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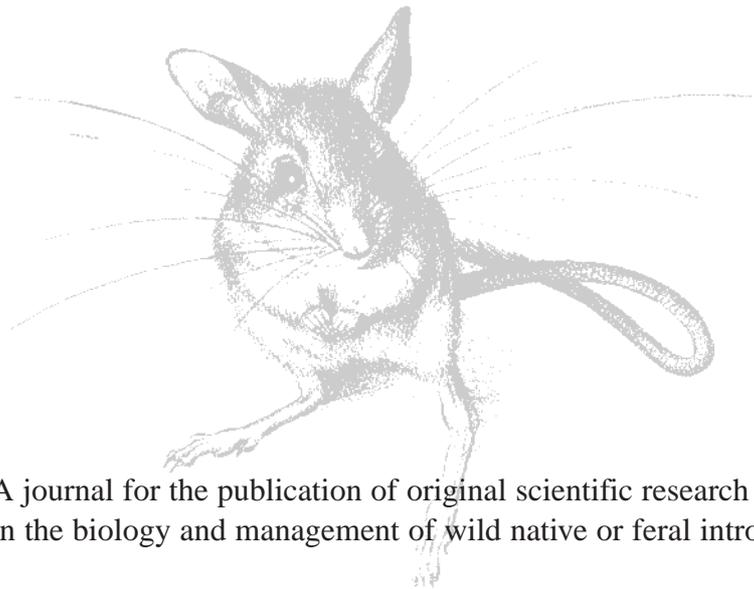
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## Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation?

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**Abstract.** Most of Australia's sheep rangelands are enclosed by a dingo-proof fence. Within these rangelands, where dingoes (*Canis lupus dingo*) are rare, red kangaroos (*Macropus rufus*) are considered to be food limited because their numbers respond to fluctuations in pasture biomass that are driven by highly variable rainfall. Outside this region, where dingoes are common, kangaroo densities are generally substantially lower, suggesting that dingoes are an important limiting factor. However, it is unclear whether dingoes can regulate kangaroo populations. In this study, red kangaroo and emu (*Dromaius novaehollandiae*) numbers were monitored for varying periods during 1978–92 by aerial survey on both sides of the dingo fence in three areas in the north of the South Australian pastoral zone. Densities of red kangaroos and emus were lower outside the fence, although the disparity varied between areas and over time. The similarity in the environments on both sides of the fence and the marked step in kangaroo density at the fence are consistent with dingoes strongly limiting these prey populations. In the north-east of the pastoral zone, where kangaroo and emu densities are greatest, the contrast in density across the fence was most pronounced. Furthermore, the trends in density over time differed across the fence. Outside the fence, red kangaroos and emus remained at low densities following drought as dingo numbers increased. Inside the fence, red kangaroo and emu populations showed a 'typical' post-drought recovery. The data therefore suggest that, in some situations, dingoes may not simply limit red kangaroo and emu populations, but also regulate them. For this to occur, predation rate would need to be density dependent at low prey densities. The availability of alternative prey, and the reduction in the numbers of all prey during drought may provide the mechanism.

### Introduction

The extent to which predators influence the dynamics of large mammalian herbivores is still debated (reviews by Skogland 1991; Boutin 1992) and, to date, the work has concentrated on ungulates. If generalisations about the influence of predators are to be drawn, kangaroos (*Macropus* spp.) in their rangeland habitat provide an important contrast. Central to the debate are the processes of limitation and regulation. Limitation is defined by Sinclair (1989) as the process that sets the equilibrium point of a population. Limiting factors can be either density dependent or density independent. Regulation is the process that returns a population to its equilibrium point and by definition this can happen only through density-dependent factors. However, density dependence does not necessarily mean regulation, because a density-dependent factor may only tend to regulate a population. It may be weak, act only at certain densities or under certain environmental conditions, and it may act with a time delay

(Begon and Mortimer 1986). According to Sinclair (1989), the interesting questions regarding population regulation concern the extent to which a particular mortality factor limits a population and the manner in which it alters the equilibrium position (i.e. whether or not the population is ever regulated). Understanding the dynamics of a population requires information on both density-dependent mortality factors and environmental stochasticity and, where predators can regulate a population, whether more than one stable state can occur (Sinclair and Pech 1996).

Within the sheep rangelands of Australia, where dingoes (*Canis lupus dingo*) are either absent or rare, red kangaroos (*Macropus rufus*) are food limited (Bayliss 1987; Cairns and Grigg 1993). Density dependence (operating as a feedback loop between kangaroos and pasture) appears weak (Caughley 1987). This should result in greater fluctuations in numbers in a stochastic environment than if it were strong (Sinclair 1989; Sinclair and Pech 1996). In certain areas with

dingoes, red kangaroos appear to be predator limited (Caughley *et al.* 1980; Thomson 1992). It is unclear, however, whether dingoes can regulate kangaroo populations, although some studies have suggested that this might be the case, with rabbits (*Oryctolagus cuniculus*) serving as alternative prey (Caughley *et al.* 1980; Corbett and Newsome 1987; Newsome 1994).

