Predation by red foxes limits recruitment in populations of eastern grey kangaroos

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Abstract   We investigated the impact of red fox (*Vulpes vulpes* Linnaeus 1758) predation on juvenile eastern grey kangaroos (*Macropus giganteus* Shaw 1790) using a replicated predator removal experiment. In two sites in Namadgi National Park, south-eastern Australia, a persistent 1080 poisoning campaign over 18 months reduced fox density by more than 85%, and to less than 10% of the fox density in two other sites with no fox baiting. Changes in the mother : young ratios and densities of kangaroo populations were monitored twice monthly along 2-km transects in each site from July 1993 to February 1995. Compared to nonremoval sites, where foxes were controlled, 25–40% more females retained juveniles over the period when these young became emergent from the pouch. This higher survival of emergent pouch young resulted in a significantly higher proportion of juveniles in kangaroo populations at fox control sites, which resulted in a significantly higher annual growth rate. We conclude that predation upon juveniles is an important limiting factor for kangaroo populations in Namadgi NP.

Key words: feral predator, juvenile survival, macropod, mother : young ratio, predator control, predator–prey interaction, vertebrate pest.

INTRODUCTION

For many large mammal herbivores (>20 kg adult body mass), juvenile mortality exerts a dominant influence on overall population dynamics (Gaillard *et al.* 1998). Understanding the causes of this mortality and its consequences to population dynamics therefore remains fundamental to understanding and managing these species. Predation upon juveniles is perhaps the most controversial source of mortality for large mammals, particularly where there are potential conflicts in attempting to conserve and manage both predator and prey (Bergerud 1988; Merriggi & Lovari 1996). Two main hypotheses to account for predator impact compete: the doomed surplus hypothesis (Errington 1946) considers that predators take the excess production of a population, while in contrast, the predator-limitation hypothesis (Boutin 1992; Van Ballenberghe & Ballard 1994) considers that predators remove individuals that would otherwise contribute to the population. However, there are very few predator manipulations testing between these hypotheses to give support to observational and modelling work, which suggested that predators can strongly influence large herbivore population dynamics by limiting juvenile recruitment (Gaillard *et al.* 1998).

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In Australia, the population dynamics of large kangaroos in semiarid areas has been the subject of extensive empirical and modelling research. For grey kangaroos, many workers have explored their broad-scale distribution (e.g. Jarman & Denny 1976; Caughley *et al.* 1988) and abundance (e.g. Caughley *et al.* 1977; Caughley & Grigg 1982; Grigg *et al.* 1985) and in arid and semiarid areas rainfall is considered a significant regulatory factor (e.g. Caughley *et al.* 1984, 1985; Caughley 1987). Outside climatically unpredictable arid environments there have been no published studies of the population ecology of eastern grey kangaroos and the factors limiting population growth remain speculative. It is likely, however, that factors other than rainfall exert strong influences on grey kangaroo population biology in temperate areas (Arnold *et al.* 1991). Anecdotal evidence suggests that predation may exert strong influences. For example, dingoes (*Canis lupus dingo* Linnaeus 1758) are considered the most significant predator of kangaroos, although early workers considered their impact negligible (e.g. red kangaroos (*Macropus rufus* Desmarest 1842) Newsome 1971, 1975). Dingoes often prey primarily upon very old animals (Newsome *et al.* 1983a,b; Oliver 1986; Thomson 1992; Wright 1993) and the very young and can inflict heavy losses (Shepherd 1981) which may dramatically limit recruitment (Robertshaw & Harden 1986, 1989). Correlative evidence comparing kangaroo densities on either side of the dingo fence in central Australia shows a significant difference consistent with the hypothesis that

dingo predation limits kangaroo numbers, particularly at low densities (Jarman & Denny 1976; Caughley *et al.* 1980). Dingo predation is even thought to have eliminated pockets of eastern grey kangaroos and red-necked wallabies (*Macropus rufogriseus* Desmarest 1817) in New South Wales (Robertshaw & Harden 1989).

