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KANGAROOS AND CLIMATE: AN ANALYSIS OF DISTRIBUTION

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SUMMARY

(1) The distributions of three partially sympatric kangaroo species, *Macropus giganteus* Shaw, *M. fuliginosus* (Desmarest) and *M. rufus* (Desmarest), were analysed to determine their climatic characteristics.

(2) *M. giganteus* occupies areas only where rainfall either has little seasonal trend or where rainfall in summer exceeds winter rainfall.

(3) *M. fuliginosus* is found in areas of uniform or winter rainfall.

(4) Seasonality of rainfall has little influence on the distribution of *M. rufus*. Instead, its distribution reflects interaction between mean annual precipitation and mean annual temperature.

(5) The extent of sympatry and allopatry appears to be determined by the independent reaction of each species to specific and differing climatic stimuli rather than by biological interaction between species.

INTRODUCTION

The eastern grey kangaroo *Macropus giganteus*, the western grey (=southern grey) kangaroo *M. fuliginosus* and the red kangaroo *M. rufus* are three of the largest species of the Macropodoidea (kangaroos, wallaroos, wallabies and rat kangaroos). The range of each overlaps to some extent with the other two, but as a generalization *M. giganteus* lives in the east of Australia, *M. fuliginosus* occurs across the south of the continent excluding Tasmania, and *M. rufus* lives in the arid and semi-arid zones that occupy most of the interior but reach the coast in Western Australia (Fig. 1).

The purposes of this study were to describe the range of climate experienced by each species, to determine the components of the climate that indexed the distributions most economically, to identify areas within the climatic tolerance of each species that are not currently occupied, and to explore the usefulness of these species in interpreting the palaeoclimate of fossil faunas. Finally, we sought to develop a methodology that would transfer easily to the study of the distribution of other species in other areas.

In restricting this analysis of distribution to characteristics of the climate we do not imply that precipitation and temperature, of themselves, determine whether a particular species inhabits a particular area. We assume that the distributions are related much more directly and causally to such attributes as land use, forage production, water supply and habitat. Nonetheless, we expect climate to provide a rough index of those attributes, the climatic variables being correlated with factors that directly influence an individual's

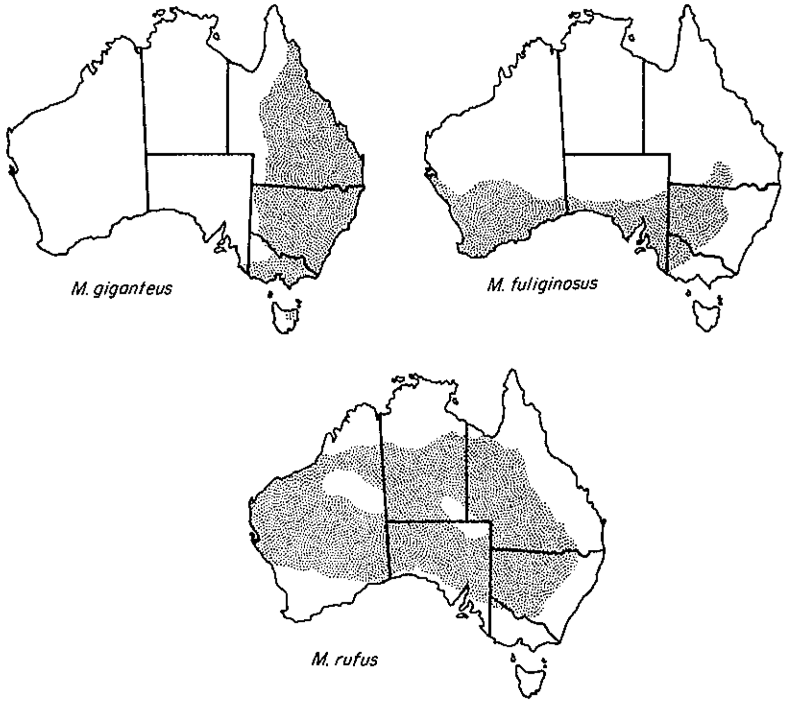

FIG. 1. The distributions of three species of kangaroos. From Caughley, Grigg & Short (1983).

probability of surviving and reproducing. Our aim here is to explore the extent to which distributions can be characterized by climate alone, the residual anomalies being identified for further study.