The data presented here were obtained from annual aerial surveys of kangaroo populations in the South Australian pastoral zone. These have provided a description of the dynamics of red kangaroo and emu (*Dromaius novaehollandiae*) populations (Pople *et al.* 1991; Cairns and Grigg 1993). In several years, these surveys were extended outside the pastoral zone, allowing a comparison of the dynamics of these populations across the dingo or barrier fence. Such a comparison should provide some insight into whether dingoes are in fact regulating kangaroo and emu populations outside the dingo fence. These data provide an obvious extension to those of Caughley *et al.* (1980), who reported the densities of kangaroo and emu populations in winter 1976 on both sides of the dingo fence in South Australia, New South Wales and Queensland.

Two questions were posed in this study. Firstly, to what extent do kangaroo and emu densities differ on either side of the dingo fence? Secondly, as densities of kangaroos and emus fluctuate over time, is there a change in the 'prey ratio', which is the ratio of density (kangaroo or emu) outside the fence to that inside the fence? If densities on either side of the

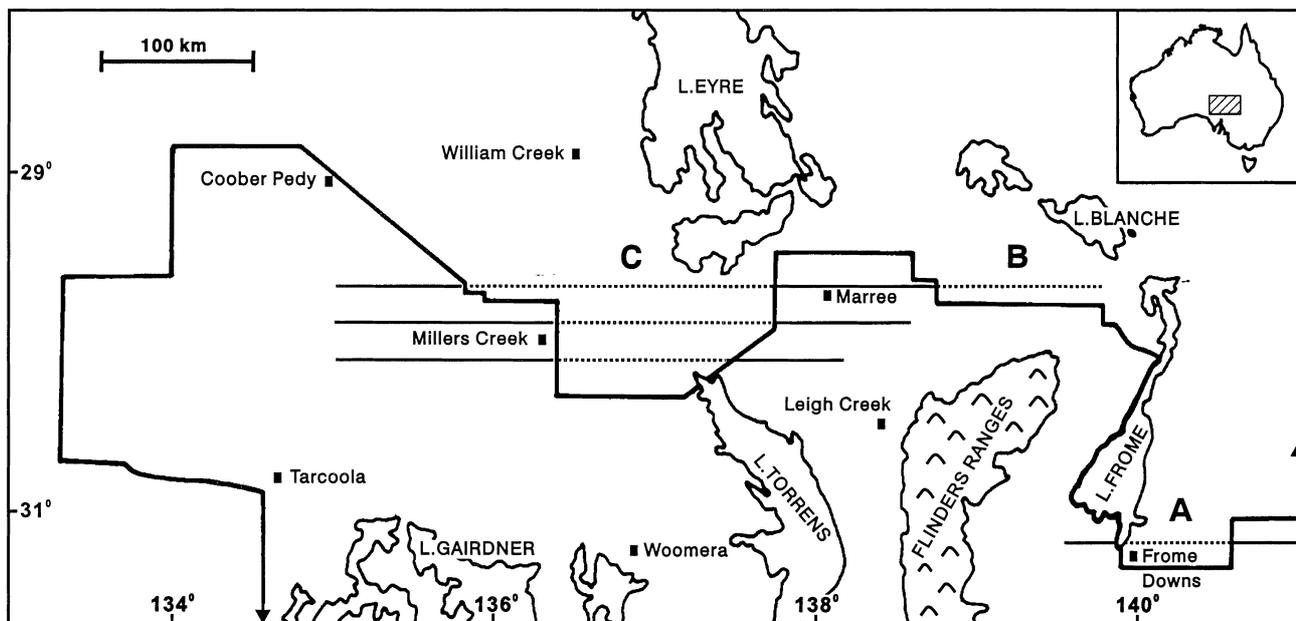
fence fluctuate in concert (i.e. the prey ratio is constant), then this would suggest that predation is density independent and dingoes are simply limiting prey numbers. If the prey ratio declines with increasing prey numbers inside the fence, then predation is density dependent and predator regulation is indicated. If the prey ratio increases in this situation, then predation is inversely density dependent and, by definition, is not regulatory. Possible confounding factors such as environmental differences across the fence must also be considered.

## Methods

### Study area

Dingoes have been controlled in the northern parts of the South Australian pastoral zone since the establishment of pastoralism there in the late 1800s. Initially, individual properties were responsible for control of dingoes, with the use of netting fences, trapping and shooting. The *South Australian Dog Fence Act* of 1946 allowed the establishment of a continuous fence extending from Fowlers Bay on the west coast of South Australia to the New South Wales border in the east. The location of the northern part of this fence is shown in Fig. 1. These control measures were later supplemented with 1080 baiting inside the fenced area. The dingo fence (and associated control measures) creates what is considered an effective barrier to dingoes. It separates the predominantly sheep-grazing lands inside the fence from country used solely for grazing cattle outside the fence.

The environment of this region of South Australia has been described by Laut *et al.* (1977), who divided it into a number of environmental provinces that were subdivided into environmental regions and then further subdivided into environmental associations. Brief descriptions of the three areas monitored in this study are given below:



**Fig. 1.** Northern section of the South Australian pastoral zone showing the dingo barrier fence (thick solid line) and survey transect lines flown inside (thin solid line) and outside (dotted line) the fence in each of three areas (A, B and C). The western edge of Area B is arbitrarily defined as 91 km west of the barrier fence east of Marree. The eastern edge of Area C is 91 km east of the barrier fence west of Marree, thereby overlapping Area B. The barrier fence extends south from Tarcoola to the Great Australian Bight and north of Area A along the New South Wales border (arrowed).

