

Comparative Ecology of Twelve Species of Nocturnal Lizards (Gekkonidae) in the Western Australian Desert

ERIC R. PIANKA AND HELEN D. PIANKA

Observations on active geckos during their natural period of nocturnal activity allow comparison of many aspects of the ecologies of 12 species, including habitat and microhabitat requirements, diets, daily and seasonal patterns of activity, body temperature relationships, reproduction, predation and broken tail frequencies. Because as many as nine species, including five congeneric *Diplodactylus*, occur together on a single study site, emphasis is placed upon ecological differences that might reduce competition and allow coexistence of such a diversity of nocturnal species.

Only slight differences in temporal patterns of activity are evident. However, foods eaten as well as habitats and microhabitats exploited differ strikingly among these gekkonids. Larger species tend to eat larger prey than smaller species. Three species are food specialists, eating essentially nothing but termites. Three others are distinctly arboreal, with the majority of specimens first sighted off the ground. Two species are semi-arboreal, one of which is restricted almost entirely to *Triodia* grass tussocks. Due to clear-cut differences in habitat requirements, three large terrestrial species of *Nephurus* are always allopatric; one is restricted to sandridges, another to sandplain-*Triodia* habitats, and still another to shrub-*Acacia* habitats. In general, sympatric species pairs with high dietary overlap tend to overlap relatively little in microhabitat and vice versa.

ALTHOUGH a fairly extensive literature on some aspects of gekkonid biology and ecology has been assembled (see literature cited), observations on nocturnal geckos during their natural period of activity are difficult to make and have been limited [see, however, Park (1938); Huey (1969, 1975); Marcellini (1971); Parker and Pianka (1974)]. Here we present such information on active geckos of 12 species in the Australian desert, and we use these data to examine and interpret ecological relationships among sympatric species of nocturnal lizards, particularly resource partitioning and competitive interactions [see Cody (1974) and Schoener (1974) for reviews of the subject].

A series of desert study areas in Western Australia support from 18 to 40 sympatric species of lizards (Pianka, 1969a, 1975), many of which are nocturnal [from 8 to 13 species or from 32 to 44% (mean 36%) of the total number of species occurring on a given area]. In this paper we describe and compare the ecologies of members of the largest nocturnal group, 12 species of gekkonid lizards. [Nocturnal skinks and pygopodids, which constitute a minor part of these lizard communities, will be treated in subsequent papers. Niche relationships of the entire lizard community have been analyzed by

Pianka (1973, 1974, 1975).] From three to nine species of geckos, including up to five species of congeneric *Diplodactylus*, occur in ecologic sympatry on the study areas (Table 1). Descriptions of the Australian desert system and all but one of the study sites and their faunas have been published (Pianka, 1969a, 1969b, 1972; Pianka and Pianka, 1970). Two of the 12 species, *Gehyra variegata* and *Heteronotia binoei*, are wide ranging, occurring virtually throughout Australia, whereas the other ten species have variously more restricted geographic ranges.

Until recently, there were few ecological investigations on nocturnal lizards, although some aspects of the ecology of a variety of eastern Australian geckos have now been examined by Bustard (1964, 1965a, 1966, 1967a, 1967b, 1967c, 1967d, 1967e, 1968a, 1968b, 1968c, 1968d, 1969a, 1969b, 1970a, 1970b, 1970c). Our prime concern here is to discern and quantify niche differences between pairs of these species which might reduce competition among them and allow ecological coexistence of so many species.

STUDY AREAS

Exact locations (Fig. 1) and descriptions of eight of the nine study sites reported on here have been published (Pianka, 1969a, 1969b; Pianka and Pianka, 1970). The ninth study site, area

TABLE 1. OCCURRENCES OF DIFFERENT GECKO SPECIES ON THE VARIOUS STUDY AREAS. See map (Fig. 1) for localities coded by letters.

Species	A	M	D	E	L	G	N	Y	R
<i>Gehyra variegata</i> ^a	x	x	x	x	x	x		x	x
<i>Heteronotia binoei</i> ^t	x	e	e	x	x	x	x	x	e
<i>Diplodactylus ciliaris</i> ^a		x		x					x
<i>Diplodactylus conspicillatus</i> ^t		x	x	x	x	x	e	x	
<i>Diplodactylus elderi</i> ^a	x	e	x	x	e	e	e		
<i>Diplodactylus pulcher</i> ^{s, t}	x								x
<i>Diplodactylus stenodactylus</i> ^t			x	x					
<i>Diplodactylus strophurus</i> ^a	x		x	x				x	
<i>Nephrurus laevis</i> ^{s, t}			x	x					
<i>Nephrurus levis</i> ^t					x	x	x		
<i>Nephrurus vertebralis</i> ^t	e	x						x	
<i>Rhynchoedura ornata</i> ^t	x	x	x	x	x	x	x	x	x
Totals (x)	6	5	7	9	5	5	3	6	4
Totals (x + e)	7	7	8	9	6	6	5	6	5

e = expected on the basis of distribution, habitat, autecology and microhabitat. x = collected. a = arboreal. s = semi-arboreal. t = terrestrial.

R, is located at about latitude 27° 05' and longitude 119° 37'. This site is a so-called "tor" area, covered with large, often exfoliating, granitic rock outcroppings and vegetated with mulga (*Acacia aneura* and *Acacia craspedocarpa*) as well as a variety of woody shrubs. An important plant in the Australian sandy deserts is so-called "spinifex," belonging to the genus *Triodia* (Burbidge, 1953); these perennial grasses, which form dense clumps up to a meter in diameter, frequently dominate the ground cover in sandplain habitats (see Pianka, 1969b, for a photograph). Areas A and M are mixed mulga-eucalypt-spinifex (*Acacia-Eucalyptus-Triodia*) habitats on desert loams, thus constituting mixtures of the "mulga" and "spinifex" habitats, respectively (Pianka, 1972). Areas D and E are desert sandhill and sandridge habitats, respectively, supporting large eucalypt trees and spinifex as well as a variety of other sandridge perennials such as *Thryptomene* and *Grevillea*. Large stretches of habitat dominated by spinifex occur in the interdunal valleys. Thus, these two areas possess both the "spinifex" and the "sandridge" habitats. Areas L and G are sandplain habitats with large eucalypts, spinifex, and a few scattered bushes, and are therefore fairly typical sandplain-*Triodia* habitat with a *Eucalyptus* canopy. Area N is a relatively "pure" spinifex flat, or a grass desert. Area Y is a nearly pure shrub desert site in a dry lakebed, with a vegetative structure very reminiscent of shrub deserts in the Great Basin of western North America. In addition to these nine major study sites (Fig.

1), we also observed and collected incidental specimens of most of these gecko species on various other areas in the Simpson, Tanami, Great Victoria, and Great Sandy deserts and these observations and specimens have been used here.

METHODS

Geckos were almost always collected during their natural period of nocturnal activity, which begins shortly after sunset and extends at least until midnight (limitations on human endurance dictated that most of our specimens were collected after dusk but before midnight). The majority of specimens were located by the eyeshine technique using Winchester 7½ volt head lanterns, but some were also collected by body shine with a kerosene lantern. Active geckos provide data on exactly where in the habitat each species forages, as well as other pertinent information on their ecology, such as time of activity, body temperature and air temperature. Notes were taken on the precise microhabitat location and orientation (angle of head and body with respect to horizontal) of every active gecko at the time of first sighting and subsequent collection. Most individuals were grabbed by the head between the thumb and forefinger and their cloacal temperature recorded within a few seconds of capture, before any appreciable change in body temperature occurred.

Occasionally, geckos were found in their diurnal retreats. These were usually under dead bark, in tree hollows or fallen logs, under fallen

debris, in termite mounds, or dug up from underground burrows. Such animals were used to augment sample sizes, but only for dietary, reproductive, and anatomical data analyses. We spent nearly 300 man-hours observing and collecting geckos at night over a 16-month period, and an entire annual cycle, from October of 1966 through January of 1968.

Some species were quite common and resulting samples are fairly large (in the hundreds of specimens), whereas others were extremely difficult to acquire in large numbers either because of cryptic behavior, restricted habitat requirements or an apparent rarity. Hence we must make somewhat tentative statements about the ecologies of such infrequently collected species. Dissection of preserved specimens provided data on stomach contents and reproductive condition. Volumes of oviducal eggs and intact stomachs were estimated to one tenth of a cc by volumetric displacement using a narrow-necked graduated cylinder. The volume of each empty stomach was similarly measured and subtracted from the first measurement to obtain an estimate of the volume of food contained in a stomach. Estimates were then made of the numbers and volumes of prey of different types in each lizard stomach as follows. Approximate volumes of individual prey items were estimated visually, by the proportion of the total volume of food taken up by that item. Prey in each stomach were counted individually, except for termites for which standards were determined, and the number per stomach estimated from the total volume of termites. Head lengths were measured to the nearest 0.1 mm with vernier calipers, as the distance from the anterior edge of the ear aperture to the tip of the snout. Eye diameters were estimated using a dissecting microscope and an ocular micrometer. Hindleg lengths were measured to the nearest mm by extending the hindleg at a right angle to the body, holding the leg as straight as possible, and placing the end of a metal ruler against the body parallel to the leg. The tip of the claw of the longest toe was taken as the end of the limb. Methods employed generally follow those described by Pianka (1965, 1967, 1969b, 1970a, 1973, 1975). Our collection of over a thousand geckos has been donated to the Los Angeles County Museum of Natural History.