Red foxes are also significant predators of macropods but it is the smaller macropods that are considered most vulnerable (Kinnear *et al.* 1988, 1998; Burbidge & McKenzie 1989; Robertshaw & Harden 1989). Several studies have identified larger species of macropods (>10 kg adult body mass) in the diet (see review by Newsome *et al.* 1997). However, this occurrence has been attributed to carrion from dingo kills (e.g. Lunney *et al.* 1990), despite observations of foxes killing the juveniles of euros (*Macropus robustus,* Gould 1841) (Hornsby 1982), red-necked wallabies (Robertshaw & Harden 1989) and grey kangaroos (Arnold *et al.* 1991). Consequently, the impact of foxes on the population dynamics of these larger species has been considered negligible (Robertshaw & Harden 1989). More recently, though, foxes have been implicated as a potential cause of significant juvenile mortality in a population of western grey kangaroos (*Macropus fuliginosus* Desmarest 1817) in woodland in Western Australia (Arnold *et al.* 1991). Poor recruitment was thought to be the principal factor limiting population growth, and fox predation was suggested as a factor.

In this paper we investigate the effect of fox predation on juvenile recruitment in populations of eastern grey kangaroos in areas of montane grassland in Namadgi NP, south-eastern Australia. Kangaroo comprises up to 45% (by occurrence) of the fox diet in the area, reaching a peak in late spring when juvenile kangaroos begin to emerge from the pouch (Fig. 1; Banks 1997). This occurrence coincided with several observations of direct predation by radio collared foxes which harassed female kangaroos with young at foot until they abandoned their young (Banks 1997). In this paper we test two predictions from the general predator-limitation model on the impact of fox predation using a spatially duplicated predator-removal experiment. If foxes limit recruitment of juvenile kangaroos then fox removal will result in higher juvenile survival (prediction 1). If predation upon juveniles limits kangaroo populations then fox removal will result in higher kangaroo population growth where foxes are removed (prediction 2).

METHODS

Study area

The study was conducted in Namadgi National Park in the Brindabella Ranges, 50 km south of Canberra, Australia. The study area consisted of montane forest (800–1100 m a.s.l.) and open grassy farmland, which was repossessed more than 15 years prior to this study. Four cleared valleys were chosen, each approximately 10 km^2 in area and separated by 7–22 km of mostly sclerophyllous forest which provided some barrier to fox movement and hence independence between sites. Kangaroos were abundant and each night moved from the remnant timbered areas to forage on the valley floor, consisting primarily of short tussock grasses (*Poa* spp.). Foxes were prevalent throughout and were likely to be the main predator of kangaroos in the area. The main mammalian prey of foxes in the area are European rabbits (*Oryctolagus cunniculus* Linnaeus 1758) (40% by occurrence) and kangaroos (up to 45%), with native small mammals, invertebrates and vegetation comprising the remainder (Banks 1997). Dingoes, major predators of kangaroos in other areas (Robertshaw & Harden 1989), were very uncommon in all sites (fewer than one individual seen every two months) due to persistent and targeted live trapping by National Parks personnel to reduce dingo impact on neighbouring sheep properties. As dingoes were essentially missing from this system it is highly unlikely fox control efforts lead to major changes in dingo predation on kangaroos.

Details of the fox removal experiment are described by Banks *et al.* (1998). In summary, there was a persistent campaign of 1080 baiting in two sites (Boboyan and Grassy) using commercially available FOXOFF baits (35 g) each containing 0.3 mg of 1080. Baiting commenced in July 1993 and reduced fox abundance from 2.8 and 3.4/km (spotlight counts) to less than 0.5/km within 6 months, and to almost zero for the next 12 months. Fox density in the two nonremoval sites (Orroral and Glendale) remained comparatively stable over this period (approximately 0.8–2.0/km) and typically fivefold higher than in fox removal sites.

Kangaroo surveys

The size and structure of the kangaroo population at each of the study sites was estimated from counts along
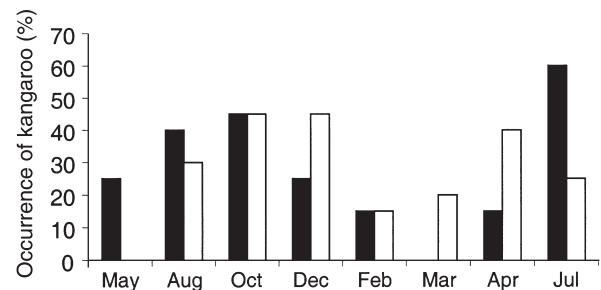
Fig. 1.   Monthly changes in the percentage occurrence of eastern grey kangaroo in fox scats collected from non-removal sites Glendale (□) and Orroral (■) during 1993–1994 kangaroo breeding season. *n* = 20 scats for each month in each site.

