Species densities of terrestrial vertebrates in Australia. Chapter 59 in A. Keast (ed.) Ecological Biogeography ...

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Geographic distributions of many Australian vertebrates are still imprecisely known. Nevertheless, approximate range maps are now available for marsupials, birds, amphibians and reptiles (Marlow, 1962; Slater, 1971, 1975; and Cogger, 1975). We exploit this data base here to examine geographic patterns in numbers of species, or 'species densities', of various taxonomic groups of vertebrates (excluding fish). Broad patterns emerging from our analysis will presumably be altered little by further refinements in taxonomy and known geographic distributions.

Following the quadrate technique of Terent'ev (1963) and Simpson (1964), we partitioned the Australian continent into 160-odd squares 150 miles (about 240 km) on a side. Using transparent overlays, we then tallied up the approximate numbers of species in various vertebrate taxa that occur in each grid. Resulting data matrices reveal various geographical trends such as latitudinal gradients in diversity as well as patterns of taxonomic complementarity (inverse correlations between the species densities of two taxa). Moreover, when coupled with information on crucial climatological variables, correlation and multivariate analyses elucidate the relative importance of various abiotic environmental factors for different groups. Finally an intercontinental comparison with the vertebrates of the continental U.S.A. reveals both general trends as well as intriguing differences between continents.

Numbers of species in various taxonomic groups included in the present analysis are as follows: marsupials (116), passerines (336), non-passerines (259), frogs (133), turtles (16), snakes (101) and lizards (351). Marine forms, such as sea birds, sea turtles and sea snakes, are excluded.

1. Geographical patterns in numbers of species

All groups examined, except lizards, tend to be most diverse in the peripheral regions of heavier rainfall. In contrast, most lizard groups, especially the agamids and geckos, reach their highest species densities in the arid inland areas. Skincid lizards in the genus *Ctenotus* are also most diverse in the Center. Lizard species densities, expecially those of agamids and varanids, tend to be somewhat lower in the east than in the west (correlation coefficients for agamids and varanids versus longitude over all 161 squares are, respectively, −0.64 and −0.59, P's$<$0.001). Species densities of non-*Ctenotus* skinks (146 species total) follow the avian and

Editor's note: Correlation coefficients between any two variables range from −1.0 to +1.0: these endpoints represent, respectively, a perfect inverse correlation (larger values of one variate are invariably associated with smaller values of the other) and a perfect positive correlation (a direct one-to-one correspondence exists between variables – given one, the other can be predicted exactly). A correlation coefficient of zero reflects a graph with perfect 'shotgun scatter' and no tendency between the two variables *x* and *y*. Thus a value of, say +0.68 is a moderately strong positive correlation (as in Fig. 11), whereas one of −0.64 (as in Fig. 14) indicates a moderately strong inverse relationship between variables.

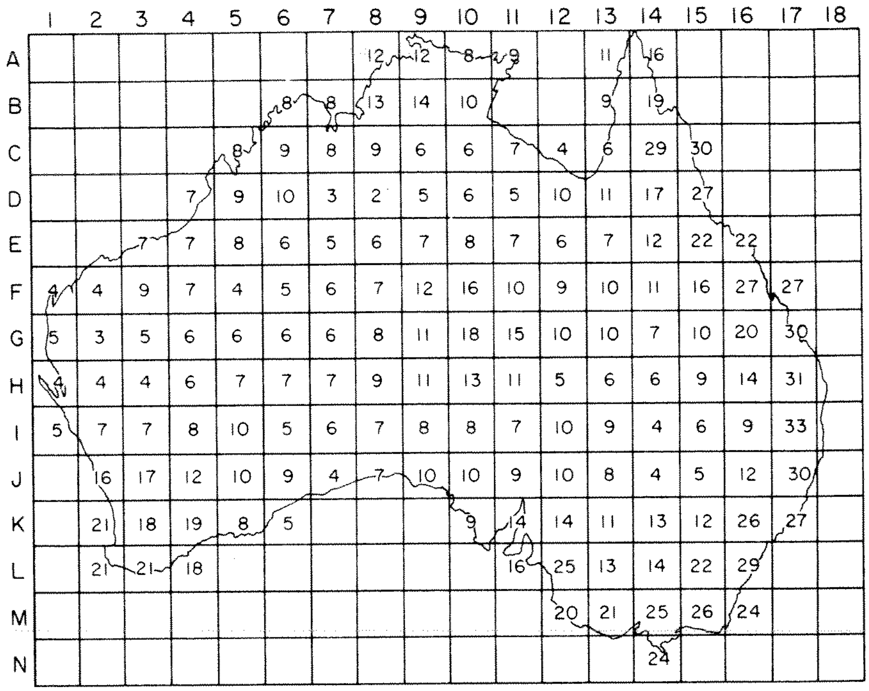

Fig. 1. Marsupial species density (116 species).

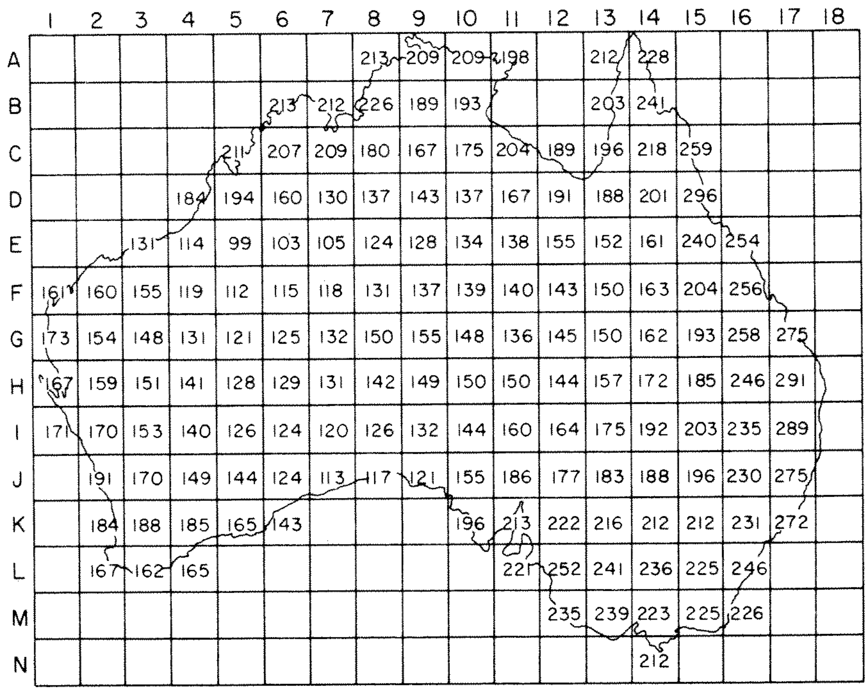

Fig. 2. Bird species density (595 species).