To quantify the variety of resources exploited by various species (niche breadths), we use the diversity index of Simpson (1949),

$$1/\sum_i p_i^2,$$

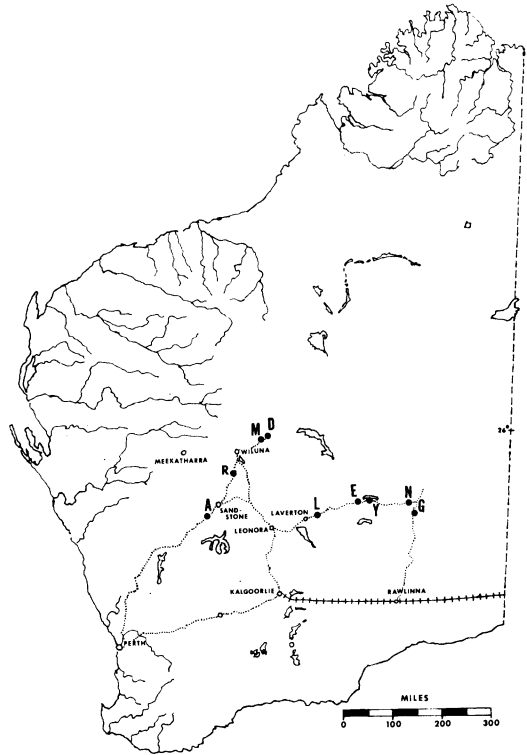


Fig. 1. Locations of the nine study areas in Western Australia.

where p_i is the proportion of the i th resource category used. When divided by the number of different resource categories, n , such niche breadth estimates vary from a minimum of near zero (actually $1/n$) to a maximum value of unity. Overlap is computed using the following formula (Pianka, 1973, 1975; May, 1975):

$$\frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of the i th resource used by the j th and the k th species, respectively. Overlap values obtained from this equation vary from zero (no overlap) to one (complete overlap).

Throughout the text, figures, and tables, standard symbols are used for the mean (\bar{x}), standard deviation (S), sample size (N), standard error of the mean ($S.E.$), Pearson product moment correlation coefficient (r) and Spearman rank correlation coefficient (r_s).

TABLE 2. HABITAT SPECIFICITIES, MICROHABITATS AND DAYTIME RETREATS (WHERE KNOWN) OF THE 12 SPECIES OF GECKOS ON THE NINE STUDY SITES.

Species	Habitat*	Microhabitat	Daytime Retreat
<i>Gehyra variegata</i>	ubiquitous	arboreal	under bark and fallen logs, in holes in trees and rock crevices.
<i>Heteronotia binoei</i>	ubiquitous	terrestrial	under logs, in litter and termite mounds, in burrows of other animals.
<i>Diplodactylus ciliaris</i>	mulga	arboreal	(?) one found in a <i>Triodia</i> tussock.
<i>Diplodactylus conspicillatus</i>	nearly ubiquitous	terrestrial	spider holes (in ground).
<i>Diplodactylus eldери</i>	<i>Triodia</i>	semi-arboreal	in <i>Triodia</i> tussocks.
<i>Diplodactylus pulcher</i>	shrub- <i>Acacia</i>	terrestrial and semi-arboreal	(?) unknown, possibly spider holes.
<i>Diplodactylus stenodactylus</i>	sandridges	terrestrial	(?) one in a small burrow.
<i>Diplodactylus strophurus</i>	shrub- <i>Acacia</i>	arboreal	(?) one in a large bush; another in a <i>Triodia</i> tussock.
<i>Nephurus laevis</i>	sandridges	terrestrial	burrows.
<i>Nephurus levis</i>	sandplain- <i>Triodia</i>	terrestrial	large burrows, often of other animals.
<i>Nephurus vertebralis</i>	shrub- <i>Acacia</i>	terrestrial	large burrows of other animals.
<i>Rhynchoedura ornata</i>	ubiquitous	terrestrial	spider holes (in ground).

*Modified from Pianka (1969a, 1972).

MICROHABITAT, HABITAT AND HABITAT SPECIFICITY

Microhabitat utilization patterns vary widely among the 12 species (Tables 2, 3, 4); some species are found in association with one (or two) microhabitat element(s) to the virtual exclusion of the others. Thus, over three-quarters of all *Rhynchoedura ornata* and *Nephurus vertebralis* were first sighted on the ground in the open spaces between plants, while 89%, 66% and 75%, respectively, of all *Gehyra variegata*, *Diplodactylus ciliaris* and *D. strophurus* were in vegetation above the ground when first sighted.

R. ornata and *Heteronotia binoei* occur throughout the Australian desert in a wide variety of habitats and on numerous different soils. Both these terrestrial species were found in mulga-dominated habitats, on sandridge areas, and in *Triodia*-dominated sandplain habitats. Because these two species occur in all types of desert habitats and are therefore widespread, they were classified as "ubiquitous" by Pianka (1969a). A third terrestrial species, *Diplodactylus conspicillatus*, found on seven of the nine areas in both shrubby and grassy habitats, was labelled "nearly ubiquitous" (Pianka, 1969a);

this species is considered further below where we compare it with *Diplodactylus pulcher*.

The three arboreal species (*Gehyra variegata*, *Diplodactylus ciliaris*, and *D. strophurus*) occurred only on study areas with large shrubs and/or trees (or rocks). Of these, *G. variegata* has the most versatile habitat requirements and is the most widespread. This extremely successful gecko species exploits a great variety of vegetation, ranging from shrubs such as *Hakea* and *Grevillea* to small trees (*Acacia aneura*, *A. craspedocarpa*, and *Eucalyptus pyriformis*) to large trees including *Eucalyptus gongylocarpa* and *E. dichromophloia*. It is also found on rocks, boulders and granitic outcrops. *G. variegata* is sorely in need of taxonomic revision, and at least two distinct taxa may be involved: a small dark rock-dwelling species and another larger paler tree-dwelling species (Mitchell 1965; Bustard 1966b). We have been similarly impressed with the difference in size and color of populations in mulga habitats (small and dark) versus those in habitats with large eucalypts (larger and paler). *D. ciliaris* and *D. strophurus* have slightly more restricted habitat requirements and are considerably less widespread than *Gehyra*, being known to occur on only three

TABLE 3. MICROHABITAT LOCATIONS OF VARIOUS GECKOS WHEN FIRST SIGHTED (PERCENTAGES).

Species	N	Terrestrial (on ground)						Arboreal (above ground)		Micro-habitat Niche Breadth
		Open	Burrows	Spinifex	Shrubs	Litter	Near Rocks	Low (1-60 cm)	High (> 60 cm)	
<i>Gehyra</i>										
<i>variegata</i> (G)	321	5.6			0.3	5.0	0.6	49.5	39.0	0.17
<i>Heteronotia</i>										
<i>binoei</i> (H)	20	45.0	10.0	5.0	5.0	20.0	5.0	5.0	5.0	0.23
<i>D. ciliaris</i> (ci)	70	11.4		7.1	10.0	5.7		34.3	31.4	0.27
<i>D. conspicillatus</i> (co)	56	66.1	5.4	19.6	7.1		1.8			0.14
<i>D. elderi</i> (e)	20	10.0		75.0*		15.0				0.11
<i>D. pulcher</i> (p)	24	41.7	12.5			8.3	4.2	33.4		0.20
<i>D. stenodactylus</i> (s)	43	30.2		23.3	41.9	2.3		2.3		0.20
<i>D. strophurus</i> (st)	52	11.5	7.7	1.9		3.8		63.5	11.5	0.15
<i>N. laevis</i> (la)	184	71.7	1.1	5.4	20.7	1.1				0.15
<i>N. levis</i> (le)	21	61.9		23.8	9.5	4.8				0.12
<i>N. vertebralis</i> (v)	14	78.6	7.1	7.1	7.1					0.09
<i>Rhynchoedura</i>										
<i>ornata</i> (R)	285	77.9	6.0	9.5	1.8	3.9	1.1			0.10

* 12 of these 15 lizards were taken at night by burning clumps of spinifex.

and four, respectively, of the nine study areas. Whereas *D. ciliaris* was almost always found in association with acacias (especially mulga, *Acacia aneura*), *D. strophurus* was found both on acacias (including mulga) and on various shrubs and mallee eucalypts on some areas as well as on small chenopodeaceous shrubs on area Y. *Diplodactylus ciliaris* and *D. strophurus* are sympatric on the sandridge study area E (Table 1); here we found *D. ciliaris* in *Grevillea*, *Acacia* and *Hakea*, frequently (though by no means always) on the slopes or crests of sandridges, whereas *D. strophurus*, which was considerably less abundant, occurred on *Thryptomene* and *Acacia* near the crests of sandridges.

Diplodactylus elderi, presumably a semi-arboreal species, appears to be intimately associated with and dependent upon spinifex. These animals were almost always found inside such grass clumps, except for a few which were invariably immediately adjacent to a tussock. We found *D. elderi* very difficult to spot and to collect; although we collected it on only three of nine areas, its habitat requirements suggest that it probably occurs on four other areas with *Triodia* (Table 1). Its prehensile tail and climbing abilities indicate that *D. elderi* must frequently climb within *Triodia* tussocks (we periodically saw eyeshine above ground in spinifex tussocks that may well have been this species).

Nephrurus levis was always collected in sandplain habitats dominated by *Triodia*. This open-dwelling terrestrial species has been classi-

fied as restricted to "spinifex" habitat (Pianka, 1969a), termed "sandplain-*Triodia* habitat" by Pianka (1972).

