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The Distribution and Abundance of Kangaroos in relation to Environment in Western Australia

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Abstract

Red and western grey kangaroos were surveyed from the air in Western Australia during the winter of 1981. The area covered, 1 528 000 km^2 or 61% of the State, excluded only the Kimberleys in the north and the Gibson and Great Sandy Deserts of the interior. Hence almost all kangaroo range within the State was surveyed, to provide an estimate of 980 000 reds and 436 000 greys. Densities were much lower than those of the eastern States. Red kangaroos were most abundant in mulga shrubland, chenopod shrubland and tussock grassland, and least abundant in hummock grassland. Densities were associated strongly with land-use categories, being high in areas used for extensive sheep grazing and low in vacant Crown Land and arable land. In contrast to reds the western grey kangaroos were confined to the south and west of the state, their distribution being related more directly to climate than to vegetation or land use. They live in the winter rainfall zone. We suggest that their restricted breeding season results in peak nutritional demands associated with lactation, and hence energy requirements, being synchronized with the spring flush of pasture following winter rains. Approximately 14% of the red kangaroo and 8% of the western grey kangaroo populations in Western Australia were harvested legally in 1981.

Introduction

The abundance and distribution of red and western grey kangaroos, *Macropus rufus* and *M. fuliginosus*, were assessed by aerial survey for 1 528 000 km^2 of Western Australia (61% of the area of that State) in the winter of 1981. The Gibson and Great Sandy Deserts and the Kimberley Division were omitted from this survey because of problems of scale and inaccessibility and because kangaroos were expected to be either at low densities or absent. Bad weather prevented the survey of small areas to the north and south-east of Perth. Estimated densities were examined against environmental variables (climate, vegetation and land use) in an attempt to determine the habitat requirements of each species of kangaroo. The broad-scale scanning survey was complemented for red kangaroo by a more intensive survey of a limited area, the Gascoyne River Basin (64 000 km^2) of central western Western Australia (Fig. 1).

For the purpose of this paper, Western Australia can be divided broadly into three environmental zones:

The south-west. This is bounded by a line running from Kalbarri in the north to Cape Arid in the south (Fig. 1). It has a mediterranean climate of hot, dry summers and warm, wet winters. Average annual rainfall varies spatially between 300 and 1200 mm. Wet and dry sclerophyll forest, temperate woodland and mallee shrublands are the primary vegetation types. Major forms of land use include forestry, intensive grazing of sheep and cattle and the cultivation of wheat.

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The pastoral zone. It forms a broad arc across Western Australia bounded to the south-west by the wheatbelt and to the east by the desert (Fig. 2). It meets the west coast between Port Hedland in the north and Kalbarri in the south and is here 700 km wide. To the south-east it narrows to less than 60 km near Eucla. To the north of this area, and entirely separated by the Great Sandy Desert, lies an extension of the pastoral zone centred on the Fitzroy River and the Kimberley Division.

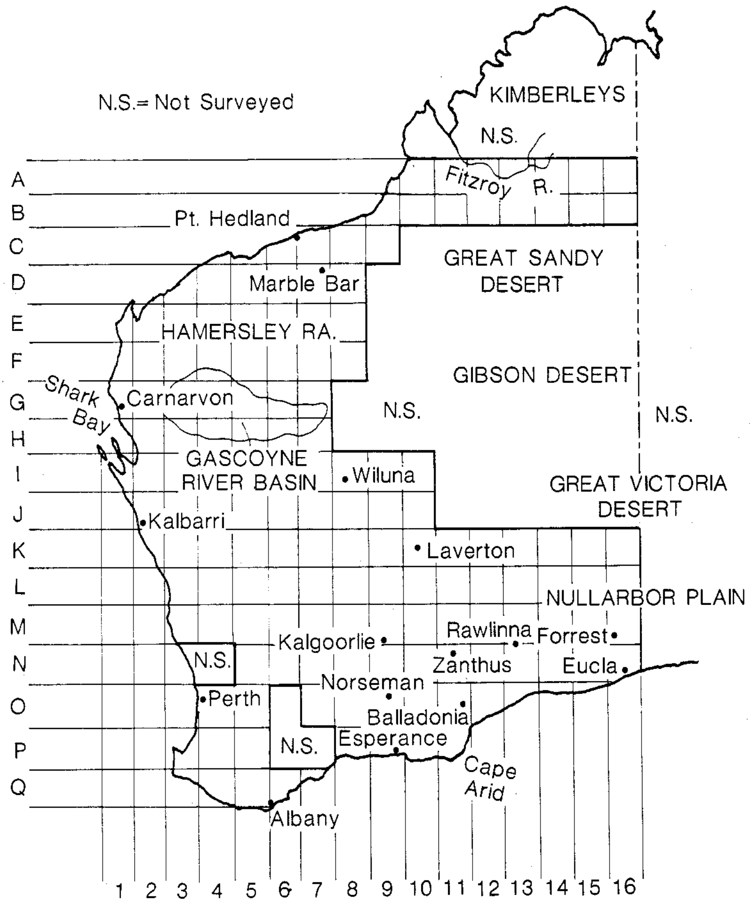

Fig 1. Western Australia, showing the area surveyed and the location of the Gascoyne River Basin.

Average rainfall varies between 200 and 350 mm across the zone, most of it falling in winter in the south but becoming progressively summer-dominant towards the north. The major vegetation is mulga, *Acacia aneura*, shrubland with a low shrub or grass understorey. Other vegetation types include eucalypt woodlands (e.g. *Eucalyptus salmonophloia, E. salubris, E. lesouefii, E. dundasii*) to the south of Kalgoorlie (Beadle 1981), the low chenopod shrublands of the Nullarbor Plain, and hummock grass, *Triodia* spp., in the north (Hamersley Range, Marble Bar, Fitzroy River) and along the eastern margin of the pastoral zone.

Extensive sheep grazing is the major land use although cattle grazing predominates in the north (Pilbara, Hamersley Range and along the Fitzroy River) and to the east where the pastoral zone abuts the deserts.

The unoccupied zone (Fig. 2). The low (<200 mm) and erratic rainfall and the absence of ground water limits even extensive pastoralism. Much of this area is dominated by parallel sand-dunes with a vegetation of hummock grass and scattered low eucalypts (for example, *Triodia basedowii* with *Eucalyptus gongylocarpa* in the Great Victoria Desert). In the south it includes much of the low chenopod shrubland of the Nullarbor Plain.

