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THE EDGE OF THE RANGE

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SUMMARY

(1) We suggest a theoretical framework for considering limits to relatively stable distributions and illustrate some of the points raised with information on the distribution of two species of kangaroos.

(2) If an attribute such as density or condition is low at the periphery but rises progressively towards the core of the distribution, its trend is described as a 'ramp'. If the level of the attribute differs little between the periphery and the core of the distribution its trend forms a 'step' at the range boundary.

(3) Should density form a ramp inwards from the boundary whereas the mean well-being of the animals (e.g. body condition, growth, weight, recruitment) forms a step, the factor limiting distribution is likely to be a resource that is utilized consumptively or preemptively.

(4) Should both density and well-being form a ramp, the implicated factor is a component of climate, an unmodifiable resource, or a facultative predator, parasite or pathogen.

(5) Should both density and well-being step at the range boundary, the factor controlling the position of the boundary is likely to be the substrate (e.g. a rock type).

(6) Two kangaroo populations were sampled at the core and periphery of their respective ranges. The southern (= 'western') grey kangaroo *Macropus fuliginosus* (Desmarest) exhibited a ramp of both density and well-being which, in combination with ecological information on this species, suggested that the edge of the range was positioned by a component of climate perhaps interacting with an unmodifiable resource.

(7) The eastern grey kangaroo *Macropus giganteus* Shaw exhibited a ramp of density but a step of well-being, implicating a renewable resource as the factor determining the inland boundary of distribution.

(8) Density and distribution are likely to be different aspects of the same thing except where the limiting factor or combination of factors is or includes a renewable resource consumed by the animals.

INTRODUCTION

Krebs (1978) considered that 'the simplest ecological question one can ask is simply: Why are organisms of a particular species present in some places and absent in others?' This paper is limited to that class of distributions robust to variation in year-to-year weather, the distribution being relatively stable over several generations. We offer a theoretical framework for considering limits to such distributions and discuss some of the points raised in the context of the distributions of two species of kangaroos.

Suppose a hypothetical species is incapable of maintaining a population in conditions that are either very hot or very cold, or in conditions that are very dry or very moist.

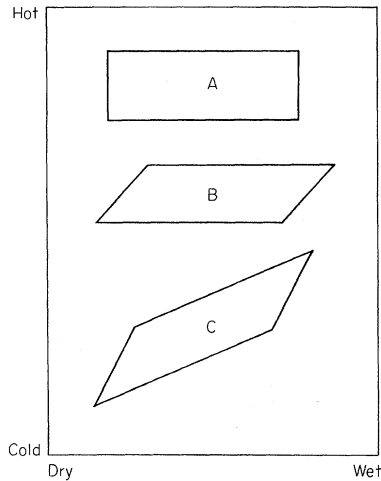


FIG. 1. Three hypothetical envelopes of the adaptability of a species to temperature and moisture: A, the two factors limit independently; B, the effect of one factor is influenced by the level of the other; C, the effect of each factor varies according to the level of the other.

Figure 1 is a diagram of its range of tolerance to those environmental factors, temperature and relative humidity, as they might be elucidated experimentally. In the first example (Fig. 1A) each factor acts independently upon the population's dynamics. The second example (Fig. 1B) illustrates the two factors operating in concert but asymmetrically, the envelope of tolerance being defined as before by both temperature and humidity but in an interactive manner. Although tolerance is circumscribed absolutely by an upper and lower limiting temperature it is demarcated within those limiting values by humidity whose effect varies with temperature. High levels of humidity are tolerated only when temperature is high, and low levels only under cold conditions. Figure 1C represents the effect of two symmetrically interacting factors. The population's tolerance of temperature varies with the level of humidity, and tolerance of humidity varies with temperature.

A range of tolerance to one or more factors, as established by experiment, does not transform directly into a geographic distribution. Bartholomew's (1958) dictum that 'the distribution of a species will be controlled by that environmental factor for which the organism has the narrowest range of adaptability or control', is something of a simplification. First, the effect of one factor may be influenced by the level of another. Secondly, since environmental factors are measured in units that differ in kind, in no absolute sense can the range of adaptability on one factor be declared broader or narrower than that on another. And thirdly, distribution is not simply a function of an organism's physiology. Whether distribution is determined by one or several factors depends critically on the geographic dispersion of the levels of each factor. Is the interval of adaptability on one factor nested geographically within the interval of adaptability on another, or do the two intervals overlap? As an example, suppose a hypothetical species is shown by experiment to be incapable of maintaining populations when temperature falls outside the interval 1–10 °C, or when relative humidity lies outside the interval 20–80%. Is distribution controlled by temperature or by humidity? Given the limits of tolerance stated above, the distribution of the species may be limited entirely by temperature (Fig. 2a), or entirely by humidity (Fig. 2b), or in some places by temperature and other places by