set transects, 1.5–2.0 km long in each site, which ranged between 400 and 700 m wide due to changes in the proximity of the forest edge in the valley. Initial observations showed that animals emerged from the forest to feed in open habitats an hour before dusk. Previous workers have identified this period as the peak time for foraging activity (Heathcoate 1987; Clancy & Croft 1991). One hour before dusk, all the animals that occurred in the area of the set transect were identified to sex and size class (small, medium or large) with the aid of binoculars (Pentax 12 × 50). Transects were surveyed twice each survey period with sites surveyed in random order. Surveys were conducted during August, October and December in 1993 and then monthly until March 1995.

Kangaroos in the area were not habituated to humans and initial attempts to conduct the survey on foot (e.g. Coulson & Raines 1985; Southwell 1989) proved futile as animals fled to the protection of cover when approached at distances exceeding 200 m. This problem of reactive movement seriously compromises attempts to estimate population size from transect counts (Southwell 1994). Therefore, observations of the kangaroos were made from the back of a moving vehicle travelling very slowly (<5 km/h) throughout all areas of the transect. Animals were calm when a vehicle approached slowly and hence less likely to be missed or counted more than once during a survey. The extra height of the vehicle also enabled a clearer identification of each animal's sex and size characteristics.

Each individual was identified to sex and size class, as the large population sizes precluded drugging and capture techniques (e.g. Arnold et al. 1986) or the identification of individual animals based upon facial or other external features (Jarman et al. 1989). Males were easily distinguished from females based on their generally larger frame, more muscular forearms, relatively larger forepaws and generally darker coats. Males also have obvious, external testes from a young age. Individuals were classified by size and development as subadult, medium or large adult (Jarman & Southwell 1986). Females do not show the same relationship between body size and age as do males and generally stop growing at 5–7 years (Norbury et al. 1988; Arnold et al. 1991). Therefore, females were classified as subadult or adult. Females were also identified as having small–medium or large pouch young, having small–medium or large young at foot or having no discernible young (Jarman & Southwell 1986). Included in the latter category were females unable to be classified because their pouches were not clearly visible (mean monthly percentage females with unclassified young was Boboyan = 11.1%; Grassy = 15.7%; Glendale = 10.1%; Orroral = 11.3%). In this case it was likely that these females had no or only very small young because the pouch becomes large and obvious

when young are medium or large sized. Young at foot are easily distinguished. Animals were considered subadult based on their small head and body size, downy appearance of their fur and other under-developed features. Sub-adults showed no association with particular females and were considered to be independent.

Assessing recruitment

If foxes cause a significant loss of newly emergent pouch young, the proportion of adult females with young should differ between treatments over the study period. Similar mother : young ratios have been used extensively in studies of ungulate population ecology, particularly in those assessing the impact of predation upon recruitment (e.g. Gasaway et al. 1992; Seip 1992; see also review by Boutin 1992). Thus, proportional changes in the numbers of females with young (in the pouch or at foot) were compared between treatments using Student's t-tests at each time period. To determine if fox predation limited recruitment, the proportions of subadults in the populations were also compared between sites with and without foxes. In all analyses, proportions were arcsine transformed (Sokal & Rohlf 1995) and compared using one-tailed tests, excluding the hypothesis that fox control could lead to reduced recruitment of juveniles (Rice & Gaines 1994).

Kangaroo population growth

To determine whether fox predation limited kangaroo population growth, mean monthly densities were calculated using the total counts from direct observations divided by the area (ha) sampled. Females with young at foot were considered as a single animal until the young became independent. The exponential rate of increase was used as an index of population growth and derived from the slope of a linear regression of $\log_e$ density against time (Caughley & Sinclair 1994) which was then converted to an annual rate. In March 1994 the areas covered during evening counts of kangaroos increased to include a more representative sample of the kangaroos at each site. This change is unlikely to have influenced changes in the proportion of females with young, but made total counts before and after this time incompatible. Hence only data from March 1994 to February 1995 (the core experimental period) were used to determine population changes.

