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SYMPATRY OF DESERT LIZARDS (*CTENOTUS*) IN WESTERN AUSTRALIA

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Abstract. Seven species of congeneric lizards (*Ctenotus*) frequently occur in ecologic sympatry in the Australian desert. The ecologies of these and seven other species are described and compared, with particular reference to niche differences.

Adult *Ctenotus* range from 45 to 118 mm in snout-vent length. Larger species take larger prey items than smaller ones. Six species do most of their foraging in the open spaces between plants, while six others forage mostly within the dense tussocks of porcupine grass (*Triodea*). The former have proportionately longer hindlegs than the latter. It is demonstrated that hindleg and head proportions are good morphological indicators of the place niche and the food niche, respectively, and that body temperature reflects the time niche in a useful way. Lizards with higher body temperatures are usually active later in the day than those with lower body temperatures. Whereas the species which forage in the open show a poor correlation between air temperature and body temperature, those that forage in shady places within vegetation have body temperatures closely correlated with ambient air temperatures. The former are dependent upon direct solar and/or substrate heat, while the latter appear not to substantially exploit these heat sources.

After analyzing the ways in which the lizards subdivide habitat space and environmental resources, it is concluded that there are at least three dimensions to the *Ctenotus* niche: place, food, and time. An analysis is presented which demonstrates that *Ctenotus* are ecologically rather tightly "packed," and it is suggested that the overall differences between pairs may represent minimal ecologic distances.

Long treated as a part of the scincid genus *Sphenomorphus,* the recently separated genus *Ctenotus* (Storr 1964) is one of the largest genera of Australian lizards. The taxonomy of the Western Australian desert species has been recently treated by Storr (1968); otherwise the genus remains poorly known. This group of lizards is of substantial ecological interest because as many as 11 species may be found living together in the same general area. The present paper examines the comparative ecology of 14 species in the Great Victoria Desert.

Skinks in the North Temperate zones tend to be secretive and retiring, typically being found in damp situations. There are no real desert species in the New World. In many ways, the Australian *Ctenotus* are ecologically more comparable to the North American teid genus *Cnemidophorus* and the European lacertids *Lacerta* and *Eremias* than they are to typical skinks. In a study on the ecology of North American flatland desert lizards, I distinguished two distinct methods of foraging, labelled the "sit-and-wait" and the "widely foraging" techniques (Pianka 1965). In North America the former method is utilized by a variety of different species, particularly iguanid lizards, while the latter technique is used by the teid *Cnemidophorus tigris.* In the Australian deserts, agamid lizards forage by the "sit-and-wait" technique, while the various *Ctenotus* forage widely in a manner similar to that used by *Cnemidophorus* in the New World. Perhaps the most striking discrepancy in the comparison of *Ctenotus* and *Cnemidophorus* is that there are so many more ecologically sympatric species of the former than there are of the latter in the respective deserts.

An analysis of the lizard species diversity of North American flatland deserts (Pianka 1967) has shown that there are never fewer than 4, or more than 10, ecologically sympatric desert lizard species. A comparable investigation of the number of species in Australian deserts (Pianka 1969) produced between 18 and 40 sympatric species on areas of a given degree of habitat complexity. A good part of this increase in total number of species is due to the genus *Ctenotus.* It is therefore of substantial interest to examine in detail the comparative ecology of desert *Ctenotus,* with particular emphasis on the mechanisms by which these congeners avoid competitive exclusion. The central concern of this paper is thus the partitioning of habitat space and environmental resources.

METHODS

Eight desert study areas, described and located by Pianka (1969), were selected and visited at irregular intervals over a 16-month period. The following parameters were recorded, if possible, for every lizard encountered: identity, date, time, air temperature (1.2 m above ground, in shade),

approximate size, position in the environment when first sighted, and subsequent movements (including whether the lizard took fright and ran or continued to walk or sit undisturbed). Wherever possible, lizards were collected, usually by shooting. Specimens collected provided considerably more data, including sex, weight, exact size (snout-vent length), tail length and whether or not the tail had been broken and regenerated. Body temperatures were recorded only for active lizards (not those dug up) and were not recorded if lizards were badly damaged or when the delay between shooting and capture seemed unduly long.

Dissection of the preserved material gave information on gonad condition (length of testes in males, average size and total number of eggs in females), and stomach contents. Twenty-five food categories were distinguished, which are listed in Table 3. Individual prey items were counted for each stomach, except in the case of termites, for which standards were determined by counts and these used to make estimates of the number per stomach. Estimates were made of the volume of each prey item as follows. The volumes of intact stomachs were measured to one-tenth of a cubic centimeter by volume displacement in a small graduated cylinder. After the contents were removed, the volume of the empty stomach was similarly determined. Using the difference between these two measures (the total volume of food in the stomach), approximate volumes of individual prey items were estimated visually to the nearest hundredth of a cubic centimeter, by the proportion of the total food volume taken up by a given prey type.

Head lengths were measured to the nearest one-tenth of a millimeter with vernier calipers, as the distance from the anterior edge of the ear aperture to the tip of the snout. Hindleg lengths were measured to the nearest millimeter by extending the hindleg at a right angle to the body, holding it as straight as possible, and thrusting a small metal rule against the body immediately anterior to the hindleg. The tip of the claw on the longest toe was taken as the end of the limb.

The Study System

There are at least 13 distinct subregions within the area climatologically considered to be desert in Australia (Figure 1). The boundaries between these subregions are sometimes difficult to pinpoint, but in other cases may be quite sharp. The latter condition is particularly true of the borders of the three major sand deserts, the Great Sandy, Simpson, and Great Victoria deserts. There are a few sandridges and substantial areas of sandplain in the Exmouth Area, the Central Ranges and the Tanami desert. Where the latter two areas contact the three great sandridge deserts, boundaries may be somewhat blurred and indistinct. Therefore, sand-specialized organisms have been able to move between the three sandy deserts to a certain degree. In like manner, the mulga scrub country in the east and west is connected by the Nullarbor Plain and its bordering zone of myall (not shown), a shrubby habitat similar to mulga. There is also a "corridor" through the southern part of the Gibson desert connecting the Western Mulga Scrub Country with the higher elevations in the Central Ranges. The stony deserts are somewhat more disjunct, although the Pilbara region is nearly connected to the Gibson desert and Sturt's Stony desert almost contacts the extensive South Australian Stony Salt Lake Country. The Great Victoria desert occupies the south central portion of the region outlined in Figure 1. It is predominantly a sandy desert with red sands supporting a vegetation consisting mainly of spinifex grasses (*Triodea*) and eucalypt trees (*Eucalyptus*). In wetter places and on harder soils, there are some tracts of mulga (*Acacia aneura*) and occasional dry lakebeds composed largely of various chenopod species (including *Atriplex*).

FIG. 1. The approximate boundaries of the various subregions of the Australian desert, based upon a variety of sources.

Although there are a limited number of weather stations in the region of the Great Victoria desert proper, most published isopleths of climatic parameters follow longitudes and, accordingly, there is probably minimal variation in climate within this particular geographic area. Differences in the lizard fauna from site to site are thus usually related to soil and vegetational differences rather than to climatic differences.

Figure 2 shows the geographical distribution of average annual rainfall in the desert area. Be-

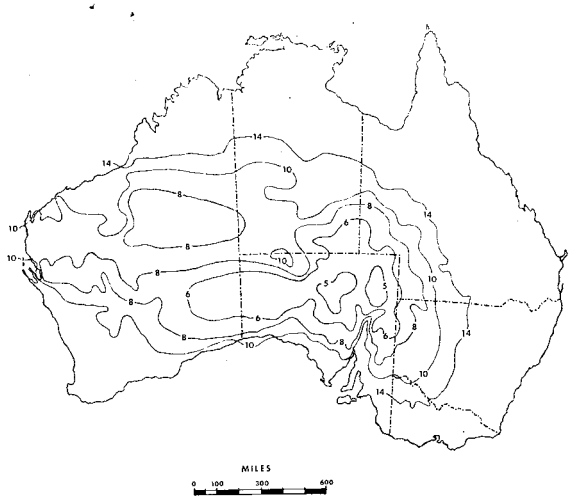

FIG. 2. Isopleths (inches) of average annual precipitation for the desert region (from the Commonwealth of Australia Yearbook, 1967). (10 in. = 25.4 cm)

cause of the higher temperatures in the north, the northern limits of "desert" conditions correspond roughly to the 14-in. isopleth. Although the Australian inland is "desert" in the dual climatological senses of receiving 10 or less inches of rain per annum and possessing an appropriate precipitation to evaporation ratio, its vegetation often does not correspond to what is usually considered "typical" desert vegetation. The Australian "deserts" are predominantly arboreal and frequently remind one of an open savannah woodland. Almost nowhere is one out of sight of either *Acacia* or *Eucalyptus* trees. Desert eucalypts such as the bloodwood (*E. gongylocarpa*) can be impressively large trees, occasionally attaining heights of 10–15 m (and frequently 8 m) with a trunk diameter of up to half a meter. The acacias are smaller trees, seldom exceeding 5 m in height with a trunk diameter of perhaps ¼ m. The most important and well known of the acacias is *Acacia aneura,* commonly referred to as "mulga." There are numerous other desert-adapted species of *Eucalyptus* and *Acacia* in the Great Sandy, Tanami and Simpson deserts.

An exceedingly important plant in the Australian desert is the grass genus *Triodea.* These perennial grasses form dense clumps up to a meter in diameter, consisting of a complex latticework core with numerous outwardly directed sharp spines, and are vaguely reminiscent of a dead cactus (Figure 3i). This plant life form is unique to the Australian continent and has been intimately involved with and related to the evolution of the genus *Ctenotus* (Pianka 1969). It is highly probable that it is the existence of such a structurally complex plant life form which has made possible the origin and ecological coexistence of so many congeneric species of *Ctenotus.*

The present study is based largely upon data collected by my wife and me during the period from October 1966 through January 1968. The source of most of the information reported here is from our collection of 735 specimens of *Ctenotus* from the Great Victoria desert.[1] However, we made observations and collections in the Simpson, Tanami and Great Sandy deserts, which are freely used. Seven of the 14 species treated here were described from our collection in 1968 by G. M. Storr of the Western Australian Museum: these are *atlas, ariadnae, calurus, dux, grandis, helenae,* and *piankai.* Before my study, there were practically no specimens known of several other species: *brooksi, colletti, leae,* and to a lesser extent, *quattuordecimlineatus.* Thus, only *leonhardii, pantherinus,* and *schomburgkii* were at all well known taxonomically before Dr. Storr's study, and the nomenclature of even these three species was in a very confused state (see Storr 1968). There have been no studies on any aspect of the ecology of *Ctenotus.*

Figure 4 presents all known locality records and depicts the probable geographic ranges of the 14 species. The stippled areas shown are, for the most part, conservative estimates of the geographic distributions, although they are based upon considerations of autecology, microhabitat and habitat as well as the actual localities of collection, which are shown as solid circles. At the bottom center of Figure 4 is a species density map of these 14 species on the Australian continent. The high species density center in the Great Victoria desert is an artifact of our intensive collecting efforts in this region. However, the map does reflect a fair correspondence between the distributions of these *Ctenotus* species and the geographic subregions of the Australian desert (compare Figures 1 and 4).