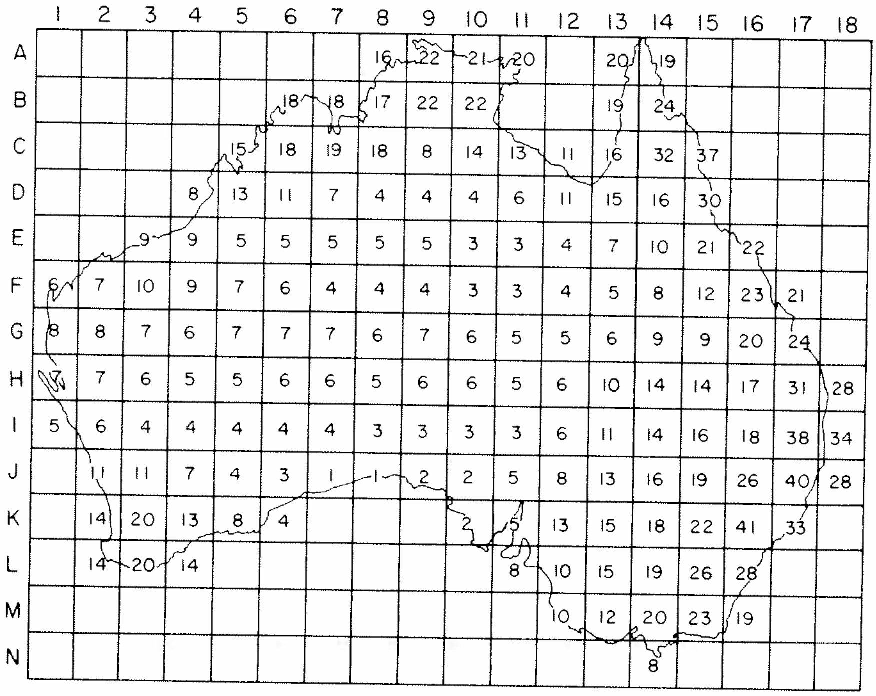

Fig. 3. Frog species density (133 species).

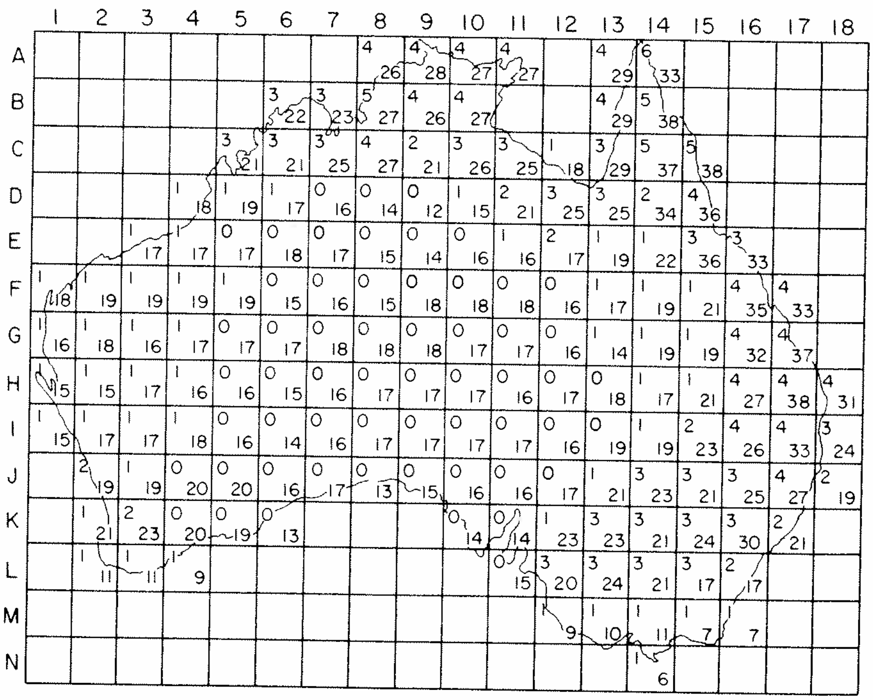

Fig. 4. Turtle and snake species densities (16 and 101 species, respectively).

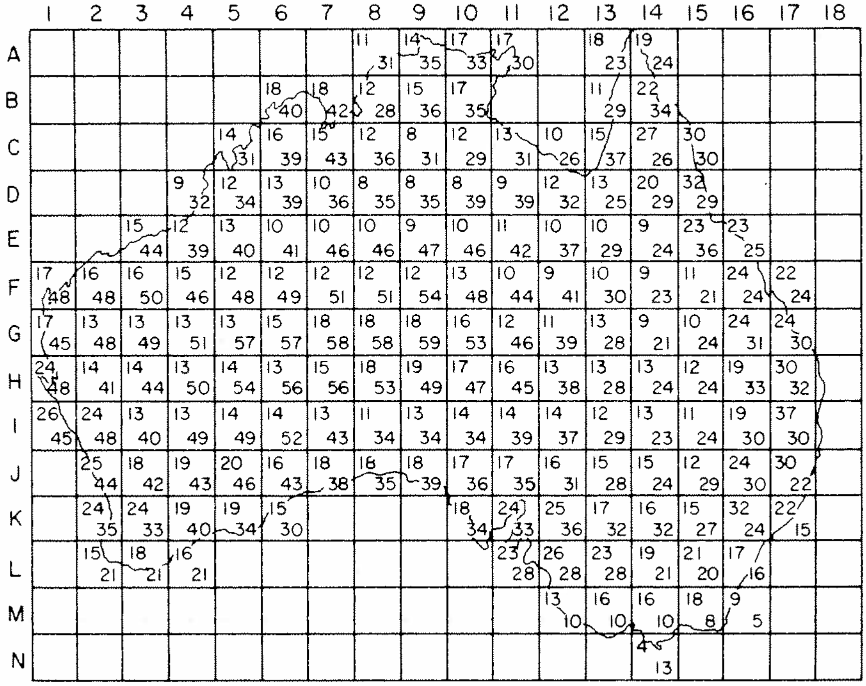

Fig. 5. Numbers of species of non-*Ctenotus* skinks (above) and other lizards (below).

mammalian pattern with higher numbers of species in wetter regions. Because of this dichotomy among Australian lizards, non-*Ctenotus* skinks are treated separately from the more typical dry-adapted lizard species throughout the remainder of this paper. Total numbers of species of marsupials, birds, frogs, turtles, snakes, non-*Ctenotus* skinks and dry-adapted lizards estimated to occur in each quadrate are shown in Figs. 1, 2, 3, 4 and 5.