Scat counts have also been used to provide indices of kangaroo abundance (e.g. Perry & Braysher 1986). However, a pilot study of scat counts revealed highly irregular temporal fluctuations indicative of differential decay rates between sites (Banks 1997)

making them unsuitable to reveal the influence of fox impact on kangaroo abundance.

RESULTS

Kangaroos in the study area were strongly seasonal breeders as most females carried well developed (medium or large-sized) pouch young during mid-winter each year. There were relatively few instances of females having both young at foot and pouch young. Within sites, some variation in the apparent progression of pouch young size occurred from survey to survey. This presumably reflected females' ability to pull the pouch tight which obscured the size of the young to the observer. As a result there was a peak in the proportion of females with young in August each year when large pouch young were highly visible. To overcome problems of identifying the size of pouch young, all sizes were pooled for purposes of analysis and any unclassified females were combined with females with no young. Similarly, the sex of subadults was often difficult to determine and hence sexes were pooled.
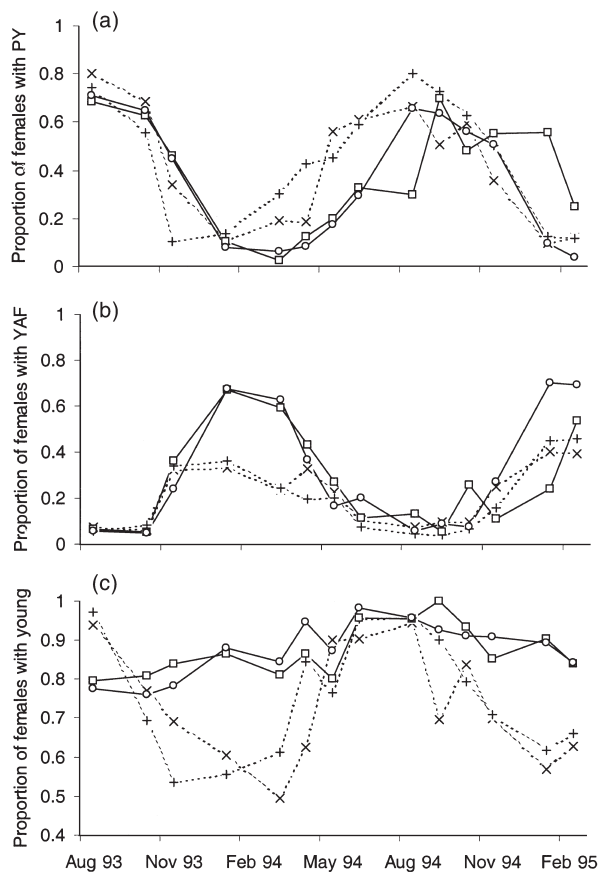
Fig. 2. Monthly proportions of female eastern grey kangaroos with (a) pouch young (PY), (b) young at foot (YAF) and (c) all types of young, in fox removal sites Boboyan (—□—), Grassy (—○—) and nonremoval sites Glendale (– – × – –), Orroral (– – **+** – –).

Changes in the proportions of females with young

The proportion of adult females with young was defined as 1 minus the proportion of females with either no young or with unknown young. During winter 1993, kangaroo populations in the two non-removal sites had slightly but not significantly larger proportions of females with pouch young than did the removal sites (Fig. 2a). From August to January these young gradually became emergent from the pouch resulting in a steady increase in the proportion of females with young at foot during this period (Fig. 2b). However, during this pouch emergence phase the proportion of females with young declined sharply in sites with foxes by around 50% (Fig. 2c). By contrast, where foxes were removed, most females kept their young over this period (Fig. 2c) and treatment differences were most apparent in the proportion of females with young at foot (Fig. 2b). As a result, in January and March 1994, the proportion of females with young was significantly higher than in sites where foxes remained ($t_2 = 30.18$; $P < 0.01$ and $t_2 = 3.51$; $P = 0.03$, respectively; one-tailed tests). This difference had disappeared in April 1994 as juveniles in all sites became independent of their mothers.

In the 1994–1995 breeding season, the response to fox control was repeated. Almost half of the females in non-removal sites appeared to lose their young over the period when young were emerging from the pouch (Fig. 2b,c), although in Boboyan the transition from pouch young to young at foot over summer appeared delayed (Fig. 2a,b). Nevertheless, a significantly higher proportion of females had young in fox removal sites compared to non-removal sites in late spring ($t_2 = 5.76$; $P < 0.01$ one-tailed test) and early summer ($t_2 = 6.52$; $P < 0.01$ one-tailed test).