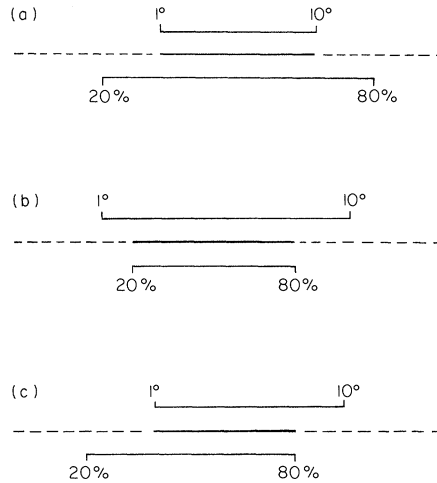


FIG. 2. A hypothetical species cannot persist where temperature is outside the range 1–10 °C or where relative humidity falls outside the range 20–80%. Which factor defines the range of the species is determined by whether, in the field, the range of adaptability on temperature lies within that defined by humidity (a), or the reverse (b), or whether they overlap such that the position of the range boundary is in some places determined by temperature and in others by humidity (c).

humidity (Fig. 2c). Thus, an explanation of the distributional limits of a species must be rooted in the geographic facts of environment as much as in the physiological facts of adaptability. The laboratory may teach us which combinations of environmental variables are within the range of adaptation, but an environmental map is needed to inform us which of these combinations are available in the field. The distribution of a species will reflect both.

A FRAMEWORK

We begin from the notion that the edge of the range marks the point at which, on average, an individual's contribution to the next generation is less than unity.

Environmental requirements

An individual's fitness will be affected by shortages of some things (e.g. heat, food, water or a place to nest) and by too much of other things (e.g. heat, water, disease or predators). The environmental factors that affect an individual's fitness (in this context its chances of surviving and reproducing) have been classified in many ways. The following informal scheme has no intrinsic merit but lends itself to a discussion on limits to distribution.

(a) A beneficial or deleterious environmental factor whose level cannot be modified by the animals: (i) a component of climate *per se* (e.g. a gradient of mean annual temperature); (ii) a specific substrate (e.g. a particular rock type that is present or absent); (iii) a source of food or water whose absolute amount cannot be reduced by the activities of the organisms but which, nonetheless, may influence distribution by being distributed heterogeneously or sparsely. As an example of the effect of heterogeneity: although the water requirement of all African elephants *Loxodonta africana* Blumenbach would be

served by a single river, the distribution of elephants is limited in many areas by a shortage of water. And as an example of the effect of sparseness: tsetse fly *Glossina* spp. must have access to blood, most of which is supplied by wild ungulates. The probability of a fly surviving and reproducing is a function of the density of those ungulates, but that fly has no effect on that density. Nor does extracting a meal from one of those animals affect the amount available to the next fly to find it. The flies face what Andrewartha & Birch (1984) call an 'extrinsic shortage' because it is not of their making. In fact, the relationship is not that simple. Tsetse flies may indirectly affect the chance of an individual obtaining a meal because the irritability of the host increases with the density of the fly (Vale 1977). A similar effect has been postulated for triatomine bugs feeding from people (Schofield 1982).

(b) A beneficial environmental factor whose use by one animal reduces the amount available to others. (i) A resource used consumptively. All individuals have access to the resource and each individual's activities influences the level of the resource available to it and to other individuals. Sinclair's (1977) account of the interaction of grass and buffalo *Syncerus caffer* Sparrman and Houston's (1982) account of the ecology of elk *Cervus elaphus* Linnaeus describe such a relationship. In the parlance of Andrewartha & Birch (1984), a shortage of this resource, caused as it is by the animals themselves, is an 'intrinsic shortage'. (ii) A resource used pre-emptively. Individuals are either winners or losers. An example is provided by nesting holes used by parrots.

(c) A deleterious environmental factor whose effect on an animal may vary with the density of its population: (i) facultative parasite, predator or pathogen; (ii) obligate predator, parasite or pathogen.

Characteristics of the population relative to the position of the range boundary

We nominate three characteristics of the population as providing clues to which environmental factors control the position of the range boundary. The first characteristic is the form of the density profile extending from the boundary into the distribution. It may form either a ramp or a step.