2. Latitudinal trends

Monotonically increasing latitudinal gradients in species densities towards the tropics, so celebrated in the literature (Wallace, 1878; Fischer, 1960; Pianka, 1966), are essentially non-existent in terrestrial vertebrates of Australia (Figs. 6, 7, 8, 9 and 10). Nevertheless, distinct latitudinal patterns in species densities, presumably related to trends in annual rainfall, do occur. The average number of parrot species tends to increase slightly towards **higher** latitudes (Fig. 8): the correlation coefficient of parrot species density with latitude over all 161 squares is $+0.50$ ($P<0.001$). The average number of species of hawks at a given latitude is fairly flat across Australia (Fig. 8), as is snake species density over most of the mid latitudes (Fig. 9). At very high and very low latitudes, however, the average number of species of snakes decreases and increases, respectively. Also, recall that snake species densities tend to be reduced in the interior (Fig. 4). Using all 161

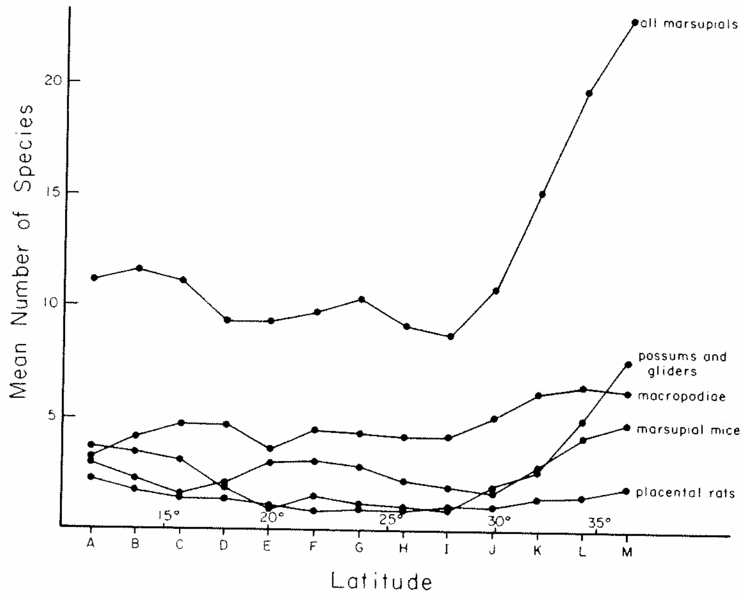

Fig. 6. Average number of species of marsupials occurring at each latitude. Placental rats are also shown.

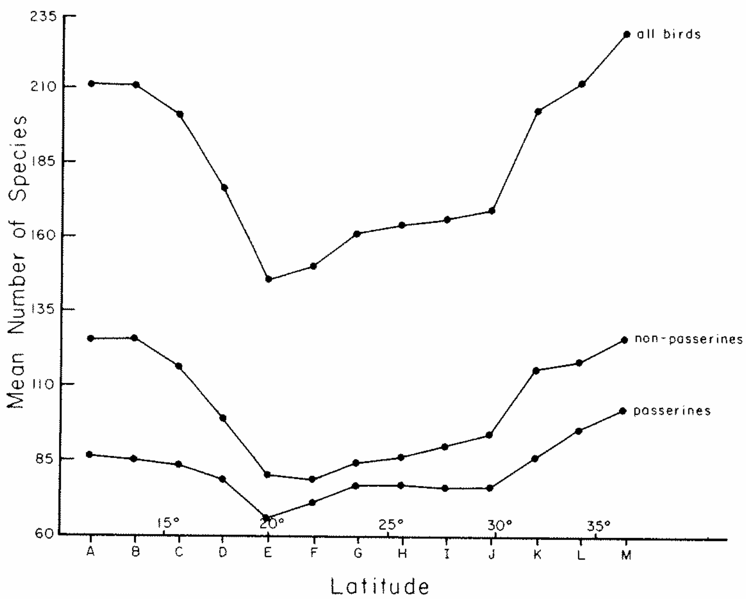

Fig. 7. Average numbers of bird species occurring at each latitude.

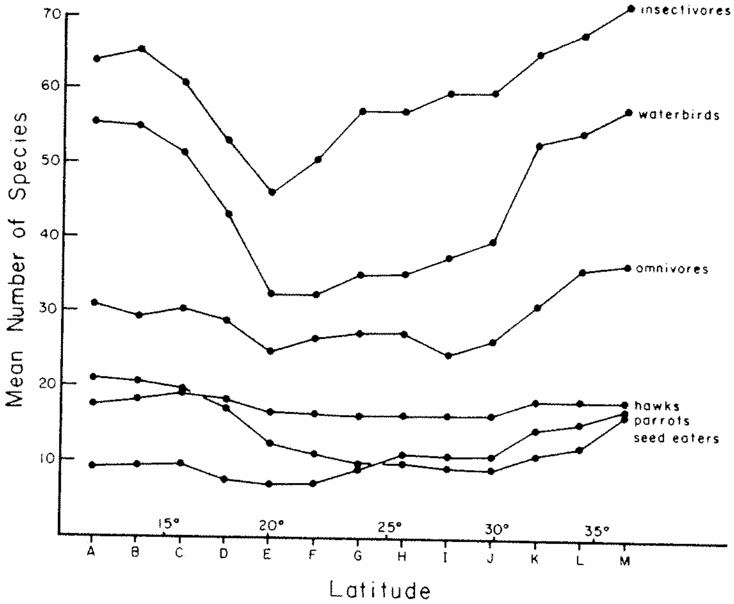

Fig. 8. Average species densities of various avian groups by latitude.

