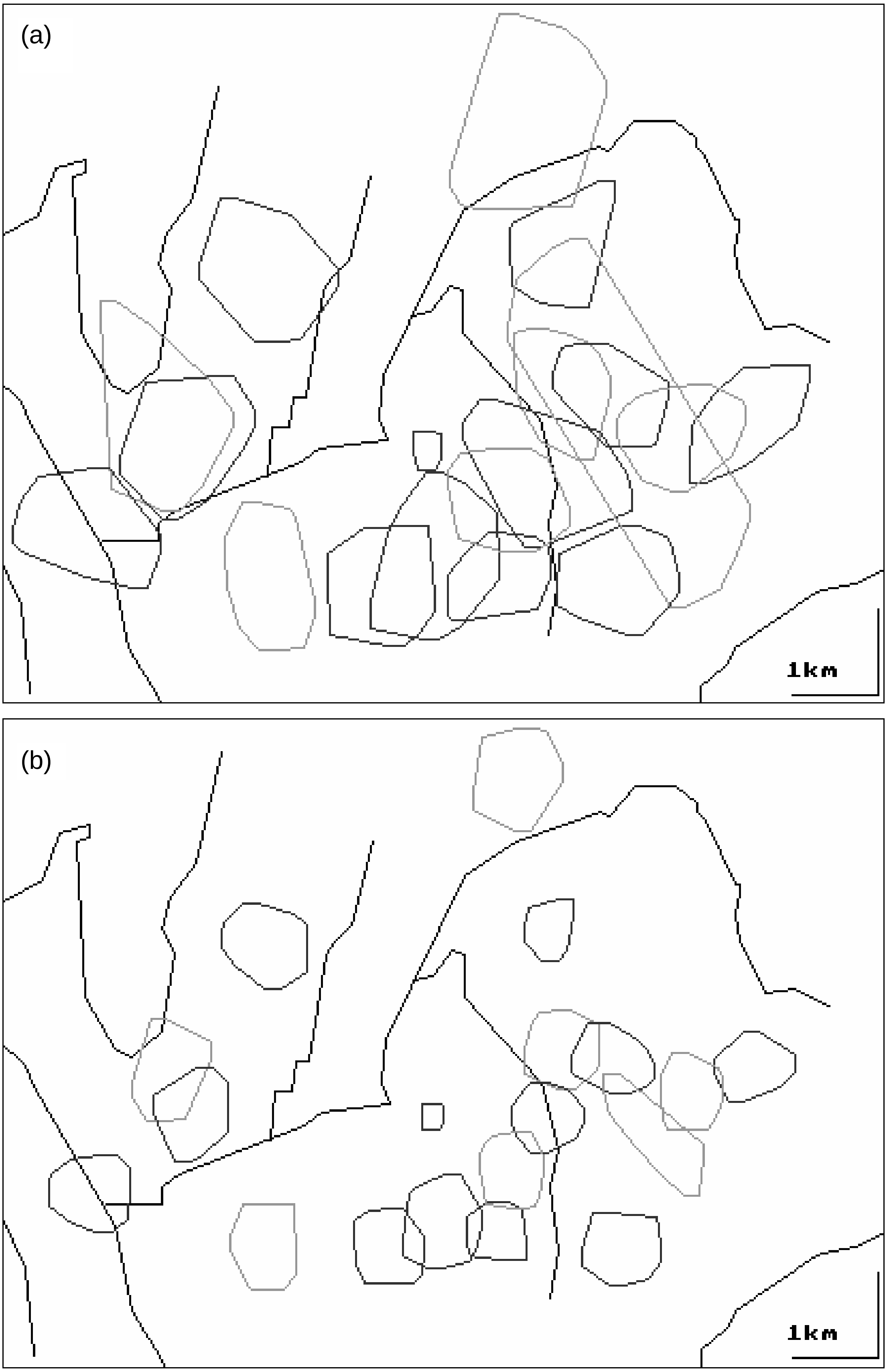


Figure 2.12. Overlap of (a) 95% MCP home ranges and (b) 50% MCP core ranges in spring 1996. Males light grey, females dark grey, backdrop map of roads in study area.

### *2.3.8 Dispersal*

Dispersal was defined as a movement of >3179m, the average span of total home range (Table 2.3). Of the 15 foxes (6 females, 9 males) radio-collared as juveniles, 6 (2 females, 4 males) were confirmed to have dispersed, signals were lost for 5 (2 females, 3 males) and 3 (1 female, 2 males) remained in the vicinity of capture (Table 2.12). All but 3 of the radio-collared juveniles were at 5 months of age when tagged, with the other 3 at 6, 8 and 10 months of age. The 8- and 10-month juveniles were both recorded as dispersers. The two male foxes that remained near their capture location both had erratic movements for some months, one never settling during the study. Of the 26 (10 females, 16 males) fitted with eartags only, 3 (2 females, 1 male) were confirmed to have dispersed, 2 (1 female, 1 male) were found dead on the site and the whereabouts of 21 (8 females, 13 males) were unknown on completion of the study (Table 2.12).

Table 2.12. Number of radio-collared and eartagged foxes confirmed as dispersing from or remaining in the study area, and the number of animals of unknown whereabouts. Adults were foxes tagged at > 1 year old, 38 of the 41 juveniles were tagged at ≤ 5 months of age, the other three radio-collared at 6, 8 and 10 months.

| | **Dispersed** | **Didn't disperse** | **Missing** |
|---|---|---|---|
| **Total radio-collared** | 12 (6 juv, 6 adults) | 28 (3 juv, 25 adults) | 9 (5 juv, 4 adults) |
| Females radio-collared | 6 (2 juv, 4 adults) | 18 (1 juv, 17 adults) | 4 (2 juv, 2 adults) |
| Males radio-collared | 6 (4 juv, 2 adults) | 10 (2 juv, 8 adults) | 5 (3 juv, 2 adults) |
| **Total eartagged** | 3 (all juv) | 2 (all juv) | 21 (all juv) |
| Females eartagged | 2 (all juv) | 1 (all juv) | 8 (all juv) |
| Males eartagged | 1 (all juv) | 1 (all juv) | 13 (all juv) |
| **Grand Total** | 15 (9 juv, 6 adults) | 30 (5 juv, 25 adults) | 30 (26 juv, 4 adults) |

In addition to the 9 juveniles confirmed to have dispersed, 6 foxes (4 females, 2 males) radio-tagged as adults shifted more than 3179m from their capture location or original home range (Table 2.13). A further 4 foxes (2 females, 2 males) radio-tagged as adults were missing on completion of the study. The percentage of radio-collared foxes that dispersed was 24% assuming missing foxes all remained in the site, and 43% assuming missing foxes all dispersed from the site.

The furthest distance recorded was a vixen that travelled 285 km, with the next greatest distance also by a vixen at 140 km. Mean and standard error of distance of dispersal excluding these extreme distances was 12.2 ± 4.3 km (males 15.9 ± 6.7 km, females 6.5 ± 1.2 km). Although the greatest distances were travelled by females, no significant difference was found in dispersal distance of males and females (*t* = 1.38, df= 7, p=0.10). Direction of dispersals fell within the range of $91^o$ – $273^o$, indicating a generally southerly direction of movement. The greatest distances were travelled by juveniles (Figure 2.13), but the difference in dispersal distance of juveniles (61.1 ± 31.6 km) and adults (5.9 ± 1.1 km) was not significant (*t* = 1.75, df= 8, p=0.12). There was no significant distance between sexes in the proportion of juveniles and adults that dispersed ($\chi^2$=0.55, df=1, p>0.05). Nor was there a significant difference in the mean age at dispersal between males and females (*t* = 1.38, df= 8, p=0.21).

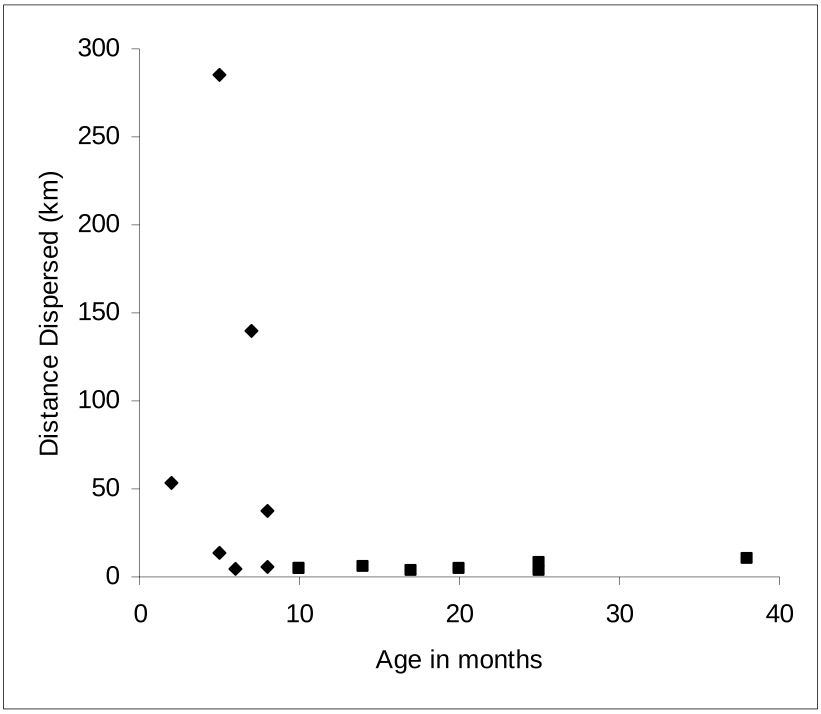


Figure 2.13. Age in months at which dispersal of foxes occurred and distance moved (km). Males depicted by squares, females by diamonds.

Of radio-collared animals, juveniles were significantly more likely to disperse than adults ($\chi^2$=5.35, df=1, p<0.01). When missing animals were pooled with confirmed dispersing animals this relationship became stronger ($\chi^2$=8.27, df=1, p<0.005).

## 2.4 DISCUSSION

### *2.4.1 Morphometrics*

Body dimensions of adult foxes in the present study are comparable to adult foxes in other studies within Australia, with a trend towards smaller size and weight than European foxes and larger size and weight than North American foxes. Weights of adult foxes in this study (males 5.4 ± 0.2 kg, females 4.9 ± 0.1 kg) were similar to findings of Bubela (1995) in alpine and subalpine NSW (males 5.2 ± 0.2 kg, females 4.6 ± 0.1 kg) and Banks (1997) in forest near Canberra (males 5.23 ± 0.27 kg, no adult females), but slightly smaller than findings of McIntosh (1963b) in the Canberra district (males 6.3 ± 0.77, females 5.5 ± 0.72). These results suggest slightly heavier foxes than those in North America (males 4.5-5.4 kg, females 4.1-4.5 kg) (Ables 1975) and slightly lighter than foxes from Europe (males 5.9-7.6 kg, females 5.1-6.5 kg) (Lloyd 1980). Head-body lengths of 679 ± 16 mm for males and 656 ± 9 mm for females were also similar to findings in alpine and subalpine Australia (males 670 ± 20 mm, females 650 ± 10 mm) (Bubela 1995), the Canberra region (males 650 mm, females 624 mm) (McIntosh 1963b) and Great Britain (males 570-777 mm, females 560-744 mm) (Lloyd 1980), and slightly larger than foxes in North America (males 639-655 mm, females 609-619 mm) (Storm *et al.* 1976).

### *2.4.2 Home range size*

This study estimated total home range size of 276-446 ha as determined by kernel and MCP analyses respectively. Other home range estimates in Australia include farmland in central Victoria, where ranges were calculated of 365-610 ha and urban fringe in Victoria where ranges were estimated to be 40-90 ha (Coman *et al.* 1991). Bubela (1995) reported home ranges of sub-alpine foxes of 160-220 ha, with ranges as large as 1010 ha in alpine habitats. In forested habitat in the ACT, Banks (1997) calculated range sizes of 154-194 ha. Foxes in semi-arid NSW were estimated to range over approximately 513 ha (Marlow 1992). Phillips and Catling (1991) found ranges of size 130-530 ha in coastal forest.

These home range results can not be directly compared as methods used to define ranges were not consistent and the numbers of animals tracked and fixes collected varied greatly. Nor were errors in each study due to factors such as topography, signal strength, tower alignment and average distance from transmitters to receivers likely to be consistent. The Coman *et al*. (1991) study used 90% Fourier transform utilisation distributions and 100% MCP and followed 2 foxes in farmland and 3 in urban fringe, but did not specify the number of fixes used. Banks (1997) tracked 7 foxes with an average of 35 fixes on each, using 100% MCP and 95% kernel utilisation distribution. Bubela (1995) tracked up to 9 foxes and equalised the number of fixes used in range estimations to 29.41, also using 100% MCP and 95% kernels. Marlow (1992) used 95% Fourier transform but did not specify numbers of foxes or fixes, while Phillips and Catling (1991) collected an enormous 451-656 fixes on each of 3 foxes and used 100% MCP. The present study followed 33 foxes with an average of 189 fixes on each for overall range estimates, with never fewer than 30 fixes used in MCP estimation or 40 in kernel estimates in seasonal estimates. This is a much larger number of animals than used in prior home range research in Australia, and estimates of ranges are based on more fixes than any of these studies with the exception of that by Phillips and Catling (1991). There is much individual variation among foxes, for example the smallest total 95% MCP range measured in this study was 76 ha and the largest 1926 ha. It is therefore important that the number of individuals tracked is as large as possible to ensure estimates are representative of the scope of behaviours in a population.

A further detail incorporated into this study was that the average displacement of “dummy” transmitter position estimates from their true locations was used to determine the width of a buffer strip around range estimates to allow for this error. While the site was topographically favourable for telemetry research, with little signal bounce and few obstacles to reception, the distances over which tracking was conducted were large, resulting in an average displacement of 187 m. While other studies checked and measured errors, they were not then incorporated into the overall estimate, but were rather used as a means of filtering unsatisfactory fixes from the data set.

Despite data from other areas of Australia not being directly comparable, some trends are evident. Overall range size in the present study is similar to range sizes in Victorian farmland (Coman *et al.* 1991) and NSW coastal forest (Phillips and Catling 1991), smaller than findings in semi-arid Australia (Marlow 1992) and alpine Australia (Bubela 1995), and larger than ranges in urban fringe (Coman *et al.* 1991). Alpine and arid Australia are the most variable environments of these listed, and likely to also contain the lowest food diversity. Conversely urban fringe would be expected to be a highly stable environment with high food diversity. Agricultural lands on the tablelands in NSW and central Victoria have relatively stable climates and high productivity, and support intermediate size ranges. These findings then fit with predictions of Voigt and Macdonald (1984) regarding the relationship between environmental stability, food diversity and home range size. Population density is also linked to fox range size, with smaller ranges at higher densities (Harris 1980). Density of foxes in the present study will be explored in detail in Chapters 3 and 5, but is similar to that in agricultural land in Victoria, higher than that supported by alpine and arid environments and lower than findings in urban areas, supporting this prediction.

The current study found ranges of male foxes to be significantly larger than ranges of females. This trend was also observed in other studies of fox home range in Australia, but was non-significant in these studies (Coman *et al.* 1991; Phillips and Catling 1991; Marlow 1992; Bubela 1995). Male ranges were found to be significantly larger than female ranges in urban Bristol (White *et al.* 1995), but no significant difference was detected in range sizes of males and females in Switzerland (Meia and Weber 1995) or Japan (Cavallini 1992).

In this study no significant difference was detected in range sizes of adults and juveniles. This was also the observation of Meia and Weber (1995) in Switzerland, who argue that, as body size and hence energetic requirements of adults and sub-adults are similar, similarity in range sizes is expected. Woollard and Harris (1990) found no difference in range size before and after dispersal, also supporting a similarity in range sizes between adults and juveniles. As range size was only estimated if there was evidence that the range area was not continually increasing with additional data points, these results may have been biased towards those juveniles remaining in their natal ranges. Animals seeking out a new range were not likely to exhibit a steady range area and so would have been excluded.

Ranges were found to be similar in size across seasons. In Australia ranges were marginally larger in winter in sub-alpine Australia, (Bubela 1995), and Phillips and Catling (1991) found a slight reduction in range area of a dog fox and a vixen from pre-denning (winter) to denning (spring) in coastal NSW. Marlow (1992) observed no seasonal differences in semi-arid Australia. Where seasonal variation has been observed in overseas studies, ranges were invariably largest in winter with a decrease in spring (Sheldon 1950; Lloyd 1980; Kolb 1984; White *et al.* 1995). This has been argued to be due to difficulties in securing food during winter (Sheldon 1950). White *et al*. (1995) found males had significantly larger ranges in winter but found no seasonal variation among females, while Meia and Weber (1995) observed no seasonal variation at all. In the present study any variations in range size associated with breeding may have operated on a shorter time scale than whole seasons. If this was the case, comparisons of shorter periods such as monthly ranges may have been necessary to detect a difference, but would have required more data to have sufficient numbers of fixes in each month. As males and females have different roles in cub-rearing, some sex-season interaction was also expected. However, no indications of such behaviour were observed and, again, possibly could only be detected with comparisons of shorter time periods.

### *2.4.3 Minimum convex polygon vs kernel analysis*

The two methods of estimating home range used in this study, 95% MCP and 95% kernels, reflected different features of fox ranges and gave differing estimates of range size. MCP analysis is a very simplistic means of defining home ranges and is heavily inflated by shifts in ranging behaviour and forays. Kernel analysis tended to yield smaller home range estimates and was not as influenced by forays or shifts in ranging behaviour. As a consequence, kernel estimates are likely to be closer to the true size of the home range. The precise shape of ranges towards the tails of the utilisation distribution is difficult to predict (Anderson 1982), and area estimations are strongly influenced by the choice of smoothing constant (Harris *et al.* 1990). While using a lower utilisation distribution may have improved accuracy, the 95% contour was used for comparison to other studies of fox movement in Australia that used similar kernel estimation (Bubela 1995; Banks 1997).

MCP analysis highlighted animals with shifting or foraying behaviour, ranges of such animals being much larger than those of other animals. Kernel estimates for these same foxes showed multiple centres of activity, often disjointed, thereby depicting the shift in behaviour as well as location of the alternative range. However, as it was common for a fox to have more than one centre of activity, examination of centres of activity alone was often not sufficient to identify animals with range shifts. Thus, by coupling MCP and kernel analyses, animals with erratic ranging behaviour such as shifts and forays could be identified.

The aim of using 95% MCPs and kernels was to exclude abnormal movements. However the selected percentile is arbitrary, and can lead to inaccurate estimates of range size if normal movements are excluded or abnormal movements included. A further consequence of inclusion of forays in MCP analysis is that range sizes can fail to stabilise. This is exemplified in this study by one individual who made a large number of forays, resulting in exclusion from home range analysis as its MCP range size failed to plateau. Difficulty then arises in deciding at what point foraying becomes the normal behaviour of the individual.

MCPs are unable to depict multiple centres of activity or ranges of a concave form. This can lead to inclusion of areas not used by the animal and a core area different to the animal’s true centre of activity. While kernel analysis can overcome this problem, choice of smoothing constant leads to differences in the level of detail depicted in the contouring. If data are oversmoothed, focal points of activity can be lost, and, conversely, if data are undersmoothed, even minor groupings of fixes show as a centre of activity. In this study least-squares cross-validation generally selected a smoothing constant which gave a unified home range with good internal detail, with some exceptions.

Approximately half of the home ranges plotted using kernel analysis were of a convex nature with a single centre of activity, while the other half had a more concave form with usually two, but sometimes three, centres of activity. Animals with more than one centre of activity included five animals who shifted range location, so these centres were not used simultaneously. MCP analysis gave much larger estimates of range size than kernel analysis where the range was of a concave nature, particularly MCP estimates of core areas. Moreover, centres of activity in MCP analysis frequently fell outside core areas depicted by kernel analysis. In studies from Europe (Lloyd 1980; White *et al.* 1995), Japan (Takeuchi and Koganezawa 1990) and North America (Storm 1965; Ables 1969b; Keenan 1981) foxes have frequently been reported to have multiple focal points of activity around areas such as dens, favourite hunting areas, abundant food supplies and resting areas. Given that fox ranges are frequently not of a convex nature, use of a home range estimation technique that does not assume convexity is highly advisable.

### *2.4.4 Nomadic foxes*

In this study seven individuals were observed with apparently nomadic behaviour, two of which settled nearby during the study and were classed as “dispersers”. Ranges of four of these (3 males, 1 female) could be included in analysis as range sizes had reached a maximum, but they were considerably larger than ranges of other foxes, and overlap plots showed them to cover the ranges of many other individuals. Two other foxes (both vixens) were also apparently nomadic but were regularly out of range of the tracking towers and hence too few fixes were available for analysis. Meia and Weber (1995) also observed a nomadic adult in a home range study in Switzerland, and recommended such animals be treated separately to the rest to avoid inflating estimates of mean home range size.

Identification of nomadic foxes in the present study, and in that by Meia and Weber (1995), was a subjective process and in the current study was based on observed movements and shifts in focal areas. Home range analysis was unable to objectively reveal animals that did not appear to range in a normal fashion, with some being included as outliers, and others excluded due to insufficient fixes or failure of ranges to plateau. Simply excluding all outliers runs the risk of excluding animals with particularly large ranges. Some of these animals qualified as dispersers, moving more than the average span of a range from their point of capture, and are discussed in more detail later. The presence of nomadic foxes raises other issues such as reliability of abundance estimation techniques that rely on animals having a steady range (such as active den counts – see Chapter 3), contact rates between foxes with implications for disease transmission, rates of recolonisation of vacated territories and whether such animals are able to successfully rear cubs.

### *2.4.5 Range overlap*

Overlap of ranges was investigated for MCP-generated ranges but not kernel-generated ranges. This was because some kernel ranges were fragmented, making interpretation difficult. The level of detail implied by kernel estimates was probably unrealistic for the purposes of overlap analysis, given the animal must have travelled between isolated areas of activity. As a broad overview of how ranges were spatially arranged, MCP depictions were considered adequate. Detailed analysis of overlap was also considered inappropriate given it could only be investigated for animals with radio-collars, with an unknown number of uncollared animals potentially overlapping the observed ranges.

Despite the crudity of MCP range shapes and only having a sample of the fox population radio-collared, a number of ranges neatly abutted without overlapping, suggesting territorial exclusion was operating. The ranges of males commonly overlapped with female ranges, giving no evidence of territorial exclusion across genders, but rarely overlapped with other males. A notable exception was a pair of adult males whose ranges, including core areas, overlapped for several seasons, with this arrangement ceasing upon the death of one of the two. The ranges of several juvenile males were observed to encompass the ranges of a number of mature males and females. These animals were apparently unsettled in a range, and it is possible that their wide-ranging movements and shifts in focal areas were due to being driven out by a resident male. Adult-juvenile overlap was also observed by Marlow (1992) in arid Australia. Other studies in Australia observed intersexual overlap of ranges and female-female overlap, but not male-male overlap (Coman *et al.* 1991; Phillips and Catling 1991; Marlow 1992; Bubela 1995), suggesting the phenomenon of male-male overlap is rare. This was also the conclusion of Poulle *et al*. (1994) in a study in France, Niewold (1980) in the Netherlands where a father and son were observed to share a range and Cavallini *et al*. in Japan (1992) where male-male overlap was observed once, although Harris and Smith (1987) found 21% of fox families in urban Bristol contained two adult dog foxes.

A much higher degree of range overlap was observed for females than males, but core areas were usually distinct, suggesting that, even where an area was shared, vixens occupied an exclusive area for most of their time. No evidence was found of vixens in shared ranges moving to an alternative range, with overlap only ceasing on death of the vixens. While cause of death was unknown, it is unlikely to be related to territorial exclusion, as evidence of range shifts would be expected if this was occurring. This pattern of range sharing with exclusive core areas could arise where rich resources were available which could support a number of vixens, but where vixens retained an exclusive area for rearing cubs. Indeed, while it was not clear what foraging or other resources were available where the largest concentration of foxes occurred, core areas of these vixens were arranged along a series of gullies, and focused around dens. Little has been described of overlap of core ranges in Australia, with Marlow (1992) observing only one vixen shared the core range of the sole tracked male at any one time in arid Australia. In the only Australian study where spatial groups were thought to occur, it was noted that ranges either significantly overlapped or virtually not at all, (Bubela 1995).

Social groups composed of a male, a dominant vixen and subordinate related vixens have been described in which there is almost complete overlap of core areas as well as the remainder of the range, and rearing of cubs is usually restricted to the dominant pair (Macdonald 1979; Reynolds and Tapper 1995). This does not appear to be the case in the present study, where range boundaries differed greatly between overlapping individuals, and individuals usually had exclusive core areas. Such interactive social behaviour as described by Macdonald (1979) is apparently a rare extreme, as most studies in which a high degree of overlap of ranges has been observed found that foxes had individual focal areas (Ables 1969b; Harris 1980; Lloyd 1980; Niewold 1980; Voigt and Macdonald 1984; Poulle *et al.* 1994). These indicate that while tolerant of other foxes within the range, behaviour is still largely solitary.

### *2.4.6 Dispersal*

In this study, twice as many foxes tagged as juveniles dispersed as remained within the vicinity of capture. This is in contrast to findings of Coman *et al*. (1991), who found of 46 tags recovered, 13 had dispersed and 33 remained in the capture vicinity. However, as most of the 33 cubs killed close to their natal dens had not reached 7 months of age, it is likely some of these were yet to disperse (Coman *et al.* 1991). Males outnumbered females 9:4 in the Coman *et al*. (1991) study, whereas in the present study similar numbers of males and females dispersed. Of the 6 juveniles monitored by Marlow (1992), 5 (all vixens) dispersed.

Mean distance of dispersal excluding exceptional movements was calculated to be 12.3 ± 4.3 km, with no difference between sexes in terms of distance travelled. This is similar that found by Coman *et al*. (1991), who calculated mean distance of dispersal to be 11 km from point of tagging, and further than the findings of Marlow (1992), where mean distance of dispersal of 5 juvenile vixens was 3.5 ± 0.4 km. In a summary of dispersal distances recorded in the northern hemisphere, Trewhella *et al*. (1988) observed the majority of foxes did not move far, but that a small proportion moved much greater distances. This was the case in the present study, as well as in the study by Coman *et al*. (1991). In Marlow's (1992) limited sample size only short distance dispersal was observed.

In all three Australian studies the furthest distances were travelled by vixens (present study 285 km, Coman *et al*. (1991) 30 km and Marlow (1992) 4.8 km) although in the study by Marlow (1992), only one male was followed, who remained in his natal range. Overseas literature suggests males are more likely to disperse than females and travel further (Ables 1975; Storm *et al.* 1976; Lloyd 1980; Saunders *et al.* 1995). The findings of the present study do not support this trend, with a similar number of males and females dispersing and no significant difference in distance travelled. Similarly, neither of the other two Australian studies (Coman *et al.* 1991; Marlow 1992) support a trend for males to move further than females, although sample sizes were small. Distance travelled by male cubs in the present study (15.9 ± 6.7) generally fell within the usual range reported from overseas of 2.8-43.5 km, and all but two movements by females were in the usual range of 1.8-38.6 km (Trewhella *et al.* 1988). Two vixens moved exceptional distances, one travelling 285 km and the other 140 km, inflating the average distance found for females (64.4 ± 41.2 km).

A trend of male foxes being more likely to disperse than females is compatible with hypotheses of social groups in which yearling vixens remain as helpers (Coman *et al.* 1991). However, in the limited sample size of present study, males and females were equally likely to disperse, which does not support this form of social grouping.

Dispersal distances are usually biased towards point of capture, as animals may not have completed their dispersal movements when killed (Ables 1975). In the present study, no shooting or poisoning of foxes occurred within the study area, so there was little risk of being killed near their capture location. If anything, this would have biased away from retrieving eartagged animals near their capture locations but would not have affected animals fitted with transmitters as they could be monitored while still alive. Bias towards point of capture probably applied to radio-collared animals, as signals were unlikely to be detected far from the site.

Three of the juvenile foxes fitted with radio-collars were older than 5 months of age. Dispersal was evidently not complete even by 10 months of age, as two of these animals, the 8 and 10 month olds, were recorded as dispersers. However it is possible they were in mid-dispersal when tagged, which would have resulted in an underestimate of their dispersal distances. Both were of poor body condition and suffering mange when captured, and both took a further number of months to settle into a range, with erratic movements in the interim. In a detailed study of movement patterns of dispersing foxes in the United States of America, Storm *et al*. (1976) observed that dispersal took the form of a directional movement to new areas rather than an erratic wandering that resulted in gradual shifts. Likewise, Zimen (1984) observed dispersal was usually a sudden, directed movement followed by a phase of slower and less directed movements while establishing in the new area. In Australia, Marlow (1992) also reported that all dispersals took place as a single change in position rather than random movement from area to area before settling. If this is also the case in the present study, it is likely these two foxes had completed any major dispersal movement they were going to undertake, if any, and were drifting in search of a vacant territory or matings. This may have also been the case for a number of other radio-collared foxes that were observed to shift activity over a number of different locations. Some of these eventually settled in a range, signals of several other unsettled foxes were lost, and one never settled during the study.

The fates of 9 radio-collared foxes in the present study are unknown. It is likely that the majority of these animals dispersed, but as some degree of collar failure is also likely, some may have remained within the site ‘invisibly’. Although dispersal of both adults and juveniles was observed, juveniles were significantly more likely to disperse, this relationship even stronger when it was assumed all missing radio-collared animals had dispersed. There was a non-significant trend for the furthest distances to be travelled by juveniles. In North America, Storm *et al*. (1976) also observed a less pronounced tendency to disperse in adults compared to juveniles, and for adult dispersal to be mostly over a shorter distance.

The distances from capture locations to final ranges for the two adult males that qualified as dispersers were above the average range span used to define dispersal (>3179m), but were not above the average male range span (4045m). It is likely that the two were in fact on a foray when trapped or shifted range as a consequence of trapping, rather than being true dispersers. One of the 4 adult females for which dispersal was detected was known to have successfully held a range and raised a cub in its initial location before shifting. It is likely that this animal was disturbed by frequent walk-in radio-tracking and moved off-site as soon as the cub was weaned. This same vixen was recaptured once in its initial range, and promptly made a several day foray to the area which was to become its future range but then returned to its original range for several more months before the permanent shift, rearing the cub in the meantime. A further two dispersing adult vixens were apparently itinerant foxes who were regularly out of range of the tracking towers and whose erratic movements qualified as dispersal. The fourth adult vixen recorded as dispersing may have been a genuine mature-age disperser or else shifted range as consequence of trap-fright. The low incidence of recaptures of foxes for which ranges were understood prior to recapture makes it very difficult to interpret the influence of trapping on ranging behaviour.

All dispersal events recorded were in a southerly direction (91°-274°), with no northerly dispersals observed. Topography to the north of the site was a series of undulating hills and steep gullies, with limited vantage points for long distance radio-signal reception. In contrast, hills to the south of the site offered wide reception over a much greater distance. This favoured detection of signals of animals leaving in a southerly direction, whereas signals of foxes dispersing to the north were less likely to be detected. The land to the west of the mountain range that ran north-south along the western boundary of the site was much flatter, offering excellent reception. It is likely, then, that the observed general southerly direction of movement was a feature of radio-signal detection, not an instinctive trend of foxes in the area. Moreover, given the relatively small number of foxes on which this observation is based, it may have been due to chance alone. Storm *et al.* (1976) found a trend towards more northerly dispersal in North America, but considered this an artefact of increased hunting intensity to the north of the country. Other studies have found dispersal to radiate in all directions from the point of tagging (Lloyd 1980; Coman *et al.* 1991). The data from the current study is not sufficiently strong to refute that this does not also occur in this site.

The proportion of animals that disperse and the distance they travel has major implications for disease spread, the spread of rabies being the primary motivation behind studies of dispersal in Europe and North America. It also has implications for rates of recolonisation of areas in which lethal control has been conducted. For example, as foxes will rapidly recolonise vacated territories and will travel great distances, removal of foxes needs to be conducted over large areas to maximise duration of lowered predator densities. The effects of dispersal into areas where fertility control has been imposed are yet to be seen, but the presence of resident, infertile foxes could potentially result in less successful colonisation of such areas by incoming dispersers. Whether being born in areas of high infertility will affect likelihood of dispersal and distance travelled from such areas is also yet to be seen. Distance of dispersal is negatively correlated with population density (Trewhella *et al.* 1988), but whether this applies when density is low due to control efforts rather than unfavourable habitat quality is not known. Thomson *et al*. (2000) found a regularly baited buffer zone around a control site was very effective at preventing recolonisation, and proposed the buffer zone was a ‘dispersal sink’: as there were vacancies in the buffer zone, dispersing foxes would settle there rather than continuing on to the core area. It is clear, with such high mobility, that gene flow must be rapid, so any resistance to poison or fertility control agents is likely to be readily transmitted over long distances.

### *2.4.7 Conclusion*

It can be seen from the results of this study, and those of other studies within and outside Australia, that fox ranging behaviour is highly varied both between and within habitats. There is considerable value in using more than one technique for estimating range area and usage, in this case Minimum Convex Polygon and kernel methods, as each has its own merits and weaknesses, reflecting different aspects of fox ranging behaviour. Some trends in fox ranging behaviour are common across a broad spectrum of habitats. These trends include a high incidence of range overlap between females and between male and female resident foxes but rarely any male-male overlap. Even within highly overlapping ranges, individual foxes commonly have separate areas of intense activity, indicating that, while tolerant of other individuals within their ranges, they are rarely sociable. A small proportion of the population of foxes in an area appears to be nomadic, some of whom later settle in a steady range. It is clear, then, that foxes may reside in an area without commanding a home range, and are therefore potentially able to mate with resident foxes, play a role in disease transmission and compete for and impact upon prey species. Such foxes may be harder to detect by census techniques that assume normal ranging behaviour such as natal den counts (Chapter 3). Dispersal of both males and females, particularly as juveniles, is a common phenomenon and can occur over large distances.

# CHAPTER 3

# DENS

## 3.1 INTRODUCTION

Counts of breeding dens during spring are regarded as being the most accurate means of estimating fox density provided the size of family groups and social structure are known (Trewhella *et al.* 1988; Saunders *et al.* 1995). The counts involve locating all breeding dens in the area then multiplying the count by the estimated number of foxes per den. This gives a population size that can be converted to a density estimate by dividing by the area searched for dens. As foxes only reliably occupy dens during the breeding season, this method can only be used to estimate annual population fluctuations, not changes within the year. Published Australian studies that used breeding den counts to estimate population size assumed a breeding pair of adults plus an average sized litter of cubs per den, and no non-territorial foxes (Coman *et al.* 1991; Marks and Bloomfield 1999). In both these studies, litter sizes were based on observed numbers of cubs at dens in their study site, averaging 3.3 cubs (Coman *et al.* 1991), and 4.36 cubs (Marks and Bloomfield 1999). In a review of the red fox in Australia, Saunders *et al.* (1995) reported mean litter size to be 4 cubs, with a maximum of around 10. Other studies of fox litter size in Australia found averages of 4.25 (McIntosh 1963b) and 3.7 (Ryan 1976). A concurrent study in central-western NSW found the main whelping period for foxes was early September (McIlroy *et al.* in press).

In a study of den usage in agricultural land in Japan, dens were classified as natal (where cubs spent about 6-8 weeks from birth), residential (for rearing litters after leaving natal dens) and temporarily visited (for periodical retreat or for advertising territories) (Nakazono and Ono 1987). Of 80 dens monitored, 12.4% were identified as natal, with little change in the number of natal dens from year to year. These were distributed fairly uniformly across the study area but were often amid a cluster of residential or temporarily visited dens. Natal dens generally developed from dens repeatedly used for temporary visits or rearing of cubs, usually persisted for long periods of time once established and could be used for multiple generations

(Nakazono and Ono 1987). While no natal dens were abandoned during the study, 35% of temporary dens were abandoned. According to Henry (1986), vixens may use the same whelping den year after year, and upon death of a vixen the site may be used by one of her daughters. He also notes that derelict dens may be renovated after long periods of vacancy. Ables (1975) and Storm *et al.* (1976) also reported dens to be occupied in multiple years but neither author quantified the number of years each den visited was used.

Dens occur in a wide variety of habitats, and in non-urban areas have been reported to include dry drainage channels, eroded gullies, hollows between tree roots, under boulders or dug in dry land on hillsides (Storm *et al.* 1976; Lloyd 1980; Henry 1986). Henry (1986) describes natal dens as typically on a hillside in sandy loam, often in forest but close to meadow or open slope. He further generalises that dens usually have multiple entrances, and are normally within 100 metres of a water source. In Japan it was also observed that foxes selectively used open land rather than wooded areas for natal dens, and it was noted that natal dens usually had more entrances than temporary dens (Nakazono and Ono 1987). Studies from North America (Sheldon 1950) and Scotland (Hewson 1986) also found natal dens to be more prevalent in agricultural land than forest. However in a study in which dens were located by radio-tracking juvenile foxes, Storm *et al.* (1976) found the majority were located in wooded areas, suggesting the apparent preference for open areas is due to dens being more conspicuous in such sites.

Techniques to locate natal dens of the red fox include aerial surveys (Sargeant *et al.* 1975; Page 1981), questionnaires (Harris 1981; Nakazono and Ono 1987), ground searches (Sheldon 1950; Insley 1977; Coman *et al.* 1991; Marks and Bloomfield 1999), monitoring radio-collared foxes (Storm *et al.* 1976; Coman *et al.* 1991; Reynolds and Tapper 1995) and even equipping prey items with radio-tags and tracking them back to dens (Voigt and Broadfoot 1983). The first three of these methods rely on observing foxes or dens, and are difficult to use where there is dense vegetative cover. The latter two methods require intensive fieldwork but are not hindered by dense cover. Active dens are readily identified by evidence such as freshly dug soil, strong odour, prints, scats or food remains, while obsolete dens often have leaf litter and cobwebs within and little or no odour (Nakazono and Ono 1987).

Evidence that an active den was used as a natal den included visual observations of cubs, cub prints or scats and areas of trampled grass (Insley 1977; Coman *et al.* 1991; Marks and Bloomfield 1999). Foxes will move their cubs to a new location if disturbed or once the cubs become quite advanced (Sheldon 1950; Storm *et al*. 1976; Insley 1977; Lloyd 1980; Harris 1981; Dekker 1983; Henry 1986; Nakazono and Ono 1987; Marks and Bloomfield 1999). Lloyd (1980) commented that vacated dens are generally of an unwholesome appearance, often displaying large quantities of unconsumed carrion.

This chapter explores use of dens by foxes in high rainfall agricultural land in the southwest slopes of NSW, and uses this to estimate density of foxes in this environment.