The Gascoyne River Basin was surveyed more intensively than the rest of the state. Its rangelands have been the focus of much research into the effect of sheep grazing on pasture composition and erosion rate of soil (Wilcox and McKinnon 1972; Williams *et al.* 1977; Williams 1978) and therefore rated a more detailed assessment of kangaroo density. The basin is an area of extensive sheep grazing in a 200–250 mm rainfall zone with a vegetation primarily of mulga shrubland.

Methods

Aerial Survey

Surveys were flown in April-June 1981. The technical details of the survey (height, speed and strip-width), methods of delineating the strip boundary, observer standardization and correction factors for differential visibility of kangaroos in different vegetation cover types were as for previous State surveys (Caughley and Grigg 1981, 1982; Short and Grigg 1982). The basic unit of survey was the degree block (1° longitude by 1° latitude). Two transects were flown (along the 15′ and 45′ of latitude) in each block where high densities of kangaroos were expected (i.e. in the pastoral zone), a sampling intensity of 0·7%. In the south-west and beyond the eastern margin of the pastoral zone a single transect was flown across the block along the 30′ of latitude (0·35%). The Gascoyne River Basin was surveyed at an intensity of 1·4%.

Analysis (Extensive Survey)

Data on 20 environmental variables were compiled for each degree block. Rainfall was estimated from maps published by the Bureau of Meteorology (1975, 1977–81, 1979), vegetation data from the 'Natural Vegetation' map (Division of National Mapping 1976) and commentary (Carnahan 1976), and land use information from the 'Land Use' map (Division of National Mapping 1979). The compiled variables were:

(i) *Rainfall variables*

Average annual rainfall, in millimetres.

Reliability of rainfall, calculated as the lower 10 percentile of rainfall expressed as a percentage of the average annual rainfall.

Winter–summer dominance of rainfall expressed on a 5-point scale, the highest value indicating winter dominance.

Annual rainfall for the three years 1978–80 as a percentage of average annual rainfall.

Annual rainfall for the five years 1976–80 as a percentage of average annual rainfall.

Rainfall during 1980, in millimetres.

(ii) *Vegetation Variables*

Percentage of each degree block dominated by mulga. This category includes areas of mulga with an understorey of low shrubs (often *Eremophila* sp.) and, in favourable situations, such perennnial tussock grasses as *Eragrostis eriopoda*; as well as areas with a ground layer of perennial grasses, e.g. *Eragrostis eriopoda* and *Danthonia bipartita*, ephemeral grasses, e.g. *Aristida* spp. and *Enneapogon* spp., and forbs, e.g. *Helipterum* spp. and *Ptilotus* spp. (Carnahan 1976).

Percentage of each degree block dominated by mallee shrubland or mallee heath. Mallee shrubland (see Beadle 1981 for major species alliances) generally occurs with an understorey of sclerophyllous and often ericoid low shrubs. Mallee heath (e.g. *Eucalpytus tetragona* with a dense sclerophyllous understorey) occurs along the southern coast on sandy duplex soils (Carnahan 1976).

Percentage of each degree block dominated by chenopods. The dominant vegetation type in this classification is the low shrubland of *Maireana sedifolia* with a lower stratum of tussock grasses which occurs on the Nullarbor Plain. It also includes smaller areas of low open woodland dominated by *Acacia sowdenii* (Carnahan 1976).

Fig. 2

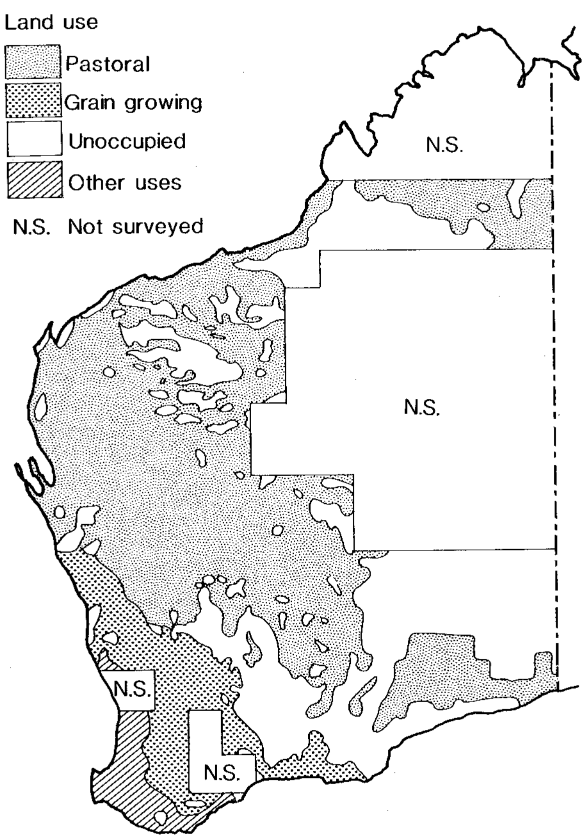

Fig. 3

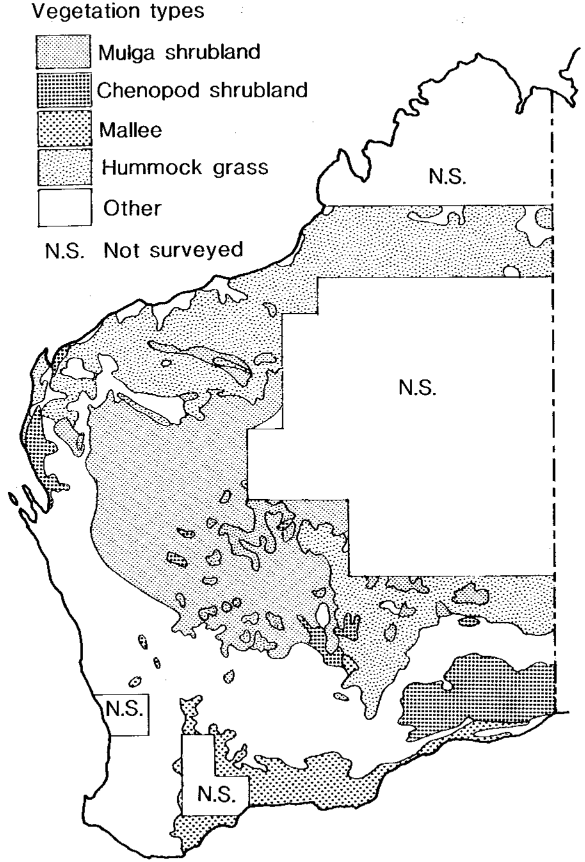

Fig. 2. Major land use types used in analysis.
Fig. 3. Major vegetation types used in analysis.