The second characteristic is the trend in mean well-being of individuals from the periphery to the core. 'Well-being' may be indexed by such as body condition, fecundity rate, mortality rate and rate of increase.

The third characteristic is the trend in intrinsic rate of increase (r_m), a statistic that may be defined, paraphrasing Andrewartha & Birch (1954), as the rate of increase of a population with a stable age distribution when no resource is limiting. It is difficult to measure in the field and is included here mainly for conceptual purposes, it being the only measure of a population's demographic vigour that, by definition being independent of density, is not confounded by the effects of pre-emptive and consumptive competition.

Table 1 shows the trends to be expected in these population characteristics as one moves into the distribution from its edge and where the position of that edge is controlled by one factor only. A gradient of climatic favourability (1a), for example, will be paralleled by a gradient in r_m because r_m indexes environmental favourability as the population's ability to increase in the absence of competition. Likewise the density of the animals is likely to parallel that trend, because the density of patches with favourable microclimate will increase with rising overall climatic favourability. We would expect average well-being also to vary in parallel.

A substrate (1b of Table 1) needed by the species provides a factor with only two levels: presence or absence. A specific rock-type provides our example but 'substrate' is used in a

TABLE 1. The likely trend in population characteristics from the periphery to the core of a species' distribution where the range boundary is controlled by a single factor

Factor affecting range boundary	r_m profile	Density profile	'Well-being' profile
Climate	1a ramp	ramp	ramp
'Substrate'	1b step	step	step
Resource unmodifiable	1c ramp	ramp	ramp
Resource used:			
consumptively	2a step	ramp	step
pre-emptively	2b step	ramp	step
Facultative ppp*	3a ramp	ramp	ramp
Obligate ppp*	3b —	—	—

* Predator, parasite or pathogen.

more general sense. The rock warbler *Origma solitaria* (Lewin) is confined to the Hawkesbury sandstone formation around Sydney, Australia (Slater, Slater & Slater 1986). Its distribution is clearly limited by the distribution of that formation. All species of wild sheep, goats and goat-antelopes of the subfamily Caprinae (*Ovis*, *Capra*, *Hemitragus*, *Psuedois*, *Rupicapra*, *Nemorhaedus*, *Oreamnos*, *Ammotragus*, *Capricornis*) live only in mountain country (Schaller 1977), the boundaries of their distributions coinciding with the break of slope. We class this as a special case of control of distribution by 'substrate'. The boundary between the sea and the land is a change of substrate marking the distributional limits of many species.

The three characteristics of the population will step at the boundary of the species' distribution if that boundary is determined solely by such a factor.

An unmodifiable resource (1c of Table 1), one that can be neither pre-empted nor reduced by consumption, acts upon population characteristics rather like a component of climate. If it controls the boundary and if its intensity is clinal the population's r_m , density and individual well-being will form a ramp.

Consider, however, case 2a of Table 1, a resource used consumptively (as against pre-emptively) which, in the absence of use by the species of interest, would exhibit a geographic trend in biomass. Intrinsic rate of increase of the species would be zero at the geographic boundary of the resource and hold to some constant positive value within the resource's distribution. Since the animals themselves do not influence the level of the resource when they are at minimal density (the conditions under which r_m is measured), the trend in r_m is stepped at the range boundary. Not so the trend in density which, being a function of the production of the resource per unit of area, would rise progressively with distance from the range boundary towards the core of distribution. Assuming that population density comes to an equilibrium reflecting the rate of production of the resource and the rate at which it is utilized, each population along the gradient, although differing in density, will have a mean rate of increase of zero. Hence, there will be no trend in well-being along that gradient because well-being parallels rate of increase. Well-being steps at the range boundary.

A contrast is a resource used pre-emptively (2b). Although the dynamics of the population dependent on such a resource differ considerably from those of a population using a resource consumptively, the expected trend in r_m , density and well-being inward from the range boundary are the same in both cases.

A geographic cline in the density or infectivity of a facultative predator, parasite or pathogen (3a of Table 1) may determine the position of the range boundary. Its effect on the trend of r_m , density and well-being is likely to be that of a climatic factor, but complicated by the interaction between the predator, parasite or pathogen and both the species of interest and the alternative hosts or prey. An obligate predator, parasite or pathogen (3b) may also determine the position of the range boundary but, since it cannot have a geographic trend in density or infectivity independent of interaction with the target species, we postulate no necessary pattern of that species' r_m , density or well-being.