HABITAT

Only *Ctenotus schomburgkii,* which has a relatively wide geographic distribution, occurs throughout all the desert habitats. Thus it is not surprising that this versatile species occurs in all the subregions of the desert (see map, Figure 4). All the other species show various degrees of habitat restriction. For instance, *brooksi, colletti, dux,* and *leae* are invariably associated with sand-ridges. Others, including *calurus, grandis, helenae, patherinus, piankai,* and *quattuordecimlineatus,* are restricted to habitats in which there is spinifex grass (*Triodea*). Only *leonhardii* is restricted to habitats containing acacias and/or

[1] Now lodged in the Los Angeles County Museum of Natural History.

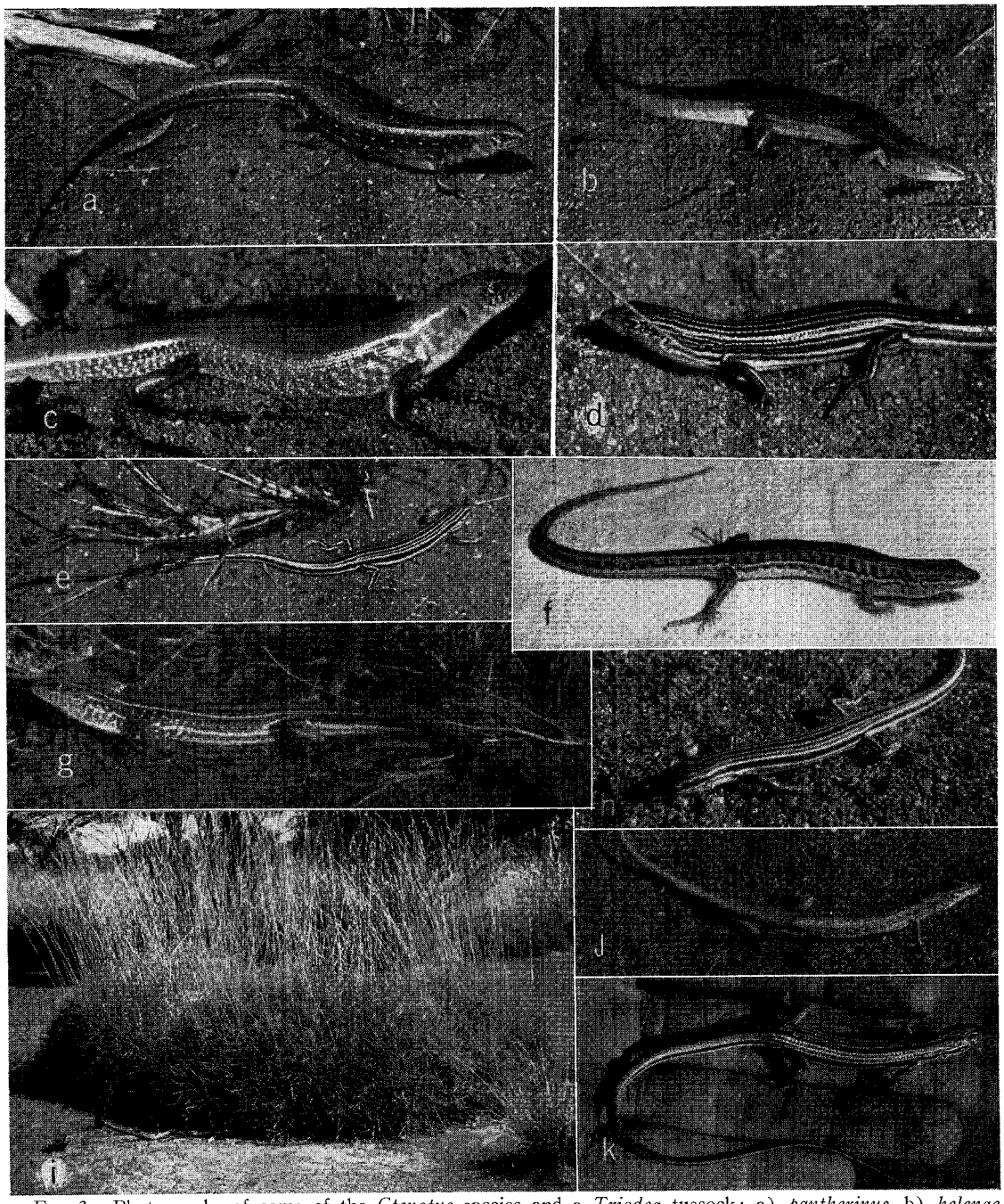

FIG. 3. Photographs of some of the *Ctenotus* species and a *Triodea* tussock: a) *pantherinus,* b) *helenae,* c) *grandis,* d) *quattuordecimlineatus,* e) *calurus,* f) *schomburgkii,* g) *leonhardii,* h) *colletti,* i) *Triodea* tussock, j) *brooksi,* k) *leae.*

chenopods. In another paper (Pianka 1969), I discuss habitat specificity in *Ctenotus* and other Australian desert lizards.

Table 1 shows which species of *Ctenotus* occurred on different study areas. It may be seen that from 2 to 11 species of *Ctenotus* coexist sympatrically. In the case of the E area with 11 species, both the spinifex-specialized and the sand-ridge-specialized species occur, the former 7 for the most part on the interdunal sandplains and the latter 4 on the sandridges proper or their edges. These 7 sandplain species occur in ecologic sympatry on at least 4 of the 8 study areas (E, L, G, and N areas).

Body Size

There are pronounced differences in the size of the different species of *Ctenotus*. Figure 5 illustrates this with histograms of snout-vent lengths for the 14 species. It may be seen that there are three overlapping but fairly distinct size groups, corresponding roughly to 25–55, 28–75, and 35–118 mm. *Ctenotus dux, leae,* and *leonhardii* are somewhat intermediate between the three groups. Figure 5 is arranged so that adult body size de-

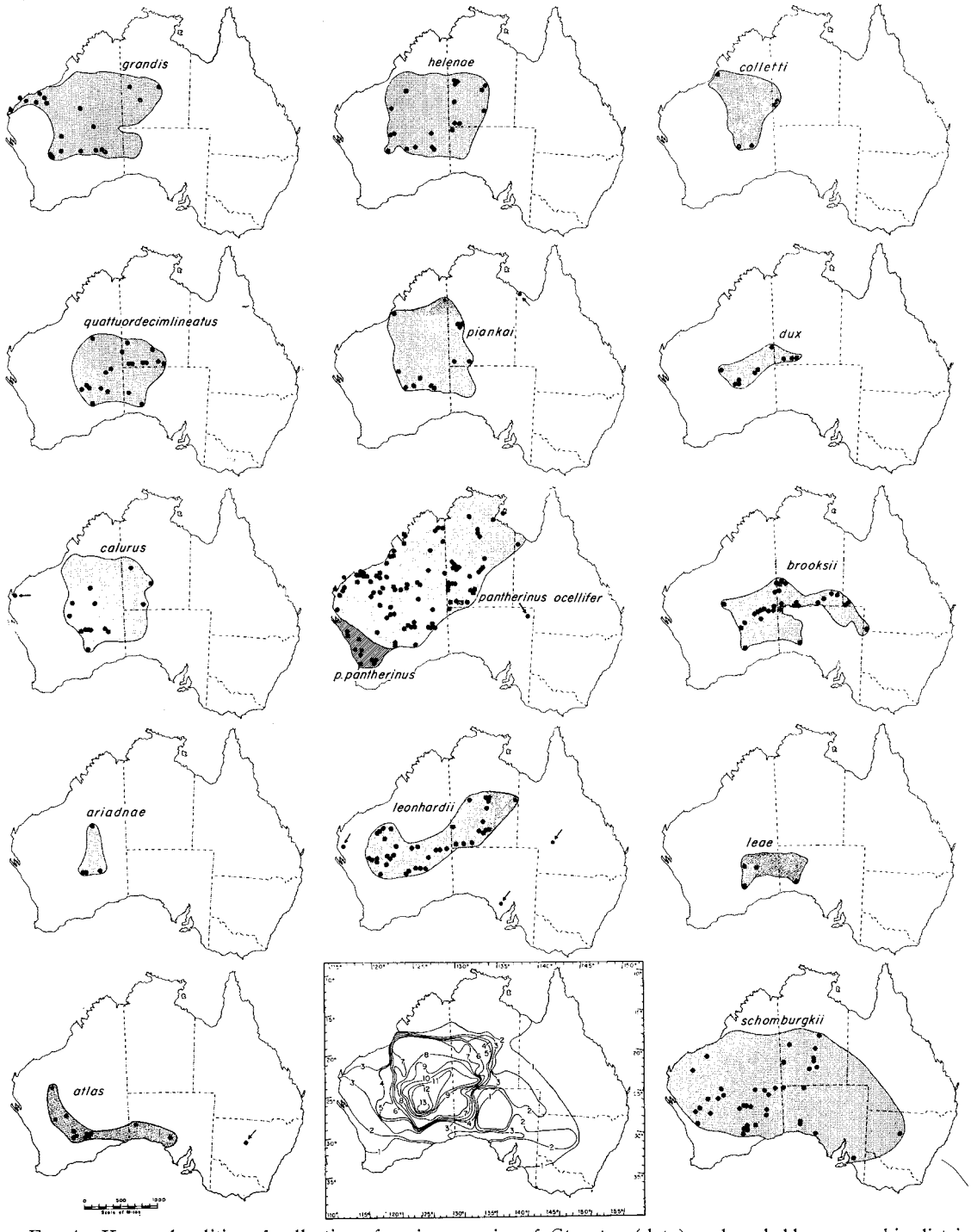

FIG. 4. Known localities of collection of various species of *Ctenotus* (dots) and probable geographic distributions, after consideration of habitat requirements, microhabitat and ecology. The map at the bottom center is a species density map of these 14 species on the Australian continent (see text).