## 3.2 METHODS

### *3.2.1 Den searches*

From 1994 to 1996 inclusive, any dens located during the course of other fieldwork or reported by locals were noted and monitored for signs of activity. However in 1995 and 1996 a systematic search approach was adopted to gain a more representative picture of den use within the site. An area of 16.4 km$^2$ was selected within the study area to encompass the scope of habitats within the site (Figure 3.1). This area was thoroughly searched for dens during August/September of each year, which is the start of the main whelping period for foxes (McIlroy *et al.* in press) so foxes were assumed to have selected and prepared a number of dens for breeding by this time, and the number of dens in use should be at its peak. A further advantage was that vegetation cover was low at this time, enabling dens to be readily located. Den searches were conducted using a motorbike to run transects of 20m intervals in open paddocks and by foot in areas where access was more difficult such as along gullies, steep slopes and wooded areas. Location (grid reference), habitat (creek bank, hollow log, base of tree, hillside), evidence of activity (freshly turned earth by the den, scats, strong odour, prints, food remains) or its absence (spider webs across entrance, leaves and grass within) and number of entrances were recorded, and a code number assigned to each den.

In November of both years, these dens were revisited to assess whether they were still active and to note any evidence that breeding took place (visual observations of cubs, cub prints or scats, areas of trampled grass). At this time vegetation cover was very dense, so only dens visited earlier could be located. This meant it was not possible to reliably establish if any new dens had been constructed since the first survey. From this it was possible to generate an estimate of how many dens foxes prepared, how many were actually used for breeding, where these dens were most likely to be located, and whether the same dens were used from year to year.

As a novel application of mark-recapture analysis, and as an alternative estimation of the total number of dens in the searched area, Petersen estimates were made of the total number of dens in 1995 and 1996 using the Seber correction to reduce bias

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1$$

Where $\hat{N}$ = estimate of population size at time of marking
$M$ = number of individuals marked in the first sample
$C$ = total number of individuals captured in the second sample
$R$ = number of marked individuals in second sample (Krebs 1999).

Assumptions of the Petersen estimate are (1) the population is closed to additions and deletions, (2) catchability is equal within each sample, (3) marking does not affect catchability and (4) marks are not lost or overlooked (Pollock *et al.* 1990; Krebs 1999). August and November counts were used as the two census periods for each year, and it was assumed that the total number of dens was unchanged between August and November. Binomial confidence intervals were obtained graphically (Krebs 1999).

A Jolly-Seber analysis was also conducted based on all four survey periods to estimate the total number of dens and the total number of active dens in the site in the two middle survey periods. This analysis allows for an open population (Seber 1982; Krebs 1999). Assumptions of Jolly Seber analysis are (1) every individual has the same probability of being caught in the *t*-th sample, whether marked or unmarked, (2) every marked individual has the same probability of surviving from the *t*-th to the (*t*+1)th sample, (3) marks are not lost or overlooked and (4) sampling time is negligible in relation to intervals between samples. The total number of natal dens could not be estimated by this method as a minimum of four sampling periods are required for this analysis but natal dens were only able to be found during the two spring survey periods.

Other applications in which mark-recapture analysis has been used include using the fossil record to estimate the number of species, speciation rates and extinction rates, estimation of the number of animals missed in aerial surveys, estimation of the number of homeless people in a city, and estimation of the number of errors in a computer program (Pollock 1997).

Survival of dens was estimated using the Kaplan-Meier method (Pollock *et al.* 1989; Krebs 1999). This method allows new dens to be added to the sample at any time, and any losses of unknown fate to be deleted from the sample without affecting the estimated survival rate (Krebs 1999). Estimates were based on all four sampling periods for all dens and active dens. Because dens can only be natal once each year it was inappropriate to consider whether they remained natal within a year, so natal dens within each year were compared giving two sampling periods.

Survival is calculated as

$$\hat{S}_k = \prod_{i=1}^{n} \left[ 1 - \left( \frac{d_i}{r_i} \right) \right]$$

Where $\hat{S}_k$ = Kaplan-Meier estimate of finite survival rate for the period
$d_i$ = number of deaths recorded at time $i$
$r_i$ = number of individuals alive and at risk at time $i$
$n$ = number of time checks for possible deaths (Krebs 1999)

A chi-square test of heterogeneity with the correction for continuity (Sokal and Rohlf 1995) was used to compare den habitat (in gullies or away from gullies) and den form (dug into the ground or under or within trees or fallen logs), and whether differences existed in habitat and form between natal and non-natal dens. This test was also used to compare habitat and form of dens initially found by radio-tracking versus those found by systematic searching. A Student's *t*-test (Sokal and Rohlf 1995) was used to compare the number of active entrances of natal and non-natal dens.

### *3.2.2 Distribution of dens*

Nearest neighbour distances between active dens and between natal dens were calculated for each year to determine whether den dispersion was aggregated, random or regular (Clark and Evans 1954; Krebs 1999). In this test the distance to the nearest neighbour of every den is measured to give a mean nearest neighbour distance. An expected distance is calculated based on the density of dens in the site, assuming a random pattern. The ratio of the observed and the expected distance gives a measure of deviation of the observed pattern from the expected random pattern, a random pattern having a ratio of 1. When clumping occurs this ratio approaches zero, and in a regular pattern the ratio approaches an upper limit of around 2.15 (Krebs 1999). The Clark and Evans test can be biased towards a regular pattern if a boundary strip is not included to allow for outermost dens potentially being closer to dens outside the study area (Krebs 1999). To avoid this bias any dens nearer to the edge of the searched area than to the nearest den were excluded from the sample. Mean density of natal dens per square kilometre was also calculated.

### *3.2.3 Number of dens used by foxes*

Radio-collared vixens were tracked regularly throughout the winter and spring period (described in Chapter 3) to locate any dens used by each individual, and also regularly followed on foot from shortly before sunset until it was too dark to see unaided to establish whether they were returning to a litter in a den.

### *3.2.4 Litter size*

To verify presence of cubs and gain an estimate of litter size, any dens showing evidence of cub-rearing during November were observed using binoculars from an hour before sunset until it was too dark to see unaided. At this time a spotlight was shone around the area to check for any foxes in the vicinity. This was repeated for up to three nights, with the maximum number of cubs seen simultaneously taken as the litter size.

### *3.2.5 Density estimation using dens*

Population abundance in spring was estimated using confirmed breeding dens, assuming 2 adult foxes and a litter of cubs as estimated in *3.2.4* occupied each breeding den. To account for foxes whose home ranges were only partly within the surveyed area, the area occupied by this number of foxes was taken as the area searched for dens (16.4 km$^2$) plus a boundary strip the width of half an average home range radius (Krebs 1999). Home range radius was estimated to be 3179m (Table 2.3), bringing the total area to 61.3 km$^2$. The calculated abundance was divided by the corrected area to give an estimation of density. Adult abundance and density during spring were also estimated by dividing the total number of active dens by the average number of dens each vixen was observed to use, then doubling to include males, assuming the sex ratio in the fox population was 1:1, as reported by McIntosh (1963b).

## 3.3 RESULTS

### *3.3.1 Location of dens*

A total of 200 dens were found within the 16.4 km$^2$ searched and an additional 11 dens were found outside the systematically searched area between 1994 and 1996 (Figure 3.1). Between 51% and 62% of dens located each year showed signs of activity during winter, the number of active dens reducing by spring (Table 3.1). Locations of all dens found to be active and all natal dens in 1994, 1995 and 1996 are shown in Figures 3.2, 3.3 and 3.4. In the two years of systematic surveying (1995 and 1996), 28% – 37% of dens found to be active in winter were still active in spring, and of those still active, 59% – 63% showed evidence that they were used as natal dens (Table 3.1, Figures 3.3 and 3.4). In the years of systematic searches, natal dens comprised 26% of active dens and 16% of all dens located within the search area in winter of 1995 and 17% of active and 9% of total dens in 1996. During the course of the study a number of new dens were created and old dens destroyed, with the maximum number of dens in existence at one time being 187 dens in 1996 (Table 3.1, Figure 3.5).

### *3.3.2 Mark-recapture analysis*

Using the Petersen estimate with the Seber correction, the total number of dens within the systematically searched area was estimated to be 105 (95% confidence interval 103 – 111) in 1995 and 185 (95% confidence interval 185 – 189) in 1996. These estimates are identical to the total number of dens identified in each year (Table 3.1) and the confidence limits are narrow around these figures.

Table 3.1 Numbers of dens located at Murringo between 1994 and 1996. Systematic searches were conducted in 1995 and 1996. The numbers of dens within the systematically searched area are shown in brackets. Proportions of dens remaining active or used as natal dens were only calculated for dens within the searched area.

| | **1994** | **1995** | **1996** |
|---|---|---|---|
| Total dens located | 38 | 110 (105) | 187 (185) |
| Dens active in winter | 23 | 68 (65) | 96 (95) |
| Dens active in spring | 24 | 26 (24) | 27 (27) |
| Natal dens | 9 | 17 (15) | 16 (16) |
| % total dens active in winter | - | - (62%) | - (51%) |
| % active winter dens still active in spring | - | - (37%) | - (28%) |
| % active spring dens used as natal dens | - | - (63%) | - (59%) |

Jolly Seber analysis estimated the number of dens within the search area to be 104 in 1995 and 184 in 1996. The 95% confidence intervals were found to be tight, but bias in the analysis resulted in the estimated number of dens not falling within the range, so they were excluded from the results. As with the Petersen estimate, these figures are very similar to the total number of dens found each year (Table 3.1). When only active dens in each survey period were considered, the total number was estimated to be 72 (95% confidence interval 46 – 154) in spring 1995 and 93 (confidence interval could not be estimated) in winter 1996. These figures are similar to the total numbers of active dens identified during the winter den searches (Table 3.1).

Using Kaplan-Meier survival estimation, the probability of dens surviving from winter to spring was 99% in 1995 and 97% in 1996. Survival from winter 1995 to winter 1996 was 84% and from spring to spring was 83%. This indicates particularly high persistence of dens from winter to spring, and also high persistence from year to year. The chance of an active den in winter still being active in spring was 28% in both years. The chance of a den being active in both winter 1995 and winter 1996 was 14%, as was chance of activity from spring to spring. Of natal dens used in 1995, 20% were again used as natal dens in 1996.

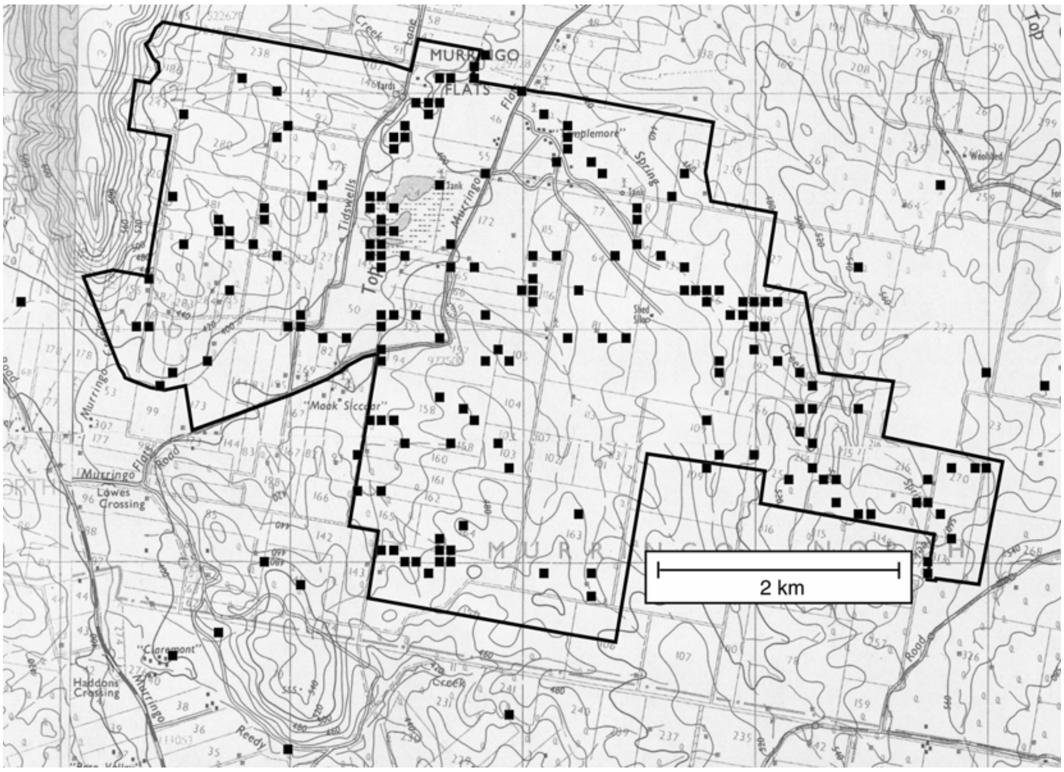


Figure 3.1. Map of study site showing locations of all dens mapped. The outlined area was systematically surveyed during both winter and spring of 1995 and 1996.

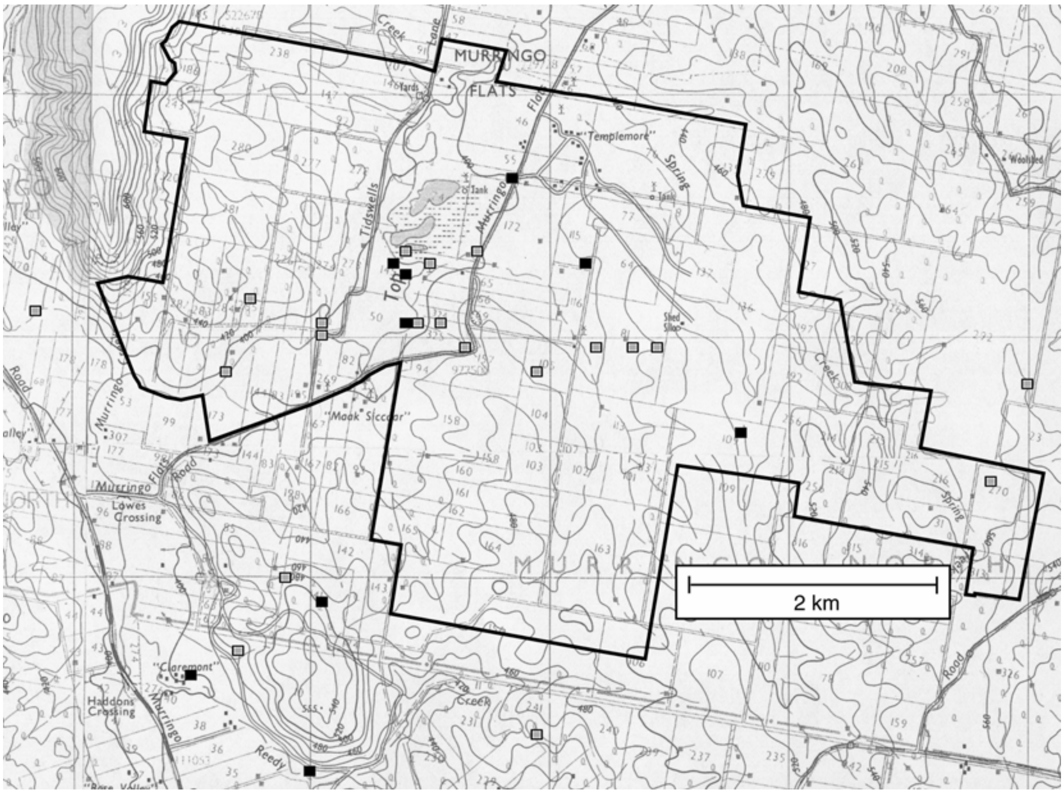


Figure 3.2 Locations of all active (grey) and natal (black) dens in 1994. The systematic search area is shown for reference only, but searches did not commence until 1995.

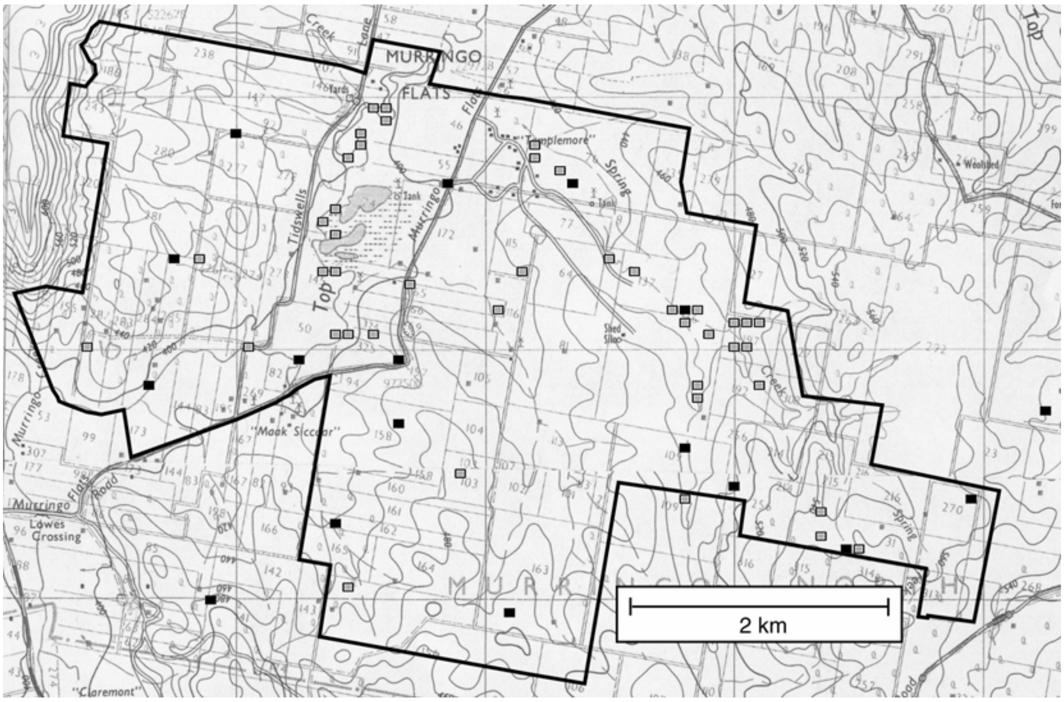


Figure 3.3. Locations of all active (grey) and natal (black) dens in 1995. The outlined area was systematically searched for dens in winter and spring of 1995 and 1996.

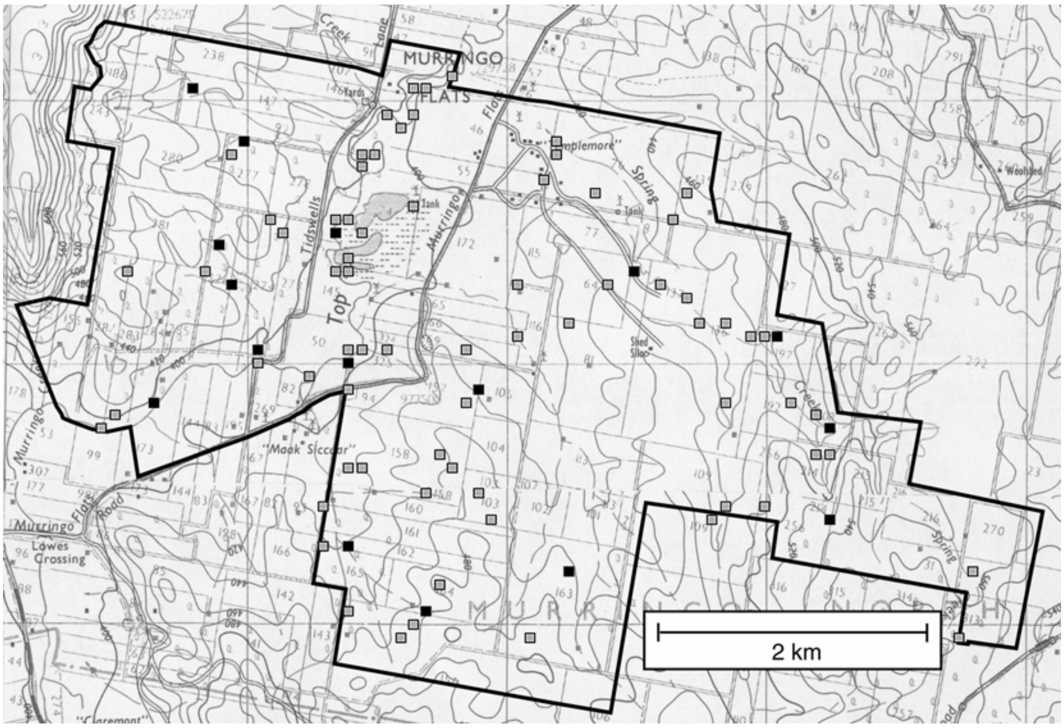


Figure 3.4. Locations of all active (grey) and natal (black) dens in 1996. The outlined area was systematically searched for dens in winter and spring of 1995 and 1996.

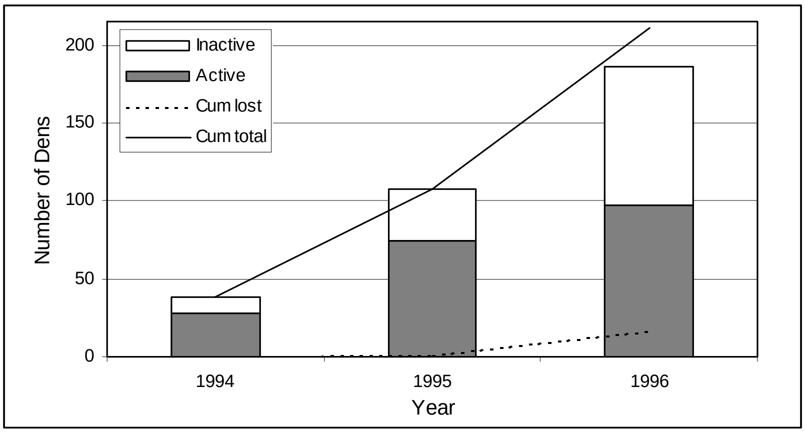


Figure 3.5. The number of active and inactive dens located in each year, the cumulative number of dens located and cumulative number of dens lost from the study site.

### 3.3.3 Search method

Of the total 200 dens located within the search area, 159 were initially located by systematic searching, 22 by radio-tracking of foxes (4 of these were located after systematic searching had taken place) and 19 located opportunistically (2 post-systematic search). Of the 11 dens outside the search area, 6 were found by radio-tracking of foxes, 4 opportunistically and 1 after being informed by a local farmer. The number of dens located in the second year (1996) of systematic surveying that had not previously been found was 79 (Table 3.1: 186-107). Thirty-nine of these were old, inactive dens that had not been found during previous surveys, 26 were freshly constructed dens, and 14 were active when found in 1996, but it was not clear whether they were newly dug or had been overlooked in the previous year’s survey.

### 3.3.4 Den habitat and form

The majority of dens were found in gullies or creeklines, with 121 dens in such areas and 90 dens on flat paddocks or hillsides (Figure 3.1). Dens were either dug into the ground or under or within trees or fallen logs. Dens along gullies were significantly more likely to be dug into soil than those away from gullies, which tended to be under or within trees or fallen logs ($\chi^2$=98.4, df=1, p<0.001). There was no significant difference between natal and non-natal dens in terms of whether they were located in gullies or away from gullies ($\chi^2$=0.01, df=1, p>0.05), or whether dug into the ground or under timber or trees ($\chi^2$=1.71, df=1, p>0.05).

The average number of entrances per den was 2.1 (± 0.1 S.E., n=211). Natal dens had significantly more active entrances (3.4, n=38) than non-natal dens (1.9, n=173) (t=2.01, P<0.001).

Search method was explored to see if the habitats in which dens were found (in gullies or away from gullies) or the type of den (whether dug or under timber) influenced their ability to be found. The ratio of dens found in gullies versus away from gullies did not differ significantly whether dens were initially located by radio-tracking, which is not affected by visibility of the den, or by systematic survey ($\chi^2$=0.52, df=1, p>0.05). Likewise dens in or under trees or logs versus dug into the ground occurred in the same ratio whether initially found by radio-tracking or systematically surveying ($\chi^2$=1.77, df=1, p>0.05).

### *3.3.5 Den dispersion*

To avoid any bias as a result of outermost dens potentially being nearest to dens outside the study area, any active dens nearer the edge of the searched area than to the nearest active den within the area were excluded from the sample. This resulted in four dens in 1995 and nine dens in 1996 being excluded from the data sets. Nearest neighbour analysis indicated active den dispersion was aggregated in both 1995 and 1996 (Table 3.2, Figures 3.3 and 3.4).

Sample size was limited for natal dens, and the spacing meant that very few were nearer to another natal den than to the edge of the site. For 1996 data, a Student’s t-test was conducted to establish whether mean distance between dens nearer the search boundary than to each other (n=11) was significantly greater than for dens nearer each other than the boundary (n=4). No significant difference was found (t=2.8, p>0.05). This indicated that bias was not likely to be a problem, so the Clark and Evans nearest neighbour test was applied to the entire natal den data set. Natal dens in 1996 were found to be regularly dispersed (Table 3.2, Figure 3.4). The 1995 data set was not sufficiently large to conduct a t-test examining potential boundary strip bias, but nearest neighbour analysis of the entire 1995 natal den data set also indicated a regular dispersion of natal dens (Table 3.2, Figure 3.3).

Table 3.2. Number of nearest-neighbour den pairs (*n*), density of dens (dens/km$^2$), mean nearest-neighbour distance (km), dispersion index (DI), deviation from random (*z*) and form of dispersion of dens, calculated at p<0.05.

| **Category** | ***n*** | **Density** | **Mean n-n distance** | **DI** | ***z*** | **Dispersion** |
|---|---|---|---|---|---|---|
| 1995 active | 67 | 4.09 | 0.16 | 0.64 | -5.7 | Aggregated |
| 1996 active | 86 | 5.24 | 0.19 | 0.85 | -2.7 | Aggregated |
| 1995 natal | 15 | 0.91 | 0.92 | 1.75 | 5.5 | Regular |
| 1996 natal | 15 | 0.91 | 0.78 | 1.50 | 3.7 | Regular |

### *3.3.6 Persistence of dens*

Dens were not always used in successive years. Twenty-nine dens were monitored for all three years of the study, of which 5 were used in all years. Of 109 dens monitored for two years, 39 were used in two successive years. A number of dens disappeared and new dens were dug between years.

The number of natal dens in the search area was similar in the search years of 1995 (17 natal dens) and 1996 (16 natal dens), and a number of dens were used for rearing cubs on more than one occasion. Of 27 natal dens followed for two or more years, 6 were used for cub rearing more than once. There were two instances in which a den used for raising cubs in one year was derelict the next but a new natal den had been created in the immediate vicinity (< 20m) of the original. Although recorded as separate dens, these were treated as single dens for analysis of persistence of a den, as location and microhabitat were virtually identical.

Non-natal dens tended not to be used on repeated occasions. Eighty-five non-natal dens were followed for two or more years, of which 17 were never active during the study period. The remaining 68 were active during at least one survey period. As mentioned earlier, dens still active in spring of each year comprised only about a third of dens active during winter. Of 17 dens remaining active in the spring of 1994 or

1995, only two dens were active in the spring of the following year, with 14 not used again. One den was active the following winter but abandoned by spring.

Evidence was collected of a succession of occupants through some dens. During the spring den searches of 1995, 6 dens which had been active in winter 1995 were found with a dead vixen in the opening. Activity ceased at these dens for the remainder of the breeding season but 4 showed signs of activity the following year. A den in which a fox died during winter 1994 was not used in the following year, but was active in 1996. Successive occupancy of a cluster of dens was observed with 3 radio-collared vixens, in which the initial occupant of a set of 5 dens raised a cub in 1994 but then shifted to a different area. Two vixens occupying nearby but separate dens then left these and assumed shared occupancy of the vacated 5 dens. In winter 1995 they withdrew residence of one of the 5 dens, which was then used as a natal den by an unmarked fox. At least one of the two had cubs in spring 1995, with the natal den different to that used by the first vixen, but both vixens died at this point so occupancy ceased. These dens were all occupied by unmarked foxes the following year (1996).

### *3.3.7 Number of dens used by vixens*

A total of 18 vixens were observed at dens. Ten of these were tracked thoroughly and found to use a total of 24 dens. The number of dens used per vixen ranged from a maximum of 5 to a minimum of 1, with a mean of 2.4 (± 0.4 SE, n=10).

There was one instance in which four advanced cubs (at least 8 weeks of age) were observed at a den which had been a rabbit warren only 4 weeks earlier, indicating the cubs had been shifted since birth.

### *3.3.8 Litter size*

Emergent cubs were successfully counted at 11 dens during the study, giving an average litter size of 2.8 cubs (± 0.4 SE, n=11), with a maximum of 5 cubs and a minimum of 1.

### 3.3.9 Density estimation

A total of 17 natal dens were located within the search area in 1995 and 16 in 1996. Assuming 2 adults and 2.8 cubs occupied each breeding den, this gives a population size of 82 foxes (34 adults and 48 cubs) in 1995 and 77 foxes (32 adults and 45 cubs) in 1996 within the search area of 61.3 km$^2$. Density of natal dens within the search area was 0.28 dens/km$^2$ in 1995 and 0.26 dens/km$^2$ in 1996. Density of foxes was calculated to be 0.55 adult foxes/km$^2$ prior to breeding and 1.34 foxes/km$^2$ post-breeding during the spring of 1995 and 0.52 adult foxes/km$^2$ prior to breeding and 1.26 foxes/km$^2$ post-breeding in 1996.

Density was also calculated using the average number of dens vixens were observed to use. In winter 1995 there were 68 active dens within the search area (1.10 active dens/km$^2$), which amounts to 28 vixens, at 2.4 dens/vixen. Assuming there was only one vixen per den and a 1:1 sex ratio, this calculated to 56 adult foxes within the search area, or 0.91 foxes/km$^2$. In winter 1996 there were 96 active dens within the study area (1.57 active dens/km$^2$), giving 40 vixens and hence 80 adult foxes within the search area. This translates to a pre-breeding density of 1.30 adult foxes/km$^2$.

## 3.4 DISCUSSION

### 3.4.1 Den usage and identification

Foxes at Murringo were found to use multiple dens, with approximately three times more dens showings signs of occupation during winter than during spring. Use of dens also varied between years, as reported in other studies from around the world (Sargeant *et al.* 1975; Storm *et al.* 1976; Insley 1977; Lloyd 1980; Harris 1981; Henry 1986; Nakazono and Ono 1987; Coman *et al.* 1991; Saunders *et al.* 1995; Marks and Bloomfield 1999). The number of natal dens was relatively constant between years, similar to findings in Japan (Nakazono and Ono 1987). The proportion of dens identified as natal was also similar to findings of Nakazono and Ono (1987), despite over five times as many dens identified per unit area in the Murringo study.

The total number of dens identified during the study increased steeply throughout the study, largely due to a number of old, inactive dens identified in the second year of searching that had been previously overlooked. The number of active dens identified did not increase as markedly as inactive dens in the second year of surveying, suggesting that active dens were identified more successfully from the initiation of searching. In a 15 year study of fox den use in Japan, Nakazono and Ono (1987) indicated it took three years of searching to reach comprehensive cover of the site. After this point the total number of recorded dens increased gently and there was a balance between newly identified dens and those that were apparently abandoned.

In terms of using dens to estimate population size, it is most important to have accurate estimates of the numbers of natal and other active dens. Inactive den numbers are irrelevant to this analysis. Thus the lower success at finding inactive dens is not detrimental to the density estimates generated by this study, although it has implications for studying general persistence of dens, turnover of occupancy of dens, patterns of distribution of dens and whether den availability is limiting fox population size.

### *3.4.2 Mark-recapture analysis*

Applying mark-recapture analysis to the data set gave similar estimates of den numbers to that observed directly. Estimates from winter to spring of each year using the Petersen estimate were particularly tight. Confidence limits were narrow, and biased upwards of the estimate. Confidence limits by this method are not symmetrical around the estimate (Krebs 1999). The assumption of the population being closed to additions and deletions (Seber 1982; Pollock *et al.* 1990; Lancia *et al.* 1994; Krebs 1999) was reasonable given very high persistence of dens over the time period and that very few new dens were likely to be dug after the winter period due to cessation of breeding. There were also no problems with recognising dens that had been previously marked, and marking did not affect the den in any way. There may have been minor violation of the assumption of equal catchability within each sample. The nature of the spring search was to revisit all dens located by systematic surveying during winter. This essentially involved retracing all ground covered in the winter survey but with the handicap of dense vegetation obscuring dens. The dense vegetation meant that dens overlooked in winter were even less likely to be found during the spring surveys. This bias would not have been as strong for active dens, as vegetation tended to be disturbed around these, but previously overlooked inactive dens were very unlikely to be identified. The very high recapture rate indicated relocation of dens was extremely successful.

The estimates of den numbers using Jolly Seber analysis also gave findings similar to that observed directly. Confidence intervals could not be calculated for most of these estimates as the analysis does not estimate standard error correctly when survival is close to 1 (White 2000). When only active dens were considered, the estimates were similar to numbers directly observed in the winters of each year but confidence intervals were very broad for the spring 1995 estimate. This fits with the general observation that success at identifying dens improved by the second year of systematic surveying, and that numbers identified in the 1995 survey were likely to be underrepresentative.

The assumptions of Jolly Seber analysis were generally reasonable, with the possible exception of the assumption that every den has the same probability of being caught in the *t*-th sample, whether marked or unmarked. Growth of vegetation hindered sightability of dens in the spring surveys, so dens not marked in the winter survey were less likely to be found in spring than marked dens. This bias would have been less pronounced for active dens than inactive dens, as disturbance of vegetation around these highlighted their presence, and was unlikely to have greatly influenced winter surveys when vegetation cover was not a problem. High persistence of all dens supports the assumption that every marked den has the same probability of surviving from the *t*-th sample to the ($t$+1)th sample. There were no problems with recognising marked dens and the lengths of the survey periods were brief compared with the intervening time intervals.

It is very difficult to find data to test the outcomes of mark-recapture experiments, as it is very rare to know the true population size with which to compare the estimates. In this study it is likely that what was observed was very near the true population size, particularly in the 1996 surveys, and this is supported by the findings of the two mark-recapture methods employed. This finding lends support to the effectiveness of this method of den searching for measuring the number of dens in an area, which can then be used to estimate population densities of foxes.

### *3.4.3 Den habitat and form*

The majority of dens, both natal and non-natal, were located in creeklines or gullies, and were usually dug into the ground. Where dens occurred away from gullies they tended to be under or within trees or fallen logs. These habitats are typical of those reported by other authors from around the world (Storm *et al.* 1976; Lloyd 1980; Henry 1986). In a study of fox denning behaviour in urban Melbourne, Marks and Bloomfield (1991) reported natal dens to be characteristically in quiet locations where they were seldom disturbed by humans. Henry (1986) described dens as usually occurring within 100m of a water source. Gullies in the Murringo site offered less risk of disturbance from general farming activities such as ploughing, sowing and harvesting of paddocks, as well as allowing more secretive movements to and from dens. Soil away from gullies was often rocky and less friable, making digging dens much more difficult. Such areas tended to be used for grazing rather than cropping, so trees, fallen timber and other potential refugia were more abundant than in cropped areas. Moreover gullies were commonly dry. It seems likely, then, that the prevalence of dens in gullies was more due to reduced risk of disturbance rather than proximity to water.

As outlined in the introduction, some studies reported that foxes preferentially use open areas for denning (Sheldon 1950; Henry 1986; Hewson 1986; Nakazono and Ono 1987) whereas Storm *et al*. (1976) found a preference for wooded areas. This is likely to be due to dens being more conspicuous in open areas, as the Storm *et al*. (1976) study was the only one which used radio-tracking to locate dens, a technique unaffected by how visible dens are. In the present study essentially all dens were found in open areas, but very little forested cover was available. There was no significant difference in location (gully, away from gully) and appearance (dug, under log etc) of dens found whether by searching for visual cues or by radio-tracking, suggesting the search technique was effective at identifying dens and thoroughly covered the area.

Dens usually had multiple entrances, as reported by Henry (1986). Natal dens had more entrances on average than non-natal dens. Nakazono and Ono (1987) observed that dens were initially very simple in structure with few entrances and became more complex with increased visitation by foxes, eventually evolving into natal dens with multiple entrances. The advantage of having multiple entrances is not clear, but it may be an adaptation to predator avoidance by providing multiple escape routes and more scope for unobserved entry and exit, or may aid with thermoregulation or ventilation.

### *3.4.4 Den distribution*

Nearest neighbour analysis of den locations indicated natal dens were regularly distributed across the study area, while non-natal active dens occurred in clusters. Vixens were observed to use more than one den, so it is likely that clusters were occupied by the same vixen. Nakazono and Ono (1987) also found regular spacing of natal dens with associated clusters of other active dens. Regular spacing of natal dens was also reported by Marks and Bloomfield (1999) and Hewson (1986), but activity in non-natal dens was not described. Territoriality is likely to be the mechanism driving this regular spacing of natal dens, with possible motivations being to ensure sufficient resources for the family group and/or to avoid cubs encountering neighbouring family groups. It is widely reported that foxes will move their cubs to a different location from the natal den, as was observed on one occasion during this study, and it is likely that the observed clusters of active dens are maintained for such a purpose. Shifting may have occurred at other dens during this study, but because the surveys were conducted quickly, covering blocks of several square kilometres each day, it was unlikely to be detected nor to have influenced counts of natal dens, as vixens would not have had time to shift cubs to another den in the vicinity during the search period.

### *3.4.5 Methodological limitations*

The methods used to locate dens may have caused biased results. During the study, newborn cubs were observed as early as mid-September, and as late as mid-December. If the area was searched too early in the breeding season the natal dens would be missed, but if delayed until later, evidence of breeding would be lost from the dens of early breeders. Visiting the dens on additional occasions would address this problem, but if counts are done on multiple occasions there is a risk that litters will be shifted to a different location and counted again. The late winter (August) search could not be conducted any later in the season as vegetation growth during spring obscured dens, which would have resulted in many dens being overlooked. All dens located in the winter search could be relocated in spring, but any dens constructed post-winter search were therefore not included unless found opportunistically.

### *3.4.6 Persistence of dens*

There were many disused dens in the area, and high turnover of which dens were occupied at any time, suggesting den availability was not a limiting factor on population size. Although based on a brief time period, the high survival estimates generated using Kaplan-Meier and Jolly Seber analyses indicate that dens are very likely to persist year after year, but that the probability of dens remaining active year after year is much lower. Although data are limited, the denning behaviour of radio-tagged vixens indicated high turnover of tenants within dens, and that vacated dens were readily re-occupied. This was also supported by observations of repossession of dens at which the occupant had died. Nakazono and Ono (1987) also reported high turnover of which dens were active in any one year, although the total number active stayed relatively steady. Natal dens were more likely to be used on repeated occasions than non-natal dens, not necessarily by the same vixen, suggesting attributes of these dens were desirable for successful cub-rearing, and there may have been competition for such locations. Other studies looking at fox den usage have also commonly found breeding dens to be used on repeated occasions, often not in consecutive years (Storm *et al.* 1976; Page 1981; Henry 1986; Nakazono and Ono 1987). Two studies reported natal dens persisting much longer than the lifespan of foxes (up to 35 years), and also observed natal dens falling into obsolescence for a number of years before being reoccupied (Storm *et al.* 1976; Nakazono and Ono 1987), indicating successive tenancy of breeding dens by vixens.