Two terrestrial species, *Diplodactylus stenodactylus* and *Nephrurus laevis*, are found only in desert sandridge habitats (Pianka, 1969a, 1972). Neither of these species was ever found more than a short distance from a sand dune or a sandridge and, indeed, the vast majority of specimens (93% of 43 specimens and 99% of 164 specimens, respectively) were taken either

TABLE 4. FREQUENCY DISTRIBUTIONS, BY NUMBER OF LIZARDS AND PERCENTAGE, OF HEIGHTS ABOVE GROUND WHEN COLLECTED FOR THE THREE ARBOREAL SPECIES. Some individuals were first sighted at greater heights (see text).

Height	<i>Gehyra variegata</i>		<i>D. ciliaris</i>		<i>D. strophurus</i>	
	N	%	N	%	N	%
on ground	29	9.9	19	29.2	7	15.9
1 to 15 cm.	93	31.9	20	30.8	24	54.4
16 to 30 cm.	33	11.3	1	1.5	5	11.4
31 to 61 cm.	35	12.0	8	12.3	2	4.5
62 to 91 cm.	28	9.6	6	9.2	4	9.1
92 to 122 cm.	25	8.6	4	6.2	2	4.5
123 to 152 cm.	13	4.4	3	4.6		
153 to 183 cm.	16	5.5	1	1.5		
over 184 cm.	20	6.8	3	4.6		
Totals	292		65		44	

TABLE 5. STOMACH CONTENTS: TOTAL NUMBER OF PREY ITEMS IN EACH FOOD CATEGORY.

Prey items	Gecko species ^a											
	G	H	ci	co	e	p	s	st	la	le	v	R
Isopods	8		1					1	2			
Centipedes	1	1							8	2	4	
Spiders	72	8	20		15+		13+	24+	105	13	16	1
Scorpions	1		1						5	4	5	
Pseudoscorpions	3											
Acarinae		1						1				
Thysanura	3						1	1	1	1		
Collembola												2
Formicidae	7+	4	2		1				15			1+
Other Hymenoptera	5	1+			1							
Locustidae	24+	1	12+		2+		2+	4+	43	10	5	
Blattidae	14+	1	7+		2			10+	17	5		
Mantids-Phasmids	2		4					1				
Neuroptera	2		2					1				
Coleoptera	103	4	63		6		29	47	236	11	2	
Isoptera	536	4+		330	20	160	15		3			1428
Homoptera-Hemiptera	113	4	8		12		7	9	18			
Diptera					6		9					
Lepidoptera	17	2	2		1+		7	4	1			
All larvae	20	5	28		2		1	8	20	10		
All pupae	1											
Unidentified insects	55	5	8		4		9	8	22	2	1	1
Lizards and sloughed skins	10	5	1						3		3	
Plant materials	1	1	2		1	2			7			8
Total number of items	998	47	161	330	73	162	93	119	506	58	36	1441

^a Abbreviations of species names coded in Table 3.

+ Indicates that additional parts and pieces were also present.

on the slopes or crests of sand dunes and sandridges.

The two remaining species, *Diplodactylus pulcher* and *Nephurus vertebralis*, were always collected in habitats with a substantial number of *Acacia* bushes or trees, and often in areas with small shrubs rather than spinifex; Pianka (1969a, 1972) classified these as "mulga" or shrub-*Acacia* species. As indicated earlier, *D. pulcher* climbs occasionally; *N. vertebralis* was invariably found on the ground. It may be significant that we never encountered *D. pulcher* in sympatry with *D. conspicillatus*; their ecologies and morphologies are very similar and their occurrence could well be mutually exclusive. Table 2 summarizes much of the above discussion. Overlap in use of microhabitats is examined under "Competition and Coexistence."

DIET

Tables 5, 6 and 7 summarize the stomach contents of 1102 geckos. Inspection of these tables

reveals that three species (*D. conspicillatus*, *D. pulcher*, and *Rhynchoedura ornata*) are termite specialists, feeding on isopterans to the virtual exclusion of all other prey, while the remaining nine species have rather generalized diets, composed of various arthropods (especially insects) and an occasional lizard or piece of plant material. Interestingly enough, the three termite specialists tend to have empty stomachs much more often (only 38, 40 and 56% contained food, $\bar{x} = 44.8\%$) than do the more generalized feeders (66 to 100% with food $\bar{x} = 81.5\%$), suggesting that food specialization is accompanied by greater variation in feeding success (Table 7).

Specialization on termites as a food source is economically feasible because these insects occur in colonies; such a clumped spatial distribution and concentrated food supply assures that the profits gained from this food source will outweigh the costs of finding it (MacArthur and Pianka, 1966). Two species of skinks in the Kalahari desert of southern Africa have specialized on termites as well (Huey et al., 1974; Huey

TABLE 6. STOMACH CONTENTS: TOTAL VOLUME, IN CUBIC CM, OF PREY IN EACH FOOD CATEGORY.

Prey items	Gecko species ^a											
	G	H	ci	co	e	p	s	st	la	le	v	R
Isopods	.28		.04					.05	.14			
Centipeds	.06	.05							.97	.55	.80	
Spiders	2.72	.17	1.41		.27		.20	1.71	3.35	1.95	1.19	.01
Scorpions	.15		.05						.37	1.19	.76	
Psuedoscorpions	.03											
Acarinae		.02						.02				
Thysanura	.08						.04	.04	.05	.08		
Collembola												.005
Formicidae	.15	.08	.03		.01				.08			.01
Other Hymenoptera	.28	.01			.01							
Locustidae	2.70	.20	3.46		.15		.14	.79	4.94	1.96	.26	
Blattidae	1.61	.17	.87		.09			1.03	2.50	.65		
Mantids-Phasmids	.09		1.03					.05				
Neuroptera	.30		.14					.01				
Coleoptera	2.35	.10	2.22		.12		.65	1.02	7.72	1.29	.17	
Isoptera	7.62	.13		3.31	.18	.99	.12		.03			8.44
Homoptera-Hemiptera	1.87	.08	.23		.11		.15	.25	.33			
Diptera					.04		.23					
Lepidoptera	.62	.14	.13		.02		.28	.49	.18			
All larvae	1.20	.09	2.43		.07		.07	.71	1.23	1.08		
All pupae	.30											
Unidentified insects	.59	.07	.22		.05		.12	.24	.92	.16	.02	.005
Lizards and sloughed skins	.68	.19	.01						1.59		1.72	
Plant materials	.04	.02	.07		.01	.02			.16			.03
Unidentified material	.88	.09	.08	.04	.01	.03	.13	.05	1.52	.62	.02	.32
Total Volume	24.60	1.61	12.42	3.35	1.14	1.04	2.13	6.46	26.08	8.88	4.94	8.82
Food Niche Breadth (Volumes)	.34	.57	.30	.05	.39	.06	.31	.33	.29	.33	.22	.05

^a Abbreviations of species names coded in Table 3.

and Pianka, 1974); ants represent a similarly concentrated and patchy food source and both the North American and the Australian deserts support an ant specialist species of lizard—*Phrynosoma platyrhinos* (Pianka and Parker, 1975) and *Moloch horridus* (Pianka and Pianka, 1970), respectively.

Prey size distributions (Table 8) also differ markedly among these Australian geckos, with the larger species eating larger prey items; prey size and head size are significantly correlated (Fig. 2). An analysis of overlap in prey size, however, adds little to what can be gained from studying overlap in prey taxa, weighted by volume (Table 6). We discuss dietary overlap further below.

ANATOMICAL CORRELATES OF THE FOOD AND PLACE NICHES

We have shown above that head length (Table 9) is correlated with the size of prey eaten

(Fig. 2); other, similar, correlations occur between morphology and ecology. Thus lizards that are usually active in open spaces between shrubs tend to have longer hindlegs (expressed as a percentage of SVL) than species that stay closer to cover (Pianka, 1969b; Pianka and Parker, 1972). A similar correlation holds among these 12 species of geckos, provided that two exceptionally long-bodied species, *Rhynchoedura ornata* and *Diplodactylus conspicillatus*, are excluded (Fig. 3). Since the latter two species typically emerge from and stay close to (as well as retreat down!) spider burrows in the open spaces between plants, selection for speedy escape into cover, presumably enhanced by long hindleg length, may be relaxed. The preceding argument is also a justification for omitting these two aberrant species in the regression and correlation coefficient shown in Fig. 3.

Toe lamellae are fairly good anatomical indicators of arboreality and terrestriality among

TABLE 7. STOMACH CONTENTS: PERCENTAGE FREQUENCY OF OCCURRENCE OF PREY ITEMS IN EACH FOOD CATEGORY BASED ON THE TOTAL NUMBER OF STOMACHS WITH FOOD.

