Does Dingo Predation Control the Densities of Kangaroos and Emus?

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Abstract

The density of red kangaroos in the sheep country of the north-west corner of New South Wales is much higher now that it was last century. It is also much higher than the present density across the dingo fence in the adjacent cattle country of South Australia and Queensland. The picture is similar for emus. Farther east, about halfway along the New South Wales–Queensland border, no difference in density between the two States could be detected for red kangaroos, grey kangaroos or emus. We examine and discard several hypotheses to account for the density contrasts in the west and the lack of them farther east, deeming it unlikely that the pattern reflects environmental gradients, or differences in plant composition and growth, hunting pressure or availability of water. Instead, we favour this hypothesis: that the past and present patterns of density are attributable directly to predation by dingoes, which can hold kangaroos at very low density in open country if the dingoes have access to an abundant alternative prey.

Introduction

This study is an attempt to explain three paradoxical observations made by a party (G. Caughley, R. G. Sinclair, D. Scott-Kemmis and G. R. Wilson) surveying the density of kangaroos in the north-west corner of New South Wales in January 1975.

The first was the density of $7 \cdot 3$ km^{-2} recorded for red kangaroos, *Megaleia rufa*, on that survey, relative to what it had been when the explorer Charles Sturt passed through in February 1845. In reporting an emu Sturt (1849, p. 275) remarked 'we have seen very few either of these birds or kangaroos in these trackless solitudes.' His base camp, manned continuously for 5½ months, was on permanent water at Depot Glen, a few kilometres north of the present town of Milparinka. The survey party visited the site in 1975 and found red kangaroo droppings in abundance along the creek. The density of red kangaroos thereabouts must have been vastly greater than it was in 1845.

The second observation was in sharp contrast. To check on the generality of the first observation the party visited another area from which circumstantial evidence indicated low kangaroo densities last century. In June 1861 Burke and Wills died of malnutrition on Cooper's Creek despite having firearms, ball and powder (Moorehead 1963). They fought for survival for two months on that stretch of creek between the site of Innaminka in South Australia and the cattle station of Nappamerry in Queensland, but apparently saw no kangaroos. On the evidence of the 1975 survey in New South Wales a similar result was expected from this visit—a present density of red kangaroos far in excess of the deduced low density of 1861. But an aerial survey along that stretch of Cooper's Creek, which was in full flow at the time, turned up no kangaroos. Apparently the density was much the same as last century.

The third observation was of a contrast in the density of red kangaroos between New South Wales on one hand and South Australia and Queensland on the other. The aerial survey of 1975 (Caughley *et al.* 1977) was restricted to New South Wales but we extended some transects a few kilometres into South Australia and Queensland. The density in these states was manifestly lower than in New South Wales, and at the time we accepted the local opinion that kangaroos kept away from the dingo fence on the border lest they be cornered against it by dingoes. Dingoes are rare in the sheep country of the north-west corner of New South Wales but common in the adjacent cattle country of Queensland and South Australia. The border fence in this area is designed to stop dingoes and hence acts also as a barrier to kangaroos.