### 3.4.7 Density estimation

The present study estimated average litter size to be 2.8 cubs, which is comparable to the findings (3.3) of Coman *et al.* (1991) in rural Victoria, but lower than other reported figures of 4.0 (Saunders *et al.* 1995), 4.25 (McIntosh 1963b) and 3.7 (Ryan 1976). A concurrent study into litter sizes in the central tablelands of NSW found average litter size to be 4.0 (n=157), and 8% of vixens to be barren (n=226) (Saunders, unpublished data). The latter study used placental scar counts to estimate litter size, which is not dependent on cubs being emergent simultaneously but does not include loss due to infant mortality, so it is expected that litter size estimates would be higher by this method.

The observed density of active dens in the present study varied between years (1.1-1.6 dens/km$^2$), averaging 1.3 dens/km$^2$. Density of natal dens was steady at 0.3 den/km$^2$, lower than Coman *et al.*'s (1991) reported 0.5-0.7 natal dens/km$^2$ in rural and semi-urban Victoria, and Marks and Bloomfield's (1999) average of 1.0 natal den/km$^2$ across 4 urban sites. Likewise, the post-breeding density of foxes was estimated to be 1.3 foxes/km$^2$, which is much lower than Coman *et al.*'s (1991) estimate of 3 foxes/km$^2$, and estimates by Marks and Bloomfield (1999) of 3-16.2 foxes/km$^2$. However, unlike the present study, these studies did not incorporate a boundary strip so their estimates are expected to be higher. Other studies in eastern Australia estimated density to be 4.6-7.2 foxes/km$^2$ on the northern tablelands of NSW (Thompson and Fleming 1994), 0.2 foxes/km$^2$ in forest on the south coast of NSW (Newsome and Catling 1992), 1.8 foxes/km$^2$ in sub-alpine NSW (Bubela 1995) and 0.9 foxes/km$^2$ in semi-arid grazing habitat in Western NSW (Marlow 1992). Density estimates in the present study appear more similar to those from less productive habitats in sub-alpine (Bubela 1995) and semi-arid Australia (Marlow 1992) than to the study in the most similar habitat on the NSW tablelands (Thompson and Fleming 1994), but this is more likely due to differences in methodology used to estimate density rather than that foxes are at particularly low densities in the present study.

The estimated density of foxes in late winter was lower using natal den counts (0.52-0.55 adult foxes/km$^2$) than that estimated using active den counts (0.91-1.30 adult foxes/km$^2$). Coman *et al.* (1991) estimated a winter density of 1.2 foxes/km$^2$ using natal den counts and 3.9 foxes/km$^2$ in late autumn using a capture/recapture technique. Active den counts and capture/recapture estimates are independent of whether foxes actually breed, and that both these studies found higher estimates by these methods rather than natal den counts suggests a significant number of non-breeding adults were present in both populations. Both Coman *et al*. (1991) and Marks and Bloomfield (1999) acknowledge this potential bias in estimates based on natal den counts. They also question the assumption of natal dens being occupied by a breeding pair of foxes, citing a number of studies where family groups with more than one vixen, and sometimes more than one adult male, were observed. While accepting that family groups may contain multiple vixens, Harris (1981) also made this assumption in his model of fox population structure in Bristol. The present study also observed dog-foxes and breeding vixens with overlapping home ranges (Chapter 2), indicating this assumption is overly simplistic.

### *3.4.1 Conclusions*

In summary, the search technique was successful at locating dens, particularly natal and other active dens. A considerable number of inactive dens were located, and there was much turnover of active dens between years, suggesting availability of suitable den locations was not limiting fox numbers. However to build a clearer picture of persistence of dens and turnover of occupants, a much longer-term study would be required. Natal dens were evenly dispersed across the site, while other active dens were clustered. Foxes tended to locate dens in gullies, dug into the soil, but also utilised resources such as hollow logs, trees and fallen timber. Estimates of fox density based on natal den counts showed little fluctuation between years, although more fluctuation was detected using active den counts. Estimates based on natal den counts can be regarded as a minimum population density for the Murringo area, as they relied upon a simplistic social structure, used minimum litter size estimates and did not take into account presence of non-breeding adults. Even so, density is relatively high compared with other rural studies. The study also provided an opportunity for a novel application of mark-recapture analysis, with the mark-recapture estimates comparing favourably with the actual observations.

# CHAPTER 4

# ACTIVITY RHYTHMS

## 4.1 INTRODUCTION

Foxes are largely nocturnal, with a tendency towards crepuscular activity, according to studies in North America (Storm 1965; Ables 1969a; Adkins and Stott 1998), Japan (Takeuchi and Koganezawa 1992) and Europe (Maurel 1980; Blanco 1986; Saunders *et al.* 1993; Cavallini and Lovari 1994; Lovari *et al.* 1994; Weber *et al.* 1994; Reynolds and Tapper 1995; Doncaster and Macdonald 1997). In Australia, foxes have been reported to be most active during the night (Jarman 1986; Bubela 1995; Saunders *et al.* 1995; Banks 1997; Meek 1998). Timing of activity can be affected by prey activity (Cavallini and Lovari 1994; Lovari *et al.* 1994) and to avoid human disturbance (Blanco 1986; Weber *et al.* 1994). Activity levels of vixens have been observed to drop during lactation (Takeuchi and Koganezawa 1992; Doncaster and Macdonald 1997), and Phillips and Catling (1991) reported that in south-eastern New South Wales a female changed from mainly nocturnal to diurnal activity during denning in October but a male fox did not change. Seasonal differences in levels of activity have also been reported. In England, Saunders *et al.* (1993) found male foxes were significantly more active in autumn and winter, while Reynolds and Tapper (1995) observed a lull in activity in the middle of the night during autumn and winter. Doncaster and Macdonald (1997) found activity was spread over a greater number of hours during winter nights but that there was no change in the number of hours active across seasons. In North America foxes were observed to be more diurnal in winter than in other seasons (Ables 1969a), whereas in Europe foxes were more diurnal during summer (Cavallini and Lovari 1991).

Predominantly nocturnal behaviour is common to the majority of the canid family (Gittleman 1989). Many carnivores exhibit peaks in activity around twilight, and this is thought to be because twilight is the prime time for hunting and food gathering, this being the overlap period for many diurnal and nocturnal prey species and a peak time for many insects (Kavanau and Ramos 1975). The visual system of the red fox is best adapted for dim light, but they also see well in daylight (Kavanau and Ramos 1975).

Information on when foxes, and indeed other species, are active is useful in many situations. For example, in this study relative density was estimated by spotlight counts from moving vehicles (Chapter 5). Preferably such surveys should be carried out at consistent levels of activity. Prior knowledge of fox activity patterns can also be useful in designing studies on ranging behaviour. In this study, the bulk of radio-tracking of foxes was carried out when they were expected to be at their most active, under the assumption that they are likely to cover more of their range during these periods (Chapter 2). Palomares and Delibes (1992) found that studies of habitat use are biased if activity patterns of the animal under study are not taken into account. Studies on energetics and metabolic rates would benefit from a profile of activity rhythms at different times of the year to assist in interpretation of results. Also control programs such as spotlight shooting are likely to be more effective if done when foxes are out and about, while a knowledge of activity patterns of predators may allow people managing stock or wildlife to predict when such populations are more likely to be at risk of predation.

In describing daily activity patterns, the underlying assumption is that there **is** a daily recurring cycle. In a review of mammalian activity rhythms, Ashby (1972) noted that in mammals there appears to be an endogenously determined periodicity of activity of approximately 24 hours, so this assumption appears justified. This chapter will present findings on fox activity rhythms, and will outline a new method of analysing data on animal activity rhythms.

## 4.2 METHODS

### *4.2.1 Data collection*

Data were collected by fixed tower radio-telemetry, virtually all by a single observer, between March 1995 and December 1996. Data were collected at all times of day, and come from a total of 34 adult foxes (20 female, 14 male). During any one month the number of foxes being studied averaged 17.9 (10.2 females and 7.7 males) and ranged from 10 to 24 foxes. Because the primary goal of the exercise was triangulation of bearings, and movement data was collected as an incidental, the data set is somewhat patchy and unevenly distributed. Radio signals tend to fluctuate when the animal is moving, and this property was used to identify active fixes. This property has been used previously for red foxes (Ables 1969a; Phillips and Catling 1991; Weber *et al.* 1994; Bubela 1995; Reynolds and Tapper 1995). Each frequency was listened to for 20 seconds (Erlinge 1980), and if any fluctuations were noted during that time the fix was deemed active; otherwise it was deemed steady. Data were pooled into 1-hour intervals and the percentage of active fixes in each interval calculated over the 24-hour period. Over the duration of the study there was an average of 141 fixes per fox, with the average for females being 136 and for males 147 fixes.

Because there were occasional gaps or hours in which there was little data, an Average Shifted Histogram approach was used to pool intervals (Härdle 1991). This involved combining each 1-hour interval with the intervals before and after, and averaging, thereby effectively giving a weight of 1 to the interval under consideration and 0.5 to the intervals before and after. This method meant that unless there were 3 successive intervals without fixes, activity ratios could still be estimated, but still retained enough definition in the data set that fluctuations in activity could be examined. A further advantage of using the Average Shifted Histogram approach to pooling intervals is that it avoids arbitrarily deciding whether to pool each interval with the one before or the one after (Härdle 1991).

### *4.2.2 Fourier analysis*

A common approach for identifying peaks and troughs in a 24-hour pattern is to repeatedly sample the proportion of animals moving at different times. When graphed, such a time series yields a histogram-like graph (eg Blanco 1986; Reynolds and Tapper 1995; Banks 1997), with steps corresponding to discrete sampling intervals. However it is reasonable to assume that the behaviour patterns this step function is based on are better described by a continuous function that respects the nature of the underlying data. This chapter now looks at how such a step function should be smoothed.

Movements of individual animals are made up of (a) cyclical components, which depend on factors such as day length and hormonal changes, and (b) “noise”, which depends on occasional and random factors such as weather, illness, proximity to predator or prey, haphazard movements by the animal and inaccuracies in data collection. When movements of categories of animals are considered, the noise component includes differences in behaviour of various subcategories. If samples are large, these subcategory differences will be largely cancelled, enabling major cyclical factors common to all subcategories to be identified. The more narrowly defined the category (eg male foxes in a particular month), the more structure (ie more cyclical components) the movement pattern is expected to have, these additional cycles being features of that category. However sample sizes for such narrow categories are liable to be small, giving less predictive value to the data.

Ideally any smoothing process should remove the noise without losing the underlying signal. The smoothing method outlined here uses truncated Fourier series (also referred to as partial sums of Fourier series) to describe the signal mathematically. In addition, the residual “roughness” after smoothing may itself provide a basis for comparison between classes of animals.

Often cyclical animal behaviour is composed of cycles upon cycles (epicycles). These cycles can reinforce or neutralise each other, giving the overall pattern. Each of these cycles can be described mathematically by means of a sine or cosine function. With enough such terms, any function can be described over a given interval to any required accuracy. Truncated Fourier series analysis does just this: the overall function is broken down into its component cycles and then truncated at an appropriate point so as to retain meaningful cycles while removing the noise components. The general form of a Fourier series (James 1993), truncated at $k$ terms for cycles within a 24 hour period is:

$$f(t) \approx A_0 + \sum_{n=1}^{k} A_n \cos(\frac{2n\pi t}{24} + \varphi_n)$$

where $f(t)$ = function being smoothed

$A_0$ = average value of the function $f$ over a 24h period

$A_n$ = amplitude of $n$th cyclical component

$\varphi_n$ = phase angle of $n$th cyclical component, which indicates the time(s) when this component peaks

In this study, $f(t)$ was the proportion of animals active at time $t$.

If a mathematical description of this form can be obtained for the data, then the periods and amplitudes of the various components can be estimated, and the components that dominate an animal's behaviour and at what times they are most influential on its movements can be interpreted. The analysis also allows comparison between different categories, such as sexes of animals or seasons, and can focus a search for an underlying biological basis for the most significant cycles. In addition, spikes or outliers can be clearly identified and, given appropriate observational data, it may be possible to identify what incidents lead to which outliers. Note that the presence in a truncated Fourier series of a term with frequency $\omega$ (say) does not, in itself, mean that the animals have a behavioural pattern with frequency $\omega$. It can also mean that a behavioural pattern of lower frequency than $\omega$ is not exactly sinusoidal, the higher frequency terms jointly indicating the degree of deviation of the pattern from the sinusoidal (Diggle 1990).

The study describes here the first time this method of Fourier series analysis has been used to describe animal activity patterns. An alternative method using discrete (rather than continous) Fourier series has been used before (see eg Diggle 1990; Semen *et al.* 1997). These authors use discrete Fourier series to fit a set of discrete sequential data. In the present study the data consisted of proportions of foxes found to be active over intervals of one hour. This does not present a 'snapshot' at a particular moment, such as the proportion of foxes active at say 12noon, 1pm and 2pm, but rather the proportions active over the continuous intervals 12noon-1pm and 1pm-2pm. Since a continuous rather than a discrete process was being modelled it was considered more appropriate to use continuous Fourier series than discrete Fourier series.

Continuous Fourier series minimise the 'Integrated Square Error' (ISE) which is a measure of the area between the data curve and the curve made by the Fourier approximation. Discrete Fourier series, on the other hand, minimise the Total Sum of Squares (SS), which is the sum of the squared distances between each data point and the Fourier approximation at the same timeslot (squaring is using in both methods to ensure positive and negative differences don't cancel each other out). Both the ISE and the SS can be expressed as sums of squares of the Fourier Coefficients. Because they relate to points rather than to an overall approximation to a curve, discrete Fourier series were not considered the appropriate tool for curve smoothing. Nevertheless a discrete Fourier approximation was made to the total data set for comparative purposes, and results found to be extremely similar (unpublished data).

A spreadsheet was set up in Microsoft EXCEL to perform a Fourier analysis and plot the resultant cycles, given the percentage of active fixes in each 1-hour interval. The final formulae are given below.

If:

$$\frac{a_0}{2} = \frac{1}{6}\sum_{i=1}^{24} p_i \qquad \text{and, for n} \geq 1$$

$$a_n = \frac{1}{n\pi}\sum_{i=1}^{24} p_i (\sin\frac{n\pi i}{12} - \sin\frac{n\pi(i-1)}{12})$$

$$b_n = -\frac{1}{n\pi}\sum_{i=1}^{24} p_i (\cos\frac{n\pi i}{12} - \cos\frac{n\pi(i-1)}{12})$$

$$\text{Then } p(t) = \frac{a_0}{2} + \sum_{n=1}^{\infty}(a_n \cos\frac{n\pi t}{12} + b_n \sin\frac{n\pi t}{12}) \qquad \text{for } 0 \leq t < 24$$

$$= A_0 + \sum_{1}^{\infty} A_n \cos(\frac{2n\pi t}{24} + \varphi_n)$$

$$\text{When } A_0 = \frac{a_0}{2}, \quad A_n = \sqrt{a_n^2 + b_n^2}, \quad \varphi_n = -\mathrm{sign}b_n \mathrm{a}\cos\frac{a_0}{A_n}$$

where $p_i$ = proportion observed active in *i*th 1-hour timeslot

$p(t)$ = Fourier approximation to proportion active at time $t$

and $t$ is measured in hours.

As mentioned above, if $t$ is in *i*th timeslot, then $p(t) = p_i$.

$p(t)$ can be approximated by the truncated Fourier series

$$A_0 + \sum_{n=1}^{k} A_n \cos(\frac{2n\pi t}{24} + \varphi_n)$$

where, by the theory of Fourier series, the ISE ∏ 0 as k ∏ ∞

### *4.2.3 Integrated square error (ISE) calculation*

Also calculated was the integrated square error (ISE) of the Fourier approximation to the data set. The ISE indicates how much variation there is from the basic rhythmic pattern, or, in other words, the degree to which the truncated series considered approximates the data.

For the above Fourier series calculations, the ISE (Wand and Jones 1995) is:

$$\int_{c}^{c+T} p(t)^2\,dt - T(A_0{}^2 + \frac{1}{2}\sum_{n=1}^{k} A_n{}^2)$$

### *4.2.4 Activity rhythms of categories*

When the total data set was broken down into categories, in many cases gaps still remained in the data set following ASH analysis, which meant the Fourier calculations could not be done. Wherever there are only a few readings in a given time slot, a slight change or any noise in the data has a large impact on the percentage recorded as active. It was arbitrarily decided that calculations would not be carried out on data sets where any time slot contained fewer than 12 readings.

Data were not collected evenly across the year, which meant the shape of the overall plot could potentially be biased towards the characteristics of the months when more data were collected. The average number of data per month was 531, with a minimum of 213 in March and a maximum of 1005 in October. No data were collected in January, April and June. Data sets which were sufficiently large were (a) Octobers, (b) all months except Octobers, and (c) daylength >13h. These sets were also able to be subdivided into males and females. Comparisons could not be made for short day length, months other than October nor between individual foxes, but some data from individual foxes is presented to illustrate profiles.

### *4.2.5 Day length correction*

Since data was collected at different times of year with varying day and night lengths, the data sets were also corrected for sunrise and sunset times in such a way that there were 12 “segments” each of day and night, with the sun rising at the beginning of segment 6 and setting at the beginning of segment 18. Day segments were calculated by dividing the time between sunrise and sunset at each period of data collection by 12. This gave the length of each segment, and data were then assigned to the segment into which the time they were collected at fell. Night segments were calculated similarly, dividing the period from sunset to sunrise into 12 equal segments. As for the “clock time” data set, this “segment time” data set was pooled into 1-segment intervals and percentage active fixes calculated. The division of “daytime” (ie the interval sunrise to sunset) into equal subintervals, and “nighttime” into the same number of equal subintervals (different in length from the daytime subintervals) seems to have been near universal in ancient human cultures and in Europe until about 1200 AD (Richmond 1956).

Both clock and segment time data sets were then broken down to look for differences in activity rhythm between sexes, individual foxes, seasons and readings at different day lengths.

### *4.2.6 Truncation of series*

Tarter and Lock (1993) provide a single-term stopping rule for deciding where a Fourier series should be truncated when estimating an unknown probability density function. While the series under study were not density functions, the rule was still considered to see what it advised. It was, however, dismissed as inappropriate due to the meaninglessly high number of terms it recommended for inclusion. As the data sets being smoothed were made up of 24 ‘steps’, it would be meaningless to include more than 24 cyclic terms. Moreover the method used to collect the data was quite rough, so many of the irregularities within the data sets were likely to be noise, not cyclical behaviour. This means that taking more and more cycles may simply be creating a better fit to the noise rather than describing behavioural patterns.

As explained earlier, the more narrowly defined the category, the more cyclical factors are likely to be identified, whereas a broad category is likely to merely show general cycles common to all subcategories included. Using the integrated square error (ISE) as a guide to how well the Fourier series approximated the data set with each additional term, it was decided to truncate the series at the point where including further terms did not greatly reduce the ISE, up to a maximum of 4 cyclic terms.

## 4.3 RESULTS

### *4.3.1 Clock time versus segment time*

In the majority of situations considered, the ISE was found to be smaller when segments corrected for daylength were used rather than those for clock time (Table 4.1). Where clock time had a smaller ISE, the difference was usually very small. This indicates that using segment time generally results in a better fit to the curve. $A_0$ values (the average percentage active in each time slot) were very similar for segment and clock time (Table 4.1), as were times and magnitudes of points of maximum and minimum activity (Table 4.2). In all cases the amplitude of the 12-segment cycle was always considerably larger than that of the 12-hour cycle (Table 4.1). Hereafter, unless otherwise stated, results presented are based on segment time rather than clock time.

### *4.3.2 Overall fox activity*

It was found that overall the daily activity patterns of foxes in the study area could be reasonably approximated by the first two cyclical terms of the Fourier series. In other words, fox activity patterns could generally be described by 24-segment and 12-segment cyclical components rising and falling sinusoidally (Figure 4.1). Activity levels rose steeply from late afternoon, peaking at around the 20th segment, then remained high all night (Figure 4.1; Table 4.2). Activity fell away shortly before dawn and reached its minimum just before midday. Overall average fox activity was 44.8% ($A_0$), and the integrated square error (ISE) after two cyclical components was 0.013, as estimated for segment time (Table 4.1). Inclusion of further components did not greatly reduce the ISE (Figure 4.2).

Table 4.1. Number of fixes of foxes, average percentage moving ($A_0$), amplitude of cycles (in segments or hours) and integrated square error (ISE) to/at point of truncation, for segment (seg) and clock time data. (– indicates truncated before cycle).

| Category | Fixes | Time | $A_0$ | 24 | 12 | 8 | 6 | ISE cutoff |
|---|---|---|---|---|---|---|---|---|
| All foxes | 4782 | Seg | 44.8 | 12.6 | 6.6 | – | – | 0.013 |
| | | Clock | 44.6 | 12.4 | 5.7 | – | – | 0.020 |
| All foxes - Oct | 1005 | Seg | 46.0 | 19.3 | 9.6 | 5.8 | 6.3 | 0.032 |
| | | Clock | 45.2 | 20.4 | 8.5 | 4.5 | 6.0 | 0.038 |
| All foxes - not Oct | 3777 | Seg | 45.2 | 13.5 | 5.0 | 5.4 | – | 0.016 |
| | | Clock | 45.2 | 13.1 | 4.2 | 5.6 | – | 0.013 |
| All foxes >13h day | 2225 | Seg | 43.5 | 15.3 | 5.5 | 3.5 | 4.9 | 0.025 |
| | | Clock | 42.9 | 16.1 | 4.1 | 2.5 | 3.7 | 0.030 |
| All females | 2764 | Seg | 46.7 | 12.6 | 7.6 | – | – | 0.012 |
| | | Clock | 46.6 | 12.4 | 6.4 | – | – | 0.023 |
| All males | 2018 | Seg | 42.2 | 13.0 | 5.1 | 4.9 | – | 0.028 |
| | | Clock | 41.8 | 12.7 | 4.6 | 4.8 | – | 0.025 |
| Females - Oct | 579 | Seg | 47.1 | 17.8 | 12.2 | 9.2 | 8.0 | 0.039 |
| | | Clock | 46.4 | 19.3 | 10.8 | 6.6 | 6.5 | 0.037 |
| Males - Oct | 426 | Seg | 44.8 | 21.6 | 5.9 | 2.9 | 5.5 | 0.069 |
| | | Clock | 44.0 | 22.2 | 5.5 | 3.6 | 6.7 | 0.067 |
| Females - not Oct | 2185 | Seg | 47.3 | 13.9 | 5.3 | 4.1 | – | 0.014 |
| | | Clock | 47.5 | 13.8 | 4.0 | 5.1 | – | 0.013 |
| Males - not Oct | 1592 | Seg | 42.2 | 13.1 | 4.7 | 8.0 | – | 0.023 |
| | | Clock | 41.9 | 12.5 | 4.6 | 7.0 | – | 0.023 |
| Females >13h day | 1250 | Seg | 46.3 | 16.9 | 8.4 | 7.0 | 7.5 | 0.035 |
| | | Clock | 46.1 | 18.2 | 7.1 | 4.1 | 7.1 | 0.047 |
| Males >13h day | 975 | Seg | 40.0 | 13.8 | – | – | – | 0.043 |
| | | Clock | 38.8 | 14.2 | – | – | – | 0.039 |

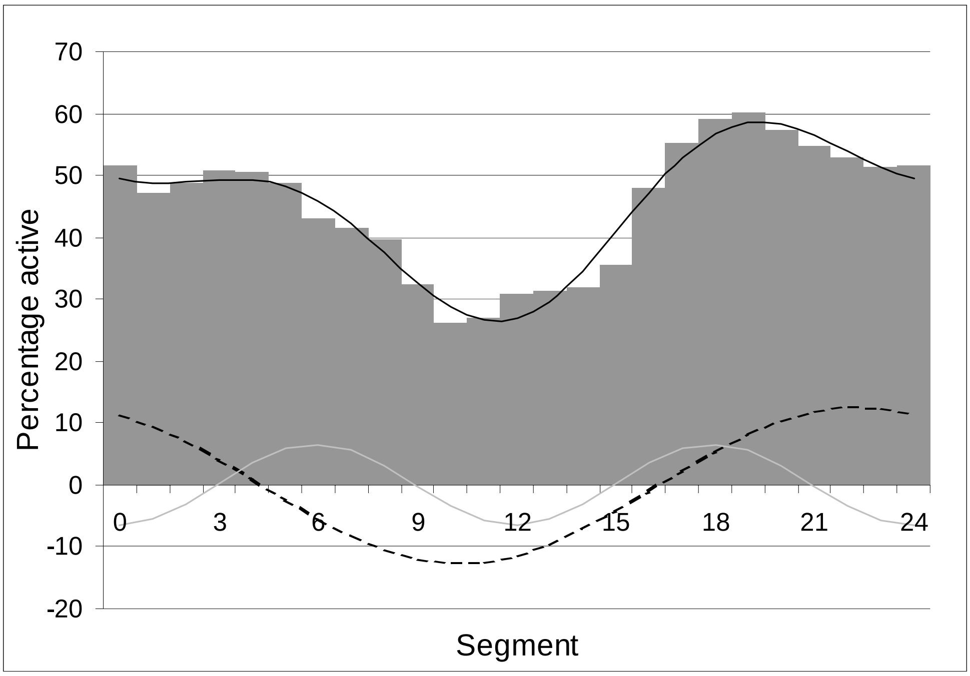


Figure 4.1. Overall fox activity rhythm, using segment time, based on 2 cyclical components.

( ▨ raw data, ——overall curve,- - - -24 seg cycle, ——12 seg cycle)

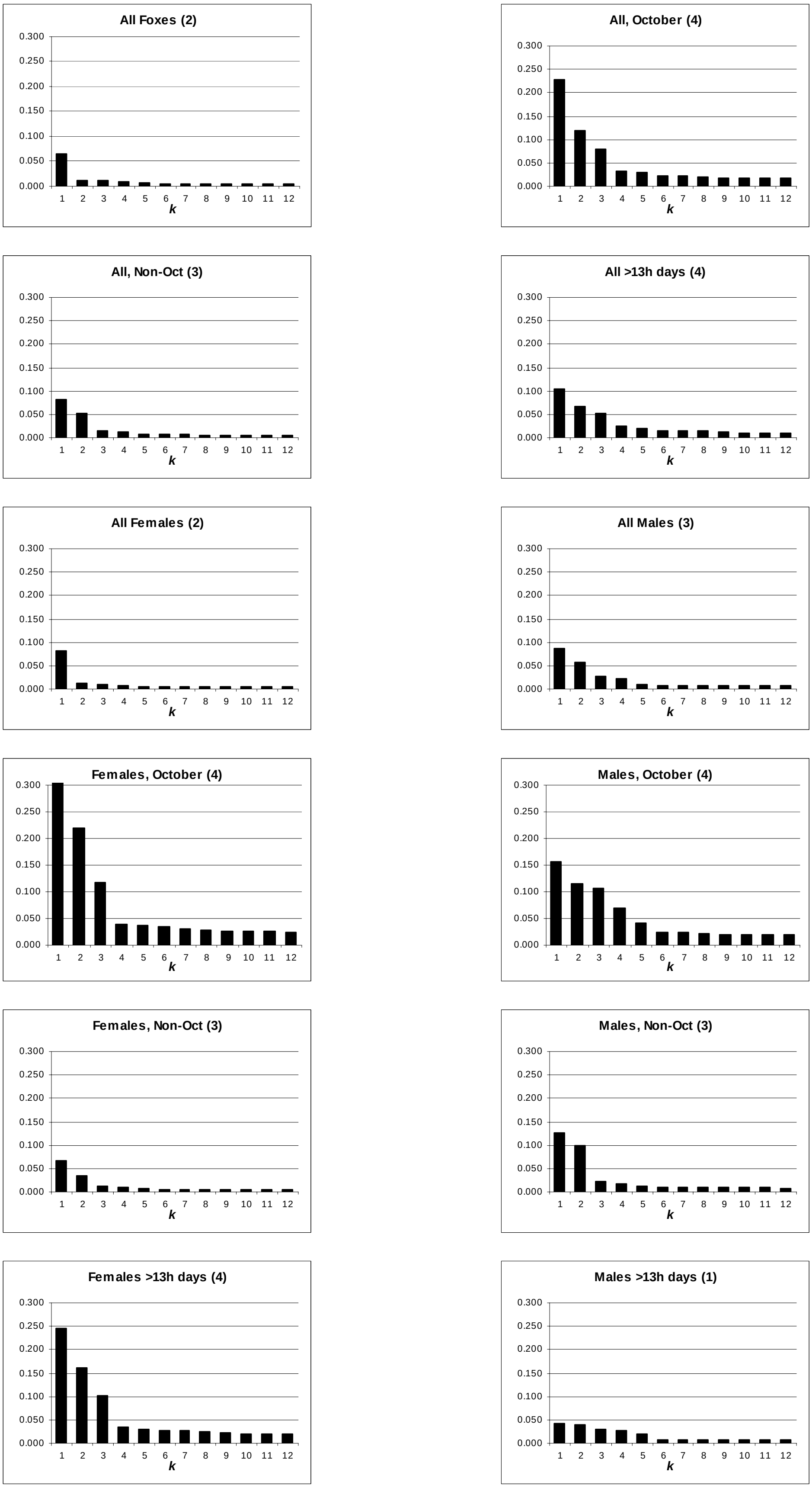


Figure 4.2. Integrated square errors (ISE) after inclusion of increasing number of cycles for all categories of foxes analysed. Number of cycles included shown in brackets.

Table 4.2. Time (in segments or hours) and percentage of foxes active at points of maximum and minimum activity for plots based on both clock and segment (seg) time.

| Category | Maximum Activity | | | | Minimum Activity | | | |
|---|---|---|---|---|---|---|---|---|
| | Time | | % active | | Time | | % active | |
| | Clock | Seg | Clock | Seg | Clock | Seg | Clock | Seg |
| all foxes | 20 | 20 | 58 | 57 | 12 | 12 | 27 | 26 |
| all foxes - Oct | 19 | 19 | 70 | 69 | 9 | 10 | 15 | 16 |
| all foxes - not Oct | 2 | 3 | 58 | 58 | 14 | 14 | 24 | 24 |
| all foxes >13h day | 22 | 22 | 62 | 62 | 9 | 9 | 24 | 24 |
| all females | 19 | 20 | 62 | 63 | 12 | 12 | 31 | 26 |
| all males | 20 | 20 | 58 | 57 | 14 | 14 | 26 | 26 |
| females - Oct | 18 | 18 | 78 | 70 | 9 | 10 | 16 | 16 |
| males - Oct | 19 | 19 | 75 | 73 | 10 | 10 | 14 | 16 |
| females - not Oct | 2 | 19 | 61 | 60 | 13 | 13 | 26 | 26 |
| males - not Oct | 3 | 3 | 56 | 60 | 14 | 14 | 21 | 21 |
| females >13h day | 22 | 22 | 68 | 71 | 9 | 9 | 22 | 23 |
| males >13h day | 21 | 20 | 54 | 55 | 9 | 9 | 25 | 26 |

### *4.3.3 Potential skewing of data*

Data were not collected evenly across the year, which meant the shape of the overall plot could potentially be skewed towards the characteristics of the months when more data was collected. To check for any indications of such distortion, data were taken for the month in which the most data were collected, October, and compared to the data set for the remaining months of the year. In this way data sets from different times of year could be compared. The average percentage of readings that were active ($A_0$) was found to be similar for both October and non-October data (46.0% October, 45.2% non-October; Table 4.1). However the overall profiles of the two data sets were quite different, with higher activity levels in the afternoon and evening in October, whereas in the non-October data set there was considerably more activity in the morning (Figure 4.3). There was also a much greater swing between minimum and maximum activity levels in October (16%-69% in October, 24%-58% non-October) (Table 4.2; Figure 4.3). The non-October data set was adequately described by 3 cycles whereas October required 4 cycles to describe the data (Figures 4.2 and 4.3).

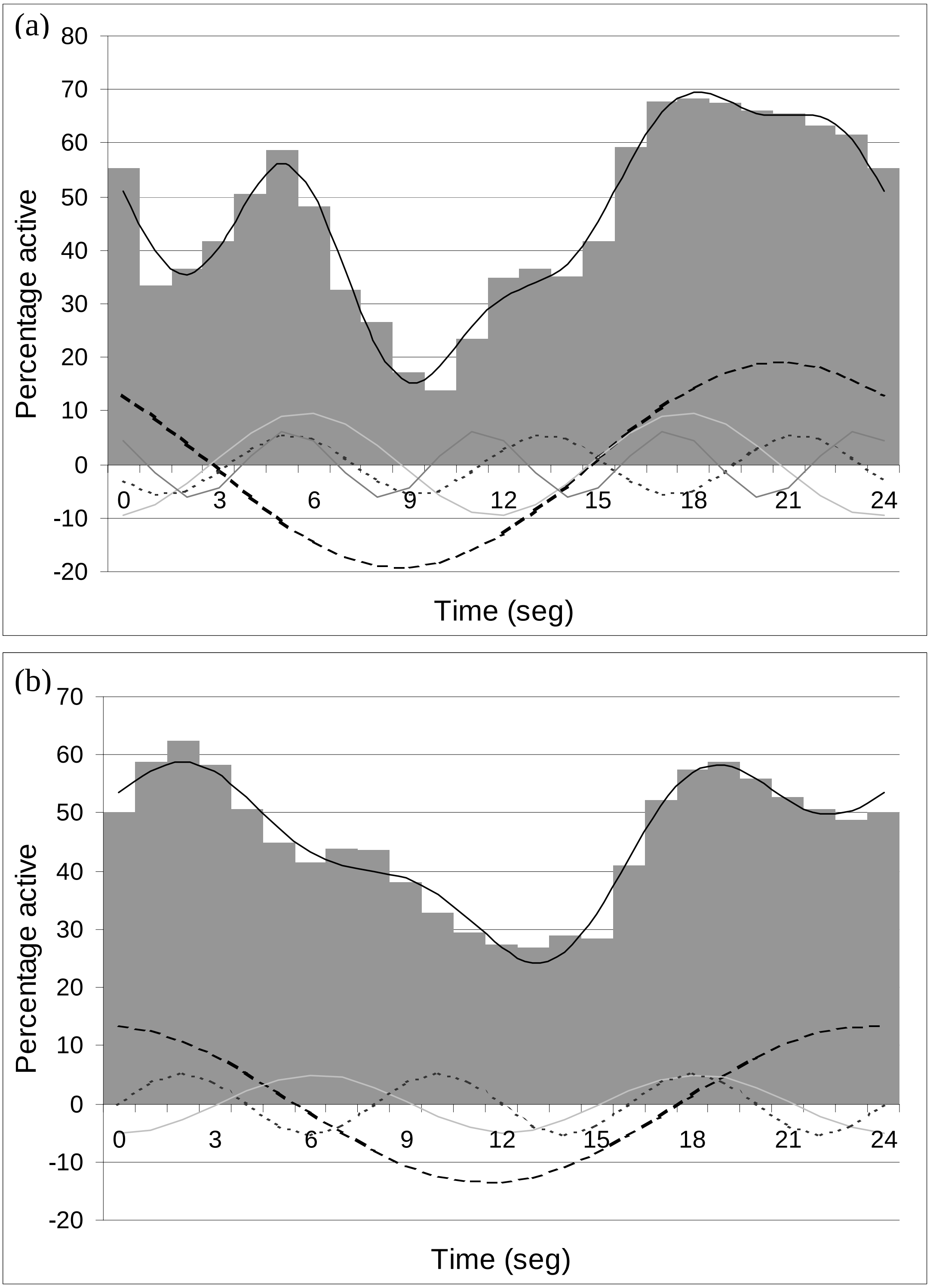


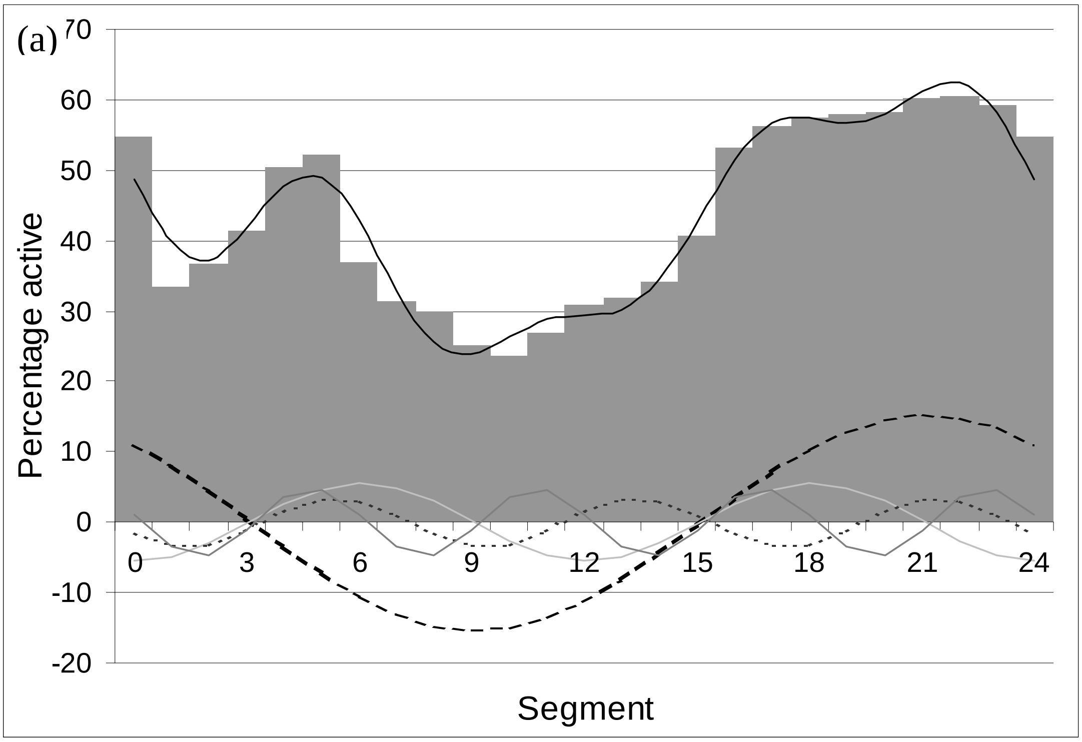
Figure 4.3. Overall fox activity curves for (a) October and (b) non-October activity plots using segment time.

