PATTERNS OF NICHE OVERLAP AMONG BROADLY SYMPATRIC *VERSUS* NARROWLY SYMPATRIC KALAHARI LIZARDS (SCINCIDAE: *MABUYA*)[1]

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Abstract. Two semiarboreal skinks (*Mabuya*) are narrowly sympatric in the Kalahari desert, whereas two terrestrial species are broadly sympatric both with one another and with the semiarboreal species. We attempt to discern reasons for these differing distributional patterns.

The narrow zone of sympatry of the semiarboreal species is partially congruent with zones of habitat change (rainfall and vegetation), suggesting that the narrow zone probably reflects adaptations of these species to geographic discontinuities of the physical environment. However, the near identity of niches (position on sandridges, microhabitats, body temperatures, times of activity, as well as types and sizes of prey) of the semiarboreal species relative to other species pairs also suggest that intense competition could restrict the zone of sympatry.

Key words: Africa; body temperatures; competition; diet; distributional patterns; lizards; niche overlap; sympatry.

INTRODUCTION

Four species of skinks of the genus *Mabuya* are common in the southern Kalahari semidesert of southern Africa. Two semiarboreal species, *Mabuya spilogaster* and *Mabuya striata sparsa* (until recently considered races of a single species [Mertens 1955]), are sympatric only along a narrow belt in the southern Kalahari (Broadley 1969). In contrast, two terrestrial species, *Mabuya occidentalis* and *Mabuya variegata punctulata*, are broadly sympatric both with one another and with the semiarboreal species.

What accounts for these broad vs. narrow zones of sympatry? In general, narrow zones can result from intense interspecific competition (Selander and Giller 1963, Schoener 1974, Cody 1974), adaptations of species to geographically discontinuous aspects of the physical environment (Huey 1969, Pianka 1969), or hybrid inferiority (Mayr 1963, Hall and Selander 1973). Here we examine data on body and head sizes, microhabitat associations, thermal relations, diets, and reproductive biologies. These data are relevant only to an analysis of the two ecological explanations. The possible role of hybrid inferiority can be discounted, nonetheless, because these *Mabuya* are readily recognizable by humans at a distance and because neither Broadley (1969) nor ourselves have found any evidence of hybridization.

In a description of the vegetation and topography of the southern Kalahari, Leistner (1967) recognized two major geographic subdivisions. Stabilized sand-ridges cover most of the southwestern sector (Fig. 1), while gently rolling sandplains occur to the northeast. Vegetation is predominantly grassy throughout. Trees occur sporadically in the sandridges and are more common in the sandplains.

METHODS

We gathered most of these data on 10 study sites while investigating lizard species density in the Kalahari from late November 1969 through mid-October 1970 (Pianka 1971). On a second visit, from mid-December 1975 through early March 1976, we obtained additional information on distributions and behavior. Various data and statistics on locations, vegetation, topography, climate, saurofauna, and avifauna of each area are given by Pianka (1971) and Pianka and Huey (1971). On one study site (area K) in the Kalahari Gemsbok National Park, the two semiarboreal species occur in sympatry (Fig. 1A). On two sites (T and D), we found *M. spilogaster* in allopatry. All other study areas supported allopatric populations of *M. striata*. The two terrestrial species also occurred on most of these sites: *M. variegata* is, however, absent from area K.

For each undisturbed lizard collected[3] or observed, we recorded microhabitat and time of activity. Cloacal and air (shaded bulb, chest height) temperatures were measured at the time of capture with Schultheis thin-bulb thermometers (body temperatures were not measured if lizards were badly damaged or when the delay between shooting and capture was long). Snout-vent lengths (SVL) were