**Area A.** This area (1300 km<sup>2</sup> inside the fence and 2000 km<sup>2</sup> outside the fence) comprised a mixture of plains, partly overlain with dunes, with low and tall chenopod shrublands, and low open woodlands of mulga trees. The environment was similar on both sides of the barrier fence, although dunefields became more extensive and hummock grasslands more common outside the fence. The transect lines flown to estimate kangaroo and emu density crossed three environmental associations belonging to two regions of which one association and both regions occurred on both sides of the fence.

**Area B.** Inside the barrier fence, this area (2300 km<sup>2</sup>) comprised either silcrete tableland with extensive dunes, or undulating plains. Vegetation ranged from low open chenopod shrubland to tall open shrubland and fringing woodland of mulga and mallee (*Eucalyptus* spp.). Outside the fence (2700 km<sup>2</sup>) the habitat is similar, although the tableland is dissected in some environmental associations while others are dominated by gibber (i.e. stone-covered) plain. Transect lines for the aerial surveys crossed four environmental associations belonging to the same region, of which two associations occurred on both sides of the fence.

**Area C.** This area was similar to area B, but more varied given its larger size (12 100 km<sup>2</sup> inside the fence and 10 600 km<sup>2</sup> outside the fence). Again, the environment was similar on both sides of the barrier fence with no obvious environmental discontinuity at the fence. Transect lines crossed eight environmental associations belonging to three regions, of which four associations and all regions occurred on both sides of the fence.

All three areas are arid, with annual rainfalls that are low (<200 mm), highly variable (coefficients of variation range 49–58%) and greatly exceeded by annual evaporation (>2800 mm). Rainfall is weakly seasonal with a late summer peak. Winters are cold and summers are very hot.

#### Aerial survey

Since 1978, kangaroos and emus in the South Australian pastoral zone have been counted during winter (July–August) by aerial survey. Surveys were conducted using strip transect sampling with fixed-wing aircraft. This has become the established method for the broad-scale monitoring of kangaroo populations (Caughley *et al.* 1976; Caughley and Grigg 1981). An aircraft (usually a Cessna 182) is flown at a ground speed of 185 km h<sup>-1</sup> (100 kts), 76 m (250 ft) above the ground. Two trained observers occupy the rear seat, counting kangaroos seen on either side of the aircraft in strips that are 200 m wide on the ground. Strip boundaries are delineated by streamers on the wing struts. The observers count in 97-s units (= 5 km × 200 m), each of which is followed by a 7-s break, during which observers record their counts (Caughley and Grigg 1981). To further ensure repeatability of the technique, surveys are flown when there is minimal cloud cover (Short and Bayliss 1985), during winter and within 3–4 h of sunrise or sunset.

The data reported here are a subset of the survey data for the pastoral zone in South Australia. The lines selected for analysis are shown in Fig. 1. In Area A, 20 km<sup>2</sup> (= 50 km × 400 m) were surveyed inside the dingo fence and 30 km<sup>2</sup> outside the fence. In Area B, 34 km<sup>2</sup> were surveyed inside the dingo fence (these were also used for calculating density estimates in Area C) and 40 km<sup>2</sup> outside the fence. In Area C, 200 km<sup>2</sup> were surveyed inside the dingo fence and 158 km<sup>2</sup> outside the fence. In area A, these transect lines were flown in 1978 and each year during 1983–92. In Areas B and C, transect lines were flown each year during 1983–87.

#### Analysis

To account for animals that are missed by observers in fixed-wing aircraft, correction factors need to be applied to counts of animals. For kangaroos, these correction factors are determined from the average canopy cover within each survey unit (Caughley *et al.* 1976) and air temperature at 76 m (Bayliss and Giles 1985). All surveys reported here were flown

in air temperatures <15°C, which require no correction for temperature. All counts of kangaroos were multiplied by 2.29, counts of emus were multiplied by 1.47 (Caughley and Grice 1982), but counts of dingoes were uncorrected.

Even when aerial surveys are broken into survey units, the transect line remains the independent sampling unit (Caughley and Sinclair 1994). In Areas A and B, only single lines were flown in each year, so no standard errors could be calculated. In Area C, three separate transect lines were flown each year, providing six sampling units inside the fence and three outside the fence on which a variance estimate could be based for each year (Fig. 1). Standard errors were calculated using ratio estimation (Caughley and Sinclair 1994). In Areas A and C, counts of kangaroos and emus on either side of the fence were compared with a paired-sample *t*-test after initial assessment for normality, using each year as a replicate. In Area C, an analysis of variance compared counts of both kangaroos and emus using 'side-of-fence' as a fixed factor and year as a random factor. Densities were log<sub>e</sub>-transformed to stabilise variances.