To summarize this framework: where the range boundary is controlled by a single factor, the nature of the factor can be determined by the geographic trend of two easily measurable population characteristics: density and well-being. Their trend in combination allows differentiation of the controlling factor into one of three groupings. Should both density and well-being form a ramp inward from the range boundary the controlling factor is likely to be a component of climate, an unmodifiable resource or a facultative predator, parasite or pathogen. Should both density and well-being form a step rather than a ramp at the boundary, the limiting factor is likely to be the 'substrate'. Should density form a ramp but well-being a step, the likely limiting factor is a resource that is used by the animals either pre-emptively or consumptively.

Of course, it will seldom be as simple as that because the boundary at any point may be controlled by two or more interacting factors, but the above scheme provides a framework and starting point for an investigation. It may be useful also for determining the point at which control of the position of the range boundary passes from one factor or combination of factors to another factor or combination.

TWO EXAMPLES FROM KANGAROOS

We will now examine some of these ideas by way of concrete examples. Our strategy was to compare density and well-being at two points within a species' distribution: near its periphery and near its core. To increase generality we made that comparison on two species of kangaroos, *Macropus giganteus* and *Macropus fuliginosus*, taking advantage of their partial overlap of distribution to restrict sampling to two sites. These were located such that each was near the core of the distribution of one species and near the periphery of the distribution of the other (Fig. 3). Hence, treatments (core vs. periphery) are not replicated, and that would normally confound site and treatment. In this case the confounding is not absolute because at each site one species acts in a sense as a control of the other. The hypotheses specify that a population characteristic will differ between sites in a predicted direction and that if both species differ between sites in that attribute they differ in opposite directions. A trend common to the two species immediately implicates a site effect additional to any treatment effect.

If an attribute (e.g. density, fecundity) is significantly lower at the periphery than at the core of distribution its geographic trend is declared a ramp. If not significantly different, or significantly different in the reverse direction, its trend is declared a step.

We are acutely aware that these decision rules may fail to differentiate an imprecise step from a ramp or a saw-toothed ramp from a step. Further, those trends were deduced for all variables other than density from but two points. The probability of misidentifying the form of a trend is thus high enough to counsel a cautious interpretation.

Field methods

Two study sites were chosen. One was in the north of New South Wales where *M. fuliginosus* was near the edge of its range and *M. giganteus* was well within its distribution. The second was in the southern third of the same State but where *M. giganteus* was near the edge of its distribution whereas *M. fuliginosus* was well within its range. The northern study area comprised 600 km² and the southern area 700 km². Neither study area could be sited to sample the precise periphery of the distribution of a species because numbers there were too low to allow sampling.

Approximately fifty mature females of each species, and a lesser number of males, were shot in each study area over the period 18–25 June 1985. Each specimen was weighed and the right crus (essentially the tibia plus the heel) was measured. The kidney fat of the left kidney was weighed and expressed as a percentage of the weight of the kidney. Pouch young were weighed and their head lengths measured. Length of head was converted to an estimate of age by the growth curves of Poole, Carpenter & Wood (1982a, b).

A sample of the stomach contents was taken from most of the sampled animals, being scored subsequently in the laboratory according to the abundance of various plant groups (grasses, forbs, shrubs, chenopods, Malvaceae and medics) determined by cuticle analysis. The method and its limitations are described by Barker (1986), the technique being modified from that described therein by extending the scoring system from three to five classes of proportional abundance.

The density of both species combined was estimated by low-level aerial survey between 1980 and 1982, the details being reported by Caughley *et al.* (1984). Subsequently it has been shown that although those estimates were corrected for visibility bias the correction factors were too low for *M. fuliginosus* (Short & Bayliss 1985) and were probably too low also for *M. giganteus*. Hence, the estimates are presented here as density indices rather than absolute densities. Because the two species cannot be differentiated with certainty from the air, the aerial surveys returned only estimates of the density of the two species combined. Dissection into its two components was achieved by applying the results of ground surveys that estimated the ratio of the two species in each of the 88 degree blocks (1° latitude by 1° longitude encloses about 11 000 km² at these latitudes) making up the zone of distributional overlap (Caughley *et al.* 1984).

Density

Figure 3 is a map of isopleths of density indices where the distributions of the two species overlap. Figure 4 shows a cross-sectional profile of density along the axis of least change in the density of *M. fuliginosus*. The cross-section is drawn through latitude–longitude intersections, each point representing an average of density in the four surrounding degree blocks. The trend of density inwards from the range boundary is clearly a ramp rather than a step for both species. The path of that cross-section is chosen for convenience only. Figure 3, showing isopleths of density, indicates that any alternative path would return much the same result. For *M. giganteus*, however, that holds only for its inland (western) boundary. Density at its eastern boundary, the Pacific coast, has not been measured.