[3] Deposited in the Los Angeles County Museum of Natural History, and the Museum of Vertebrate Zoology, University of California, Berkeley.
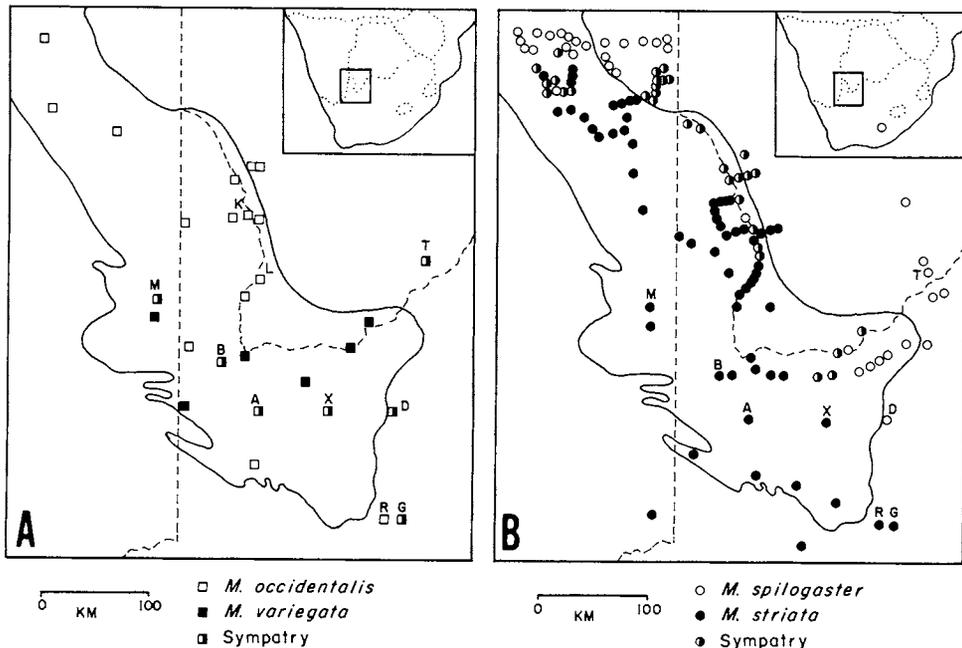
FIG. 1. Approximate localities of *Mabuya occidentalis* and *M. variegata* (A, left) and of *M. striata* and *M. spilogaster* (B, right) in the southern Kalahari Desert. Extralimital records exist for all species. Dune region enclosed by solid line. Study sites marked by letter.

later measured on freshly-captured material, but head lengths were measured on preserved specimens with vernier calipers. Gonadal state (length and width of testes, average size and total number of eggs and/or embryos) and stomach contents were determined by dissection. We recognized 33 prey categories (in Table 7 a few minor categories are consolidated), and approximated the volume of individual prey items in each category by placing contents of stomachs on millimetre-ruled graph paper. The area covered with a depth of ≈ 1 mm approximates volume of prey in μl (= cubic millimetres). Total volume of prey per stomach estimated by this procedure compares closely with volumes estimated by volumetric displacement. Largely digested material and recognizable parts were recorded, but were omitted from prey size distributions unless original sizes could be estimated.

To quantify the variety of microhabitats used or foods eaten (niche breadths), we use the diversity index of Simpson (1949), $1/\Sigma_i^n p_i^2$, where p_i is the proportion of the ith resource category used. Overlap is computed using the following symmetric formula (Pianka 1973, 1974, 1975, May 1975):

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

where p_{ij} and p_{ik} are proportions of the ith resource used by the jth and kth 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 ($\bar{x}$), sample size (N), standard error of the mean (SE), Pearson product-moment correlation coefficient (r), and Spearman rank correlation coefficient (r_s).

RESULTS

Distributions

Locality records of the semiarboreal *Mabuya* in the southern Kalahari are plotted in Fig. 1B (data of Broadley 1969, the Umtali Museum [D. G. Broadley, *personal communication*], the Transvaal Museum [W. D. Haacke, *personal communication*], plus our observations and collections). *Mabuya striata*, though found primarily in sandridge areas, also occurs outside this region in the south at sites R and G. *Mabuya spilogaster* is sympatric with *M. striata* along the eastern sector of the sandridge areas and is allopatric in the flatland desert to the northeast. (In the northern portion of the sandridge areas, *M. spilogaster* replaces *M. striata* in the sandridges). The belt of sympatry is apparently very narrow compared with the extensive geographic overlap of fossorial skinks (*Typhlosaurus*) in the same region (see Fig. 1 of Huey and Pianka 1974). Similarly, the two terrestrial species of *Mabuya* occur on all or most of our study areas (Pianka 1971, Broadley 1975) and are thus broadly sympatric with each other and with *M. striata* and *M. spilogaster* (Fig. 1A).