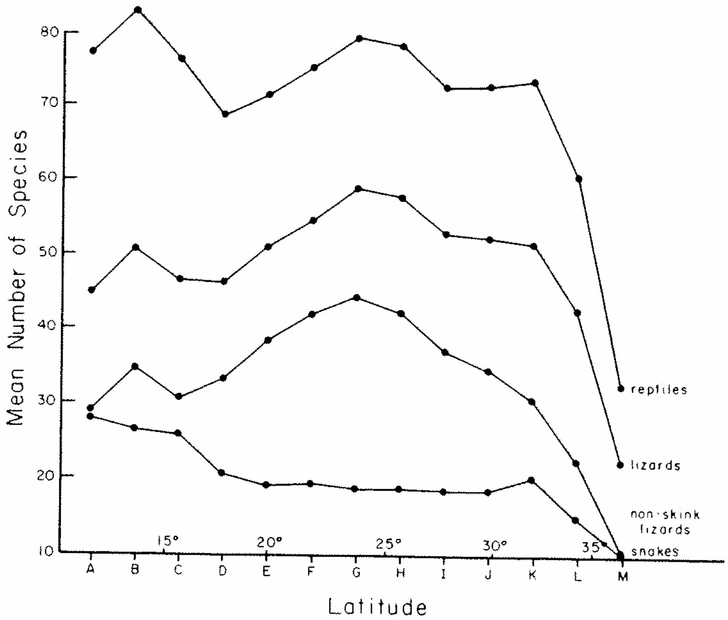

Fig. 9. Average species densities of major reptilian groups by latitude.

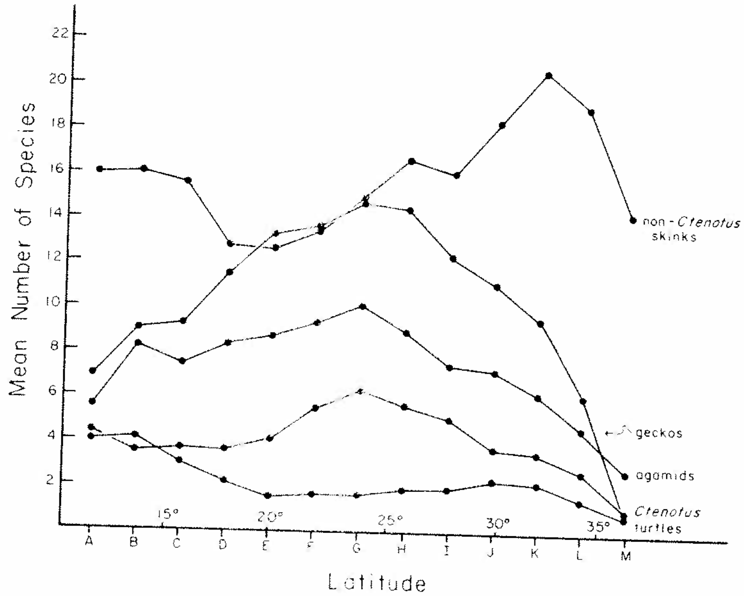

Fig. 10. Average species densities of various lizard groups and turtles by latitude.

squares, snake species numbers are negatively correlated with latitude ($r = -0.47$, $P < 0.001$). As indicated above, most avian groups are richer at the northern tropical, wet eastern coast, and the southern wet temperate margins of the continent than they are in the dry interior (Figs. 2, 7 and 8). In marked contrast, most lizard groups (excluding the non-*Ctenotus* skinks) follow the opposite pattern, attaining their greatest species richness near the tropic at middle latitudes (Figs. 5, 9 and 10). Marsupial species density is high along the wet eastern coast and in the wet southeast and southwest (Fig. 1). The average number of species of marsupials at a given latitude is fairly flat over the northern two-thirds of the continent but climbs abruptly in the wet southern fringe (Fig. 6).

3. Wet tropics versus wet temperate zones

To compare species densities of various groups in the tropics with those in the temperate zones in areas with similar annual rainfall, we selected 15 tropical squares corresponding roughly to the Cape York Peninsula south to about latitude 20°S plus most of the Darwin–Arnhem Land area and compared these with 15 wet temperate zone squares consisting approximately of Victoria and the southernmost part of New South Wales plus the wet southwestern corner (roughly from Geraldton to Albany). Table 1 summarizes the average numbers of species of various groups in each of these regions. Somewhat surprisingly, the wet temperate area supports as many avian species as does the wet tropics (except for seed-eating birds). Interestingly enough, except for lizards, reptile species densities tend to be significantly higher in the tropics whereas marsupials show the opposite

Table 1. Mean number of species in 15 wet tropical and 15 wet temperate squares. Standard deviation, Mann-Whitney 'U' statistic and significance levels are also given.

Taxonomic group	Wet tropics		Wet Temperate		'U' Test results	
	$\bar{X}$	SD	$\bar{X}$	SD	'U'	P
All Marsupials	15.5	7.6	21.1	4.5	55.0	<0.01
Macropods	5.5	3.4	6.5	1.5	41.5	<0.01
Marsupial Mice	3.1	1.3	4.5	1.2	9.0	<0.0001
All Birds	217.9	29.3	216.0	29.5	117.5	>0.05
Passerines	92.7	16.4	95.1	18.4	66.5	<0.05
Non-Passerines	125.3	15.0	120.9	13.0	101.0	>0.05
Water Birds	53.9	4.9	55.3	4.2	107.5	>0.05
Insectivorous Birds	68.5	11.6	68.5	11.2	107.5	>0.05
Omnivorous Birds	33.7	7.3	34.4	7.3	100.5	>0.05
Seed-eating Birds	21.5	4.6	13.7	3.4	17.5	<0.001
Frogs	22.1	6.3	17.4	5.7	160.0	>0.05
All Reptiles	83.0	11.7	56.7	21.4	35.5	<0.001
Turtles	4.1	1.0	1.7	0.9	12.5	<0.0001
Snakes	30.9	4.6	15.2	6.0	0.5	<0.0001
All Lizards	48.0	7.8	39.8	15.6	75.0	>0.05

trend with more species in the temperate zone than in the tropics. Frogs, dry-adapted lizards and non-*Ctenotus* skinks do not differ significantly in species numbers between the wet tropics and the wet temperate zones.