Percentage of each degree block dominated by the hummock grasses *Triodia* spp. and *Plectrachne* sp. Major species include *Triodia basedowii* in the south and centre of the State, and *T. pungens* and *Plectrachne schinzii* in the north. Commonly, hummock grass occurs either with isolated trees or as a savannah woodland of either *Acacia pachycarpa* or *Eucalyptus brevifolia* in the north, *A. aneura* in the centre, or *E. gongylocarpa* in the south of the State (Beadle 1981).

Percentage of each degree block dominated by tussock grass and graminoids. These may occur as an understorey to tall shrublands of mulga and to low shrublands of chenopods (Carnahan 1976).

Growth form of the tallest stratum of vegetation. Each degree block was assigned a value of between 1 and 5 according to the scale: *1*, low shrubs <2 m; *2*, tall shrubs >2 m; *3*, low trees <10 m; *4*, medium trees 10–30 m; *5*, tall trees >30 m.

Foliage cover of tallest stratum expressed as a percentage.

Diversity of vegetation within a degree block measured as the number of distinct vegetation types crossed per survey line. It varied between one and five.

Major vegetation types are mapped in Fig. 3.

(iii) *Land use variables*

Average density of stock (beef beasts per square kilometre) within a degree block. Eight sheep equal one beef beast (Division of National Mapping 1979).

Percentage of block in which cattle grazing predominates.

Percentage of block in which sheep grazing predominates.

Percentage of block dominated by wheat farming.

Percentage of block comprising national park land or other nature conservation reserves.

Percentage of block in which the major land use is other than above. Almost all land in this catagory is vacant Crown Land unsuitable both for cultivation and for extensive grazing, but included also is an area used for commercial forestry in the south-west.

Major land use categories are mapped in Fig. 2.

After an initial examination of scattergrams of kangaroo density versus each environmental variable, kangaroo densities were logged (ln[kangaroo density+0·01]) to improve linearity. A correlation matrix of environmental variables indicated a high degree of intercorrelation between variables. Hence variables were transformed by principal components analysis (Kim 1975) to provide a reduced number of orthogonal components. Components (axes) highly correlated with kangaroo density were then entered into a step-up multiple regression (Kim and Kohout 1975), transformed kangaroo density being the dependent variable and the principal components independent variables. The advantage of this approach over using the original variables in the multiple regression is that, due to their orthogonality, the relative contribution of each component (independent variable) to the value of y is given by the magnitude of its standardized coefficient. This is not true of a multiple regression using intercorrelated 'independent' variables.

Analysis (Gascoyne River Basin)

The distribution of red kangaroos within the Gascoyne River Basin was compared with published maps of geology and vegetation (Wilcox and McKinnon 1972).

Results

Numbers and Densities of Kangaroos

Numbers (±SE) and densities (±SE) of red and western grey kangaroos are listed in Appendix 1 and mapped in Figs 4 and 5. Approximately 980 000 red kangaroos and 436 000 western grey kangaroos were estimated as present in the surveyed area. Red kangaroos attained medium densities north-east of Carnarvon (4–5 per square kilometre), and between Rawlinna and Forrest on the Nullarbor Plain (3–7 per square kilometre). Of an area of about 948 000 km^2 in which red kangaroos were recorded, 73% had a density of less that 1 per square kilometre.

Like the red kangaroo, western grey kangaroos were generally sparse outside several small areas of concentration. Greys reached highest densities at two points abutting the south coast; at Albany (5–6 per square kilometre) and at Balladonia (2–7 per square kilometre).

Densities were below 1 per square kilometre in 74% of their surveyed range of 474 000 km^2.

Environmental Influences on Density and Distribution of Kangaroos

Twelve orthogonal components were extracted from the original 18 intercorrelated variables. The components most highly correlated with logged kangaroo density (Table 1) were then entered into a step-up multiple regression, the transformed kangaroo density being the independent (y) variable. The resulting equation accounted for 52% of the variance of y in the case of the red kangaroos and 31% for grey kangaroos. The standardized and unstandardized coefficients are presented in Table 2. The loadings of environmental variables on each principal component used in the regression are given in Table 3.

Table 1. Correlation matrix of transformed kangaroo densities with principal components

Components used in further analysis are in italics

Principal component	Red kangaroo	Western grey kangaroo	Principal component	Red kangaroo	Western grey kangaroo
1	−0·05	*−0·39*	7	0·08	−0·02
2	*−0·28*	*0·28*	8	*−0·47*	*0·18*
3	*0·24*	0·07	9	−0·17	0·14
4	*−0·33*	0·09	10	*−0·30*	*0·25*
5	−0·12	0·04	11	−0·06	0·12
6	−0·08	−0·06	12	−0·17	−0·16

Table 2. The standardized and unstandardized coefficients and constants for multiple regression of transformed kangaroo density on principal components

Component	Red kangaroo		Western grey kangaroo	
	Standardized coefficient	Unstandardized coefficient	Standardized coefficient	Unstandardized coefficient
PC 1	–	–	−0·382	−0·770
PC 2	−0·236	−0·520	0·261	0·537
PC 3	0·259	0·606	–	–
PC 4	−0·307	−0·655	–	–
PC 8	−0·431	−1·024	0·155	0·345
PC 10	−0·292	−0·741	0·233	0·553
Constant	–	−2·118	–	−3·330

(i) *Red kangaroos*

The five most important components for this species, ranked by importance, were:

P.C. 8: a vegetation component comprising a strong negative loading on 'mulga' (percentage of each grid square dominated by mulga) and a positive loading on 'hummock grass' (percentage of each grid square dominated by hummock grass). Red kangaroo density was negatively correlated with this component, indicating that areas of mulga woodlands commonly had high densities of red kangaroos, but areas of hummock grass had low densities (see Table 4).

P.C. 4: a land use component comprising a strong negative loading on 'sheep' (percentage of grid square where sheep grazing predominates) and a strong positive loading on 'other land use'. Red kangaroo density was negatively correlated with this component. Thus higher densities of red kangaroos were found in areas where the grazing of sheep is the major activity, and lower densities were found in the large tracts of unused Crown Land to the east and south of the pastoral zone.

P.C. 10: a climatic component reflecting reliability of rainfall. Red kangaroo density was negatively correlated with this component, indicating the favourability of areas of erratic rainfall to this species.

