

Original papers

The geographical distribution of rarity

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Summary. This paper asks the question: are most species that are censused as rare in particular localities rare throughout most of their geographic ranges, or are they common in substantial portions of their ranges elsewhere? The first alternative is labeled *suffusive rarity* and the second *diffusive rarity*. To answer this and similar questions, rarity can be measured as the fraction of censuses from some locality (e.g., a quadrat) in which a species occurs (*occurrence rarity*), or the relative or absolute abundance of the species averaged over all censuses from some locality (*abundance rarity*). The question was analyzed for occurrence-rarity data from Australian terrestrial birds distributed over 1° (10⁴-km²) quadrats. The great majority of species that are rare in a particular quadrat are not rare and are often common in a substantial number of other quadrats, i.e., these avian species are much closer to the diffusive than suffusive portion of the rarity continuum. The data also show that 1) the distribution of sizes of geographic ranges, whether breeding or total, is highly skewed, appearing exponential to more concave; 2) species are much rarer in their nonbreeding than breeding ranges; 3) more widespread species, whether breeding or total ranges are considered, tend to occur more rarely in a slightly but significantly greater fraction of their ranges; and 4) hawks and owls, typified by high abundance rarity, show occurrence rarity in a greater fraction of their ranges than the average nonraptorial species. Although continental birds may be especially predilected toward diffusive rarity, the present analysis points to identification of centers of abundance as major ways of preserving those species contributing most to recorded instances of rarity. Similar analyses with other kinds of organisms would be most welcome.

Key words: Rarity – Geographic distributions – Occurrence frequency – Birds (Australian terrestrial)

others, or are they typically rare in all censuses? How this question is answered encapsulates crucial information about the nature of rarity. If the first possibility is correct, then rarity is by and large a matter of spillover from places where a species is common. An understanding of rarity then mainly involves an understanding of the dispersal powers of that species, i.e., how it diffuses across the landscape. Preservation of that species then mainly involves preservation of its spatial center of abundance. If the second possibility is correct, that species rare somewhere are rare everywhere, then the crucial biological properties involved in understanding rarity are more numerous, and include problems of individual mate location, the degree of specialization and abundance of appropriate resources. Preservation of such species then focuses less on specific areas, and preservation may involve putting aside very large areas. Obviously there is a continuum between the two extreme possibilities, and it is of interest to determine where along the continuum species of particular groups lie.

This paper has the following purposes. First, the concepts just introduced will be named and made operational, so that the determination just mentioned can be performed. Then, rarity will be empirically examined for a particular system, the terrestrial birds of the continent of Australia. The recent publication of *The Atlas of Australian Birds* (Blackers et al. 1984), a stupendous volume amassing an enormous amount of data, makes possible a partial answer to the above question about rarity. How rarity relates to the total size of geographic ranges and whether ranges are breeding or breeding plus migratory will also be examined. Finally, speculation about the generality of the result obtained for Australian birds will be given together with relationships to previous characterizations of rarity, e.g., Rabinowitz (1981) and Brown (1984).

Concepts

Diffusive vs suffusive rarity

The degree of rarity is a species property. To the extent that a species conforms to one or the other extreme of the rarity continuum discussed above, it can be said to show diffusive vs suffusive rarity. *Diffusive rarity* characterizes a species that is rare in certain parts of its range but common in other parts. Because the former parts tend to occur at the periphery of ranges (Brown 1984 and below), the pattern is one of apparent diffusion from a center (or centers) of abundance; diffusive rarity is maintained by dif-

An ecological census lists occurrences or abundances for species at some locality during some short period of time. It is a common observation for a collection of such censuses that some species are moderately to very rare, in the sense that they occur in relatively few censuses and/or occur at relatively low abundances (Preston 1948, through Rabinowitz 1981, gives an overview). This paper asks the following question about such rarity. Are the species that are rare in censuses from particular localities typically common in

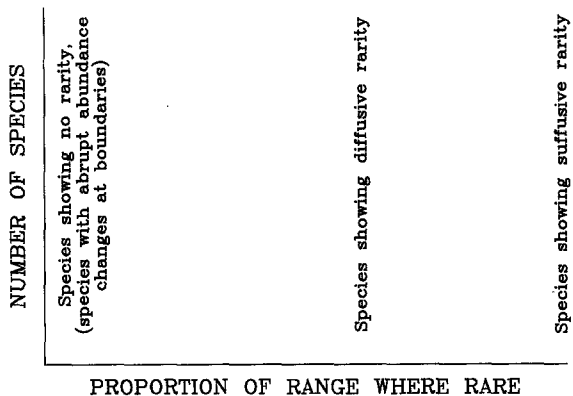


Fig. 1. A rarity continuum. Species having different fractions of their ranges where rare are arranged along this continuum to characterize rarity in some group. To the left margin, common species occur. The diffusive-to-suffusive portion of the continuum is from left-of-center to the right margin; it spans species that are rare in a moderate fraction of their ranges to species rare in their entire ranges

fusion from without. *Suffusive rarity* characterizes a species that is rare everywhere; the species' range is completely covered or filled, i.e., suffused, with rarity, in the somewhat metaphorical sense that a darkened room is suffused with a weak light or a chalky complexion with a reddish tinge. It is the second of these sorts of rarity that alone is included in Rabinowitz's (1981) "seven kinds of rarity," and that some may consider the only genuine rarity; Rabinowitz for example refers to the first type as "pseudo-rarity." But the first can be far commoner than the second, as we shall see below.

Occurrence vs abundance rarity

To locate a rare species along the diffusive-suffusive continuum, one must divide the species' range into sectors,

e.g., quadrats of equal size. For each quadrat, the species is scored as to its degree of rarity therein. Computation of the fraction of total quadrats where the species is rare then locates it along a commonness-to-rarity continuum, of which the diffusive-suffusive continuum is a portion (Fig. 1). A species that is rare everywhere (to the extreme right of Fig. 1) shows suffusive rarity. A species that is rare in a substantial number more shows diffusive rarity in the former quadrats (middle to mid-left part of Fig. 1). Species rare nowhere show no kind of rarity (to the extreme left of Fig. 1).

A variety of decisions are needed to make the rarity continuum of Fig. 1 operational.

First, we need to set the boundaries of diffusive and suffusive rarity, situations-in-between, and situations showing no kind of rarity. Such a decision will probably typically be arbitrary, and when making qualitative comparisons, exact boundaries are not really crucial (see below).

More importantly, we need to define what is meant by rarity in individual quadrats of a species range. For this purpose, I distinguish occurrence from abundance rarity. *Occurrence rarity* exists when a species occurs in a small number of censuses performed at places within the given quadrat. *Abundance rarity* exists when the species has a small abundance averaged over censuses performed within the given quadrat. This average may or may not include censuses where the species does not show up at all (i.e., where abundance is zero). Further, it may be based on relative abundance (abundance scaled to abundances of the other species in the census) or absolute abundance (abundance without regard to abundances of other species, e.g., numbers per unit area) or something else (see last section below). Either occurrence rarity or abundance rarity can be used as the axes for Fig. 1. Table 1 gives the formulae that define occurrence and the various kinds of abundance rarities.

Table 1. Formulae for computing occurrence and abundance, and their relation to the determination of diffusive vs suffusive rarity

Formula	Suffusive rarity	Diffusive rarity
<p>OCURRENCE of Species <i>j</i> in Quadrat <i>q</i> =</p> $O_{jq} = \frac{\text{Number censuses in Quadrat } q \text{ with Species } j}{\text{Total censuses in Quadrat } q (T_q)}$	O_{jq} small in most <i>q</i>	O_{jq} small in a substantial number of <i>q</i> , not small in a substantial number of <i>q</i>
<p>ABUNDANCE of Species <i>j</i> in Quadrat <i>q</i></p> <p>ABSOLUTE ABUNDANCE =</p> $A_{jq} = \frac{\sum_i^{T_q} \text{number of individuals of Species } j \text{ in Census } i}{\text{Total censuses in Quadrat } q (T_q)}$ <p>A_{jq} may alternatively be computed by substituting density for number in the preceding formula.</p>	A_{jq} or A'_{jq} small in most <i>q</i>	A_{jq} or A'_{jq} small in a substantial number of <i>q</i> , not small in a substantial number of <i>q</i>
<p>RELATIVE ABUNDANCE =</p> $A'_{jq} = \frac{\sum_i^{T_q} \text{number of individuals of Species } j \text{ in Census } i}{\sum_j \sum_i^{T_q} \text{number of individuals of Species } j \text{ in Census } i}$ <p>T_q equals the number of censuses in Quadrat <i>q</i>, and <i>j</i> is summed over all species.</p>		

Occurrence and abundance measures of rarity must be correlated to some extent. A species having a low occurrence, i.e., found in a few censuses only, must statistically have a low abundance as well, provided zeros are included in the latter's computation. In contrast, the converse is not statistically necessary, but it is likely: a species having a small abundance (i.e., number per unit area) is likely to occur in a few censuses, all other things being equal. However, were such a species conspicuous, e.g., as are certain hawks, then they would often be seen even at low densities and would be reported in most censuses. Thus while occurrence and abundance rarity should be correlated, the correlation should not be symmetrical. Below this correlation is examined further empirically.