TABLE 1. Species occurrences on eight study areas in Western Australia[a]

Species	Areas[b] A	M	D	E	L	G	N	Y
Ctenotus grandis	x	x	e	x	x	x	x	
Ctenotus helenae		x	x	x	x	x	x	
Ctenotus pantherinus	x	x	x	x	x	x	x	
Ctenotus leonhardii	x	x						x
Ctenotus quattuordecimlineatus				x	x	x	x	
Ctenotus ariadnae					x			
Ctenotus atlas	x							
Ctenotus dux			x	x				
Ctenotus leae				x				
Ctenotus schomburgkii	x	x	e	x	x	x	e	x
Ctenotus brooksi				x				
Ctenotus calurus		x	x	x	x	x	x	
Ctenotus piankai			e	x	x	x	x	
Ctenotus colletti				x				
Total	5	6	7	11	8	7	7	2

[a]x=collected, e=highly expected.
[b]Exact locations of these sites are given in Pianka (1969). A and M are habitats with mixtures of acacias, eucalypts and spinifex grass on desert loams. These two sites lie in the broad ecotonal area between typical shrub desert (*Acacia*-chenopod) and typical grass desert (*Eucalyptus-Triodea*). The D and E areas are desert sandhill and sandridge habitats, respectively, and support large *Eucalyptus* trees, *Triodea*, as well as a variety of other specialized sandridge perennials. The L and G areas consist of sandplain habitats with large eucalypt trees, a few scattered shrubs and spinifex. The N area is "pure grass desert" containing almost nothing but *Triodea* spp. The Y area is a relatively pure shrub desert, consisting of chenopods and other small shrubs in a dry lakebed.

creases from top to bottom (subsequent figures follow the same format). On the basis of size alone, it might be predicted that there would be little interspecific competition between the very small species and the adults of the larger species. Juveniles of these large species, however, should encounter more interspecific competition due to their greater overlap with small species.

FORAGING TECHNIQUES

Six of the 14 species do most of their foraging in the open spaces between plants, these are: *leonhardii, leae, schomburgkii, brooksi, calurus,* and probably *dux*. Six others appear to do the ma-

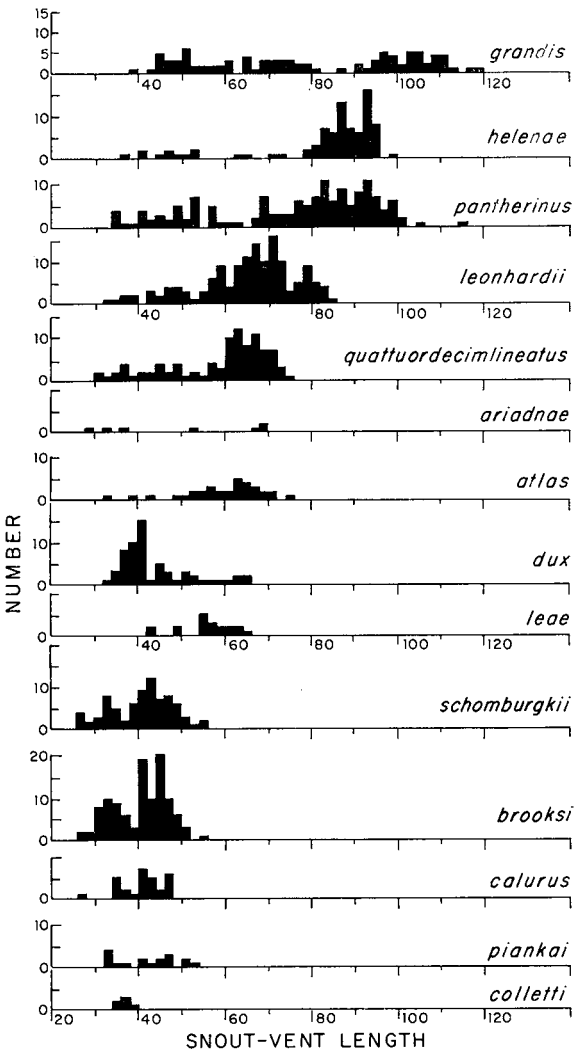

FIG. 5. Frequency distributions of snout-vent lengths in mm. Although females are slightly larger than males in some species, sexual size differences are very slight and probably of little ecologic importance.

TABLE 2. Location of various *Ctenotus* when first sighted (percentages)

Species	N	Open sun	Open shade	Litter sun	Litter shade	Spinifex in open sun	Spinifex in open shade	Spinifex under tree sun	Spinifex under tree shade	Other bushes sun	Other bushes shade	Overall sun	Overall shade
ariadnae (*ar*)	5	20.0					80.0					20.0	80.0
atlas (*at*)	24	4.2				20.8	66.6	4.2	4.2			29.2	70.8
brooksi (*br*)	72	36.1				13.2	7.6			35.4	7.6	84.7	15.2
calurus (*ca*)	48	44.8	5.2			20.8	25.0				4.2	65.6	34.2
colletti (*co*)	4	25.0		25.0			25.0				25.0	50.0	50.0
dux	49	20.4				36.7	16.7			24.8	2.4	81.9	19.1
grandis (*gr*)	66	13.6				9.1	74.2				3.0	22.7	77.2
helenae (*h*)	79	5.1				7.6	49.4	1.3	31.6	1.3	3.8	15.3	84.7
leae	21	38.1				4.8	9.5			19.0	28.6	61.9	38.1
leonhardii (*leon*)	101	21.7	2.0	2.5	9.4	3.9	26.7			16.8	16.8	44.9	55.0
pantherinus (*pa*)	81	3.7				19.8	66.5		6.2	1.9	1.9	25.4	74.6
piankai (pi)	9	11.1				11.1	77.7					22.2	77.7
quattuordecimlineatus (*qu*)	99	9.1	1.0			9.6	78.2			1.0	1.0	19.7	80.2
schomburgkii (*sch*)	95	32.6	4.2	6.8	7.9	17.8	21.1			7.5	3.2	63.7	36.4

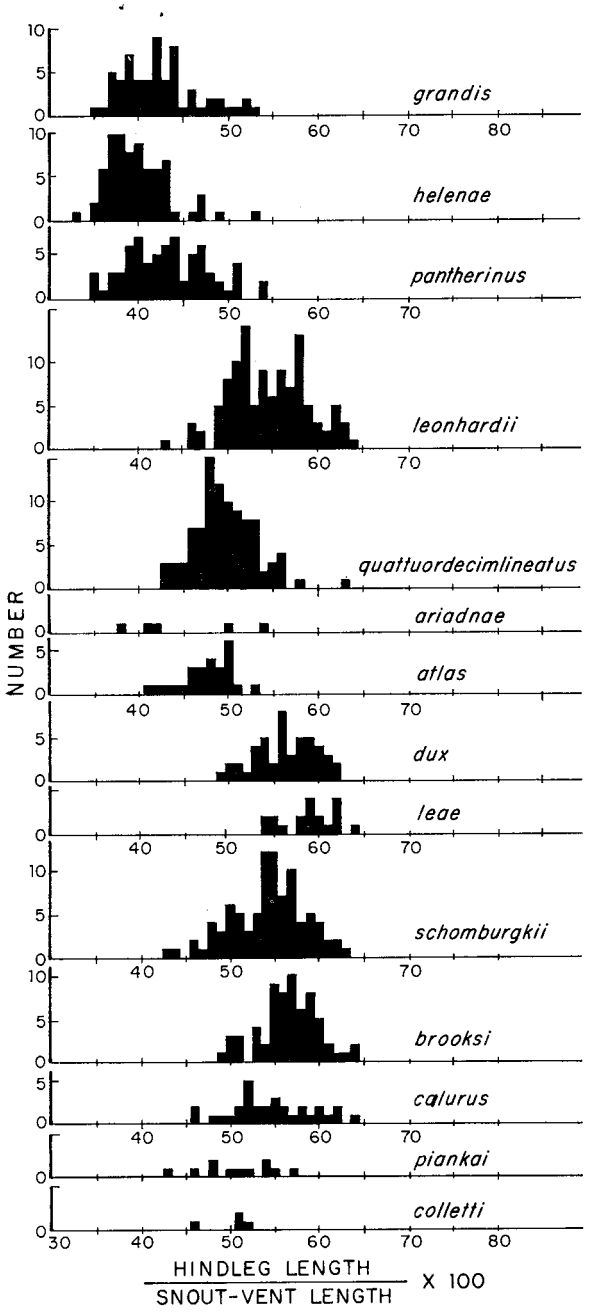

FIG. 6. Frequency distributions of hindleg length as a percentage of snout-vent length.

jority of their foraging within or at the edges of the dense tussocks of spinifex grass; these are *grandis, helenae, pantherinus, quattuordecimlineatus, atlas,* and *piankai.* There is not enough information available on either *ariadnae* or *colletti* to know for certain where they forage, but their diets and anatomy allow some tentative conclusions.

In order to quantify differences in foraging

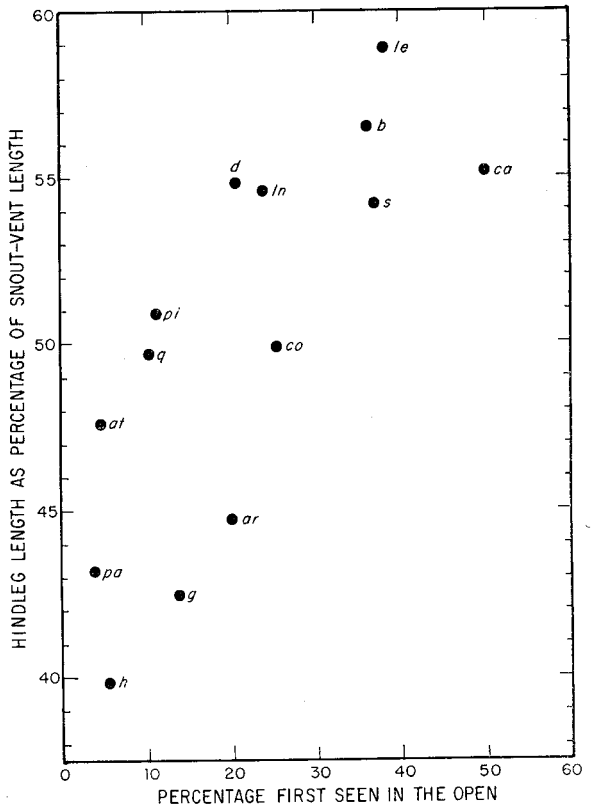

FIG. 7. Plot of the mean hindleg length (as a percentage of snout-vent length) versus the percentage of individuals first observed in the open (see Figure 6, Table 2, and text). Note that open foraging species have proportionately longer hindlegs than those which forage in more closed in places. ar = *ariadnae,* at = *atlas,* b = *brooksi,* ca = *calurus,* co = *colletti,* d = *dux,* g = *grandis,* h = *helenae,* le = *leae,* ln = *leonhardii,* pa = *pantherinus,* pi = *piankai,* q = *quattuordecimlineatus,* s = *schomburgkii.*

technique, the exact microhabitat location of each lizard when it was first sighted (or heard) was recorded (Table 2). In addition, it was noted that species which forage in the open have proportionately longer hind legs than those which spend most of their time in the more closed-in places (Figures 6 and 7). Hence hind leg proportions can be used as a morphological indicator of the "place niche."