METHODS

Surveys

Distributions were mapped largely by aerial survey between 1980 and 1982. The planes were flown at 75 m above the ground on east–west transects. Two observers, one on either side of the plane, each scanned a strip 200 m wide. The unit of resolution was the degree block (1° of latitude by 1° of longitude, about 12 000 km^2), and presence or absence was assessed on transects running from one side of it to the other. Most degree blocks were sampled by two transects, others by four, and some areas of very arid desert were allocated only a single transect per block. Details of the individual surveys were provided by Caughley, Grigg & Short (1983) and in publications referred to therein. *M. giganteus* and *M. fuliginosus* cannot be differentiated with confidence from the air and so their respective distributions within their region of overlap were mapped from the ground (Caughley *et al.* 1984). The distribution of *M. giganteus* in Tasmania and in the eastern highlands of Australia was taken from Strahan (1983). By these various methods each species was scored as present or absent on each of the 687 degree blocks into which Australia can be divided.

Climatic variables

Continent-wide surfaces of monthly mean minimum and mean maximum temperature, and nineteen regional surfaces of monthly precipitation, were constructed from Laplacian smoothing spline functions fitted to data from meteorological stations (M. F. Hutchinson & H. Nix, unpublished). These provided estimates of climate as a function of latitude, longitude and elevation for any point on the land surface.

The climatic variables derived from the surfaces were used in turn to derive twelve selected variables for each degree block, characterizing annual, seasonal and extreme components of the climatic environment: (1) annual mean temperature; (2) minimum temperature of the coldest month; (3) maximum temperature of the hottest month; (4) annual temperature range (3–2); (5) mean temperature of the wettest quarter (3 months); (6) mean temperature of the driest quarter; (7) annual mean precipitation; (8) precipitation of the wettest month; (9) precipitation of the driest month; (10) annual precipitation range (8–9); (11) precipitation of the wettest quarter; (12) precipitation of the driest quarter. 'Quarter' refers to any three consecutive months, not to spring, summer, autumn and winter. The value of a climatic variable assigned to a degree block was a mean of that variable sampled at 121 points within the block.

Analysis

The 687 values of each climatic variable (from the 687 degree blocks) were sorted to find the highest and lowest values of each. That range was divided into fifteen equal intervals and the frequency of blocks containing a particular species was plotted against those fifteen intervals for each variable. This was repeated for each species. Means and standard deviations were calculated for each frequency distribution to indicate central tendency and spread of each species along each of the twelve climatic gradients.

Discriminant functions were calculated to discriminate between the climates characterizing the distributions of the three species. Only the 482 degree blocks containing at least one species were used for this purpose. Blocks were divided into seven groups: those with *M. giganteus* only, those with *M. fuliginosus* only and those with *M. rufus* only, the three combinations of two co-occurring species, and the blocks containing all three.

TABLE 1. Mean and spread of the climate of degree blocks on which each species of kangaroo occurs. Precipitation is in mm, temperature in °C

	Species of *Macropus*								
	M. giganteus			*M. fuliginosus*			*M. rufus*		
Climatic variable	Mean	S.D.	C.V.%	Mean	S.D.	C.V.%	Mean	S.D.	C.V.%
(1) Mean annual temperature	18·9	3·8	20	17·9	1·7	10	21·6	2·8	13
(2) Min. temp. coldest month	4·5	3·1	69	4·8	1·1	24	6·3	2·6	42
(3) Max. temp. hottest month	33·0	3·9	12	33·0	2·4	7	36·6	2·4	7
(4) Annual temp. range (3–2)	28·0	3·4	12	28·0	2·8	10	30·1	2·3	8
(5) Mean temp. wettest quarter	22·4	7·2	32	17·0	7·0	41	26·0	6·0	23
(6) Mean temp. driest quarter	15·8	3·9	24	19·1	4·1	21	18·1	4·0	22
(7) Mean annual precip.	599·7	333·1	56	303·4	169·8	56	277·1	138·1	50
(8) Precip. wettest month	90·0	63·3	70	42·9	34·6	81	49·9	34·6	69
(9) Precip. driest month	25·6	16·7	65	14·0	6·1	44	9·0	7·3	81
(10) Annual precip. range (8–9)	65·3	61·0	93	30·8	32·4	105	41·8	35·1	84
(11) Precip. wettest quarter	237·7	150·5	63	115·3	90·3	78	130·7	87·9	67
(12) Precip. driest quarter	86·6	54·2	62	47·5	22·3	47	32·8	22·4	68