A third kind of procedural decision may affect empirical analyses of rarity continua, and this is quadrat size. In cases in which a species distribution is smeared evenly over the landscape, even down to the level of individual home ranges, quadrat size has little effect on the sorts of analyses done in this paper. However, were a species patchily distributed, quadrat size may make a difference. The phenomenon is well investigated in plant ecology in particular, e.g. Greig-Smith (1964), Kershaw (1964, esp. p 104ff), Pielou (1969). The main result is that the variance of abundance within patches is highest when the scale of sampling quadrats is the same as the scale of patchiness. To illustrate in part, suppose quadrats were much larger than the scale of patchiness of the species in question. Then the fraction of censuses having the species, assuming nearly perfect and evenly distributed censusing within the quadrat, will be some relatively intermediate number, i.e., not very close to zero or one. Now suppose quadrats were smaller, on the scale of patchiness of the given species. Then many quadrats will give either close to zero percent occurrence or close to 100 percent occurrence. Thus the variance of the rarity distribution will increase, and in particular, the fraction of quadrats where the species is very rare will increase. (This variance can again decline with smaller quadrats still [Kershaw 1964].)

To determine if this sort of somewhat artifactual increase in rarity might be going on, several other kinds of data can be observed. If the species has many quadrats where rare *and* quadrats where common with few in between, quadrat scale and species patch scale may be similar. If visual inspection of how rare, common and intermediate quadrats are distributed shows patchiness, especially throughout the geographical range of the species and not just at the range perimeter, the same conclusion is supported. For certain simple situations, this visual inspection can be replaced by precise statistical analyses (Krishna Iyer 1949, Pielou 1969, p 107ff). In contrast, if a species having more quadrats where rare than any other kind also has fewer quadrats where common, or if patches where rare are not randomly intermingled with patches where common, the patchiness effect is not supported. Then, factors besides a patchiness effect are responsible for occurrence rarity, the most obvious of which is that the species occurs at very low average densities within the quadrat or in very few places there.

Also mitigating against finding a patchiness effect is the behavior of census-takers. Natural habitat is in many places now quite patchy due to human disturbance. But census-takers are likely to select patches of natural habitat only, ignoring places where most species do not occur and

thereby in effect "homogenizing" the quadrat toward non-patchiness. Natural patchiness may still give the above effect, but this would be substantially less than if unnatural patchiness were a problem. Nonetheless, for the present sort of study, it is best to select quadrat sizes much larger than the scale of whatever patchiness might exist.

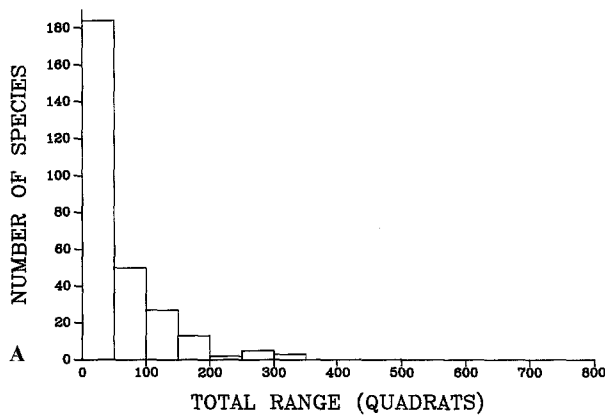
Methods

I have just reviewed a variety of possible problems in determining the spatial distribution of rarity in real situations. I now give in some detail an example with real data. Because those data were not collected for purposes of this analysis, a number of procedural decisions are already made for us.

The data consist of separate distribution maps for all the strictly terrestrial (i.e., not including freshwater) bird species of the Australian continent (Blakers et al. 1984). Each species' map is composed of quadrats, in this case 100×100 km (1°), which are classified in two ways. First, quadrats within which breeding was recorded are separated from quadrats within which no breeding was recorded. These are henceforth referred to as "breeding" and "non-breeding" quadrats. Second, quadrats are divided into three groups on the basis of the fraction of censuses having the given species. These fractions are less than 11%, 11–40%, and greater than 40%. The three kinds of quadrats are henceforth referred to as "quadrats where rare," "intermediate quadrats," and "quadrats where common," respectively.

The program resulting in the atlas data, performed under the auspices of the Royal Australasian Ornithologists Union, is perhaps the most vast and impressive of its kind. Census and compilation details can be obtained from Blakers et al. (1984), but some are important to mention here. Census-takers were urged to be very careful about identifications, erring on the conservative side and giving details of doubtful cases; these were later evaluated by a central group of experts. The minimal unit of recording for this project, which we are informally calling a "census," is actually a record sheet which may contain observations from a portion of a day or may represent a longer time, say a several month period. Censuses thus fall on the side of completeness in comparison to censuses for other such studies. An effort was made by the atlas compilers to cover the entire continent of Australia, and each quadrat was represented by at least one census. The actual distribution of censuses per quadrat, for those quadrats touching the continent itself, is 1–5 censuses, 11.6%; 6–25 censuses, 27.2%; 26–50 censuses, 19.4%; over 50 censuses, 41.8%. Moreover, a smoothing procedure was used for quadrats having fewer than 50 censuses; the procedure averages a given quadrat with the eight surrounding quadrats to a degree weighted negatively by number of censuses within the given quadrat (Blakers et al. 1984, p 679). This very clever procedure goes a long way toward averting the bias that would otherwise be associated with infrequently sampled quadrats: quadrats having fewer than 9 censuses, for example, could never be designated "quadrats where rare" for particular species; rather, rare species would typically be counted as not occurring in such quadrats at all. Only for clusters of infrequently sampled quadrats would this artifact exist; given the distribution of sampling intensities (above), these could not be very common, and in fact inspection of maps reveals few, if any, such clusters. The

BREEDING PASSERINES



BREEDING PASSERINES

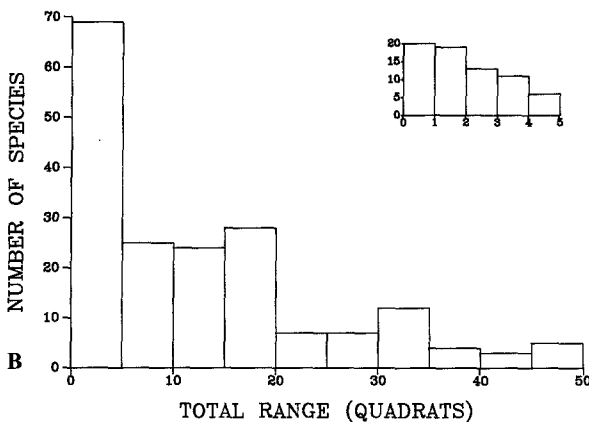


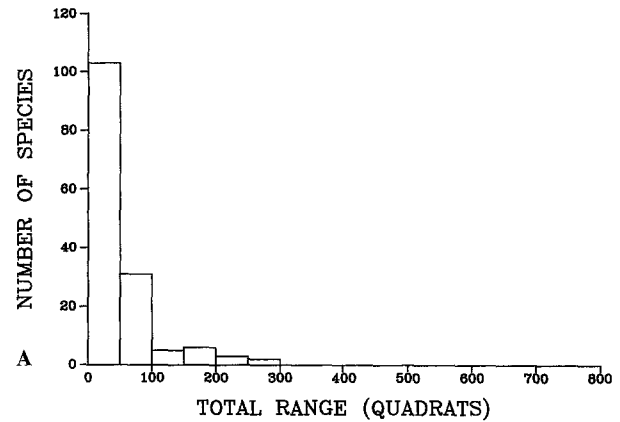
Fig. 2A, B. Distribution of geographic range size for Australian terrestrial breeding passerines, three scales. **A** Quadrats in groups of 50. **B** First category of "top," in groups of 5. *Insert, B* First category of **B** in groups of 1. 1 quadrat = 10^4 km²

smoothing procedure does bias the data against finding species on the leftmost portion of the continuum of Figure 1, i.e., those with abrupt abundance changes at boundaries. If this bias exists, however, the results to be reported below are all the more surprising.