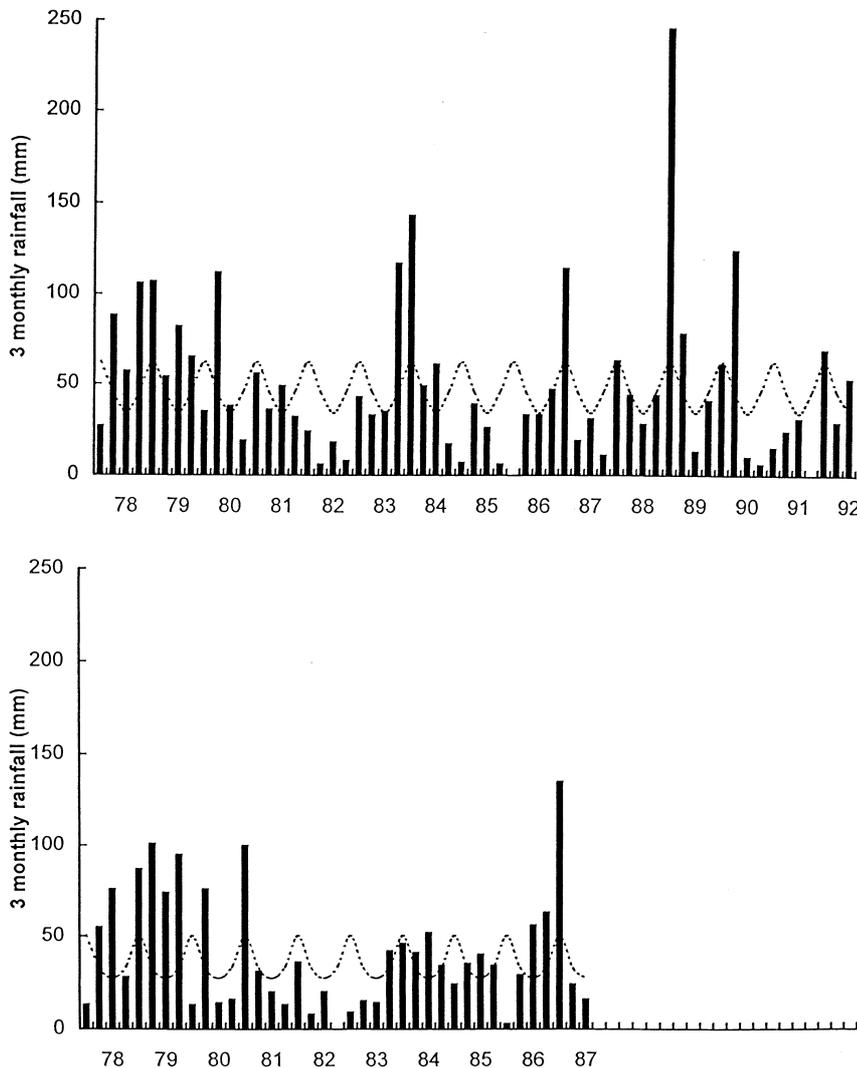
Caughley *et al.* (1980) suggested that the change in kangaroo density with increasing distance from the dingo fence would reflect the impact that dingoes are having on the population. This trend in density will form a step at the fence if that fence is an effective barrier to dingoes and if dingoes strongly limit kangaroo populations. Given that there were several years of data available in the present study, unit densities were first standardised over the entire transect line for each year. These were calculated as the difference between each unit density and the mean unit density for the transect, divided by the standard deviation of unit densities for the transect, yielding a standard deviate or *z* score which is a measure of standard deviations from the mean. Mean *z* scores ( $\pm$ s.e.) for each unit were then calculated across years. For Area C, the mean was calculated across the three survey lines and across years.

#### Results

Rainfall during the study period was characterised by a drought in 1982–83 that resulted in a dramatic decline in kangaroo populations in eastern Australia (Caughley *et al.* 1985). At Frome Downs in Area A, rainfall was above average in late 1983 and early 1984, but another dry period lasted until mid-1986 (Fig. 2a). In contrast, rainfall at Millers Creek in Area C was close to average during 1984–85 (Fig. 2b). The pattern of rainfall during 1978–87 at Marree in Area B closely followed that recorded at Frome Downs. Rainfall at Frome Downs was generally above average from mid-1986 to early 1990, but 1990–91 was again dry.

These rainfall patterns are broadly reflected in the trends in red kangaroo and emu numbers inside the dingo fence with little time lag (Figs 3–5). The trends for both species in each area were similar and mirrored the trends in the entire pastoral zone for that period (Pople *et al.* 1991; Cairns and Grigg 1993). The decline in red kangaroo numbers in 1991 in Area A was certainly far greater than that recorded in the broader region, which showed a more gradual decline to the level in 1992.

Numbers of kangaroos and emus were generally lower outside the fence. The difference was most marked in Area A and became obvious at higher densities in Areas B and C. There was a significant fence effect in Area A for both kangaroos ( $t_{10} = 6.26$ ,  $P < 0.001$ ) and emus ( $t_{10} = 4.06$ ,  $P < 0.01$ ), but none in Area B (kangaroos:  $t_4 = 0.88$ ,  $P > 0.4$ ; emus:  $t_4 = 1.16$ ,



**Fig. 2.** Three-monthly (Jan.–Mar., Apr.–Jun., Jul.–Sep., Oct.–Dec.) rainfalls (bars) relative to the three-monthly long-term average (dotted line) during 1978–1992 at (a) Frome Downs (mean annual rainfall = 189 mm, s.d. = 110) in Area A and (b) Millers Creek (mean annual rainfall = 143 mm, s.d. = 83) in Area B. Long-term average rainfall is lowest in winter (Jul.–Sep.). Locations are shown in Fig. 1.