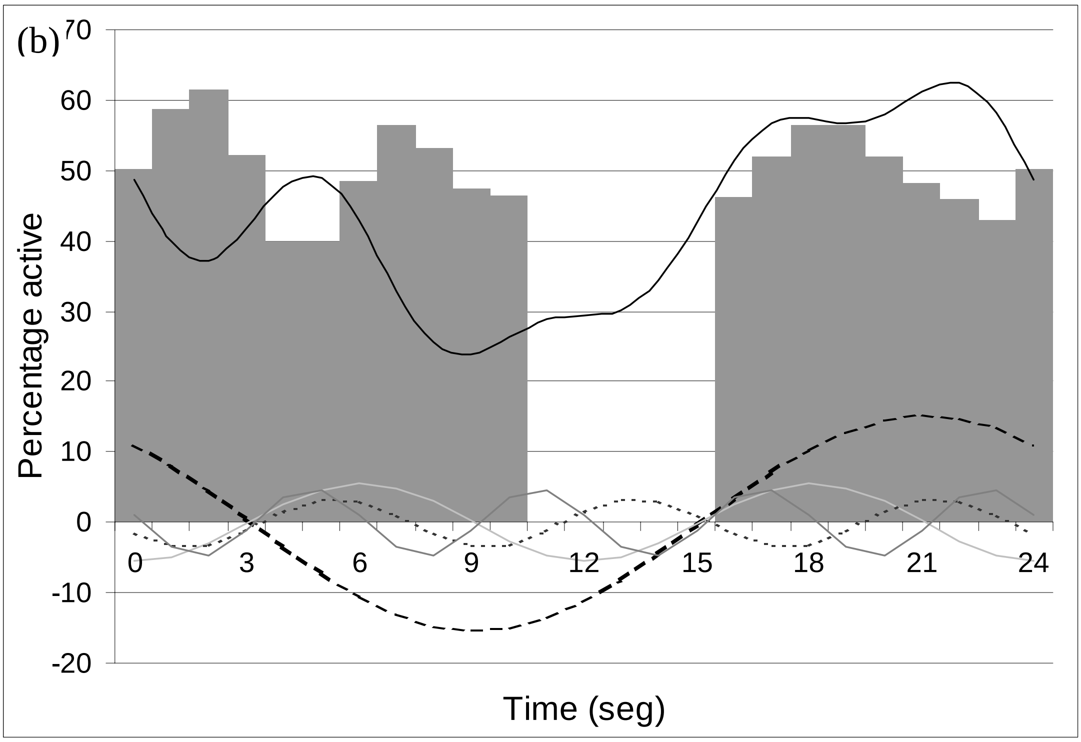
( ▬ raw data, — overall curve, - - - 24 seg cycle, — 12 seg cycle, ······ 8 seg cycle, — 6 seg cycle)

### *4.3.4 Day length*

Fourier calculations were carried out on the data set from day length >13h (Figure 4.4a), but gaps in the data set meant the <11h data could not be analysed. To see if there were differences in pattern between the different day length data sets, the curves for >13h (Figure 4.4b) and total fox data (Figure 4.4c) were superimposed on the data for <11h of daylight, and assessed by eye for goodness of fit.

It was found that when day length was >13h, 4 cycles were required to approximate the data. The bulk of activity took place in the early evening, with much less activity after midnight (Figure 4.4a). Activity levels were at a minimum in the 9th segment (Table 4.2), and $A_0$ was relatively low (43.5%; Table 4.1). When the curve for >13h was superimposed on the data for <11h of daylight, it could clearly be seen that the patterns were very different: at shorter daylength, activity levels appeared to be high essentially all night, especially in the early morning (Figure 4.4b). In other words there appeared to be more activity in the very early morning and less in the evening when there were limited daylight hours. This same shifting of activity from evening to morning could be observed to a lesser degree in the curve for total fox data superimposed on the plot of <11h data (Figure 4.4c). Lack of daytime data meant no comment could be made on daytime activity at this time of year. While no minima and maxima or $A_0$ values could be calculated, overall activity levels appeared to be higher for shorter daylength, with peaks later in the morning and earlier at night than when days were longer (Figure 4.4 b,c).





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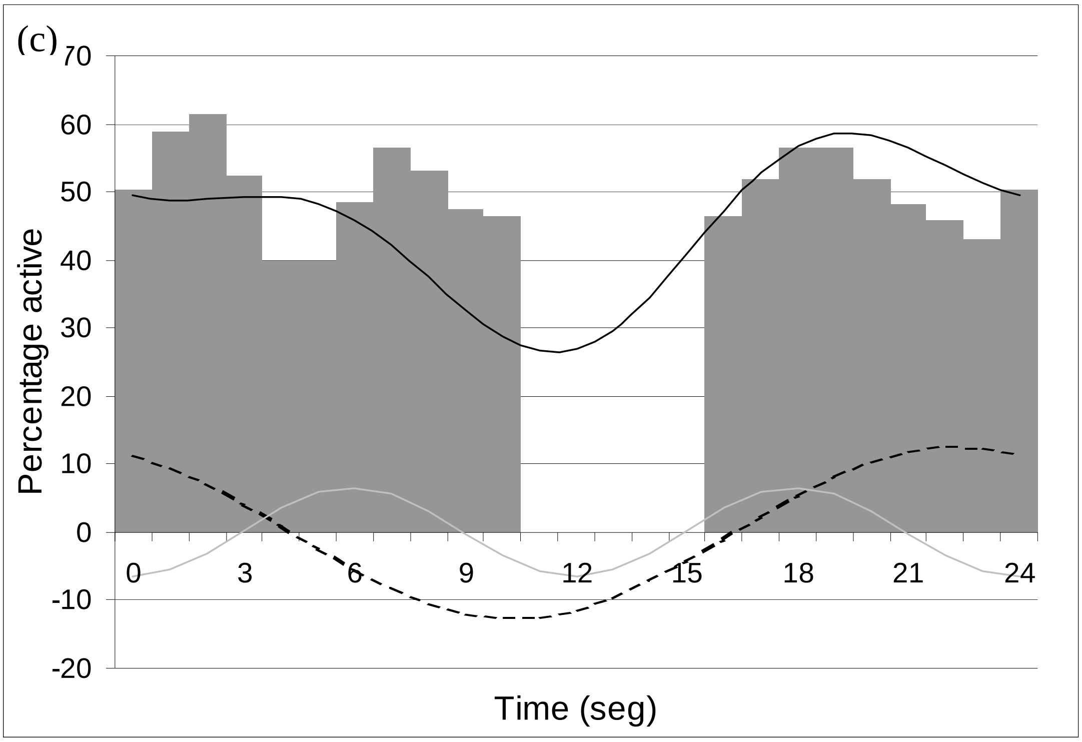


Figure 4.4. Activity rhythms of foxes (a) when daylight >13h for all foxes, (b) Fourier approximation to data when daylight >13h, superimposed on <11h data, using segment time and (c) Fourier approximation to pooled fox data, superimposed on <11h data.

( ▨ raw data, — overall curve, - - - 24 seg cycle, — 12 seg cycle, ········ 8 seg cycle, — 6 seg cycle)

### *4.3.5 Males versus females*

The percentage of foxes active ($A_0$) was higher for females (46.7%) than males (42.2%) (Table 4.1). Maximum activity of both sexes was in the 20th segment and minimum activity was in the 12th segment for females and the 14th for males (Table 4.2), with the lull in male activity more prolonged during the day (Figure 4.5b). The overall pattern for females was very clearly described by only considering the 24-segment and the 12-segment cyclical components, as indicated by the very small ISE at this point (ISE after 2 cycles 0.012; Table 4.1). In contrast, three cyclical components were required to adequately describe male activity, with ISE after 3 components higher at 0.028 (Table 4.1). This suggests males are subject to an additional 8-hour activity rhythm, and indicates that 24- and 12-segment cycles are less reliable as predictors of male activity rhythms.

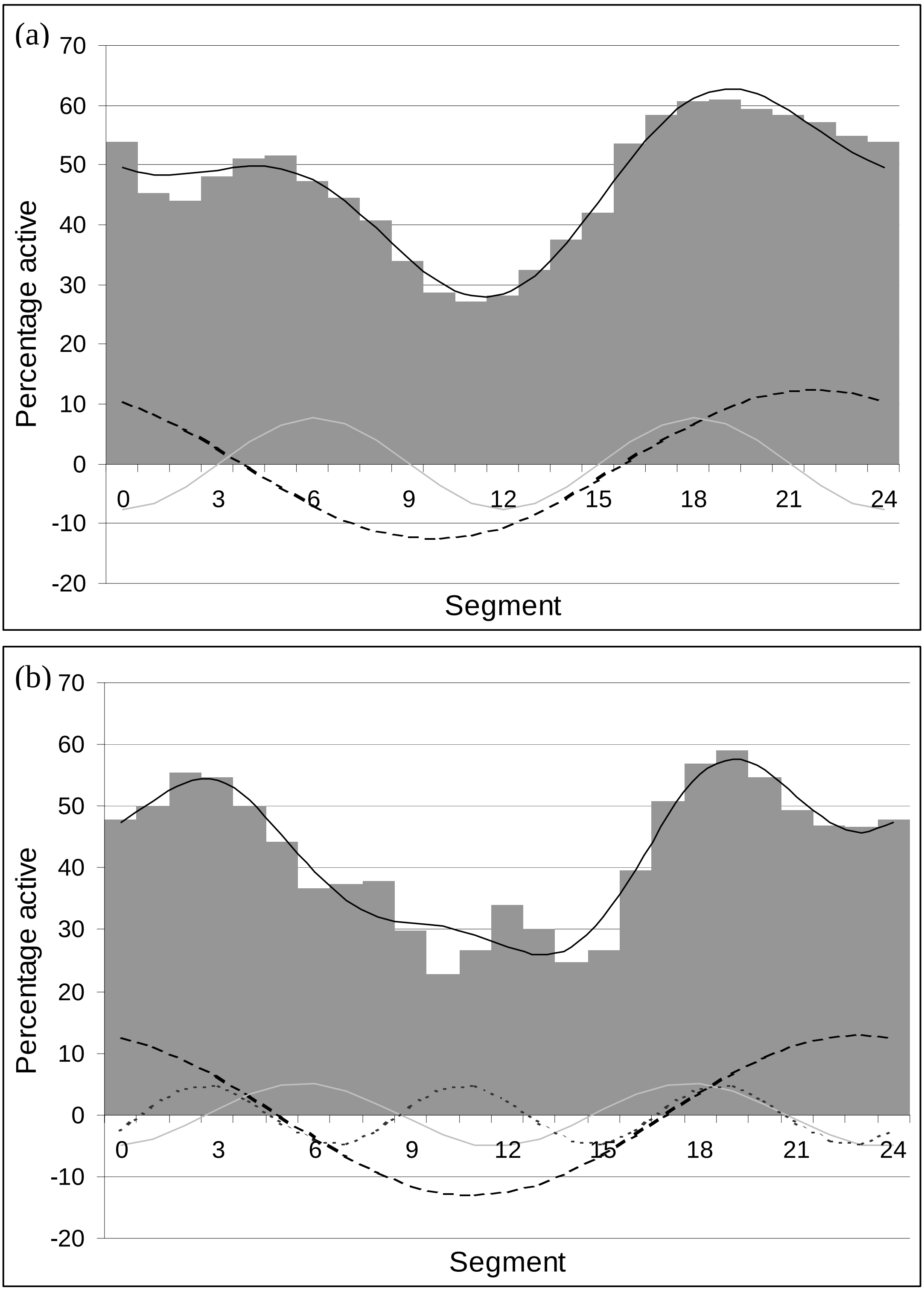


Figure 4.5. Activity rhythms for (a) all female foxes and (b) all male foxes, using segment time.

( ▨ raw data, —— overall curve, - - - 24 seg cycle, —— 12 seg cycle, ⋯⋯ 8 seg cycle, —— 6 seg cycle)

### *4.3.6 Time of year*

Three cyclical components were required to describe activity patterns when the months other than October were pooled, and the ISE was lower for females (0.014) than for males (0.023) (Table 4.1; Figures 4.6a,b). Inclusion of the 8-segment component much more greatly reduced the ISE for males than females (ISE 0.023 down from 0.100 for males, 0.014 down from 0.034 for females; Figure 4.2), indicating the relatively greater significance of the 8-segment cyclical component to males. $A_0$ values were higher for females (47.3%) than for males (42.2%) (Table 4.1).

In October, average activity levels were again higher for females than males ($A_0$ = 47.1 for females, $A_0$ = 44.8 for males; Table 4.1), indicating that females are consistently more active and predictable in their movements than males. Maximum activity was earlier in the evening in October compared with the rest of the year (Table 4.2). Female foxes were slightly less active in October than the rest of the year (Table 4.1, Figures 4.6a, 4.7a), while male foxes were more active in October than in other months (Table 4.1, Figures 4.6b, 4.7b). The amplitude of the 12-segment cycle was markedly greater for females in October (12.2) than in other months (5.3) (Table 4.1), and there was a distinct lull in activity during the night with a second, smaller, peak just before dawn (Figure 4.7a). The third segment peak in overall activity of males was not present in October, and minimum activity was considerably lower in October (16% in Oct, 26% total males; Table 4.1, Figure 4.7b). Four cyclical components were required to describe male and female fox activity, with ISEs lower for females than for males at the point of truncation (0.039 for females, 0.069 for males; Table 4.1). However the ISE after the 12-segment component was considerably higher for females (0.219) than males (0.116), indicating greater importance of 8- and 6-segment cyclical components to females in October (Figure 4.2).

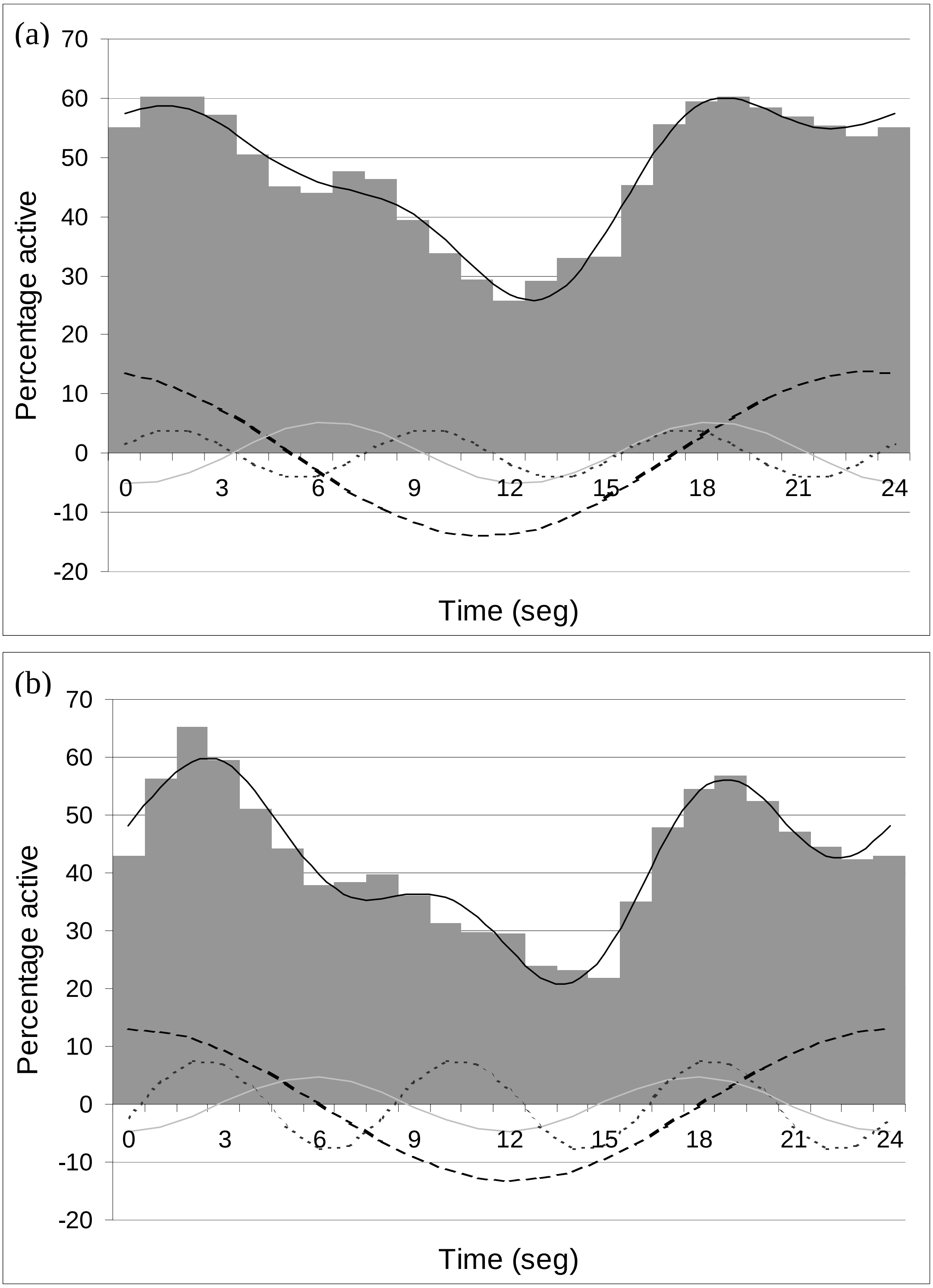


Figure 4.6. Activity rhythms all months except October for (a) female foxes and (b) male foxes, using segment time.

( ▨ raw data, —— overall curve, - - - 24 seg cycle, —— 12 seg cycle, ······ 8 seg cycle, —— 6 seg cycle)

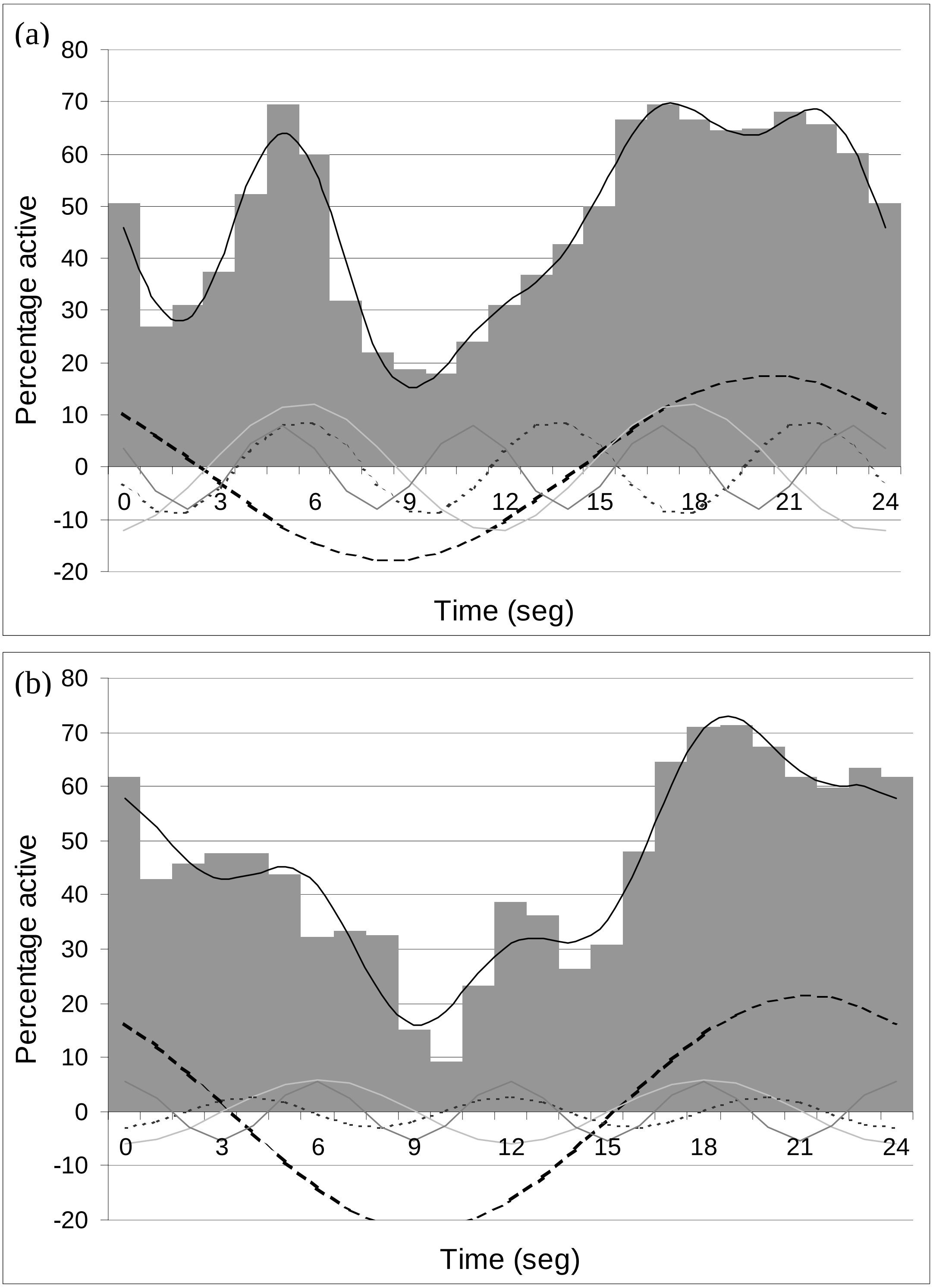


Figure 4.7. Activity rhythms in October for (a) female foxes and (b) male foxes, using segment time.

( ▨ raw data, —— overall curve, - - - 24 seg cycle, —— 12 seg cycle, ········ 8 seg cycle, —— 6 seg cycle)

Activities of males and females were markedly different to each other when daylight >13h (Figure 4.8a,b). Four cyclical components were required to describe female activity, while males could be clearly described by a single cyclical component, with the 24-segment component completely dominating male activity (Figure 4.2). Even after the 4th component, the ISE for females (0.035) remained comparable to that of males after just one cycle (0.043) (Table 4.1). This indicates female activity is considerably more complex than male activity at this time of year. The increased amplitude of the 12-segment component observed in females in the October data set was diminished in the >13h daylight plots (Figures 4.7a, 4.8a). Average male activity levels were at the lowest recorded when daylight >13h ($A_0$ = 40.0%), while female activity levels were considerably higher than males, and comparable to females at other times ($A_0$=46.3%) (Table 4.1). Maximum activity of females (71%) was considerably higher than males (55%), although minima were very similar (females 23%, males 26%) (Table 4.2).

### 4.3.7 *Individual foxes*

Data for many individual foxes could not be analysed due to gaps in the data sets. Overall profiles of the five more data-rich individuals were examined by eye to see if any individual traits were apparent, revealing that activity patterns varied greatly between foxes (Figures 4.9a-e). The relative importance of the various cycles differed between individuals, as did times and amplitudes of the various peaks. The small number of fixes in some time intervals meant the data sets were unlikely to be reliable, so no further analysis was carried out.

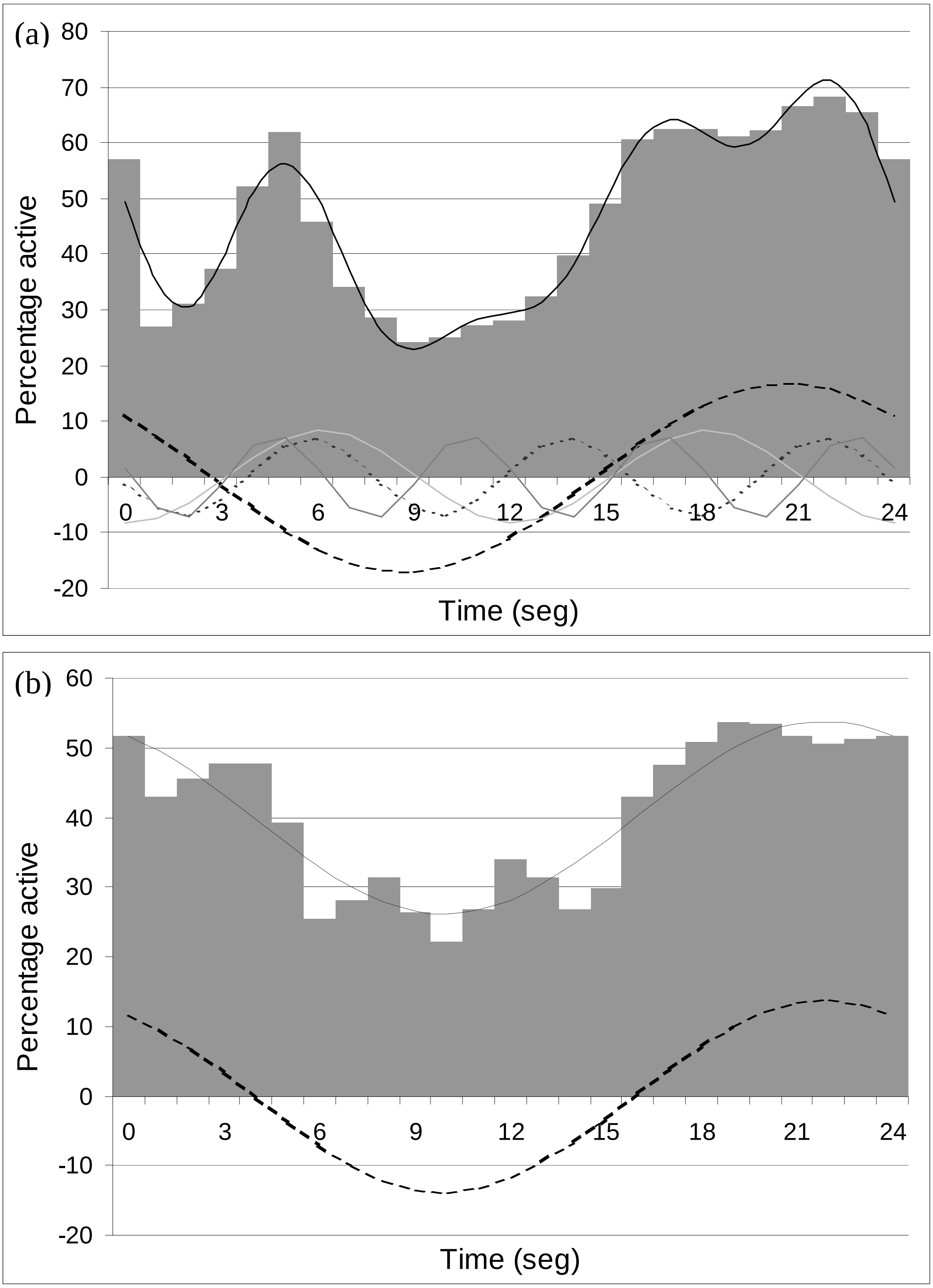
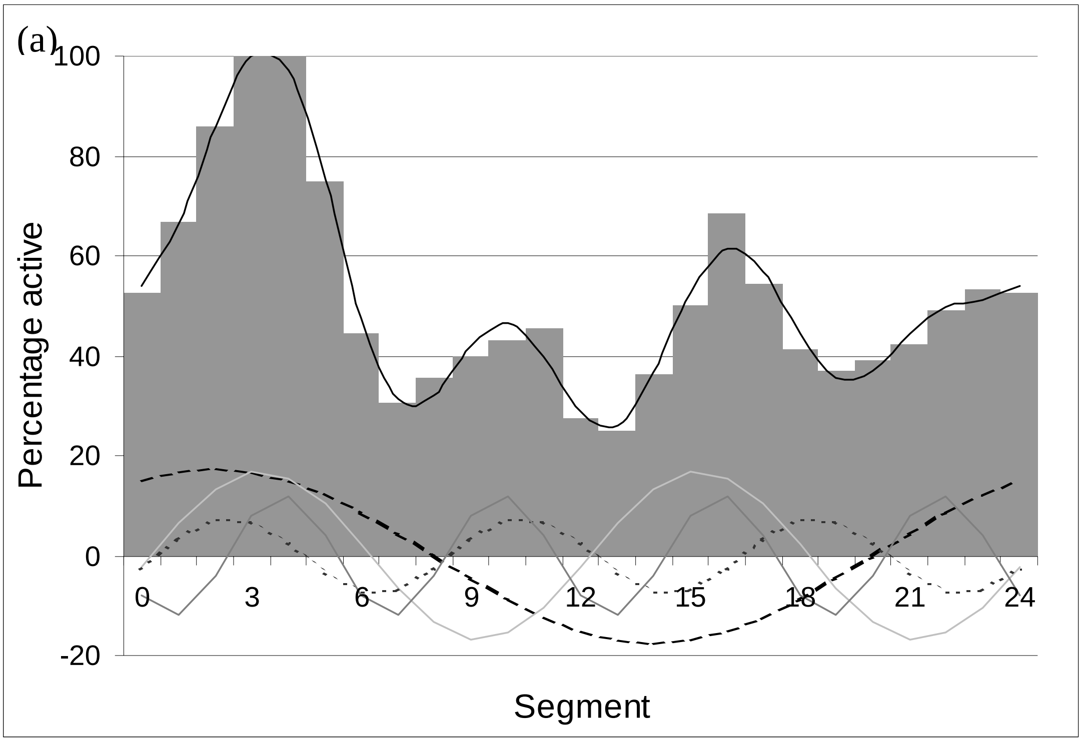
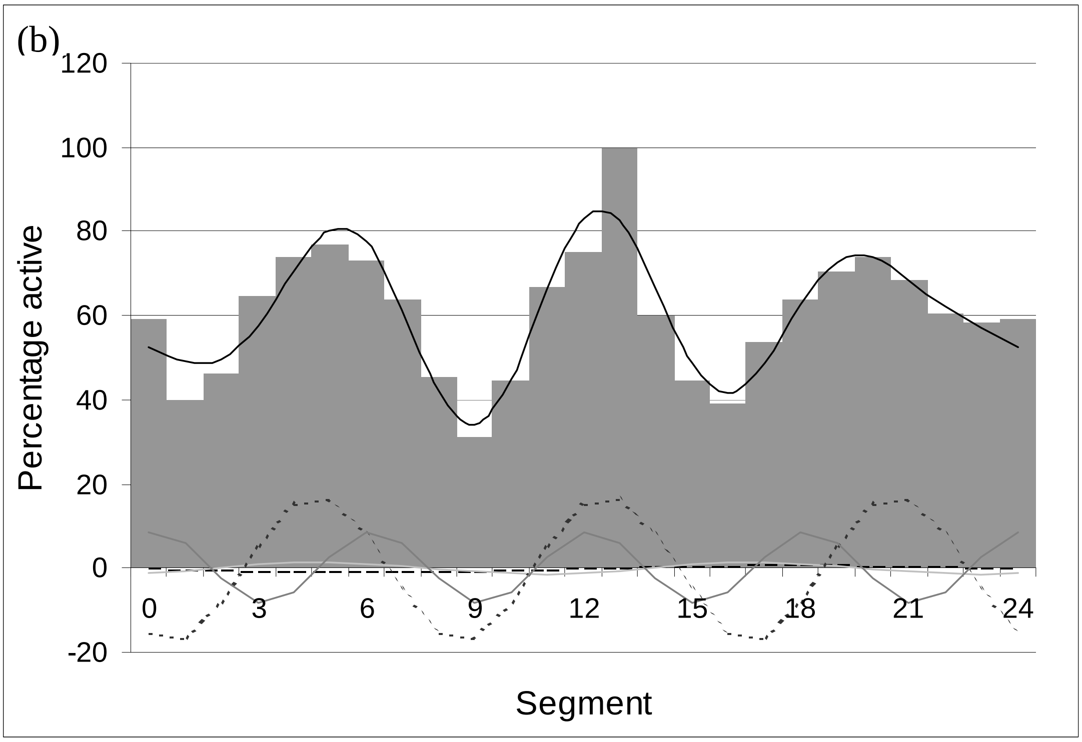


Figure 4.8. Activity rhythms when daylight >13h for (a) female foxes and (b) male foxes, using segment time.

( ▨ raw data, — overall curve, - - - 24 seg cycle, — 12 seg cycle, ······ 8 seg cycle, — 6 seg cycle)





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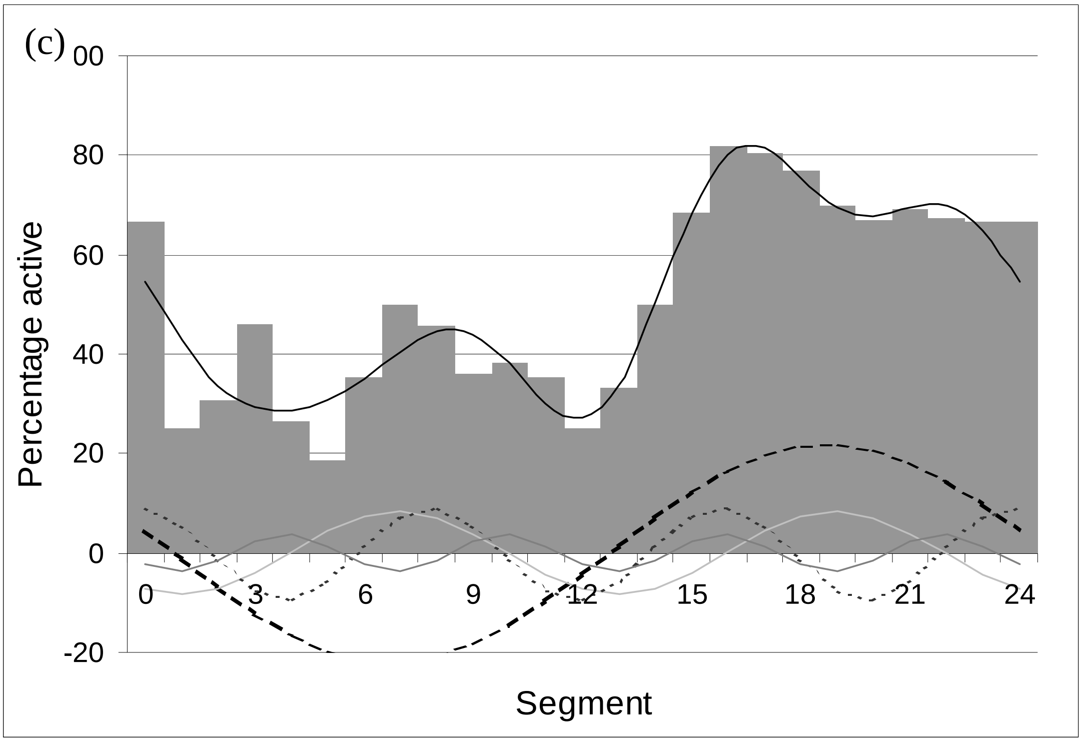

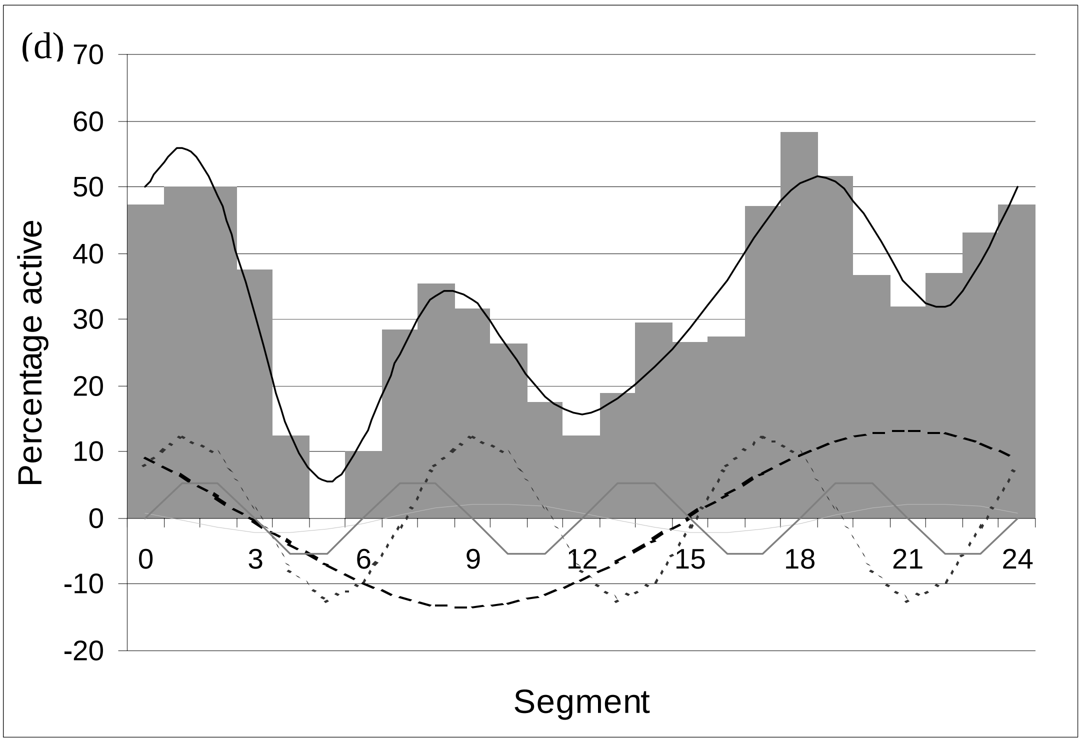

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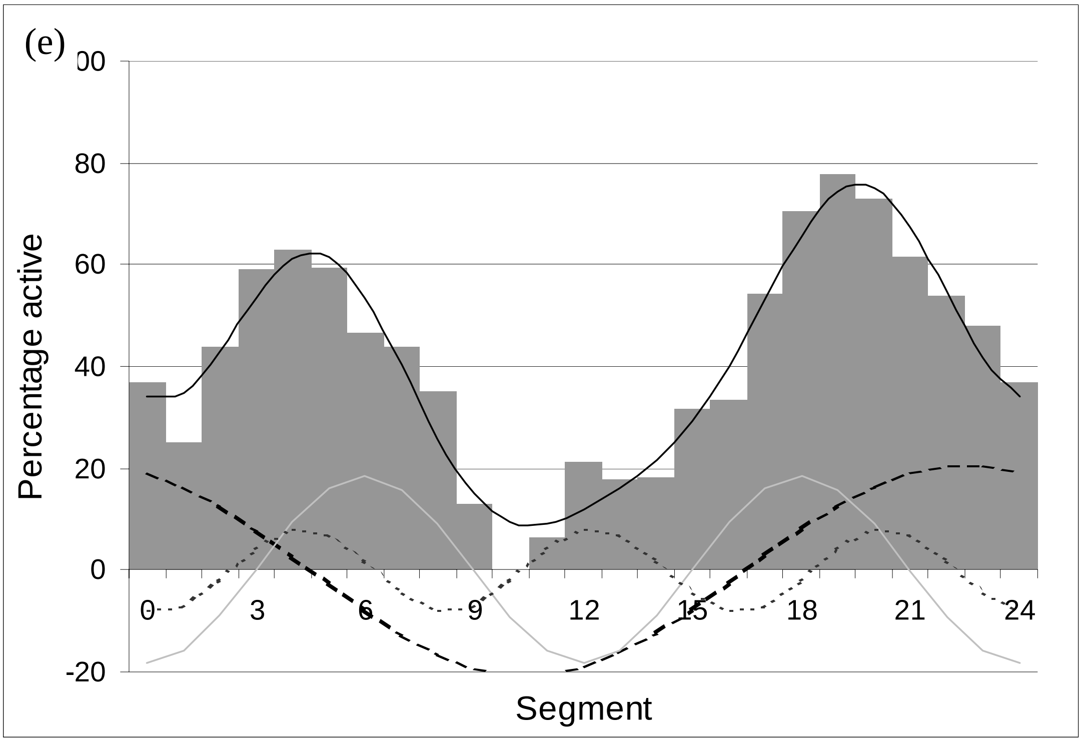


Figure 4.9. Overall activity curves for five individual foxes: (a) female tag 269 (b) female tag 86, (c) female tag 260, (d) male tag 450 and (e) male tag 90.