4. Correlations with environmental factors

We computed correlations between species densities of various groups in each of the 161 squares and five climatological variables: (1) average total annual number of hours of sunshine, (2) average annual precipitation, (3) coefficient of variation in annual precipitation, (4) average annual temperature, and (5) length of the growing season as measured by the average number of frost-free days (most Australian climatic data were obtained from Gentilli, 1974). Results are summarized in Tables 2 and 3. The taxa fall into two major (and several minor) groups: (1) typical dry-adapted lizards reach highest diversities in sunny, dry, warm places with variable rainfall (Fig. 11), and (2) all other groups are most diverse in less sunny, wetter places with less variability in annual rainfall. The latter group divides into three subgroups: turtles, snakes and seed-eating birds have diversified in warmer regions while marsupials, non-*Ctenotus* skinks, passerines and insectivorous birds reach their highest diversities in somewhat cooler zones (Table 3). Frogs and non-passerines are intermediate in that species numbers show no correlation with annual temperature (Table 3).

Numbers of species of dry-adapted lizards are plotted against annual hours of sunshine in Fig. 11, while Figs. 12 and 13 plot species densities of birds and frogs, respectively, against average annual precipitation.

Table 2. Correlation coefficients between various taxonomic groups and five climatological variables over the 161 squares. Coefficients greater than 0.16 are significant at the $P<0.05$ level, those greater than 0.21 at the $P<0.01$ level and those greater than 0.32 are significant at the $P<0.001$ level.

Taxonomic Group	Annual hours of sunshine	Annual precipitation	C. V. precip.	Annual temp.	Frost-free days
Marsupials	−0.67	0.54	−0.39	−0.33	−0.30
All Birds	−0.63	0.69	−0.43	−0.07	−0.11
Passerines	−0.59	0.59	−0.32	−0.19	−0.22
Non-Passerines	−0.61	0.71	−0.47	0.01	−0.03
Water Birds	−0.62	0.67	−0.50	−0.01	−0.03
Insectivorous Birds	−0.60	0.57	−0.32	−0.25	−0.27
Omnivorous Birds	−0.56	0.59	−0.33	−0.13	−0.16
Seed-eating Birds	−0.48	0.80	−0.43	0.33	0.26
Frogs	−0.56	0.73	−0.44	0.04	−0.10
All Reptiles	0.24	0.02	0.21	0.30	0.18
Turtles	−0.45	0.77	−0.45	0.34	0.20
Snakes	−0.18	0.57	−0.18	0.43	0.28
All Lizards	0.44	−0.37	0.40	0.09	0.04
Non-*Ctenotus* Skinks	−0.42	0.28	−0.15	−0.25	−0.28
All Other Lizards	0.68	−0.54	0.50	0.22	0.18
Agamids	0.59	−0.47	0.40	0.24	0.19
Geckos	0.73	−0.52	0.67	0.25	0.18
Ctenotus	0.42	−0.40	0.22	−0.02	−0.03
Varanids	0.49	−0.23	0.34	0.46	0.42

Table 3. Various taxa placed into ecological groupings based on the signs of correlations between their species densities and environmental variables.

Taxonomic group	Hours of sunshine	Annual precip.	C. V. in precip.	Annual temp.	Frost-free days
Marsupials	−	+	−	−	−
Non-*Ctenotus* Skinks	−	+	−	−	−
Passerines, Insectivorous and Omnivorous Birds	−	+	−	−	−
Non-Passerines and Water birds	−	+	−	0	0
Frogs	−	+	−	0	0
Seed-eating Birds	−	+	−	+	+
Turtles	−	+	−	+	+
Snakes	−	+	−	+	+
Dry-adapted Lizards	+	−	+	+	+

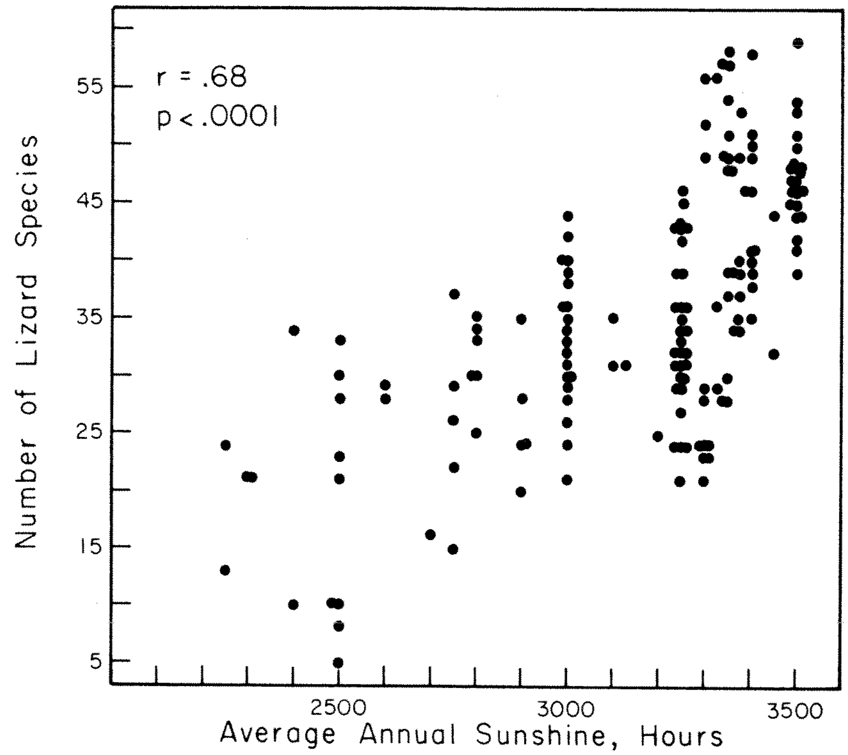

Fig. 11. Number of dry-adapted species of lizards (all lizards except non-*Ctenotus* skinks) plotted against average annual hours of sunshine.