P.C. 3: a vegetation component comprising a positive loading on 'chenopod' (percentage of each grid square dominated by chenopods) and 'tussock grass' (percentage of each grid square dominated by tussock grasses) and a negative loading on 'growth form of the tallest stratum of vegetation'. Density of red kangaroos was related positively to this component. Reds were at high densities in areas where chenopods and tussock grass were common and where the value for 'vegetation growth form' was low (i.e. where the tallest stratum of the vegetation is made up of shrubs rather than forest trees).

P.C. 2: a component largely reflecting climate. Annual average rainfall, rainfall during 1980, reliability of rainfall, and stock density all load positively on this component, which was negatively correlated with red kangaroo density. Hence densities of red kangaroos increased as annual averge rainfall, reliability of rainfall and stock density declined. Rainfall during 1980 is included because of its correlation with annual average rainfall.

Table 3. Loadings of environmental variables on principal components used in the regressions

Variables	Loading on principal component No.: 1	2	3	4	8	10
Average annual rainfall	−0·04	*0·91*	−0·20	0·04	0·20	0·09
Reliability of rainfall	−0·36	0·49	−0·04	0·18	0·13	*0·49*
Winter–summer dominance of rainfall	*−0·82*	0·18	0·01	0·06	0·09	0·22
Rainfall (1978–80)	*0·93*	−0·11	0·10	0·16	−0·18	−0·02
Rainfall (1976–80)	*0·92*	0·04	0·13	0·20	0·04	0·18
Rainfall (1980)	0·56	*0·70*	−0·21	−0·06	−0·01	−0·14
Mulga	0·00	−0·16	−0·13	−0·26	*−0·70*	−0·04
Mallee	−0·05	0·08	−0·07	0·03	−0·01	0·03
Chenopod	−0·17	−0·16	*0·75*	0·11	0·17	0·00
Hummock grass	*0·77*	−0·06	−0·24	0·04	*0·32*	−0·22
Tussock grass	0·08	−0·04	*0.83*	0·06	0·01	0·05
Growth form of vegetation	−0·16	0·27	*−0·56*	0·25	0·21	0·19
Foliage cover of vegetation	−0·27	0·41	0·10	0·00	−0·15	0·14
Diversity of vegetation	0·05	0·07	−0·05	0·01	0·09	0·02
Stock density	−0·18	*0·79*	−0·06	0·02	0·00	0·03
Cattle	0·36	0·15	0·04	−0·10	−0·01	−0·03
Sheep	−0·28	−0·14	−0·04	*−0·73*	−0·20	−0·04
Wheat	−0·21	0·11	−0·12	−0·04	0·10	0·06
National Park	0·02	−0·05	0·06	0·03	0·04	0·01
Other land use	0·14	−0·02	0·07	*0·92*	0·15	0·04

(ii) *Western grey kangaroos*

Of the five components most highly correlated with the transformed grey kangaroo density, three (P.C. 1, 2 and 10) indicate the importance of climate to the distribution and abundance of this species. The fifth component (P.C. 12) was eliminated from the analysis despite a significant correlation with grey kangaroo density. It contained only residual unexplained variance in the matrix of environmental variables unaccounted for in the previous 11 components (0·8% of the total variance).

The four most important components for grey kangaroos, ranked by importance, were:

P.C. 1: a bipolar component with 'winter-summer dominance of rainfall' having a negative loading and rainfall over the previous 3 and 5 years (1978–80, 1976–80) and 'hummock grass' (percentage of each degree block dominated by hummock grass) having a positive loading. Kangaroo density was negatively correlated with this component, indicating high densities of grey kangaroos at high values of 'winter-summer dominance' (i.e. the winter rainfall zone) and low densities in areas of hummock grass. Rainfall for the 3- and 5-year periods before the survey (1978–80, 1976–80) was below average over much of the surveyed areas of Western Australia, largely due to the failure of winter rains. Hence

Fig. 4

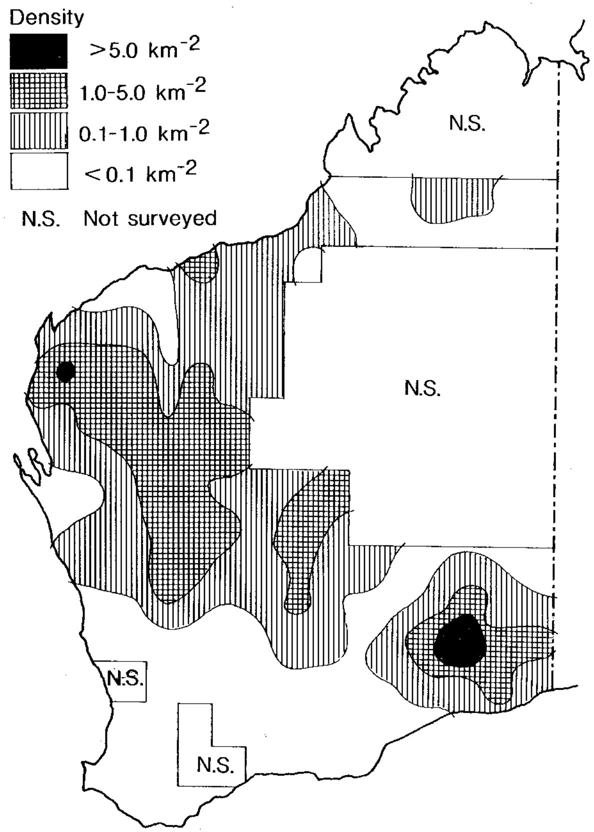

Fig. 5

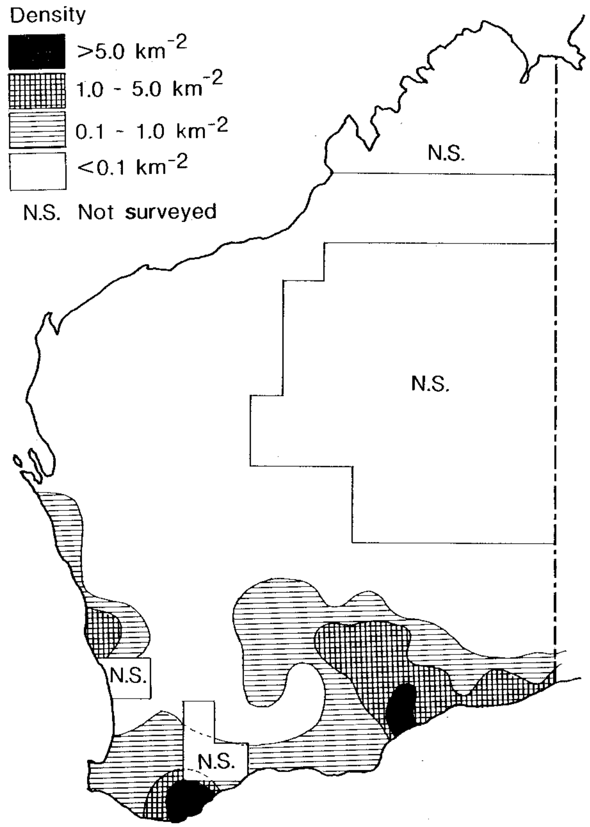

Fig. 4. Densities of red kangaroos in Western Australia.
Fig. 5. Densities of western grey kangaroos in Western Australia.

these variables are inversely related to the variable 'winter-summer dominance of rainfall'.