$P > 0.3$ ). In Area C, there was a significant fence effect for kangaroos ( $F_{1,4} = 51.26$ ,  $P < 0.01$ ), but not for emus ( $F_{1,4} = 1.4$ ,  $P > 0.3$ ), although there was a suggestion of a side-of-fence  $\times$  year interaction ( $F_{4,32} = 2.53$ ,  $P = 0.06$ ). During 1983–87, the trends in kangaroo and emu numbers were similar on either side of the fence. During 1987–92, the trends in emu and kangaroo numbers in Area A differed markedly on either side of the fence. While numbers increased inside the fence following good rainfall (Fig. 2a), numbers outside remained low and never reached their pre-1986 levels (Fig. 3).

Associated with the suppression of kangaroo and emu numbers during 1986–92 outside the fence in Area A were sightings of dingoes during aerial surveys. The number of dingoes seen peaked in 1989–90, coinciding with a peak in kangaroo and emu numbers. In 1990 and 1991, when kangaroo numbers declined sharply inside the fence, dingoes were also recorded inside the fence. Only three sightings of

dingoes were made from the air in Areas B and C, each outside the fence.

The mean standardised density of red kangaroos in units either side of the fence in each area is shown in Fig. 6. There was a marked step in kangaroo density at the eastern fence in Area A (Fig. 6a) and the western fence in Area C (Fig. 6c). Density did not drop as sharply or as consistently at the other three fencelines, but nor was there a gradual decline in density that would suggest an environmental gradient influencing kangaroo density.

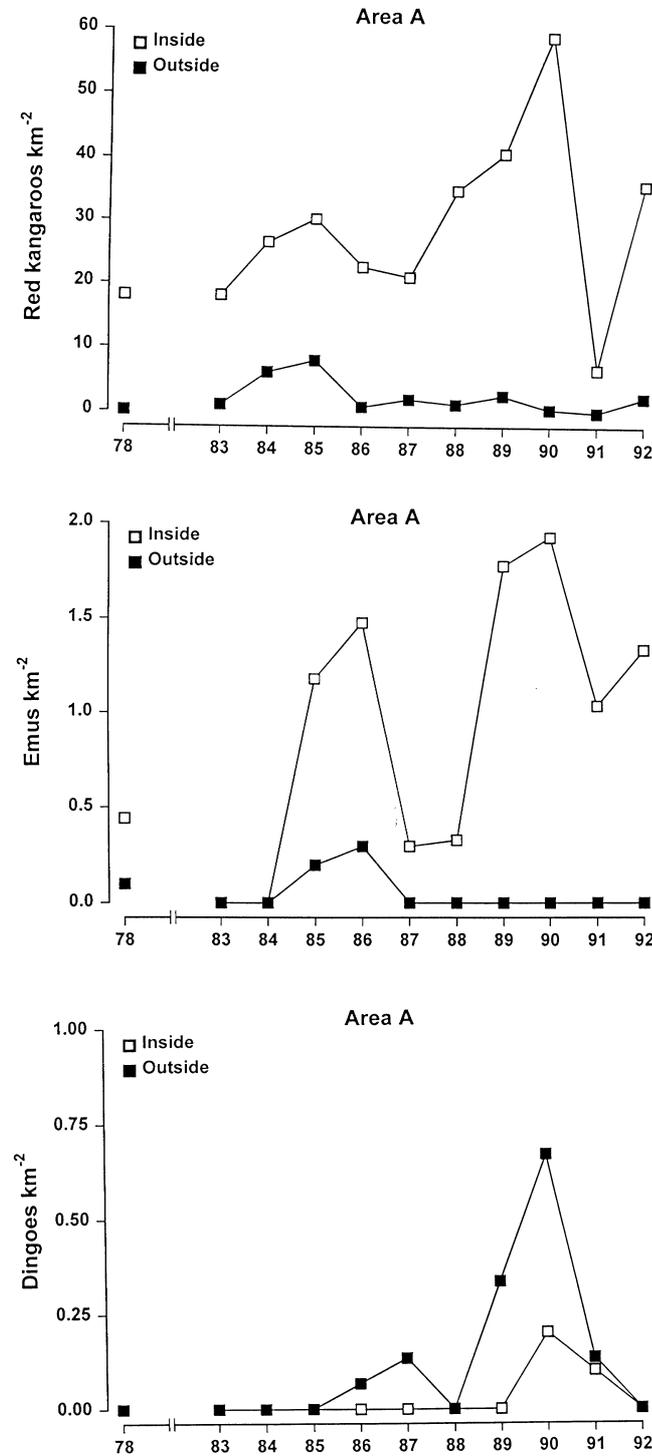
### Discussion

Lower densities of red kangaroos and emus outside the dingo-exclusion fence in three distinct pastoral regions of South Australia support the assertion of Caughley *et al.* (1980) that this is the result of dingo predation. There was a marked fall in kangaroo density across the fence in each area that could not be explained by an environmental gradient, and