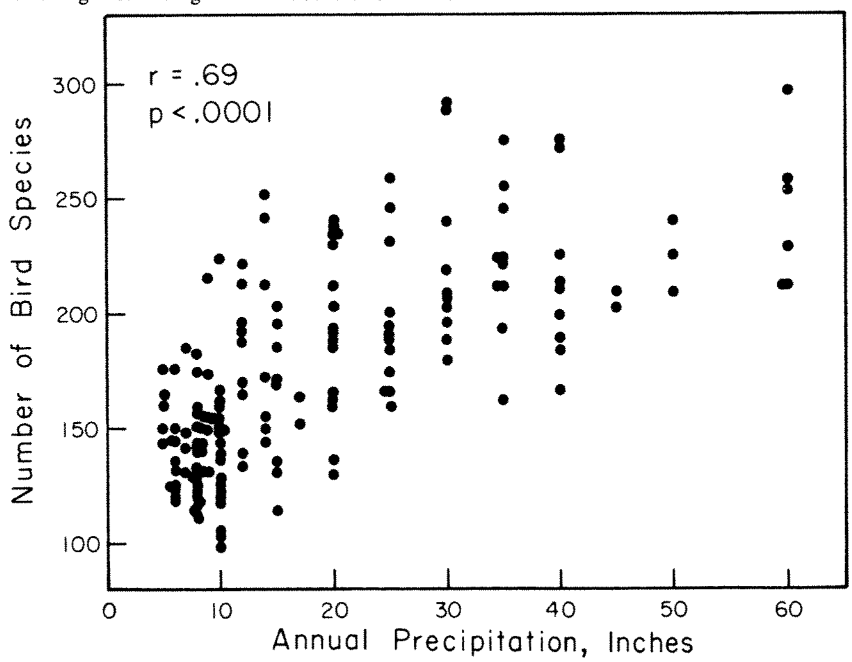

Fig. 12. Number of species of birds plotted against average annual precipitation.

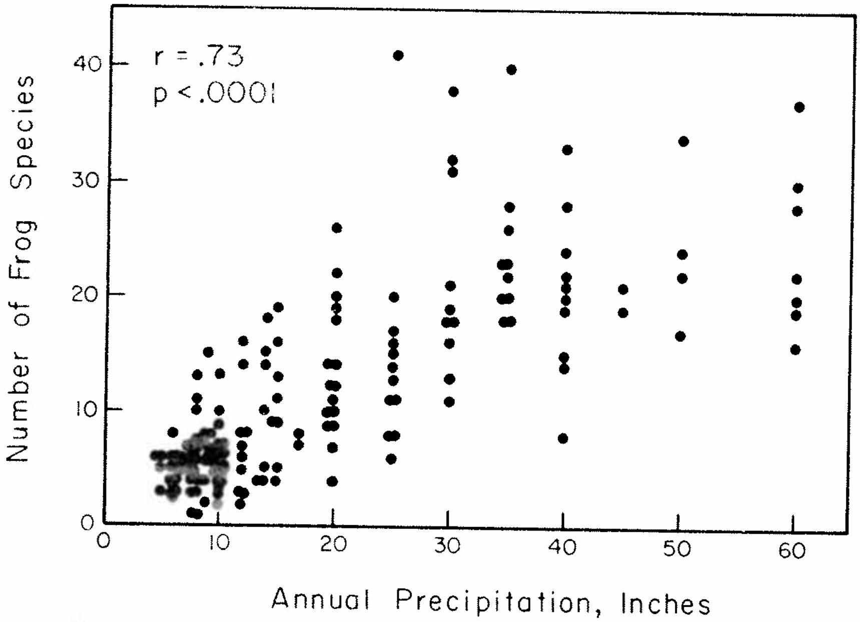

Fig. 13. Number of frog species plotted against average annual precipiation.

Because many of the five climatic variables are variously intercorrelated (r's range from -0.67 to 0.84 – see Schall & Pianka, 1978), we used partial correlation to hold constant the effects of one or more variables in stepwise multiple regressions. The resulting relationship between residual unexplained variance in species density and a given climatic variable was thus used to order variables by the degree to which they reduce the residual variance. Such stepwise multiple regressions using the five climatic variables as independent variables reduce variance in species densities by the following amounts: marsupials (60%), birds (59%), frogs (65%), turtles (62%), snakes (45%), all lizards (only 22%), non-*Ctenotus* skinks (29%) and other 'dry-adapted' lizards (50%) (see also Table 6).

5. Taxonomic complementarity

Community structure could well be influenced by competition between higher taxa. For example, Brown & Davidson (1977) presented convincing evidence for competition between granivorous ants and rodents in the North American desert. In comparing factors influencing the diversity of desert mammals in Australia and North America, Morton (1977) suggests that seed-harvesting ants and granivorous birds may partially replace seed-eating rodents on the former continent. G. M. Storr (personal communication) once suggested that Australian budgerigahs could well be ecological replacements for American pocket mice (*Perognathus*) and kangaroo rats (*Dipodomys*), since these small seed-eating parrots breed rapidly and form dense populations following spinifex (*Triodia*) seeding after heavy desert

Table 4. Matrix of correlation coefficients of species densities between various taxonomic groups over all 161 squares to show taxonomic complementarity between dry-adapted lizards and birds.

	Marsupials	Birds	Passerines	Non-Passerines	Insectivorous birds	Omnivorous birds	Seed-eating birds
Marsupials	—	0.72	0.77	0.64	0.76	0.72	0.61
Frogs	0.71	0.83	0.79	0.80	0.77	0.80	0.78
All Reptiles	0.05	0.08	0.08	0.07	0.15	0.06	0.15
Turtles	0.44	0.76	0.65	0.78	0.65	0.67	0.79
Snakes	0.37	0.60	0.55	0.60	0.56	0.55	0.71
All Lizards	−0.19	−0.32	−0.28	−0.33	−0.19	−0.30	−0.29
Non-*Ctenotus* Skinks	0.62	0.60	0.61	0.55	0.68	0.55	0.41
Dry-adapted Lizards	−0.51	−0.64	−0.60	−0.63	−0.54	−0.59	−0.52
Agamids	−0.48	−0.63	−0.60	−0.61	−0.54	−0.63	−0.47
Geckos	−0.42	−0.50	−0.41	−0.53	−0.39	−0.37	−0.37
Varanids	−0.50	−0.43	−0.49	−0.36	−0.43	−0.48	−0.27