One species (*Ctenotus calurus*), first encountered in the open 50% of the time, has a qualitatively unique foraging behavior; these lizards are continually on the move, lashing their bright blue tails as they progress through the open spaces between shrubs. They are nervous and wary, but occasionally an individual pauses to dig up an insect larva. Other species also forage widely, doing some digging and some climbing for prey, but none lash their tails as does *C. calurus. C. atlas, helenae, quattuordecimlineatus,* and *piankai* were

TABLE 3. Stomach contents: total number of prey items in each food category

Prey items	*Ctenotus* species[a]													
	gr	*h*	*pa*	*leon*	*qu*	*ar*	*at*	*dux*	*leae*	*sch*	*br*	*ca*	*pi*	*co*
Isopods			1											
Gastropods			3		1									
Centipedes		1		10	1									
Aranae	2	4	6	9	21	1	1	18	8	10	26	6	11	2
Scorpionidae	1			3	1									
Rhaphidoidea										1				
Thysanura			1		4				1		1			8
Formicidae	78	31	24	15	10		1	3	4	2	96	1	3	
Other Hymenoptera	2	7	11	10	3			2	1		10			
Locustidae	1	26	8	21	20	1	7	12	2	1	4	1	3	1
Blattidae	4	7	1	2			1			3	1			1
Mantids-Phasmids		1		5	8			6	2				1	
Neuroptera								1						
Coleoptera	13	27	14	13	21		8	26	1	9	37	2		
Isoptera	2,475	2,779	1,786	831	206	54	151	39		968	10	133		5
Diptera	1		2		2			4	1	2	1			
Lepidoptera	6	5	1	2	15	1	1	7					3	
Homoptera-Hemiptera	2	2	6	41	117	4	15	39	49	5	45		18	3
Insect eggs					4					1	3			
All pupae					1			2			2			
All larvae	49	49	8	29	61		1	5	8	11	26	11	2	2
Unidentified insects	34	21	6	12	13	2		7	5	3	5	3		
Lizards and sloughed skins	4	1	3	2	2		1	1			1	2		
Floral parts, plants	17		30	6	5			9	7		17			
Vegetative parts	123	72	5	33	18			2	11	2			2	
Total number of items	2,812	3,033	1,916	1,044	534	63	187	183	100	1,018	285	159	43	22

[a]Abbreviations of species names are coded in Table 2.

TABLE 4. Stomach contents: total volume, in cubic cm, of prey in each food category

Prey items	*Ctenotus* species[a]													
	g	*h*	*pa*	*leon*	*qu*	*ar*	*at*	*dux*	*leae*	*sch*	*br*	*ca*	*pi*	*co*
Isopods			0.02											
Gastropods			0.15		0.02									
Centipedes		0.15		1.67	0.04									
Aranae	0.25	0.41	0.41	0.56	0.44	.02	0.01	0.31	0.27	0.17	0.55	0.10	0.11	0.12
Scorpionidae	0.50			0.26	0.01									
Rhaphidoidea										0.01				
Thysanura			0.05		0.14				0.03		0.01			0.10
Formicidae	1.20	0.61	0.25	0.18	0.17		0.01	0.01	0.08	0.01	0.52	0.01	0.02	
Other Hymenoptera	0.55	0.49	0.27	0.41	0.10			0.06	0.10		0.37	0.03		
Locustiade	0.05	2.80	0.48	1.81	0.68	0.06	0.45	0.74	0.22	0.01	0.20		0.05	0.01
Blattidae	1.15	2.95	0.05	0.43			0.10			0.28	0.01			0.01
Mantids-Phasmids		0.10		0.38	0.53			0.27	0.10				0.06	
Neuroptera								0.03						
Coleoptera	2.00	2.10	0.37	0.32	0.68		0.20	0.46	0.01	0.18	0.78	0.01		
Isoptera	41.68	31.57	15.68	8.60	2.04	0.91	1.48	0.14		3.85	0.03	0.94		0.04
Diptera	0.05		0.07		0.03			0.08	0.02	0.005	0.03			
Lepidoptera	0.41	0.30	0.15	0.45	1.92	0.02	0.06	0.40					0.03	
Homoptera-Hemiptera	0.25	0.10	0.21	1.07	2.39	0.06	0.21	0.44	0.71	0.06	0.59		0.12	0.01
Insect eggs					0.09					0.07	0.19			
All pupae					0.07			0.13			0.09			
All larvae	3.70	3.11	0.59	4.65	3.00		0.01	0.07	0.13	1.30	0.51	0.45	0.06	0.06
Unidentified insects	1.60	0.55	0.10	0.46	0.23	0.04	0.06	0.12	0.14	0.05	0.06	0.01	.01	
Lizards and sloughed skins	3.30	0.50	0.12	0.33	0.13		0.01	0.03			0.03	.01		
Floral parts, plants	0.95		2.42	0.66	0.29			0.26	0.45		0.33			
Vegetative parts	2.70	1.02	0.08	1.29	0.66			0.04	0.85	0.04			0.04	
Unidentified plant parts		0.05		0.54						0.02				
Unidentified material		1.20	0.95	1.19	0.64		0.16	0.29		0.29	0.41	.03	0.06	
Total volume	60.34	48.01	22.42	25.36	14.32	1.11	2.76	3.88	3.11	6.34	4.75	1.59	0.56	0.35

[a]Abbreviations of species names are coded in Table 2.

TABLE 5. Stomach contents: percentage composition, by number (data of Table 3), and corresponding food species diversity

Prey items	*Ctenotus* species[a]													
	gr	*h*	*pa*	*leon*	*qu*	*ar*	*at*	*dux*	*leae*	*sch*	*br*	*ca*	*pi*	*co*
Isopods			0.05											
Gastropods			0.15		0.19									
Centipedes		0.03		0.95	0.19									
Aranae	0.07	0.13	0.31	0.86	3.93	1.58	0.53	9.84	8.00	0.98	9.12	3.77	25.58	9.09
Scorpionidae	0.03			0.28	0.19									
Rhaphidoidea										0.09				
Thysanura			0.05		0.75				1.00		.35			36.36
Formicidae	2.77	1.02	1.25	1.43	1.87		0.53	1.64	4.00	0.19	33.68	0.62	6.97	
Other Hymenoptera	0.07	0.23	0.57	0.95	0.56			1.09	1.00		3.50			
Locustidae	0.03	0.85	0.41	2.01	3.75	1.58	3.74	6.56	2.00	0.09	1.40	0.62	6.97	4.55
Blattidae	0.14	0.23	0.05	0.19			0.53			0.29	.35			4.55
Mantids-Phasmids		0.03		0.47	1.50			3.28	2.00				2.32	
Neuroptera								0.55						
Coleoptera	0.46	0.89	0.73	1.24	3.93		4.27	14.21	1.00	0.88	12.98	1.25		
Isoptera	88.01	91.62	93.21	79.59	38.58	85.71	80.74	21.31		95.08	3.50	83.64		22.73
Diptera	0.03		0.10		0.37			2.19	1.00	0.19	.35			
Lepidoptera	0.21	0.16	0.05	0.19	2.81	1.58	0.53	3.83					6.97	
Homoptera-Hemiptera	0.07	0.06	0.31	3.92	21.91	6.34	8.02	21.31	49.00	0.49	15.78		41.86	13.64
Insect eggs					0.75					0.09	1.05			
All pupae					0.19			1.09			0.70			
All larvae	1.74	1.61	0.41	2.77	11.42		0.53	2.73	8.00	1.08	9.12	6.91	4.65	9.09
Unidentified insects	1.20	0.69	0.31	1.14	2.43	3.17		3.83	5.00	0.29	1.75	1.88		
Lizards and sloughed skins	0.14	0.03	0.15	0.19	0.37		0.53	0.55			.35	1.25		
Floral parts, plants	0.60		1.56	0.57	0.94			4.92	7.00		5.96			
Vegetative parts	4.37	2.37	0.26	3.16	3.37			1.09	11.00	0.19			4.65	
Food species diversity	0.56	0.46	0.40	0.98	1.98	0.61	0.80	2.28	1.68	0.30	2.06	0.71	1.64	0.69

[a]Abbreviations of species names are coded in Table 2.

TABLE 6. Stomach contents: percentage composition, by volume (data of Table 4), and corresponding food species diversity

Prey items	*Ctenotus* species[a]													
	gr	*h*	*pa*	*leon*	*qu*	*ar*	*at*	*dux*	*leae*	*sch*	*br*	*ca*	*pi*	*co*
Isopods			0.09											
Gastropods			0.67		0.14									
Centipedes		0.31		6.58	0.28									
Aranae	0.41	0.85	1.83	2.21	3.07	1.80	0.36	7.99	8.69	2.68	11.58	6.29	20.00	34.25
Scorpionidae	0.83			1.03	0.07									
Rhaphidoidea										0.16				
Thysanura			0.22		0.98				0.96		0.21			28.70
Formicidae	1.99	1.27	1.12	0.71	1.19		0.36	0.26	2.57	0.16	10.95	0.63	3.64	
Other Hymenoptera	0.91	1.02	1.20	1.62	0.70			1.55	3.92		7.79			
Locustidae	0.09	5.83	2.14	7.14	4.75	5.40	16.31	19.07	7.07	0.16	4.21	1.89	9.09	2.87
Biattidae	1.91	6.14	0.22	1.70			3.62			4.42	0.21			2.87
Mantids-Phasmids		0.20		1.50	3.70			6.96	3.22				10.91	
Neuroptera								0.77						
Coleoptera	3.31	4.37	1.65	1.26	4.75		7.25	11.86	0.32	2.85	16.42	0.63		
Isoptera	69.08	65.75	69.94	33.91	14.24	81.98	53.63	3.61		60.72	0.63	59.11		11.21
Diptera	0.09		0.31		0.21			2.06	0.64	0.08	0.63			
Lepidoptera	0.68	0.62	0.67	1.77	13.41	1.80	2.17	10.31					5.45	
Homoptera-Hemiptera	0.41	0.20	0.94	4.22	16.68	5.40	7.61	11.34	22.83	0.95	12.42		21.82	2.87
Insect eggs					0.63					1.10	4.00			
All pupae					0.49			3.35			1.89			
All larvae	6.13	6.47	2.63	18.34	20.95		0.36	1.81	4.18	20.45	10.74	28.30	10.91	17.15
Unidentified insects	2.65	1.14	0.45	1.81	1.61	3.60	2.17	3.09	4.50	0.79	1.26	0.63	.01	
Lizards and sloughed skins	5.47	1.04	0.53	1.30	0.91		0.36	0.77			0.63	0.63		
Floral parts, plants	1.58		10.79	2.60	2.02			6.70	14.47		6.95	1.89		
Vegetative parts	4.47	2.12	0.35	5.08	4.60			1.03	27.33	0.63			7.27	
Unidentified plant parts		0.10		2.12						0.31				
Unidentified material		2.49	4.24	4.69	4.47		5.80	7.47		4.57	8.64		10.91	
Food species diversity	1.16	1.33	1.13	2.00	2.22	0.74	1.38	2.28	1.78	1.18	2.19	1.12	1.13	1.58

[a]Abbreviations of species names are coded in Table 2.

