Adult Goliath Heron, of Zululand, standing near its nest in a *Phragmites* patch. For a report on the biology of this bird, see page 537.

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This volume was prepared with the assistance of Cynthia Collins, Katherine Hoskins, and Lyle Rosbotham.

Ecological Dynamics of Australian Desert Lizards: or, the L-Area Revisited

Grant Recipient:	Eric R. Pianka, Department of Zoology, University of Texas, Austin, Texas.
Grants 1977, 1829:	For a study of ecology and diversity of desert lizards in Western Australia.

During postdoctoral studies in the Great Victoria Desert of Western Australia in 1966-1968, I discovered what are very probably the richest lizard faunas on Earth (Pianka, 1969a). One red sandridge site supports at least 40 different species of lizards! In addition to a diverse fauna of fairly typical lizards, these include small nearly legless subterranean skinks, snake-like pygopodids, as well as very intelligent mammal-like varanid lizards. Areas in the Kalahari semidesert of southern Africa, practically identical in their basic climate and general physiognomy (but markedly different in their biota) support fewer than half as many species of lizards (Pianka, 1971). How do so many different species of lizards partition resources and manage to coexist in the Australian deserts? Some preliminary results and ideas have been offered (Pianka, 1969a, 1969b, 1971, 1973, 1975, 1981).

A major goal of the present research was to assess the stability of these lizard assemblages and to try to determine how duplicable earlier results might be. For example, I wanted to find out whether resource usage patterns were stable. I also hoped to better characterize the resources used by apparently rare species.

SPECIES RICHNESS

With the help of funding from the National Geographic Society (including the generous loan of a four-wheel-drive Toyota Landcruiser field vehicle), I returned to the Great Victoria Desert from June 1978 through March 1979. Little change was evident on study areas. More than 3000 new lizard specimens were collected along with supporting field data: Sample sizes for most species, including many "rare" ones, were doubled, greatly increasing my confidence in estimates of resource usage. Two sites were chosen for detailed study, one of which (the "L-area") had been examined on the previous expedition. A second study site, "Red Sands," was found to support at least 42 different species of desert lizards, including the fabulous perentie *Varanus giganteus* (the second largest living species of lizard, penultimate only to the Komodo monitor *Varanus komodoensis*). In the remainder of this report, I focus on the L-area.

This large lizard collection (now lodged permanently in the Western Australian Museum in Perth) was shipped back to Texas, where the lizards were measured and dissected. Reproductive status was determined (sex, testes length, egg number, and egg volume). Stomachs were removed and contents measured and identified. Prey, largely insects, were assigned to some 275 different food categories by type, color, and size. For example, ants and termites were placed into size and color categories by family to generate some 97 ant and 58 termite resource states (here I examine a condensed version of this data set, using just 19 prey categories). Data matrices of utilization coefficients by lizard species were constructed and analyzed with the aid of a computer. The diversity of foods eaten ("dietary niche breadth") was calculated for each species and dietary overlaps were computed for all possible pairs of species. A comparable analysis of microhabitat use patterns was also undertaken. Estimates of both dietary and microhabitat niche breadths are uncorrelated with number of lizards, an indication that sample sizes are adequate to characterize patterns of resource use. These data were compared with other information gathered earlier. Considerable species-specificity and substantial fidelity in the use of food types and microhabitats is evident among many of these Australian desert lizards. For example, some species are termite-specialists whereas others virtually never eat termites; still other species eat ants to the exclusion of other prey. Diet and microhabitat utilization patterns of most species, even those of generalists such as the gecko *Heteronotia binoeii*, proved to be remarkably consistent in time. Also, in site-to-site comparisons, each species is typically its own closest neighbor in niche space. Tables 1 and 2 summarize results obtained for eight relatively abundant species in the L-area in 1966-1968 and again in 1978-1979 (overall estimates based upon all the specimens of each species collected on all study sites are still more conservative, varying relatively little between 1966-1968 and 1978-1979). Some shifts in resource use were also evident in certain species in the L-area.