Breeding season

Before proceeding to an examination of indices of well-being among the four samples, we first compared the two species in terms of breeding season and dietary intake because a

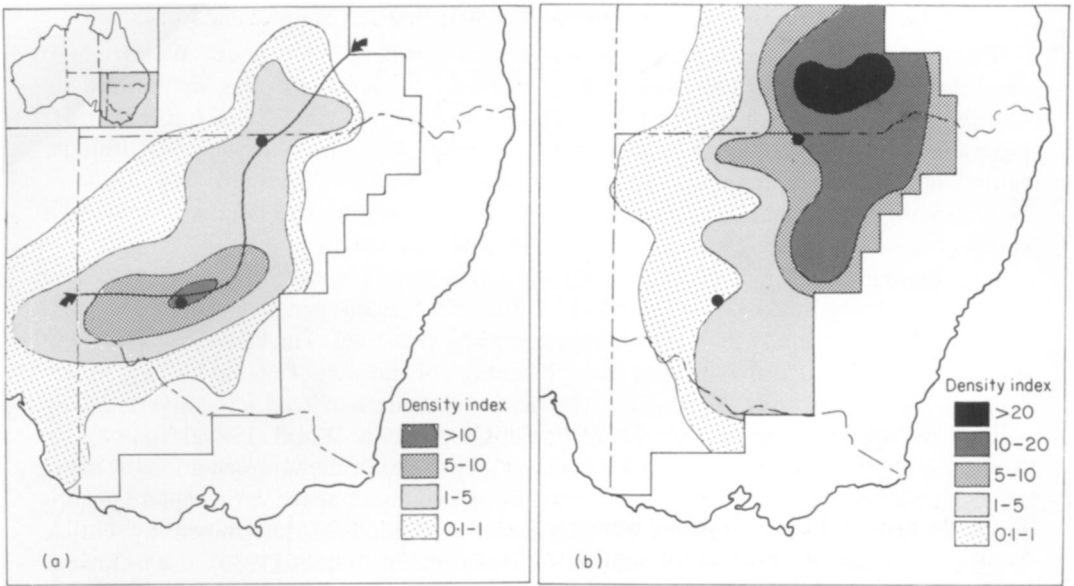


FIG. 3. Isopleths of density indices for *M. fuliginosus* (a) and *M. giganteus* (b) within their zone of sympatry. The darker the shading the higher the density. Filled circles indicate the sampling areas, and the line indicated by arrows in (a) marks path of the cross section of Fig. 4.

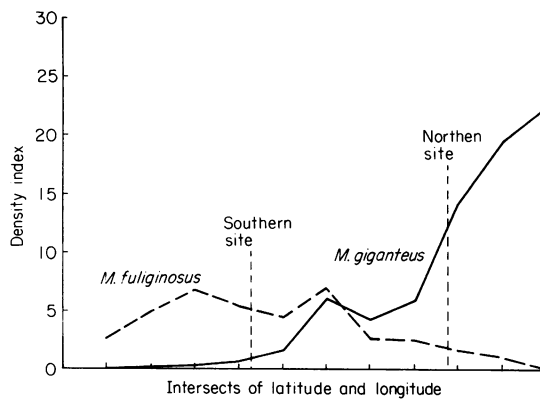


FIG. 4. The trend of density for *M. fuliginosus* and *M. giganteus* along a transect through the axis of least change in density of the first species.

difference of seasonality in these might well confound comparisons of body condition. The seasonal cycle of fat deposition and mobilization is influenced by a female's milk production which is itself influenced strongly by the age of her pouch-young. Differences in diet at time of sampling might have a similar effect.