TABLE 7. Stomach contents: percentage frequency of prey items in each food category, and total numbers of stomachs on which these frequencies are based

Prey items	*Ctenotus* species[a]													
	gr	*h*	*pa*	*leon*	*qu*	*ar*	*at*	*dux*	*lxae*	*sch*	*br*	*ca*	*pi*	*co*
Isopods			1.49											
Gastropods			4.47		1.07									
Centipedes		1.33		8.65	1.07									
Aranae	3.27	5.33	5.97	8.65	17.20	20.00	3.84	21.27	37.50	10.12	33.87	22.22	50.0	40.0
Scorpionidae	1.63			1.92	1.07									
Rhaphidoidea										1.26				20.0
Thysanura			1.49		4.30				6.25		1.61			
Formicidae	34.42	18.66	16.41	6.73	10.75		3.84	4.25	25.00	2.53	33.87	3.70	10.0	
Other Hymenoptera	3.27	9.33	4.47	7.69	3.22			4.25	6.25		12.90			
Locustidae	1.63	29.33	11.94	18.26	17.20	20.00	19.23	23.40	12.50	1.26	6.45	3.70	30.0	20.0
Blattidae	4.91	9.33	1.49	1.92			3.84			3.79	1.61			20.0
Mantids-Phasmids		1.33		1.92	8.60			10.63	6.25				10.0	
Neuroptera								2.12						
Coleoptera	16.39	29.33	10.44	7.69	12.90		15.38	23.40	6.25	7.59	38.70	7.40		
Isoptera	75.40	64.00	79.10	58.65	18.27	40.00	61.53	12.76		84.81	1.61	77.77		20.0
Diptera	1.63		2.98		2.15			4.25	6.25	2.53	1.61			
Lepidoptera	6.55	6.66	1.49	1.92	9.67	20.00	3.84	12.76					20.0	
Homoptera-Hemiptera	3.27	2.66	10.44	18.26	41.93	60.00	23.07	36.17	62.50	6.32	41.93		70.0	20.0
Insect eggs					4.30					1.26	3.22			
All pupae					1.07			4.25			3.22			
All larvae	16.39	16.00	5.97	16.34	29.03		3.84		18.75	7.59	30.64	25.92	20.0	40.0
Unidentified insects	36.06	20.00	8.95	11.53	13.97	40.00	11.53	8.51	31.25	3.79	8.06			
Lizards and sloughed skins	6.55	1.33	4.47	1.92	2.15		7.69	2.12			1.61	7.40		
Floral parts, plants	11.47		1.49	5.76	3.22			12.76	25.00		8.06			
Vegetative parts	22.95	22.66	7.46	17.30	19.35			4.25	68.75	1.26			20.0	
Unidentified plant parts		1.33		14.42						1.26				
Total number of stomachs	61	72	67	104	93	5	26	47	16	79	62	27	10	5

[a]Abbreviations of species names are coded in Table 2.

observed to climb around within spinifex tussocks, sometimes reaching heights of a foot or more above ground. However, because of difficulties of observation and small sample sizes, it is not definitely known whether these species are more arboreal than the others. In any case, all *Ctenotus* are very active and forage widely.

FOOD

Most lizards are fairly opportunistic feeders, taking without preference whatever prey items they encounter within a broad range of types and sizes. Seasonal changes in diet frequently reflect distinct changes in food availability. Smaller species and/or individuals tend to take smaller prey than larger species and/or individuals (for example, see Schoener 1967, 1968). Because differences in microhabitat and foraging techniques may often result in exposure to different prey species, dietary differences between species can sometimes be useful indicators of niche differences.

Table 3 lists the total number of prey items in each of 26 categories. Tables 4, 5, 6, and 7 list, respectively, the total volume, the percentage by number, percentage by volume, and the frequency of occurrence of each prey type.

Food species diversities, calculated with Shannon's (1949) information theoretic measure, $-\Sigma p_i \log_e p_i$ (where p_i is the proportion of the total prey in each prey category), based on numbers and volumes are given at the bottom of Tables 5 and 6, respectively. The breadth of the food niche is indicated by these measures.

Similarly, Table 8 gives the frequency distribution of prey sizes (volumes), mean prey sizes and prey size diversity for each of the species. Larger *Ctenotus* eat bigger prey than do the smaller species, but this tendency is obscured by the great numbers of termites eaten by most species. The mean volume of the 10 largest prey items is more indicative of any upper limit on prey size (Table 8, bottom). The correlation between this measure and mean head length is shown in Figure 8.

TIME OF ACTIVITY

Because air and substrate temperatures are strongly time dependent, a lizard's temporal activities must be closely geared to its thermoregulatory requirements. Species which are active all year long often shift their daily periods of activity and encounter a similar thermal environment in both the winter and summer. Many lizards with a bimodal daily pattern of activity during the summer months (i.e. early in the day when the environment is warming and later when it is cooling down again) change to a unimodal, mid-day

TABLE 8. Prey size distributions, prey size diversity, mean prey size, and the mean size of the largest 10 prey items (in cubic mm.)

Prey size categories (in mm³)	*Ctenotus* species[a]													
	ar	*at*	*br*	*ca*	*co*	*dux*	*gr*	*h*	*leae*	*leon*	*pa*	*pi*	*qu*	*sch*
Trace (.005)	1	11	126	68		70	25	912	5	3	405	13	138	839
.006-.014	8	158	81	67	18	39	968	1100	39	829	1385	24	147	136
.015-.024	53	10	37	20		31	1385	864	21	98	77	4	147	23
.025-.034		4	17	5		18	229	104	9	18	13	1	44	9
.035-.044	1	1	8		1	9	35	18	3	7	6	1	13	3
.045-.054		3	6	1	1	4	54	42	4	36	20		27	2
.055-.064	1	4	6			2	15	1	3	3	5	1	5	2
.065-.074			4		1	3	12	3	6	4	4		4	3
.075-.084			2						1	6	9		5	
.085-.094			1					14		4	2		2	
.095-.104			3	3	1	5	13	21	6	21	10	1	10	
.105-.175		2	1			1	12	5	2	8	1		7	1
175-.224		1		1			8	3		8	1		2	1
.225-.274									1	1			1	
.275-.324								2		4	1			
.325-.374						1				2				
.375-.424								1		3	1			
.425-.474											1			
.475-.524							3	2		1				
.525-.624										1				
.625-.724							2							
.725-.824								1						
over .825							1	1					1	
Total no. measured prey items	64	194	292	165	22	183	2762	3094	100	1057	1941	45	554	1019
Mean volume of largest 10 items	.026	.088	.091	.064	.029	.121	.485	.490	.123	.385	.190	.033	.185	.082
Prey size diversity	.61	.80	1.58	1.23	.72	1.72	1.23	1.39	1.91	.95	.91	1.25	1.81	.63
Mean prey size	.018	.014	.016	.010	.016	.020	.022	.016	.033	.023	.012	.011	.026	.006

[a]Abbreviations of species names are coded in Table 2.

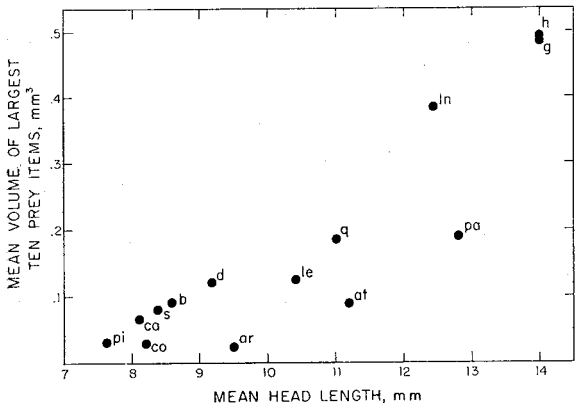

FIG. 8. Plot of the mean volume of the 10 largest prey items (in mm³) against mean head length. Points marked as in Figure 7.

pattern during the winter months (see Mayhew 1964). Although a lizard's thermoregulation is influenced by its place and food niche, body temperature, because it is easily quantified, is a convenient and useful indicator of the "time niche." There are distinct daily and seasonal patterns of activity in *Ctenotus;* some of these are reflected in Figures 9, 10, and 11.

Figure 9 demonstrates that *Ctenotus calurus* is active later in the day during winter months than it is during the summer.

Figure 10 shows the frequency distribution of times of collection. Although seasonal and day to day changes somewhat obscure daily patterns, there are nonetheless distinct differences within this group of lizards. For instance, although sample sizes are small, *Ctenotus leae* and *piankai* have a unimodal mid-day period of activity, whereas *schomburgkii* and *brooksi,* with lower mean body temperatures, display bimodal daily patterns, being active early and late. Patterns for other species are less clear in this figure, and are more conveniently depicted in Figure 11, which plots frequency distributions of active body temperatures. This figure exemplifies the utility of body temperature as an indicator of the time niche; *leonhardii*[2] and *leae,* both mid-day open foraging forms, have higher mean body temperatures than other species.

An interesting empirical relation between the time and place niche is shown in Figure 12, where the correlation coefficient of air temperature versus

[2] The sharp kurtosis of the *leonhardii* body temperature distribution suggests that this species is pushing scincid physiological limits, and indeed, it has the highest mean body temperature yet recorded for any skink (Brattstrom 1965, Licht et al. 1966).