I treated the data just described as follows. For each species, the number and frequency (number/total) of quadrats where rare, quadrats where common, and intermediate quadrats were counted from the atlas maps. These were the raw data used in nearly all analyses. I computed these quantities separately for breeding quadrats, nonbreeding quadrats, and all quadrats combined. I then grouped species into three taxa: passerines, nonpasserines, and all species combined. I could then examine rarity properties of particular subclasses of species, e.g., the distribution of the species-specific fractions of quadrats where rare for breeding passerines. In addition, I did some analyses for hawks and owls separately, to characterize patterns for species known to occur in low densities nearly everywhere. Note that the definition of rarity necessarily adopted here is "occurrence rarity," not "abundance rarity."

In total, 456 species distributed over 810 quadrats form the data used in this study. All terrestrial species included in Blackers et al. (1984) were used except those restricted to the island of Tasmania (these were not used because a finer set of quadrats only was given for them).

BREEDING NONPASSERINES



BREEDING NONPASSERINES

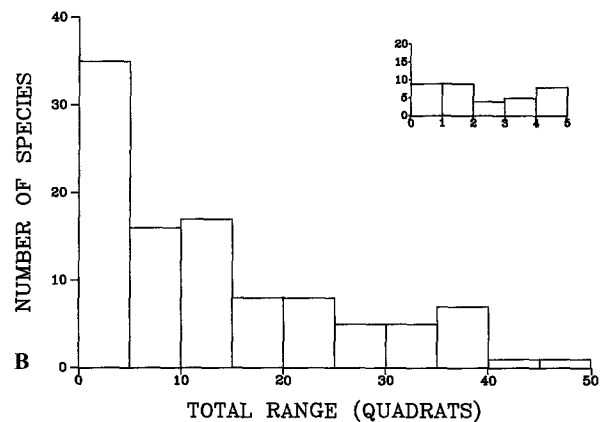


Fig. 3A, B. Distribution of geographic range size for Australian terrestrial breeding nonpasserines, three scales. **A** Quadrats in groups of 50. **B** First category of "top," in groups of 5. *Insert, B* First category of **B** in groups of 1. 1 quadrat = 10^4 km²

Results

Distribution of the sizes of species geographic ranges

Before presenting the analysis of occurrence rarity, I examine the distribution of species-range areas for all terrestrial species over all quadrats of the Australian continent. Were most species very widespread, we might expect, were diffusion important, many quadrats where rare simply because ranges are so large. In fact, distributions of range size are strikingly skewed toward small values (Figs. 2-4). Modes of such distributions lie at the smallest range-size category using a 10^4 -km² scale, i.e., ranges between 0 and 5×10^5 km². Distributions appear strikingly concave, even more so than exponential.

To examine the highly skewed nature of range-size distributions further, the first category used in the previous analysis was broken down into 5-quadrat intervals. Even here, the mode for breeding ranges (Figs. 2, 3) lies at the smallest category, 0- 5×10^4 km². The mode for total ranges lies at the next smallest category (Fig. 4). These distributions are still quite skewed and concave-looking. To carry things further, the first category of this finer-scale plot was itself broken down into 1-quadrat intervals (insert graphs, Figs. 2-4). Even now the smallest category contains the mode for breeding ranges of passerines.

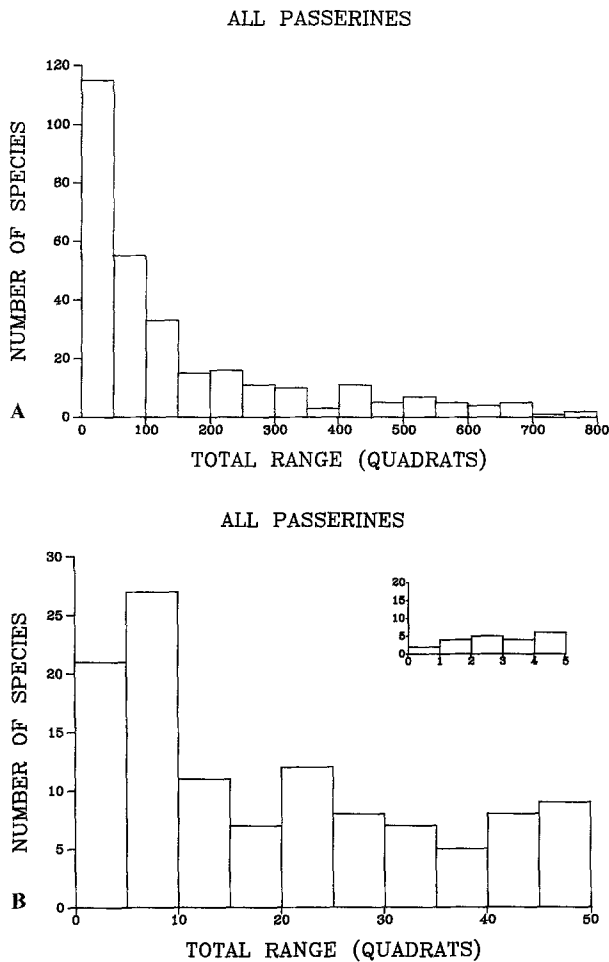


Fig. 4A, B. Distribution of geographic range size for total range (breeding and nonbreeding) of Australian terrestrial passerines, three scales. **A** Quadrats in groups of 50. **B** First category of "top," in groups of 5. *Insert, B* First category of **B** in groups of 1. 1 quadrat = 10^4 km²

The conclusion from this analysis is that the distribution of geographic range sizes in Australian terrestrial birds is strikingly skewed toward small sizes, appearing somewhat more concave than exponential. These distributions recall the "hollow" curves first found for endemic species by Willis (1922; see also Rapoport 1982, Anderson 1985 [and included references]). It is possible such distributions, should they turn out to be more general, represent a "macroscopic rule," albeit of unknown significance. Further, the range data show that many species of Australian birds have quite restricted ranges, and in this sense of rarity (cf. Rabinowitz 1981), are quite rare. It must be reiterated, however, that the atlas data do not necessarily report the entire ranges of the component species; rather they give the ranges within the study continent. In many cases they do represent the entire range, as Australasian birds tend to be very endemic (Sibley and Ahlquist 1985). In a substantial number of cases, however, species have distributions in Australia restricted to tropical Queensland and occur farther north as well, into New Guinea and surrounding islands (e.g., Kikkawa 1982; Beehler et al. 1986). The number of potential quadrats that could be added from these areas is rela-

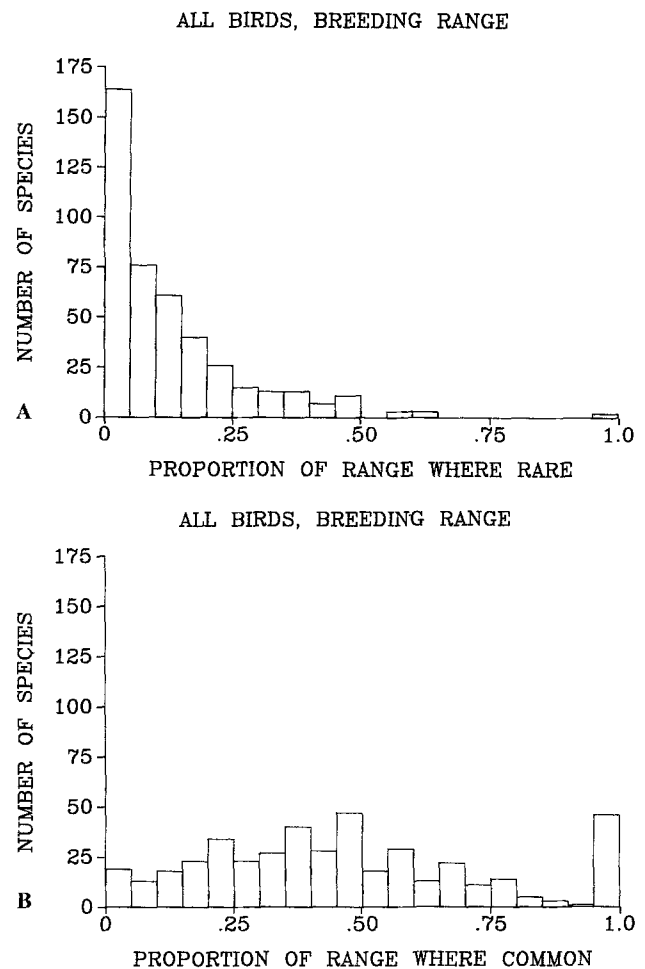


Fig. 5. **A** Distribution of rarity for breeding ranges of all Australian terrestrial bird species, a realization of the rarity continuum of Fig. 1. Note that most species have a very small proportion of their breeding ranges where not rare. **B** Distribution of commonness for breeding ranges of all Australian terrestrial bird species. Note that most species have a large proportion of their breeding ranges where common