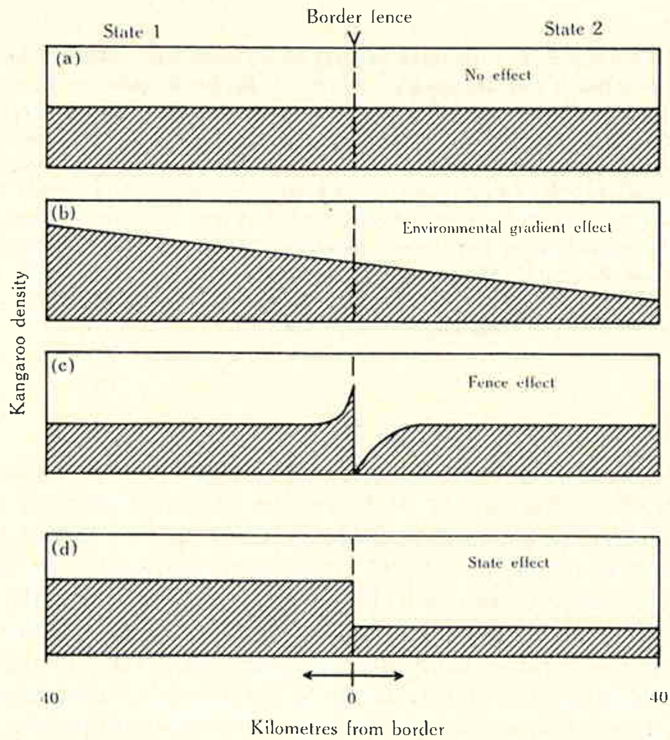


Fig. 1. Ways in which density of a species might change relative to the position of a State border fence.

Those three observations generated the questions for this study:

(1) Why does the trend in red kangaroo density between last century and now differ between New South Wales and the other two States?

(2) Does the density of red kangaroos differ now between States (Fig. 1)?

(3) If so, does density climb smoothly from one State into another, as it might if density followed an environmental gradient (Fig. 1*b*), or is density stepped at the border (Figs 1*c*, 1*d*)?

(4) If density steps at the border, is this an effect of the fence itself acting as an aid to dingo predation or as a barrier to upwind drift or some other directional

dispersal of kangaroos (Fig. 1*c*), or is the difference in density a result of the States providing discrete and disparate environments (Fig. 1*d*)?

(5) What variables are associated with observed trends in density between States?

Jarman and Denny (1976) also addressed some of these questions. Their findings are compared with ours later in this paper.

Methods

Design

The density of red kangaroos was compared in August 1976 between States along transects crossing the border at right angles (Fig. 2). These comparisons were made:

A. New South Wales with South Australia across a dingo fence;

B. Queensland with South Australia across a border fence;

C1. New South Wales with Queensland (far west) across a dingo fence;

C2. New South Wales with Queensland (central west) across a border fence;

Surveys A, B and C1 were located close together where the three States meet, thereby controlling to some extent the environmental differences between comparisons. Survey C2 was positioned farther east where the densities of eastern grey kangaroos, *Macropus giganteus*, could be included in the comparison. Fig. 2 maps the transects.

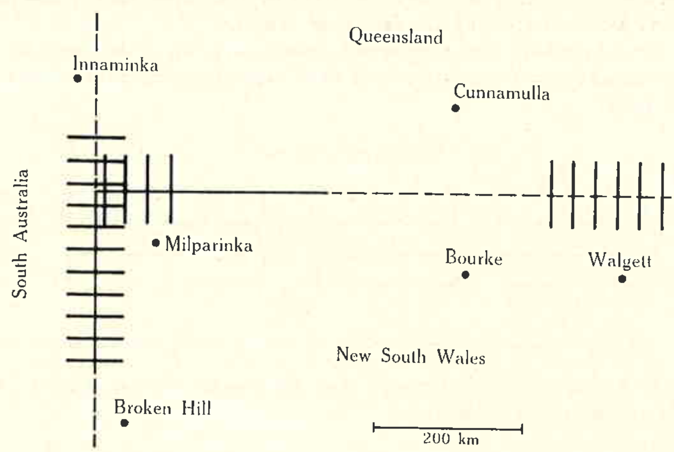


Fig. 2. Aerial survey transects in relation to State borders. The border is drawn as a continuous line where the border fence is a barrier to dingoes.

Transects began 40 km inside one State and ended 40 km inside the other. Each transect was covered by a single overflight, the sections in each State being paired by time of day, weather conditions, direction of traverse, and fatigue of observers. Parallel transects were separated by 28 km and were run in alternate directions so that an observer scanning north on one run would scan southward on the next. The aircraft was flown at 185 k.p.h. (100 knots) at a height of 75 m (250 ft) above ground.