( ▨ raw data, —— overall curve, - - - - 24 seg cycle, —— 12 seg cycle, ········ 8 seg cycle, —— 6 seg cycle)

## 4.4 DISCUSSION

### *4.4.1 Pattern of activity*

The results of this study support those reported elsewhere in Australia (Jarman 1986; Phillips and Catling 1991; Bubela 1995; Saunders *et al.* 1995; Banks 1997; Meek 1998) and overseas (Storm 1965; Ables 1969a; Maurel 1980; Blanco 1986; Takeuchi and Koganezawa 1992; Saunders *et al.* 1993; Cavallini and Lovari 1994; Lovari *et al.* 1994; Weber *et al.* 1994; Reynolds and Tapper 1995; Doncaster and Macdonald 1997; Adkins and Stott 1998) that foxes are predominantly nocturnal, with a major peak in activity about an hour after sunset, fairly high activity all night and minimum activity around noon. When there were more night hours the overall activity level seemed to be higher, whereas when nights were short, there was a huge peak in activity soon after dark but little action in the remaining night hours. This is in contrast to findings of Doncaster and Macdonald (1997) who found fox activity levels were higher on short summer nights than long winter nights, although the total number of hours foxes were active each night was similar throughout the year in urban Oxford. Similarly, Reynolds and Tapper (1995) found foxes were generally less active in the middle of long nights in autumn and winter than in other seasons in rural southern England.

Activity levels of female foxes were lower in October than in other months. This is when females are most likely to be lactating (McIntosh 1963b; Ryan 1976; McIlroy *et al.* in press), and a drop in activity of lactating females has been observed by other authors (Takeuchi and Koganezawa 1992; Doncaster and Macdonald 1997). Males were observed to be more active in October than at other times of year in the present study.

Other studies have found that activity rhythms of prey species have an influence on when foxes are active (Cavallini and Lovari 1994; Lovari *et al.* 1994). In summer, insects were a major dietary component in the present study (Chapter 6), and it is likely that summer evenings were a prime time for feeding on insects, potentially explaining the high levels of activity at that time (Figure 4.4a). In a study on captive foxes it was found that peaks in fox activity corresponded with periods of wakefulness of rabbits, with active phases from 20:00h to 01:00h and from 07:00h to

08:00h (Dallaire and Ruckebusch 1974). Eating tended to occur in the evening phase, even though food was available in the morning.

### *4.4.2 Cyclical components of fox behaviour*

The major new result in the present study is that general fox behaviour could be clearly described by a 24-segment and a 12-segment cyclical component in many situations considered, indicating this to be a robust trend. Of the categories considered, the 24-hour or -segment cyclical component always had the largest amplitude, indicating it to be the primary cycle driving fox activity patterns (Table 4.1). The 12-segment cyclical component usually had the next largest amplitude.

Not only does the length of the 12-segment cycle correspond to the periods of light and dark, but the peaks tended to occur very close to the start of the 6th and 18th segments, the times of sunrise and sunset. This suggests some factor associated with sunrise and sunset triggers movement. If sunrise and sunset have an influence on fox movements, it would be expected that segment time would give a better fit than clock time. This is because when clock time data is pooled over the full year, movements in response to sunrise and sunset will occur at different times along the time-axis, essentially blurring the effect. The finding that using segment time generally gives a better fit to the data supports the hypothesis that sunrise and sunset have a considerable influence on movements. Moreover the finding that the amplitude of the 12 unit cycle was diminished when clock time was used rather than segment time indicates that using clock time blurs out these effects of sunrise and sunset on fox activity patterns. The timing of the 24-segment component did not appear to be linked to sunrise or sunset. According to Ashby (1972), the entrainment of the 24 hour daily rhythm of mammals appears to be caused by the periodicity of the rapid changes in light intensity of dawn and dusk, so this could well be the underlying biological basis to the 12-segment cycle.

The average percentage of foxes moving in each time interval, $A_0$, covered a remarkably small range, but within this females were found to be generally more active and regular in their movements than males. While there were differences between categories, these were generally not large, and all fell in the range 40.0% to

47.3% (Table 4.1). This suggests that the average activity level of foxes in this locality is primarily a feature of the species rather than of the season or category of animal considered. Phillips and Catling (1991) monitored fox activity from June to November, and found a female fox was active 51-59% of the time, and two male foxes to be active 41% of the time. Cavallini and Lovari (1994) found total activity ranged from 46.5-55.0% of the time for four foxes, while the fifth was significantly lower at 34.6% of the time. Both these studies presented mean activity levels of individual foxes rather than mean activity levels of all foxes in a category, and sample sizes were small. The greater range of mean activity levels reported in these studies therefore do not contradict findings of the present study that mean activity levels fall into a narrow range irrespective of season or sex. Values of these percentages are not directly comparable due to differences in data collection and analysis. Doncaster and Macdonald (1997) reported that foxes were nocturnal and active for a similar length of time each night irrespective of the time of year.

It was found that more narrowly defined data sets usually required more cycles than larger, more general sets (Table 4.1). In a more general category, these specific traits would be swamped by other data and dismissed as noise, and these results bear out the expectation that the more narrowly defined the category, the more cycles specific to that category are to likely to be found. However, the more narrowly defined the category, the smaller the data set becomes, rendering the data more susceptible to the effects of noise, as can be seen from the larger ISEs at the point of truncation for smaller data sets than for larger data sets (Table 4.1, Figure 4.2).

The relative importance of further cyclical components varied when more specific categories were considered. For example, in October the 12-segment component for females became much more pronounced. This coincides with lactation (McIntosh 1963b; Ryan 1976; McIlroy *et al.* in press), and possibly reflects this. Ideally, data would be available to analyse month by month to see how trends varied throughout the year. Coupling rhythmic data with appropriate observational data could portray a more complete picture of what factors are underlying apparently complex behaviour. For instance, females were much more complex in their behaviour than males when days were longer, which begs the question of what females do in summer that is so different to males? Maurel (1980) reported that there was considerable variation in activity patterns between individual foxes, and, given suitable data, analysis of cyclical components of movements of individual foxes may shed light on the nature of this variation.

### *4.4.3 Fourier series as a new tool for describing activity rhythms*

The results presented here demonstrate the use of Fourier series not only as a tool for smoothing a histogram, but as a systematic means of identifying the cyclical components underlying the overall movement patterns of animals over a 24h period. The terms in the resultant expression clearly show magnitude and timing of the various cycles, enabling comparison between categories, or even between different localities or species. When comparing results of different studies, caution should be exercised in comparing amplitudes of the various data sets, as what is interpreted as movement can vary between observers, terrain, transmitters etc. However relative magnitudes of cycles are still comparable, as are timings of peaks and troughs. The decision as to where to truncate the series remains subjective, with it not necessarily clear where movement ceases to be cyclic and degenerates into noise. In this study a cautious approach was chosen based on the likelihood of considerable noise in the data sets. Kronmal and Tarter (1968), when dealing with smoothing histograms and estimating probability density functions (rather than smoothing time series graphs as done here) suggest omitting those terms for which $A_k^2 < 8/(n+1)$ ie $A_k < 0.57$ in this instance. Here, rather more terms have been discarded to ensure that roughness which may be the result of inaccuracies in data collection are smoothed out.

The Fourier method of analysis also provides scope for removing the rhythmic components and looking at what is left. This noise component may, too, contain much useful information that could be interpreted given observational data. A further feature of this method of analysis is that the integrated square error (ISE) provides an estimate of how well the equation generated fits the data.

The method is quite unreliable for small samples, the ISE necessarily being higher when sample size is small. A large sample dampens the influence of irregularities in data collection, allows properties to be accurately found, and thus allows the basic trends to be analysed. Given a more precise method of assessing whether or not the animal was moving, (eg Doncaster and Macdonald 1997 used movement sensitive radio-transmitters), such large data sets may not be so essential. Another important requirement is that data sets not have gaps. Because these data were collected as a side topic in a study focussed on ranging behaviour, they are incomplete. Nonetheless even this partial data indicates clear trends. Uneven collection of data from different times of the year may have had an influence on the basic trends in this study, so it would be advisable to design data collection to be more evenly distributed.

This study has considered only fox activity rhythms within a 24h period. It is likely that other, larger, cycles also occur, such as annual cycles in activity. Given an appropriate data set it would be possible to apply this same approach to test for larger cycles, and also verify that there is indeed a 24h periodicity to fox movements.

### *4.4.4 Conclusion*

In summary, fox behaviour was clearly described by a 24-segment and a 12-segment cyclical component. The 24-segment component was the dominant driving force, with the 12-segment component of lesser amplitude. The 12-segment cyclical component appeared to be stimulated by the rising and setting of the sun. Coupled, these cycles gave an overall pattern of predominantly nocturnal behaviour, with a peak in activity around 2 hours after sunset, a lesser peak before dawn and minimum activity around noon. Female foxes were generally more active than males, but during October female activity was much reduced. These patterns are similar to those reported in other studies in Australia and overseas. In contrast to other studies, fox activity was overall higher on winter nights than on summer nights. Use of Fourier series provides a systematic means of identifying cyclical components of movement behaviour, and enables comparison of these cyclical components between individuals, categories of animals, localities and even species. Given suitable data, this method could be adapted to periods longer than 24 hours.

# CHAPTER 5

# POPULATION DYNAMICS

## 5.1 INTRODUCTION

The subject of population dynamics focuses on changes in the number of individuals in a population and the factors that affect population size. A population's rate of increase is determined by its size, by the number of individuals entering through births and immigration and the number leaving through deaths and emigration (Krebs 1985). These factors will each be discussed.

The simplest measure of a population's rate of increase is the ratio of estimates of population size in two successive years, this being the finite rate of increase ($\lambda$) (Caughley 1980). For birth-pulse populations, such as foxes, these estimates must be made at the same time of year (Caughley 1980). A more useful expression of rate of increase is the instantaneous rate of increase ($r$), where a particular rate of increase has the same value as the equivalent rate of decrease, but with the sign reversed (Caughley 1980). These two expressions of rate of increase are related by the equation $\log_e\lambda = r$.

A rate of increase depends on the mean fecundity at each age and mean survival at each age. If these are constant for sufficiently long, the population will converge towards a stable age distribution and rate of increase becomes constant (Caughley 1980). A special case of the stable age distribution is the stationary age distribution, when $r = 0$ (Caughley 1980). This property is often used in the construction of life tables for populations where rate of increase ($r$) is constant (usually zero) and survival schedules are either calculated from the frequencies of age at death or from fecundity rates and age frequencies (Caughley 1980). Life tables and fecundity schedules were not the focus of the present study as larger sample sizes than the study design allowed would be needed. Caughley (1980) recommends at least 150 age determinations.

Foxes are a birth-pulse species, and in Australia cubs are born around September/ October each year (McIntosh 1963b; Ryan 1976; McIlroy *et al.* in press).

Hence, fox densities are expected to be at their highest immediately after breeding then taper off due to mortality and dispersal to a lowest point just before the next influx of cubs. Studies in Australia that monitored trends in fox abundance support this, with fox abundance found to peak in summer (Marlow 1992; Pech *et al.* 1992; Banks 1997; Thomson *et al.* 2000).

Relative indices of abundance for fox populations have been collected using measures such as spotlighting counts (Newsome *et al.* 1989; Marlow 1992; Tapper *et al.* 1996; Banks 1997) and trapping success (Thomson *et al.* 2000), signs of fox presence such as animal tracks (Thomson *et al.* 2000), bait or scent-station visitation (Trewhella *et al.* 1991; Thompson and Fleming 1994; Banks 1997), scat counts (Cavallini 1994; Banks 1997), and by success rates (capture effort) of lethal methods such as cyanide baiting (Algar and Kinnear 1992; Thomson and Algar 2000; Thomson *et al.* 2000) and shooting (Hewson 1984a; Heydon *et al.* 2000). A relative index of population size is sufficient to measure rates of change, but a measure of absolute abundance is necessary to estimate true population sizes or densities (Caughley 1980). Absolute abundance of foxes has been measured by methods such as breeding den counts (Trewhella *et al.* 1988; Coman *et al.* 1991; Saunders *et al.* 1995; Marks and Bloomfield 1999), distance sampling (Buckland *et al.* 1993; Lancia *et al.* 1994) based on spotlight counts (Lugton 1992; Marlow 1992; Newsome and Catling 1992; Heydon *et al.* 2000), index-removal-index (Thompson and Fleming 1994) and home range size and occupancy (Newsome and Catling 1992; Bubela 1995).

The annual rate of increase of a vertebrate population typically fluctuates gently for most of the time around a mean of zero, with favourable conditions resulting in population increase, and unfavourable conditions resulting in decline (Caughley and Sinclair 1994). Hone (1999b) examined counts of foxes from 43 unmanipulated populations across Australia and found their rates of increase were normally distributed around a mean of zero. Such studies, based on successive counts of adults, are measuring the change in adult population size.

Fox fecundity is commonly measured by examination of placental scars in samples of vixens (eg McIntosh 1963b; Fairley 1970; Ryan 1976; Storm *et al.* 1976; Englund 1980a; Allen 1983; Harris and Smith 1987; Lindstrom 1988; Lindstrom 1994;

Marlow *et al.* 2000). Foxes are sexually mature from 10 months of age (Storm *et al.* 1976). There is evidence that the annual reproductive performance of yearling vixens is lower than older vixens (Harris 1979; Englund 1980a; Allen 1984). The mean litter size in Australia has been estimated as 4.25 (McIntosh 1963b), 3.7 (Ryan 1976) and 3.7 (Marlow *et al.* 2000). Environmental conditions can affect fecundity, with higher proportions of barren foxes in drought conditions than observed in more favourable conditions (Pech *et al.* 1997). However average litter size appears to be relatively unchanged by environmental conditions (Pech *et al.* 1997). Studies of urban foxes in England have found fecundity to be related to population density and survivorship, with a high proportion of barren vixens in a high density fox population with a stable environment (Harris 1979), and a higher incidence of barren vixens where survival rates were higher (Harris and Smith 1987).

The oldest fox in a sample of 154 from an area of minimal fox control in Wales was 10 years of age (Lloyd 1980), but this and other studies have found it is rare for foxes to live beyond 3 years (eg Fairley 1969; Harris 1977; Lloyd 1980; Yoneda and Maekawa 1982; Coman 1988; Marlow *et al.* 2000). The usual causes of mortality of foxes in Europe (Harris 1978b; Reynolds and Tapper 1995) and North America (Storm *et al.* 1976) appear to be human-related, but are poorly understood in Australia (Saunders *et al.* 1995). High levels of human-related mortality is a trait common to most furbearers (Clark and Fritzell 1992). Storm *et al*. (1976) found more than 80% of tagged foxes died as a result of shooting, trapping or road accidents in a study in North America. A study of mortality of urban foxes in Britain found 61% of adult foxes died from road accidents and a further 18% were deliberately killed by people (Harris 1978b). Disease accounted for 10% of deaths, fights for 3%, parturition for less than 1% and the remaining 7% were from misadventure or of unknown causes (Harris 1978b). A recent survey in Britain found the numbers of foxes deliberately culled were close to estimates of annual productivity in British fox populations, and therefore likely to be the chief cause of fox mortality (Heydon and Reynolds 2000). In Australia, mortality of foxes has been linked to changes in environmental conditions, with fox numbers observed to fall following drought-related decline in rabbit numbers (Myers and Parker 1975; King and Wheeler 1985; Newsome *et al.* 1989; Pech *et al.* 1997).

A number of studies in Australia and overseas have presented distributions of ages of foxes based on samples of dead animals (eg Storm *et al.* 1976; Harris 1977; Lloyd 1980; Yoneda and Maekawa 1982; Coman 1988; Marlow *et al.* 2000). These studies all found survival rates to be lowest in the first year of life (Storm *et al.* 1976; Harris 1977; Lloyd 1980; Yoneda and Maekawa 1982; Coman 1988; Marlow *et al.* 2000). Only one published studies in Australia has attempted to construct a life tables based on such data (Marlow *et al.* 2000). The life table of Pech *et al*. (1997), although considering Australian circumstances, was based on life table data of Storm *et al*. (1976) from North America. Both these studies (Pech *et al.* 1997; Marlow *et al.* 2000) assumed a rate of increase of zero, based on the absence of management in the populations studied.

Higher ratios of juveniles to adults are found in areas of intensive control than in areas with light control (Phillips 1970; Harris 1977; Lloyd 1980; Yoneda and Maekawa 1982). Other authors have interpreted observed juvenile:adult ratios as indicative of the level of fox control, or lack thereof, in their single-site studies (Coman 1988; Marlow 1992; Marlow *et al.* 2000).

The method used to collect age structure samples can have a great influence on the ages of animals collected, with a general tendency to collect a disproportionately high number of young foxes (Ables 1975; Harris 1977; Englund 1980a; Coman 1988). Bias in age structure with different techniques appears to vary between locations. For example Coman (1988) observed significantly more yearlings in shot samples than those collected in battues. Given this, Coman (1988) cautions against directly comparing age structures based on different methods of collection unless some estimate of “capture bias” is known. Lugton (1992) found greater bias towards juveniles using cyanide than shooting in semi-arid Australia, but commented that samples collected by shooting also appeared to be biased towards younger foxes. In contrast to this, Marlow *et al*. (2000) found cyanide baits were extremely successful at collecting a large sample of foxes across all age cohorts in semi-arid Western Australia. Kay *et al*. (2000) found a significantly higher ratio of adults to juveniles using trapping rather than shooting, as well as a significantly higher ratio of males to females in the trapped sample.

Success per unit effort can also differ between localities. For example Marlow *et al*. (2000) observed that they had much greater success with proportionately less effort than that of Coman (1992) in a fox eradication exercise in Victoria, and suggested their success was most likely due to the use of cyanide. However Coman (1992) commented that a range of techniques had initially been used in his study, including the poisons cyanide and strychnine, but discarded in favour of night-shooting and battues due to their low success rate.

Unless the population under study is closed, immigration and emigration also play a role in its dynamics (Krebs 1985). Dispersal is a common phenomenon amongst foxes (Lloyd 1980; Trewhella *et al.* 1988), and distance travelled can be great (Ables 1965; Lloyd 1980; Trewhella *et al.* 1988). Studies have found foxes will readily and rapidly reinvade areas from which they have been removed (Clark and Fritzell 1992; Coman 1992; Saunders *et al.* 1995; Thomson *et al.* 2000). Dispersal is covered in detail in Chapter 2.

The present study aimed to monitor fluctuations in fox population size, rate of increase, survival and the extent of immigration and emigration of foxes in a population not subject to management.

## 5.2 METHODS

### *5.2.1 Relative fox abundance*

Relative fox abundance was assessed by quarterly spotlight counts conducted over 3 consecutive nights timed to coincide with critical times during the fox's biological year as described by Saunders *et al*. (1995). Counts in June/July were to estimate numbers during the mating season, counts in September/October were just before the influx of cubs, counts in December/January included recently emergent cubs and counts in March occurred before major dispersal of sub-adults. Spotlight counts used in this study are described by Kay *et al*. (2000). A single observer used a 100W spotlight while standing in the tray of a vehicle moving at 10-15 km/h. A set transect of 21.2 km was followed each time, and the same observer (myself) conducted all spotlight counts. Counts were made on both sides of the vehicle, and commenced an hour after sunset. When an animal was sighted the vehicle halted while details (approximate distance to animal, species, whether visibly tagged, number of individuals, time and habitat) were recorded. Details were recorded for all mammalian species (rabbits, hares, brushtail possums, cats and eastern grey kangaroos) sighted other than livestock. Given the distances over which foxes were visible, it was usually not possible to tell whether the animal was tagged or radio-collared. Attempts were made to individually identify any radio-tagged animals by pointing telemetry equipment at all foxes caught in the spotlight and scanning possible frequencies. However this practice was abandoned when it was found that signals of other collared foxes in the area made it impossible to reliably identify the sighted fox. Quarterly spotlight censuses were carried out from July 1994 until June 1997, with the omission of summer 1994. An additional spotlight count was conducted in January 1996 after a particularly low census result in November 1995, to check that the low result was not due to a sightability problem. In June 1997 foxes were culled from the site. A follow-up count was conducted in January 1998 to assess whether the population size had returned to pre-cull levels. All estimates are reported as numbers of each species observed per kilometre of spotlight transect.

### *5.2.2 Numerical response*

The numerical responses of foxes to changing densities of rabbits, hares, brushtail possums and eastern grey kangaroos, as estimated by spotlighting counts, were evaluated using the Pearson product-moment correlation coefficient (Sokal and Rohlf 1995). Lag phases of 3, 6, 9 and 12 months were also assessed for any responses in predator abundance to changes in prey density (Pech *et al.* 1992). The numerical relationship between cat and fox abundance was also examined by correlation.

### *5.2.3 Rate of increase*

Average annual instantaneous rate of increase (*r*) of the fox population was calculated by linear regression of the natural logarithm of the number of foxes sighted in successive years at the same time of year (Caughley and Sinclair 1994; Johnson 1994). Four estimates of annual instantaneous rate of increase were calculated, one for each season using $\log_e N = a + rt$, where $N$ = population size, $r$ = instantaneous rate of increase, $t$ = time of census and $a$ = fitted value of $\log_e N$ when $t = 0$.

Finite rate of increase ($\lambda$) was estimated as $\lambda = (N_{t+1})/N_t$ for counts of foxes in successive years at the same time of year. This followed the method of Eberhardt (1987), and was calculated for each of spring, summer, autumn and winter.

### 5.2.4 *Absolute fox abundance*

Absolute abundance of foxes was estimated by index-manipulation-index (Caughley 1980). Population size prior to manipulation ($Y_1$) is calculated from indices of abundance before and after removal of a known number of animals as $Y_1 = I_1C/(I_1\text{-}I_2)$, where $Y_1$ = population size at time of first index, $I_1$ = first index of abundance, $I_2$ = second index of abundance and $C$ = number of animals removed between first and second index. The proportion removed is estimated as $p^* = (I_1 - I_2)/I_1$, and the proportion remaining as $q^* = 1 - p^*$. The variance of the population estimate is approximated as $\text{var}(Y) \approx Y^2(q^*/p^*)^2(1/I_1 + 1/I_2)$ (Caughley and Sinclair 1994). This method of analysis assumes the population is closed. To minimise bias due to animals leaving or entering the population, it is important to carry out the three stages of the experiment (index of abundance, removal, index of abundance) in as short a time interval as possible (Caughley and Sinclair 1994).

Spotlighting was used as the index of abundance, with the same transect sampled on three consecutive nights immediately before and after the culling period. This transect was a shortened version of the transect used for quarterly spotlight surveys, as culling could not be conducted over the full area covered by the regular survey transect. Culling took place over a two-week period in June 1997 using a combination of cyanide baiting (Algar and Kinnear 1992), trapping and shooting.

Cyanide was administered using M-44 cyanide ejectors (Marks *et al.* 1999). These contain a cyanide capsule mounted above a spring-loaded plunger. When an animal tugs on the bait, in this case lamb, the device is triggered, ejecting cyanide powder into the mouth of the animal. For the two weeks prior to the cull period, foxes were free fed daily with buried lamb baits at over a hundred locations within the study area. Cyanide baits were then buried in locations with consistent bait take. If not successful within three days, the baits were relocated, with baiting effort dispersed across the study area. Victor Softcatch™ leghold traps (Woodstream Corporation) were set as described in Chapter 2 at locations across the baited area bearing evidence of fox presence such as scats, tracks or strong fox odour. Night shooting was carried out as outlined in Marlow *et al*. (2000) from a slow moving vehicle along tracks through the baited area using a 100W spotlight to sight foxes. To minimise risk of foxes becoming spotlight shy and hence the estimation becoming biased negatively, only very accurate shooters were used so very few targeted animals were missed. A day was also spent visiting dens using fox terriers to drive foxes out. Foxes fleeing from dens were shot.

Population size was also estimated using a Peterson estimate, the simplest of the mark-recapture population size estimators (Caughley and Sinclair 1994; Krebs 1999). This was the only mark-recapture technique that could be applied within the framework of the cull, using the number of radio-collared animals within the culled area as the total number marked. Prior to commencing culling, preliminary calculations were carried out to estimate the number of marked animals that would need to be culled to achieve a standard error of about 10% of the population size (Caughley 1980).

The population size estimates were divided by the total sampling area to give an estimate of population density. Sampling area was measured in two ways. The first approach was to measure the area over which cyanide baiting, trapping and shooting were conducted together with a boundary strip around this of half an average home range diameter (Krebs 1999). Secondly, each death location was defined as a capture point, and the area sampled at each capture point was then calculated as a circle of half an average home range diameter around that point (Otis *et al.* 1978; Krebs 1999). The total sampled area was then the total area covered by these circles. In both methods the estimate of home range diameter (3179m) (Chapter 2) was used.

### *5.2.5 Age, reproductive status and body condition*

All fox carcasses collected during the cull were weighed and measured. Kidney fat (KFI) was measured as an index of body condition (Winstanley *et al.* 1998). Left and right kidneys and associated peritoneal fat were removed from each fox and standardised by cutting the peritoneal fat parallel to the kidney as viewed from the caudal pole (Riney 1982). Kidneys were blotted dry and weighed with and without associated fat (Winstanley *et al.* 1998), and kidney fat index calculated as KFI = 100*(weight of kidneys plus fat/ weight of kidneys without fat) (Riney 1982). Age was estimated according to tooth wear (Harris 1978a), and classified as < 1 year old, 1 year old or > 1 year old. Uteri were taken from female foxes for examination of placental scars (Lindstrom 1994). This sample was contributed to a much larger study into fox fecundity which will be reported elsewhere (McIlroy *et al.* in press, Saunders, unpublished data). Stomachs were collected, labelled with capture location, date and an identifying code and stored at –20$^{o}$C to provide information on diet (Chapter 6).

Age profiles and sex of foxes culled by each of the four methods (shooting, cyanide, trapping and fox terriers) were compared using a contingency table. Body condition of foxes culled by each method were compared using a one way analysis of variance.

### *5.2.6 Survival estimation*

Survival of foxes fitted with radio-transmitters was estimated using Kaplan-Meier analysis adapted to include staggered entry of animals into the study (Pollock *et al.* 1989). This estimator gives the probability of survival to an arbitrary time $t$, as well as 95% confidence intervals. The analysis distinguishes between animals that died and animals lost (censored) from the sample due to causes such as transmitter failure or dispersal. Assumptions of this analysis are that animals of a particular sex and age class have been sampled randomly, that survival times are independent for different animals, that capture and radio-tagging of the animal does not influence its future survival, that the censoring mechanism is random and that newly tagged animals have the same survival function as previously tagged animals (Pollock *et al.* 1989). Survival of radio-collared animals was monitored from July 1994 until June 1997. Survival patterns were compared from July – June for each of the three years animals were monitored using a log-rank test adapted for staggered entry (Pollock *et al.* 1989). Seasonal trends in survival were examined by pooling data across years (Caughley 1980), and monthly survival was compared across years using a log-rank test (Pollock *et al.* 1989). Survival patterns for the breeding season (August – November) for each year were compared using a log-rank test.

### 5.2.7 Causes of death

Cause of death and age at death were noted for located radio-collared foxes that died during the study prior to the cull. Any other foxes found dead in the study area vicinity were also examined for age and cause of death. In addition to estimation of age by tooth wear, age was estimated by examination of sequential deposition of cementum annuli in canine teeth (Harris 1978a; Johnson *et al.* 1979). As foxes are monoestrous with a distinct breeding season, foxes could be placed into an annual cohort. Aging was undertaken by Matson's Laboratory (USA) using known age references.

### 5.2.8 Sensitivity of finite rate of increase ($\lambda$) to changes in life history parameters

Survival, fecundity and rate of increase for a population with overlapping generations and reproduction at discrete yearly intervals are linked in Lotka's equation as $\Sigma l_x e^{-rx} b_x = 1$, where $l_x$ is the probability of survival from birth to age $x$, $b_x$ is the rate of production of female offspring per female of age $x$ and $r$ is the instantaneous rate of increase (Caughley 1980). Assuming no age-specific differences in adult survival or fecundity, following Sibly *et al*. (1997), substituting $\lambda = e^r$, and denoting the age of first reproduction as $\alpha$, this can be simplified (Lande 1988) and rearranged to:

$$\lambda^{\alpha} (1 - s/\lambda) = l_{\alpha} b, \quad (1)$$

where $s$ is adult survival per year, $l_{\alpha}$ is survival from birth to first reproduction and $b$ is the number of female offspring per female per year.

Sensitivities of $\lambda$ to changes in fecundity ($b$), survival to first reproduction ($l_\alpha$), annual adult survival ($s$) and age of first reproduction ($\alpha$) were calculated by implicit differentiation as in Lande (1988):

$\delta\lambda/\delta b = \lambda/bT$, $\delta\lambda/\delta l_\alpha = \lambda/l_\alpha T$, $\delta\lambda/\delta s = \lambda(T-\alpha+1)/sT$ and $\delta\lambda/\delta\alpha = -\lambda(\ln(\lambda/s))/T$ where $T = \alpha+s/(\lambda-s)$ is the generation time of the population. The larger the value of the partial derivative the higher the sensitivity.

Instantaneous and finite rates of increase of foxes were calculated using equation 1 and data from Table 2 of Pech *et al*. (1997) representing average, drought and ideal conditions, and this was compared to rate of increase calculated by Pech *et al*. (1997). Sensitivities of $\lambda$ to changes in life history parameters were also calculated using these data using the equations outlined above.

These same calculations were then made using adult survival ($s$) data from the present study but retaining fecundity and juvenile survival data from Pech *et al*. (1997).

### *5.2.9 Immigration and emigration*

The proportion of radio-collared animals lost (either by death or emigration) between each spotlighting census was assumed to be representative of losses from the population. This was compared to change in population size according to spotlighting results. Where spotlighting results indicated an increase in population size or a lesser decline than indicated by telemetry results, this increase was attributed to immigration except during periods where births took place. In periods where births took place, the proportion of immigrants could not be partitioned from births. Whether there was overall movement into or out of the site was tested using a paired Student's *t*-test (Sokal and Rohlf 1995) of the differences between survival of radio-tagged foxes and the observed change in population according to spotlighting for each period. Emigration (dispersal) was covered in detail in Chapter 2.

## 5.3 RESULTS

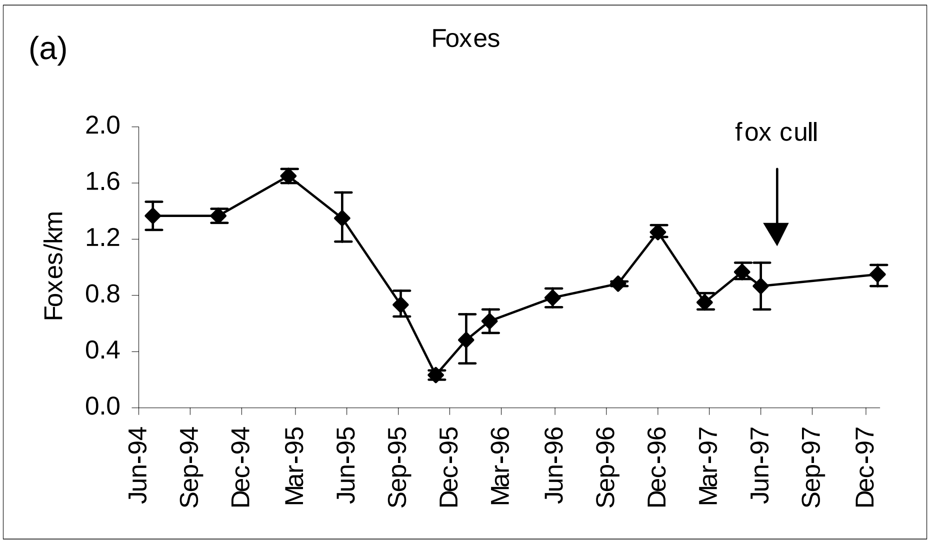
### *5.3.1 Relative fox abundance*

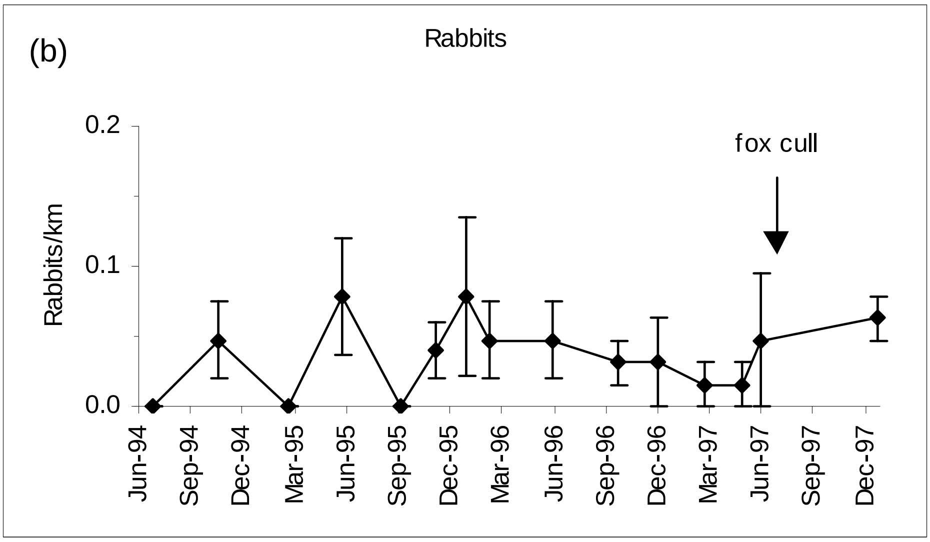
Foxes were the most commonly sighted mammal on the spotlighting transect, with rabbits, hares, cats, brushtail possums and eastern grey kangaroos also frequently sighted (Figure 5.1 a – f). Spotlighting censuses revealed the fox population to fluctuate widely over the duration of the study (Figure 5.1a). Numbers were initially high but fell steeply after March 1995, reaching their lowest point in November 1995. Numbers rose gradually after this time and became relatively stable at a lower level than that observed at the start of the study. By January 1998, numbers were slightly lower than those observed in the previous summer, but similar to that immediately before the cull (Figure 5.1a).

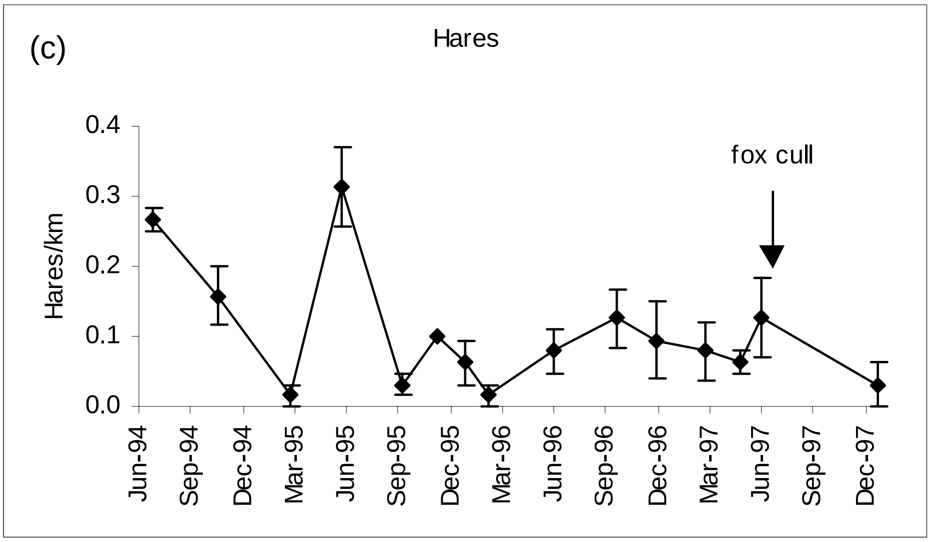
Rabbits were regularly sighted at very low numbers, with no major changes in population size observed (Figure 5.1b). Hare numbers fluctuated over the study, and, while more commonly sighted than rabbits, numbers were low (Figure 5.1c). Consistently low numbers of cats were sighted across the study (Figure 5.1d). Brushtail possum sightings fluctuated over the study, with the highest numbers observed in January 1996 and lowest in February 1996 (Figure 5.1e). Numbers of eastern grey kangaroos also fluctuated across the study, being most abundant at the start of the study in July 1994 and the finish in January 1998, and least common from June 1995 until May 1997 (Figure 5.1f).

### *5.3.2 Numerical response*

No significant correlations were found between foxes and numbers of rabbits ($r$ = 0.28, n = 14, p = 0.34), hares ($r$ = 0.40, n = 14, p = 0.16) or brushtail possums ($r$ = 0.13, n = 14, p = 0.67), but numbers of foxes and kangaroos were significantly correlated ($r$ = 0.59, n = 14, p = 0.03). No significant relationships were found between numbers of foxes and rabbits, hares, brushtail possums and eastern grey kangaroos for lag phases of 3, 6, 9 and 12 months ($p>0.05$ for all). Nor was there a significant relationship between numbers of foxes and cats ($r$ = 0.07, n =14, p=0.82).







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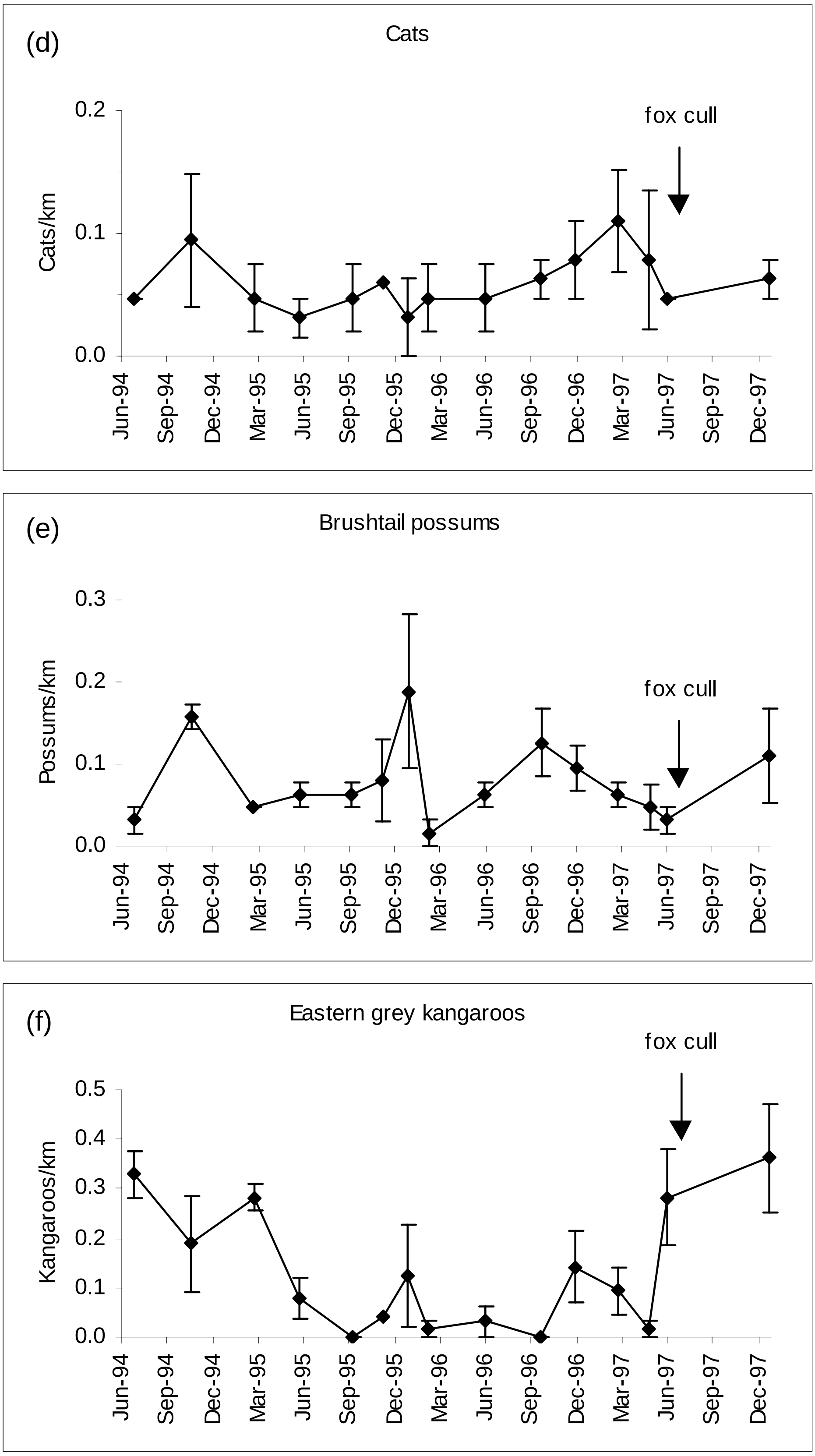

Figure 5.1. Mean and standard error of number of animals spotlighted per km on a 21.2km transect at Murringo. Foxes were culled from the site in June 1997.