RESULTS

Table 1 gives the mean and spread of the climate of blocks containing each species. For example, the first row of the table shows that blocks containing *M. rufus* have on average a higher mean annual temperature than do those containing *M. giganteus*, and that those containing the southern species *M. fuliginosus* have the lowest. However, *M. giganteus* copes with a greater range of mean annual temperatures (S.D. = 3·8 °C, C.V.% = 20) than do the other two species, reflecting its greater latitudinal range (Fig. 1).

Figs 2 and 3 provide four examples comparing the frequency distributions of occurrence of the species along climatic gradients. The extremes of each scale mark the limits of the Australian climate on a degree-block basis. Fig. 2 features annual averages—mean annual precipitation and mean annual temperature—whereas Fig. 3 features components of seasonality: precipitation of the wettest quarter and mean temperature of the wettest quarter.

The discriminant analysis indicated that the blocks containing each species only, and combinations of species, could generally be discriminated into the seven combinations by use of six of the climatic variables: mean annual temperature, minimum temperature of the coldest month, maximum temperature of the hottest month, mean temperature of the driest quarter, mean annual precipitation, and precipitation of the driest quarter. Sixty-six per cent of blocks were correctly identified within the seven categories by use of two discriminant function axes.

Fig. 4 summarizes that analysis by showing the discriminant space occupied by each of the species, irrespective of whether it occurred alone or in combination with one or both of

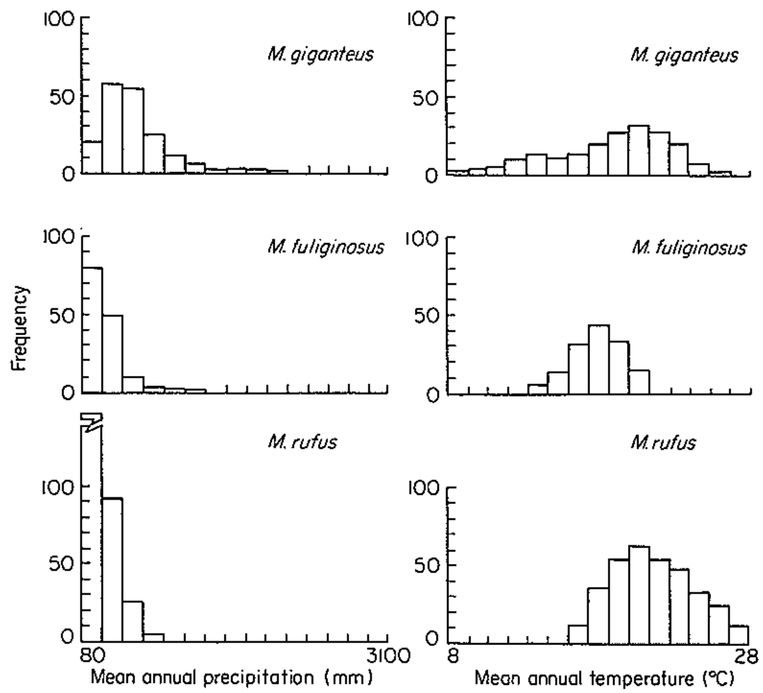

FIG. 2. Frequency of degree blocks containing each species along gradients of mean annual precipitation and mean annual temperature.