Two observers (G.C. and J.C.), one on each side of the aircraft, counted animals on a strip demarcated by streamers attached to the wing struts. These were so positioned that they marked off a 200-m-wide strip when the plane was at survey altitude. Each 5 km of track an electronic whistle sounded for 7 s, in which time the observers wrote down the number of animals seen since the previous whistle. The area traversed during the pause was not included in the estimate of density. Hence a standard transect measuring 80 by 0·4 km, excluding gaps, could be divided transversely into halves, one half in each State, and longitudinally into halves representing the fields of view of the two observers. It could also be subdivided into 32 elements of 1 km^2. Fig. 3 diagrams the elements within a transect and the gaps between them. By subdividing transects in this way it becomes possible to split a beam of white variability into a spectrum of contributing effects: States, species, observers, transects, and distance from the border.

A further comparison of densities between States was made by a transect down the border, the aircraft being positioned directly above the fence. Each observer scanned a 200-m-wide strip whose inner boundary was positioned 25 m out from the fence. At the same time the pilot (G.C.G.) counted animals within 10 m either side of the fence.

Analysis

Transects were treated as a random factor; States, species, observers and distance from the border as fixed factors. Before the data were subjected to analysis of variance each count was increased by 0·375 to eliminate zeros and then square-rooted to homogenize variances (Anscombe 1948).

Since each analysis comprises a mix of fixed factors and one random factor, the denominator of the *F*-ratio testing the significance of a fixed factor is the mean square of interaction between that factor and the random factor 'transects' (Zar 1974, appendix C). The denominator for testing an interaction between two fixed factors is the mean square of the three-way interaction between these factors and 'transects'. Because the levels of factor 'transects' are unreplicated, neither that factor, nor any interaction incorporating it, can be tested for significance. But those tests are redundant for our purposes; they would answer no question we care to pose.

The densities in the figures are corrected for visibility bias by multiplying observed densities by 2·29 in the open country of the western study area and by 2·42 in the more timbered eastern area. Derivation of these factors is given by Caughley *et al.* (1976).

An index to density of emus, *Dromaius novaehollandiae*, is given as the frequency of occurrence per 5 km of track (representing a sampling unit of 2 km^2) and dingo density is indexed as the number seen per 5 km of track.

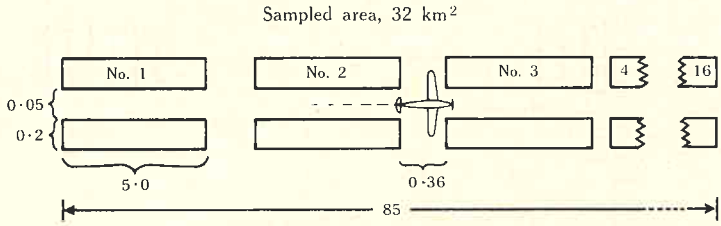


Fig. 3. The anatomy of a transect. The components are not to scale. All measurements are in kilometres.

Results

New South Wales–South Australia

Fig. 4 compares the density of red kangaroos in New South Wales with that in South Australia north of that State's dingo fence, at three levels of resolution. The top comparison is of density measured in intervals of 5 km outward from the border for 40 km in each direction. Density in New South Wales was 166 times higher than in South Australia: 12·00 km^{-2} against 0·07 km^{-2}. The difference is not an artefact of the Sturt National Park in New South Wales; density on transects within the park did not differ significantly from that on the transects south of the park (F = 2·86, 1/6 d.f.).

Analysis of variance (Table 1) indicated that the difference was real, accounting for 77% of the total variability of the data. Within the limits of sampling variation the observers (G.C. and J.C.) did not differ in counting efficiency and there was no observer × State interaction. Analysis of counts from New South Wales revealed no significant difference in density by distance from the border (F = 0·64; 7/56 d.f.).