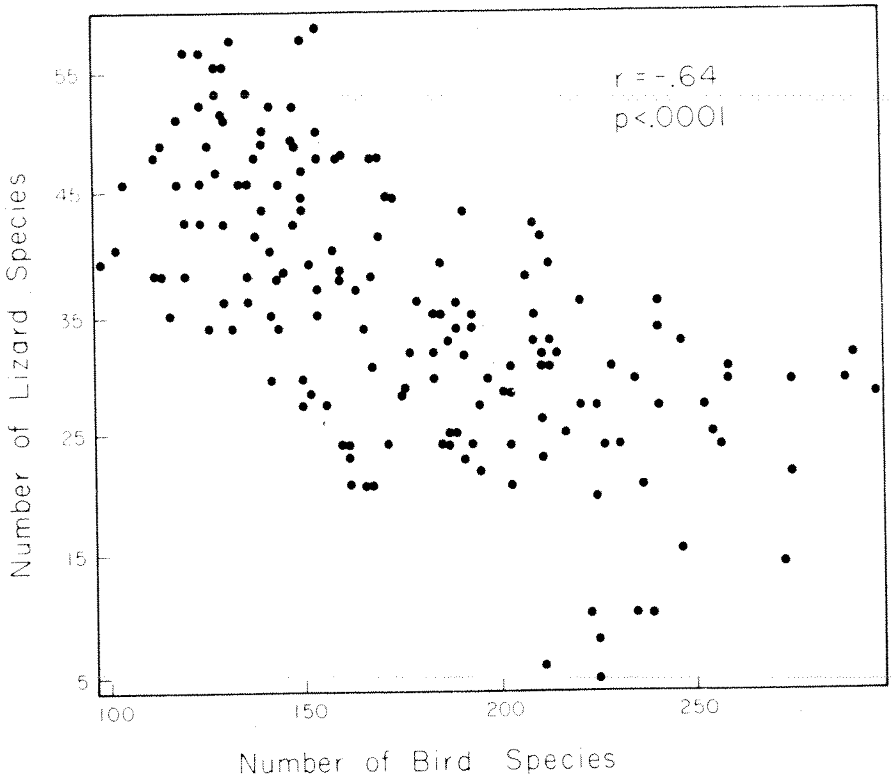

Fig. 14. Plot of species density of dry-adapted lizards versus number of bird species.

rains. Such taxonomic complementarity might be reflected in inverse correlations between the species densities of pairs of higher taxa.

Some of the more interesting correlations among various taxa over the 161 squares are summarized in Table 4. Correlations among the various avian groups (not shown) are all positive and fairly strong ranging from 0.64 to 0.97 (mean 0.82). The correlation between numbers of non-*Ctenotus* skink species and species density of other lizards is not significant ($r = -0.08$). Species densities of turtles and snakes are positively correlated $r = 0.79$, $P < 0.001$), as are various dry-adapted lizard groups among themselves. Species densities of frogs and the wet-adapted reptile groups (turtles, snakes and non-*Ctenotus* skinks) are invariably positively correlated with bird species numbers, whereas numbers of species of dry-adapted lizard groups all correlate negatively with avian species densities (Table 4). Fig. 14 shows the inverse correlation between the species densities of birds and those of dry-adapted lizards. Note that this taxonomic complementarity need not be a result of interspecific competition among higher taxonomic groups, but that it might just as well reflect simply different responses to prevailing environmental conditions by organisms with fundamentally different body plans. Elsewhere (Schall & Pianka, 1978), we suggest that ectothermic lizards are favored in open sunny areas where the costs of thermoregulation are low and that, by virtue of their ability to become inactive and lower metabolic rates during periods of stress, lizards have an advantage over endothermic birds and mammals in harsh and unpredictable deserts.

6. Comparison with North American vertebrates

We performed an exactly comparable analysis of patterns of species density among terrestrial vertebrates of the continental United States (Schall & Pianka, 1978). The total numbers of species of birds, mammals and snakes are remarkably similar in the U.S. and Australia (Table 5). Salamanders are absent from Australia for historical reasons. Frogs are more diverse in Australia, whereas the U.S. turtle fauna is richer. There are 3.5 times as many lizard species in Australia (Table 5). North American lizards are ecologically more homogeneous than Australian lizards, which occupy a broad range of niches, having usurped the ecological roles of some North American mammals, snakes and perhaps even arthropods (Pianka, 1969; see also chapter in this volume). For example, large and intelligent varanid lizards are important tertiary predators in the central deserts of Australia, a role filled by carnivorous mammals such as the coyote and kit fox in North America.

Australia and the U.S. overlap by only about 14° of latitude (25° to about 39° – see Fig. 15). The two continents differ in striking ways. Australia has experienced negligible glaciation, is considerably flatter than the U.S., and has about 3–4 times as much desert and semi-arid areas as North America. Australia also has a sharper precipitation gradient than the U.S. and is thermally less variable. Australian precipitation is more variable than that of the U.S. and tends to be greatest along the coasts. Comparison of the same

Table 5. Approximate total numbers of species of various vertebrate taxa in Australia and the continental United States.

Taxonomic group	Australia	United States
Mammals	224	296
Birds	650	620
Frogs	133	52
Toads	1 (introduced)	25
Salamanders	0	99
All Amphibians	134	176
Turtles	16	50
Snakes	101	104
Lizards	351	99
Totals, all terrestrial vertebrates	1476	1345
Area in 10^6 km^2	7.69	7.83

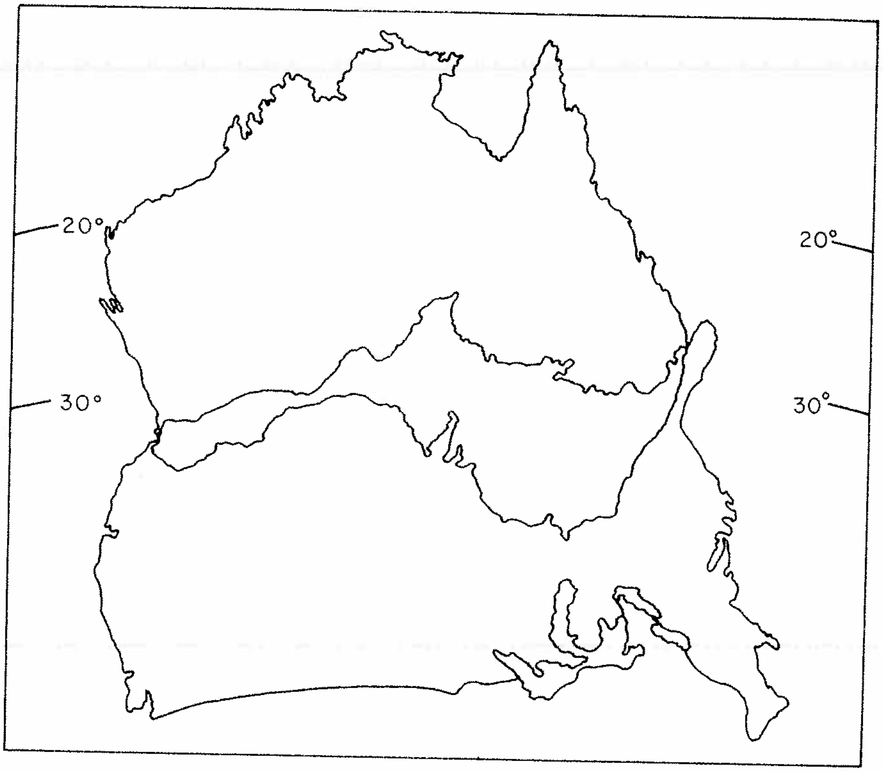

Fig. 15. Outlines of Australia and the continental United States superimposed with latitude and west coasts aligned.