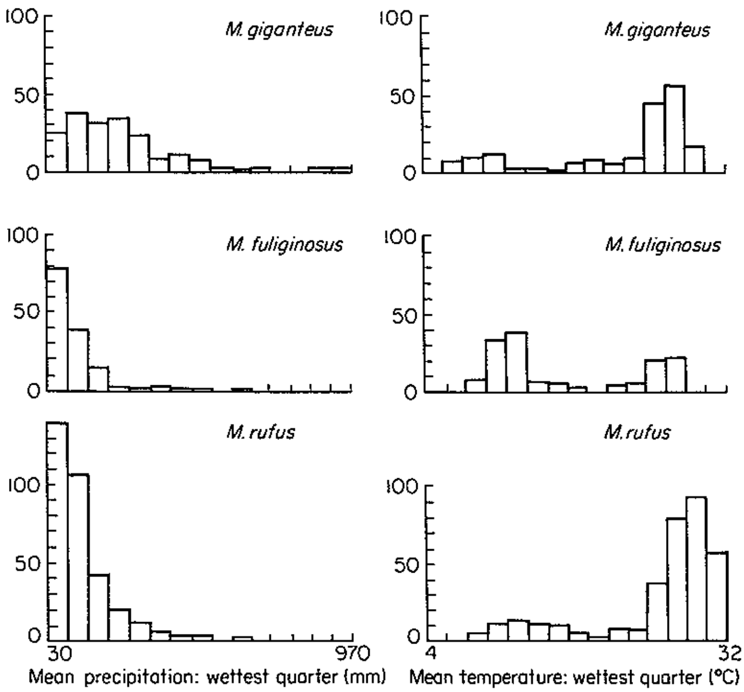

FIG. 3. Frequency of degree blocks containing each species along gradients of mean precipitation of the wettest quarter and mean temperature of the wettest quarter.

the others. The first discriminant function split the blocks largely according to whether they were cold and wet (left) or hot and dry (right). Along the second axis the blocks were split largely according to seasonal polarity, whether rain fell mainly in winter (lower), at a

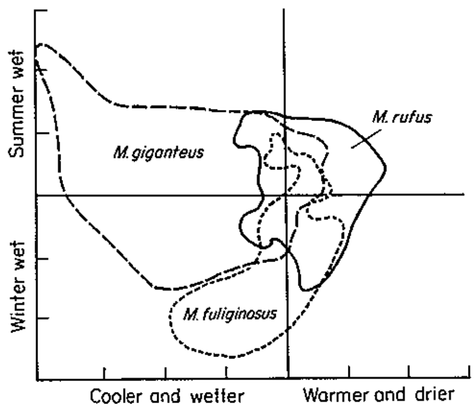

FIG. 4. Distributions of the three species of kangaroos within the space defined by two discriminant functions. The first (x-axis) featured annual mean temperature, maximum temperature of the hottest month, minimum temperature of the coldest month and mean annual precipitation. The second (y-axis) featured annual mean temperature, precipitation of the driest quarter and temperature of the driest quarter.

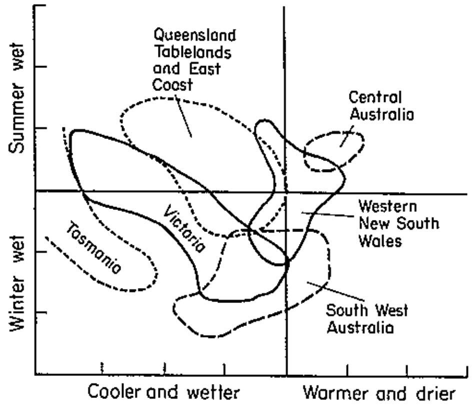

FIG. 5. The position of the climate of selected regions of Australia within the discriminant function axes of Fig. 4.