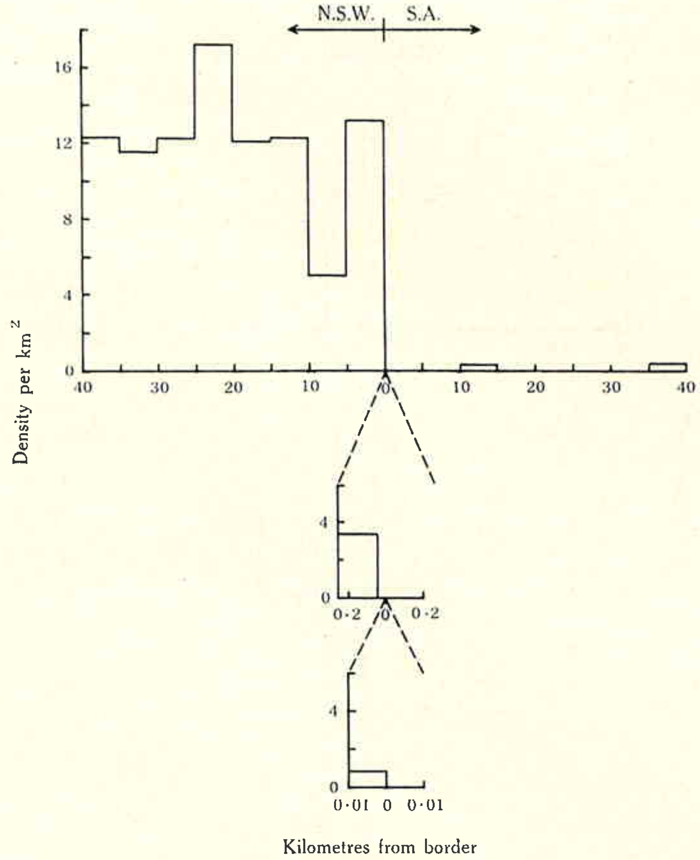


Fig. 4. Comparison of density of red kangaroos across the border between New South Wales and South Australia.

Table 1. Analysis of variance of red kangaroo densities compared between New South Wales and South Australia

*** $P<0.001$

Source	Sum of squares	Degrees of freedom	Mean square	Variance ratio
States	236·95	1	236·95	52·89***
Observers	1·43	1	1·43	1·25 NS
Transects	23·96	7	3·42	—
States × observers	0·75	1	0·75	0·85 NS
States × transects	31·37	7	4·48	—
Transects × observers	7·96	7	1·14	—
States × observers × transects	6·13	7	0·88	—
Total	308·55	31		