TABLE 2. Mean age of pouch-young collected 18–25 June 1985, by area and species

Area	<i>N</i>	Mean age (days)	S.D.
<i>M. giganteus</i>			
North	36	168	56
South	33	174	81
<i>M. fuliginosus</i>			
North	24	167	57
South	45	204	60
Analysis of variance:			
Species:		$F=1.67, P>0.1$	
Area:		$F=3.71, 0.1>P>0.05$	
S × A:		$F=1.97, P>0.1$	

Both species of kangaroo breed throughout the year but with a marked peak of production in the summer months. Since comparisons of body condition and reproductive rate between species might be confounded by breeding seasons somewhat out of phase, the ages of the pouch young were first tested for a difference in mean age (Table 2). Analysis of variance revealed no significant overall difference between the species but suggested the possibility that the animals bred in the south about a fortnight earlier than in the north. The spread of the season of births, as indexed by the standard deviation of pouch-young ages, was estimated as between 56 days in the north for *M. giganteus* and 81 days for that species in the south. The standard deviations for *M. fuliginosus* lay between those extremes. Conversion of the extreme standard deviations to variances and dividing the largest by the smallest gave a ratio of 2.09. That test statistic for heterogeneity of variance (and hence of the spread of the four calculated seasons of birth) must exceed 2.61 for significance at the 5% level of probability.

Diet

Table 3 presents analyses of stomach contents. No significant difference was detected between kangaroo species in the frequency of various plant groups in the diet. However, there was some suggestion of a difference between the northern and southern areas across kangaroo species, but not quite to the 5% level of probability sought. Certainly the area in which an individual kangaroo was shot was an immensely more powerful predictor of its recent diet than was the species to which it belonged: the mean square for area was 114 times greater than that for kangaroo species when shrub intake was considered, and 138 times greater for intake of grasses.

Well-being: body condition

Mean kidney-fat indices for lactating females are presented in Table 4. The analyses summarized therein indicate that there was no overall difference between the two areas (kangaroo species pooled) but that there was a difference between species, the mean index of *M. fuliginosus* being higher than that of *M. giganteus* irrespective of area. Within each species, body condition was higher in the core area of its distribution than in the peripheral zone, condition of *M. giganteus* being higher in the north than in the south and for *M. fuliginosus* being higher in the south than in the north.

Two additional indices of body condition provided a picture differing from that presented by kidney fat. Regression of cubed root of body weight on length of crus (Table 5) suggested that in the south the animals were somewhat heavier for a given length of crus

TABLE 3. Mean indices of the abundance of plant groups in the stomach contents of female kangaroos, by area and species: *Mg*, *M. giganteus*; *Mf*, *M. fuliginosus*

Plant group	Northern area		Southern area	
	<i>Mg</i>	<i>Mf</i>	<i>Mg</i>	<i>Mf</i>
Grasses	3.54	3.50	3.06	3.27
Forbs	2.70	2.70	3.53	3.50
Shrubs	0.89	1.04	0.73	0.47
Chenopods	0.98	0.76	0.76	0.92
Malvaceae	0.24	0.94	0.04	0.08
Medics	0.00	0.00	1.23	1.21
Kangaroos (<i>n</i>)	49	50	52	48
Analyses of variance				
Intake of grasses				
Kangaroo spp: $F < 1, P > 0.5$				
Areas: $F = 3.80, 0.1 > P > 0.05$				
R × A: $F < 1, P > 0.5$				
Intake of shrubs				
Kangaroo spp: $F < 1, P > 0.5$				
Areas: $F = 3.62, 0.1 > P > 0.05$				
R × A: $F < 1, P > 0.5$				

TABLE 4. Kidney-fat indices of lactating females, by area and species. One asterisk indicates significance at <5%, two at <1% and three at <0.1%; N.S. indicates lack of significance: *Mg*, *M. giganteus*; *Mf*, *M. fuliginosus*

<i>N</i>	Index	Area	Status	Spp.	North	South	North	South
					<i>Mg</i>	<i>Mg</i>	<i>Mf</i>	<i>Mf</i>
36	7.87	North	Core	<i>Mg</i>	—	*	N.S.	N.S.
37	5.87	South	Edge	<i>Mg</i>	—	**	***	
24	8.55	North	Edge	<i>Mf</i>	—	—	N.S.	
45	9.40	South	Core	<i>Mf</i>	—	—	—	
Analysis of variance:								
Species: $F = 12.93,$					$P < 0.005$			
Area: $F < 1$					$P > 0.5$			
S × A: $F = 5.90,$					$P < 0.025$			

than they were in the north, and specifically that *M. fuliginosus* in the south was heavier than either *M. fuliginosus* or *M. giganteus* in the north. A check was run by comparing the body weights of lactating females because they comprised the largest homogeneous subset of the animals sampled. Table 6 confirms that on average the animals are heavier in the south than in the north irrespective of species. Consequently, the interpretation of the trends must be cautious because of a possible confounding of effect and site.