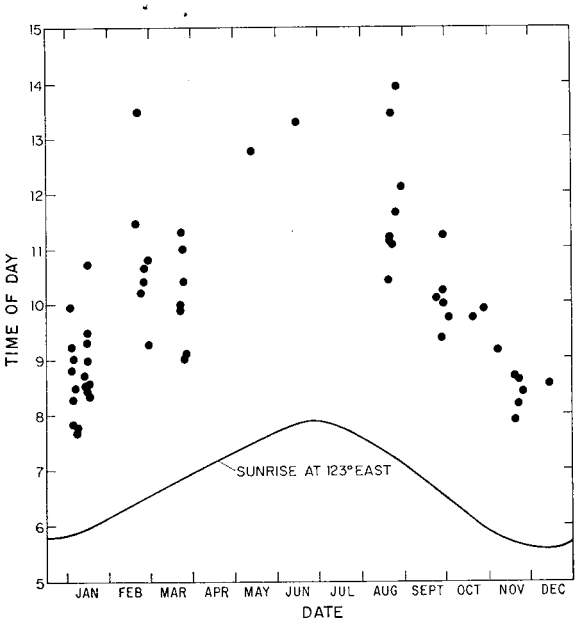

FIG. 9. The time of day each *Ctenotus calurus* was observed is plotted against the date, showing that these lizards are active later in the day during the winter than in the summer. Approximate time of sunrise at a longitude midway between study areas (all located between latitudes 26°14 and 28°31 S) is shown, suggesting that the time lag from sunrise until the lizards become active also changes seasonally. Somewhat similar patterns occur in other species.

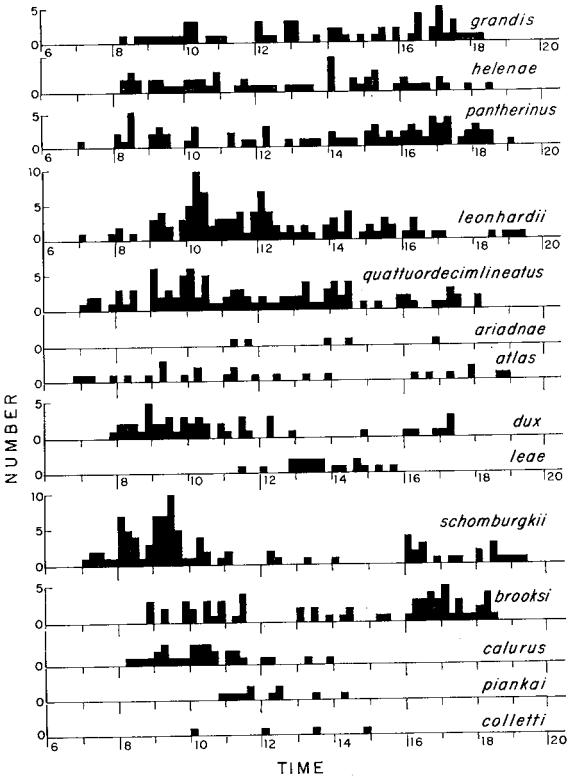

FIG. 10. Frequency distributions of the time of collection. Note that some species, such as *brooksi* and *schomburgkii*, have a bimodal diel pattern of activity, whereas others, such as *leae*, *calurus*, and *piankai* have a unimodal activity pattern. Day to day weather changes and seasonal trends, such as the one depicted in Figure 9, somewhat obscure these daily patterns.

body temperature is plotted against the hindleg's percentage of the snout-vent length (the same ordinate as that of Fig. 7). Open foraging species' body temperatures are not well correlated with ambient air temperature, whereas those which forage within spinifex tussocks show a much better correlation (Table 9). Unfortunately, I did not record substrate or black-bulb temperatures during this study, but this figure suggests that substrate and/or solar heat are relatively more important to open foraging species.

Ctenotus also possess distinct seasonal patterns of activity. While my data are less than satisfactory for certain uncommon species, they are adequate for *leonhardii, pantherinus, quattuordecimlineatus,* and *schomburgkii* and perhaps for *calurus* and *helenae* (Table 10). Several species, particularly *atlas* and *grandis,* were most conspicuous several weeks after cyclone Elsie during January and February of 1967. Others, such as *brooksi, dux,* and *leae,* occurred on only one or two study areas and were therefore not adequately sampled. *C. ariadnae, colletti,* and *piankai* are too rare to provide sufficient data. Generally, larger species and/or individuals have a shorter active season than smaller individuals or species (for instance compare *leonhardii* and *schomburgkii*).

REPRODUCTION

Breeding usually takes place between October and February. Although there were no yolked follicles in the females of five species, at least one female in each of the other nine species had either enlarged ovarian or oviducal eggs. These data, presented in Table 11, suggest that *pantherinus* is significantly more fecund than most other species. Even *helenae,* which attains nearly the size of *pantherinus,* was never observed to have a clutch of more than six, whereas one large *pantherinus* female carried nine ovarian eggs 8 mm in diameter. Clutches of seven eggs occur regularly in *leonhardii* and *pantherinus.*

PREDATION

I have recorded reptilian predators on 9 of the 14 species considered here. The small monitor lizard, *Varanus eremius,* eats *calurus, grandis, pantherinus,* and *quattuordecimlineatus* (Pianka 1968). The larger *Varanus gouldi* takes *atlas, colletti, helenae, leonhardii, quattuordecimlineatus,* and *schomburgkii* (Pianka 1970). Both monitors

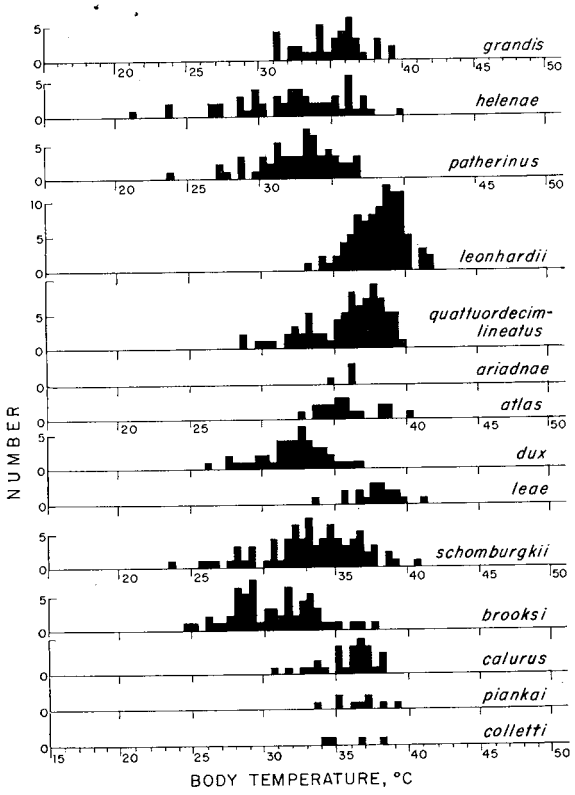

FIG. 11. Frequency distributions of body temperatures of active lizards, a useful indicator of the time niche (see text). Statistics for these distributions are presented in Table 9.

almost certainly prey upon all 14 species, but whereas *V. eremius* usually catch *Ctenotus* above ground by a combination of surprise, stalking and pursuit, *V. gouldi* usually dig them out of frequently dead-end burrows. I have also found *atlas, helenae*(?), *leonhardii,* and *pantherinus*(?) in the stomachs of various desert-dwelling elapid snakes. It is doubtful that very many *Ctenotus* fall prey to avian or mammalian predators, because birds and mammals are unable to pursue the lizards into dense *Triodea* tussocks. Predation by *Varanus* and snakes has probably been the

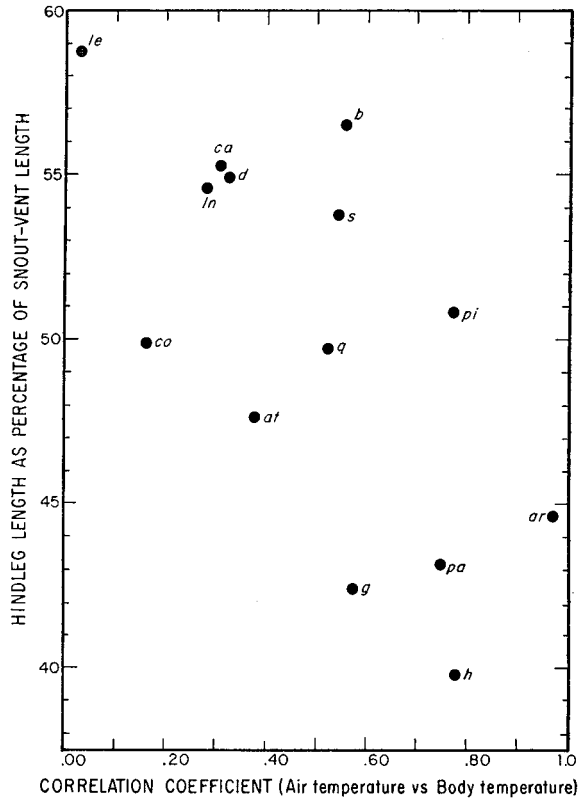

FIG. 12. The hindleg length (as a percentage of snout-vent length) is plotted against the correlation between air temperature and body temperature. This plot demonstrates that the long-legged species which forage in the open exploit solar and substrate heat sources, rather than the air, which appears to be the heat source of the shorter-legged species that forage in shady places within the vegetation. Symbols as in Figure 7.

TABLE 9. Air and body temperature statistics[a]

Species	Air temperature			Body temperature			r_{AT-BT}
	$\bar{X}$	SD	N	$\bar{X}$	SD	N	
ariadnae	29.7	4.53	5	35.8	0.92	4	.970
atlas	29.3	4.86	26	34.5	3.96	23	.330
brooksi	20.1	4.40	67	30.6	2.81	61	.556
calurus	26.4	3.82	32	35.6	1.93	29	.275
colletti	27.5	3.90	4	35.9	1.83	4	.160
dux	19.8	3.88	50	32.0	2.32	45	.295
grandis	25.4	4.78	58	34.2	3.32	43	.574
helenae	26.1	5.13	73	32.8	4.13	64	.776
leae	27.7	3.76	19	37.7	1.72	18	.031
leonhardii	29.8	4.20	106	38.0	1.91	92	.250
pantherinus	26.4	5.95	74	33.1	3.11	67	.759
piankai	28.2	3.56	11	35.5	3.31	10	.780
quattuordecimlineatus	27.6	4.61	100	35.8	2.67	79	.519
schomburgkii	26.6	4.85	89	33.3	3.38	77	.538

[a] $\bar{X}$=mean, SD=standard deviation, N=number of observations, r_{AT-BT}=correlation coefficient between air temperature and body temperature.