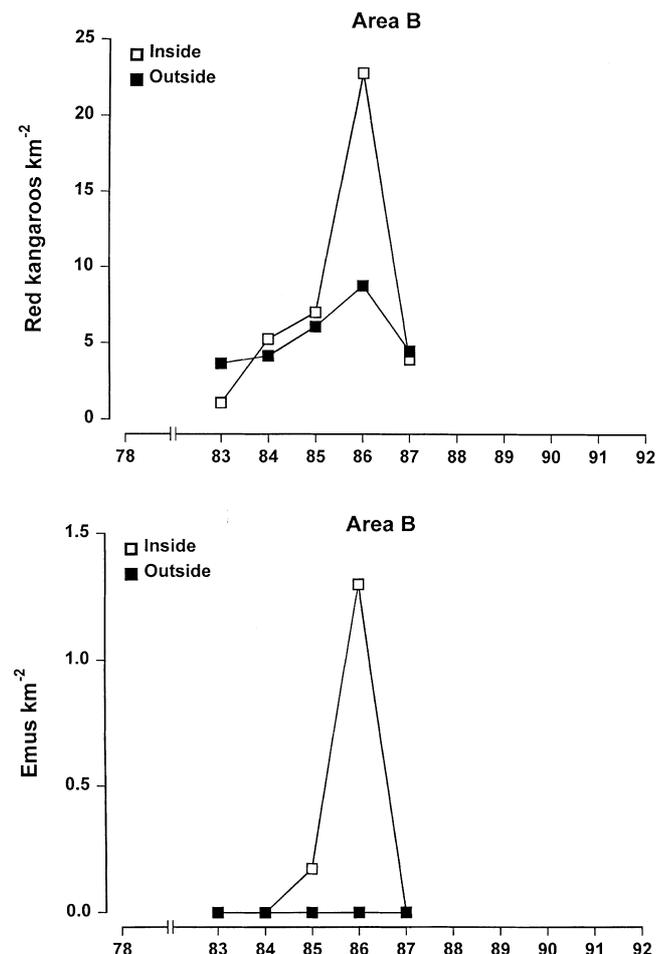
overall differences in the environment across the fence were negligible. This fence effect was evident over a number of years. The results are similar to those obtained by Caughley *et al.*

*al.* (1980) in winter 1976 in north-western New South Wales. The fence appeared to have a smaller effect in Area B than in Areas A and C. This may have been the result of higher dingo numbers in the latter two areas, but the data on dingoes are poor. Alternatively, it may simply have been the result of the smaller sample of kangaroo and emu numbers in Area B.

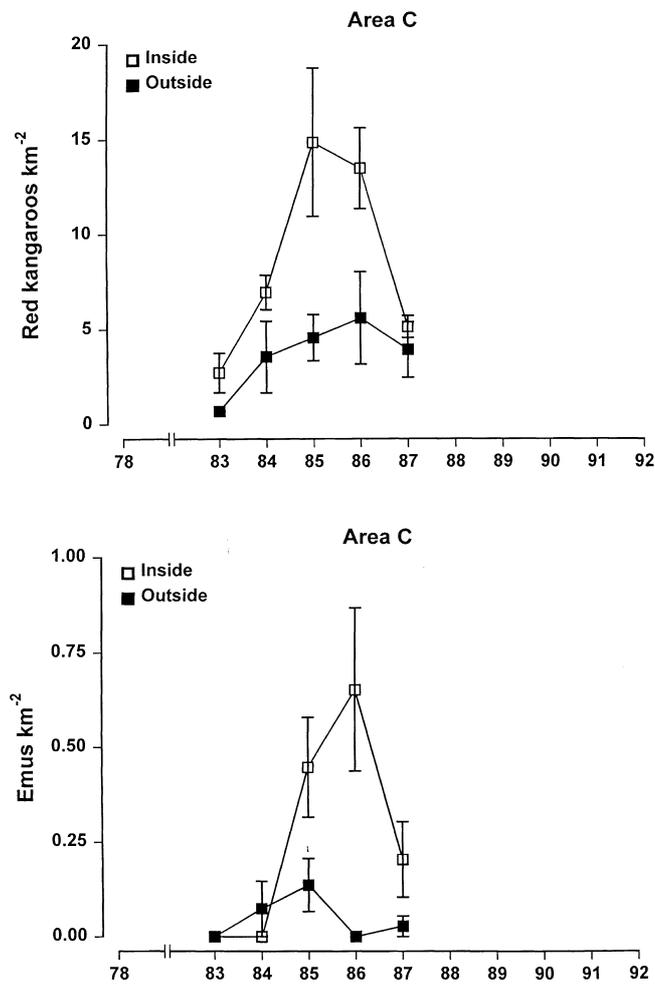
The most plausible alternative hypothesis considered by Caughley *et al.* (1980) was that, because mostly sheep are grazed inside the dingo fence and cattle outside, sheep may have altered the vegetation to favour kangaroos more than did cattle. A similar pattern of grazing exists across the dingo fence in northern South Australia. However, in north-western New South Wales, Landsat imagery showed no discontinuities in vegetation at the dingo fence (Caughley *et al.* 1980). Furthermore, in northern New South Wales, Caughley *et al.* (1980) found no marked differences in kangaroo numbers on either side of the fenceline separating predominantly cattle country in Queensland from predominantly sheep country in



**Fig. 3.** Densities (animals km<sup>-2</sup>) of (a) red kangaroos, (b) emus and (c) dingoes inside (open symbols) and outside (closed symbols) the dingo fence in Area A during 1978–92.