P.C. 2: a component largely reflecting rainfall. A positive correlation of this component with density indicates that high densities of grey kangaroos were in areas of high average annual rainfall and areas of high stock density.

P.C. 10: a component with a positive loading on reliability of rainfall. A positive correlation of the transformed kangaroo density with this component indicates that high densities of grey kangaroo occur in areas of reliable rainfall.

P.C. 8: a vegetation component with a high negative loading on 'mulga' and a positive loading on 'hummock grass'. Grey kangaroo density is positively correlated with this component, unlike red kangaroo density which shows the reverse relationship. The low densities of grey kangaroos in a few degree blocks containing hummock grass to the east of Kalgoorlie (Table 4), when compared with their virtual absence in mulga woodland, is the cause of the significant correlation with grey kangaroo density.

Table 4. Density of red and western grey kangaroos by habitat

Only degree blocks within the range of distribution of each species are considered. A density from a degree block was included for a habitat type only if that habitat type occurred on greater than 50% of the transect or transects flown (10% for national parks). Sources. Division of National Mapping (1976, 1979). n.a., not available

Habitat type	Red kangaroo		Western grey kangaroo	
	Mean density per sq. km	No. of degree blocks	Mean density per sq. km	No. of degree blocks
Chenopod shrubland	1·34	18	1·08	10
Mulga	1·21	30	0·43	1
Extensive pastoral (sheep)	0·84	51	0·55	18
Extensive pastoral (cattle)	0·84	24	0·26	1
National park and nature conservation reserve	0·76	13	0·81	16
Unoccupied	0·62	42	0·72	21
Hummock grassland	0·33	43	0·71	6
Wheat	0·11	6	0·22	10
Eucalypt woodland[A]	0·07	7	1·24	8
Mallee[A]	n.a.	–	1·07	10
Managed forests[B]	n.a.	–	0·86	5

[A] Excludes those areas substantially cleared for cereal cropping.
[B] Likely to be an underestimate due to poor conditions for flying and visibility.

The Gascoyne River Basin

Red kangaroos reached highest densities (>3 per square kilometre) in the north-west of the Gascoyne Basin (Fig. 6*a*; Mangaroon, Minnie Creek) and in restricted areas to the south of Mt Clere and south-east of Three Rivers. Low densities (<1 per square kilometre) occurred in the south-west (Gascoyne Junction) and in the central north (Waldburg and Teano Ranges).

The distribution of red kangaroos within the Basin was not clearly related to geological provinces (Fig. 6*b*). There was no significant difference in density of red kangaroos between provinces ($0 \cdot 10 < P < 0 \cdot 05$), although kangaroos occurred at a mean density two to three times greater in the Archean (2·9 per square kilometre) and Eastern Tributaries (2·1 per square kilometre) provinces than in the Permian (1·0 per square kilometre) and Eastern Uplands (0·5 per square kilometre). The Bangemall and Sanddune provinces had intermediate densities. Density contours, however, tended to cross geologic boundaries at right angles rather than to follow them.

The distribution of red kangaroos did appear to be related to pasture groups within the Basin. Aerial survey lines on which kangaroo density was above average differed in pasture composition from those along which kangaroo density was below average ($F_{8,468} = 3 \cdot 51$, $P < 0 \cdot 001$). The former had a significantly greater proportion of stony chenopod pasture and significantly less hill pasture. Stony chenopod pasture makes up 21% of the Gascoyne Basin and is the most productive of the major pasture groups within the Basin, having a stocking rate of 6·2–12·4 sheep per square kilometre (Wilcox and McKinnon 1972). This pasture type occurs as a tall shrubland of *Acacia victoriae*, *A. tetragonophylla* and *A. eremea* with an understorey predominately of *Maireana* spp. and a ground flora of halophytic annuals. Wilcox and McKinnon (1972) regarded much of this pasture type as being 'severely overused, degraded and eroded' as a result of overstocking. One exception to the pattern of high kangaroo densities in areas where stony chenopod pasture is a major habitat type was in that area surrounding Gascoyne Junction in the Permian geologic province. Hill pasture (also 21% of the Basin), by contrast, is among the least productive of pasture types, having a stocking rate of 2·3–4·6 sheep per square kilometre. It is much less degraded than the stony chenopod pasture, largely due to its inaccessibility to sheep. In this pasture type, *Acacia aneura*, *A. linophylla*, *A. tetragonophylla* and *A. eremea* form a low, sparse canopy over an understorey which includes small shrubs of *Cassia* and *Eromophila* spp. After effective rains annual provide sparse short-term grazing (Wilcox and McKinnon 1972).

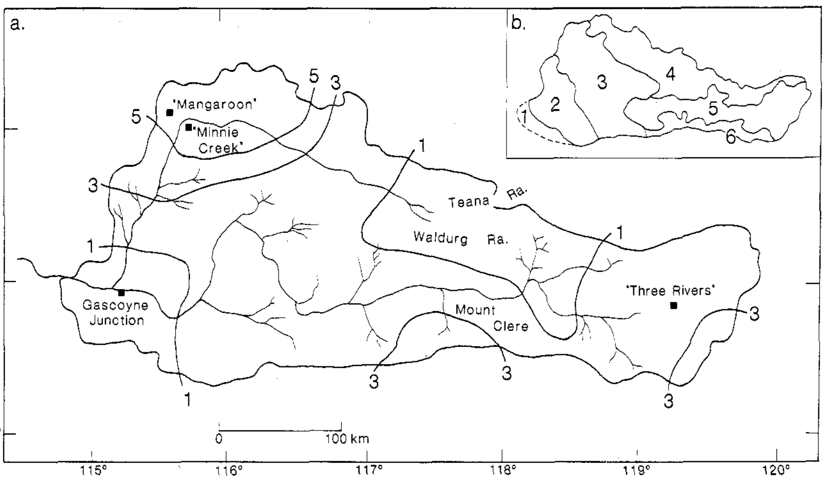

Fig. 6. (*a*) Densities of red kangaroos in the Gascoyne River Basin. (*b*) Geologic provinces: (1) Sanddune; (2) Permian; (3) Archean; (4) Bangemall; (5) Eastern tributary; (6) Eastern upland.