### 5.3.3 Rate of increase

Average annual finite rate of change ($\lambda$) estimates based on successive years for each season are shown in Table 5.1. Estimates based on counts in autumn, winter and spring were less than 1, indicating a decrease in population size, but the estimate based on summer counts indicated an increasing population. Average annual instantaneous rate of increase ($r$) was slightly negative when based on counts in autumn, winter or spring, and slightly positive when based on summer counts (Table 5.1). However none of these estimates of $r$ was significantly different from zero as analysed by ANOVA (Table 5.1).

Table 5.1. Annual finite rate of increase ($\lambda$) and average annual instantaneous rate of increase ($r$) based on the number of foxes sighted per km calculated for each season from July 1994 to January 1998. A "–" indicates no estimate was possible.

| Season | $\lambda_{95-94}$ | $\lambda_{96-95}$ | $\lambda_{97-96}$ | $r_{95-94}$ | $r_{96-95}$ | $r_{97-96}$ | mean $r$ | $F$ | df | p |
|---|---|---|---|---|---|---|---|---|---|---|
| Autumn | – | 0.37 | 1.23 | – | -0.99 | 0.21 | -0.39 | 1.28 | 1,1 | 0.46 |
| Winter | 0.99 | 0.58 | 1.24 | -0.01 | -0.54 | 0.22 | -0.16 | 2.54 | 1,2 | 0.25 |
| Spring | 0.54 | 1.19 | – | -0.62 | 0.18 | – | -0.22 | 0.93 | 1,1 | 0.51 |
| Summer | – | 5.47 | 0.75 | – | 1.70 | -0.29 | 0.71 | 1.51 | 1,1 | 0.43 |

### 5.3.4 Absolute fox abundance

Preliminary calculations were carried out to estimate the number of marked animals that would need to be culled to achieve a standard error of about 10% of the population size using a Petersen estimate following the procedure of Caughley (1980). Eleven radio-tagged animals were known to be alive within the proposed cull area. The total population size was estimated at 50 foxes, requiring 9 marked animals to be among those culled. The same calculations were then repeated using a population size of 100 animals, with the outcome that 10 of the 11 marked animals would need to be culled. This was considered an unrealistically high proportion of marked animals.

After initial spotlighting counts, a total of 19 foxes was culled from within the census area, one of which was radio-collared. An additional fox was killed just outside the census area and 3 foxes killed in the area shortly before the initial census. Estimates of population size were based on the 19 foxes culled within the census area.

The Petersen estimate of fox abundance and its standard error of population size, based on 11 marked animals and recapture of 19 animals, one of which was marked, was calculated to be 110 ± 60. Index-manipulation-index abundance estimation gave a population estimate, and standard error, immediately prior to the cull of 66.5 ± 76.9 foxes (Table 5.2). Only a small proportion of the animals in the population was culled, leading to a large standard error. Population density based on a population size of 67 foxes was 1.4 foxes/km$^2$ when the area occupied by the population was measured as the culled area plus a boundary strip of half an average home range span, and 3.2 foxes/km$^2$ when area was defined by circles of an average home range span around each death location (Table 5.2). Population density using the Petersen abundance estimate of 110 foxes was 2.4 foxes/km$^2$ when area occupied by the population was measured as the culled area plus a boundary strip, and 5.3 foxes/km$^2$ when area was defined by circles around each death location (Table 5.2).

Table 5.2. Absolute density estimates based on spotlighting indices (mean ± se) and removal of a known number of animals (IMI) and using a Petersen estimate. Cull area was measured by a boundary strip around the area in which baiting, trapping and shooting took place (method 1) and by a buffer around locations where animals were killed (method 2). Population density was calculated using IMI and Petersen population estimates and both methods of area estimation.

| | |
|---|---|
| 1st index of abundance ($I_1$) | 14.0 ± 1.7 |
| 2nd index of abundance ($I_2$) | 10.3 ± 1.7 |
| No. animals removed ($C$) | 19 |
| Population estimate at first index ($Y_1$) | 66.5 |
| Variance (standard error) | 5907 (76.9) |
| Petersen population estimate ± standard error | 110 ± 60 |
| Area of cull (km$^2$) – method 1 | 45.9 |
| Area of cull (km$^2$) – method 2 | 20.9 |
| Population density estimate (foxes/km$^2$) IMI/ Petersen | 1.4/ 2.4 (using area 1) |
| Population density estimate (foxes/km$^2$) IMI/ Petersen | 3.2/ 5.3 (using area 2) |

### 5.3.5 *Age and body condition of culled foxes*

Four different methods were used to cull the 23 foxes from the site (Table 5.3). Shooting yielded foxes of a range of ages whereas those collected by cyanide and trapping were all young (Table 5.3). One fox driven from a den by terriers was one year of age while the other two obtained by this method were older again (Table 5.3).

However these differences in age profiles of foxes by each method were not significantly different ($\chi^2$ = 11.8, df =6, p=0.067). Nor was there a significant difference in sex of animals collected by the four methods ($\chi^2$ = 6.5, df =3, p=0.088). Body condition of the three foxes killed by trapping was noted to be much poorer than condition of foxes by other methods (Table 5.3), however a one way analysis of variance did not find this difference to be significant (Table 5.4).

Table 5.3. Sex, age (based on tooth wear) and body condition (kidney fat index) of foxes culled by shooting, cyanide baiting, trapping and using fox terriers to drive foxes from dens. The percentage of foxes culled by each method is also shown.

| **Technique** | **Shooting** | **Cyanide** | **Trapping** | **Terriers** | **Total** |
|---|---|---|---|---|---|
| No. foxes | 11 (48%) | 6 (26%) | 3 (13%) | 3 (13%) | 23 |
| Males | 4 | 3 | 0 | 3 | 10 |
| Females | 7 | 3 | 3 | 0 | 13 |
| Age = 0 | 7 | 5 | 3 | 0 | 15 |
| Age = 1 | 3 | 1 | 0 | 1 | 5 |
| Age >1 | 1 | 0 | 0 | 2 | 3 |
| KFI mean ± se | 136.5 ± 4.9 | 132.6 ± 10.0 | 114.3 ± 4.7 | 131.7 ± 7.3 | 131.9 ± 3.7 |

Table 5.4. One way analysis of variance of kidney fat index of foxes culled by the techniques of shooting, cyanide, trapping and using fox terriers.

| **Source of Variation** | **Sum of Squares** | **DF** | **Mean Square** | **F** | **p** |
|---|---|---|---|---|---|
| Between Groups | 1156.56 | 3 | 385.519 | 1.34921 | 0.29 |
| Within Groups | 5143.26 | 18 | 285.737 | | |
| Total | 6299.82 | 21 | | | |

### *5.3.6 Survival estimation*

The Kaplan-Meier survival function modified for staggered entry of animals showed survival to be very high for the first 11 months of the study before falling steeply for the next 16 months then levelling for the remaining 10 months of the study (Figure 5.2). Survival of foxes was significantly lower in the second year of the study (0.56, July 1995 – June 1996) than in the first year (0.96, July 1994 – June1995) ($\chi^2_1$ = 5.23, $\chi^2_2$ = 5.09, $\chi^2_3$ = 4.99, df = 1, p<0.05 for all; Figure 5.3). However no significant differences were found between survival in the first (0.96) and third (0.75) years ($\chi^2_1$ = 1.52, $\chi^2_2$ = 1.50, $\chi^2_3$ = 1.25, df = 1, p>0.05 for all), or between the second (0.56) and third (0.75) years of the study ($\chi^2_1$ = 1.46, $\chi^2_2$ = 1.40, $\chi^2_3$ = 1.38, df = 1, p>0.05 for all) (Figure 5.3). The number of tagged animals at risk in each month was 15.2 ± 2.2

(mean and standard error) from July 1994 – June1995, 22.5 ± 1.4 from July 1995 – June 1996 and 18.9 ± 0.8 from July 1996 – June 1997.

Monthly survival was not found to be significantly different across years (Table 5.5). When data were pooled across years, survival was found to be lowest between July and October, reaching a minimum in September (Figure 5.4). Foxes were significantly less likely to survive the breeding season (August to November) of 1995 than that of 1994 ($\chi^2_1 = 4.24$, $\chi^2_2 = 4.08$, $\chi^2_3 = 4.05$, df=1, $p<0.05$). No significant differences were found between breeding seasons of 1994 and 1996 ($\chi^2_1 = 1.47$, $\chi^2_2 = 1.44$, $\chi^2_3 = 1.43$, df = 1, $p>0.05$ for all) or 1995 and 1996 ($\chi^2_1 = 2.36$, $\chi^2_2 = 2.22$, $\chi^2_3 = 2.22$, df = 1, $p>0.05$ for all).

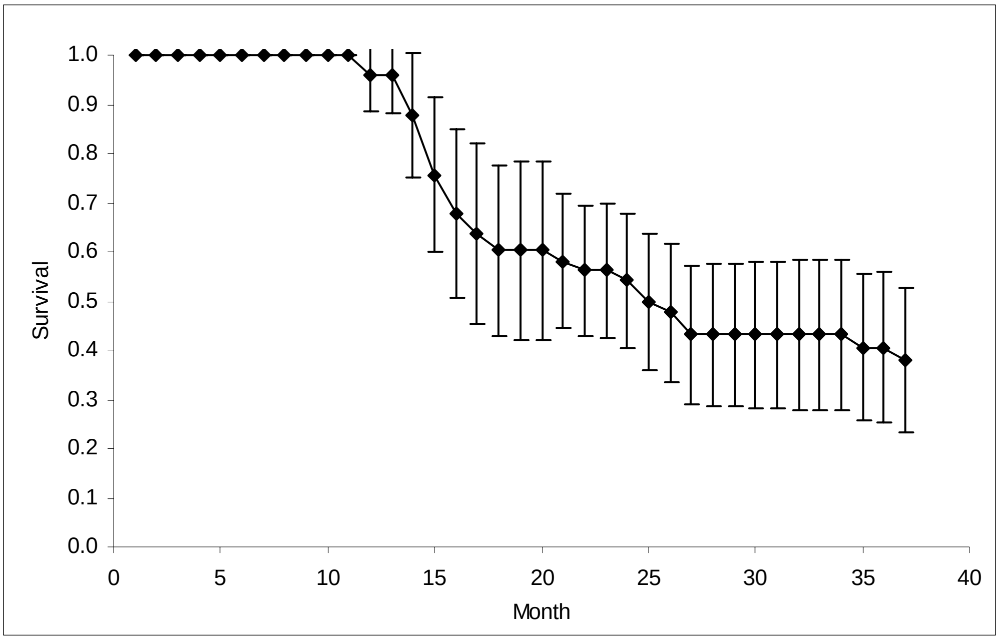

Figure 5.2. The Kaplan-Meier survival function and upper and lower 95% confidence intervals, modified for staggered entry of animals, for adult foxes radio-tagged at Murringo, July 1994 – July 1997.

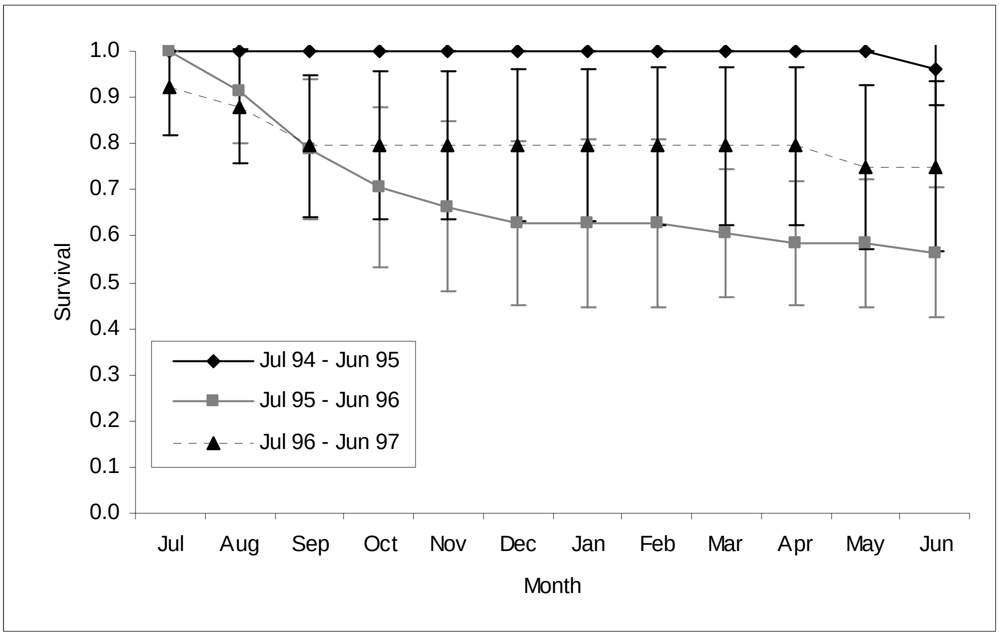

Figure 5.3. Comparison of survival between years of radio-tagged adult foxes at Murringo, July 1994 – July 1997. Error bars are 95% confidence intervals.

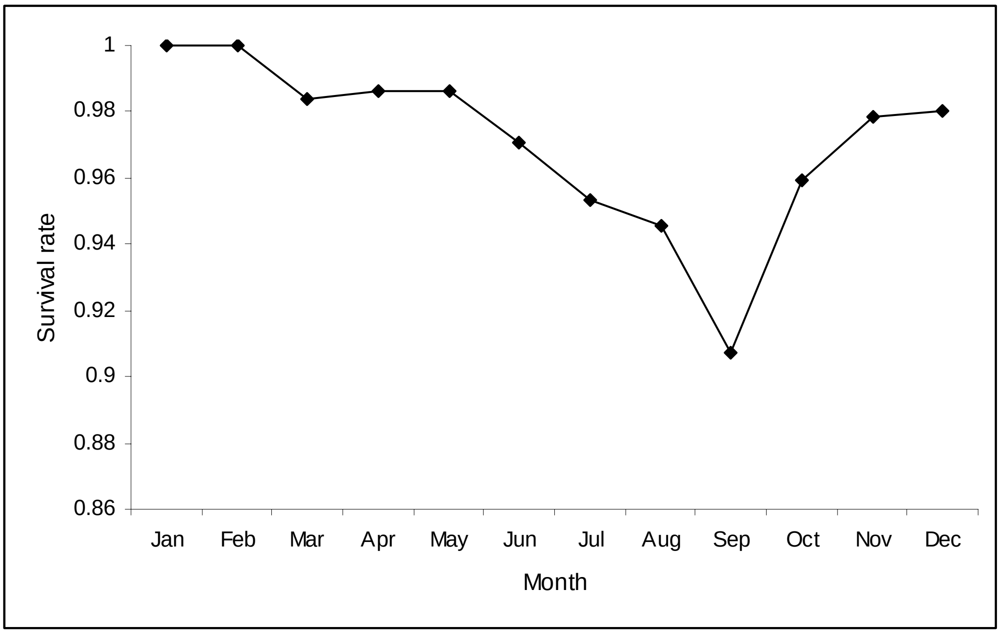

Figure 5.4. Seasonal variation in the rate of survival per month of radio-collared foxes at Murringo. Data from July 1994 to July 1997 are pooled.

Table 5.5. Comparison of monthly survival across the three years of the study from July 1994 to July 1997. “-“ indicates no deaths occurred during that month. Log-rank $\chi^2$ values were calculated using the first method by Pollock *et al*. (1989), with 1 degree of freedom.

| | Years 1-2 | | Years 2-3 | | Years 1-3 | |
|---|---|---|---|---|---|---|
| | $\chi^2$ | *p* | $\chi^2$ | *p* | $\chi^2$ | *p* |
| Jan | - | - | - | - | - | - |
| Feb | - | - | - | - | - | - |
| Mar | 0.52 | >0.05 | 0.59 | >0.05 | - | - |
| Apr | 0.90 | >0.05 | 0.57 | >0.05 | - | - |
| May | - | - | 1.65 | >0.05 | 1.59 | >0.05 |
| Jun | 0.00 | >0.05 | 0.59 | >0.05 | 0.64 | >0.05 |
| Jul | - | - | 1.88 | >0.05 | 0.25 | >0.05 |
| Aug | 0.81 | >0.05 | 0.35 | >0.05 | 0.39 | >0.05 |
| Sep | 1.60 | >0.05 | 0.17 | >0.05 | 1.08 | >0.05 |
| Oct | 1.20 | >0.05 | 2.06 | >0.05 | - | - |
| Nov | 0.65 | >0.05 | 1.12 | >0.05 | - | - |
| Dec | 0.78 | >0.05 | 1.00 | >0.05 | - | - |

### *5.3.7 Causes of death*

Bodies of 15 radio-collared foxes were recovered and examined for cause of death. One died of 1080 poisoning at a nearby site, 3 dispersed from the site of which 2 were shot and cause of death was not specified for the other, and 11 died of apparently natural but unknown causes within the site. A further 2 uncollared vixens were found dead of apparently natural causes at the mouth of dens within the study site. All those that died of apparently natural causes had attained at least one year of age (Table 5.6).

A further 35 foxes were recovered from the vicinity of the study site, of which 27 were shot, 7 were roadkills and one was killed by a tractor (Table 5.7). Approximately equal numbers of males and females were shot, and while 59% (16/27) were less than 1 year of age, 11% (3/27) attained an age of 4 years or greater (Table 5.7). Six of the seven roadkill foxes were males, all less than one year of age, with the other a yearling vixen. The fox that died of other causes was a yearling male.

Table 5.6. Age in years and sex of foxes that died of natural causes within the study site at Murringo estimated from examination of cementum annuli.

| Age | Male | Female | Total |
|---|---|---|---|
| 1 | 1 | 3 | 4 |
| 2 | 2 | 2 | 4 |
| 3 | 0 | 1 | 1 |
| 4 | 0 | 2 | 2 |
| 6 | 1 | 0 | 1 |
| 10 | 0 | 1 | 1 |
| Total | 4 | 9 | 13 |

Table 5.7. Age structure of foxes shot, roadkilled or dead of other cause from the Murringo vicinity between 1994 and 1997 estimated from examination of cementum annuli. The male fox in the “other” category was mowed in a hay paddock. Sex of animals is shown in brackets.

| Age | Shot | Roadkill | Other |
|---|---|---|---|
| 0 | 16 (8 unknown, 4 male, 4 female) | 6 (male) | |
| 1 | 6 (1 unknown, 3 male, 2 female) | 1 (female) | 1 (male) |
| 2 | 1 (unknown) | | |
| 3 | 1 (female) | | |
| >3 | 3 (2 male, 1 female) | | |
| Total | 27 (10 unknown, 9 male, 8 female) | 7 (6 male, 1 female) | 1 (male) |

### *5.3.8 Sensitivity of finite rate of increase ($\lambda$) to changes in life history parameters*

Using equation 1, instantaneous rate of increase ($r$) was calculated to be 0.03/year under average conditions, -0.92/year under drought conditions and 0.67/year under ideal conditions (Table 5.8).

Under average conditions, finite rate of increase ($\lambda$) was most sensitive to a small change in adult survival ($s$) followed by a change in survival to age of first reproduction ($l_\alpha$), but was relatively robust to changes in age at first reproduction ($\alpha$) and fecundity ($b$) (Table 5.8). Under drought conditions, a change in survival to first reproduction had the greatest influence on $\lambda$, followed by adult survival, while under ideal conditions adult survival followed by survival to first reproduction had the most influence on $\lambda$ (Table 5.8).

Using adult survival estimates from the present study, a change in adult survival was found to have the greatest influence on $\lambda$, followed by survival to age of first reproduction then fecundity then age at first reproduction for all years studied (Table 5.8).

Table 5.8. Data on age at first reproduction ($\alpha$), adult survival per year ($s$), survival from birth to first reproduction ($l_\alpha$) and female young/female/year ($b$), and calculated annual finite ($\lambda$) and annual instantaneous ($r$) rates of increase, generation interval ($T$) and sensitivities of $\lambda$ to changes in $b$, $l_\alpha$, $s$ and $\alpha$. ([1] data calculated from Pech *et al.* (1997), [2] data from present study, Year 1 = July 1994-June 1995, Year 2 = July 1995-June 1996, Year 3 = July 1996-June 1997).

| | Average[1] | Drought[1] | Ideal[1] | Year 1[2] | Year 2[2] | Year 3[2] |
|---|---|---|---|---|---|---|
| $\alpha$ | 1 | 1 | 1 | 1 | 1 | 1 |
| $s$ | 0.63[1] | 0.32[1] | 0.79[1] | 0.96[2] | 0.56[2] | 0.75[2] |
| $l_\alpha$ | 0.346[1] | 0.178[1] | 0.95[1] | 0.346[1] | 0.346[1] | 0.346[1] |
| $b$ | 1.15[1] | 0.43[1] | 1.22[1] | 1.15[1] | 1.15[1] | 1.15[1] |
| $\lambda$ | 1.03 | 0.40 | 1.95 | 1.36 | 0.96 | 1.15 |
| $r$ | 0.03 | -0.92 | 0.67 | 0.31 | -0.04 | 0.14 |
| $T$ | 2.58 | 1.24 | 1.68 | 3.41 | 2.41 | 2.89 |
| $\delta\lambda/\delta b$ | 0.35 | 0.75 | 0.95 | 0.35 | 0.35 | 0.35 |
| $\delta\lambda/\delta l_\alpha$ | 1.15 | 1.81 | 1.22 | 1.15 | 1.15 | 1.15 |
| $\delta\lambda/\delta s$ | 1.63 | 1.25 | 2.47 | 1.41 | 1.71 | 1.53 |
| $\delta\lambda/\delta\alpha$ | -0.20 | -0.07 | -1.05 | -0.14 | -0.21 | -0.17 |

### *5.3.9 Immigration and emigration*

Spotlighting results indicated at least as great a decline as that observed in radio-collared animals from July 1994 until January 1996 aside from the two periods where births occurred (October 1994 – March 1995 and November 1995 – January 1996). This would suggest no evidence of immigration to the site (Table 5.9). Conversely, again with the exception of when births occurred (December 1996 – March 1997), spotlighting results from January 1996 until May 1997 indicated increases in population size (Table 5.9). As these increases were not due to births, they were attributed to immigration. There was no evidence of immigration in the final period of the study from May 1997 to June 1997, with the survival of telemetered foxes similar to the change in population size across that period (Table 5.9). A paired *t*-test of the differences between survival and population change according to spotlighting indicated no overall movement of foxes into or out of the site ($t$ = -1.28, df =12, p= 0.22).

Of 50 foxes radio-tracked between July 1994 and July 1997, 24% were confirmed to have dispersed and the signals of a further 20% were lost, indicating that a maximum of 44% of radio-tagged animals may have dispersed during the study.

Table 5.9. Survival of radio-tagged foxes between spotlighting censuses and change in population size according to spotlighting results for each period. Where survival of radio-tagged foxes indicated a drop in population size but spotlighting results indicated an increase, the increase was attributed to immigration unless births also occurred in that period.

| Period | Survival of radio-tagged foxes | Change in numbers by spotlighting | Survival – Change | Immigration |
|---|---|---|---|---|
| July 94 – Oct 94 | 1.00 | 1.00 | 0 | no |
| Oct 94 – Mar 95 | 1.00 | 1.21 | -0.21 | ? + births |
| Mar 95 – Jun 95 | 0.89 | 0.82 | 0.07 | no |
| Jun 95 – Sep 95 | 0.88 | 0.55 | 0.33 | no |
| Sep 95 – Nov 95 | 0.77 | 0.31 | 0.46 | no |
| Nov 95 – Jan 96 | 0.89 | 2.12 | -1.23 | ? + births |
| Jan 96 – Mar 96 | 1.00 | 1.26 | -0.26 | yes |
| Mar 96 – Jun 96 | 0.82 | 1.28 | -0.46 | yes |
| Jun 96 – Oct 96 | 0.70 | 1.12 | -0.42 | yes |
| Oct 96 – Dec 96 | 0.95 | 1.43 | -0.48 | yes |
| Dec 96 – Mar 97 | 0.94 | 0.60 | 0.34 | ? + births |
| Mar 97 – May 97 | 1.00 | 1.29 | -0.29 | yes |
| May 97 – Jun 97 | 0.94 | 0.89 | 0.05 | no |
| Mean | | | **0.16** | |

## 5.4 DISCUSSION

### *5.4.1 Rate of increase*

While the overall rate of increase of foxes in the present study (1994-1997) was found to be zero in each season examined, population size was observed to fluctuate considerably within the three years they were monitored in the absence of any management activity. For rate of increase to fluctuate around a mean of zero is typical of vertebrate populations (Caughley and Sinclair 1994). Given the small number of data points on which the regression analysis of rate of increase was conducted (a maximum of 4 points), only a very strong trend in population size would have been detectable in this time frame. However a zero rate of increase was expected in the present study as no fox management had been conducted in the area for many years and fox numbers were expected to be limited by resources rather than management, so a longer study is likely to have nevertheless observed a mean zero rate of increase. This is further supported by findings in a collation of data on rate of increase of pest mammals in Australia in which mean annual instantaneous rate of increase of foxes was not found to be significantly different from zero (Hone 1999b).

In the present study there was a naturally occurring steep decline in fox numbers from 1994 to 1995, and an increase in numbers from 1995 through to cessation of monitoring in 1997. All of the counts prior to September 1995 were conducted during a drought, with no vegetation to hamper visibility on spotlight counts. Regular rain after this point (Figure 1.4) resulted in considerable vegetation growth. However there was no evidence to suggest that reduced sightability of animals may have been responsible for the apparent drop in numbers, as fluctuations in numbers of other species on the spotlight count such as rabbits, cats and brushtail possums did not mirror this drop in fox numbers. Although fox numbers peaked in autumn in this study (Figure 5.1a) as distinct to summer as reported in other Australian studies (Marlow 1992; Pech *et al.* 1992; Banks 1997; Thomson *et al.* 2000), the summer counts in the present study were conducted before fox cubs were readily visible, and the autumn counts were the first that included the pulse of cubs.

### *5.4.2 Survival*

Annual survival of radio-collared foxes was particularly high in 1994 (0.96) and significantly lower in 1995 (0.56). Survival in the third year of the study (0.75) fell between estimates from 1994 and 1995, and did not differ significantly from either of the first two estimates. This range encompasses the level of mortality of adult vixens (0.39) estimated by Marlow *et al*. (2000), which translates to annual survival of 0.61. In the present study all radio-collared animals that died within the study area had attained at least one year of age, so survival estimates are more comparable to those found for older foxes. The range of annual survival estimates from the present study are also comparable to findings of Pech *et al*. (1997) (range of 0.53 – 0.93) for foxes greater than one year of age.

Pollock *et al*. (1989) recommend a minimum of 20 tagged animals at all times and preferably higher for good precision. Monthly sample sizes in the present study were slightly below the recommended minimum in the first (15.2 ± 2.2 SE) and third (18.9 ± 0.8 SE) years of monitoring, but above this figure in the second year (22.5 ± 1.4 SE). Hence, while precision in the present study is not high, it should provide a reasonable estimate of survival.

Survival of radio-collared foxes was observed to be lowest from July to October (Figure 5.4). This is during the breeding season of foxes (Saunders *et al.* 1995), when energetic demands are at their greatest and fat reserves at their lowest (Winstanley 1997). It is possible, then, that this increase in mortality was due to breeding-related stress: the cost of reproduction as observed in red deer (*Cervus elaphus*) (Clutton-Brock *et al.* 1983). Mortality was also observed to be higher in 1995 than in 1994 or 1996. These findings are driven by the death of seven vixens between August and October in the breeding season of 1995, six of these of apparently natural causes. Two uncollared vixens were also found dead at the entrances to dens in the site during this period. These vixens were of a range of ages, all at least one year old. This suggests the high mortality of vixens in this season was not simply due to a cohort of vixens collared at the same age reaching the end of their lifespan together, but rather a real phenomenon. Spotlighting results from this period (Figure 5.1a) indicate that the population as a whole declined during this period, supporting that mortality was more widespread than just radio-collared vixens.

In the present study rainfall was above average prior to the start of data collection but below average rainfall occurred from February 1994 until January 1995 (Figure 1.3). Above average rainfall occurred from January 1995 through to November 1996, and below average rainfall again from November 1996 until completion of the study. Pech *et al*. (1997) assumed that below average rainfall reduces survival and fecundity. In this study survival was actually lowest in the period of above average rainfall. The period of drought declaration prior to this wet period was only of 15 months duration, and it is possible impacts of the drought had a lag effect that only became evident once the drought had broken. One such possible lag effect is that foxes may have been in excellent condition leading into the drought, and had sufficient fat reserves that drought-induced mortality only became evident a year later. Another possibility is that fecundity was low during the drought, resulting in low recruitment the following year. Alternatively, mortality of herbivores such as sheep and cattle may have been very high during the drought, creating an abundant supply of carrion over that period. Once the drought ended, herbivore mortality may have dropped, resulting in a shortage of carrion to support such high fox numbers.

### *5.4.3 Sensitivity of finite rate of increase ($\lambda$) to changes in life history parameters*

Analysis of the sensitivity of finite rate of increase ($\lambda$) to changes in life-history parameters using results from Pech *et al*. (1997) and from the present study found the two most influential life-history parameters were adult and juvenile survival (Table 5.8). Changes in fecundity and age at first reproduction had much less impact on finite rate of increase (Table 5.8). The analysis used to determine sensitivity of $\lambda$ relied on a simplified version of the Lotka equation, losing age-specific details (Lande 1988). However, rates of increase calculated by the simplified equation were similar to estimates of Pech *et al*. (1997), which retained age-specific details. Although never before applied to fox data, this indicates that such a simplification is appropriate. There were differences in $\lambda$ calculated from spotlighting indices (0.99, 0.58 and 1.24; Table 5.1) and using the simplified Lotka equation (1.36, 0.96 and 1.15; Table 5.8), indicating either the estimates of $l_\alpha$ and/or $s$ from Pech *et al*. (1997) were not strictly applicable to the present study, or that immigration and emigration were influencing the rate of increase of the population as measured by spotlighting. Using equation 1, instantaneous rate of increase (*r*) was calculated to be 0.03/year under average conditions, -0.92/year under drought conditions and 0.67/year under ideal conditions (Table 5.8). This compares to estimates by Pech *et al.* (1997) using the same data of 0.063, -0.94 and 0.752 under average, drought and ideal conditions respectively.

Fertility control is being explored as an alternative to lethal control to manage foxes in Australia (Tyndale-Biscoe 1994b). The major implication of this finding for management of foxes using fertility control is that a small change in fecundity may cause less change in the rate of increase of foxes than lethal control. However this does not consider relative costs of units of effort by either form of control, and if fertility control was relatively less expensive this approach could be the more favourable alternative.

### *5.4.4 Numerical response of foxes to prey species*

In the present study foxes were by far the most commonly sighted mammal on the spotlighting transect, with numbers of prey species, such as rabbits and hares, very low. No numerical responses of foxes to numbers of rabbits, hares or brushtail possums were detected, either immediate or with a time lag of 3, 6, 9 or 12 months. Numbers of foxes correlated positively with numbers of kangaroos, but no lag relationship was found. It is unlikely this relationship was a numerical response of a predator to a prey species as there is no evidence that foxes prey on mature kangaroos, although they will prey on juvenile kangaroos (Banks 1997). If there is indeed a relationship, it is more likely that fox and kangaroo numbers were both related to another factor not measured in this study.

Based on low numbers of prey mammals sighted and the lack of a numerical response, it appears that mammals were not important prey species in this area and that foxes were feeding on alternative food sources. This is different to the semi-arid studies where rabbits were the key prey species (Myers and Parker 1975; King and Wheeler 1985; Catling 1988; Pech *et al.* 1992). Rabbits were a major prey species in other diet studies on the tablelands of NSW (eg McIntosh 1963a; Croft and Hone 1978; Banks 1997; Molsher *et al.* 1999), and the lack of rabbits in the present study is unusual. This may explain why the impact of drought on fox numbers in the semi-arid studies appeared to be so direct compared to the present study. Fox dietary observations will be addressed in Chapter 6.

### *5.4.5 Lifespan and causes of mortality*

The oldest fox collected in the present study was a vixen estimated to be 10 years of age. This is as old as the oldest fox reported in the United Kingdom by Lloyd (1980), and older than any foxes collected in a number of other studies around the world (Fairley 1969; Storm *et al.* 1976; Harris 1977; Yoneda and Maekawa 1982; Coman 1988; Marlow *et al.* 2000). Foxes that died of apparently natural causes over the course of the study were, not surprisingly, generally older than those dying of human-induced causes. This indicates that foxes are capable of lengthy lifespans if they can avoid human intervention. Causes of mortality for radio-collared foxes were human-related for those that dispersed from the site and apparently natural for those remaining within the site. Precise cause of death of radio-collared foxes within the site could not be identified due to the degree of decomposition when located, but human-related causes could be ruled out as no poisoning or shooting took place anywhere near the home ranges of these individuals, and they were not roadkilled. Sarcoptic mange has been identified as a cause of death in other studies (Tullar and Berchielli 1981; Lindstrom *et al.* 1994), but was rarely observed in the present study. In fact two foxes suffering mange when first radio-collared both recovered over the course of the study. Recovery from mange has also been reported by Storm *et al*. (1976).

### *5.4.6 Bias in culling techniques*

When a variety of techniques were used to cull foxes from the study site, there was a trend towards differing age profiles of foxes culled by the various techniques. While not significant, sample sizes for some techniques were very small, and there was insufficient power to detect a significant difference. The trend detected was that a range of ages of foxes, weighted towards subadults, were collected by night shooting. Cyanide and trapping, on the other hand, resulted in almost exclusively subadult foxes. Moreover the three foxes collected by trapping were of poorer body condition than the six that took cyanide baits. This suggests only naïve foxes are likely to be caught by cyanide or traps, and that foxes need to also be very hungry to step into a trap. Night shooting resulted in a younger age profile of foxes than that known to occur in the site from observations of natural mortality, so is likely to still favour young, naïve foxes, but is apparently less biased than the profile generated by cyanide baiting or trapping. In contrast to results of the first three methods, the limited sample of foxes driven from dens by terriers were weighted towards older animals. It is possible that older, more dominant foxes are more likely to hold an established den site, and hence by killing foxes in dens, such animals may be favoured.

Differences in age profiles by different techniques have been found by other authors (Ables 1975; Harris 1977; Englund 1980a; Coman 1988; Lugton 1992; Kay *et al.* 2000; Marlow *et al.* 2000), with the biases of each technique towards particular age groups not consistent across studies. The present study was more like the findings of other studies in eastern Australia (Coman 1988; Lugton 1992; Kay *et al.* 2000) than Western Australian findings (Marlow *et al.* 2000). There was no strong evidence in the present study that the method used to collect foxes was biased in favour of a particular sex of animals, unlike findings of Kay *et al*. (2000) in which the ratio of males to females was significantly higher in a trapped sample than in a shot sample. If the trends observed here are real, the implications are that the removal or collection technique can have a big impact on the age profile of animals collected, which can only be corrected for if some estimate of “capture bias” is known for each study (Coman 1988).

Night shooting was not initially planned to be used in the cull as it had the potential to compromise the index of abundance, with cyanide baiting and trapping initially intended to be the sole means of culling foxes. When it became apparent that insufficient foxes could be collected by trapping and baiting alone, night shooting and use of dogs were incorporated into the cull. If the cull had continued without the use of night shooting and dogs, only subadult foxes and a single yearling would have been collected. Such low success using cyanide baits is in contrast to the success with this technique of Marlow *et al*. (2000), but similar to findings of Coman (1992), where shooting was more successful than use of poison. The present study suggests there may be other factors underlying the difficulty of culling foxes in eastern Australia, as cyanide was not found to be an efficient method of culling.

### *5.4.7 Absolute density estimation*

The estimates of absolute abundance calculated using a Petersen estimate (2.4-5.3 foxes/km$^2$) and index-manipulation-index (1.4-3.2 foxes/km$^2$) are similar to other estimates for temperate grazing areas in eastern Australia, with Coman *et al*. (1991) estimating 3.9 in central Victoria and Thompson and Fleming (1994) estimating 4.6-7.2 in the northern tablelands of NSW. The method used to estimate density in the northern tablelands study did not incorporate a boundary strip to take into account foxes whose home ranges only partly overlapped the study area (Thompson and Fleming 1994), so these density estimates are higher than if a boundary strip had been included as in the present study. As only a small proportion of the population was successfully culled, the two methods used to estimate density in the present study (Petersen estimate and index-manipulation-index) gave estimates with very large standard errors. In sites where culling is more successful, these methods of density estimation may be able to give more precise estimates.

### *5.4.8 Immigration and emigration*

No immigration was detected prior to January 1996, but from this point until May 1997 the population was noted to rise outside the breeding season, indicating immigration was occurring. The start of the period during which immigration was observed was immediately following a major drop in fox numbers in the site (Figure 5.1a), and is likely to have been foxes moving into the area to occupy vacancies left by dying animals. This suggests that whatever caused such high mortality within the site at that time was relatively localised, with surplus foxes in surrounding areas able to quickly move in.

The results of this study indicate immigration and emigration played a significant role in the dynamics of this population. Over the duration of the study, no overall trend in direction of movement either into or out of the site was detected. However even during the period when no immigration was detected, emigration still took place. Given there was no management of foxes in the study area, while baiting programs and shooting still took place in the surrounding districts, it is not surprising to observe a general movement out of the study area during this period to occupy vacancies left by control programs. The trend of general movement out of the site reversed following a period of high mortality within the site, with greater movement into the site. This demonstrates that foxes will readily and rapidly move into areas where the population has been reduced whether by control programs or through natural mortality events. The ability to rapidly recolonise areas has also been observed by other authors in Australia (Saunders *et al.* 1995; Thomson *et al.* 2000), with the implication that management programs for foxes need to be over a very large area or repeated very frequently if numbers are to be held at depressed levels for any length of time (Saunders *et al.* 1995). The high mobility of foxes also indicates that immigration and emigration regularly play a significant role in fox population dynamics. Thomson *et al*. (2000) found most recolonisation by foxes of a large depopulated area in Western Australia occurred during autumn, attributing this to autumn being the peak period for juvenile dispersal.