On the L-area, 530 lizard specimens representing 27 species were collected in 1966-1968. Tracks of the wary, large monitor *Varanus gouldi* were regularly noted although no specimens of these elusive lizards were sighted. The spinifex gecko *Diplodactylus elderi* was listed as "highly expected on the basis of geographic range, habitat, autecology, and micro-

Table 1. Diets of Eight Species (Representing Three Families) of Lizards on the L-area in 1966-1968 and in 1978-1979 (Percentages, by Volume)

	Amphibolurus Isolepis		*Moloch Horridus*		*Crypto-blepharus Boutoni*		*Egernia Striata*		*Ctenotus Grandis*		*Ctenotus Helenae*		*Gehyra Variegata*		*Rhynchoe-dura Ornata*	
PREY	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79
CATEGORY																
Centipedes		0.2						1.5		6.6		0.5				
Spiders	0.4	0.8			12.7	22.7	0.1	0.8	1.3	0.2	0.9	2.3	6.6	3.1		
Ants	24.8	49.2	100.0	100.0		9.1	3.8	8.1	2.8	0.7	1.0	0.7	1.2	0.4	0.4	0.5
Wasps	4.6	2.3				1.2	0.1	0.4			1.1	0.4	1.8	0.2		
Grasshoppers and crickets	3.5	9.8			17.5	6.0	0.2	0.8	0.1		5.3	5.6	9.5	7.3		
Roaches		1.1				9.1	0.3	3.7	1.5		10.1	6.7	4.1	21.2		
Mantids		0.2			7.8	1.2							0.5	0.7		
Beetles	3.9	3.7			4.3	16.9	2.1	6.3	0.5	2.2	1.5	4.3	7.3	18.5		
Termites	33.4	23.9			15.8	10.6	86.2	70.3	72.9	89.2	69.6	73.7	49.4	15.1	99.4	96.7
Hemipterans	5.0	2.4			16.2	6.0	0.1	0.2		0.05		0.2	6.9	9.7		
Diptera		3.0			1.0	7.9								0.2		
Lepidoptera	1.0				3.9		0.3		0.8		0.6	2.6	1.7	6.5		
Insect larvae	20.5	1.9			6.8		2.8	0.05	7.0		7.1	0.2	5.5	3.9		
Miscellaneous unidentified insects	3.1	0.6			14.0	5.4	0.7	3.1	1.0	0.8	0.7		2.7	4.8		2.4
Vertebrates						3.3	3.1	1.5	6.5			2.7	0.4	8.0		
Plant material		0.7					0.2	3.1	5.5		2.1	0.2			0.1	0.5
Total volume of prey, (cc)	13.48	97.66	5.70	3.86	0.51	1.66	37.93	53.76	50.64	61.54	40.69	17.10	12.26	21.85	2.30	2.10

TABLE 2. Percentage Utilization of Various Microhabitats Among Eight Lizard Species (Representing Three Families) on the L-area in 1966-1968 and again in 1978-1979

	Amphibolurus Isolepis		*Moloch Horridus*		*Crypto-blepharus Boutoni*		*Egernia Striata*		*Ctenotus Grandis*		*Ctenotus Helenae*		*Gehyra Variegata*		*Rhynchoe-dura Ornata*	
MICROHABITAT CATEGORY	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79	66-68	78-79
Open sun	66.0	32.6	71.4	42.9	3.7		2.6	28.6	11.1	21.9	6.4	7.1				
Grass sun	20.8	55.2		21.4	3.7		5.3	9.5	8.9	12.5	6.4	14.3				
Bush sun		0.4						4.8								
Tree sun		0.5			5.6	1.9					2.1					
Other sun						10.4	9.2	21.4								
Open shade		0.6			3.7		27.6						3.5	1.5	86.0	93.5
Grass shade	13.2	9.6	28.6	7.1			26.3	9.5	80.0	65.6	75.5	71.4		3.0	2.0	3.2
Bush shade		0.6					5.3	4.8					0.9	1.5		
Tree shade		0.4		28.6	1.9						9.6	3.6	3.9	3.7		3.2
Other shade						0.9	23.7	21.4					0.9	5.7	12.0	
Low sun					25.0	36.8										
Low shade		0.2			13.9	6.6							39.0	39.5		
High sun					30.6	34.0						3.6				
High shade					12.0	9.4							51.8	45.0		
Total number of lizards	53	513	7	7	27	53	37	21	45	32	47	28	114	200	50	62