TABLE 10. Numbers of specimens of each species observed during the months indicated from late 1966 through early 1968

Species	Jan.	Feb.	Mar.	Apr.	May	June	Aug.	Sept.	Oct.	Nov.	Dec.	Totals across
ariadnae		4										4
atlas	8	8	2	1					4	2	2	27
brooksi					44	24		4	1	1	1	75
calurus	18	7	7		1	1	8	5	3	6	1	57
colletti					1	1		1		1	1	5
dux					33	2	8	5		1	1	50
grandis	3	42	15		1	3			5		1	70
helenae	8	46	11		4			3	1	6	3	82
leae					7			12		1	1	21
leonhardii	36	12	30	2	1		8	1	3	2	36	131
pantherinus	19	6	8		11	13	7	1	4	10	4	83
piankai	2	1	1		1	1	1	1		3		11
quattuordecimlineatus	33	21	25		2			18	2	16		117
schomburgkii	15	6	12	4	8	2	5	12	10	16	22	112
Number of days spent in field	18	18	14	1	18	11	18	20	21	22	22	

TABLE 11. Frequency distributions of clutch sizes for female *Ctenotus*

No. of eggs	*Ctenotus* species[a]								
	ar	*at*	*ca*	*co*	*h.*	*leae*	*leon*	*pa*	*sch*
1		1			1				2
2		1	4	1	3		1		2
3					7	1	2	1	2
4	1		2		3	2	2	2	2
5					3			1	
6					2			1	
7							7	4	
8								1	
9								1	
Mean	4.0	1.5	2.7	2.0	3.5	3.7	5.8	6.1	3.0

[a]Abbreviations of species names are coded in Table 2.

selective force which has resulted in *Ctenotus* becoming so very wary and difficult to observe and collect.

DISCUSSION: ECOLOGIC OVERLAP

Prior to this study, no one had reported ecological coexistence of more than four congeneric species of lizards (Milstead 1957, 1961; Schoener 1968). It is, therefore, of some interest to analyze niche differences among *Ctenotus*.

Only 7 of the 14 species regularly occur in true ecologic sympatry, these are: *calurus, grandis, helenae, pantherinus, piankai, quattuordecimlineatus,* and *schomburgkii.* On the L-area *ariadnae* is added to this list, and *brooksi, colletti, dux,* and *leae* occur on the sandridges of the E-area (Table 1). However, essentially nothing is known about *ariadnae,* and the sandridge species are not truly syntopic with most of the seven sandplain *Ctenotus.* Hence it will be sufficient to examine in detail niche differences among only these seven species.

Before proceeding, some considerations concerning ecologic distance are in order. Three distinct components of the overall ecologic distance between species are diagramed in Figure 13. First is the distance (in as many dimensions as appropriate) between the centers of the two niches. The second is the total amount of resource shared by the two species (niche overlap). Third is the competitor's relative usage of these shared resources. The first measure, d, is equal to the effective ecologic distance, e_d, only when there is no niche overlap (Fig. 13A).[3] Niche overlap (stippled in Fig. 13) reduces the effective ecologic distance between competitors. Furthermore, overlap affects two competitors equally only when their niche breadths (and/or population sizes) are identical (Fig. 13B). If niche breadths are unequal, the competitor with the narrower niche must share relatively more of its required resources (Fig. 13C). I have shown that *Ctenotus* niches usually overlap broadly in the manner shown by Figure 13 B and C; this overlap must be quantified before niche differences can be adequately analyzed.

A number of different measures of overlap have been suggested by various authors. Some of these are reviewed by Horn (1966), and others have been suggested since (Cody 1968; Levins 1968; MacArthur and Levins 1967; Pico, Maldonado, and Levins 1965; Schoener 1968). MacArthur and Levins (op. cit.) derive the following useful measure of overlap between two normal distributions:

$$\text{overlap} = e^{-[(\bar{x}_1 - \bar{x}_2)^2/2\sigma_1\sigma_2]}$$

where $\bar{x}_1$ and $\bar{x}_2$ are the means and σ_1 and σ_2 the standard deviations of the two distributions. This measure varies from zero (no overlap) to one

[3] It is interesting that the character displacement concept seems to be based upon d, rather than e_d.

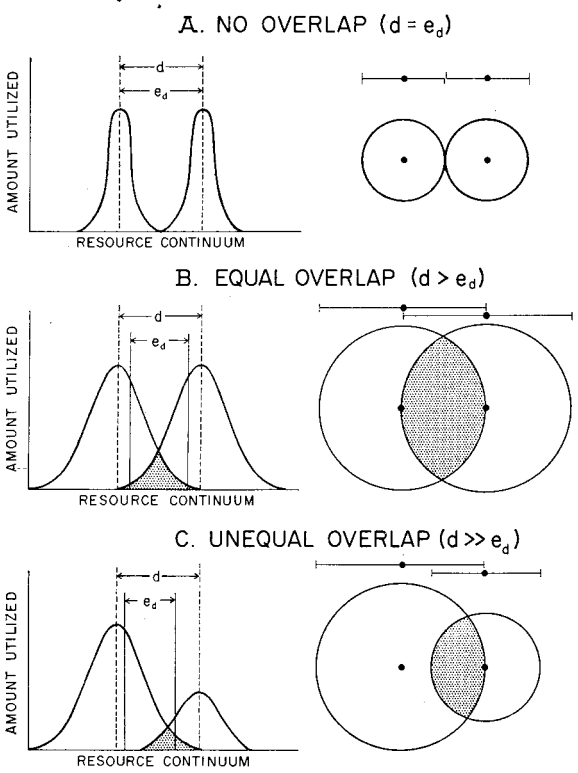

FIG. 13. Diagrammatic representations of the three components of ecologic distance. A.) abutting niches with no overlap, effective ecologic distance, e_d, equals the distance, d, between the centers of the two niches. There is no direct competition in this case. B.) overlapping niches of equal breadth, e_d is symmetrically less than d. Competition is equal and opposite. C.) overlapping niches of unequal breadth, e_d is asymmetrically much less than d. Competition is not equal and opposite, but is more intense on the population with the smaller niche. Three different, but equivalent, geometric representations are shown.

(complete overlap). Horn's (op. cit.) information theoretic index, R_o, does not require ordering of the distributions under comparison, and also varies from zero at no overlap to unity at complete overlap. Both measures give values of unity when one distribution is completely included within the other. However, as Horn points out, various degrees of departure from linearity between any two indices are to be expected.

I used MacArthur and Levins' index (above) to quantify overlap where normality could be approximated and Horn's R_o where it could not (Table 12). Data used to compute these values have been presented in Tables 2, 5, 6, 8, and 10 and in Figures 6 and 11.

Place niche

Examination of Table 2 demonstrates that four of the seven species (*grandis, pantherinus, piankai,* and *quattuordecimlineatus*) were first observed either inside or in the shade of spinifex from 66 to 78% of the time. This grass is also an important microhabitat element for *helenae,* which is frequently found in spinifex underneath trees. Even the two open-foraging forms, *calurus* and *schomburgkii,* were often first sighted in or near spinifex. Because of the heavy usage of one microhabitat component, overlap in microhabitat is consistently fairly high (mean = .81). Overlap in hindleg length distributions (as a percentage of snout-vent length, from Figure 6) is much more variable and has a lower mean (.37). Only four species pairs show higher than average overlap in both measures of their place niche: *calurus* × *schomburgkii, grandis* × *pantherinus, helenae* × *pantherinus,* and *piankai* × *quattuordecimlineatus.* A fifth pair, *grandis* × *helenae,* showing approximately average overlap in microhabitat, has higher than average overlap in all other niche components measured.

Food niche

Four different measurements of the food niche also give a wide range of overlap values. Overlap in head length is mostly all-or-none, a reflection of the fact that three of the seven species are small, three large, and only one species (*quattuordecimlineatus*) is intermediate in size. Overlap in prey size is not well correlated with overlap in head length, reflecting the importance of termites in most diets. Overlap in diet by food items (number and volume) is high for all species pairs except those with *quattuordecimlineatus* and *piankai.* Examination of Tables 5 and 6 shows that my sample of *piankai* did not contain any termites, and that *quattuordecimlineatus* contained them in considerably smaller proportions than were present in most other species' diets, where they constitute a major food item. Dietary overlap between *quattuordecimlineatus* and *piankai* is, however, moderate. As in their place niche overlap, the pairs *calurus* × *schomburgkii* and *helenae* × *pantherinus* show very high overlap in all four aspects of their food niches. A distinct difference exists in the size of prey taken by *grandis* and *pantherinus.* Hence two of the four species pairs with high overlap in place niche have fairly different food niches; only *calurus* × *schomburgkii* and *helenae* × *pantherinus* overlap broadly in both food and place niches.

Time niche

MacArthur and Levins (1967) point out that if resources are being rapidly renewed individuals can compete only when they are active within a fairly short time of each other. Persistent differences in time of activity between congeneric liz-

TABLE 12. Overlap along various dimensions of the niche for all combinations of the seven species frequently occurring in ecologic sympatry

Species pair[a]	Place niche		Food niche				Time niche		Means across
			Prey items						
	Microhabitat (A)	Hindleg (B)	by number (A)	by volume (A)	Prey size (A)	Head length (B)	Season (A)	Body temperature (B)	
ca x *gr*	.80	.03	.93	.85	.70	.00	.60	.86	.60
ca x *H*	.62	.00	.95	.87	.96	.00	.73	.61	.59
ca x *pa*	.71	.06	.94	.85	.91	.00	.88	.60	.62
ca x *pi*	.76	.69	.17	.41	.96	.84	.88	1.00	.71
ca x *qu*	.76	.45	.75	.67	.90	.03	.87	1.00	.68
ca x *sch*	.88	.98	.95	.94	.85	.96	.85	.67	.89
gr x *h*	.80	.80	.99	.91	.84	1.00	.88	.93	.89
gr x *pa*	.92	.98	.98	.93	.67	.90	.58	.94	.86
gr x *pi*	.98	.15	.13	.28	.71	.00	.50	.93	.46
gr x *qu*	.98	.16	.71	.58	.85	.32	.66	.87	.64
gr x *sch*	.72	.02	.96	.87	.35	.00	.52	.97	.55
h x *pa*	.89	.70	.95	.82	.87	.83	.74	1.00	.73
h x *pi*	.78	.02	.28	.60	.79	.00	.61	.77	.48
h x *qu*	.80	.02	.83	.84	.72	.15	.71	.66	.59
h x *sch*	.59	.00	.94	.83	.34	.00	.83	.99	.57
pa x *pi*	.92	.24	.10	.36	.95	.00	.89	.76	.53
pa x *qu*	.94	.26	.70	.64	.80	.63	.73	.64	.67
pa x *sch*	.68	.04	.98	.85	.69	.01	.84	1.00	.64
pi x *qu*	.98	.96	.64	.78	.87	.01	.82	1.00	.76
pi x *sch*	.68	.77	.09	.34	.76	.67	.79	.80	.61
qu x *sch*	.71	.48	.68	.66	.70	.07	.76	.71	.60
Means down	.81	.37	.70	.71	.77	.31	.75	.84	.65