### *5.4.9 Conclusion*

In conclusion, this study found that considerable fluctuations can occur in fox numbers in the absence of management, but that, in accordance with predictions by Caughley and Sinclair (1994), these fluctuations were around a mean rate of increase of zero. Foxes in the area were capable of attaining up to 10 years of age, and natural mortality occurred at greater ages than would be predicted from samples of foxes collected by lethal means. The method used to collect samples of foxes can potentially result in bias in the age profiles of samples, and this aspect needs further clarification. Immigration and emigration played a measurable role in dynamics of this population in the absence of human manipulation, supporting findings of other studies that foxes are capable of long distance movements and rapid recolonisation of vacated areas. Analysis of the sensitivity of rate of increase to changes in survival and fecundity found the most important factors were juvenile and adult survival, indicating that lethal control may be a more efficient form of management for foxes than fertility control, although relative costs were not considered.

# CHAPTER 6

# DIET AND FOOD AVAILABILITY

## 6.1 INTRODUCTION

Where foxes occur around the world, they are well known to be opportunistic feeders, and, while predominantly carnivorous, will consume insects, edible fruits and other vegetable matter (Henry 1986). They also scavenge for food, making heavy use of carrion and other refuse (Ables 1975; Lloyd 1980).

Of dietary studies in south-eastern Australia, the majority have been clustered either in forested areas of south-eastern New South Wales and north-eastern Victoria, or in semiarid NSW, Queensland and South Australia. Only two published studies on fox diet have been carried out in higher rainfall agricultural land in NSW (McIntosh 1963a; Croft and Hone 1978), and one in Victoria (Coman 1973a). Nevertheless, these studies support findings from overseas that foxes are opportunistic predators and scavengers, relying mostly on mammalian prey. Where rabbits are plentiful, they usually constitute the most abundant item in scats and stomachs (McIntosh 1963a; Martensz 1971; Coman 1973a; Ryan and Croft 1974; Brunner *et al.* 1975; Bayly 1978; Croft and Hone 1978; Seebeck 1978; Lowe 1982; Baker and Degabriele 1987; Catling 1988; Marlow 1992; Lugton 1993a; Banks 1997; Molsher 1999). Other mammals make up the bulk of fox diets where rabbits are less common or absent (Green and Osborne 1981; Triggs *et al.* 1984; Brown and Triggs 1990; Lunney *et al.* 1990; Brunner *et al.* 1991; Banks 1997). Two studies have found scavenged carcasses, primarily eastern grey kangaroo, to be heavily utilised rather than live prey (Palmer 1995; Molsher 1999). Bubela (1995) found invertebrates to compose the bulk of fox diet in subalpine NSW, with mammals contributing only a small portion. However this study did not examine diet during winter, at which time a different study found small native mammals to compose the staple diet of foxes (Green and Osborne 1981)

The usual approach to identifying food items consumed by foxes is through analysis of scats or stomach contents. Items in stomach contents are much more readily identified and less affected by relative efficiency of digestion than scat contents (Brunner and Wallis 1986), but the method involves killing the fox, which gives a one-off snapshot of that fox's diet. Moreover killing the animal is not always an option: in this study killing of foxes in or near the study site would have compromised the outcomes of other aspects of the work. Being non-invasive, scat collection can be carried out on an ongoing basis with minimal interference to study animals (Brunner and Wallis 1986). In analysis of stomach contents, it is possible to estimate the relative importance of prey species by determining both percentage and volume occurrence of each prey species in the predator stomach (Hyslop 1980). Scat analysis can only show percentage occurrence, however Brunner and Wallis (1986) regard this as a minor disadvantage as several studies (Coman and Brunner 1972; Coman 1973b; Coman 1973a) have shown little difference between percentage occurrence and percentage volume for more important food items in stomachs.

Simply identifying food items consumed by foxes is of limited value. It provides information on the range of items utilised by the species at that time, which is useful for identifying shifts in patterns of prey consumption or differences between areas (Coman 1973a; Brunner *et al.* 1975; Hyslop 1980; Triggs *et al.* 1984; Wallis and Brunner 1987). It can also reflect differences in predation patterns between species of predator living in the same habitat (Triggs *et al.* 1984). Analysis of predator stomachs and scats is also commonly used to identify presence of rare prey (Brunner *et al.* 1976; Friend 1978). However, to relate consumption to preferences of the predator or its impact on prey species, a measure of food availability is necessary (Brunner and Wallis 1986).

The sheer scope of potential food sources makes it difficult to quantify fox food availability. Henry (1986) states that prey generally appears to be taken in approximate proportion to its abundance. However a number of studies from different parts of the world have found foxes appeared to ignore potential prey species, while apparently seeking out other species (Macdonald 1977). In a study of fox diet in Poland, Goszczynski (1974) found small rodents were a constant component of fox diet independently of their population density, but that among small rodents, consumption of the common vole *Microtus arvalis* paralleled changes in its availability. Six studies have been carried out in Australia that measured a number of potential food sources and compared this with occurrence in diet of foxes (Green and Osborne 1981; Catling 1988; Lunney *et al.* 1990; Marlow 1992; Bubela 1995; Banks 1997). As with overseas studies, it appears that when availability of prey is measured, it often doesn't correspond with any accuracy to occurrence in diet. Green and Osborne (1981) found mammals to be the dominant prey species during winter in the Australian Alps, with insects the primary food resource during snow-free months. They reported disproportionately high predation on *Mastacomys fuscus*. Findings of Bubela (1995) supported these results in a later study in the same area, with similar dietary components and a relatively high incidence of *Mastacomys fuscus* in scats. A study by Marlow in arid western NSW (1992) found rabbits to be the preferred prey species even when their availability was low but that foxes would switch to small marsupials even though they were also in low numbers at those times. Banks (1997) noted that rabbits occurred in fox diet frequently in sites where rabbits were less abundant in Namadgi National Park, Australian Capital Territory. Studies by Catling (1988) and Lunney *et al*. (1990) did not report a significant discrepancy between availability of prey and occurrence in diet. At Yathong Nature Reserve in semi-arid western NSW, Catling (1988) recorded abundance of rabbits but not other prey species. He found rabbits to be the dominant component of fox diet, and found predation by foxes corresponded with a slight time lag to rabbit abundance. Lunney *et al*. (1990) found mammals, generally native, were the most common dietary group, but, lacking any statistical analysis, they could only comment that occurrence appeared to roughly correspond with mammal abundance found by other survey techniques. Mammal abundance data were not presented.

The impact of predation on prey species is determined not only by what proportion of prey is taken, but also by characteristics of the population dynamics of both the predator and the prey species. How predators respond to prey is influenced by the density of the prey species. To measure the impact on prey, this predator response is often divided into a functional response – number of prey eaten per predator at different prey densities – and a numerical response – response of predator population to change in prey density (Solomon 1949).

Generally predators operate on the third trophic level (Begon *et al.* 1996), with their dynamics affected by prey availability which is in turn affected by foliage availability which is affected by external factors such as climate. Feedback may occur at all trophic levels. Scavenging, unlike predation, does not affect the rate at which resources are produced. Instead it is dependent on the rate at which some other force renders the resource available. This relationship between scavenger and food is described by Pimm (1982) as donor controlled, with the donor (prey) controlling the density of the recipient (predator) but not the reverse. Having no direct feedback between consumer and resource, it differs from traditional Lotka Volterra models of predator-prey interactions (Begon *et al.* 1996).

Functional responses are commonly categorised into Types I, II and III, based on findings of Holling (1959) (Figure 6.1). A Type I response indicates that as more resource becomes available, more is consumed per capita. It is difficult to conceive a situation in which the predator does not become satiated due to constraints such as handling time and stomach capacity (Holling 1959). However a Type I response is observed if such prey levels are never reached in reality (Boutin 1995). Where such levels are achieved, a Type II response is observed, with consumption approaching a maximum as availability increases. This gives a negative density dependent relationship, with a smaller proportion of the prey population consumed with increasing density. In some situations, a Type III response is observed, where, at low prey densities, an increasing proportion of the prey population is taken as prey availability increases. Beyond a threshold density the response is as for Type II. Examination of the functional response of predators to differing levels of carrion availability can yield information on the importance of carrion as a food source. This study does not intend to dwell on the technicalities of classifying response types as this is probably of lesser importance than quantifying carcass consumption to shed light on how important carrion is as a food source.

Putman (1983) studied disappearance and decomposition of small rodent carcasses in the Oxfordshire countryside. Decay was initially rapid, slowing exponentially over time. During summer and autumn, carcasses were largely decomposed after 7 or 8 days if not discovered by a scavenger.

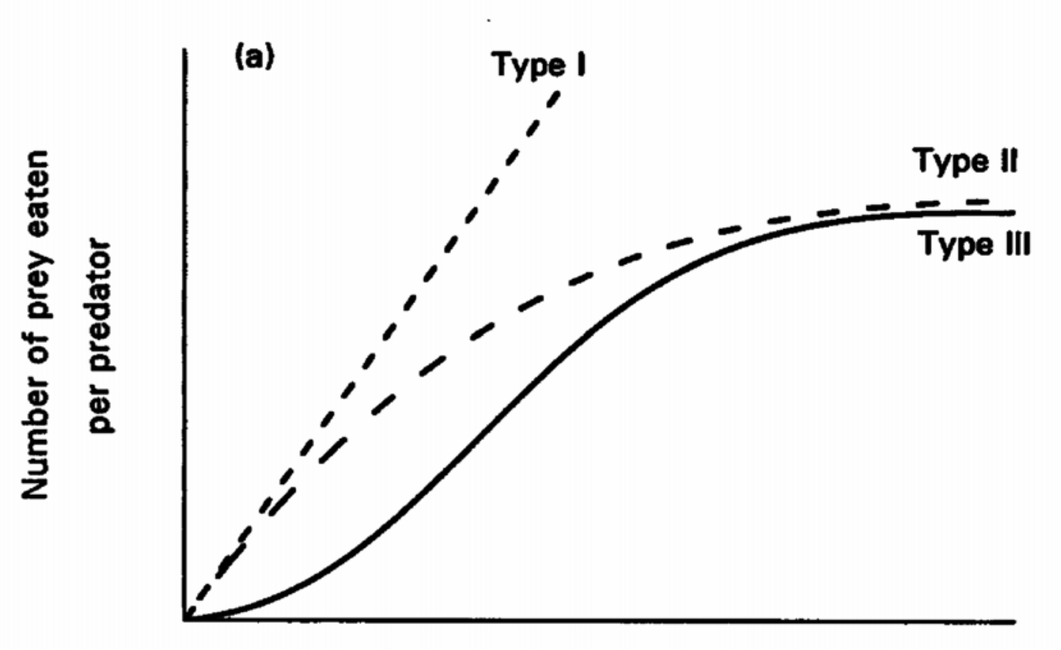

Figure 6.1. Type I, II and III functional response curves of a predator to differing prey densities (after Caughley and Sinclair 1994 Figure 10.2).

Given an estimate of energy requirements of foxes and calorific value of available carrion, it is possible to examine how much of a fox's energy needs can be met through scavenging, and compare this to what is actually observed. Saunders *et al.* (1993) estimated energy demands of foxes by directly measuring movement parameters and applying generalised models of energy expenditure for each activity. These models were based on measurements on many vertebrate species under laboratory conditions, and hence are not ideal for extrapolation to field conditions. Nor do they take into account energy requirements of growth and reproduction (Saunders *et al.* 1993). A more accurate method used for measuring field metabolic rate (FMR) is the doubly labelled water (DLW) technique (Lifson and McClintock 1966; Nagy 1989). This technique measures turnover of isotopically labelled water injected into free-living animals, however only a few studies have applied the DLW technique to carnivores (Green *et al.* 1984; Chevalier 1989; Geffen *et al.* 1992; Nagy 1994; Covell *et al.* 1996; Winstanley 1997). Winstanley (1997) provides the most applicable estimate to this study of red fox field metabolic rates, with FMR ranging between 318-582 kJ/kg/day. This study was carried out concurrently with my study in the same vicinity.

To maintain energy reserves, some species opt to consume their food upon acquisition and lay down large amounts of body fat while others cache food for later consumption (Cuthill and Houston 1997). Foxes do not carry much body fat but are known to cache excess food (Macdonald 1976; Sargeant 1978). The majority of caches are returned to, usually soon after caching, particularly if the cache contained preferred prey (Scott 1943; Macdonald 1976; Henry 1977). To what degree caching behaviour occurs in Australia is not well understood, with only one study describing this behaviour (Saunders *et al.* 1999). This study was carried out in the central tablelands of NSW, and used non-toxic baits containing radio-transmitters. It was found that approximately 10% of offered baits were cached, at a mean distance of 156m from the original location. The majority of cached baits were retrieved within six days. While not a primary aim of my study, intense monitoring of food supply enabled some investigation of whether caching occurred in the study site.

In this chapter, major food items of foxes in the central tablelands of NSW are described and related to their availability. The role of foxes as scavengers will also be discussed in the context of their energy requirements.

## 6.2 METHODS

### *6.2.1 Diet*

Fox stomachs collected during 1996 and 1997 from farmland around Orange, NSW (approximately 150km north of this study site), as part of a different study (Winstanley 1997) were donated to the project. Stomachs were stored frozen then thawed immediately prior to analysis. Stomachs were slit open and total contents weighed. These contents were then rinsed through interlocking geology sieves (phi 2 and phi 1.0) over an empty bucket and separated into fresh mammal, mammal carrion, bird, invertebrate, reptile, amphibian, plant and miscellaneous categories. Smaller items such as maggots were trapped in the fine sieve, while soil and other fine material was caught in the bucket. Volumes of food items were estimated by water displacement (Coman 1973a). Where volumes were less than 2mL, they were recorded as trace. Soil quantity was categorised by eye into trace, moderate and much.

Obvious putrescence or presence of maggots among vertebrate remains were considered evidence that the vertebrate was consumed as carrion. Large animals such as sheep and cattle were also considered to have been taken as carrion.

It is possible to identify mammalian remains to species level using microscopic examination of medulla patterns in hair as outlined in Brunner and Coman (1974). However the dominant mammalian food items, rabbits and hares, have very similar hair structure (Croft and Hone 1978; Reynolds and Aebischer 1991), and could not be identified to species level with confidence. For this reason hair analysis was simply used to separate lagomorph (hare or rabbit) from non-lagomorph. Only two published studies of fox diet in Australia acknowledged the potential for confusion between rabbit and hare, and conceded some hare samples may have been misidentified as rabbit (McIntosh 1963a; Croft and Hone 1978). Three other studies included hare in species lists but did not comment on how these were identified (Coman 1973a; Green and Osborne 1981; Lunney *et al.* 1990). Other studies simply listed rabbit, and, according to an expert on hair analysis, it is general practice to assume lagomorph remains are rabbit unless there is particular interest in looking more closely (Barbara Triggs, pers comm). Data on availability of rabbits and hares was collected during spotlight counts for foxes (Figures 5.1 b,c), so separating relative contributions of rabbits and hares could have revealed patterns in dietary preference. Availability of mammals not detectable by spotlighting was not measured, so partitioning other mammalian food items to species level was not considered necessary.

### *6.2.2 Food availability*

It was not possible to measure all potential food resources. However carrion availability and grasshopper abundance were measured as indicators of food availability. In addition, all non-livestock mammals sighted on quarterly spotlight counts were recorded (Figures 5.1a-e), providing a relative index of abundance throughout the study.

*Carrion availability*

A concurrent study into impacts of fox predation on lambing success was able to supply information on availability of lambs and losses both due to direct predation and other causes during three successive lambing seasons (Saunders *et al.* 1997). Initially, carrion availability was planned to be based on records of stock deaths supplied by property managers, however difficulty of collating such data meant this approach was abandoned.

During the lambing season of 1996, one 130 ha paddock was intensively monitored to estimate how consumption of lamb carcasses related to availability. Lambing yields a considerable quantity of carrion but only for a very short period of time each year. From the day the first newborn lamb was observed in the paddock, five transects of average width 70m and length 1.1 km were followed daily, with approximately 30% of the paddock thoroughly searched. Any new carcasses were weighed, and cause of death determined (following Rowley (1970)), how much of carcass had been consumed prior to finding and whether this was done by fox or some other species were noted. An identifying number was painted on the side of each carcass and on the ground beside it to indicate if the carcass was moved. Old carcasses were visually assessed daily to record any scavenging over the previous night. Any carcasses showing signs of scavenging by foxes were weighed the following day to allow calculation of amount consumed. Scavenging by birds was also recorded. Carcasses scavenged by birds typically exhibited talon or beak holes in the body, pecking of eyes or tongue, or removal of intestines through the anus. Unscavenged carcasses were weighed at least weekly to monitor background rate of decay. Daily transects continued for seven weeks, by which stage peak lambing was passed and no new carcasses had appeared for over a week.

To assess whether fox numbers increased in the paddock during lambing, or stayed steady, a weekly spotlight transect was followed through the lambing paddock, starting the week before lambing commenced. The transect was 1.2 km in length and took approximately 20 minutes to complete. Unlike spotlight counts described in Chapter 5, these counts were carried out using a 50W handheld spotlight and battery pack, with the observer riding on the back of a four-wheel motorbike.

### *Grasshoppers*

Grasshopper counts were carried out approximately bimonthly between March 1996 and January 1998 to establish when peak abundance occurred. Counts were based on a line transect method outlined by Southwood (1978), and involved counting the number of grasshoppers that were flushed in a 300m walked transect. Ten transects were walked each sampling period, 7 in pasture and 3 in crop paddocks, and sampling was only carried out between 11am and 3pm on sunny days to ensure maximal activity.

### *6.2.3 Energy requirements*

The gross energy values of mass of lamb carcasses available each day and consumed each day were estimated based on the average energy value of fresh animal carcasses of 3181 kcal/kg (13360 kJ/kg) (National Academy of Sciences 1968).

Energy requirements of foxes were calculated using findings of Winstanley (1997) which estimated specific energy expenditure to range between 318-582 kJ/kg/day. Average weight of foxes was calculated from data collected when trapping foxes (5.1 kg ± 0.1 se; Table 2.2). Estimates of how many foxes could potentially be supported by the total carcasses in the lambing paddock, and how many could be supported by the amount consumed, were calculated from these data. The estimated number of foxes consuming carrion was converted to a density estimate by dividing the estimate by the area of the lambing paddock plus a boundary strip the width of half the average home range span (3179m; Table 2.3) (Krebs 1999) around the lambing paddock

### *6.2.4 Analysis*

To estimate the rate of decay of carcasses in the absence of scavenging, the weights of each unscavenged carcass were plotted against time after death. Fewer weights were available for older carcasses, as few remained unscavenged as time progressed. For this reason a weighted regression analysis was carried out using SAS (SAS Institute Inc 1996). This rate of decay was used to back-calculate approximate daily mass of each carcass on days when not actually weighed, from which total biomass available and amount removed from scavenged carcasses was estimated.

The time after death at which foxes cease to regard lamb carcasses as a food source was established by analysing the number of days after death when lambs were scavenged. Two regression models were tested. First, a constant effect model where the number of carcasses scavenged was regressed on time of first scavenging and time of most major scavenging. Second, an exponential decay model where the natural logarithm of the number of carcasses scavenged was regressed on time of first scavenging and time of most major scavenging.

To analyse the relationship between amount of carrion consumed and amount available, first the potential for differential preferences for fresher and older carcasses was considered. Separate regressions of amount consumed against that available were carried out for carcasses at each day since death on the expectation that there would be a weaker or non-existent relationship for carcasses of decreasing desirability. A further possibility existed that foxes would not consider old carcasses when there was an abundance of fresh ones, but would eat them when there was no alternative. To remove the influence of carcasses of other ages, partial correlation analyses were carried out (Sokal and Rohlf 1995; SAS Institute Inc 1996) for carcasses of each age since death, with the partial variable being all carcass matter of age other than n. Partial correlation analyses were also carried out for cumulative carcasses to age n with the partial variable being all older carcasses, and cumulative available carcasses of minimum age n, with the partial variable being all fresher carcass matter.

Two functional response models were tested on data relating the amount consumed versus the amount available. The type I response was tested using linear regression. The type II response was tested using non-linear regression (procedure NLIN, SAS Institute Inc 1996) following the modified Michaelis-Menton equation:

$y = Ax^C/(B + x^C)$

where $A$ is the asymptote of the functional response, $B$ is the value of $x$ when $y = A/2$ and $C = 1$ in a Type II response (Marshal and Boutin 1999).

## 6.3 RESULTS

### *6.3.1 Diet*

A total of 148 stomach contents were analysed. The overall diet of foxes was found to be dominated by volume by vertebrate prey, both fresh and carrion (Table 6.1). The vertebrate categories were predominantly mammals, with birds, reptiles and amphibians occurring in 13% of stomachs and contributing only 1% of the total volume (Table 6.1). Invertebrates contributed the next most sizeable proportion of fox diet, occurring in 73% of fox stomachs, and contributing 21% of volume. Plant matter occurred in the majority of stomachs but contributed little to volume (Table 6.1). Of the vertebrate component of fox stomach contents, carrion was the most frequent occurrence and, along with lagomorphs, contributed the most sizeable portion of volume (Table 6.1). Lamb, mouse and other mammalian prey occurred relatively rarely and contributed little to volume.

When seasons were considered separately, carrion and lagomorph were both a dominant component of stomach volume in all seasons, particularly in winter and spring (Table 6.1). Lamb contributed a considerable portion of volume during winter but was insignificant in other seasons. The lamb category only included lamb clearly taken as prey, while scavenged lamb and sheep were included with carrion. As with the pooled results, mice and other prey occurred infrequently and contributed little to volume. Invertebrates occurred in the majority of stomachs in all seasons, with 100% of summer stomachs containing invertebrates. In terms of volume, invertebrates (including grasshoppers) composed a considerable portion of fox diet in summer and autumn, occupying 39% and 35% of stomach contents respectively, but contributed little to volume of winter and spring stomachs. While plant matter was a frequent occurrence in stomach contents of all seasons, it contributed very little volumetrically in any season.

Table 6.1. Total and seasonal percentage occurrence (O%) and volume (V%) of food categories (lagomorph, lamb, mouse, other prey, vertebrate carrion, bird, herpetofauna, plant, invertebrate and miscellaneous) in the diet of foxes from the Orange district of NSW, as determined by stomach contents analysis. (*n* =148 total stomachs, *n* =42 winter, *n* =21 spring, *n* =12 summer, *n* =73 autumn)

| Food Category | Total | | Spring | | Summer | | Autumn | | Winter | |
|---|---|---|---|---|---|---|---|---|---|---|
| | O% | V% | O% | V% | O% | V% | O% | V% | O% | V% |
| Lagomorph | 19.6 | 32.5 | 23.8 | 49.0 | 16.7 | 22.9 | 17.8 | 28.7 | 21.4 | 32.7 |
| Lamb | 6.1 | 7.1 | 0.0 | 0.0 | 0.0 | 0.0 | 4.1 | 1.5 | 14.3 | 19.2 |
| Mouse | 5.4 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 4.1 | 0.3 | 11.9 | 2.0 |
| Other prey | 5.4 | 2.1 | 0.0 | 0.0 | 8.3 | 1.3 | 5.5 | 1.5 | 7.1 | 4.1 |
| Carrion | 48.0 | 30.1 | 52.4 | 32.7 | 33.3 | 34.1 | 41.1 | 24.5 | 61.9 | 35.5 |
| Bird | 7.4 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 12.3 | 0.4 | 4.8 | 0.7 |
| Herp. | 5.4 | 0.5 | 23.8 | 2.9 | 0.0 | 0.0 | 2.7 | 0.1 | 2.4 | 0.0 |
| Plant | 57.4 | 3.9 | 61.9 | 1.7 | 41.7 | 1.3 | 57.5 | 6.7 | 59.5 | 1.7 |
| Invert. | 73.0 | 21.3 | 81.0 | 11.6 | 100.0 | 39.3 | 80.8 | 34.7 | 47.6 | 3.1 |
| Misc. | 18.9 | 1.5 | 33.3 | 2.1 | 8.3 | 1.1 | 16.4 | 1.6 | 19.0 | 1.0 |

### *6.3.2 Food availability*

When the study commenced, the landowner was using dog biscuits as supplementary fodder for cattle, and these were stockpiled in two large heaps as well as available in a number of feed troughs. Foxes were observed foraging at troughs and at one of the stockpiles. These stockpiles were depleted around winter 1995 and not replenished for the remainder of the study. It is likely that while they were available these dog biscuits were a significant dietary component.

#### *Carrion availability*

A total of 97 lamb carcasses were located and monitored during the lambing season of 1996. The area searched was estimated to cover 30% of the paddock area, extrapolating to a total of approximately 320 carcasses available in the paddock.

A plot of availability of fresh carcasses against time (Figure 6.2) reveals most deaths occurred during the first week of lambing, with a second pulse of deaths in the third week. Very few deaths occurred beyond the third week. Deaths of lambs were associated with spells of cold, wet weather.

Scavenging of carcasses was found to usually occur *in situ*, with only 5 carcasses moved up to 100m from their original location. All carcasses could be accounted for throughout the monitoring period, indicating that little or no caching of carcasses was occurring.

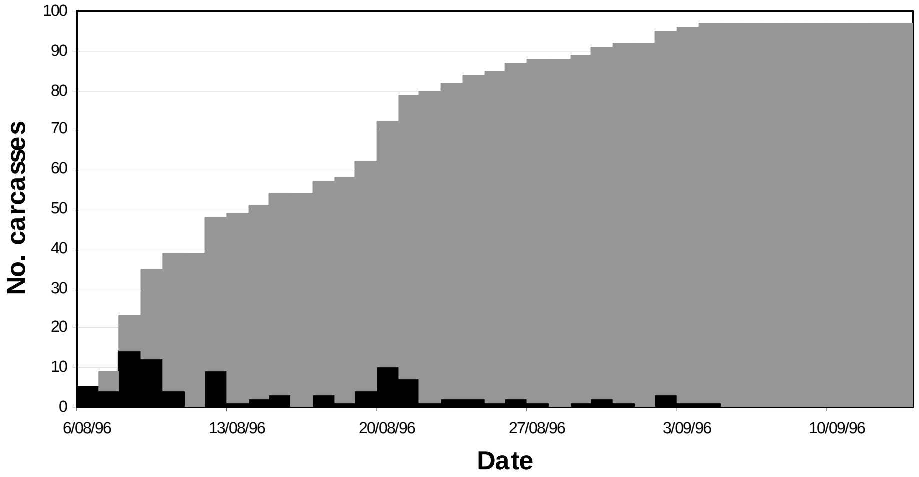

Figure 6.2. Number of fresh (■) and cumulative total (▒) lamb carcasses available on each day during lambing in 1996.

*Grasshoppers*

Grasshopper counts carried out between March 1996 and January 1998 showed grasshoppers to appear in December, rise to a peak in March, taper off through autumn and completely disappear by June (Figure 6.3). No distinction was made between different species of grasshoppers and locusts, and no correction was carried out to convert counts to biomass of grasshoppers per unit area.

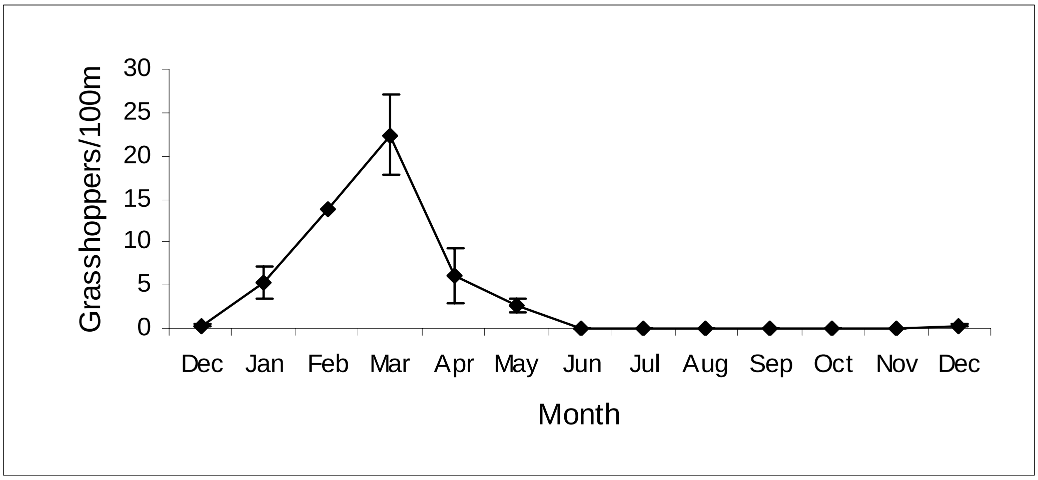

Figure 6.3. Average monthly grasshopper abundance in the study site (data were collected between March 1996 and January 1998).

### *Rate of decay of carcasses*

A highly significant linear relationship (F = 720; df = 1,33; $p < 0.005$, $r^2 = 0.956$; $n$ = 2 to 67) was found describing the rate of decay of carcasses in the absence of scavenging (Figure 6.4). The fitted equation was,
weight (kg) = -0.118*age (days) + 4.303.

This relationship indicated a constant loss of matter of 0.118 kg per day.

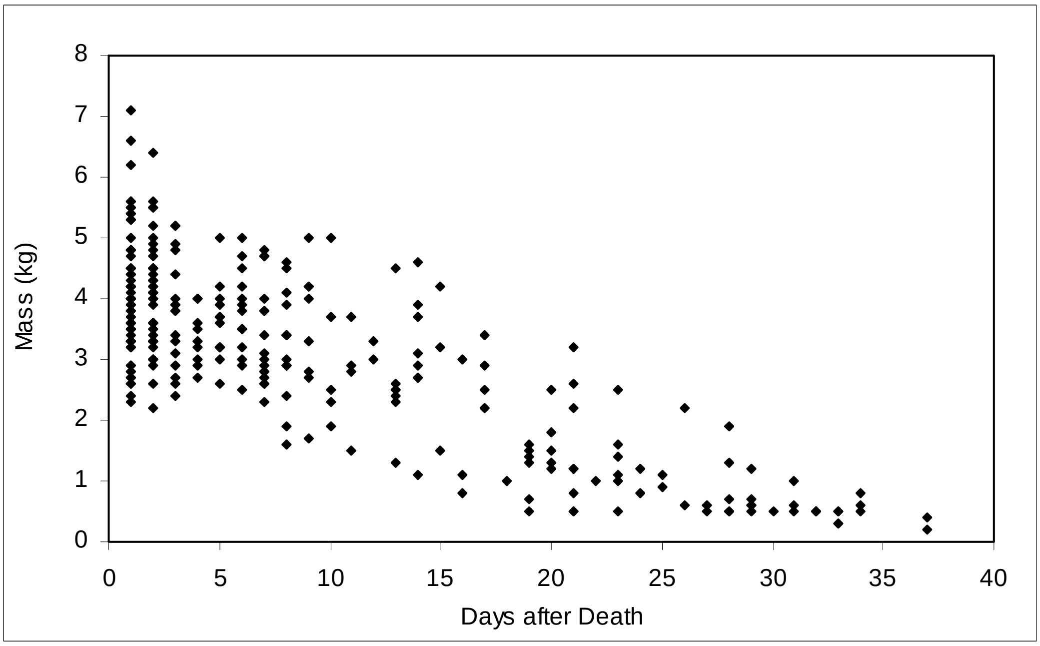

Figure 6.4. Rate of decay of lamb carcasses in the absence of scavenging.

### *Time after death when carcasses were scavenged*

The main scavenging appeared to also be the initial scavenging event, with little difference between plots of initial scavenging and plots of main scavenging events (Figure 6.5). However some carcasses were repeatedly revisited for progressive scavenging, while others remained unscavenged. Both the constant effect model and the exponential decay model gave highly significant results for both initial and main scavenging events (Figure 6.5). However the relationship between scavenging and carcass age was found to be better explained by the exponential decay model ($r^2$ = 0.52, $p<0.001$ for initial scavenging, and $r^2$ = 0.59, $p<0.001$ for main scavenging).

### *Preference for fresh carcasses over old*

There was a significant positive correlation between the availability of carcasses that were one day old and their consumption ($r^2$ = 0.54; df=29; $p<0.005$), when the availability of other carcasses was corrected for. All other ages gave non significant results. When cumulative carcasses to age $n$ were considered, significant correlations ($p>0.05$) were only found for carcasses up to day 3 (day 1 $r$ =0.54, day 2 $r$ =0.45, day 3 $r$ =0.38). With increasing quantities of older matter this correlation became weaker. No significant relationships were found for cumulative available carcasses of minimum age n, indicating there was no preference for older carcasses.

### *Relationship between amount consumed and amount available*

Two functional response models were tested to see which, if any, explained the relationship between consumption and availability. Given the finding that no significant correlations between consumption and availability occurred for older carcasses, the functional response models were only tested for fresh carcasses. A highly significant relationship was found for the type I functional response model ($y = 0.07x - 0.22$) (Figure 6.6; Table 6.2). Using non-linear least squares regression to fit functional response curves to the data, convergence was achieved with the equation $y = -7345.2x/(-113059.1 + x)$ (Figure 6.6; Table 6.2) for the type II model. As there was no evidence of a sigmoidal relationship at low levels of food availability, a type III model was not fitted. Plots of type I and II curves show essentially no difference in shape in the range of the data used (Figure 6.6), and even when extrapolated over a much larger range, deviate only slightly. Both regressions had highly significant outcomes (Table 6.2).

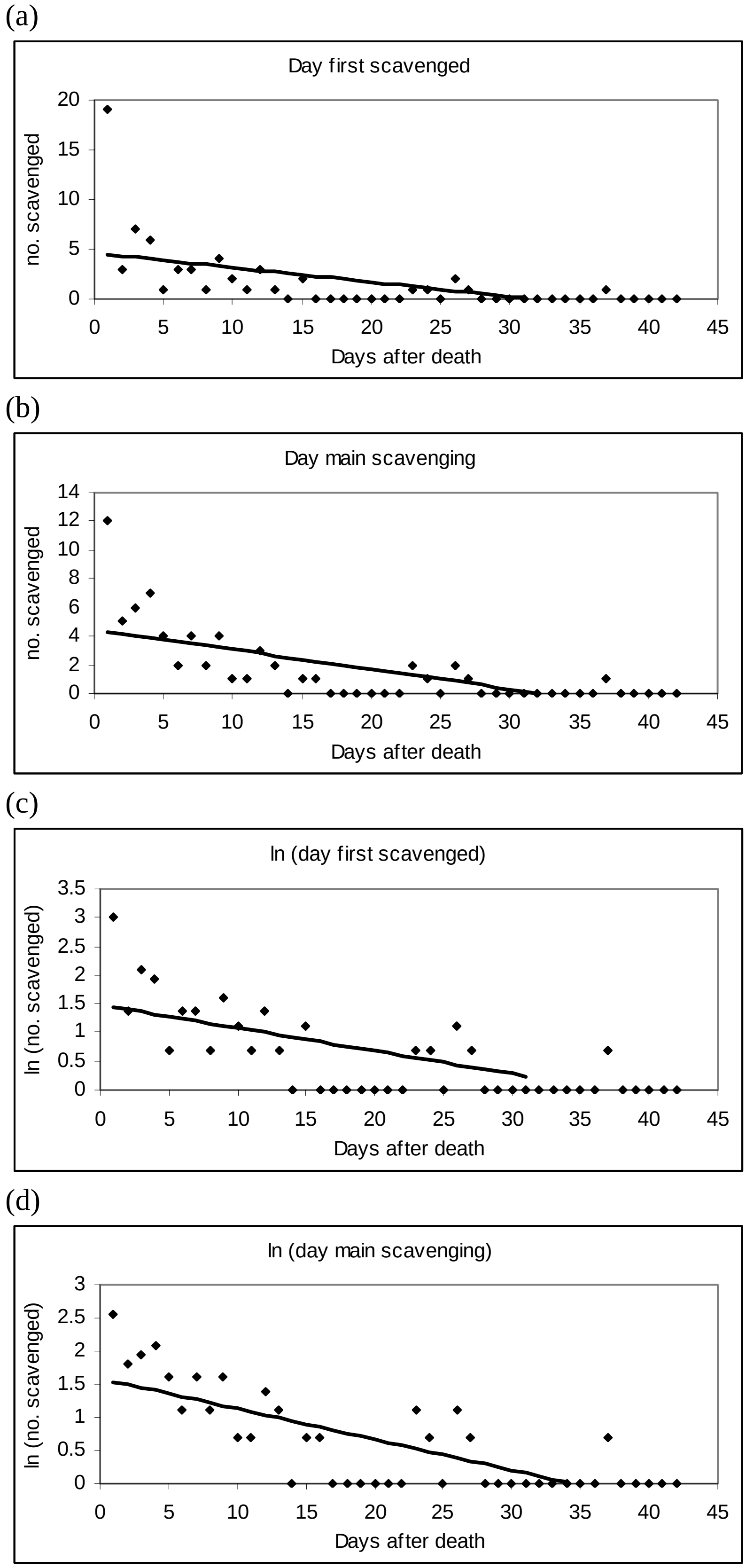

Figure 6.5. Number of days after death when scavenging of carcasses occurred. (a) time of first scavenging $r^2 = 0.31$, p=0.0001. (b) time of main scavenging $r^2 = 0.48$, p<0.0001. (c) ln (time of first scavenging) $r^2 = 0.52$, P<0.0001. (d) ln (time of main scavenging) $r^2 = 0.59$, p<0.0001.

Table 6.2. The fit of functional response models fitted to data for consumption of fresh lamb carcasses.

| Model | $r^2$ | df | F | p |
|---|---|---|---|---|
| Type I | 0.57 | 29 | 37.49 | <0.0001 |
| Type II | 0.66 | 29 | 56.92 | <0.0001 |

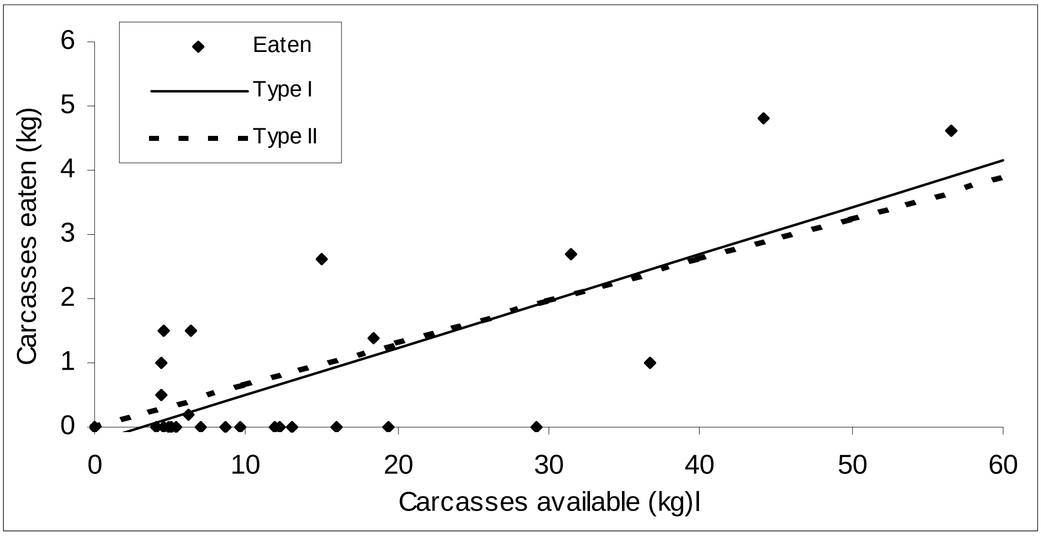

Figure 6.6. Quantity of fresh (one day old) carcass eaten against availability during August and September 1996. Both Type I and Type II functional response curves are plotted.