Prey items	Gecko species ^a											
	G	H	ci	co	e	p	s	st	la	le	v	R
Isopods	2.2		1.6					2.3	1.4			
Centipedes	.4	3.7							4.8	8.3	28.6	
Spiders	35.3	29.6	31.1		57.2		25.0	39.5	42.8	54.1	57.1	.6
Scorpions	.4		1.6						3.5	16.7	28.6	
Psuedoscorpions	1.3											
Acarinae		3.7						2.3				
Thysanura	1.3						2.5	2.3	.7	4.2		
Collembola												.6
Formicidae	3.9	11.1	3.3		4.8				2.8			.6
Other Hymenoptera	1.7	3.7			4.8							
Locustidae	13.4	3.7	32.9		23.8		7.5	20.9	27.6	37.5	35.7	
Blattidae	6.5	3.7	13.1		9.5			25.6	11.7	20.9		
Mantids-Phasmids	.9		6.6					2.3				
Neuroptera	.4		3.3					2.3				
Coleoptera	22.8	11.1	49.2		19.1		42.5	39.5	60.0	25.0	14.3	
Isoptera	28.4	7.4		100.	14.3	100.	10.0		.7			98.7
Homoptera-Hemiptera	25.4	14.8	13.1		23.8		22.5	20.9	8.3			
Diptera					4.8		15.0					
Lepidoptera	7.3	7.4	3.3		9.5		12.5	9.3	.7			
All larvae	8.2	18.5	29.5		9.5		2.5	16.3	11.7	12.5		
All pupae	.4											
Unidentified insects	23.7	18.5	13.1		19.1		22.5	16.3	15.2	8.3	7.1	.6
Lizards and sloughed skins	4.3	18.5	1.6						2.1		35.7	
Plant materials	1.3	3.7	3.3		4.8	20.			4.8			5.3
Total number of stomachs containing food	232	27	61	21	21	10	40	43	145	24	14	155
Number of stomachs examined	287	41	75	55	26	25	43	53	173	36	14	274
% stomachs with food	80.9	65.9	81.2	38.2	80.8	40.0	93.0	81.1	83.8	66.7	100.0	56.4

^a Abbreviations of species names coded in Table 3.

geckos, with arboreal species having enlarged lamellae and/or toe pads while terrestrial species have much more elongated pointed toes and smaller lamellae (see Glauert, 1961; Kluge, 1967 for illustrations). Werner (1969) found that eye sizes, expressed as a percentage of SVL, are greater in ground-dwelling geckos than in climbing species. Table 10 summarizes relevant statistics for the twelve species considered here; excluding the occasional climber *Diplodactylus pulcher* and considering *D. elderi* to be arboreal, the overall statistics in the four arboreal species are significantly (t-test, $P < .05$) different from those for the seven terrestrial species (bottom, Table 10), in support of Werner's finding.

TEMPORAL PATTERNS OF ACTIVITY

Because geckos emerge from their diurnal retreats shortly after sunset, their activity pat-

terns vary seasonally as daylength changes, with somewhat later emergence during summer. Expressing times of activity in terms of "hours since sunset" reduces variation due to such seasonal shifts in activity times and greatly facilitates comparisons among species (Pianka, 1973, 1975). Fig. 4 shows histograms of the numbers of geckos collected at different times since sunset. These data are biased in that our collecting effort diminished as the night progressed; however, any observed differences between species, all of which were sampled over the same period of time, presumably would reflect real differences in activity patterns should these be present. However, unlike diurnal lizards (Pianka, 1973, 1975), temporal differences in daily activity among these nocturnal lizard species are very slight and none are statistically significant (Table 11). Thus, there is little if

TABLE 8. PREY SIZE DISTRIBUTIONS, MEAN PREY SIZE AND THE MEAN SIZE OF THE LARGEST TEN PREY ITEMS (IN CC).

Prey volume (cc)	Gecko species ^a											
	G	H	ci	co	e	p	s	st	la	le	v	R
Trace ($\leq .005$)	50	1			25	80	3	2	14			809
.006 – .014	293	8	30	330	15	80	37	23	69			621
.015 – .024	356	11	22		15		21	26	66			4
.025 – .034	62	2	11		3		7	13	69			7
.035 – .044	13	5	6		3		4	7	32	2		
.045 – .054	26	1	21		1		7	15	14	1	3	
.055 – .064	9		3						15			
.065 – .074	11		2		1		1	4	7			
.075 – .084	13		10		1			2	5	7	6	
.085 – .094	3						1		2			
.095 – .104	8	1	13		2			5	37	21	2	
.200	13	2	8					5	17	12	3	
.300	7		8					1	9	5	1	
.400			1					1	2		1	
.500	1		2						4	1		
.600			1								2	
.700										1		
over .800								1	1	2	1	
Total numbers of mea- sured prey items	865	31	139	330	66	160	81	105	363	52	19	1441
Mean prey volume	.024	.032	.077	.010	.015	.006	.022	.056	.049	.154	.136	.006
Mean volume of largest 10 prey items	.300	.078	.380	.010	.058	.010	.055	.280	.400	.480	.370	.027

^a Abbreviations of species names coded in Table 3.

any diurnal separation in time of activity of these lizards within the time period we observed them (seasonal patterns of activity do appear to differ slightly among species—Table

12). Time niche breadths vary among these geckos, however, with the daily activity of some species, such as *D. stenodactylus*, being relatively concentrated and that of others more

TABLE 9. STATISTICS ON HEAD LENGTHS (MM) AND HINDLEG LENGTHS, THE LATTER EXPRESSED AS A PERCENTAGE OF SNOUT-VENT LENGTH.

Species	Head Length				Hindleg Length			
	\bar{x}	S	SE	N	\bar{x}	S	SE	N
<i>Gehyra variegata</i>	11.97	1.85	0.11	281	38.4	2.08	0.12	286
<i>Heteronotia binoei</i>	10.62	1.74	0.28	40	50.4	3.94	0.62	41
<i>Diplodactylus ciliaris</i>	16.81	1.09	0.24	20	43.5	1.55	0.39	16
<i>Diplodactylus conspicillatus</i>	9.76	0.97	0.13	55	31.6 40.1	2.17	0.29	55
<i>Diplodactylus elderi</i>	8.80	1.81	0.25	26	41.5	3.99	0.55	26
<i>Diplodactylus pulcher</i>	9.84	1.06	0.21	25	41.7	2.59	0.52	25
<i>Diplodactylus stenodactylus</i>	10.62	2.36	0.36	43	41.4	3.23	0.49	43
<i>Diplodactylus strophurus</i>	14.97	2.02	0.27	55	45.0	2.24	0.30	45
<i>Nephurus laevis</i>	15.40	3.61	0.27	173	52.1	3.98	0.30	173
<i>Nephurus levis</i>	18.26	4.37	0.74	35	51.5	4.31	0.73	35
<i>Nephurus vertebralis</i>	17.94	3.70	0.99	14	51.6	4.81	1.29	14
<i>Rhynchoedura ornata</i>	8.29	0.73	0.04	274	38.6 47.9	1.94	0.12	274 272

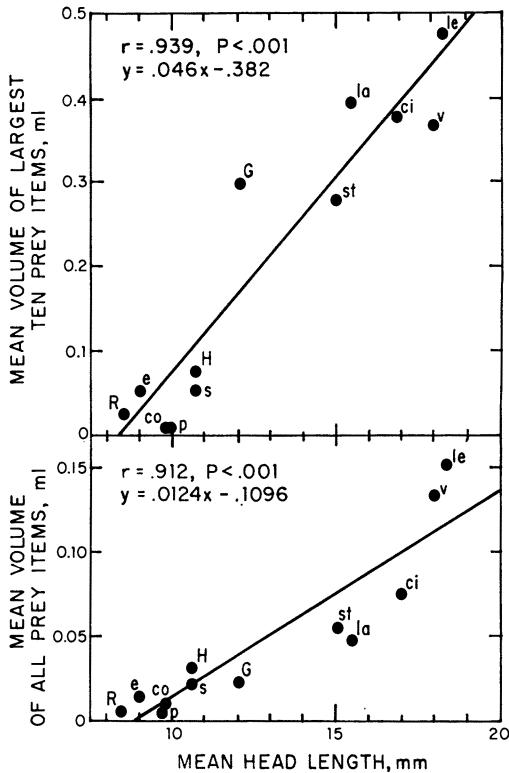


Fig. 2. Two plots of mean head length against prey size. Upper panel shows the nearly linear relationship of average head length and the mean volume of the largest ten prey items. Lower panel plots the average volume of all prey items against mean head length. Both correlations are highly significant statistically (P 's $< .001$).

spread out such as *D. pulcher* (Fig. 4, variances in Table 11, and seasonal niche breadths in Table 12).

Provided that resources are rapidly renewed, competition may be reduced or avoided through differences in times of activity, on either a daily or a seasonal basis. Resource partitioning by means of such temporal separation of activities appears to be relatively limited among many animals (Ricklefs, 1966; Schoener, 1974), but it is somewhat more prevalent in predatory species, especially terrestrial poikilotherms such as lizards (Pianka, 1969b, 1973, 1975; Schoener, 1974, 1976). It is interesting to speculate on what factors might have favored the evolution of different activity times among sympatric diurnal lizards and to ask why such temporal separation of activity apparently has not arisen among these nocturnal lizards. Whereas diurnal lizards actively thermoregulate in numerous

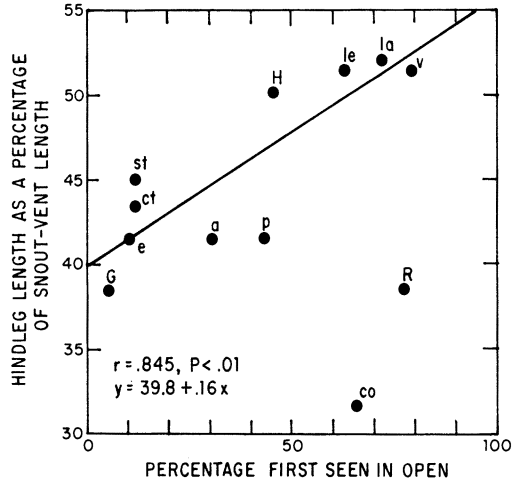


Fig. 3. Average hind leg length, expressed as a percentage of snout-vent length, plotted against the percentage of geckos first sighted in the open. Excluding the two aberrant long-bodied termite specialists that retreat into narrow spider holes, the correlation is highly significant statistically.

ways including adjusting their time and place of activity (Huey and Slatkin, 1976), nocturnal geckos are passive thermoregulators at night (see also Parker and Pianka, 1974; Huey and Slatkin, 1976, and next section of this paper showing high correlations between air and body temperatures among these geckos). Air and substrate temperatures are strongly time dependent, both during day and night. However, during the daylight hours, shading effects, coupled with differential heating of various microhabitats, create a thermally diverse environment. Although a thermal mosaic persists after dark due to differential rates of cooling, spot-to-spot variability in temperature is less than during daylight hours. Thus a nocturnal poikilotherm has less opportunity to thermoregulate than a diurnal one; moreover, being active over a period of time requires tolerating a range of temperatures. Interestingly enough, the average of the standard deviation in body temperature for these 12 species of geckos ($3.88 \pm .44$) is significantly higher (t-test, $P < .05$) than the same statistic calculated from Table 9 of Pianka (1969) for 14 species of diurnal skinks of the genus *Ctenotus* ($2.67 \pm .50$). Huey (1975) states "because...geckos prefer temperatures higher than those at which they are nocturnally active, it is unlikely that one would observe temporal activity segregation: all geckos should be active as early as possible in the evening." This seems to be the case (Fig. 4).