habitat" (Pianka 1969a). During the 1978-1979 expedition, some 1565 new lizard specimens representing 32 species were captured in the L-area. Only one species that was collected in 1966-1968 was not encountered on the second trip (*Egernia kintorei*, a very uncommon large nocturnal skink); five new species were recorded, including *Varanus gouldi* and *Diplodactylus elderi* (both mentioned above). Tracks of the enormous *Varanus giganteus* were seen, but these exceedingly intelligent lizards always evaded sighting and easily eluded capture.

RELATIVE ABUNDANCE

Relative abundance of various species in the L-area, as reflected in the numbers actually collected, did not remain constant but fluctuated fairly substantially (Table 3, left side). Abundance of some species varied upward or downward by factors of three or more, but most changed less. Regardless of the direction (increase versus decrease), the average magnitude of change in relative abundance is 2.69 (SD = 1.64, n = 26). Apparent changes in the abundance of the very uncommon species could easily be artifacts and probably should not be taken too seriously. While these differences are doubtlessly attributable, in part, to differences among collectors, I nevertheless gained the distinct impression that at least two species had markedly increased in abundance (*Amphibolurus isolepis* and *Ctenotus calurus*), whereas several other species seemed to have definitely declined more or less drastically (*Ctenotus grandis*, *Ctenotus helenae*, *Gehyra variegata*, and *Rhynchoedura ornata*). In the light of these apparent changes in relative abundance, closer scrutiny of resource utilization patterns among species is instructive (Tables 1 and 2).

DIET AND MICROHABITAT

Foods available to these lizards appear to have undergone some changes between 1966-1968 and 1978-1979, at least as reflected in what the entire saurofauna actually ate (see below).

These changes may be deemed as relatively conservative in that composition of prey categories changed by less than an order of magnitude (calculated by percentage). Nonetheless, grasshoppers and crickets and insect larvae seem to have dropped precipitously whereas ants and vertebrates show strong increases (the apparent change in vertebrate foods is an artifact to the extent that it reflects my own heightened effort to collect *Varanus*). Note that the diversity of foods eaten by all lizards increased slightly, partially due to the decrease in the importance of termites. (The L-area is unusual among my Australian study areas in its very high values for termite consumption.)

Prey Category	% Composition 1966-1968	% Composition 1978-1979	Change in Relative Importance
Centipedes	0.3	1.2	+ 4.0
Spiders	1.2	0.7	- 1.7
Scorpions	1.5	1.7	+ 1.1
Ants	5.5	12.4	+ 2.3
Wasps	0.6	0.6	1.0
Grasshoppers and crickets	13.3	7.5	- 1.8
Roaches	2.5	2.9	+ 1.2
Mantids and phasmids	0.2	0.4	+ 2.0
Neuropterans	—	0.1	(+)
Beetles	3.1	4.4	+ 1.4
Termites	50.4	41.8	- 1.2
Hemipterans	1.2	1.6	+ 1.1
Diptera	0.01	0.7	+70.0
Lepidoptera	1.2	0.4	- 3.0
Insect eggs and pupae	0.2	0.1	- 2.0
All insect larvae	5.7	1.0	- 5.7
Miscellaneous arthropods	1.8	3.0	+ 1.7
Vertebrates	5.2	18.3	+ 3.5
Plant materials	6.0	1.4	- 4.3
Total volume of food (cc)	249.1	477.5	
Diversity of foods eaten by all lizards	3.48	4.28	

Although there is no reason to suspect that availability of microhabitats should have altered appreciably over the decade between my two visits, the following summarizes data on microhabitat utilization of the entire L-area saurofauna in 1966-1968 versus 1978-1979.

The fraction of lizards first sighted in the sunshine at the edge of porcupine grass tussocks increased fourfold whereas those observed in grass shade decreased. Overall diversity of microhabitats used by all individuals of all lizard species declined.