Fig. 5

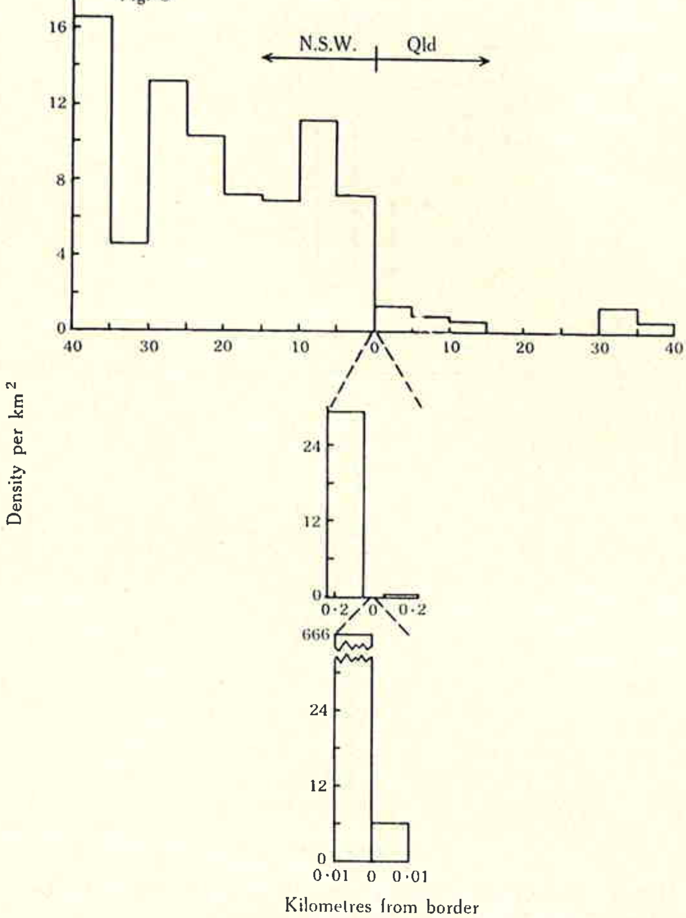
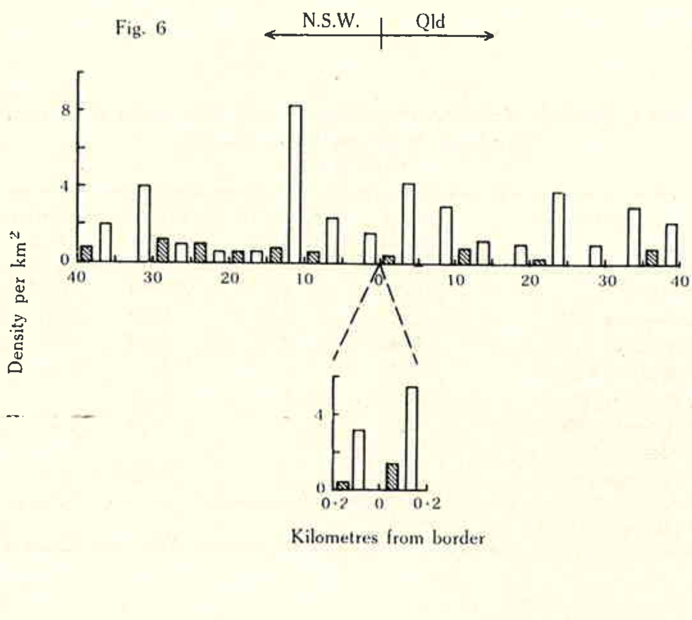

N.S.W.
Qld
16
12
8
4
0
40 30 20 10 0 10 20 30 40
Density per km²
24
12
0
0·2 0 0·2
666
24
12
0
0·01 0 0·01
Kilometres from border

Fig. 6


N.S.W.
Qld
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Density per km²
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Kilometres from border

The two smaller histograms of Fig. 4 compare densities measured very close to the border on the 220-km transect along the fence. A density difference between the two States, although not as marked as in the extensive comparison, is again suggested by these counts.

These results in combination suggest that there may be a fence effect (see Fig. 1*c*) in the immediate vicinity of the border but that it is trivial compared with the massive difference in density maintained for at least 40 km out from the border in either direction, far beyond any possible influence of the fence itself. There is no discernible trend in density that might implicate an environmental gradient. Rather, the step in density at the border indicates a State effect (Fig. 1*d*), probably reflecting a marked difference in the environment of the two States.

The contrast in kangaroo density between States appears again in the counts of emus. The New South Wales density index of 0·52 drops to 0·02 in South Australia, a highly significant ($F = 67{\cdot}9$; 1/7 d.f.) 26-fold difference. Likewise, the density of dingoes differs between States, but in the opposite direction. New South Wales returned a density index of zero against 0·11 observed per 5 km of track for South Australia ($F = 6{\cdot}5$; 1/7 d.f.).

Queensland–South Australia

At the spacing set by the survey design only three transects could be fitted into this zone because the border fence extends only 60 km north from Queensland's southern border. No significant difference ($F = 1{\cdot}0$; 1/2 d.f.) could be detected between the densities of red kangaroos in the two States which averaged 0·17 km^{-2} overall. No kangaroo was seen on either side of the flight path on the transect directly along the border.

Likewise, no significant difference ($F = 1{\cdot}8$; 1/2 d.f.) in emu density was detectable between States, the index averaging 0·17 overall. Only one dingo was seen (in Queensland) on this survey.

We interpret these findings as indicating no effect of fence or State on the densities of red kangaroos and emus in these two areas.

New South Wales–Queensland (far west)

At the spacing set by the survey design only four transects could be fitted across the New South Wales–Queensland border between South Australia and the Bulloo overflow. The transect along the fence was limited to 90 km.