TABLE 10. STATISTICS ON DIAMETERS OF THE EYES OF ADULT GECKOS, EXPRESSED BOTH AS A PERCENTAGE OF HEAD LENGTH AND AS A PERCENTAGE OF SNOUT-VENT LENGTH. Both eyes on each individual were measured to the nearest 0.1 mm with an ocular micrometer and averaged; ten specimens of each species were measured (except for *H. binoei*, where the sample size was nine).

Species	% of Head Length			% of Snout-Vent		
	\bar{x}	S	SE	\bar{x}	S	SE
<i>Gehyra variegata</i> ^a	22.3	1.9	0.59	5.4	.48	.15
<i>Heteronotia binoei</i> ^t	23.3	1.6	0.54	5.9	.41	.14
<i>Diplodactylus ciliaris</i> ^a	20.9	1.9	0.60	4.7	.45	.14
<i>Diplodactylus conspicillatus</i> ^t	24.3	2.4	0.76	4.0	.31	.10
<i>Diplodactylus elderi</i> ^a	22.2	1.2	0.39	5.1	.34	.11
<i>Diplodactylus pulcher</i> ^{s, t}	26.8	2.1	0.65	5.1	.51	.16
<i>Diplodactylus stenodactylus</i> ^t	24.3	3.4	1.07	5.4	.63	.20
<i>Diplodactylus strophurus</i> ^a	21.9	1.4	0.43	5.0	.36	.12
<i>Nephrurus laevis</i> ^t	25.2	1.4	0.45	6.8	.37	.12
<i>Nephrurus levis</i> ^t	24.5	2.2	0.68	6.7	.73	.23
<i>Nephrurus vertebralis</i> ^t	27.4	4.4	1.38	7.3	1.21	.38
<i>Rhynchoedura ornata</i> ^t	30.3	3.8	1.19	5.4	.53	.17
Overall statistics for the four arboreal species	21.8	1.7	0.26	5.1	.47	.07
Overall statistics for the seven terrestrial species	25.6	3.6	0.43	5.9	1.21	.15

a = arboreal. s = semi-arboreal. t = terrestrial.

BODY TEMPERATURE RELATIONSHIPS

As in the North American *Coleonyx variegatus* (Parker and Pianka, 1974), body temperatures of active Australian geckos are very strongly correlated with ambient air temperatures, with correlation coefficients ranging from .71 to .99 (Table 13). These correlations tend to be highest in the arboreal species and lowest in the termite specialists. Most, but not all, mean body temperatures are slightly higher than mean air temperatures. As might be expected, body temperatures of active geckos vary markedly with the seasons (Figs. 5 and 6). These very strong correlations between gecko body temperatures and ambient thermal conditions suggest that nocturnal species have less opportunity to thermoregulate than diurnal ones (compare, for example, with data of Pianka, 1969b).

Licht et al. (1966) presented statistics on the body temperatures selected in thermal gradients by individuals of four of the species here considered: *Gehyra variegata* (\bar{x} = 35.3, N = 7), *Heteronotia binoei* (\bar{x} = 30.0, S = 1.86, N = 6), *Diplodactylus conspicillatus* (\bar{x} = 34.3, S = 4.56, N = 3), and *Rhynchoedura ornata* (\bar{x} = 34.0, S = 0.69, N = 8). On the basis of these and other observations, Licht et al. suggested that two distinct groups of geckos exist, one relatively "thermophilic" (including *Gehyra*,

Diplodactylus, and *Rhynchoedura*) and another less thermophilic one (including *Heteronotia*). However, active body temperatures of *Heteronotia* in nature differ little from those of the putatively thermophilic species (Table 13). Indeed, average body temperatures of these active geckos in nature are invariably significantly lower than the above-mentioned "preferred" values (t -tests, P 's < .05); moreover, body temperatures in nature are also much more variable, except in *Diplodactylus conspicillatus* (Table 13). Aver-

TABLE 11. STATISTICS ON TIMES OF ACTIVITY, EXPRESSED IN HUNDREDTHS OF AN HOUR SINCE SUNSET.

Species	\bar{x}	SE	N	S ²
<i>Gehyra variegata</i>	1.37	0.04	259	0.47
<i>Heteronotia binoei</i>	1.60	0.17	17	0.49
<i>Diplodactylus ciliaris</i>	1.58	0.10	71	0.69
<i>Diplodactylus conspicillatus</i>	1.52	0.09	52	0.43
<i>Diplodactylus elderi</i>	1.63	0.19	18	0.62
<i>Diplodactylus pulcher</i>	1.67	0.22	25	1.20
<i>Diplodactylus stenodactylus</i>	1.40	0.08	44	0.25
<i>Diplodactylus strophurus</i>	1.36	0.11	51	0.61
<i>Nephrurus laevis</i>	1.37	0.55	174	0.36
<i>Nephrurus levis</i>	1.79	0.14	23	0.43
<i>Nephrurus vertebralis</i>	1.39	0.17	13	0.38
<i>Rhynchoedura ornata</i>	1.40	0.06	268	0.88

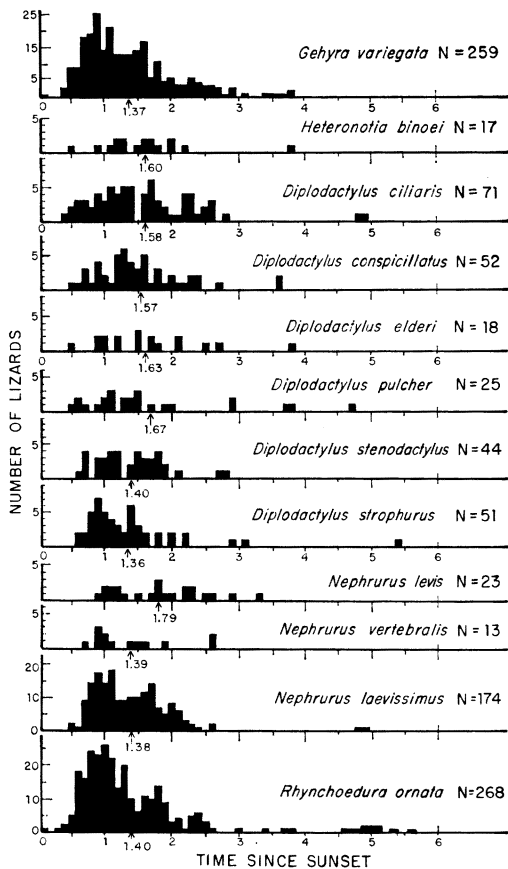


Fig. 4. Frequency distributions of times of activity of all twelve species, expressed in hours since sunset to correct for seasonal shifts in activity patterns. Means are indicated with arrows and sample sizes are given at the right side of each panel. Table 11 gives statistics computed from these data.

age body temperatures of active geckos are low-est for the three species of *Nephurus* and highest for the three termite specialists (Table 13). Many of the differences between species in air and body temperature statistics are statistically significant. For example, *Diplodactylus stenodactylus* and *Nephurus laevisissimus*, which occurred only on sandridge areas D and E (Table 1), differ significantly in both their air and body temperature statistics (*t*-tests, *P*'s < .001). Such differences probably stem from differential seasonal peaks of activity (Table 12), with higher temperature species being active during warmer months and species with lower temperatures such as *Nephurus* being active in the winter and early spring.

The relatively high thermal preferences of geckos in laboratory gradients could well reflect

optimal temperatures for digestive processes (Regal, 1966; Bustard, 1967d; Skoczylas, 1970; Vance, 1973; Lillywhite et al., 1973). Body temperatures of animals in their daytime retreats are probably considerably higher than those of active lizards at night (Huey, 1976). A. R. Main (pers. comm.) suggested that geckos hiding in spider burrows during the day may well regulate their body temperatures by moving up and down into warmer or cooler temperatures. One cool morning, we observed a *Diplodactylus strophurus* actually basking in full sunlight on a branch; we were, unfortunately, unable to record this animal's body temperature. Nevertheless, above considerations partially resolve the apparent disparity between body temperatures observed in laboratory thermal gradients and those actually realized under field conditions at night (see also Huey and Slatkin, 1976).