TABLE 1. Snout-vent length statistics (in millimeters) of adult *Mabuya*

Species	Distribution	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N
		♂ ♂		♀ ♀	
M. striata	allopatry	82.9 ± .72	121	83.7 ± .56	137
	sympatry	86.7 ± .93	63	87.8 ± 1.16	48
M. spilogaster	sympatry	72.8 ± .95	36	69.5 ± .83	54
	allopatry	67.0 ± .75	88	70.0 ± .62	131

Body size and head size

Snout-vent length (in millimetres, $\bar{x} \pm$ SE) varies considerably among the four species of Kalahari *Mabuya* (adults + juveniles): *M. striata*, 73.7 ± 0.75 ($N = 535$); *M. spilogaster*, 64.8 ± 0.64 ($N = 354$); *M. occidentalis*, 79.4 ± 0.91 ($N = 226$); and *M. variegata*, 38.3 ± 0.54 ($N = 111$). Mean head lengths (in millimetres) vary similarly: *M. striata*, 14.45 ± 0.12 ($N = 571$); *M. spilogaster*, 13.22 ± 0.10 ($N = 388$); *M. occidentalis*, 14.81 ± 0.14 ($N = 235$); and *M. variegata*, 7.64 ± 0.08 ($N = 109$).

These overall differences between *M. striata* and *M. spilogaster* hold even when only adult males and females are considered. Mean SVL of sympatric adult *M. striata* of both sexes are significantly longer (*t*-tests, P values $< .001$) than those of the corresponding sex of sympatric adult *M. spilogaster* (Table 1). (*Mabuya striata* also have longer maximal [known] SVL than *M. spilogaster* [107 mm vs. 86 mm]. Adult *M. striata* of both sexes are significantly longer [P values $< .01$] in sympatry than in allopatry [Table 1]. Adult male *M. spilogaster* [$P < .001$], but not adult female *M. spilogaster* [$P > .5$], are also significantly longer where sympatric with *M. striata* [Table 1].) Because both species become larger in sympatry, the difference between mean SVL of the two sympatric populations (16.3 mm) is similar to that between two allopatric populations (14.4 mm, males and females lumped in these comparisons).

Microgeographic distributions in sympatry

We recognize four microgeographic subdivisions of dunes in sandridge areas: street, base, slope, crest. (In comparisons among species throughout this paper, data for sympatric *M. striata* and *M. spilogaster* are from area K only. Our samples of *M. occidentalis* from K are limited, and we thus pool data from all sandridge areas for this species. Similarly, because *M. variegata* is absent from area K, we use data pooled from other sandridge localities.) Microgeographic associations show significant overall heterogeneity (Table 2, *G*-test, $P < .025$), with *M. striata*, *M. spilogaster*, and *M. occidentalis* forming a homogeneous set ($P > .05$). The apparent dissimilarity of *M. variegata* may merely be an artifact of the relative difficulty of observing and capturing this small species in the tall bunch grasses which predominate on dune crests. In any case, overlap is high for all species comparisons (Table 5).

Microhabitat associations

Table 3 gives percentages of undisturbed animals in 16 microhabitat categories for allopatric and sympatric populations. Both *M. variegata* and *M. occidentalis* are primarily terrestrial, while *M. striata* and *M. spilogaster* are semiarboreal. The terrestrial species, nonetheless, differ considerably in microhabitats (overlap = .261) because *M. occidentalis* is strongly associated with bushes and shrubs, whereas *M. variegata* is generally associated with bunch grasses (we do not distinguish between lizards collected next to or in bunch grasses: rather, both are lumped into the ground-grass category). In contrast, the semi-arboreal species are nearly identical in microhabitats (.975), and, in fact, these species do not differ significantly in microhabitat associations in sympatry (*G*-test, $P > .5$).