A simplistic first hypothesis might be that abundance fluctuates directly with prey availability. If so, doubling the availability of ants would be expected to lead to doubling the density of myrmecophagous species. Likewise, abundance of termite-specialists would be expected to "track" termite availability. Provided one can assume that values in the above tabulation reflect real changes in availability, this hypothesis is easily tested and rejected: *Moloch horridus*, an obligate ant-specialist, decreased by a factor of three even though ants increased more than twofold. Also, although termites decreased slightly (from 50% to 42%) in the overall diet of all lizards, the relative abundance of an obligate termite-specialist *Diplodactylus conspicillatus* increased by 50% (another termite-specialist, *Rhynchoedura ornata*, fluctuated in the opposite direction, decreasing to about 40% of its former abundance). A related observation of interest can be made for *Ctenotus calurus*, the species that increased the most dramatically (450%): This tiny blue-tailed skink almost doubled its consumption of termites from 1966-1968 to 1978-1979 (from 44.3% to 81.2%), in spite of the fact that termites decreased in the overall diet of all lizards. The fraction of insect larvae in its diet fell from 51.3% to only 2%, whereas in the overall diet of all lizards, larvae decreased from 5.7% to 1.0%.

Microhabitat Category	% Utilization 1966-1968	% Utilization 1978-1979	Change in Relative Importance
Subterranean	1.2	1.9	+1.6
Open sun	14.4	18.6	+1.3
Grass sun	6.8	30.8	+4.5
Bush sun	0.1	0.2	+2.0
Tree sun	1.0	0.4	- 2.5
Other sun	0.8	0.8	1.0
Open shade	14.9	5.9	- 2.5
Grass shade	28.5	20.5	- 1.4
Bush shade	0.7	0.6	- 1.2
Tree shade	2.3	1.6	- 1.4
Other shade	3.4	1.6	- 2.1
Low sun	1.5	1.7	+1.1
Low shade	9.4	6.0	- 1.6
High sun	2.1	1.8	- 1.2
High shade	13.0	7.5	- 1.7
Total no. of lizards	516	1423	
Diversity of microhabitats used by all lizards	6.36	5.37	

Yet another interesting, although unfortunately rare, species is the flap-footed legless lizard *Pygopus nigriceps*, a nocturnal denizen of the open spaces with an unusually high consumption of scorpions (the diet by volume of 16 individuals consisted of 34% scorpions). In the overall diet of all lizards, the importance of scorpions was trivial and did not change appreciably (only 1.5% to 1.7%). Nonetheless, *Pygopus* declined drastically in relative abundance from 1.5% to a mere 0.2%.

CONCLUSIONS

Dietary and microhabitat niche breadths, and changes therein, are

TABLE 3. Lizards Collected in the L-Area, Their Abundance, Diet, and Microhabitat and Relative Change Between Collecting Trips

SPECIES	1966-1968		1978-1979		CHANGE IN RELATIVE ABUNDANCE
	NO.	%	NO.	%	
Amphibolurus inermis	9	1.70	5	0.32	- 5.30
A. minor	8	1.51	12	0.77	- 1.96
A. isolepis	55	10.38	530	33.87	+3.30
Moloch horridus	9	1.70	9	0.58	- 2.90
Varanus eremius	3	0.57	13	0.83	+1.46
V. gouldi	tr	—	4	0.26	+
V. tristis	6	1.13	18	1.15	+1.02
Ctenotus ariadnae	5	0.94	11	0.70	- 1.34
C. calurus	11	2.08	147	9.39	+4.50
C. grandis	45	8.49	39	2.49	- 3.40
C. helenae	53	10.00	31	1.98	- 5.05
C. pantherinus	8	1.51	21	1.34	- 1.13
C. piankai	2	0.38	3	0.19	- 2.00
C. quattuordecimlineatus	46	8.68	183	11.69	+1.35
C. schomburgkii	7	1.32	40	2.56	+1.94
Cryptoblepharus boutoni	27	5.09	53	3.39	- 1.50
Egernia kintorei	1	0.19	0	—	-
E. inornata	2	0.38	2	0.13	- 2.90
E. striata	37	6.98	68	4.35	- 1.60
Lerista bipes	6	1.13	53	3.39	+3.00
L. muelleri	0	—	6	0.38	+
Menetia greyii	3	0.57	4	0.26	- 2.20
Morethia butleri	0	—	1	0.06	+
Delma fraseri	0	—	4	0.26	+
Lialis burtonis	2	0.38	2	0.13	- 1.10
Pygopus nigriceps	8	1.51	3	0.19	- 7.95
Diplodactylus conspicillatus	6	1.13	27	1.73	+1.50
D. stenodactylus	0	—	1 (2)	0.06	+
D. elderi	0	—	4	0.26	+
Gehyra variegata	114	21.51	202	12.91	- 1.67
Heteronotia binoei	1	0.19	1	0.06	- 3.17
Nephrurus levis	6	1.13	4	0.26	- 4.35
Rhynchoedura ornata	50	9.43	64	4.09	- 2.31
Total no.	530 + tr		1565		