tively small, however, given the land masses involved. Of course, for species ranging farther north, this is not the case, but such species are relatively few; e.g., 308 of the 324 species of Australasian passerines listed in Schodde (1975) are endemic to the Australasian region (Sibley and Ahlquist 1985). A second more minor caveat with these data is that they are based on quadrats, not actual land areas, so that ranges calculated by this method are somewhat large, as coastal quadrats are not entirely composed of land. This sort of error should not affect the relative range sizes much nor the patterns of Figs. 2-4. In any event, to some extent the Australian avifauna could be a special case, and compilations of this sort for other groups would be most welcome.

Spatial distribution of rarity

I now present the major empirical result of this paper.

First, consider breeding quadrats only. Figure 5A plots the distribution of the fraction of quadrats where rare for all species. Notice that extremely few species occur in more than 50 percent of their ranges as "rare." The vast majority

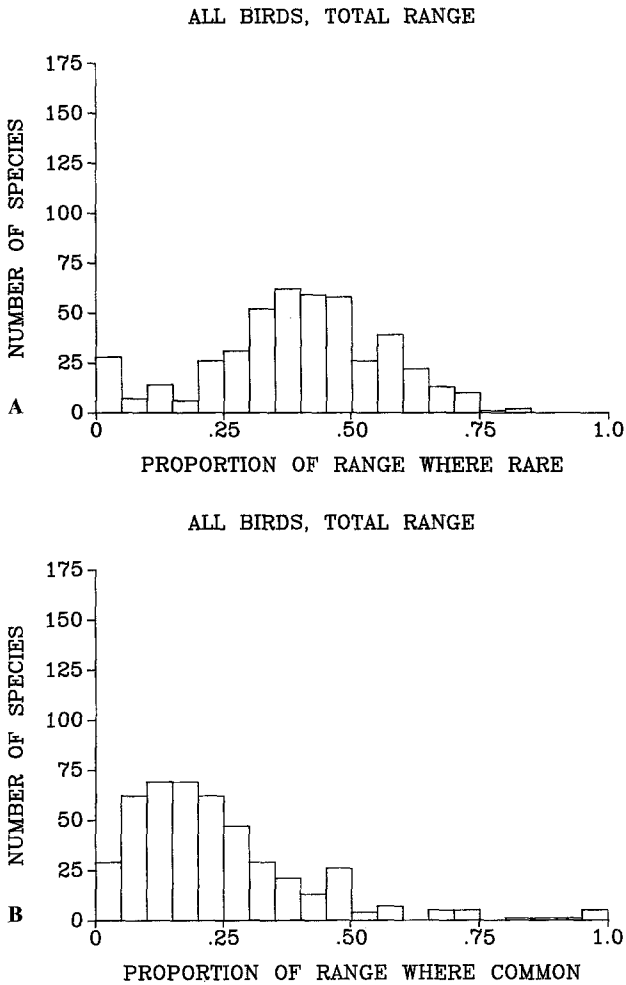


Fig. 6. **A** Distribution of rarity for total ranges (breeding and nonbreeding) of all Australian terrestrial bird species, a realization of the rarity continuum of Fig. 1. Note that most species have a small proportion of their ranges where not rare. **B** Distribution of commonness for total ranges of all Australian terrestrial bird species. Note that most species have a small-to-moderate proportion of their ranges where common

of species have most of their quadrats in the “not rare” category, i.e., quadrats where common and intermediate quadrats. Figure 5B plots the distribution of the fraction of quadrats where common. This shows that close to half the species have breeding ranges consisting mostly of quadrats where common. Hence the question in the introduction is answered thusly for Australian terrestrial breeding birds: most species that are rare somewhere are not rare and are often common in some to many other places; diffusive rather than suffusive rarity is overwhelmingly supported.

When all quadrats are included, nonbreeding as well as breeding, graphs are shifted toward a greater fraction of quadrats where rare (Fig. 6). Not surprisingly, species tend to be commoner in quadrats where they breed (Table 2; see next section also). Nonetheless, the main result, that nearly all species are common over a substantial portion of their ranges, still holds.

Taxonomic breakdown of the above figures is further illuminating. Nonpasserine species tend to have a greater fraction of quadrats where rare than passerine species (Table 2). While differences are not great, they do suggest that perhaps certain nonpasserine groups, i.e., those consisting of very large birds with large individual home ranges, show occurrence rarity more frequently than most species. To test this, “hawks plus owls” and “hawks” were analyzed separately (Table 2, right columns). For breeding quadrats, the fraction of quadrats where rare for hawks and owls is almost double that for passerines. Differences are less extreme for nonbreeding quadrats or for hawks analyzed separately. Differences in breeding or total ranges are statistically significant for passerines vs hawks plus owls, and for total ranges for passerines vs hawks (*t*-test on means), pointing to the reality of differences between kinds of birds in rarity plots. The fact that hawks and owls, known for their substantial abundance rarity (low densities), also show relatively great occurrence rarity, supports the arguments above that these two kinds of rarity should be correlated.

Figures 7–9 give those passerine species whose range properties fall closest to the average breeding, nonbreeding and total passerine ranges in terms of fractions of the three types of quadrats.

Table 2. Mean (\bar{x}) and standard deviation (SD) for frequencies of various kinds of quadrats, classified by rarity

	Passerines		Nonpasserines		All Species		Hawks & Owls		Hawks	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Breeding ranges										
	N=284		N=150		N=434		N=27		N=19	
Quadrats where rare	0.120	0.141	0.142	0.166	0.127	0.150	0.207	0.222	0.163	0.111
Intermediate quadrats	0.397	0.215	0.425	0.237	0.406	0.223	0.516	0.213	0.566	0.103
Quadrats where common	0.484	0.267	0.433	0.278	0.466	0.272	0.276	0.213	0.271	0.154
Nonbreeding ranges										
	N=295		N=158		N=453		N=27		N=19	
Quadrats where rare	0.501	0.208	0.535	0.180	0.513	0.199	0.526	0.160	0.548	0.159
Intermediate quadrats	0.358	0.157	0.333	0.135	0.349	0.151	0.393	0.119	0.387	0.124
Quadrats where common	0.141	0.161	0.132	0.153	0.138	0.158	0.076	0.060	0.065	0.054
Total ranges										
	N=298		N=158		N=456		N=27		N=19	
Quadrats where rare	0.370	0.169	0.439	0.169	0.394	0.172	0.476	0.162	0.482	0.158
Intermediate quadrats	0.375	0.139	0.347	0.129	0.365	0.136	0.421	0.117	0.418	0.112
Quadrats where common	0.255	0.175	0.214	0.177	0.241	0.177	0.104	0.076	0.100	0.079