Recruitment

During May–June, juveniles became independent of their mothers which was reflected in a small peak in the proportional representation of subadults in the population (Fig. 3). After fox control began in
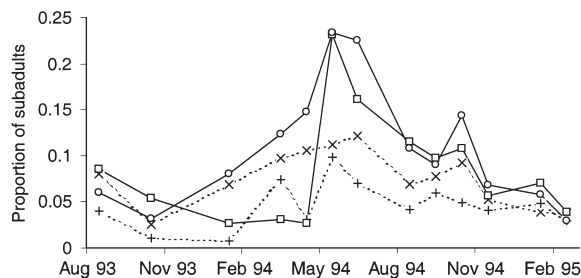
Fig. 3. Monthly proportion of subadult kangaroos in fox removal sites Boboyan (—□—), Grassy (—○—), and nonremoval sites Glendale (– – × – –), Orroral (– – **+** – –).

mid-1993, there was a significantly higher proportion of subadults in the population at fox removal sites from May–September 1994 (May $t_2 = 18.45$; $P < 0.01$: September $t_2 = 2.66$; $P = 0.05$; one-tailed tests). This pattern follows on from the changes in females with young, strongly indicating that fox removal resulted in significantly higher recruitment.

Population growth

Kangaroo densities at all sites were high (>2/ha). However, density estimates based on the observational data probably overestimated the true density, as individuals appeared to use a much wider area than the open grassland where counts were conducted. Seasonal and daily variation in climatic conditions appeared to influence surveys strongly, with kangaroo counts being lowest during winters and highest in October (Fig. 4).

Sampling limitations notwithstanding, from March 1994 to February 1995 kangaroo population growth was significantly higher where foxes were removed ($t_2 = 4.32$; $P = 0.04$; two-tailed test) with densities increasing in removal sites (Grassy annual $r = 0.47$; Boboyan $r = 0.55$) but more stable in non-removal sites (Glendale $r = 0.08$; Orroral $r = -0.14$). This pattern suggests that fox removal resulted in a higher number of kangaroos observed in open habitats. At removal sites, the most substantial changes in kangaroo numbers coincided with the peak in subadults in the population in May–August (Fig. 3). Unfortunately, the study ended prior to the second postexperimental pulse of independent subadults entering the population (April–May 1995).

DISCUSSION

The experimental reduction of foxes led to a clear increase in the proportion of juvenile kangaroos
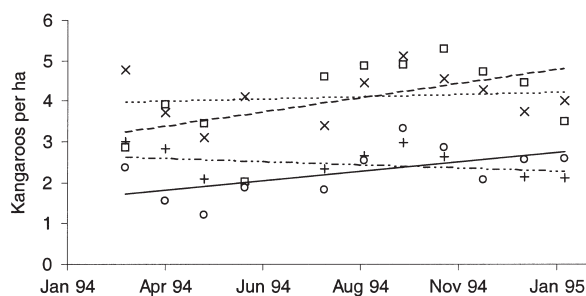
Fig. 4. Monthly average density of eastern grey kangaroos (all individuals) observed at the four study sites in Namadgi National Park during 1994–1995. Values represent the mean of two surveys per month together with regression lines representing population growth trends for fox removal sites Boboyan (□, – –) and Grassy (○, ——), and nonremoval sites Glendale (×, ……), and Orroral (+ , –··–).

surviving the period when they were newly emergent from the pouch. Where foxes were not removed there was a steady decline in the proportion of females with young and a comparable increase in the numbers of females with no young. In the fox removal sites, most females had young until the end of summer. This was followed by a pulse in the numbers of subadults observed in the fox removal sites during early autumn; this pulse did not occur where foxes remained. Importantly, these patterns were consistent between replicate sites. These results support prediction 1 that fox predation limits recruitment of juvenile kangaroos in nonremoval sites.