TABLE 3.—*(continued)*

	DIET			MICROHABITAT		
SPECIES	1966-1968	1978-1979	CHANGE	1966-1968	1978-1979	CHANGE
Amphibolurus inermis	4.33	2.89	- 1.5	1.80	5.00	+2.8
A. minor	3.50	3.51	1.0	3.84	3.90	+1.02
A. isolepis	4.48	3.19	- 1.4	2.01	2.38	+1.2
Moloch horridus	1.00	1.00	1.0	1.69	3.16	+1.9
Varanus eremius	1.41	2.14	+1.5	4.03	2.89	- 1.4
V. gouldi	2.77	2.44	- 1.1	1.55	3.60	+2.3
V. tristis	1.34	1.46	+1.1	1.92	2.13	+1.1
Ctenotus ariadnae	1.42	1.33	- 1.07	2.94	1.86	- 1.6
C. calurus	2.17	1.30	- 1.67	1.97	2.58	+1.3
C. grandis	1.85	1.25	- 1.47	1.52	2.02	+1.3
C. helenae	1.99	1.80	- 1.11	1.70	1.86	+1.1
C. pantherinus	1.30	1.04	- 1.25	1.47	1.65	+1.1
C. piankai	3.57	1.47	- 2.43	2.00	1.00	- 2.0
C. quattuordecimlineatus	5.51	1.55	- 3.55	1.49	2.10	+1.4
C. schomburgkii	1.01	1.30	+1.29	3.38	3.36	- 1.01
Cryptoblepharus boutoni	7.59	7.97	+1.05	5.07	3.63	- 1.4
Egernia kintorei	1.44	—	—	1.00	—	—
E. inornata	1.17	1.00	- 2.3	5.47	2.67	- 2.1
E. striata	1.34	1.97	+1.5	4.63	5.10	+1.1
Lerista bipes	3.83	1.90	- 2.0	1.00	1.28	+1.3
Lerista muelleri	—	3.58	—	—	1.39	—
Menetia greyii	2.00	1.29	- 1.55	2.57	1.60	- 1.6
Morethia butleri	—	1.00	—	—	2.00	—
Delma fraseri	—	1.92	—	—	1.00	—
Lialis burtonis	1.13	—	—	1.00	2.00	+2.0
Pygopus nigriceps	1.49	1.47	- 1.01	1.28	2.00	- 1.6
Diplodactylus conspicillatus	1.00	1.02	+1.02	1.80	2.31	+1.3
D. stenodactylus	—	1.00	—	—	1.00	—
D. elderi	—	2.47	—	—	1.00	—
Gehyra variegata	3.64	7.57	+2.1	2.36	2.74	+1.2
Heteronotia binoei	1.80	1.00	- 1.8	1.00	1.00	1.0
Nephrurus levis	5.30	—	—	2.67	3.00	+1.1
Rhynchoedura ornata	1.01	1.07	+1.06	1.33	1.14	- 1.2
MEAN	2.55	2.13	1.51*	2.30	2.32	1.46*
STANDARD DEVIATION	1.68	1.71	0.60*	1.27	1.10	0.45*

**Based on absolute values*

summarized in Table 3 (right side). The "compression hypothesis" asserts that microhabitats tend to be more labile than diets (MacArthur and Pianka, 1966; MacArthur and Wilson, 1967; Schoener 1974; Schoener et al., 1979). This hypothesis does not seem to be supported by the present data. The average magnitude of observed change in niche breadth (irrespective of sign) among all species was similar for foods (1.51) and microhabitats (1.46). Average food niche breadth declined slightly (2.55 to 2.13), whereas average microhabitat niche breadth remained approximately constant (2.30 versus 2.32). Variance in niche breadth among species was lower in microhabitat than in diet.