Fig. 5 gives densities of red kangaroos in this area at the same three levels of resolution. Table 2 summarizes an analysis of variance of the survey extending out 40 km from the border in both directions. Red kangaroos averaged 9·87 km^{-2} in New South Wales as against 0·61 km^{-2} in Queensland, 'States' accounting for 85% of variance in numbers. Analysis of the New South Wales counts revealed no significant heterogeneity in density at different distances south of the border ($F = 1{\cdot}9$;

Fig. 5. Comparison of density of red kangaroos across the border between New South Wales and Queensland in the far west.

Fig. 6. Comparison of density of red kangaroos (hatched bars) and eastern grey kangaroos (open bars) across the border between New South Wales and Queensland in the mid-west.

7/21 d.f.). However, the lower two histograms of Fig. 5 indicate that there is indeed a fence effect, the kangaroos in New South Wales reaching higher than average densities within 200 m of the fence (28 km^{-2}) and very much higher densities (666 km^{-2}) at the fence; but the results of the extensive survey show that this is very much a local effect. On the Queensland side of the border there appears to be a fence effect whose influence extends for about 15 km north, manifesting as a ramp of density running up to the fence. We suspect that this reflects nothing more mysterious than a break in the fence within the previous 6 months, that allowed leakage of kangaroos from New South Wales into Queensland, particularly as the ramp of density was produced largely by counts in only one transect.

Table 2. Analysis of variance of red kangaroo densities compared between New South Wales and Queensland (western area)
** $P<0\cdot01$

Source	Sum of squares	Degrees of freedom	Mean square	Variance ratio
States	79·92	1	79·92	53·64**
Observers	0·66	1	0·66	3·67 NS
Transects	5·91	3	1·97	—
States × observers	1·22	1	1·22	2·53 NS
States × transects	4·48	3	1·49	—
Transects × observers	0·54	3	0·18	—
States × observers × transects	1·45	3	0·48	—
Total	94·17	15		

Emus were more abundant in New South Wales ($F = 23\cdot9$; 1/3 d.f.), where they returned a density index of 0·47 as against 0·09 in Queensland. Relative densities of dingoes could not be assessed because we saw none on these transects.

Our interpretation of these results is much the same as for the New South Wales–South Australia comparison. There is no discernible trend in density that would implicate an environmental gradient. Rather the density breaks abruptly at the border. The marked 'State' effect transcends the localized 'fence' effect.

New South Wales–Queensland (central west)

This survey comprised six 80-km transects crossing the border at right angles and one transect of 160 km along the border. Fig. 6 shows the results separately for red kangaroos and eastern grey kangaroos. Red kangaroos averaged 0·63 km^{-2} in New South Wales and 0·28 km^{-2} in Queensland but these are not significantly different. The equivalent densities for grey kangaroos were 2·57 and 2·37 km^{-2}. Flying conditions were poor during this survey, the aircraft dancing around too much for efficient observation. Hence the estimated densities are probably too low but, since each transect sampled both States, that bias will not jeopardise comparison between the States.

Table 3 summarizes the analysis of variance on the counts of kangaroos. Of those comparisons for which an F-ratio is available, only the density of red kangaroos as against that of grey kangaroos is significant. There was no discernible difference in the density of kangaroos, species pooled, between the two States, 'States' accounting for only 1% of the variablity of the counts. Neither did the density of emus differ between States ($F = 0 \cdot 8$; 1/5 d.f.). Their density index was 0·14 over all.