*Fox abundance during lambing period*

Spotlight counts of foxes through the lambing paddock between August and September 1996 revealed no obvious trend in fox abundance (Figure 6.7). A regression analysis of sightings against time gave a non-significant result ($r^2$ =0.02, df=7, p=0.72).

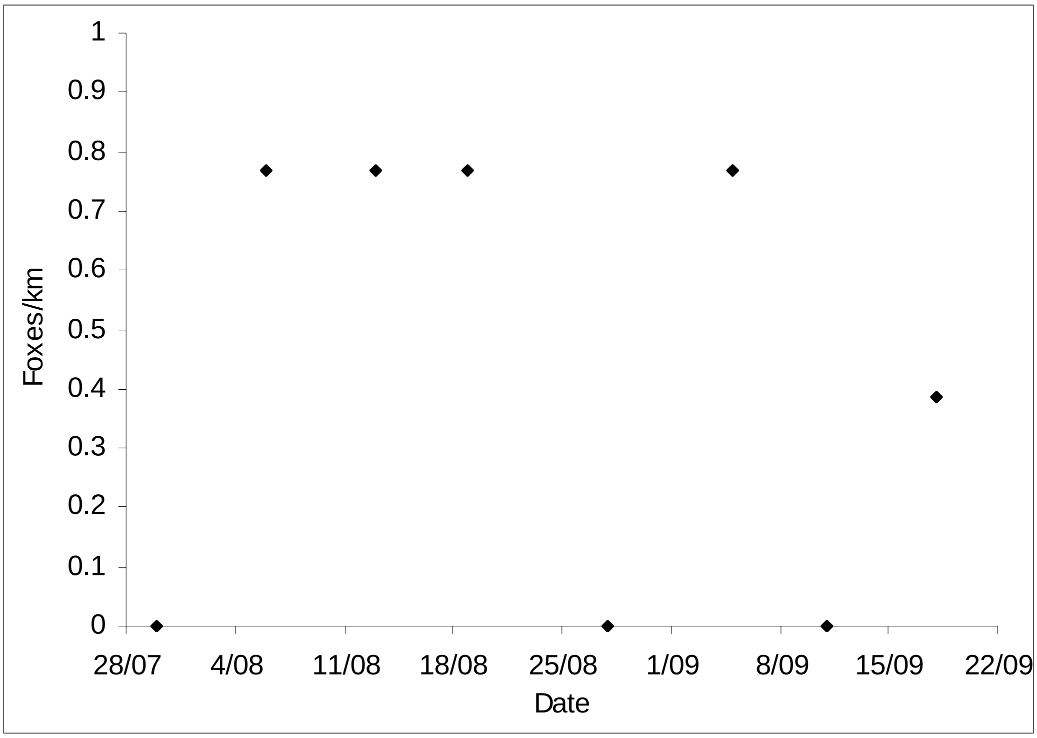

Figure 6.7. Number of foxes sighted per km on the weekly spotlight transect through the lambing paddock during July, August and September, 1996.

### *6.3.3 Energy requirements*

It was calculated from results of searching the lambing paddock that approximately 320 lamb carcasses were available for scavenging. Given that freshly dead lamb carcasses weighed an average of 4.1 kg, this amounts to approximately 1312 kg of carcass matter in that paddock alone over the 5 weeks. The average daily quantity of carcass present over the period was calculated to be 435.7 ± 27.4 kg, while the average daily consumption of carcass was 9.4 ± 1.3 kg. The daily available gross energy provided by carcasses in this paddock alone computes to sufficient food for 2440 to 4464 foxes, while the daily amount removed from the paddock could support 53 to 96 foxes (Table 6.3). Considering fresh carcasses alone, the mean daily availability was 43.1 ± 8.3 kg, which could support between 240 and 440 foxes. Actual fresh carcass matter consumed was 2.42 ± 0.81 kg, supporting 13 to 24 foxes (Table 6.3).

Table 6.3. Average daily availability and consumption of carcasses (kg±se) estimated across the entire lambing paddock in winter 1996, gross energy value of available and consumed carcasses (kJ) and potential number of foxes these could support.

| Carcasses | Available | Energy kJ | Foxes | Consumed | Energy kJ | Foxes |
|---|---|---|---|---|---|---|
| Total | 435.7±27.4 | 5 821 039 | 2440 - 4464 | 9.4±1.3 | 125 585 | 53 - 96 |
| Fresh | 43.1±8.3 | 574 480 | 240 - 440 | 2.42±0.81 | 32 064 | 13 - 24 |

The area of the lambing paddock plus boundary strip was 15.6 km$^2$. Density of foxes based on total carcass matter removed from the paddock was 3.4-6.2 foxes/km$^2$, and density based on removal of fresh carcasses only was 0.8-1.5 foxes/km$^2$.

## 6.4 DISCUSSION

### 6.4.1 *Fox diet in the Orange district*

The diet of foxes in the Orange district was found to be broadly similar to findings of other Australian studies into fox diet, with the staple foods being mammalian prey and carrion (McIntosh 1963a; Martensz 1971; Coman 1973a; Ryan and Croft 1974; Brunner *et al.* 1975; Bayly 1978; Croft and Hone 1978; Seebeck 1978; Green and Osborne 1981; Lowe 1982; Triggs *et al.* 1984; Baker and Degabriele 1987; Catling 1988; Brown and Triggs 1990; Lunney *et al.* 1990; Brunner *et al.* 1991; Marlow 1992; Lugton 1993a; Palmer 1995). Studies in agricultural land in south eastern Australia found that rabbits and sheep constitute the most important dietary items, followed by mice (McIntosh 1963a; Coman 1973a; Croft and Hone 1978). Rabbits and sheep were abundant where stomachs were collected for these studies, as they were for the present study. Interpretation of broad patterns of fox diet was limited by unequal sample sizes in each season. It could be seen that peaks in invertebrate occurrence and volume in fox diet corresponded with peaks in their availability (Table 6.1 and Figure 6.3).

It was not always clear whether the occurrence of lamb in fox stomachs was by direct predation or through scavenging of freshly dead carcasses, and in these cases presence was attributed to predation rather than scavenging. This very likely led to an overestimation of the extent of direct predation and an underrepresentation of the degree of scavenging in fox diet. Given the strong preference for freshly dead carcasses that was established in this study, this bias could be quite considerable as there was no opportunity for carcasses to show signs of putrescence. A study on scavenging and predation of lambs in north-west Scotland where sheep mortality is heavy found the number of scavenged lamb carcasses to be almost double the number of live lambs taken (Hewson 1984b).

### *6.4.2 Scavenging of lamb carcasses*

This study traced the fate of 97 individually marked carcasses during a lambing season, and found all scavenging occurred within the lambing paddock. The fate of all monitored carcasses could be accounted for throughout the monitoring period. No carcasses were completely removed, and of the five carcasses that were shifted any distance from their original location, the furthest distance moved was 100m. A sample of 22 lambs within the study area were fitted with radio-collars during this period as part of a separate study, and of these none was removed outright from the lambing paddocks (Saunders *et al.* 1997). This suggests carcasses were not being removed from the paddock prior to discovery. These findings provide no evidence that caching of lamb carcasses was occurring. Saunders *et al*. (1999) found 10% of 1080 baits fitted with radio-transmitters were cached. In the current study, a strong preference was found for fresh lamb over older carcasses. Unlike the manufactured baits used by Saunders *et al*. (1999), which were based on dried meat and so are relatively well preserved, any fresh carcasses that were cached may become unpalatable, and this may explain why caching of lambs was not observed.

Saunders *et al.* (1997) found that percentage losses of both ewes and lambs between ultrasounding in June and marking in September were consistent from year to year on Spring Valley, but that losses on Templemore were more varied, with particularly high losses of ewes during 1996 (Figure 6.8). These results indicate large quantities of carrion were consistently available each winter, with some years particularly abundant.

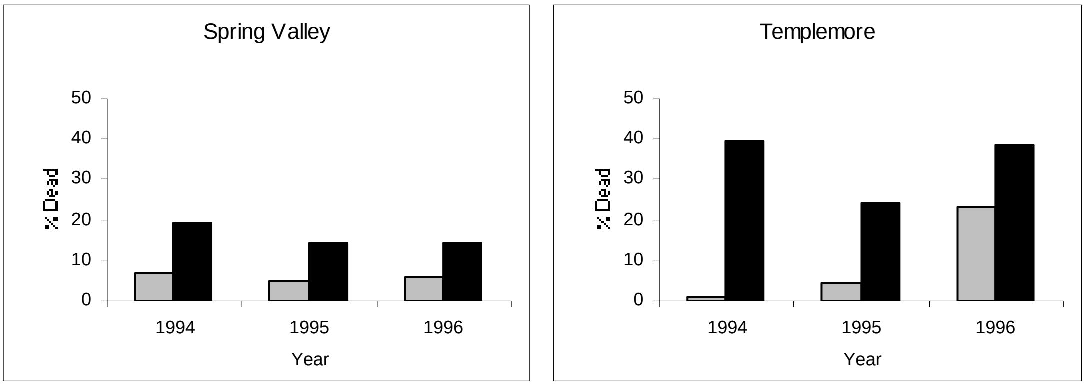

Figure 6.8. Percentage losses of ewes (■) and lambs (■) between ultrasounding of flocks (June) to marking of lambs (September) on Spring Valley and Templemore properties. Data from Saunders *et al.* (1997).

This study found lamb carcasses decayed at a constant rate over time. This trend contrasts with findings of Putman (1983) who reported exponential decay of small mammal carcasses in Oxfordshire. In this study the decay of total lamb biomass was examined, not the rate of decay of each individual carcass, and measurements were of carcasses at a wide range of stages of decay. If individual carcasses were decaying exponentially, this may have been obscured by the pooling of carcasses at different points in the decay process. Few unscavenged carcasses remained for weighing towards the end of the sampling period, rendering sample sizes of carcasses at advanced stages of decay very small.

Scavenged carcasses were not included in measurements of rate of decay as the relative proportions of matter lost through decomposition and scavenging could not be partitioned. Opening of carcasses by scavengers has been found to accelerate the rate of decay by exposing soft tissues to desiccation and colonisation by blowfly larvae and other agents of decay (Ellison 1990). In the present study scavenged carcasses also appeared to decompose faster than intact carcasses, which would have biased estimates of total matter available upwards. However rate of decomposition is not a factor in biomass of fresh carcasses, so estimates of fresh carcass availability would not be subject to this bias.

Scavenging on lamb carcasses was predominantly on carcasses only one day old. Observations in the field suggested that foxes were preferentially consuming fresh carcasses while they were available but when they became more scarce, older carcasses were exploited. In an attempt to explore this further, partial correlation analyses were performed to measure consumption of carcasses of each age while removing any influence of carcasses of other ages. The only significant relationship found was for fresh carcasses (one day old) when availability of each age was considered separately, but significant results were found for up to three days old when carcasses to that age were pooled. Given the lack of a significant relationship for days 2 and 3 when considered separately, the relationship to day 3 was attributed to dominance of day 1 carcasses in the sample.

Functional response analyses (Holling 1959; Marshal and Boutin 1999) were performed on fresh carcasses as no significant relationships were found between consumption and availability for older carcasses. A type II functional response fitted the observed pattern best, but the type I model was also highly significant. No evidence of saturation was observed, with the amount consumed rising linearly with increasing availability. The functional response measurement was of a group of foxes, not individuals. As each fox would reach saturation at different times and possibly by consuming different food items, this could have obscured the outcome. Presumably a group saturation point would have been reached eventually, but was not detected in this study. A type II functional response of foxes eating rabbits was reported by Pech and Hood (1998).

The area searched was estimated to cover 30% of the paddock area. From this it was estimated that there were approximately 320 carcasses available in the paddock. Estimation of the number of foxes that could potentially be supported by this lambing paddock alone revealed sufficient food for as many as 4000 foxes over the lambing period (Table 6.3). The daily quantity of carcass matter removed from the paddock was estimated to support up to 96 foxes, while fresh carcass consumed could meet energy needs of 13 to 24 foxes. This is a very crude estimation of energy supply and requirements, with no consideration of other nutritional requirements foxes may have, or how calorific value of carcasses may change with decay. However it does indicate there was an excess of food available during the lambing season. Lambing was occurring simultaneously in additional paddocks in the vicinity so this paddock was not the sole source of carrion for these foxes. However, while possibly an overestimation, these figures indicate carrion is in great abundance at this time of year, and a significant quantity is consumed by foxes.

In this study it was assumed that carcass matter removed by scavengers other than foxes was negligible. Ravens and the occasional bird of prey were seen scavenging carcasses and tongues and eyes were removed from many carcasses, but the quantity of matter removed appeared small. Hewson (1984b) similarly reported that birds scavenged a high proportion of lamb carcasses, but usually only removed eyes and tongues in a study in Scotland.

### *6.4.3 Management implications*

Foxes are an annual breeder (Saunders *et al.* 1995), with the population size restricted to the number of foxes that can survive the most resource-scarce time of year. Energy demands are at their highest in late winter and spring because of breeding, and by the end of spring the fat reserves of foxes are at their lowest (Winstanley 1997). This study observed stomach contents were filled almost exclusively with carrion and prey vertebrates at this time of year, whereas in other seasons invertebrates made a greater contribution. The reduced range of available foods and increased metabolic demands suggest late winter and spring may be a bottleneck period in determining the size of the fox population. If this is so, a management strategy could be to reduce the availability of carrion during late winter and spring, to restrict the number of foxes surviving this period. Such strategies could take the form of conducting lambing in autumn rather than spring, or by removal of carcasses from paddocks. However benefits from such a strategy would need to be weighed against possible increased pressure on alternative prey when food became limited, such as considered in relation to the fall in rabbit availability due to rabbit calicivirus disease (Newsome *et al.* 1997).

### *6.4.4 Conclusion*

In summary, the results of this study were broadly similar to those of other studies, in that the primary food items of foxes were mammalian prey and carrion, with invertebrates taken when abundant. Foxes made heavy use of lamb carcasses during lambing in late winter/ early spring. A strong preference was found for fresh carcasses, and there was no evidence that lamb carcasses were cached. A possible management strategy could be to restrict carcass availability in late winter/ spring to reduce the number of foxes able to be supported through this apparently resource-limited period, although any effects of prey switching as a result of such a strategy would need to be considered.

# CHAPTER 7

# GENERAL DISCUSSION

In this chapter I outline the major findings of this study and compare these to findings of other studies of fox ecology in Australia. The topics covered by this thesis: ranging behaviour, dispersal, density estimation, denning behaviour, activity rhythms, population dynamics and diet, will be covered in sequence. I then outline implications of these findings for management of foxes in Australia.

## 7.1 ECOLOGY OF THE RED FOX

### *7.1.1 Ranging behaviour and social structure*

Foxes are predicted to have smaller ranges in more stable environments with higher food diversity (Jarman 1986; Bubela 1995; Saunders *et al.* 1995; Banks 1997; Meek 1998). In Australia the largest ranges are found in semi-arid and alpine habitats (Marlow 1992; Bubela 1995), and the smallest ranges are found in urban habitats (Coman *et al.* 1991). Mean ranges in the present study were of intermediate size and most similar to range sizes in agricultural land in Victoria (Coman *et al.* 1991) and coastal forest in NSW (Phillips and Catling 1991). While ranges in the present study fitted within the overall pattern relating to environmental stability and food diversity, a great degree of individual variation was observed. Measured ranges varied from 76 ha to 1926 ha, with differing degrees of overlap with neighbouring foxes. As also observed by Meia and Weber (1995), some foxes did not occupy a steady range, and were instead nomadic in their movements.

In the present study, groups of animals were observed with a high degree of overlap of ranges, but usually with distinct non-overlapping core areas. Other animals were observed to have neatly abutting ranges with no overlap suggesting territorial exclusion. This suggests foxes had individual territories, but that in some cases these individual territories were nested within a group territory. It is clear that the broad spatial arrangement of foxes must involve overlap of home ranges, as with an average home range of 276 ha (kernel) or 446 ha (MCP), a system of non-overlapping monogamous pairs would result in an adult fox density of 0.45-0.72 foxes/km$^2$, when estimated densities were higher (Table 7.1). However the estimated density of the fox population based on natal dens falls in this range (0.52-0.55 adult foxes/km$^2$; Table 7.1) suggesting little overlap of breeding foxes. Moreover, there were some vixens observed with completely overlapping core ranges, and only one natal den was detected in these areas. This suggests there was a high proportion of non-breeding foxes in the area, and that suppression of breeding may have occurred.

Little has been described of overlap of core ranges in Australia, and the only study in Australia considered to have social groups with a dominance hierarchy (Bubela 1995) did not give sufficient detail to assess whether patterns of overlap were similar to the current study. Studies from Europe (Harris 1980; Lloyd 1980; Niewold 1980; Poulle *et al.* 1994) and North America (Ables 1969b; Voigt and Macdonald 1984) have reported a similar pattern to that observed here, with highly overlapping ranges but individual focal areas, indicating this is a common spatial arrangement.

Five hypotheses relating to group formation in mammals are summarised in Bubela (1995). These are the Resource Dispersion Hypothesis (RDH) (Kruuk 1978; Macdonald 1979; Macdonald 1983; Doncaster and Macdonald 1992), the Constant Territory Size Hypothesis (CTSH) (Lindstrom 1980; von Schantz 1984b), the Territory Inheritance Hypothesis (TIH) (Lindstrom 1986), the Resource Productivity-Variance Model (RPVM) (Powell 1989) and the Prey Renewal Hypothesis (PRH) (Waser 1981). The present study did not set out to measure temporal and spatial distribution of resources to test such hypotheses, but one prediction of the RDH is relevant to this study. This prediction is that adult group size will be smaller where available prey are more homogeneously dispersed (Bubela 1995). In the present study the largest group of foxes with overlapping core areas (Figures 2.7 and 2.8) occurred near two concentrated food resources: the local tip and a large pile of dog biscuits the landowner used as supplementary cattle fodder during the drought. Ranging behaviour did not appear to be focused around either of these resources, but they fell within range boundaries. Upon cessation of the drought, dog biscuits were no longer available. This is also when many of the animals in that group died, and no overlap of core areas was observed in the area the following year (Figures 2.11 and 2.12). These observations support the RDH prediction, and suggest the formation of a group in this environment may have been an anomaly due to the richness of the dog biscuit resource.

### *7.1.2 Dispersal*

How far foxes disperse is positively correlated with home range size and negatively correlated with population density (Trewhella *et al.* 1988). It is also thought that foxes disperse further in more heterogeneous habitats (Trewhella *et al.* 1988), and that the proportion of foxes that disperse also differs according to habitat (Zimen 1984). Dispersal patterns in this study were similar to those observed elsewhere (Trewhella *et al.* 1988; Coman *et al.* 1991), in that distances were mostly short but with some exceptional distances travelled. As observed in North America (Storm *et al.* 1976), juveniles were more likely to disperse than adults and moved further (Figure 2.13), but adult dispersal was not uncommon.

The Territory Inheritance Hypothesis (Lindstrom 1986) proposes that a female offspring’s decision to stay or disperse is based on the relative probability of gaining breeding status in the natal range versus an unoccupied territory. In this site there appeared to be a significant number of non-breeding foxes and adult survivorship was high. Levels of dispersal were high compared to those observed by Coman (1991) in similar habitat. It is possible that the chance of gaining breeding status was relatively low in the present study, and that the high proportion of dispersals observed was related to this.

Where groups of foxes form, they are usually composed of a dominant male and female and a number of subordinate, usually related vixens (Macdonald 1979). While young vixens may remain, young males are expelled from these groups (von Schantz 1981). It is also commonly observed that males are more likely to disperse than females (Ables 1975; Storm *et al.* 1976; Lloyd 1980; Saunders *et al.* 1995). This is possibly related to a proportion of females not being expelled. The current study found no difference in the proportion of males and females that dispersed, which does not support a social system in which females may remain in their natal ranges while males disperse.

Marlow *et al*. (2000) suggested the predominant social system of foxes across Australia was likely to be mated pairs or dominance hierarchies with only one subordinate, but that in higher rainfall areas, where fox densities appear to be higher, there may be a higher incidence of dominance hierarchies with multiple subordinates. The findings of the present study, in one such higher rainfall area, are supportive of this prediction, with evidence that breeding vixens were well spaced and non-breeding vixens overlapped these ranges.

### *7.1.3 Population density*

Home ranges of foxes tend to be smaller at higher population densities (Harris 1980). Within Australia, the largest ranges and lowest densities of foxes are found in semi-arid and alpine habitats (Marlow 1992; Bubela 1995; Marlow *et al.* 2000), ranges and densities in productive agricultural land are intermediate (Coman *et al.* 1991; Thompson and Fleming 1994), and the smallest ranges and highest densities are found in urban habitats (Marks and Bloomfield 1999), indicating this trend also applies to Australia.

In the present study, density of adult foxes was estimated using counts of active and natal dens (Chapter 3), quantity of carcasses (total and fresh only) removed from a lambing paddock (Chapter 6) and destructively on completion of the study using index-manipulation-index and Petersen estimates (Chapter 5). Estimates ranged from a minimum of 0.52 adult foxes/km$^2$ using natal den counts to an upper estimate of 6.2 adult foxes/km$^2$ based on removal of carcasses (Table 7.1). Both these extremes were estimated in spring 1996, indicating the range of estimates was greater than explained by fluctuations in the fox population between dates of estimation, and that the technique used to estimate density had a major effect on the estimate (Table 7.1).

All techniques used to estimate density in the present study included a boundary strip of half the average span of a home range around the area studied, as described by Krebs (1999), dramatically increasing the area over which the estimated number of foxes was thought to occur and thereby diluting the estimate. Estimates from the present study appear lower than those of other authors in similar habitats in Australia This may be because boundary strips were not included in their density estimates (3 foxes/km$^2$ Coman *et al.* 1991; 4.6-7.2 foxes/km$^2$ Thompson and Fleming 1994). Boundary strips of half a home range span may have been excessive as home range results from this study indicate considerable overlap of ranges, so foxes in addition to those counted would have been utilising the boundary strips. However, as core ranges were found to be generally exclusive (Figures 2.7-2.12), a boundary strip of half an average core span may have been more appropriate.

Table 7.1 Density of adult foxes/km$^2$ based on natal den counts, active den counts, removal of carcasses (all carcasses and fresh carcasses only) from a lambing paddock, index-manipulation-index and Petersen estimate, and date when estimation was conducted. The chapter in which each method is outlined is listed under details.

| **Density estimation technique** | **Adult foxes/km$^2$** | **Date of estimate** | **Details** |
|---|---|---|---|
| Natal den counts | 0.55 | November 1995 | Chapter 3 |
| Natal den counts | 0.52 | November 1996 | Chapter 3 |
| Active den counts | 0.91 | November 1995 | Chapter 3 |
| Active den counts | 1.30 | November 1996 | Chapter 3 |
| Total carcass removal | 3.4-6.2 | September 1996 | Chapter 6 |
| Fresh carcass removal | 0.8-1.5 | September 1996 | Chapter 6 |
| Index-manipulation-index | 1.4-3.2 | June 1997 | Chapter 5 |
| Petersen estimate | 2.4-5.3 | June 1997 | Chapter 5 |

The study site readily lent itself to the estimation of fox abundance using active and natal den counts, as dens were easily located in this habitat. However to estimate density from natal den counts a knowledge of the social structure of foxes is required, while if using active den counts it is necessary to know how many dens each fox uses, a trait that the present study revealed had much individual variation. Social organisation is very difficult to elucidate given the elusive nature of foxes so breeding pairs are commonly assumed (eg Harris 1981; Coman *et al.* 1991; Marks and Bloomfield 1999), with no correction for non-breeders in the population. The natal den counts in the present study can be considered as a minimum population estimate as it relied upon a simplistic social structure, used minimum litter size estimates and did not take into account non-breeders. Active den counts include those used by non-breeders, and the number of dens used by vixens can be estimated by close monitoring of radio-tagged animals. Assumptions in the estimation were that all active dens were located, a 50:50 sex ratio and only one vixen per active den. That estimates based on active den counts were higher than those based on natal den counts suggests a significant number of non-breeding foxes were present (Table 7.1).

Estimates of density based on carcass removal assumed that all carcasses removed were taken by foxes. The sheer scale of matter removed from the site, enough to meet the energy needs of 53-96 foxes, suggests this is an unlikely assumption. Some scavenging may have occurred by birds of prey and ravens and decomposition processes such as desiccation and consumption by maggots may have been underestimated. Decomposition was not an issue when considering fresh carcasses only, and density estimates based on fresh carcasses were more comparable to estimates by other techniques.

The destructive density estimation techniques used, Petersen estimate and index-manipulation-index, gave estimates with very large standard errors due to the small proportion of the population culled and the small sample size. In addition to the fact that the destructive nature of these techniques means they are not always appropriate within a study design, unless a significant proportion of the population can be culled, these methods can only give a broad indication of the number of foxes present.

### *7.1.4 Den usage and availability*

There were many disused dens in the study area and there was a high turnover of occupants and which dens were occupied. This suggests dens were not a limited resource. The number of natal dens was similar across the two years studied, but more active dens were identified in the second year of study. In a 14-year study, Nakazono and Ono (1987) found similar numbers of natal dens and active dens from year to year, but found they located progressively more dens for the first three years of their study as their searches became more effective before numbers stabilised. As also found by other studies (Storm *et al.* 1976; Page 1981; Henry 1986; Nakazono and Ono 1987), natal dens were more likely than active dens to be used on repeat occasions, not necessarily by the same vixen, so it is possible that these dens have particularly desirable attributes for which there may have been competition. If any suppression of breeding was occurring in the site, one mechanism by which it could be applied is through dominant foxes occupying the most favourable natal den sites.

### *7.1.5 Fox activity rhythms*

In this thesis, a new method of analysing data on activity rhythms within a 24-hour period using Fourier series (James 1993) is presented. The method provides a systematic means of identifying cyclical components of movement behaviour, and enables comparison of these cyclical components between individuals, categories of animals, localities and even species. Given suitable data, this method could be adapted to periods longer than 24 hours.

By dividing the day into 24 segments, 12 each of day and night, fox behaviour was clearly described by a 24-segment and a 12-segment cyclical component. The 24-segment component was the dominant influence, with the 12-segment component of lesser amplitude. Ashby (1972) noted that in mammals there appears to an endogenously determined periodicity of activity of approximately 24 hours, apparently entrained by the periodicity of the rapid changes in light intensity of dawn and dusk. The 12-segment cyclical component appeared to be stimulated by the rising and setting of the sun. Coupled, these cycles gave an overall pattern of predominantly nocturnal behaviour, with a peak in activity around 2 hours after sunset, a lesser peak before dawn and minimum activity around noon. This pattern is similar to that reported in other studies in Australia (Jarman 1986; Bubela 1995; Saunders *et al.* 1995; Banks 1997; Meek 1998) and overseas (Storm 1965; Ables 1969a; Maurel 1980; Blanco 1986; Takeuchi and Koganezawa 1992; Saunders *et al.* 1993; Cavallini and Lovari 1994; Lovari *et al.* 1994; Weber *et al.* 1994; Reynolds and Tapper 1995; Doncaster and Macdonald 1997; Adkins and Stott 1998).

### *7.1.6 Population dynamics*

This study found that considerable fluctuations can occur in fox numbers in the absence of management, but that, in accordance with generic predictions by Caughley and Sinclair (1994), these fluctuations were around a mean annual rate of increase ($r$) of zero. Annual adult survival in the absence of human intervention was high (0.56-0.96), similar to that reported by Pech *et al*. (1997). Of the 13 foxes that died of natural causes within the study area, four were above 3 years of age, with the oldest being 10 years. Other studies in Australia (Coman 1988; Marlow *et al.* 2000) and overseas (Fairley 1969; Ables 1975; Storm *et al.* 1976; Harris 1977; Lloyd 1980; Yoneda and Maekawa 1982) have observed very few foxes survive beyond three years of age.

Causes of mortality are typically human-related (Storm *et al.* 1976; Harris 1978b; Reynolds and Tapper 1995), so the high survivorship of foxes in the present study is most likely because of the lack of human intervention. Dead foxes collected in the vicinity of the study area during the study were all shot or roadkilled, while 13 foxes within the study area died of natural causes and only one died of human-related misadventure. However foxes dying of natural causes outside the study area were unlikely to be found, so no comment can be made on how frequent an occurrence natural death is in the presence of control efforts. No attempt was made to elucidate natural causes of death due to the state of decomposition of bodies found.

Litter sizes estimated from sightings of emergent cubs in the present study (2.8) were slightly lower than litter sizes estimated by the same technique elsewhere in Australia (3.3, Coman *et al.* 1991; 4.4, Marks and Bloomfield 1999). Density estimates based on active den counts showed greater fluctuation between years than those based on natal den counts (Table 7.1). This suggests that if there was a similar level of breeding in both years, that there were more non-breeders present in 1996 than in 1995. This corresponds with spotlighting observations, in which counts of foxes in spring 1996 were marginally higher than counts in spring 1995. Comparing natal den locations and home ranges, in 1995 there was one natal den in the range of five vixens, two vixens shared another (and were in fact observed in the den simultaneously) and no natal den was found in the range of one vixen. In 1996, a natal den was found in the ranges of each of six vixens, and no natal dens were found in the ranges of two other vixens. Where multiple vixens overlapped one natal den, or where no natal dens were found in the home range, it indicates either these animals did not breed or natal dens were overlooked.

### *7.1.7 Diet*

The staple dietary items of foxes on the central tablelands were mammalian prey and carrion, among which lagomorphs and sheep were the most common. Invertebrates were a large component of fox diet when they were most abundant in summer and autumn. The three published studies of fox diet in agricultural land in southeastern Australia also found foxes to rely mostly on mammalian prey, principally rabbits, sheep (taken as carrion) and mice (McIntosh 1963a; Coman 1973a; Croft and Hone 1978). Other studies in Australia have also found invertebrates to be an important food resource for foxes during the warmer months (McIntosh 1963a; Croft and Hone 1978; Green and Osborne 1981; Bubela 1995; Palmer 1995).

The stomachs analysed were not strictly representative of fox diet within the study area, as they came from the Orange district rather than immediately near the study area at Murringo, over 150 km away. Rabbits and other small mammals were relatively uncommon in spotlight counts in the Murringo study area, whereas they were in great abundance where foxes were collected (Roy Winstanley, personal communication). A numerical response of foxes predators (foxes) to numbers of mammalian prey (rabbits, hares and brushtail possums) (Caughley and Sinclair 1994) was not detected from spotlighting data. This suggests foxes were not reliant on these mammals in the current study. A lack of dependence on prey mammals is unusual, in that studies in Australia have found that, where rabbits were not abundant, introduced rodents (Brunner *et al.* 1991) and native mammals (Green and Osborne 1981; Triggs *et al.* 1984; Brown and Triggs 1990; Lunney *et al.* 1990) made up the bulk of fox diet, although a study in south-western Queensland found foxes to be primarily consuming mammalian carrion (Palmer 1995).

Dead lambs appeared to be of great dietary importance during the lambing period in late winter, with many carcasses showing evidence of scavenging. Foxes showed a strong preference for freshly dead lamb over more stale carcasses, and the daily quantity of fresh lamb removed from one lambing paddock alone in winter 1996 was estimated to feed 13-24 foxes (Table 6.3). No evidence of caching of lambs was detected, although this may be because cached lamb becomes unpalatable.

When the study commenced, the landowner was using dog biscuits as supplementary fodder for cattle, and these were stockpiled in two large heaps as well as being available in a number of feed troughs. Foxes were observed foraging at troughs and at one of the stockpiles. These stockpiles were depleted around winter 1995 and were not replenished for the remainder of the study. It is likely that these dog biscuits were a significant dietary component, and the observed drop in fox numbers in spring 1995 (Figure 5.1a) may have been related to the loss of this food resource.

## 7.2 MANAGEMENT AND RESEARCH IMPLICATIONS

Foxes are managed in Australia and elsewhere for conservation, production, disease and harvesting objectives. The outcomes of the research reported here have implications for fox control methods and tactics, rather than for management objectives themselves.

### *7.2.1 Social system*

Caughley *et al.* (1992) predicted that, in the theoretical situation where the breeding of a dominant female suppresses breeding in subordinate females in her group, sterilisation of the dominant female could in fact promote breeding in subordinates. An experiment to test whether sterilisation of the dominant vixen releases subordinates to breed had mixed results (Bubela 1995), and this issue remains unresolved. In Australia, the basic social unit of the fox is generally considered to be breeding pairs (Saunders *et al.* 1995). The observations in this study suggest a more complex social structure. It is likely that in other areas in Australia with similar or higher densities, foxes have a similar social structure to that observed in the present study. The model of Caughley *et al.* (1992) suggests that sterilisation of the dominant vixen would need to release breeding in more than one subordinate for the number of litters produced to increase. Further work should then be directed at establishing whether multiple non-breeding vixens per breeding vixen even occur to a significant degree in Australia before more effort is concentrated on clarifying whether release of reproduction in subordinates occurs.

A small number of nomadic foxes were among those radio-tagged in this study. Whether nomads can rear cubs is not known, but they have the potential to mate with resident foxes. Whether sterilised resident vixens could be displaced by fertile nomads is not known. This could potentially undermine the effectiveness of fertility control, which has been suggested as a possible fox control method (Tyndale-Biscoe 1994a).

### *7.2.2 Dispersal*

In this study twice as many foxes tagged as juveniles dispersed from the site as remained. Such a high proportion of foxes dispersing from the site, with a small proportion travelling very large distances, indicates there is potential for rapid spread of diseases. If resistance arises to either poisons or fertility control agents, then this could also spread rapidly through dispersing foxes. Foxes will rapidly recolonise areas where density has been reduced (Coman *et al.* 1991; Clark and Fritzell 1992; Thomson *et al.* 2000), which means management programs need to be conducted frequently and over a large area, if any lasting benefit is to be gained, although Banks *et al*. (1998) reported fox numbers stayed low in a relatively small control area. The present study found juveniles were more likely to disperse and travelled further, but adult dispersal was also observed. Juvenile foxes were more readily baited, trapped and shot than older foxes. Thomson *et al*. (2000) found that regular baiting in a buffer zone around a control area was effective at preventing recolonisation of the core, likely because vacant territories were available for foxes to settle in within the buffer area so they did not continue on to the core. Baiting to intercept dispersing foxes is possibly successful because the targets are mostly juvenile foxes.

### *7.2.3 Density estimation*

Active and natal den counts were achievable in this habitat, where dens were highly visible. Den counts were labour intensive, but gave a repeatable result. Estimates based on active den counts included non-breeding foxes, and so were considered more accurate. However natal den counts were important for assessing non-destructively the number of breeding foxes in the population. Whether nomadic foxes use dens to the same degree as resident foxes is not known, and needs to be explored to establish if active den counts include nomads. Removal of fresh carcasses from a lambing paddock gave a density estimate comparable to those from natal den counts, but assumed all carrion removed was taken by foxes and that foxes ate nothing but carrion, both unlikely assumptions.

Index-manipulation-index and Petersen estimates did not give a precise result in this study as insufficient foxes were killed to get an accurate estimate. However both methods have potential given an adequate knockdown of the population under study. Findings of this study suggest a boundary strip of half the span of an average core range rather than a home range may be more appropriate for estimating population density.

### *7.2.4 Activity rhythms*

A clearer understanding of activity rhythms of foxes has implications for management and research. Indices of fox abundance that require foxes to be active in order to detect them, such as spotlight counts, track counts, trapping success and bait station visitation, will be biased if carried out at differing levels of activity. Studies using radio-telemetry to establish habitat usage are biased if they do not take into account the activity patterns of the animal under study (Palomares and Delibes 1992). Likewise studies of ranging behaviour of foxes will give a more complete picture of areas visited by foxes if they include times of peak activity. Knowledge of activity rhythms is of benefit in interpretation of energetics studies (eg Saunders *et al.* 1993). In terms of fox control, use of spotlight shooting is more likely to be effective if carried out when foxes are most active. Activity rhythm data on predators could help to predict when prey species are more likely to be at risk of predation, and enable appropriate precautions to be taken.

### *7.2.5 Population dynamics*

Findings from the present study are in agreement with other studies (eg Coman 1988; Kay *et al.* 2000; Marlow *et al.* 2000), in that the various methods used to catch or cull foxes targeted different age groups within the population. Cyanide and trapping tended to select for younger, naïve foxes. Shooting was less biased than cyanide or trapping, but still gave a lower age profile than that known to occur in the site. As management programs are likely to be more successful at targeting younger foxes, this needs to be considered when modelling likely outcomes of control such as application of a sterilising bait. Hobbs *et al*. (2000) predicted that fertility control is more likely to be successful if the average age at sterilisation is less than the generation interval (the mean age of foxes giving birth), so greater success at targeting younger foxes may in fact be an advantage.

Sensitivity analysis (Lande 1988) found adult and juvenile survival to be the two most influential life-history parameters on rate of increase. This suggests a change in fecundity, as could occur with fertility control (Tyndale-Biscoe 1994a), may cause less change in the rate of increase than lethal control. In the long-term, however, both methods may produce similar results (Barlow *et al.* 1997). The relative costs per unit effort were not considered, but fertility control would need to be less expensive to be an efficient alternative if this is in fact the case. Bomford (1990) observed that where managing for conservation, costs of fertility control must be less than conventional control unless there are other advantages to justify the additional expense such as reduced impact on non-target species. Where managing on agricultural land, any management must be cost effective in terms of production, and fertility control would need to give the biggest return in production per dollar spent to be justifiable (Bomford 1990).

### *7.2.6 Diet*

Sufficient fresh lamb carrion was available in one lambing paddock alone during late winter to meet the energy needs of up to 440 foxes, with this figure higher again if less fresh carrion was included (Table 6.3). These findings indicate an abundance of food at the most energetically demanding time of year for foxes. In late winter and spring other food items such as invertebrates were not available. Being an annual breeder (Saunders *et al.* 1995), the population is limited to the number of foxes that can survive through the most resource-scarce time of year. The reduced range of food items available during late winter coupled with the high energetic demands associated with reproduction suggest that, without lamb carrion, late winter could be a resource bottleneck. A possible management strategy would be to minimise the amount of carrion available during late winter and spring to reduce the number of foxes supported through this bottleneck. Options to achieve this include lambing in autumn rather than winter/spring and removal of carrion from paddocks.

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