The difference in the proportion of females with young in removal and nonremoval sites suggests that foxes were responsible for approximately 25–35% of juvenile mortality during the first season but only 25% in the second season. The difference was caused by interannual difference in nonremoval sites where fewer than 30% of females had young at foot immediately prior to the young becoming independent in February 1994, but 55–62% of females had young at foot in the second season. The reason for this difference is not clear. However, the study ended before most juveniles would have become independent of their mothers, and it is not clear if all these juveniles would have been recruited.

Significant losses of juveniles in kangaroo populations may be common. Caughley (1962) found that 65% of juvenile red kangaroos died between the ages of 150 and 200 days old, the period when they would be emerging from the pouch (Dawson 1995). Shepherd (1987) also found that very poor recruitment contributed to population decline during drought. Poole (1973) found a mortality rate of 1.82% every 28 days during the pouch emergence period and associated this mortality with drought. In semiarid New South Wales, most juvenile euros also die during the period when juveniles are just emerging from the pouch (Dawson 1995). High juvenile mortality has also been observed for western grey kangaroos (Arnold *et al.* 1991) in areas where foxes were abundant and only 27% of juvenile kangaroos survived after permanent pouch emergence. However, there were marked, interannual fluctuations in the survival of newly emergent young, with rainfall during early spring and summer exerting strong influences (Arnold *et al.* 1991). At Namadgi, substantially more rain fell in 1993 than in 1994 and the winter–spring period was especially dry in 1994. If food affected juvenile survival, recruitment in 1994 should have been poorer than in 1993. However, there were fewer individuals observed in nonremoval sites during 1994 and the lower density may have led to higher *per capita* recruitment. Alternatively, there were also fewer foxes in control sites in spring 1994 than in spring 1993 (Banks 1997). From the data collected here it is difficult to distinguish between these explanations.

Several other workers have recorded high predation rates upon juvenile kangaroos. Shepherd (1981) recorded high predation rates upon juvenile red kangaroos with 97% of individuals killed by dingoes being juveniles. Similarly, Robertshaw & Harden (1986) found that dingoes preyed primarily upon juvenile swamp wallabies (*Wallabia bicolor*). In each case the high mortality of juveniles caused by predators was thought to be a principal factor limiting population growth. High rates of predation upon juveniles are common for other large mammal species (e.g. Messier *et al.* 1986; Bartman *et al.* 1992; Huggard 1992; Turner *et al.* 1992; Festa-Bianchet *et al.* 1994; Kunkel & Mech 1994). For many of these species, most mortality occurs within 2 weeks of birth when young are most vulnerable (Bergerud & Elliot 1986), although the danger may be delayed if the young are hidden soon after birth (Espmark 1969). However, fewer than half the published studies which have manipulated predator numbers for large mammalian prey have identified a significant impact of predation upon cow:calf ratios (e.g. moose *Alces alces*, Boutin 1992; caribou *Rangifer tarandus*, Bergerud 1988) and the ability of predators to limit populations of large mammals remains controversial (Bergerud *et al.* 1983; Bergerud & Snider 1988; Thompson & Peterson 1988; Bartman *et al.* 1992).

The data from Namadgi indicated that fox predation may have limited kangaroo populations, but are not entirely conclusive. Population growth rates were higher where foxes were removed and essentially stable in nonremoval sites. At fox-removal sites, increases in the numbers of adult kangaroos were observed in July 1994, directly after the period when the surviving juveniles were likely to become independent and this recruitment most likely caused much of the observed population growth. This result was consistent in both fox-removal sites and gives some support to prediction 2 that fox predation limits kangaroo population growth. However, this increase could have also been partly due to animals becoming more conspicuous due to behavioural responses of kangaroos which spent more time further from refuge after the reduction in predation risk from foxes (Banks 1997). Moreover, population growth was modest in all sites despite greater than 45% of females having young at the end of the previous breeding season suggesting a proportion of individuals were not absorbed into the populations regardless of fox control. This also suggests that some other factor must have partly compensated for predator control.

Predation has been considered to be insignificant to juvenile recruitment compared to food stress in large kangaroos (Dawson 1995), being limited largely to removing starving individuals (the 'doomed surplus', Sinclair & Arcese 1995). However, there is limited direct evidence that food stress can affect juvenile survival. Death by starvation is probably rare (Dawson 1995), with food stress increasing an animal's vulnerability to predation and disease (Speare *et al.* 1989; Arundel *et al.* 1990; but see Sinclair & Arcese 1995). For example, juvenile red kangaroos attracted to waterholes suffer heavy predation (Shepherd 1981). High mortality of subadults during winter has also been associated with elevated parasite loads induced by food stress (Arundel *et al.* 1990). Females may lose pouch young over this period if unable to meet the lactational demands of the developing young under severe nutritional stress (Dawson 1995).