A related prediction of optimal foraging theory is that diets tend to contract when foods are abundant but expand when foods are scarce. One might also expect relative abundance of consumers to vary directly with prey abundance. Of the 7 species that increased in relative abundance, food niche breadths decreased as predicted in 4, increased in 2, and stayed constant in 1 (the termite-specialist *Diplodactylus conspicillatus*). Two species changed little in relative abundance and their food niche breadth remained fairly constant. Of the 15 species that declined in abundance, diets expanded (as expected) in only 2, contracted in 6, and changed little among 7 others (the latter include both food specialists and food generalists).

These data may also be exploited to test the hypotheses that abundance of ecologically similar species fluctuate either in phase with one another, or out of phase with one another—more so as compared with ecologically more dissimilar species. The first hypothesis emerges from a noncompetition argument asserting only that species track resources, whereas the second suggests beneficial or detrimental coactions among species such as might arise from interspecific competition.

In an effort to perform such a test, I computed the direction and magnitude of changes in relative abundance among all possible pairs of species. Using lumped data from both visits, overall ecological similarity was estimated as the product of dietary overlap times microhabitat overlap. The relative change in the abundance of each pair of species was expressed as the ratio of the change in each ($\Delta N_i/\Delta N_j$). No correlation emerged from comparison of this matrix of changes in abundance versus the above-mentioned matrix of overall ecological similarity, either among all 33 species (r = -0.011) or using just 11 species for which sample sizes are more adequate (r = -0.001). Nor do the elements in the matrix of changes in abundance correlate with dietary overlap (r = +0.006). While these negative results are less than satisfying, at least they seem to support neither of the above hypotheses. Rather, they suggest either that stochasticity in this system is considerable or that abundance of each species varies more or less independently of the abundance of other species.

REFERENCES

MacArthur, R. H., and Pianka, E. R.
1966. On optimal use of a patchy environment. Amer. Naturalist, vol. 100, pp. 603-609.

McArthur, R. H., and Wilson, E. O.
1967. The theory of island biogeography. Princeton University Press, Princeton.

Pianka, E. R.
1969a. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology, vol. 50, pp. 498-502.
1969b. Sympatry of desert lizards *(Ctenotus)* in Western Australia. Ecology, vol. 50, pp. 1012-1030.
1971. Lizard species density in the Kalahari desert. Ecology, vol. 52, pp. 1024-1029.
1973. The structure of lizard communities. Ann. Rev. Ecol. Systematics, vol. 4, pp. 53-74.
1975. Niche relations of desert lizards. Pp. 292-314 *in* "Ecology and Evolution of Communities," M. Cody and J. Diamond, eds. Harvard University Press, Cambridge, Mass.
1981. Diversity and adaptive radiations of Australian desert lizards. Pp. 1375-1392 *in* "Ecological Biogeography in Australia," A. Keast, ed. D. W. Junk, The Hague, Netherlands.
1982. Observations on the ecology of *Varanus* in the Great Victoria desert. W. Austral. Naturalist, vol. 15, pp. 37-44.

Pianka, E. R., and Giles, W. F.
1982. Notes on the biology of two species of nocturnal skinks, *Egernia inornata* and *Egernia striata*, in the Great Victoria desert. W. Austral. Naturalist, vol. 15, pp. 44-49.

Schoener, T. W.
1974. The compression hypothesis and temporal resource partitioning. Proc. Nat. Acad. Sci., vol. 71, pp. 4169-4172.

Schoener, T. W.; Huey, R. B.; and Pianka, E. R.
1979. A biogeographic extension of the compression hypothesis: Competitors in narrow sympatry. Amer. Naturalist, vol. 113, pp. 295-298.

Simpson, E. H.
1949. Measurement of diversity. Nature, vol. 163, p. 688.

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