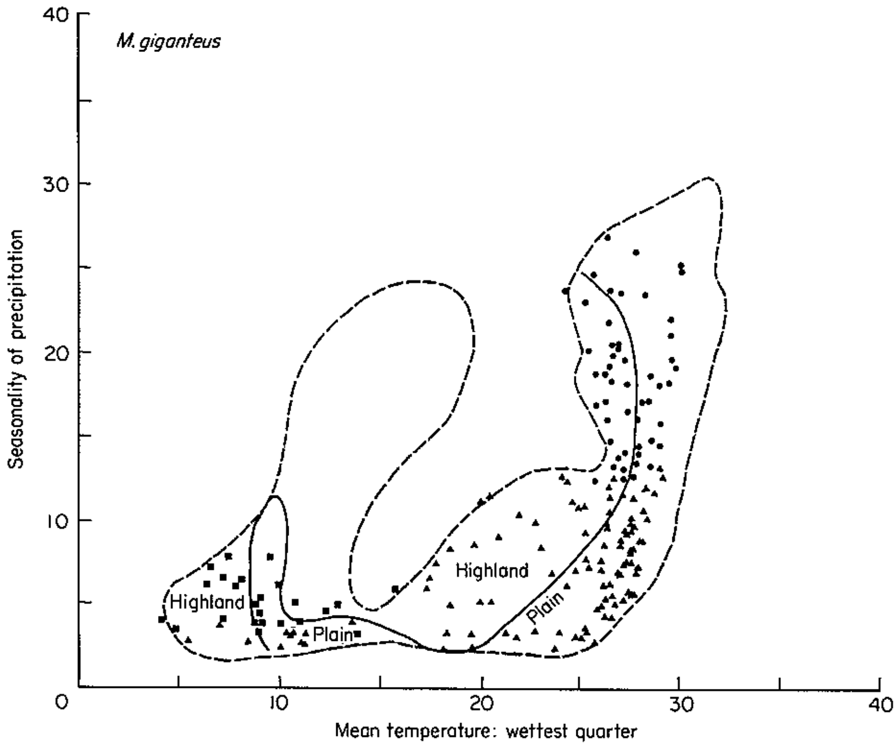

FIG. 6. The climate of degree blocks containing *M. giganteus* expressed in terms of seasonality of precipitation (difference between wettest and driest months as a proportion of mean annual precipitation) and of mean temperature of the wettest quarter. Symbols indicate those occupied blocks north of latitude 25 °S (●), those between 25 °S and 35 °S (▲) and those south of 35 °S (■). The dashed outline encloses the climate of all degree blocks in Australia and the continuous line separates the eastern coastal highlands from the inland plains.