REPRODUCTION

Ovigerous females, with eggs in their oviducts, were collected for all species except *Nephurus vertebralis* (Table 14). All females either with enlarged yolked ovarian eggs or with eggs in their oviducts were used to determine clutch sizes. Female *Gehyra* invariably lay a single, rather hard-shelled egg. All other species, except *Diplodactylus pulcher*, inevitably contained two eggs. Two *D. pulcher* females had a single oviducal egg and three other females each carried two oviducal eggs; these females may have oviposited one egg and retained the other, as is known in the eublepharine gekkonid *Coleonyx variegatus* (Parker, 1972). The mean volume of an oviducal egg varies by an order of magnitude among the 11 species, from 0.14 cc in *Heteronotia* to 1.63 cc in the much larger *Nephurus lewis*. The ratio of total clutch volume of oviducal eggs to total female body weight (including the clutch), an estimate of reproductive effort (Ballinger and Clark, 1973), varies from 5.1% in *Gehyra* to 19.1% in *Diplodactylus conspicillatus*. Means and standard errors of this ratio are listed in Table 14 for 11 species. Species with more generalized ecological requirements tend to have higher niche overlaps and lower reproductive efforts than those with more specialized requirements such as the termite specialists (Fig. 7).

PREDATION AND BROKEN TAIL FREQUENCIES

Reptiles are among the major predators of geckos in the Australian deserts, although owls,

TABLE 12. NUMBERS OF GECKOS COLLECTED PER MAN-HOUR IN VARIOUS MONTHS ON AREAS WHERE EACH SPECIES OCCURRED OR WAS THOUGHT TO OCCUR (ACTIVE GECKOS ONLY).

Species	Spring			Summer			Autumn			Winter		Seasonal Niche Breadth
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	August	
<i>Gehyra variegata</i>	1.3	1.0	2.2	0.8	0.9	3.8	3.4	1.3	1.3	6.0	1.1	.64
<i>Heteronotia binoei</i>	0.0	0.1	0.02	0.05	0.0	0.11	0.14	0.0	0.5	2.6	0.0	.16
<i>Diplodactylus ciliaris</i>	0.8	1.7	0.5	0.5	0.7	—	—	—	0.4	2.6	1.4	.50
<i>Diplodactylus conspicillatus</i>	0.0	0.5	0.3	0.5	1.1	0.4	0.2	0.0	0.0	—	0.1	.44
<i>Diplodactylus elderi</i>	0.0	0.2	0.02	0.1	0.3	0.1	0.0	0.1	0.0	—	0.0	.38
<i>Diplodactylus pulcher</i>	—	0.2	0.0	0.5	0.4	0.0	1.2	0.0	—	—	—	.25
<i>Diplodactylus stenodactylus</i>	0.0	1.8	0.8	0.0	1.7	—	—	—	0.0	—	0.6	.31
<i>Diplodactylus strophurus</i>	0.1	0.8	0.3	0.3	0.5	0.0	1.2	0.0	0.0	—	0.3	.43
<i>Nephrurus laevisissimus</i>	4.0	2.5	1.6	1.7	2.8	—	—	—	2.4	—	3.2	.59
<i>Nephrurus levis</i>	0.1	0.5	0.2	—	0.6	0.2	0.1	—	—	6.0	0.0	.15
<i>Nephrurus vertebralis</i>	—	0.5	0.6	0.6	0.0	—	—	—	0.0	—	0.0	.27
<i>Rhynchoedura ornata</i>	0.5	1.3	1.0	1.8	0.7	1.6	1.1	4.0	0.3	0.0	0.2	.54
Total Number of Man-Hours Expended	24.2	50.4	45.7	41.5	61.5	17.9	14.8	0.8	3.8	1.2	21.3	

dingos and introduced European foxes doubtless also take their share. The varanid lizards *Varanus caudolineatus*, *V. gilleni*, *V. gouldi* and *V. tristis*, are variously known to capture *Gehyra variegata*, *Heteronotia binoei*, *Diplodactylus ciliaris*, *D. conspicillatus*, *D. pulcher* and *Rhynchoedura ornata* (Pianka, 1969c, 1970b, 1971), presumably from their daytime retreats. All three species of *Nephrurus* eat *Rhynchoedura ornata* and one *N. vertebralis* contained a *Diplodactylus conspicillatus* in its stomach. Several snakes of the genera *Pseudechis* and *Demansia* also contained *Gehyra* in their stomachs. The pygopodid lizard *Lialis burtoni* and nocturnal

skinks *Egernia striata* and *E. kintorei* are also probable predators.

Gekkonid tails and tail break frequencies have attracted considerable attention (Bustard, 1964, 1968b; Bustard and Hughes, 1966; Congdon et al., 1974; Parker, 1972; Werner, 1968). Among the 12 species under consideration here, the incidence of tails broken in nature varies widely, from less than 1% in the knob-tailed *Nephrurus laevisissimus* to 72.7% in *D. elderi* (Table 15). Except for *D. ciliaris* and *D. strophurus*, which along with *D. elderi* possess tail glands that secrete a noxious sticky mucous which probably repels potential predators (Bustard, 1964), arboreal species tend to have higher

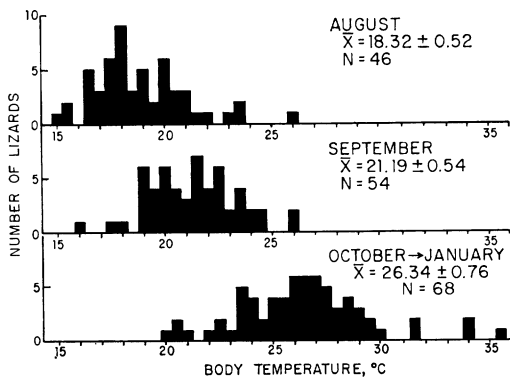


Fig. 5. Frequency distributions of body temperatures of *Nephrurus laevisissimus* at three different times of year. All means differ significantly (t-tests, $P < .001$).

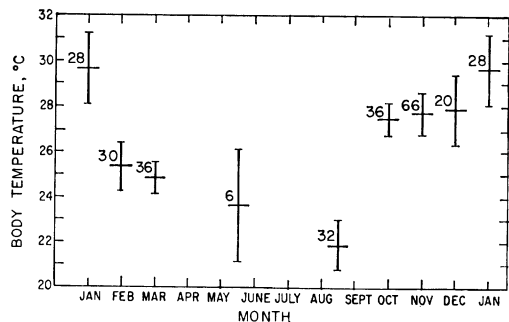


Fig. 6. Body temperatures of active *Gehyra variegata* at monthly and/or bimonthly intervals, to show seasonal changes. Horizontal bars are means and vertical lines plot two standard errors on either side of the mean. Numbers inside the figure represent sample sizes.

TABLE 13. STATISTICS ON AIR TEMPERATURES AND BODY TEMPERATURES FOR ACTIVE GECKOS. The last column is the correlation coefficient between AT and BT.

Species	Air Temperature				Body Temperature				r
	\bar{x}	SE	S	N	\bar{x}	SE	S	N	
<i>Gehyra variegata</i>	25.5	0.25	4.1	269	26.5	0.24	4.0	262	.90
<i>Heteronotia binoei</i>	25.1	0.97	5.2	29	27.0	0.69	3.5	25	.91
<i>Diplodactylus ciliaris</i>	25.8	0.66	5.6	71	25.4	0.67	5.7	71	.99
<i>Diplodactylus conspicillatus</i>	27.5	0.49	3.6	54	27.7	0.51	3.6	50	.88
<i>Diplodactylus elderi</i>	25.6	1.00	4.2	18	26.2	1.13	4.1	13	.97
<i>Diplodactylus pulcher</i>	27.5	0.69	3.5	25	27.7	0.76	3.7	24	.71
<i>Diplodactylus stenodactylus</i>	25.1	0.68	4.4	42	26.6	0.58	3.5	36	.92
<i>Diplodactylus strophurus</i>	25.5	0.68	5.0	53	25.3	0.67	4.8	52	.97
<i>Nephurus laevis</i>	22.8	0.30	3.9	171	22.5	0.32	4.1	172	.93
<i>Nephurus levis</i>	22.3	0.74	4.1	31	23.2	0.58	3.2	30	.86
<i>Nephurus vertebralis</i>	24.1	0.92	3.4	14	24.1	0.93	3.5	14	.97
<i>Rhynchoedura ornata</i>	26.7	0.21	3.3	265	27.4	0.19	2.9	237	.82

incidences of broken tails than terrestrial species as suggested by Werner (1968) (but see Parker, 1972). Surprisingly, however, *D. elderi*, which apparently uses its prehensile tail for climbing and its caudal glandular secretion in defense, has the highest incidence of broken regenerated tails among the species examined. These facts indicate intense predation pressures on *D. elderi*, and suggest that there must be a very considerable selective advantage to tail loss (see also Congdon et al., 1974). In the two species abundant enough to examine variation in frequencies of broken tails among areas, *Gehyra* and *Rhynchoedura*, such variation between areas is relatively slight. Elsewhere Pianka (1969c), has speculated that smaller individuals of the pygmy varanid lizard *Varanus caudolineatus* may actually deliberately harvest

the tails of *Gehyra* individuals that are too large to be subdued in their entirety.