Ecologists studying arboreal *Anolis* lizards emphasize the utility of comparing "structural niches" (perch height and perch diameter) in analyses of differences in microhabitat between arboreal species (Rand 1964, Schoener 1968, 1974, but see Andrews 1971). Table 4 presents such "structural niche" data (percentages) for individuals of *M. striata* and *M. spilogaster*. Overlap in sympatry is very high (.928). Both tend to use larger perch diameters and to occur closer to the ground in sympatry. Whether analyzed by using "structural niches" or alternative microhabitat categories, overlap in microhabitat associations is

TABLE 2. Microgeographic associations on dunes (percentages) of *Mabuya* in sympatry at area K (except for *M. variegata* and *M. occidentalis*, see text)

Species	N	Position on dune			
		flat	base	slope	crest
M. striata	135	53.3	7.4	22.2	17.0
M. spilogaster	94	54.3	5.3	28.7	11.7
M. occidentalis	138	47.5	6.9	24.6	21.0
M. variegata	103	47.1	16.0	30.1	6.8

TABLE 3. Locations of *Mabuya* where first sighted (percentages). Sunny days only. Sympatric populations from K-area (except *M. variegata* and *M. occidentalis*, see text)

Microhabitat	M. spilogaster allopatry	M. spilogaster sympatry	M. striata sympatry	M. striata allopatry	M. occidentalis	M. variegata
Ground						
Sun						
open	4.8	2.5	0.9	0.4	4.3	....
grass	....	....	....	1.0	3.4	23.3
bush	5.0	8.0	8.8	4.8	26.7	5.5
tree	5.5	2.5	2.2	4.6	0.9	....
log	1.7	2.5	....	0.6	1.2	1.4
Shade						
open	1.5	....	....	0.4	1.2	2.7
grass	....	....	....	0.6	7.1	58.9
bush	3.4	3.1	6.6	7.8	39.4	4.1
tree	8.8	2.5	5.3	5.6	0.9	....
log	0.8	....	....	2.0	1.2	2.7
Arboreal						
Sun						
low (< 30 cm)	2.1	0.6	6.6	6.2	1.9	....
high ($\geqslant 30$ cm)	25.8	22.2	19.5	21.5	5.3	....
log	15.5	23.5	22.6	13.9	....	....
Shade						
low	1.7	6.8	4.9	3.0	1.9	1.4
high	21.2	22.2	18.6	27.1	3.4	....
log	1.3	3.7	4.0	0.6	....	....
Sample size (N)	238	81	113	251	161	73
in sun (%)	61.3	61.7	60.6	53.8	44.9	30.1
arboreal (%)	67.6	79.0	76.2	72.3	12.5	1.4
Microhabitat niche breadth	6.5	5.9	6.8	6.3	4.2	2.5

nearly complete between the semiarboreal species, but is very limited for all other paired comparisons (Table 5).

Seasonal and daily activity patterns

Seasonal activity patterns, estimated by the relative percentage of individuals captured in different seasons (Table 6), show that *M. occidentalis* differs from the other species in being primarily active in summer. Indeed, we found no active individuals of this species in winter. All other species are active in winter when conditions are favorable and have relatively high overlaps in seasonal activity patterns (Table 5).

TABLE 4. Percentage utilization of various perch diameter and height categories in allopatry and sympatry. Bold-faced marginal entries are row totals across and column totals down. Sample sizes indicated above each matrix

$N = 229$ Allopatric *M. striata*

Height above ground	$< 1''$	$1''-3''$	$3''-6''$	$> 6''$	∞	Total
$> 3'$	1.0	13	9	13		**36**
$1'-3'$		6	6	16		**28**
$2''-11''$	.4	2	5	2		**9.4**
$< 2''$				9	18	**27**
	1.4	**21**	**20**	**40**	**18**	

$N = 105$ Sympatric *M. striata*

Height above ground	$< 1''$	$1''-3''$	$3''-6''$	$> 6''$	∞	Total
$> 3'$	1	2	2	15		**20**
$1'-3'$	1	1	8	20		**30**
$2''-11''$	2	2	12	3		**19**
$< 2''$	1			14	16	**31**
	5	**5**	**22**	**52**	**16**	

$N = 79$ Sympatric *M. spilogaster*

Height above ground	$< 1''$	$1''-3''$	$3''-6''$	$> 6''$	∞	Total
$> 3'$			8	15		**23**
$1'-3'$	1	1	10	17		**29**
$2''-11''$	1	1	6	1		**9**
$< 2''$	1			17	21	**39**
	3	**2**	**24**	**50**	**21**	