Other pasture groups (stony short grass–forbs, chenopod, wandarrie, mulga short grass–forbs, sanddune halophyte, sandplain and river) did not differ significantly between the high and low density survey lines.

Discussion

Red Kangaroos

Red kangaroos occurred at an average density of 0·87 per square kilometre in the pastoral zone of Western Australia in 1981, compared with densities of 2·8 per square kilometre in Queensland in 1980 (Caughley and Grigg 1982), 9·7 in New South Wales in 1980 (J. Caughley and Bayliss 1982) and 4·6 in South Australia in 1979 (Caughley and Grigg 1981). Low densities in Western Australia relative to the other three States may, in part, be attributable to the pattern of rainfall over the five years before the Western Australian survey. The years 1976 and 1977 were drought years ($<0 \cdot 65$ of annual average rainfall) over much of the range of red kangaroos; and in the central west (Kalbarri, Carnarvon, Wiluna) 1979 was also a drought year.

The lower density of red kangaroos in Western Australia compared with that in New South Wales and South Australia is mirrored by the corresponding sheep densities for the pastoral zones in each state (W.A., 3·6; S.A., 8·2; N.S.W., 15·3 per square kilometre [Division of National Mapping 1979 and Bureau of Agricultural Economics 1981]), suggesting a crude correspondence in habitat requirements for the two species. It is borne out by the analysis of the survey data, where the principal component having sheep grazing as the major contributing variable correlated strongly with red kangaroo density. The correspondence between extensive sheep grazing country and good red kangaroo habitat is suggested also by a zone, centred on Zanthus, where red kangaroos occur at an effective density of zero (<0·1 per square kilometre) between two high-density areas to the north-west and south-east, matching an equivalent break in the pastoral zone. This area, of mallee to the south-west of Zanthus, and of *Eucalyptus–Triodia* shrubland to the north, divides the pastoral zone in two.

In general, the western boundary of distribution of red kangaroos closely follows the western boundary of the pastoral zone. It approximates the 250-mm isohyet of rainfall, except immediately to the south of Kalbarri where red kangaroos extend into areas receiving 400 mm per annum. Marlow (1962) suggested the 500-mm isohyet as the high-rainfall limit of red kangaroo distribution; Newsome (1965*a*) the 375-mm isohyet. The general absence of red kangaroos in the >250-mm rainfall zone in Western Australia appears to reflect the unsuitability of cereal-growing areas, and eucalypt woodland (*E. salmonophloia*, *E. salubris* and others) and the open scrub of *Acacia* (mainly *A. resinomarginea*) and *Casuarina* (*C. acutivalvis* and *C. corniculata*) as habitat. Both the latter habitat types are characterized by an understorey of low sclerophyllous shrubs (Carnahan 1976) unlikely to be favoured by red kangaroos, which are primarily grazers (e.g. Griffiths and Barker 1966; Storr 1968; Bailey *et al.* 1971; Ellis *et al.* 1977).

While there is a close agreement between the western boundaries of red kangaroo distribution and the pastoral zone, there is no such agreement to the east. Red kangaroos reach medium densities on the Nullarbor Plain on chenopod shrubland well to the north of the pastoral zone. We do not know whether these densities are permanent or whether they are opportunistic following good localized rain immediately before the survey.

Reds were found to favour mulga woodlands (1·21 per square kilometre) but to occur at low densities in areas with a ground cover of hummock grass (0·33 per square kilometre) (P.C. 3 and Table 4). In New South Wales, red kangaroos show a similar preference for mulga woodlands. In an analysis of the environmental factors affecting the distribution and abundance of red kangaroos in New South Wales, Sinclair (1980) found 40% of the population concentrated in areas of mulga woodland (16% of the survey area). Red kangaroos do not favour hummock grassland (Newsome 1965*a*, 1965*b*; Storr 1968). One exception to that apparent rule was the occurrence of medium densities of red (5 per square kilometre) to the north-west of Carnarvon. The explanation for this may lie in these two degree blocks having received recent localized falls of rain, resulting in a flush of green growth not apparent in the surrounding areas. This, and the medium densities on the northern Nullarbor Plain reported above, suggest the possibility of opportunistic movements by red kangaroos over considerable distances to areas where feed is locally green and abundant. Brooker (1977) observed concentrations of reds on the Nullarbor Plain in areas where local storms had improved the food supply. Denny (1982) suggested movements of up to 30 km by marked kangaroos taking advantage of localized rainstorms in north-western New South Wales. While both long-distance movements by individuals (200 km, Bailey 1971; 300 km, Denny 1982) and medium-scale movements by populations (>34% of red kangaroos at Tero Creek, N.S.W., moved a distance of 24 km or greater, Bailey 1971) have been reported, long-distance movement as a drought-evasion strategy has yet to be demonstrated. Certainly, red kangaroos appear to be sedentary when feed and water are available locally (Frith and Calaby 1969, p. 91; Priddel, personal communication).

The two other principal components correlated strongly with red kangaroo density included a vegetation component (chenopod shrubland–tussock grassland) and a climatic component (annual average rainfall, reliability of rainfall) linked to density of domestic stock. The average density of red kangaroos in degree blocks containing greater than 50% chenopod shrubland was 1·34 per square kilometre, and that for tussock grassland 1·15 per square kilometre. Both include essentially the same areas of the Nullarbor Plain (low shrubland of chenopods with a lower stratum of tussock grasses). Greatest densities of red kangaroos were found in the more arid areas of the State (<250 mm rainfall), but some were in areas with >250 mm, particularly the northern summer-rainfall zone. Similarly, rainfall was less reliable in those degree blocks where red kangaroos were found than in degree blocks where western grey kangaroos occurred (50% compared to 62%). Sinclair (1980) found reds in New South Wales, also, to occur where rainfall was lowest and most erratic—in the north-west of that State. Density of domestic stock was correlated with both total rainfall and reliability of rainfall; hence this variable was linked with the climatic variables in the analysis.

The legal harvest of red kangaroos in Western Australia in 1981 was 133 000 (Prince, personal communication) representing 13·6% of the total population estimated here as 976 000.