five climatic variables over all quadrates on both continents reveals significant differences: average hours of sunshine, coefficient of variation in annual precipitation, average annual temperature, and the length of the frost-free period are all significantly greater in Australia than in the U.S.A., whereas average annual precipitation is significantly lower in Australia (t′-tests, all $P<0.001$). However, there are also similarities between the climates of the two continents: Intercorrelations among the five environmental variables are virtually identical on both continents (Schall & Pianka, 1978). Hence, as one moves across an environmental gradient in any given climatic variable the other four change in similar ways in both areas.

Intercontinental comparisons show certain intriguing differences as well as some similarities that may reflect truly general trends (Morton, 1977; Schall & Pianka, 1978). For example, whereas species density of Australian birds is positively correlated with average annual precipitation ($r=0.69$, Fig. 12), the numbers of species of North American birds vary inversely with average annual precipitation ($r=-0.70$). Nevertheless, in stepwise multiple regressions the five climatological variables enter in nearly the same order and reduce overall variance in species density by similar amounts (Table 6). Patterns of species density of turtles are very similar on the two continents, with precipitation being the most important variable (r's $=0.73$ and 0.79).

Table 6. Squared coefficients of multiple determination (R-squared values) and sequences of entry of independent variables into stepwise multiple regressions for various groups on two continents.

Taxon	North America		Australia	
	Pptn	0.49	Pptn	0.48
	Temp	0.58	Temp	0.57
All Birds	CV	0.60	CV	0.58
	Sun	0.60	FF	0.59
	FF	0.61	Sun	0.59
	Pptn	0.69	Pptn	0.53
	Temp	0.70	FF	0.62
Frogs	CV	0.75	CV	0.64
	Sun	0.75	Temp	0.65
	FF	0.75	Sun	0.65
	Pptn	0.54	Pptn	0.59
	Temp	0.65	Temp	0.60
Turtles	CV	0.67	FF	0.62
	Sun	0.67	Sun	0.62
	FF	0.68	CV	0.62
	Sun	0.55	Sun	0.46
All Lizards versus	Temp	0.78	Pptn	0.47
'Dry-adapted'	Pptn	0.83	Temp	0.50
Lizards	CV	0.84	FF	0.50
	FF	0.84	CV	0.50
	Temp	0.61	Pptn	0.33
	CV	0.64	Sun	0.41
Snakes	Sun	0.66	CV	0.42
	Pptn	0.68	Temp	0.43
	FF	0.69	FF	0.45
	Pptn	0.54	Sun	0.45
Mammals	CV	0.60	FF	0.48
versus	FF	0.64	Pptn	0.55
Marsupials	Sun	0.66	Temp	0.58
	Temp	0.66	CV	0.60

Code: Pptn = average annual precipitation, Temp = average annual temperature, CV = coefficient of variation in annual precipitation, Sun = average annual total hours of sunshine, FF = average annual number of frost-free days.

Annual precipitation is also the most important variable for frogs on both continents (r's = 0.80 and 0.73). Similarly, the variable that correlates most strongly with the number of lizard species (both all lizards and dry-adapted lizards in Australia) is sunshine on both continents (r's = 0.74 and 0.68, Fig. 11). In fact, the signs of correlation coefficients with all five climatic variables are identical in the U.S. and Australia for both turtles and lizards. Stepwise multiple regression reduces variance in species density of Australian dry-adapted lizards by only 50%, compared to a full 84% for U.S.

lizards (Table 6; Schall & Pianka, 1978). Species densities of snakes and mammals show rather puzzling divergent patterns on the two continents (Table 6). Temperature is more important than precipitation for U.S. snakes, whereas the reverse is true in Australia. U.S. mammal species densities correlate negatively with precipitation ($r = -0.73$) but positively with hours of sunshine ($r = 0.55$), whereas Australian marsupials show the opposite trend (respective r's $= 0.54$ and -0.67). Morton (1977) reaches similar conclusions in his comparison of factors influencing diversity of desert mammals on the two continents. Reasons for such intercontinental differences are elusive and merit further study. As distributions of Mexican vertebrates become available, it will be of interest to see if the continents differ at lower latitudes.

Differences between the faunas of the two areas could be a direct consequence of the fundamental climatic and latitudinal differences. Are there more species of lizards in Australia simply because there is 3–4 times as much desert on that continent? To attempt to answer this question, we selected and compared quadrates with crudely comparable climatic conditions on both continents.* In 15 such matched pairs of quadrates, including both arid and mesic areas, the number of species of lizards is consistently higher in Australia than in the U.S. (Mean 3.1×, range 2.0× to 5.8×). Ground-level studies in the Australian sandridge desert have also demonstrated that four times as many lizard species coexist locally on areas than on North American sites (Pianka, 1969, and Pianka chapter in this volume). In the same 15 pairs of climatically-matched quadrates, species numbers of snakes average 1.6 times as many species in North America than in Australia (range 0.8 to 3.5). In these climatologically similar quadrates, species densities of turtles are consistently lower in Australia than in the U.S. bird species numbers tend to be higher in the U.S. than in Australia in arid matched quadrates, whereas the reverse is true of mesic matched pairs. Morton (1977) argues that mammal species densities are much higher in North American desert areas than in Australian deserts.

As reliable range maps become available for these and other taxa from other parts of the world, extension of this sort of analysis should allow us to gain further insights into the complexity of interactions that determine global patterns in species richness.

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* Of course, a perfect match was impossible: Australian quadrates tended always to have slightly longer growing seasons, for example.

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