Table 3. Analysis of variance of red and grey kangaroo densities compared between New South Wales and Queensland (eastern area)
** $P<0 \cdot 01$

Source	Sum of squares	Degrees of freedom	Mean square	Variance ratio
Kangaroo species	28·66	1	28·66	28·92**
States	0·74	1	0·74	0·47 NS
Observer	0·06	1	0·06	0·08 NS
Transects	6·30	5	1·26	—
Species × State	0·01	1	0·01	0·01 NS
Species × observer	0·45	1	0·45	0·45 NS
Species × transect	4·96	5	0·99	—
State × observer	0·30	1	0·30	0·58 NS
State × transect	7·81	5	1·56	—
Observer × transect	4·13	5	0·83	—
Species × State × observer	1·17	1	1·17	1·55 NS
Species × State × transect	7·22	5	1·45	—
Species × observer × transect	5·16	5	1·03	—
State × observer × transect	2·88	5	0·58	—
Species × State × observer × transect	3·69	5	0·74	—
Total	73·54	47		

Discussion

Fig. 7 summarizes schematically our measurements of the density of kangaroos in relation to the State borders. Jarman and Denny's (1976) survey of the western study area provides a similar picture.

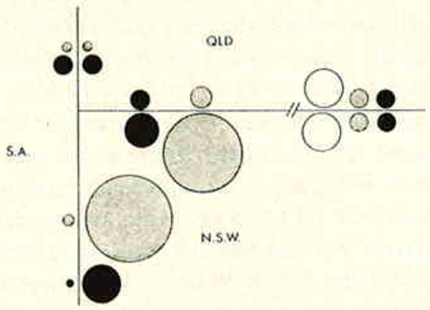

Fig. 7. Schematic representation of the densities of red kangaroos (hatched circles), grey kangaroos (open circles) and emus (solid circles) relative to the position of State borders. The area of each circle is proportional to density but the scales differ between kangaroos and emus.

In the western area these surveys are enough to invalidate some of the more plausible hypotheses accounting for the observed density contrasts between States. The sharp break in density at the border dismisses gradients in soil or aridity as the cause. The finding that the density differences between States hold 40 km from the border rules out explanation of the contrast by any local fence effect. Instead the difference has something to do with environmental conditions specific to the States themselves. The pattern of density cannot be explained easily as a response to the border fence sealing dispersal routes. It would be plausible that the contrast between New South Wales and South Australia reflects an inability of kangaroos in South Australia to move east during droughts, were it not for the low density of Queensland kangaroos which are not constrained to the same extent.

Jarman and Denny (1976) investigated the possibility that differential shooting pressure might be responsible for the density differences across the borders. They concluded that it was not high enough to explain the difference, and we agree.

Similarly, Jarman and Denny (1976) sought an explanation in the density of watering points on either side of the New South Wales–South Australian border. It differed by a factor of three, being $2 \cdot 3$ km^{-2} in New South Wales and $0 \cdot 7$ km^{-2} in South Australia (their table 4). That difference seems inadequate to explain kangaroo densities differing by a factor of over 100.

That leaves only two hypotheses that we consider credible: that the density contrasts reflect either differing vegetations or differing rates of predation by dingoes. Newsome (1971, 1975) and Frith (1973) suggested that the red kangaroo increases when cattle and sheep modify a vegetation to produce a disclimax. In the western study area the grazing regimes of domestic stock differ between States. North-west New South Wales is predominantly sheep country with a sheep: cattle ratio of about 30 (R. Farrands, personal communication). The adjacent areas of South Australia and Queensland have a ratio much closer to parity. It could be argued that vegetational changes caused by stock differ between States consequent on their differing ratios of sheep to cattle, and that vegetational changes caused mainly by sheep have favoured red kangaroos more than have those caused by cattle. That hypothesis would account neatly for the break in kangaroo density at the borders and it carries a testable corrolate prediction that plant composition and production will show discontinuities at the borders.

One of us (G.H.) looked for such discontinuities on Landsat scene 1563-23535 (grid reference 103/080, 6 February 1974) which is centred at the junction of the three States.

On the Queensland–South Australian border the vegetational response appeared similar in both States. A drop in response in South Australia was not detectable until 10 km from the border. On the New South Wales–South Australian border the vegetational response was poorer for both States than it was on the same meridian above Cameron's Corner, but it was constant across the border. The western 20 km of the New South Wales–Queensland border runs across dunes. There is no great variation in vegetational response across the border but Queensland appeared marginally better off. Differences become more pronounced 10 km away from the border with a greater vegetational response in Queensland. Further east the drainage divide of the Grey Range runs close to the border in New South Wales. Vegetational response is low in the vicinity of the divide and for the surrounding areas of high ground. Forage availability is higher in Queensland along most of this section of border.