Western Grey Kangaroos

Western grey kangaroos occurred through much of southern Western Australia from Shark Bay in the north, south and east to Eucla on the border with South Australia. Isolated animals were observed as far inland as Laverton and the Great Victoria Desert Nature Reserve (Fig. 1, K16, L16). Western grey kangaroos have been recorded on the northern fringes of the Nullarbor, mainly in *Acacia sowdenii* woodland (Fig. 1, L14) by W. D. L. Ride (personal communication in Kirsch and Poole 1972) and by Brooker (1977), and, after an exceptionally wet year, as far inland as Wiluna (Oliver 1966). Grey kangaroos were recorded at a mean density of 0·81 per square kilometre within their boundary of effective distribution in Western Australia (the 0·1-km^{-2} isopleth, Fig. 5) but including that area within the hook of density <0·01 per square kilometre largely corresponding to the wheat belt. Caughley and Grigg (1981) recorded an average density of western grey kangaroos of 1·22 per square kilometre in the pastoral zone of South Australia. However, if that area beyond their 0·1-km^{-2} isopleth of density is excluded, this density adjusts to 1·55 per square kilometre. The lower density in Western Australia is probably attributable to the presence of significant areas cleared for wheat-growing and large tracts of uncleared mallee within the range of *M. fuliginosus* in that State. Short and Grigg (1982) regarded both habitat types as suboptimal for kangaroos.

The analysis indicated that the most important variable affecting the distribution of western greys was climatic: seasonality of rainfall. *M. fuliginosus* is found in those areas of the state where winter rainfall (May–October) exceeds summer rainfall (November–April). Such rainfall results in a flush of pasture growth in late winter and spring. Nix (1976) plotted mean plant growth index values for each season. Significant plant growth occurs only at values above 0·1. The distribution of western greys in Western Australia is contained within or roughly corresponds to the 0·1 isopleth for winter and spring. Frequency of births in free-living western greys peaks between October and February (Brooker 1977; Bayliss 1980) with young first emerging from the pouch at an age of about 320 days (Poole 1975). If the major lactational stress on the mother is 9–12 months after birth—winter through to early summer—it coincides with the time of favourable plant growth, resulting presumably in a higher survival of young. Also, the greater availability of green feed at this time may ease the pouch young's transition from a total milk diet to one which includes herbage.

The second and third most important principal components in the analysis were also climatic. These components suggested the importance of a high and reliable rainfall to the occurrence of western greys. Stock density was included in the second component, it being strongly correlated with average annual rainfall. These components reflect the confinement of western greys to the south and west of the State.

In this study greys reached highest densities either where there was a mix of mallee, pastoral land and national park, or a mix of forest, mallee, intensive grazing, and national park. Such diverse areas are more likely to supply the grey kangaroo's requirements for shelter and grazing. This agrees with Scott-Kemmis (1979), who suggested that grey kangaroos in New South Wales never reached high densities in extensive tracts of any single vegetation, soil or landform but rather favoured a heterogeneity of land systems. The lowest grey densities within the south-west were in the wheatbelt immediately to the east of Perth (Figs 2, 5; Table 4), and west of Norseman where the vegetation is a mix of open *Casuarina* scrub and tall mallee shrubland. Much of the latter areas has infertile sandy soil and, at the time of survey, appeared to be devoid of surface water and ground cover.

Thirty-four thousand western grey kangaroos were legally harvested in Western Australia during 1981 (Prince, personal communication), representing 7·8% of the estimated population of 434 000.

The Gascoyne River Basin

Wilcox and McKinnon (1972) estimated that approximately 15% of the Gascoyne Basin was badly eroded, 52% somewhat less eroded and 33% in acceptable condition. They attributed this deterioration in range condition directly to overstocking, recommending a reduction in livestock numbers from 417 000 to 237 290 sheep units in an attempt to prevent further erosion and to assist in rangeland rehabilitation. Kangaroos have been harvested at a heavy rate within the basin in an attempt to assist rehabilitation. Forty-one thousand kangaroos were taken in 1977, but the harvest rate dropped to 14 500 in 1980 after a succession of drought years. With an estimated population of 120 000, red kangaroos contributed approximately 78 000 sheep units (1·5 kangaroos = 1 sheep) (McIntosh 1966; Griffiths and Barker 1966; Hume 1974) to the 165 000 sheep units (Wilcox, personal communication) run commercially in the Basin in 1981. Hence sheep and cattle contribute approximately two-thirds of the grazing pressure to this catchment and red kangaroos one-third.

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Appendix 1. Estimated Numbers and Densities of Red and Western Grey Kangaroos in Western Australia

See Fig. 1. for block numbers. Values are ± standard errors.

Block No.	Red kangaroos Numbers	Red kangaroos Density	Western grey kangaroos Numbers	Western grey kangaroos Density
A-9	1329	0·66	0	0
A-10	0	0	0	0
A-11	0	0	0	0
A-12	587	0·05	0	0
A-13	2934	0·25	0	0
A-14	1878	0·16	0	0
A-15	0	0	0	0
A-16	0	0	0	0
B-8	1048	0·46	0	0
B-9	0	0	0	0
B-10	3152	0·27	0	0
B-11	0	0	0	0
B-12	0	0	0	0
B-13	0	0	0	0
B-14	0	0	0	0
B-15	0	0	0	0
B-16	0	0	0	0
C-6	9243	1·17	0	0
C-7	10884	0·95	0	0
C-8	2782	0·24	0	0
C-9	0	0	0	0
D-3	0	0	0	0
D-4	1374	0·12	0	0
D-5	0	0	0	0
D-6	2877	0·25	0	0
D-7	690	0·06	0	0
D-8	1381	0·12	0	0
E-2	3709	0·39	0	0
E-3	9141	0·80	0	0
E-4	8455	0·74	0	0
E-5	0	0	0	0
E-6	2714 ± 2707	0·24 ± 0·24	0	0
E-7	1314 ± 708	0·12 ± 0·06	0	0
E-8	6284	0·55	0	0
F-1	892	0·24	0	0
F-2	56828	5·01	0	0
F-3	49449 ± 797	4·36 ± 0·07	0	0
F-4	44857 ± 12691	3·95 ± 1·12	0	0
F-5	4083	0·36	0	0
F-6	16349 ± 14527	1·44 ± 1·28	0	0
F-7	3989 ± 3983	0·35 ± 0·35	0	0
F-8	2269	0·20	0	0
G-1	7517	1·35	0	0
G-2	5877 ± 1200	0·52 ± 0·11	0	0
G-3	21461 ± 2401	1·91 ± 0·21	0	0
G-4	18515 ± 1402	1·64 ± 0·12	0	0
G-5	10445 ± 803	0·93 ± 0·07	0	0