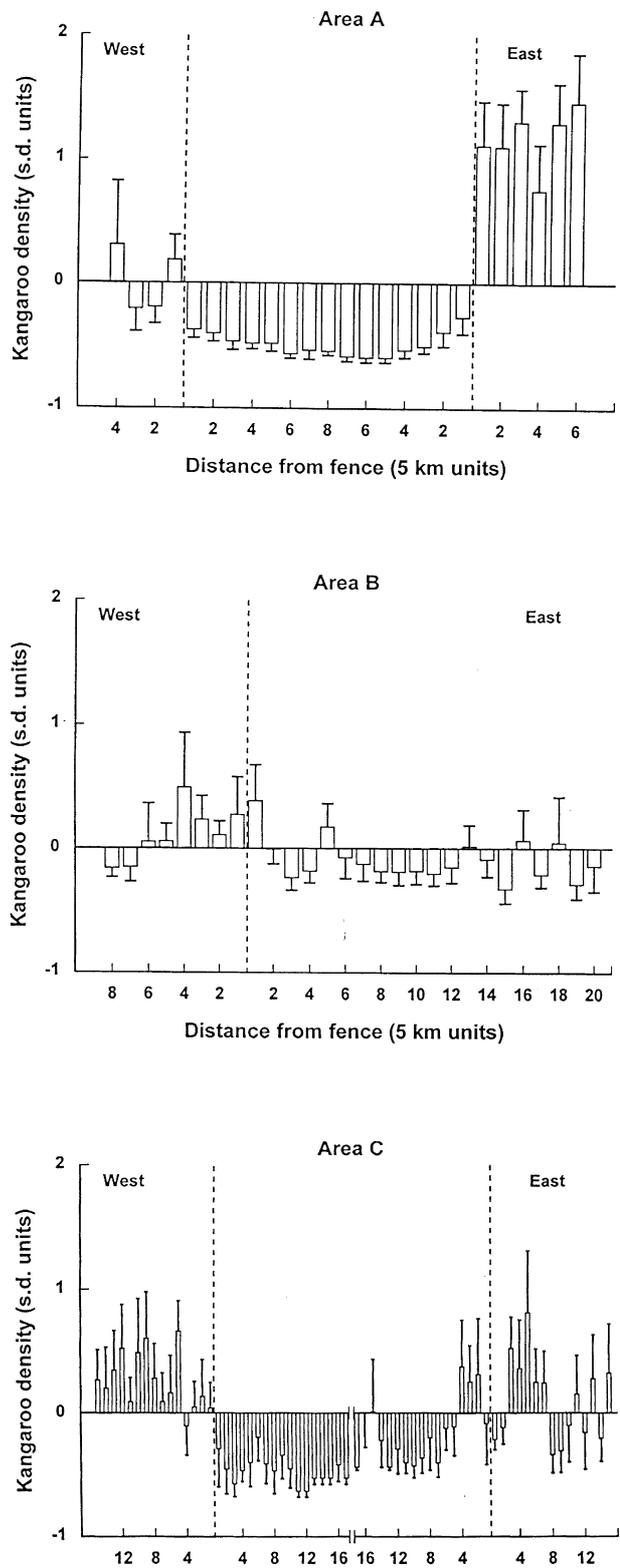
**Fig. 4.** Densities (animals km<sup>-2</sup>) of (a) red kangaroos and (b) emus inside (open symbols) and outside (closed symbols) the dingo fence in Area B during 1983–87.



**Fig. 5.** Densities (animals km<sup>-2</sup>) ( $\pm$ s.e.) of (a) red kangaroos and (b) emus inside (open symbols) and outside (closed symbols) the dingo fence in Area C during 1983–87.

New South Wales. Since dingoes are rare in these areas and the environments across the fence are similar, any effect of grazing should have been manifested.

The data from the present study are only suggestive, but combined with work elsewhere, particularly on dingo diet, provide a strong argument for predator regulation of kangaroo and emu populations. Prey switching appears to be an important mechanism for these dynamics. Throughout much of southern and central Australia, dingoes prey primarily on rabbits, but, as rabbit numbers decline, dingoes increasingly take larger prey, including red kangaroos. They also feed on carcasses of cattle that die during the drought (Corbett and Newsome 1987; Newsome 1990; Corbett 1995). Dingoes exhibit a flexible social structure, allowing them to increase group size to exploit large prey such as kangaroos and become more solitary when only small prey are available (Thomson 1992). Other factors are also important, including



**Fig. 6.** Standardised (i.e. z scores) densities ( $\pm$ s.e.) of red kangaroos counted in consecutive survey units across the dingo fences (vertical dashed line) in (a) Area A, (b) Area B and (c) Area C. Distances along transect lines (Fig. 1) are given relative to the fence.

the increased vulnerability of kangaroo populations during drought when they become concentrated around areas of remaining food and water (Newsome 1965). It is also worth noting that, even in the absence of rabbits in north-western Australia, dingoes appear capable of strongly limiting red kangaroo populations and possibly regulating them (Thomson 1992).