Kangaroo densities were very high in removal sites following fox control, and nutritional stress cannot be discounted as a cause of some losses (Bartman *et al.* 1992). Some animals may have died (though no carcasses of subadult animals were found) or dispersed but not all were absorbed into the population. Also, it was not possible to determine whether surviving individuals themselves contributed to population growth through breeding, as juveniles produced by younger mothers typically have poorer survival prospects (Poole 1983). While it is possible that females could have bred in their first season (Clarke & Poole 1967), breeding would have been later in the season and it is unlikely they would have produced independent juveniles prior to the completion of the study.

Therefore, we conclude that fox removal led to the observed population growth through increased survival of young, although the limits to this growth should be the focus of future research. In terms of Errington's (1946) 'doomed surplus' hypothesis, it is likely that a proportion of the juvenile animals taken by foxes would not have survived to maturity and that a proportion of those which did survive would not have contributed to population growth (see also Bartman *et al.* 1992). This is particularly true of predators preying principally upon juveniles of populations at high densities. At Namadgi it is possible that fox predation upon juveniles merely shifted kangaroo population density to slightly higher levels, closer to the carrying capacity determined by the prevailing resource availability (Sinclair 1989). For future studies, the key to understanding the total impact of foxes upon kangaroo population lies with the fates and reproductive successes of juveniles that survive following fox control.

Other explanations of treatment effects

It is not likely that the behavioural responses of kangaroos to fox removal could have caused such dramatic and consistent differences in the numbers of females with young being observed. While many ungulate species hide their young to avoid predation (Espmark 1969), as does the red-necked wallaby (Johnson 1995), this behaviour has not been recorded

in eastern grey kangaroos despite intensive and detailed studies of their social behaviour (e.g. Croft 1989; Jarman & Coulson 1989; Russell 1989). Similarly, there was no change in the total numbers of females over the summer period, indicating that the increase in the proportion of females with no young represents juvenile kangaroos being lost from the population, rather than females either hiding themselves or their young. Moreover, this mother : young ratio has been used extensively as a reliable index of juvenile mortality for many large mammal species (e.g. Poole 1983; Shepherd 1987; see also review by Boutin 1992).

Food stress can also cause juvenile mortality. As juveniles spend more time out of the pouch, their diet changes, from primarily milk to an increasing component of herbage (Dawson 1995). Where resources are inadequate, young animals may not have developed suitable gut morphology or gut fauna to handle poor quality food. Consequently, they can suffer most greatly from food limitation and starvation (Dawson 1995), leading to high juvenile mortality. At Namadgi though, most females bred each season which suggests that food was not limiting reproductive activities (although only the severest conditions will cause any hiatus in breeding; Kirkpatrick & McEvoy 1966; Poole 1973, 1983). Also, while there appeared to be site differences in the quality of food as eaten by rabbits (Banks *et al*. 1999), these differences occurred only between the two removal sites; there were no differences between treatments to cause a consistent bias which may confound interpretation of the fox removal results.

Density-dependent processes may also limit resource availability for kangaroos, which may lead to high juvenile mortality (Caughley 1987). However, kangaroo densities were interspersed between treatments, with the highest density occurring at a removal site (Boboyan). Also, rainfall over the study period was similar throughout the total study area (Banks 1997), suggesting that differential rainfall events were unlikely to have caused consistent biases in food availability for kangaroos. Moreover, whereas fox removal caused rabbit numbers to increase 6.5- and 12-fold (Banks *et al*. 1998) after 18 months, enhanced kangaroo recruitment was observed in the first breeding season which was within 4 months of the experiment commencing and prior to any significant increases in rabbit abundance. Importantly though, kangaroo peaked in the fox diet during the period when juvenile kangaroos appeared to be lost from the populations. Thus, despite low replication, it is highly probable that fox control was the primary cause of increased survival of juvenile kangaroos in fox-removal sites.

ACKNOWLEDGEMENTS

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