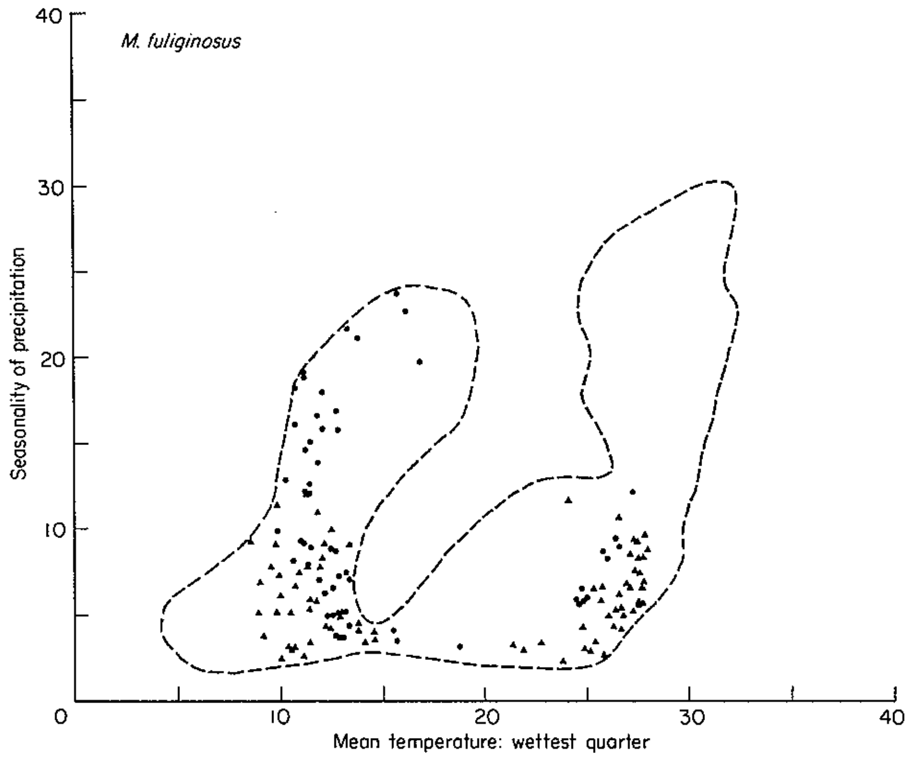

FIG. 7. The climate of degree blocks containing *M. fuliginosus* expressed in terms of seasonality of precipitation and of mean temperature of the wettest quarter. Symbols indicate those occupied blocks east (▲) and west (●) of the apex of the Great Australian Bight. The dashed outline encloses the climate of all degree blocks in Australia.

relatively constant rate throughout the year (middle), or predominantly in summer (upper). The three species have a common range in the climatic zone characterized by low seasonality of rainfall and a semi-arid mean annual precipitation and temperature. Fig. 5 shows the climate of selected geographic regions of Australia within the space defined by the two discriminant function axes.

The effect of seasonality on distribution was investigated further by calculating the difference between precipitation of the wettest and driest months as a percentage of mean annual precipitation and graphing that against mean temperature of the wettest quarter. The y-axis is thus an index of seasonality of rainfall. Separation of those indices along the x-axis splits them into two discrete columns, one containing blocks where rain falls predominantly in summer and the other containing blocks where the rain falls predominantly in winter. The columns rise from a base value of about 10, below which rainfall is relatively constant throughout the year, the difference between precipitation of the wettest and driest months being $\leq 10\%$ of mean annual precipitation.

Fig. 6 shows where Australia falls within this characterization of climate, and the range of *M. giganteus* within those limits. The points are separated according to whether each block is on the inland plains or in the coastal highlands, and identified to latitude by symbol. *M. giganteus* occurs only in areas of uniform rainfall or where summer rainfall predominates. Fig. 7 is the equivalent plot for *M. fuliginosus*, the symbols differentiating the western half of its range (west of the apex of the Great Australian Bight at longitude 130° East) from the eastern half. In contrast to *M. giganteus* it occurs only in the zone of predominantly winter or uniform rainfall.

Fig. 8 indicates that the distribution of *M. rufus* is unrelated to seasonality of rainfall, the species occurring in areas of uniform rainfall and in those dominated by either summer or winter rainfall. In Fig. 9, therefore, its distribution is displayed simply as a function of mean annual precipitation and of mean annual temperature. The Australian climate does not test the red kangaroo's tolerance of aridity, there being no arid boundary to its distribution (Fig. 9). It occupies the driest blocks on the continent. The humid boundary, which determines how close the distribution approaches the coast, is an interactive function of mean annual precipitation and mean annual temperature. Only 400 mm mean annual precipitation is tolerated where mean annual temperature is 16 °C, but that rises to 700 mm at 27 °C.

DISCUSSION

The analyses of this paper are restricted to presence or absence of kangaroos in relation to climatic variables. More intricate analyses are possible, incorporating density indices of