COMPETITION AND COEXISTENCE

There are considerably more species of nocturnal lizards on study areas in the deserts of Western Australia than there are on similar areas in the Sonoran desert of North America, and somewhat more than on study sites in the Kalahari desert of southern Africa (Pianka, 1971a, 1973, 1975). Moreover, among the study sites reported on here, as many as nine species of geckos, including five species of *Diplodactylus*, occur together on area E. Since geckos dominate the nocturnal saurofauna in most deserts, understanding their niche relationships is of some interest (Pianka, 1973, 1975). We now

TABLE 14. CLUTCH SIZES, CLUTCH VOLUME OVER BODY WEIGHT STATISTICS FOR FEMALES CARRYING OVIDUCAL EGGS, AND MEAN VOLUMES OF OVIDUCAL EGGS FOR ELEVEN SPECIES OF GECKOS.

Species	Clutch Size	Clutch Volume/Body Weight $\times 100$			Egg Volume	
		\bar{x}	SE	N	\bar{x}	N
<i>Gehyra variegata</i>	1	5.12	0.28	29	.19	20
<i>Heteronotia binoei</i>	2	9.90	1.16	3	.14	5
<i>Diplodactylus ciliaris</i>	2	11.55	0.78	14	.52	31
<i>Diplodactylus conspicillatus</i>	2	19.11	1.39	9	.57	17
<i>Diplodactylus elderi</i>	2	14.32	0.68	3	.21	6
<i>Diplodactylus pulcher</i>	1-2	14.66	2.21	5	.41	7
<i>Diplodactylus stenodactylus</i>	2	10.26	1.66	3	.20	6
<i>Diplodactylus strophurus</i>	2	12.15	0.74	14	.47	27
<i>Nephurus levis</i>	2	16.05	0.20	2	1.63	2
<i>Nephurus laevis</i>	2	15.62	1.33	7	1.08	11
<i>Rhynchoedura ornata</i>	2	16.36	0.73	27	.21	46

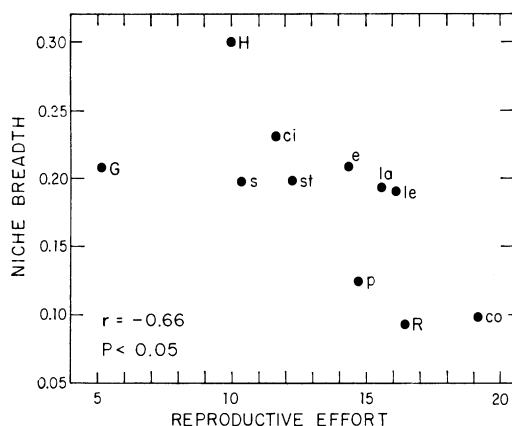


Fig. 7. Plot showing the inverse relationship between niche breadth and reproductive effort (average wet weight of an oviducal clutch as a percentage of total wet weight of an ovigerous female).

examine resource partitioning among these gecko species that could reduce competition and therefore allow coexistence of species, promoting the high species densities observed in the Australian deserts.

Closely related animal species often differ in 1) time of activity, 2) the foods they eat, either prey types or sizes ("trophic" or "food niche" of Pianka, 1973), and/or 3) their use of space, such as their habitats and micro-habitats ("place niche" of Pianka, 1973). Because times of activity differ relatively little among these species, the temporal niche dimension is not considered further. As indicated above, there are pronounced differences among these species of geckos in both the sizes and types of prey they exploit. Species with larger heads tend to eat larger prey items than those with smaller heads (Fig. 2). Three species (*Diplodactylus conspicillatus*, *D. pulcher* and *Rhynchoedura ornata*) eat virtually nothing but termites. Overlap in both food and microhabitat is very high among these three termite-specialized species (Table 16). Only two of the three occurred together in syntopy on our study areas: *Rhynchoedura* occurs on all areas, but *D. pulcher* and *D. conspicillatus* never occurred together (Table 1). Also, note that dietary overlap among termite specialists is nearly complete, but that dietary overlap between termite specialists and other gecko species (excepting *Gehyra*, which eats quite a few

TABLE 15. PERCENTAGES OF BROKEN TAILS AND SAMPLE SIZES AMONG VARIOUS SPECIES OF TERRESTRIAL, SEMIARBOREAL AND ARBOREAL GECKOS, WITH SOURCES.

Habits—Species	Sample Size	Percent Broken	Source
Arboreal Species			
<i>Gehyra variegata</i>	269	66.5	this paper
<i>Diplodactylus ciliaris</i>	70	8.6	this paper
<i>Diplodactylus strophurus</i>	53	11.3	this paper
<i>Diplodactylus williamsi</i>	80	8.8	Bustard (1964)
<i>Hemidactylus turcicus</i>	250	61.2*	Werner (1968)
<i>Ptyodactylus hasselquisti</i>	218	50.5*	Werner (1968)
Semi-arboreal Species			
<i>Diplodactylus eldери</i>	22	72.7	this paper
<i>Diplodactylus pulcher†</i>	25	32.0	this paper
Terrestrial Species			
<i>Heteronotia binoei</i>	40	52.5	this paper
<i>Diplodactylus conspicillatus</i>	54	18.5	this paper
<i>Diplodactylus stenodactylus</i>	40	30.0	this paper
<i>Nephrurus laevis</i>	169	0.6	this paper
<i>Nephrurus levis</i>	35	8.6	this paper
<i>Nephrurus vertebralis</i>	14	7.1	this paper
<i>Rhynchoedura ornata</i>	266	25.2	this paper
<i>Coleonyx variegatus</i>	353	48.7	Parker (1972)
<i>Stenodactylus stenodactylus</i>	61	18.0*	Werner (1968)
<i>Ceramodactylus doriae</i>	28	25.0*	Werner (1968)

* Includes tails broken by human handling as well as those incurred naturally.

† Perhaps better classified as terrestrial.

TABLE 16. OVERLAP IN DIET* (ABOVE DIAGONAL) AND MICROHABITAT† (BELOW DIAGONAL) AMONG TWELVE SPECIES OF GECKOS (CODED AS IN TABLE 3). Overlap index used is that of Pianka (1973). Boldface entries represent pairs that were not sympatric on study areas.

	G	H	ci	co	e	p	s	st	la	le	v	R
G	1	.72	.49	.81	.85	.81	.53	.54	.51	.49	.25	.81
H	.18	1	.67	.28	.79	.28	.56	.77	.71	.68	.58	.28
ci	.95	.34	1	.00	.68	.00	.59	.78	.83	.85	.24	.00
co	.09	.87	.27	1	.43	1.00	.15	.00	.00	.00	.00	1.00
e	.03	.27	.18	.40	1	.43	.64	.85	.69	.76	.39	.43
p	.54	.79	.56	.77	.13	1	.15	.00	.00	.00	.00	1.00
s	.05	.57	.32	.70	.48	.43	1	.66	.79	.55	.20	.15
st	.86	.21	.76	.19	.06	.71	.11	1	.81	.85	.40	.00
la	.09	.84	.27	.96	.20	.76	.75	.18	1	.82	.42	.00
le	.09	.84	.28	.99	.48	.74	.74	.19	.95	1	.52	.00
v	.09	.85	.25	.98	.22	.79	.63	.19	.98	.96	1	.00
R	.09	.86	.24	.98	.26	.80	.60	.19	.97	.96	1.00	1

* Based on 20 prey categories, by volume (data of Table 6).

† Based on 8 microhabitat categories (data of Table 3).

termites) tends to be low, frequently near zero (Table 16).

Of the 66 possible interspecific pairs among the 12 species, all but ten (boldface entries in Table 16) were actually found in sympatry on one or more of the nine study areas. These allopatric species pairs are represented by solid dots in Fig. 8, whereas pairs that occur in sympatry are indicated by open circles. Two pairs

of termite specialists, *Rhynchoedura* × *D. conspicillatus* and *Rhynchoedura* × *D. pulcher*, have extremely high overlap in both diet and microhabitat (Fig. 8). These two species also eat prey of the same size (Table 8), and use similar daytime retreats, spider burrows (Table 2). The mechanism(s) by which these ecologically nearly identical species coexist is (are) elusive, but could stem from the very concentrated nature of their termite food source. Also, we may have overestimated the actual extent of dietary overlap since these gecko species could eat different species or castes of termites as is known for South African skinks in the genus *Typhlosaurus* (Huey et al., 1974; Huey and Pianka, 1974). Except for these two pairs with perplexingly high overlap, there seems to be a distinct upper limit on dietary overlap of about 0.85 (Fig. 8). Moreover, many pairs with high overlap in microhabitat overlap relatively little in diet and vice versa (Fig. 8).

ACKNOWLEDGMENTS

We thank William S. Parker and especially Raymond B. Huey for useful comments on the manuscript. Virginia Denniston, Glennis Kaufman and Michael Egan assisted with laboratory work and data processing. Glen M. Storr and A. R. Main provided encouragement and valuable advice on field techniques. The Department of Zoology at The University of Western Australia served as a base for our operations and provided many other courtesies. We are also deeply indebted to our sturdy and dependable landrover, Matilda, which performed faith-

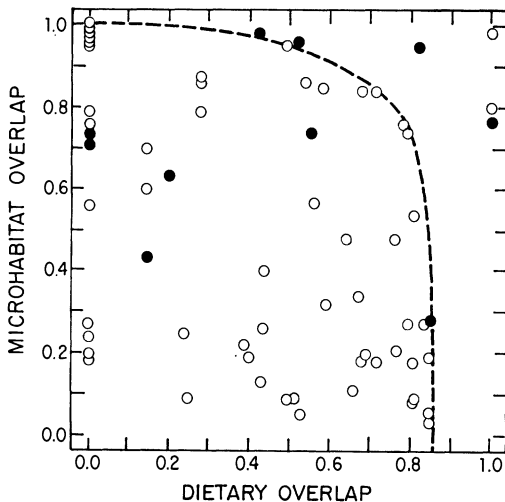


Fig. 8. Microhabitat overlap is plotted against overlap in diet for all interspecific pairs among the twelve species. Open symbols represent pairs known to occur in sympatry, closed ones indicate those we did not find sympatric on our study areas. See text.

fully as our life support system in the vast Australian desert. Field work during the daylight hours would have been impossible without the aerosol insect repellent, Scram, to ward off the Australian bushfly, *Musca vetustissima*. Finally, of course, the research could not have been carried out without the financial assistance provided by grants from the National Institutes of Health and the National Science Foundation.