[a]Abbreviations of species names are coded in Table 2.
A=Horn's (1966) overlap index, R_o. B=MacArthur and Levins' (1967) index.

ards could thus be an effective way of avoiding interspecific competition. That such differences between various *Ctenotus* occur has already been documented. Two different measures of overlap in the time niche are presented in Table 12. The first is based upon seasonality of activity, using the data of Table 10. *Ctenotus grandis,* because of its sharply seasonal activity, consistently shows the least overlap in this component of its time niche. One of the species pairs with high overlap in place and food, *helenae* × *pantherinus,* has only average overlap in seasonality of activity. The second measure of the time niche used is the active body temperature, based on statistics presented in Table 9. There is low overlap here between *calurus* and *schomburgkii; calurus* has a distinctly higher mean body temperature than *schomburgkii* and is active slightly later in the day (see Table 9 and Figure 10). Thus, in addition to the qualitative difference in modes of foraging (see section on foraging techniques), there is a temporal separation of *calurus* and *schomburgkii.*

Some broad ecological differences between the seven species are clear. The two small open-foragers forage at different times and in slightly different ways. The five spinifex-foraging species break down into three size groups: small (*piankai*), medium (*quattuordecimlineatus*) and large (*pantherinus, helenae* and *grandis*). Interspecific competition must be alleviated by these size differences. The most perplexing species pairs are those between the three large spinifex-foraging species. I have shown that *helenae* somewhat favors spinifex under trees, and that *pantherinus* takes smaller prey than *grandis.* Only 2 of the 21 species pairs have average or above average overlap in all 7 measures: these are *grandis* × *helenae* and *helenae* × *pantherinus.* There are some subtle qualitative differences between members of these two pairs, but the fact remains that ecologically they are exceedingly close. One possible interpretation is that *helenae* is a superior competitor when in competition with *pantherinus,* but inferior with *grandis,* and that *pantherinus* "swamps" out *helenae* with its high fecundity. Another hypothesis might be that the spinifex microhabitat is an extremely productive one and that this allows greater-than-average niche overlap. All three species eat very large quantities of termites (65–70% by volume). Of course, it might also be that I have not measured the relevant variables.

An intriguing consistency in the average over-

TABLE 13. Niche breadths for certain components along each of the three niche dimensions. Values are H/H_{max} (see text). The rightmost column is the mean of the place, food, and time niche, and weights the three equally

Species	Place microhabitat	Food				Time season	Mean
		Prey numbers	Prey vol.	Prey size	Mean		
calurus	.574	.217	.348	.392	.319	.821	.571
grandis	.357	.174	.360	.392	.309	.508	.391
helenae	.565	.143	.413	.443	.333	.608	.502
pantherinus	.452	.124	.351	.290	.255	.883	.530
piankai	.296	.509	.568	.398	.492	.821	.536
quattuordecimlineatus	.335	.615	.689	.576	.627	.704	.555
schomburgkii	.791	.093	.366	.201	.287	.933	.670
Means	.481	.268	.442	.385	.375	.754	.536

lap between species pairs (right column, Table 12) suggests a minimal ecologic distance between competitors. With the exception of three high-overlap pairs, these values all fall between .46 and .76. Even more striking is the convergence in overlap values obtained when mean overlaps are calculated for each of the seven species: these range only from .59 to .68. Then again, perhaps the only significance of these numbers is that they illustrate the "central limit theorem," which states that, almost regardless of the shape of a distribution, the sampling distribution of common statistics (including the mean) tends to be approximately normal.

MacArthur and Levins (1967) develop the theoretical basis for relationships between niche overlap, niche breadth, niche dimensionality and environmental uncertainty. Levins (1968) carries the theory still further. It is not possible to say exactly how many independent dimensions there are to the *Ctenotus* niche, but I can confidently assert that these lizards are using at least three: place, food, and time.

Table 13 summarizes data on niche breadth for some of the measurements used in Table 12 (only information theoretic entries are used). The measure is H/H_{max} (Horn 1966; Levins 1968) where H is Shannon's diversity measure

$$-\Sigma p_i \log p_i$$

and H_{max} equals $\log N$ (N = number of i categories). This ratio can never exceed one, and cannot fall below zero. Use of the expression allows one to compare niche breadths even where different numbers of categories are used, and makes possible interspecific comparison of mean niche breadths (far right, Table 13). Similarly to the case with niche overlap, the species have widely different niche breadths for any given component (.17 to .93), but mean niche breadths vary only from .39 to .67, with most being about .50.

Perhaps the best way to determine whether or not these trends derive from the central limit theorem is by comparing similar parameters for different taxa. One would predict that most insects, being relatively r-selected compared with vertebrates, should have more variable overlap values (both higher and lower). By such a comparison it should be possible to determine whether these results from lizards measure ecologic distances or are merely an artifact of the averaging process.

The only such data known to me are those for *Drosophila* presented by Pico, Maldonado and Levins (1965) and Levins (1968, Table 3.7, page 52). Levins (op. cit.) asserts that overlap values should be weighted by niche breadth to give realistic competition coefficients (alphas). Thus his "community matrix" is asymmetrical: interspecific competition is not equal and opposite, but according to Levins, it affects the population with the broader niche relatively more. Earlier I developed an argument for exactly the opposite: that interspecific competition is stronger on the population with the narrower niche. Using the data on food niche of Pico et al. (1965), I computed R_o and H/H_{max} values for the same groups of *Drosophila* in the same area as those Levins used in his Table 3.7.

These values and those presented in Tables 12 and 13 of this paper were then multiplied to give alpha matrices. Tables 14 and 15 present alpha matrices for *Drosophila* and *Ctenotus* in each of the three dimensions: food, place and time. The fourth matrix in each table is the overall alpha matrix, the product of the first three. It is interesting that although the variances of the seasonal and food alphas are not statistically different, the variances in microhabitat and overall alphas are, with the *Drosophila* values significantly greater (F tests, $P < .001$). Fruitflies clearly have much higher and more variable alphas than do these lizards.

TABLE 14. Alpha matrices for three dimensions of the *Drosophila* niche. From Pico, Maldonado, and Levins (1965) and Levins (1968).[a]

	mel	*lat*	*will*	*dunn*	*ana*
Microhabitat : Place					
mel	x	.30	.42	.61	.16
lat	.72	x	.92	.72	.60
will	.88	.81	x	.96	.47
dunn	.90	.44	.67	x	.38
ana	.18	.28	.25	.29	x
Means	.67	.46	.57	.65	.49
Overall mean = .55 Variance = .070					
Seasonal : Time					
mel	x	.61	.76	.55	.75
lat	.70	x	.79	.48	.50
will	.95	.85	x	.57	.59
dunn	.34	.26	.29	x	.63
ana	.60	.35	.38	.81	x
Means	.65	.52	.56	.60	.62
Overall mean = .59 Variance = .039					
Food					
mel	x	.86	.69	.85	.88
lat	.79	x	.69	.87	.87
will	.79	.85	x	.83	.81
dunn	.74	.83	.63	x	.87
ana	.77	.83	.62	.84	x
Means	.77	.84	.66	.85	.86
Overall mean = .80 Variance = .007					
Overall : Place x Time x Food					
mel	x	.16	.22	.28	.11
lat	.40	x	.55	.30	.26
will	.66	.59	x	.45	.22
dunn	.23	.10	.12	x	.21
ana	.08	.08	.06	.20	x
Means	.34	.23	.24	.31	.12
Overall mean = .26 Variance = .032					

[a] *mel* = *Drosophila melanogaster*, *lat* = *D. latifasciaeformis*, *will* = *D. willistoni* group, *dunn* = *D. dunni*, *ana* = *D. ananassae*.

TABLE 15. Alpha matrices for three dimensions of the *Ctenotus* niche, calculated from figures in Tables 12 and 13. Compare with Table 14[a]

	ca	*gr*	*h*	*pa*	*pi*	*qu*	*sch*
Microhabitat : Place							
ca	x	.29	.35	.32	.23	.26	.70
gr	.46	x	.46	.41	.29	.33	.57
h	.35	.29	x	.40	.23	.27	.47
pa	.41	.33	.51	x	.28	.32	.54
pi	.43	.35	.45	.41	x	.33	.54
qu	.43	.35	.46	.42	.29	x	.56
sch	.50	.26	.34	.31	.20	.24	x
Means	.43	.31	.43	.38	.26	.29	.56
Overall mean = .38 Variance = .012							
Seasonal : Time							
ca	x	.31	.45	.77	.72	.60	.79
gr	.49	x	.54	.51	.41	.46	.48
h	.60	.45	x	.65	.50	.50	.77
pa	.72	.30	.45	x	.73	.51	.78
pi	.72	.26	.37	.78	x	.57	.74
qu	.71	.34	.43	.64	.67	x	.71
sch	.70	.27	.51	.74	.65	.53	x
Means	.66	.32	.46	.68	.61	.53	.71
Overall mean = .57 Variance = .025							
Food : Prey items by volume							
ca	x	.31	.36	.30	.23	.46	.35
gr	.30	x	.37	.33	.16	.40	.32
gr	.31	.33	x	.29	.34	.58	.31
pa	.30	.34	.34	x	.21	.44	.32
pi	.14	.10	.25	.13	x	.54	.13
qu	.24	.21	.34	.22	.45	x	.24
sch	.33	.31	.34	.30	.19	.46	x
Means	.27	.27	.33	.26	.26	.26	.48
Overall mean = .31 Variance = .011							
Overall : Place x Time x Food							
ca	x	.03	.06	.07	.04	.07	.19
gr	.03	x	.09	.07	.02	.06	.13
h	.07	.09	x	.08	.04	.08	.11
pa	.09	.03	.07	x	.04	.07	.13
pi	.05	.01	.04	.04	x	.10	.10
qu	.07	.03	.07	.06	.09	x	.10
sch	.12	.02	.06	.07	.03	.06	x
Means	.07	.04	.06	.07	.04	.07	.13
Overall mean = .07 Variance = .001							

[a] Species names coded in Table 2.

Hence, the available data support my hypothesis that the relatively K-selected lizards are more tightly "packed-in" than more r-selected insects. Whether or not the lizard values represent minimal ecologic distances is a more difficult question to resolve, but it seems highly likely if only because this ecologically sympatric assemblage of congeners represents the most diverse known.

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