Landsat imagery revealed no discontinuities of vegetation at the border. The observed gradations appeared to be uninfluenced by the position of the border. In the absence of corroborative ground surveys we are reluctant to make too much of a Landsat image recorded in one season of one year. However, the available evidence argues against the hypothesis that contrasts in kangaroo density mirror contrasts in vegetation.

The contrasts in kangaroo and emu densities found between States in the far western study area where the fence is a real barrier were not repeated in the mid west. But there the border fence is no barrier to kangaroos (R. Condon, personal communication; M. L. H. Burns, personal communication) and no dingoes have been recorded there for many years either in Queensland (M. W. Sheehan, personal communication) or in New South Wales (R. Condon, personal communication). The ratio of sheep to cattle is about 8 in that area of Queensland and about 30 across the border in New South Wales.

This study has documented a phenomenon but has not revealed a cause. We have presented and discarded several hypotheses to account for the reported contrasts in density, and are left with only one—the distribution pattern reflects different levels of predation by dingoes.

Jarman and Denny (1976) also suspected that dingoes had something to do with the density contrasts, but they pictured the effect as indirect. They write that 'While it is debatable whether a predator can control the density of a prey species on which it depends, we think that in these densities dingoes may well be limiting the kangaroos' freedom of use of open pastures. This might limit the food available to kangaroos and hence limit their numbers.'

Our interpretation is more direct. We envisage the primitive densities of red kangaroos as being kept very low by dingo predation, whereas dingo numbers would have been determined not by the abundance of kangaroos but by that of a suite of smaller prey species: rodents of the genera *Rattus*, *Notomys*, *Pseudomys* and *Leporillus*, and marsupials of the genera *Bettongia*, *Lagorchestes*, *Onychogalea*, *Chaeropus*, *Perameles*, *Macrotis*, *Antechinomys* and *Sminthopsis*. Most of these are now either extinct or uncommon inland, but their place in the dingo's economy has been taken by the European rabbit. Green and Catling (1977) report that rabbit is the commonest component of the dingo's diet in the arid zone.

Prey–predator theory predicts that, with a single species of predator and of prey, the equilibrium level of prey will be determined largely by characteristics of the predator, and that of the predator by characteristics of both prey and predator (May 1976). A predator usually cannot force the prey to very low density because its own numbers will decrease reciprocally as its food supply declines. That tight dynamic mutuality is uncoupled when the prey comprises more than one species. Then it is possible, theoretically at least, for a species of prey to be pushed to minimal density, or to extinction, by a predator whose diet, and hence density, is sustained by other species of prey. That effect is expected if either of two conditions is met. First, if the threatened prey is taken at a higher rate than alternative prey its numbers will be lowered disproportionately. And secondly, if its intrinsic rate of increase is significantly lower than that of alternative prey it will be less capable of reacting demographically against the weight of predation compressing its density. We suspect that the second mechanism is in play when dingoes prey upon kangaroos in the presence of rabbits.

We deduce that present densities of kangaroos and dingoes in the cattle country of South Australia and Queensland are of the same order as they were 150 years ago.

But in the sheep country of those States and in New South Wales, where dingoes have been eliminated or held by continual persecution at very low densities, red kangaroo numbers are one or two orders of magnitude higher than they were last century.

Since the density of kangaroos and emus is determined by a complex of factors we do not argue that predation alone sets its level. Modification of vegetation by stock, and the increased availability of watering points this century, may well have played a part in determining the densities we see today. But we consider that most of the contrast in densities that we report here is a direct effect of predation: that kangaroos and emus in open country cannot maintain high densities when preyed upon by dingoes having access to an abundant alternative prey.

Acknowledgments

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