LITERATURE CITED

- BALLINGER, R. E., AND D. R. CLARK. 1973. Energy content of lizard eggs and the measurement of reproductive effort. *J. Herpetology* 7:129-132.
- BRAIN, C. K. 1962. Observations on the temperature tolerance of lizards in the central Namib Desert, Southwest Africa. *Cimbebasia* 4:1-5.
- BRATTSTROM, B. H. 1952. Diurnal activities of a nocturnal animal. *Herpetologica* 8:61-63.
- BUSTARD, H. R. 1964. Defensive behavior shown by Australian geckos, genus *Diplodactylus*. *Herpetologica* 20:198-200.
- . 1965a. The systematic status of the Australian geckos *Gehyra variegata* (Dumeril & Bibron, 1836) and *Gehyra australia* Gray, 1845. *Herpetologica* 20:259-272.
- . 1965b. Observations on Australian geckos. *Herpetologica* 21:294-302.
- . 1966. The *Oedura tryoni* complex: East Australian rock-dwelling geckos. (Reptilia: Gekkonidae). *Bull. Brit. Mus. (Nat. Hist.)* 14:1-14.
- . 1967a. Defensive display behavior of the Australian gecko *Nephurus asper*. *Herpetologica* 23:126-129.
- . 1967b. Gekkonid lizards adapt fat storage to desert environments. *Science* 158:1197-1198.
- . 1967c. Reproduction in the Australian gekkonid genus *Oedura* Gray 1842. *Herpetologica* 23:276-284.
- . 1967d. Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. *Copeia* 1967:753-758.
- . 1967e. A mechanism for greater predator survival during cold torpor in gekkonid lizards. *Brit. J. Herpetol.* 4:7-8.
- . 1968a. The ecology of the Australian gecko, *Gehyra variegata*, in northern New South Wales. *J. Zool., Lond.* 154:113-138.
- . 1968b. Temperature dependent tail autotomy mechanism in gekkonid lizards. *Herpetologica* 24:127-130.
- . 1968c. Temperature dependent activity in the Australian gecko *Diplodactylus vittatus*. *Copeia* 1968:606-612.
- . 1968d. The ecology of the Australian gecko *Heteronotia binoei* in northern New South Wales. *J. Zool., Lond.* 156:483-497.
- . 1969a. The population ecology of the gekkonid lizard *Gehyra variegata* (Dumeril & Bibron) in exploited forests in Northern New South Wales. *J. Anim. Ecol.* 38:35-51.
- . 1969b. The ecology of the Australian geckos *Diplodactylus williamsi* and *Gehyra australis* in northern New South Wales. Parts I and II. Koninkl. Nederl. Akad. Wet. Amsterdam Proc. Series C, 72:451-477.
- . 1970a. The population ecology of the Australian gekkonid lizard *Heteronotia binoei* (Gray) in an exploited forest. *J. Zool. Lond.* 162:31-42.
- . 1970b. The role of behavior in the natural regulation of numbers in the gekkonid lizard *Gehyra variegata* (Dumeril & Bibron). *Ecology* 51:724-728.
- . 1970c. Australian lizards. Collins, Sydney and London.
- . 1970d. Activity cycle of the tropical house gecko, *Hemidactylus frenatus*. *Copeia* 1970:173-176.
- . 1971. A population study of the eyed gecko, *Oedura ocellata* Boulenger, in northern New South Wales, Australia. *Copeia* 1971:658-669.
- , AND R. D. HUGHES. 1966. Gekkonid lizards: average ages derived from tail loss data. *Science* 153:1670-1671.
- CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, N. J.
- CONGDON, J. D., L. J. VITT AND W. W. KING. 1974. Geckos: Adaptive significance and energetics of tail autotomy. *Science* 184:1379-1380.
- GLAUERT, L. 1961. A handbook of the lizards of Western Australia. Handbook No. 6. Western Australian Naturalists Club, Perth.
- HUEY, R. B. 1969. Ecological relations of sympatric *Phyllodactylus* in the Sechura desert of Peru. Unpubl. M.A. Thesis, University of Texas at Austin.
- . 1975. Comparative ecology of sympatric geckos (*Phyllodactylus*) in the Sechura Desert of Peru.
- . 1976. Thermal biology of some tropical desert lizards from Peru. *Copeia* 1976: in press.
- , AND E. R. PIANKA. 1974. Ecological character displacement in a lizard. *Amer. Zoologist* 14:1127-1136.
- , AND M. SLATKIN. 1976. A cost-benefit model of lizard thermoregulation. *Quarterly Review of Biology*: in press.
- , E. R. PIANKA, M. E. EGAN AND L. W. COONS. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards (*Typhlosaurus*). *Ecology* 55:304-316.
- KING, W. 1959. Observations on the ecology of a new population of the Mediterranean gecko, *Hemidactylus turcicus* in Florida. *Quart. J. Fla. Acad. Sci.* 21:317-318.
- KLUGE, A. G. 1967. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Australian J. Zool.* 15:1007-1108.
- LIGHT, P., W. R. DAWSON, V. H. SHOEMAKER AND A. R. MAIN. 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* 1966:97-110.
- LILLYWHITE, H. B., P. LIGHT AND P. CHELGREN. 1973. The role of behavioral thermoregulation in the growth energetics of the toad, *Bufo boreas*. *Ecology* 54:375-383.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Amer. Nat.* 100:603-609.
- MARCELLINI, D. L. 1971. Activity patterns of the gecko *Hemidactylus frenatus*. *Copeia* 1971:631-635.
- MITCHELL, F. J. 1965. Australian geckos assigned

- to the genus *Gehyra* Gray. (Reptilia, Gekkonidae). Senck. biol. 46:287-319.
- PARK, O. 1938. Studies in nocturnal ecology 7. Preliminary observations on rain forest animals. Ecology 19:208-223.
- PARKER, W. S. 1972. Aspects of the ecology of a Sonoran desert population of the western banded gecko, *Coleonyx variegatus* (Sauria, Eublepharinae). Amer. Midl. Natur. 88:209-224.
- , AND E. R. PIANKA. 1974. Further ecological observations on the western banded gecko, *Coleonyx variegatus*. Copeia 1974:528-531.
- PIANKA, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Unpubl. Ph.D. Thesis, University of Washington, Seattle.
- . 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333-351.
- . 1960a. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology 50:498-502.
- . 1969b. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012-1030.
- . 1969c. Notes on the biology of *Varanus caudolineatus* and *Varanus gilleni*. Western Australian Naturalist 11:76-82.
- . 1970a. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703-720.
- . 1970b. Notes on the biology of *Varanus gouldi flavirufus*. Western Australian Naturalist 11:141-144.
- . 1971a. Lizard species density in the Kalahari desert. Ecology 52:1024-1029.
- . 1971b. Notes on the biology of *Varanus tristis*. Western Australian Naturalist 11:180-183.
- . 1972. Zoogeography and speciation of Australian desert lizards: an ecological perspective. Copeia 1972:127-145.
- . 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53-74.
- . 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci. USA. 71:2141-2145.
- . 1975. Niche relations of desert lizards, p. 292-314. In: "Ecology and Evolution of Communities," a symposium volume in honor of Robert MacArthur, M. Cody and J. Diamond (eds.). Harvard University Press, Cambridge, Mass.
- , AND W. S. PARKER. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. Copeia 1972:493-508.
- , AND ———. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141-162.
- , AND H. D. PIANKA. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. Copeia 1970:90-103.
- PIANKA, H. D., AND E. R. PIANKA. 1970. Bird censuses from desert localities in Western Australia. Emu 70:17-22.
- REGAL, P. J. 1966. Thermophilic response following feeding in certain reptiles. Copeia 1966:588-590.
- RICKLEFS, R. E. 1966. The temporal component of diversity among species of birds. Evolution 20:235-242.
- ROSE, F. L., AND C. D. BARBOUR. 1968. Ecology and reproductive cycles of the introduced gecko, *Hemidactylus turcicus* in the southern United States. Amer. Midl. Natur. 79:159-168.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.
- . 1976. Competition and the niche, in press. In: Biology of the Reptilia, D. W. Tinkle and W. W. Milstead (eds.). Academic Press, New York.
- SIMPSON, E. H. 1949. Measurement of diversity. Nature 163:688.
- SKOCZYLAS, R. L. 1970. Influence of temperature on gastric digestion in the grass snake, *Natrix natrix* L. Comp. Biochem. Physiol. 33:793-804.
- VANCE, V. J. 1973. Temperature preference and tolerance in the gecko, *Coleonyx variegatus*. Copeia 1973:615-617.
- WERNER, Y. L. 1968. Regeneration frequencies in geckos of two ecological types (Reptilia: Gekkonidae). Vie et Milieu 19:199-221.
- . 1969. Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylidae). Israel J. Zool. 18: 291-316.

DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF TEXAS, AUSTIN, TEXAS 78712. Accepted 17 Sept. 1974.