The fluctuations in kangaroo and emu numbers in Area A (Fig. 3) fit the pattern of 'environmentally modulated predation' described by Newsome *et al.* (1989) and Newsome (1990). One scenario to explain such dynamics is as follows. Dry conditions in 1985–86 (Fig. 2a) led to a decline in numbers of red kangaroos, emus and, presumably, rabbits. Outside the barrier fence, dingoes would have switched from rabbits as their primary prey to kangaroos, emus and any other available food. As pasture conditions improved, kangaroo numbers increased inside the barrier fence, but outside the fence kangaroo numbers were suppressed by a dingo population that was taking an increasing proportion of an increasing kangaroo population. For regulation to occur, predation by dingoes must have been density dependent at this stage (i.e. the proportion of the kangaroo population that is killed by dingoes increases with increasing kangaroo density).

In contrast, the severe drought in 1982–83 did not result in regulation of kangaroos in any of the three areas monitored here. While drought appears to be an important mediator for regulation of kangaroo populations by dingoes, it does not always result in regulation. In this study, information on alternative prey such as rabbits, rodents and cattle carrion is lacking. However, the apparent increase in dingo numbers coinciding with the suppression of what would otherwise have been increasing kangaroo and emu populations, suggests that the numerical response of dingoes, and not just their functional response, played an important role in regulating these prey.

In a recent review of the causes of density dependence and the life stage in which it occurs in mammal populations, Sinclair (1996) observed that smaller species are often regulated by predators, while large terrestrial herbivores, including kangaroos, tend to be regulated by food. Most studies of large mammals in which density dependence has been recorded have found that fecundity and early juvenile survival declined with density, with increases in adult mortality reported less commonly (see also review by Gaillard *et al.* 1998). While these patterns are consistent with the demography of red kangaroos inside the dingo fence, the situation in this area is artificial. Outside the fence, dingo predation appears regulatory at least some of the time and both subadult and adult kangaroos are taken (Oliver 1986; Thomson 1992).

The hypothesis that predator regulation of herbivores becomes more likely along a gradient of increasing primary productivity (Fretwell 1987) has been offered some support

from studies on ungulate populations (Messier 1995). However, more important influences appear to be migratory behaviour, which allows migrants to escape predator regulation (Fryxell *et al.* 1988), large body size, where predators are simply outgrown (Sinclair 1995), the presence of other limiting factors (e.g. other predators, drought, culling and disease) that keep prey within a density range that can be regulated (Messier 1995) and, finally, the presence of alternative prey that maintains the predator population (Sinclair 1995). Red kangaroos are not migratory, but are highly mobile (Norbury *et al.* 1994), which may allow them to persist in the face of heavy dingo predation. They appear to be regulated in areas of low productivity, but the influence of primary productivity needs to be tested by comparing kangaroo population dynamics along a productivity gradient. There may be no regulation in Areas B and C where productivity is lower. Nevertheless, the more immediate determinants of dingo regulation of kangaroos appear to be perturbation of prey populations by drought and the availability of alternative prey, as discussed above.

Inside the dingo fence, wedge-tailed eagles (*Aquila audax*) and presumably foxes (*Vulpes vulpes*) prey on juvenile red kangaroos (Robertshaw and Harden 1989), but the most substantial removal is undoubtedly through the commercial harvest of adult kangaroos. The impact of the latter is restricted by an annual quota of 15–20% of the population, although the actual harvest has often fallen well short of the quota. A higher proportion tends to be taken during drought when kangaroos are easier to shoot (see above) and there is increasing pressure from graziers to increase the harvest. Thus, commercial harvesting tends to have an inversely density-dependent (i.e. depensatory) effect on the kangaroo population. If harvest rate increases during drought, then it will tend to amplify the fluctuations in population size. This will be counterbalanced to some extent by greater compensation of harvest mortality during drought than when food is abundant. Nevertheless, the combined effect of this predation on the dynamics of kangaroo populations, while further limiting population size, is minor compared with the impact of a fluctuating food supply. This is in stark contrast to the influence of predation on the dynamics of the kangaroo populations on the other side of the dingo fence.

Conclusive evidence that dingoes can regulate kangaroo numbers would require experimental removal of dingoes: an increase in kangaroo numbers relative to controls following removal of dingoes would suggest limitation. If kangaroos have increased beyond the unstable equilibrium below which they can be regulated, then allowing dingoes to return after this increase should result in kangaroos remaining at a higher density relative to controls. Such an experimental approach has been suggested by Sinclair (1989) and was used by Pech *et al.* (1992) to demonstrate a two-state predator–prey system involving foxes, cats and rabbits in western New South Wales.

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