G-6	22926 ± 1420	2·04 ± 0·13	0	0
G-7	11649 ± 529	1·03 ± 0·05	0	0
H-2	2003 ± 678	0·18 ± 0·04	0	0
H-3	10954 ± 4231	0·98 ± 0·38	0	0
H-4	16508 ± 1745	1·48 ± 0·16	0	0
H-5	33936 ± 2452	3·04 ± 0·22	0	0
H-6	13461 ± 1690	1·20 ± 0·15	0	0
H-7	23526 ± 2844	2·10 ± 0·25	0	0
I-2	*617 ± 615*	*0·06 ± 0·06*	*263 ± 262*	*0·03 ± 0·03*
I-3	908 ± 235	0·08 ± 0·02	0	0
I-4	3682 ± 1190	0·33 ± 0·11	0	0
I-5	20636 ± 10380	1·86 ± 0·94	0	0
I-6	17895 ± 2174	1·62 ± 0·20	0	0
I-7	5607 ± 249	0·51 ± 0·02	0	0
I-8	3342 ± 1887	0·30 ± 0·17	0	0
I-9	9108 ± 6851	0·82 ± 0·62	0	0
I-10	20583 ± 19215	1·86 ± 1·73	0	0
J-2	*310 ± 309*	*0·03 ± 0·03*	*10130 ± 9474*	*0·99 ± 0·93*
J-3	4132 ± 3449	0·38 ± 0·31	0	0
J-4	4565 ± 3217	0·42 ± 0·29	0	0
J-5	17678 ± 2770	1·61 ± 0·25	0	0
J-6	14579 ± 12720	1·33 ± 1·16	0	0
J-7	12624 ± 1979	1·14 ± 0·18	0	0
J-8	4073 ± 995	0·37 ± 0·10	0	0
J-9	22187 ± 13627	2·02 ± 1·38	0	0
J-10	5579 ± 246	0·51 ± 0·02	0	0
K-2	*2179*	0·37	3298	0·56
K-3	2609	0·24	0	0
K-4	4239	0·39	0	0
K-5	17596 ± 1153	1·62 ± 0·11	0	0
K-6	13435 ± 5630	1·24 ± 0·52	0	0
K-7	8929 ± 4396	0·82 ± 0·40	0	0
K-8	4402 ± 2926	0·41 ± 0·27	0	0
K-9	12105 ± 2926	1·11 ± 0·27	0	0
K-10	3301 ± 1317	0·30 ± 0·12	660 ± 659	0·06 ± 0·06
K-11	3695	0·34	0	0
K-12	761	0·07	0	0
K-13	761	0·07	0	0
K-14	4674	0·43	0	0
K-15	0	0	0	0
K-16	0	0	543	0·05
L-3	0	0	0	0
L-4	0	0	0	0
L-5	11627	1·08	0	0
L-6	4970 ± 3646	0·46 ± 0·34	0	0
L-7	0	0	654 ± 651	0·06 ± 0·06
L-8	2016 ± 560	0·19 ± 0·05	2524 ± 2515	0·23 ± 0·23
L-9	12536 ± 6335	1·16 ± 0·59	4614 ± 3367	0·43 ± 0·31
L-10	1635 ± 326	0·15 ± 0·03	0	0
L-11	0	0	2153	0·2
L-12	646	0·06	646	0·06
L-13	4414	0·41	0	0
L-14	20348	1·89	0	0
L-15	0	0	0	0
L-16	4845	0·45	1077	0·10
M-3*	6237	0·65	10076	1·05
M-4*	1173	0·11	2559	0·24
M-5	0	0	0	0
M-6	0	0	746	0·07
M-7	0	0	0	0
M-8	0	0	3599	0·34
M-9	3959 ± 3215	0·37 ± 0·30	2147 ± 2131	0·20 ± 0·20
M-10	2159 ± 714	0·20 ± 0·07	12236 ± 1429	1·15 ± 0·13
M-11	0	0	12956 ± 7859	1·22 ± 0·74

M-12	3845 ± 3816	0·36 ± 0·36	27376 ± 19314	2·57 ± 1·81
M-13	53040 ± 24370	4·97 ± 2·29	2755 ± 41	0·26 ± 0·00
M-14	76600 ± 33708	7·18 ± 3·16	0	0
M-15	31879 ± 20871	2·99 ± 1·96	0	0
M-16	14856 ± 1013	1·39 ± 0·10	0	0
N-5	0	0	0	0
N-6	0	0	0	0
N-7	0	0	0	0
N-8	0	0	2495 ± 2483	0·24 ± 0·24
N-9	356 ± 355	0·03 ± 0·03	356 ± 355	0·03 ± 0·03
N-10	0	0	1425 ± 1419	0·14 ± 0·13
N-11	713 ± 710	0·07 ± 0·07	19244 ± 14901	1·82 ± 1·41
N-12	1038 ± 1034	0·10 ± 0·10	48108 ± 9992	4·56 ± 0·95
N-13	4030 ± 669	0·38 ± 0·06	23173 ± 2340	2·19 ± 0·22
N-14	4774 ± 72	0·45 ± 0·01	5884 ± 5857	0·56 ± 0·55
N-15	14105 ± 14042	1·34 ± 1·33	31087 ± 26937	2·94 ± 2·55
N-16	2767 ± 2454	0·30 ± 0·26	2749 ± 1247	0·29 ± 0·13
O-4	0	0	626	0·06
O-5	0	0	4174	0·40
O-7	0	0	0	0
O-8	0	0	0	0
O-9	0	0	0	0
O-10	0	0	1461	0·14
O-11	0	0	4487	0·43
O-12	0	0	72739	7·36
O-13	0	0	3171	0·57
P-3	0	0	1639 ± 1539	0·25 ± 0·24
P-4	0	0	3094	0·30
P-5	0	0	4847	0·47
P-8	0	0	4130	0·43
P-9	0	0	7888	0·88
P-10	0	0	6627	0·69
P-11	0	0	1311	0·15
Q-3	0	0	13866	3·08
Q-4	0	0	6062	0·62
Q-5	0	0	19968	1·96
Q-6	0	0	43995	5·66
Total	980629		435618	

*Ground surveys indicate that no red kangaroos are present in blocks M-3 and M-4 (R. I. T. Prince and K. L. Miller, personal communication). Thus some kangaroos may have been misidentified from the air.

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