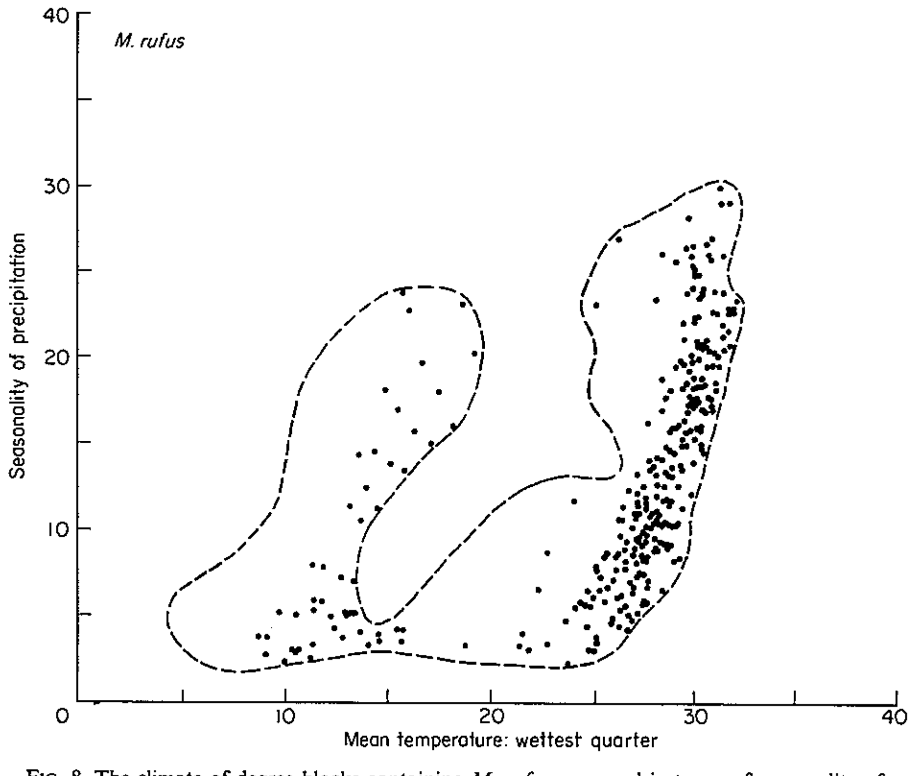

FIG. 8. The climate of degree blocks containing *M. rufus* expressed in terms of seasonality of precipitation and of mean temperature of the wettest quarter. The dashed outline encloses the climate of all degree blocks in Australia.

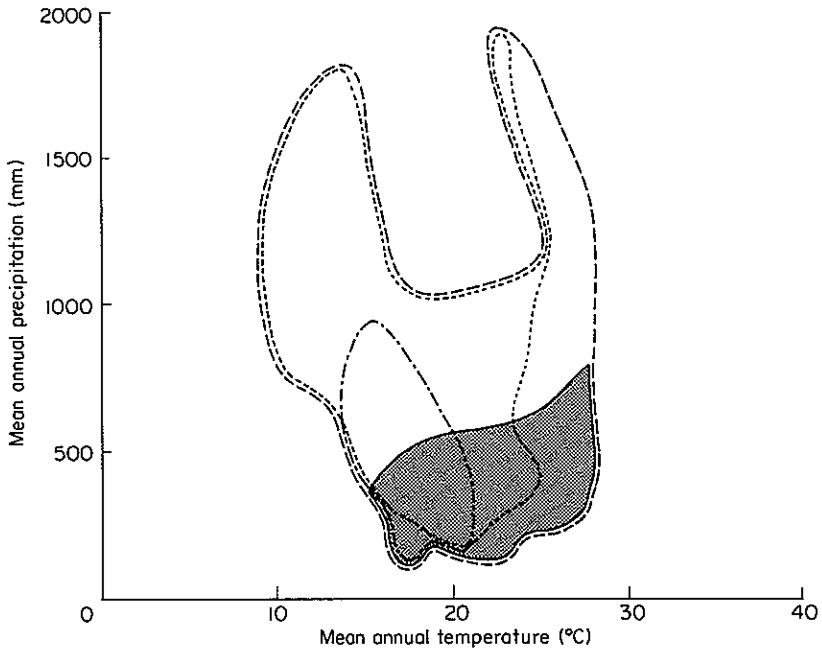

FIG. 9. The climate of degree blocks containing *M. rufus* (stippled) in terms of mean annual temperature and mean annual precipitation within the climatic envelope for Australia as a whole (– – –). Climatic envelopes for *M. giganteus* (- - -) and *M. fuliginosus* (– · – · –) are provided for comparison.

kangaroos and components of their habitat—see for example the study by Short *et al.* (1983) on kangaroos in Western Australia—but for the purposes of this paper we seek the major climatic variables that influence the distributions of the three species across the continent.