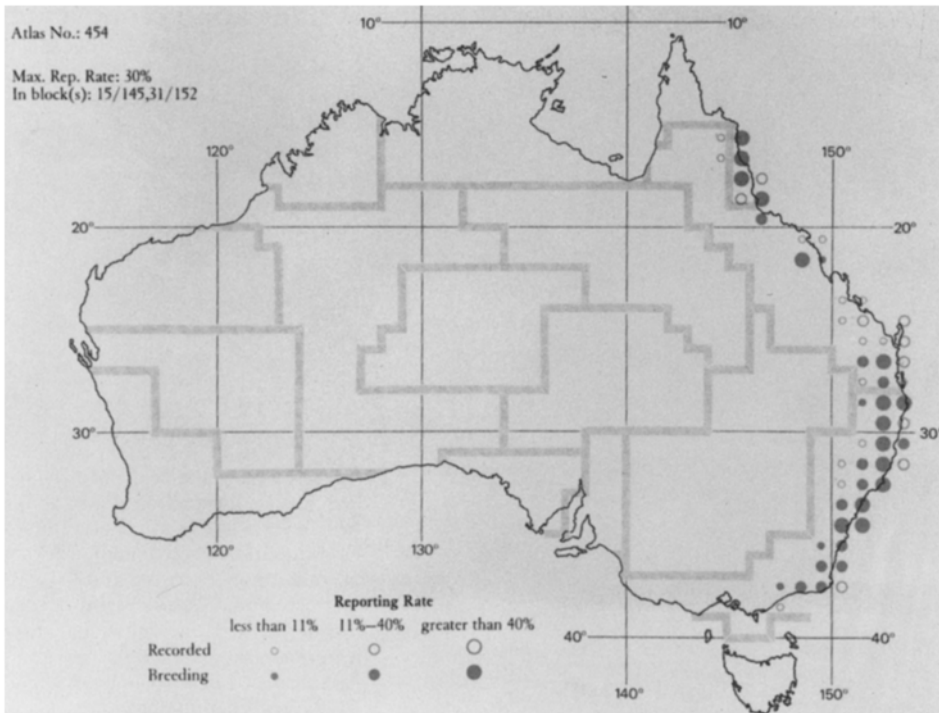
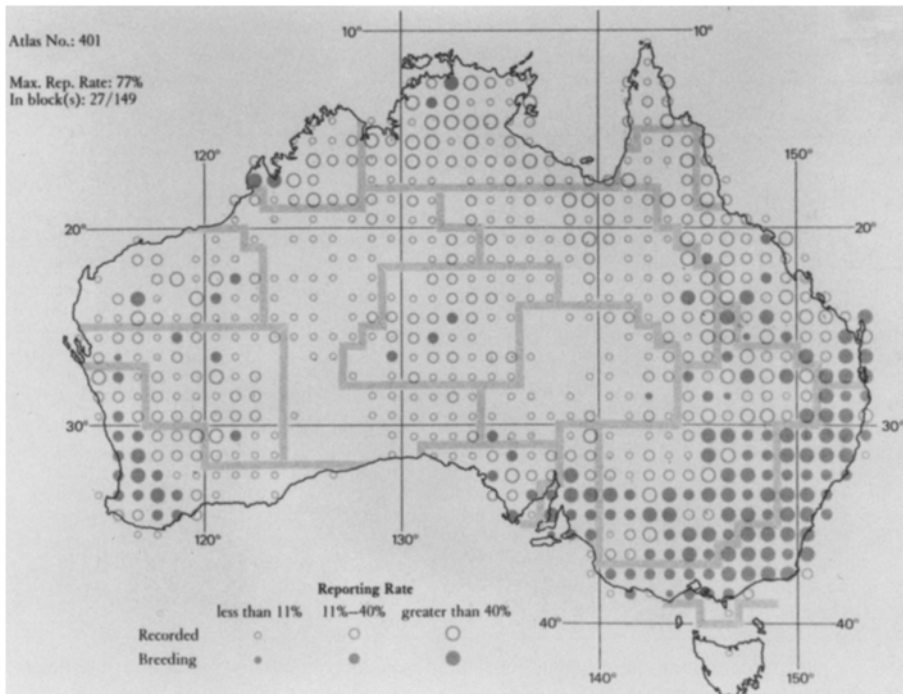


Fig. 7. Atlas map of that passerine species having the nearest to the average frequencies of quadrats where rare, intermediate quadrats, and quadrats where common for a breeding range. Species is the Brown Gerygone (*Gerygone mouki*). Boundaries are biogeographical regions designated in the atlas. (Reproduced from Blakers et al. [1984] with permission)



Rufous Whistler
Pachycephala rufiventris



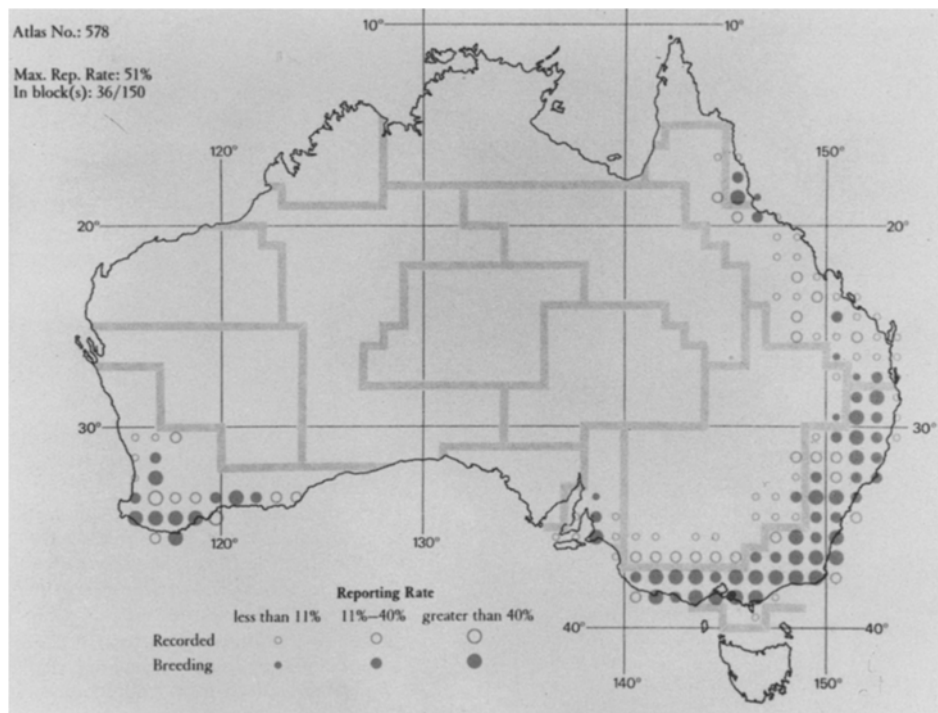
Fig. 8. Atlas map of that passerine species having the nearest to the average frequencies of quadrats where rare, intermediate quadrats, and quadrats where common for a nonbreeding range. Species is the Rufous Whistler (*Pachycephala rufiventris*). (Reproduced from Blakers et al. [1984] with permission)

Relation of occurrence rarity to total range size

Given the very great variation in total size of geographic range, we might expect any tendency for the fraction of rare or common quadrats to vary with total range to be detectable with these data. One possibility, for example, is that species are mainly rare at the periphery of their ranges, so that as total range size increases, the fraction of quadrats where rare declines as the ratio of perimeter to area declines. Using somewhat different methodologies than the present paper, Bock and Ricklefs (1983), Brown

(1984), Bock (1984) and Lacy and Bock (1986) found that the greater the range size, the greater the average abundance (density) over the range.

The Australian data show the opposite trend. Although slopes are small, a significant tendency for larger ranges to have a greater fraction of quadrats where rare exists. Regression statistics are summarized in Table 3. For comparative purposes, frequencies of the three kinds of quadrats (rare, intermediate, common) for passerines are plotted in Fig. 10 against total number of quadrats (breeding and nonbreeding; independent variables for regression statistics



White-naped Honeyeater
Meliphreptus lunatus

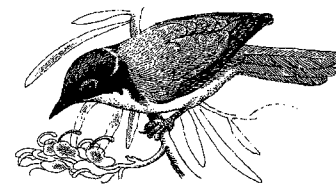


Fig. 9. Atlas map of that passerine species having the nearest to the average frequencies of quadrats where rare, intermediate quadrats, and quadrats where common for a total range (breeding and nonbreeding). Species is the White-naped Honeyeater (*Meliphreptus lunatus*). (Reproduced from Blakers et al. [1984] with permission)

Table 3. Regression statistics for frequencies of various kinds of quadrats vs totals*