Well-being: recruitment

The percentage of mature females carrying pouch-young was used to compare recruitment rates among the four populations. Table 7 shows that observed productivity of *M. giganteus* was higher in the north than in the south but the difference did not attain

TABLE 5. Slope coefficients (b) of regression of cubed root of body weight on length of crus. Three asterisks indicate significance at <0.1%; N.S. indicates a lack of significance: *Mg*, *M. giganteus*; *Mf*, *M. fuliginosus*.

N	b	Area	Status	Spp.	North	South	North	South
					<i>Mg</i>	<i>Mg</i>	<i>Mf</i>	<i>Mf</i>
72	0.0056	North	Core	<i>Mg</i>	—	N.S.	N.S.	N.S.
80	0.0060	South	Edge	<i>Mg</i>	—	—	***	N.S.
70	0.0052	North	Edge	<i>Mf</i>	—	—	—	***
73	0.0060	South	Core	<i>Mf</i>	—	—	—	—

TABLE 6. Mean weights in kg (and sample size) of lactating females, by area and species

Area	<i>M. giganteus</i>	<i>M. fuliginosus</i>
North	21.43 (36)	21.31 (24)
South	23.65 (37)	24.57 (45)

Analysis of variance:

Species:	$F < 1, P > 0.5$
Area:	$F = 20.7, P < 0.001$
S × A:	$F < 1, P > 0.5$

TABLE 7. Percentage of mature females carrying a pouch young, by area and species. Two asterisks indicate significance at <1%; N.S. indicates a lack of significance: *Mg*, *M. giganteus*; *Mf*, *M. fuliginosus*

N	% lact.	Area	Status	Spp.	North	South	North	South
					<i>Mg</i>	<i>Mg</i>	<i>Mf</i>	<i>Mf</i>
39	92	North	Core	<i>Mg</i>	—	N.S.	**	N.S.
41	80	South	Edge	<i>Mg</i>	—	—	N.S.	N.S.
39	62	North	Edge	<i>Mf</i>	—	—	—	**
51	88	South	Core	<i>Mf</i>	—	—	—	—

significance at the 5% level of probability. *M. fuliginosus* was significantly more productive in the south than in the north.

Discussion of examples

Table 8 summarizes the results from the two kangaroo species. Density of *M. fuliginosus* formed a ramp from the range boundary as did three of four measurements of mean individual well-being. By the reasoning outlined previously it can cautiously be deduced that the edge of the range is positioned in this area by a component of climate, by an unmodifiable resource, by a facultative predator, parasite or pathogen, or by two or more such factors acting in concert. We reject, albeit tentatively, control of the range boundary by 'substrate' or by a resource that the animals use pre-emptively or consumptively.

TABLE 8. The deduced trend of population parameters from the periphery of the range towards its core

Parameter	<i>M. giganteus</i>	<i>M. fuliginosus</i>
Density	ramp	ramp
Well-being:		
kidney fat	ramp	step
growth rate	step	ramp
adult weight	step	ramp
recruitment rate	step	ramp

The list of factors implicated in the placement of the range boundary can now be culled by using knowledge of the ecology of *M. fuliginosus*. We can reject an effect of predators, parasites or pathogens because there is no indication that these have a significant influence on r_m . That leaves a component of climate and/or an unmodifiable resource. *M. fuliginosus* occurs where the difference between wettest and driest months is less than 10% of mean annual rainfall. When seasonality of rainfall exceeds that threshold the species is limited to those areas where winter rainfall predominates (Caughley *et al.* 1987). Although capable of breeding in all months of the year it produces most births in summer. Apparently the association with winter rain has little to do with breeding physiology. The mechanism of its dependence on winter rainfall has yet to be discovered but the fact of it is clear enough. Very likely the species needs that suite of grasses and forbs that responds to winter rains. Tropical (summer rain) grass species tend not to grow in winter, even when unseasonal rains occur (Mott & McComb 1975; Orr 1975). The part of the boundary investigated in this study is near the geographic switch in a north-south gradient from uniform to summer rainfall.

The other implicated factor, an unmodifiable resource, need not be rejected because the winter-rainfall grasses may act as such a factor, decreasing towards the north in a way that is not modified by the kangaroos.

Density formed a ramp for *M. giganteus* also but, in direct contrast to *M. fuliginosus*, three of four indices of individual well-being formed a step. Accepting the majority verdict of a step implicates a resource as the determinant of the range boundary. The ecology of *M. giganteus* rules against that resource being of a kind used pre-emptively. It suggests a resource such as food whose use by one animal reduces the amount available to another.