The distributions of the two grey kangaroos, *M. giganteus* and *M. fuliginosus*, are associated closely with seasonality of rainfall. Both occupy areas where the difference between precipitation of the wettest and driest months is less than about 10% of annual precipitation. But where the rainfall is more seasonal *M. giganteus* occurs only in areas where summer rainfall predominates, whereas *M. fuliginosus* occurs only where winter rainfall predominates. The distribution of the red kangaroo *M. rufus* is not related to seasonality of rainfall. Instead, the climate of its distribution can be defined most economically in terms of mean annual precipitation and mean annual temperature.

The distributions reported here appear to be relatively stable. Only *M. giganteus* appears to have expanded its range since European colonization, apparently extending further inland in response to an increase of watering points provided by the sheep grazing industry (Caughley *et al.* 1984). There is no evidence that the range of *M. fuliginosus* has changed over the last 100 years. Similarly for *M. rufus*. Archer, Flannery & Grigg (1985) suggested that its range last century extended to the east coast, but John Calaby (personal communication) informs us that the only evidence for the massive contraction of range that such a nineteenth century distribution would imply is a single skin of doubtful provenance purportedly from Port Macquarie that almost certainly was transported to the coast from the inland plains.

These three species have been used as palaeoclimatic indicators, and although they may still be useful in that regard their overlap of distribution and hence of climatic tolerance has been underestimated previously. Horton (1984), in advocating *M. rufus* as an indicator of aridity, thought that it overlapped with 'grey kangaroos' only 'in a small area of southern Queensland'. In fact, the overlap between *M. rufus* and *M. giganteus* is about 880 000 km^2, that between *M. rufus* and *M. fuliginosus* about 810 000 km^2, that between *M. giganteus* and *M. fuliginosus* about 470 000 km^2, and about 420 000 km^2 is common to the ranges of all three species. Horton gave 250 mm as the isocline of mean annual rainfall circumscribing the range of *M. rufus* but, as Fig. 8 demonstrates, the humid boundary of distribution lies between 400 mm and 700 mm according to the level of mean annual temperature.

Flannery & Gott (1984) reported a fossil deposit dated insecurely as 20 000 years B.P. in southern Victoria. Three of the mammals therein—*M. rufus*, *M. giganteus* and *M. agilis*—are extant and therefore provide clues on the palaeoclimate. The authors assumed that the Pleistocene form of *M. agilis* must have had environmental requirements differing from its modern descendents because these are today restricted to the tropics. Neither was the presence of *M. giganteus* used as a climatic indicator because of 'a wide tolerance of habitat.' They deduced from the presence of *M. rufus* that the climate at time of deposition was more arid than now. However, the co-occurrence of those three species need not be anomalous. They jointly indicate a rainfall not necessarily much lower than the present mean annual of 718 mm. The major difference indicated between the palaeoclimate and the modern climate is not so much aridity as summer dominance of the rainfall.

Fig. 7 shows that *M. fuliginosus* occupies blocks in both the east and the west of Australia. In regions where seasonality of rainfall is low it tolerates climates in the east that are both hotter and colder than those of the blocks that it occupies in the west. The west of Australia has no areas of comparable climate. This species appears to have occupied all areas in which the climate is suitable.

In contrast, *M. giganteus* does not occur in the west of Australia even though there are eighteen blocks there that fall within the range of its climatic tolerance in the east. We interpret this as the effect of the arid Nullarbor Plain acting as a barrier to dispersal now and for some time in the past. The absence of *M. giganteus* in the west cannot reflect competitive exclusion by *M. fuliginosus* because the two species co-exist over 470 000 km^2 in the east. The climate of the Nullarbor Plain falls within the tolerance of *M. fuliginosus* and thus provides no barrier to east–west dispersal of that species. Similarly, dispersal of *M. rufus* is not constrained by climatic barriers, there being few areas appearing to have a suitable climate that are not in fact occupied.

This study allows some understanding of why a species inhabits a particular area and, almost as important, why it does not inhabit another. For example, none of the three species lives in the north of Australia above latitude 14° S but, we suggest, for different reasons: that it is too hot for *M. giganteus*, too wet for *M. rufus*, and both too hot in summer and too dry in winter for *M. fuliginosus*.

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