	Passerines			Nonpasserines			All Species		
	<i>b</i> **	SE	<i>R</i>	<i>b</i>	SE	<i>R</i>	<i>b</i>	SE	<i>R</i>
Breeding ranges									
<i>Dependent Variable</i>	<i>N</i> = 284			<i>N</i> = 150			<i>N</i> = 434		
Quadrats where rare	0.1304 ^d	0.0195	0.370	0.1325 ^d	0.0326	0.317	0.1304 ^d	0.0169	0.348
Intermediate quadrats	0.1537 ^d	0.0251	0.342	0.1132 ^b	0.0417	0.218	0.1404 ^d	0.0217	0.297
Quadrats where common	-0.1779 ^d	0.0299	0.334	-0.1489 ^b	0.0466	0.254	-0.1676 ^d	0.0253	0.304
Nonbreeding ranges									
	<i>N</i> = 295			<i>N</i> = 158			<i>N</i> = 453		
Quadrats where rare	0.1577 ^d	0.0226	0.378	0.0809 ^b	0.0266	0.237	0.1323 ^d	0.0174	0.338
Intermediate quadrats	0.0586 ^b	0.0181	0.186	0.0700 ^b	0.0211	0.256	0.0603 ^d	0.0138	0.201
Quadrats where common	-0.1542 ^d	0.0191	0.427	-0.1173 ^d	0.0247	0.356	-0.1405 ^d	0.0150	0.403
Total ranges									
	<i>N</i> = 298			<i>N</i> = 158			<i>N</i> = 456		
Quadrats where rare	0.1589 ^d	0.0177	0.463	0.1097 ^d	0.0239	0.344	0.1461 ^d	0.0144	0.430
Intermediate quadrats	0.0665 ^d	0.0152	0.246	0.0952 ^d	0.0191	0.371	0.0742 ^d	0.0120	0.279
Quadrats where common	-0.1669 ^d	0.0165	0.507	-0.1759 ^d	0.0239	0.508	-0.1721 ^d	0.0136	0.511

* All regressions are arcsin (frequency) 1/2 vs log₁₀ (total number quadrats in particular type of range). *b* = regression coefficient, SE = standard error of regression coefficient, *R* = correlation coefficient

** Superscripts denote two-tailed probability of no difference from zero: ^a = 0.01 ≤ *P* < 0.05, ^b = 0.001 ≤ *P* < 0.01, ^c = 0.0001 ≤ *P* < 0.001, ^d = *P* < 0.0001

for the same data are total breeding or nonbreeding ranges). In contrast to fraction of quadrats where rare, regression slopes for fraction of quadrats where common plotted against range are significantly negative. Intermediate quadrats typically show intermediate results. All regression slopes are significantly different from zero; sample sizes are huge, however, and the data are somewhat dependent (see next section).

The net result of these comparisons is to show that spe-

cies having larger ranges tend to be rare in a greater fraction of their ranges and to be common in a lesser fraction of their ranges. Thus widespread species contribute disproportionately to rarity at any site, which as we have just seen, is mainly diffusive. Were this trend great, it would mean that the total number of rare occurrences, summed over species and quadrats, would come mainly from a few widespread species. However, as Table 3 and Fig. 10 show, the trend in absolute terms is very slight.

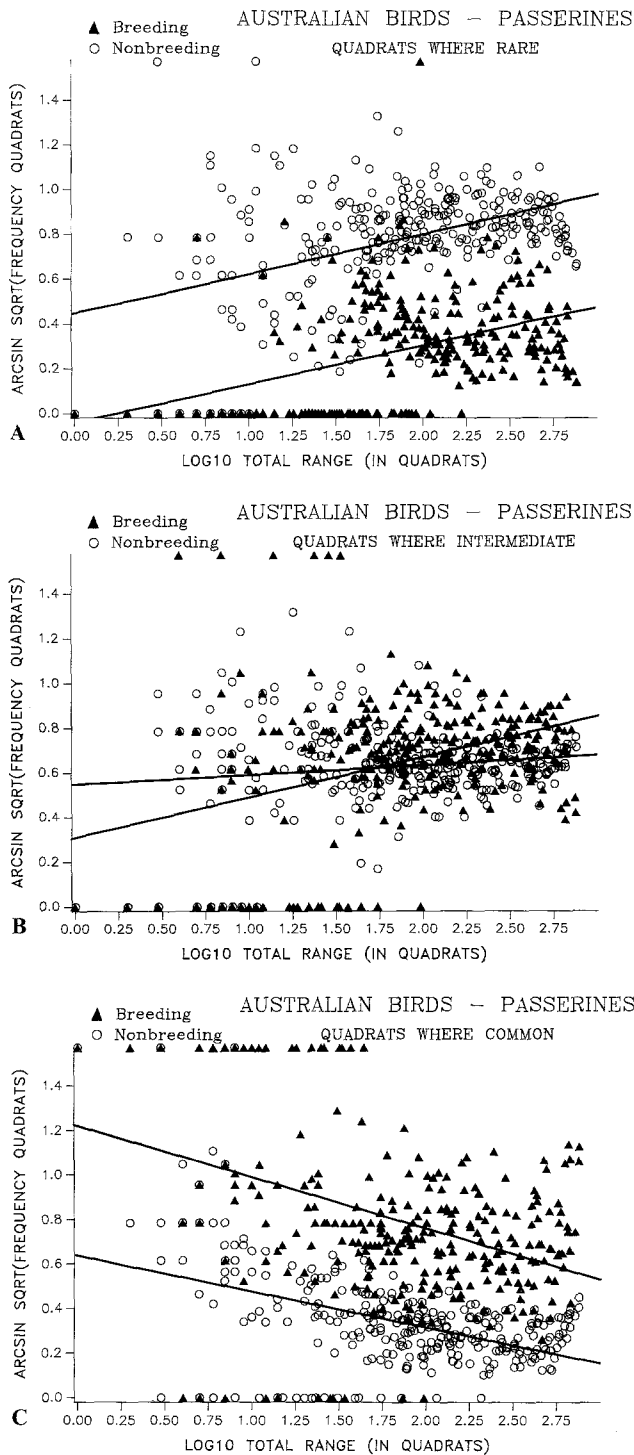


Fig. 10A-C. Frequency of quadrats where rare (A), intermediate quadrats (B) and quadrats where common (C) vs total range (breeding and nonbreeding)

Breeding and nonbreeding quadrats within particular groups (passerines, nonpasserines, all species combined) show no statistically significant differences in regression slopes (Table 3). On the other hand, huge differences in intercepts exist (Fig. 10). Because regressions on range size are significantly different from zero, yet breeding and nonbreeding quadrats do not differ in slope, analysis of covariance is suggested as a way to assess the significance of the differences between breeding and nonbreeding quadrats.

Arcsin transformed frequency was the dependent variable and \log_{10} total range size (breeding and nonbreeding, as in Fig. 10) the covariate. In all comparisons, statistical significance is extreme, with breeding data having a much smaller proportion of quadrats where rare than nonbreeding data and vice versa for quadrats where common (Table 4). Given the low magnitude of the covariate slope, differences between adjusted means from these ANCOVAs (Table 4) are only a slightly better estimate of differences between breeding and nonbreeding quadrats than are the raw data of Table 2.

Relation of the number of quadrats where rare to the number of quadrats where common

The previous analysis showed no significant differences between breeding and nonbreeding quadrats for any group. Regressions, however, are marred by the partial statistical dependence of the variables; the independent variable "total range size" is computed from the number of quadrats where rare, quadrats where common, and intermediate quadrats. The latter quantities and the total are also used in computing the fraction of the various quadrat types used as dependent variables. Were the total dominant numerically in the regression, a hyperbolically negative relation is expected as a "null" relationship. In fact, regressions are different in sign, and significantly so, rather than all being negative. Nonetheless, a treatment in which the variables are statistically entirely independent might reveal more differences between the types of quadrats than the previous analysis.

Toward this end, the number of quadrats where rare was regressed against the number of quadrats where common, and vice versa, for all groups. Because species ranges vary over about 4 orders of magnitude in the Australian data, and because some species ranges have no quadrats of one or the other type, the transformation $\log_{10}(N+1)$ was used. One might hypothesize that breeding quadrats should show less of a tendency to add quadrats where rare than to add quadrats where common as the total increase, as breeding ranges should contain individuals having a certain degree of commonness.

Although there is a lot of scatter, plots of rare vs common quadrats for breeding ranges appear roughly parabolic, whereas those for nonbreeding ranges appear more linear. Figure 11 gives these plots for passerines; other taxonomic groups have similar plots. Quadratic regression was used to test whether or not regressions are significantly parabolic – a significantly negative coefficient for the independent variable squared (the quadratic term) indicates a significant downturn of the plot, i.e., a parabolic curve.