GENERAL DISCUSSION

Most studies of distribution have followed the lead of Bodenheimer (1938, 1958) in matching presence or absence of a species to climate by climatographic techniques of varying complexity. In recent times that methodology has been advanced further by botanists than by zoologists. They have added density, and in some cases growth rate, to presence or absence, studying how these vary along major environmental gradients (see reviews by Austin, Cunningham & Fleming (1984) and Austin (1985) where the work of R.H. Whittaker in particular is identified as formative). These methods certainly provide an answer but it is usually an answer about correlation rather than about causality.

Caughley *et al.* (1987) presented a climatographic analysis of the distributions of the two kangaroo species featured here. It leaves us unsatisfied. The ecological understanding gained from that methodology stops well short of blinding insight. We have therefore

tried a different tack in this paper, attempting to get a step closer to ecological causality. This procedure differs from the climatographic approach in that the nature of the limiting factor or factors is deduced from characteristics of the population rather than from a coincidence of boundary with the value of an environmental variable; and the methodology allows for the possibility that the distribution is limited at some places by one factor or combination of factors and at other places by another factor or combination.

Andrewartha & Birch (1954) considered that distribution and density are different aspects of the same thing: where conditions are favourable density is high; where unfavourable density is low; and the edge of the range is the zero-density resultant of conditions being just not quite good enough. More specifically, they considered the edge of the range as that environment 'indicated by the position of the isopleths for zero increase' (Andrewartha & Birch 1954). They defined zero increase as a zero finite intrinsic rate of increase (i.e. $\lambda = 0$) equivalent to an r_m of minus infinity, but their notion is more correctly expressed as $r_m = 0$. Rogers & Randolph (1986) express much the same idea, postulating that the edge of the range is that location where mortality from abiotic (i.e. density-independent) sources balances fertility. Hence, on the edge of the range there are either not enough resources for an individual even when it shares them with few other individuals, or other components of the environment (e.g. predators, diseases, the direct effect of weather) raise death rate above birth rate despite there being enough resources.

If the limiting factor is a component of climate, or the 'substrate', or an unmodifiable resource, or a facultative predator, parasite or pathogen, then our conclusions as summarized in Table 1 suggest that density and individual well-being will trend spatially in parallel under the influence of a common driving variable. In that case, distribution and density would indeed be different aspects of the same thing, as may be the case with *M. fuliginosus*.

But consider the case of density within the distribution being determined by the intrinsic dynamics of the animals, by the intrinsic dynamics of a consumptively utilized resource, and by the interaction between the animals and the resource. Variations in density within the distribution may be large, reflecting geographic variation in the rate of renewal of that resource, but rate of increase will hold everywhere to a mean of zero because such interaction leads inevitably to an equilibrium. Hence, the strength of competition between animals for the resource will also be a constant across the distribution. In these circumstances, density and distribution will not be determined in the same way. We suggest the signature of such a decoupling is a ramp of density and a step of well-being. Such may be the case for *M. giganteus*.

Rogers' and Randolph's approach, stemming from previous work by Rogers (1979), seeks to explain distribution in terms of a density-independent fertility, and a variable mortality that may be divided into biotic (density-dependent) and abiotic (density-independent) components. We admire this approach in that it ties distribution to basic demographic parameters whereas we were forced to index these by measures of 'well-being'. The simplifying assumption of a density-independent fertility may well be appropriate to tsetse flies, the animal from which Rogers derived his model, but it does not hold for those other groups, vertebrates in particular, whose fertility is variable and reactive to both biotic and abiotic influences. Nonetheless, the underlying idea is attractive and may possibly be approximated for animals with varying fertility by dissecting rate of increase (the resultant and fertility and mortality), rather than mortality alone, into biotic and abiotic components.

This paper provides a tentative theoretical framework for considering relatively stable distributions and suggests a means whereby the ecological determinants of the boundary might be identified. In contrast, Taylor (1986) explored the properties of labile distributions which he considered explicable only in terms of behaviour and dynamics at both the individual and the population levels. He stressed the role of migration, and the inapplicability of standard equilibrium models.

We suspect that the stable distribution is no more than a special case of the labile distribution and that any useful theory of distribution must encompass both. That has not been attempted here, but we suggest two lines of investment that might lead to a reconciliation. First, a labile distribution may be viewed as a temporal sequence of 'stable' distributions. Secondly, a stable distribution may be viewed largely as an interaction of population dynamics with climate. A labile distribution, on the other hand, may be viewed as an interaction of population dynamics with weather, behaviour providing the tracking mechanism. In that sense, stable and labile distributions differ more in degree than in kind.

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