As shown in Table 5, all three breeding-quadrat regressions have negative coefficients for the quadratic term; one (passerines) is significant ($0.01 < P < 0.05$), and one (all species) is marginally significant ($P = 0.051$). In contrast, nonbreeding-quadrat regressions have positive quadratic coefficients in two of three cases, and none is statistically different from zero. These results mostly support the hypothesis given above. But when regressions are reversed (common vs rare quadrats), signs are about the same and patterns are, if anything, stronger (Table 5). Hence, the best that can be concluded from these data is that breeding ranges have more globular plots than nonbreeding ranges; the latter seem to rise to some ceiling and then level off.

Table 4. Analysis of covariance for frequencies of various kinds of quadrats, classified by rarity: breeding vs nonbreeding frequencies compared. Covariate is \log_{10} (number quadrats in breeding plus nonbreeding range)

	F ^a	P	Adjusted Means ^b		Sample Sizes	
			Breeding	Nonbreeding	Breeding	Nonbreeding
Passerines						
Quadrats where rare	666.1	<0.0005	0.278	0.774	284	295
Intermediate quadrats	0.88	0.35	0.647	0.627	284	295
Quadrats where common	378.1	<0.0005	0.792	0.341	284	295
Nonpasserines						
Quadrats where rare	364.0	<0.0005	0.312	0.817	150	158
Intermediate quadrats	7.24	0.008	0.681	0.603	150	158
Quadrats where common	149.8	<0.0005	0.724	0.330	150	158
All species						
Quadrats where rare	1028	<0.0005	0.290	0.789	434	453
Intermediate quadrats	5.56	0.019	0.659	0.619	434	453
Quadrats where common	525.4	<0.0005	0.769	0.337	434	453

^a With 1 df

^b arcsin (frequency) 1/2 in radians

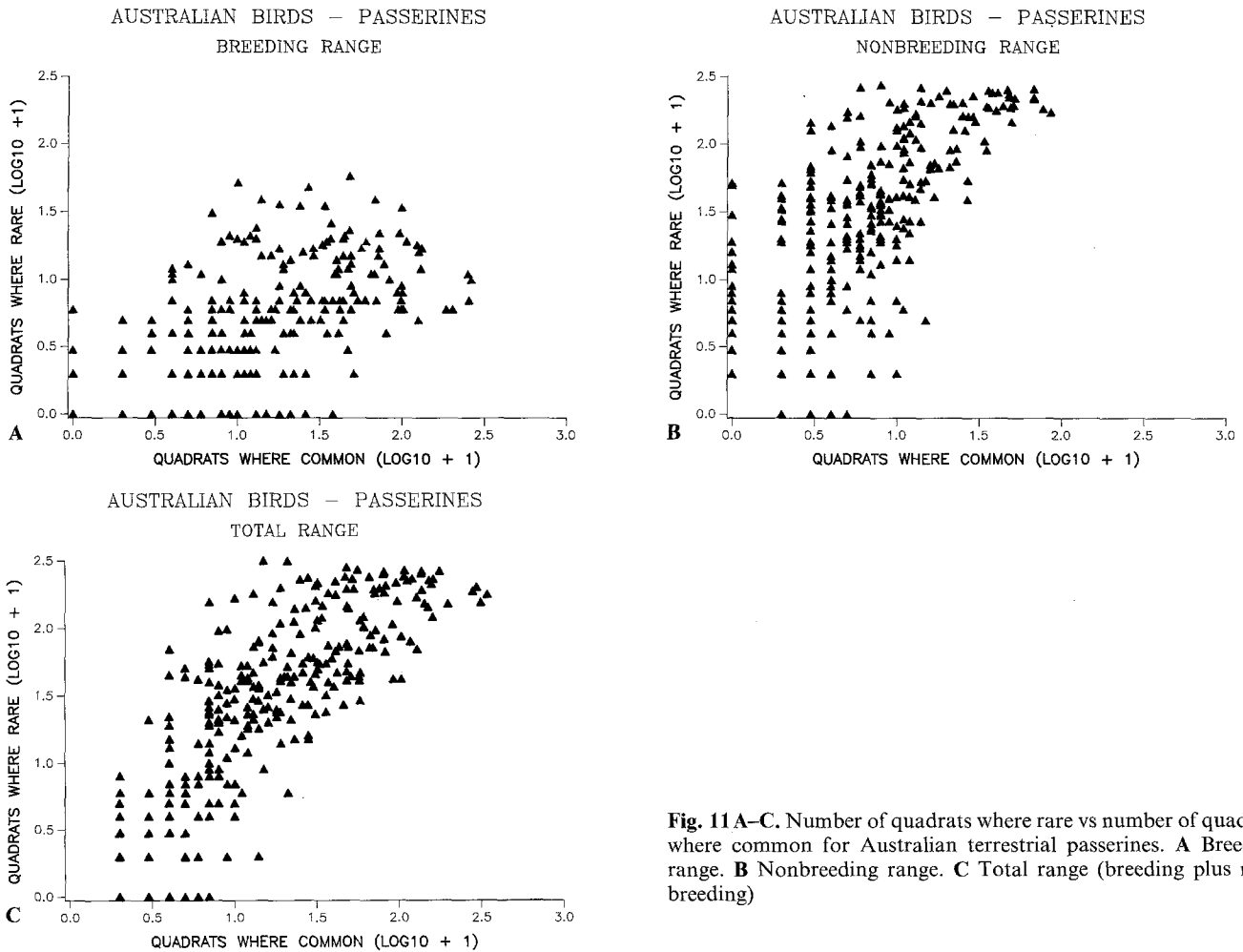


Fig. 11A-C. Number of quadrats where rare vs number of quadrats where common for Australian terrestrial passerines. **A** Breeding range. **B** Nonbreeding range. **C** Total range (breeding plus nonbreeding)

Another kind of ambiguity mars the quadratic analysis. While no statistical dependency exists, two physical dependencies are likely. The first is that numbers of quadrats where rare and numbers of quadrats where common should be correlated if there is *any* tendency for regressions to

have fixed proportions of the types, because the larger the range, the larger the number of each type of quadrat. In apparent agreement, for all but two of the regressions the coefficient of the linear term is positive (Table 5), and these two are not significant. The second is that if there exists

Table 5. Quadratic regression statistics for number of quadrats where rare on number of quadrats where common, or vice versa*

	Rare on Common			Common on Rare		
	b^{***}	b^2	R	b	b^2	R
Breeding Ranges**						
Passerines	0.900 ^d	-0.149 ^a	0.681	1.240 ^d	-0.349 ^b	0.686
Nonpasserines	0.544 ^a	-0.050	0.484	0.988 ^d	-0.338 ^a	0.506
Total	0.754 ^d	-0.106	0.613	1.180 ^d	-0.365 ^d	0.626
Nonbreeding Ranges						
Passerines	0.851 ^d	0.115	0.675	-0.148	0.235 ^d	0.720
Nonpasserines	1.165 ^c	-0.138	0.648	0.025	0.158 ^b	0.666
Total	0.981 ^d	0.011	0.666	-0.082	0.204 ^d	0.701
Total Ranges						
Passerines	2.018 ^d	-0.380 ^d	0.815	0.234 ^a	0.148 ^d	0.810
Nonpasserines	2.045 ^d	-0.455 ^c	0.717	0.295	0.080	0.694
Total	2.033 ^d	-0.408 ^d	0.776	0.285 ^c	0.108 ^c	0.762

* All regressions use $\log_{10}(N+1)$ for all variables. b = regression coefficient for linear term, b^2 = regression coefficient for quadratic term, R = multiple correlation coefficient

** Sample sizes as in Table 3

*** Superscripts denote two-tailed probability of no difference from zero: ^a = $0.01 \leq P < 0.05$, ^b = $0.001 \leq P < 0.01$, ^c = $0.0001 \leq P < 0.001$, ^d = $P < 0.0001$

an upper limit to range size (which here would be the entire continent of Australia, 810 quadrats), for randomly selected data ranges with many quadrats where common must have few quadrats where rare and vice versa (see Figs. 2–4 for range sizes). This would cause the plots eventually to bend downwards toward either axis, which perhaps is happening in the nonbreeding and total regressions. It is difficult to argue that anything more than these physical constraints is needed to explain the signs resulting from quadratic regression.

Relation between number of quadrats of each kind within a species' range for quadrats having adjacent degrees of rarity (a test of patchiness)

Above I argued that if quadrat size is of the same order as individual species' patch sizes, an artifactually large number of quadrats where rare (and quadrats where common) might be obtained. In the present study, quadrats are 1° -blocks (10^4 km²), huge areas that are unlikely to be this small. Average home-range sizes for terrestrial birds vary from 10^{-2} to 10^1 km² (Schoener 1968), so that if patchiness is at the scale of home ranges, it is on average about 10^{-4} – 10^{-5} as much as quadrat size. Nor does inspection of the individual species' maps (e.g., Figs. 7–9) suggest any marked patchiness in types of quadrats – rather smooth gradients from common to rare seem the rule. Nevertheless, the test suggested above, to ascertain if species with mainly quadrats where rare have more intermediate quadrats (i.e., “adjacent” quadrats) than quadrats where common (i.e., “nonadjacent” quadrats), and vice versa, was performed, as it was relatively simple to do so.

The following values were obtained for the first and second types of tests just listed, respectively, where “adjacent” means that the patchiness hypothesis is not supported (ties are excluded): Breeding passerines (adjacent vs nonadjacent: 8 vs 2, 91 vs 3); all passerines (adjacent vs nonadjacent: 123 vs 13, 29 vs 9); breeding nonpasserines (adjacent

vs nonadjacent: 6 vs 0, 43 vs 2); all nonpasserines (adjacent vs nonadjacent: 8 vs 2, 9 vs 4). Thus there is certainly no overwhelming degree of patchiness suggested by these data, and the opposite seems more likely: according to this test at least, the quadrat scale of the present study is appropriate. One caveat exists, however; the smoothing process described under “methods” could have resulted in more intermediate quadrats than in the actual distributions. It is impossible to assess how serious this problem is, except to point out again that many of the quadrats required little or no smoothing.

Discussion

The main empirical conclusion of this paper is that, among Australian terrestrial birds, diffusive rarity is the more common by far. In other words, the vast majority of species that are rare at any particular locality (quadrat) are common in a substantial fraction of other localities within their ranges. This is particularly true of species in their breeding ranges but is true for total ranges, breeding and nonbreeding, as well. Widespread species, because they have somewhat more localities (quadrats) in which they are rare, disproportionately contribute to the trend but not nearly so much as to invalidate conclusions about the “typical” rare occurrence. No evidence was found for ranges at this scale to be patchy in occurrence rarity and commonness; rather, evidence suggests relatively smooth gradients from common to rare regions. This picture agrees with the one painted by Brown (1984) with different data and methodology, except for the conclusion about the relation of rarity to total range size.

Species occur much more commonly in their breeding ranges than in their nonbreeding ranges. The latter contain substantially more quadrats on average (see below), so that localities (quadrats) where species are rare are much more likely to be those where they do not breed than where they do breed. Much overall distributional rarity appears to be

caused by diffusion of individuals away from their species-specific breeding ranges. Moreover, if occurrence and abundance rarity are substantially correlated, as we have argued they should be and supported with some indirect evidence above, species must typically occur in their breeding ranges at some relatively high density, i.e., minimum-population-size requirements are suggested (e.g., Goel and Richter-Dyn, 1974).

Along with these conclusions, we need to recall that the atlas data forced two decisions upon us that may not have been made the same way were they guided by the objectives of the present study.

First, numerical designations of quadrats where rare, intermediate quadrats, and quadrats where common followed those in the atlas. Although Blakers et al. (1984) do not discuss this, presumably the boundaries of 11 and 40 percent were set to provide roughly equal numbers of quadrats of each of the three kinds. In fact, numbers summed over all terrestrial species (marine and fresh water species are also included in the atlas) are as follows (rare, intermediate, common): Passerine breeding ranges: 1697, 6042, 6722; nonpasserine breeding ranges: 929, 2976, 2521; passerine total ranges: 18853, 17400, 9435; nonpasserine total ranges: 13408, 10941, 4424. Breeding ranges have more quadrats where common, total ranges have even more (absolutely) where rare. Obviously, it is possible to define rarity or commonness out of existence by other choices of boundaries, but the present choice is reasonably satisfactory here because a substantial number of all three quadrat types result and choice was made without regard for expectations of the present study. The most reasonable change would be to shift boundaries downward, making the three types closer to equality for total ranges. Then, however, distributions would shift even farther from suffusive rarity than they now are. It should also be noted that the category " $<11\%$ " is the only one likely to change totals much, as certain quadrats now scored as zero occurrence (and hence not even considered) will almost certainly be added to this category as more information accumulates. This kind of change would shift distributions toward the right of the rarity continuum, i.e., toward suffusive rarity, but given the smoothing of occurrence frequencies in the atlas (see above), the effect would likely be quite small.

Second, we had to use occurrence rarity only; we could not evaluate abundance rarity in addition. While the two should be strongly correlated, some conspicuous species will be frequently sighted yet occur at low densities, e.g., many raptors. It might be thought that abundance rarity is more desirable for this kind of analysis. Perhaps in some ways it is, but on the other hand, one might not really wish to consider rare a raptorial or other species that occurred at low densities but was seen in nearly all censuses. Were abundance rarity (either relative or absolute) used in this kind of analysis, perhaps it would be best to scale it to the abundance of the species (or kind of species) considered, averaged over the entire range. Use of occurrence rarity, because it ignores moderate-to-large differences in abundance, to some extent effects such a scaling and brings low and high density species to a more equal footing than would use of abundance rarity.

An implication of these data seems to be that to preserve most of the species recorded as rare, summed over localities, one should concentrate on preserving the "centers" of abundance of such species, i.e., those places where the spe-

cies are common. This suggests that attention be given to the particular geographic location of preserves. The latter has perhaps received less recent attention than that devoted to the sizes of preserves (e.g., Diamond 1976; Simberloff and Abele 1976; Terborgh 1976; Wilcox and Murphy 1985; Quinn and Harrison, unpublished work). Put in a more common-sense fashion, where immigration from elsewhere is the major origin of those individuals comprising most of the rare species in some place, preservation of immigration sources is essential. Concentrating on the spatial distribution of rarity, and in particular on centers of abundance, is quite important where rarity is diffusive, probably more so than concentrating on size of preserves. The latter would perhaps be more important were most species suffusively rare, i.e., occurred as rare species most places in their ranges. Certainly, suffusively rare species may more often be those designated "endangered;" the latter species are also likely to have small geographic ranges. Endangered species with small ranges are unlikely to contribute much to the total number of rare species recorded in all censuses throughout a large region, even though conservation efforts may be differentially (and of course rightly) directed towards them. It is also recognized that the scale of my study may be coarser than that practical for preserve size in some cases.

To what extent are the results with Australian terrestrial birds typical of similar analyses using other organisms? As this is the first such analysis, one can only speculate. Several features of our study taxon may predilect it toward diffusive rarity.

First, Australian birds are distributed across a vast land area with few major structural barriers (e.g., mountains, seas), and much of which is unproductive. Expansion and contraction of ranges, and unsuitability of much of the area much of the time, should favor diffusive patterns. In contrast, birds able to exist at all on small islands may be chronically more likely to fill the entire island, resulting in a more even spatial distribution of occurrence and abundance. This contrast has already been suggested to exist between open and closed systems (summary in Wiens et al. 1986; Schoener 1986); e.g., the North American shrubsteppe birds studied by Wiens (1986) and Rotenberry vs the Galápagos island birds studied by Grant (1986) and Schluter, among others.

Second, birds are extremely mobile, often to the point of nomadism, and it may be that because of the openness and barrenness of much of the terrain, Australian birds are even more mobile than other continental birds. Mobile organisms might diffuse readily from centers of abundance, especially during nonbreeding times, causing much rarity to be immigrant-related. Nomadism may also thin out the ranges of widespread species, giving the opposite relation between rarity and range size (a positive one; Fig. 10) than those found by Brown (1984) and Bock and Ricklefs (1983). Other terrestrial taxa are mostly less mobile than birds, either because of their terrestrial locomotion (e.g., most mammals and reptiles), or sessile adult stage (plants), or their small size (e.g., arthropods).

Possibly the above differences will result in the phenomena reported here to exist on a smaller scale for other organisms, so that most instances of rarity in the latter, e.g., prairie grasses (Rabinowitz 1981), are indeed contributed by suffusively rare species. Certainly analyses for other groups similar to the present one should be quite intriguing,

in part because of such differences. A problem with many taxa, e.g., nearly all insects, however, is that we just don't have the distributional information that now exists for certain birds – what may appear suffusively rare with incomplete information may turn out to be diffusively rare when more thoroughly known. At the least, centers of commonness should be looked for in such organisms, particularly where preservation is an issue.

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