$N = 195$ Allopatric *M. spilogaster*

Height above ground	$< 1''$	$1''-3''$	$3''-6''$	$> 6''$	∞	Total
$> 3'$		5	11	12		**28**
$1'-3'$	2	6	6	19		**33**
$2''-11''$		3	9	2		**14**
$< 2''$			1	5	21	**27**
	2	**14**	**27**	**38**	**21**	

Perch diameter categories
$< 1'', 1''-3'', 3''-6'', > 6'', \infty$

Structural niche breadth

9.1	7.6	6.9	8.6

TABLE 5. Matrix of overlap values between pairs of *Mabuya* in the Kalahari. From top to bottom, overlap values represent microgeography, microhabitat, season of activity, time of activity in summer, prey taxa, and prey size

	M. spilogaster	M. occidentalis	M. variegata
M. striata			
	.990	.994	.982
	.975	.225	.056
	.970	.529	.833
	.919	.898	.499
	.915	.542	.337
	.965	.685	.639
M. spilogaster			
		.983	.977
		.290	.035
		.809	.936
		.951	.450
		.776	.404
		.762	.705
M. occidentalis			
			.952
			.261
			.941
			.495
			.643
			.984

Daily activity patterns show considerable seasonal variation (Table 6). The resulting necessity of separating these data by seasons results in small sample sizes, and we have therefore pooled data from all localities for each species. During summer months most species pairs overlap considerably in time of activity (Table 5). Exceptions are comparisons involving *M. variegata*, a species which was observed predominantly late in the afternoon. (This trend

may not be real: these small and cryptic lizards bask on or near bunch grasses in the late afternoon and may merely be more conspicuous or easier to capture at that time.)

Body temperatures

Body temperatures of Kalahari *Mabuya* (Table 7) show highly significant heterogeneity by analysis of variance ($P < .001$). *Mabuya occidentalis* differs from the remaining species ($P < .01$, Student-Newman-Keuls test), which among themselves are not significantly different ($P > .05$, S-N-K test). The relatively high mean body temperature of *M. occidentalis* correlates with the tendency of this species to be active primarily in summer.

Mean body temperatures of sympatric *M. striata* and *M. spilogaster* do not differ significantly (Table 7, $P > .05$); neither do mean body temperatures of sympatric and allopatric populations of each species (P values $> .10$). Our larger samples contradict an earlier suggestion that *M. spilogaster* might be active at lower body temperatures than *M. striata* (Brain 1969).

Prey taxa and prey size

Diets are summarized in Table 8 (frequencies by volume represented by each prey category in the total diet) and Table 10 (prey size distributions). *Mabuya* are generalized predators on arthropods (Table 8), though concentrating primarily on beetles, ants, and termites (particularly *Hodotermes mossambicus* and *Trinervitermes* sp.). Overlap in prey taxa is highest between the semiarboreal species

TABLE 6. Percentage of lizards active during hourly intervals (all study areas combined) during three seasons (8 = 0800 to 0859 h). N = number of lizards observed during each season, % = percentage of total lizards observed during each season (for *M. striata* and *M. spilogaster*, calculated from data from K area only)

| Species | \multicolumn{13}{c}{Time of activity} | N | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | | |
| **M. striata** | | | | | | | | | | | | | | | |
| summer | | 2.6 | 22.7 | 12.3 | 19.5 | 7.1 | 1.9 | 3.9 | 3.9 | 5.2 | 13.6 | 5.2 | 1.9 | 154 | 23.7 |
| spring + fall | 0.4 | | 0.9 | 14.5 | 18.8 | 14.5 | 9.8 | 7.5 | 8.6 | 10.2 | 5.9 | 0.4 | 0.4 | 255 | 57.0 |
| winter | | | 1.1 | 1.1 | 6.8 | 13.6 | 29.5 | 27.3 | 12.5 | 8.0 | | | | 88 | 19.3 |
| **M. spilogaster** | | | | | | | | | | | | | | | |
| summer | 0.6 | 11.5 | 23.7 | 15.4 | 9.6 | 9.0 | 0.6 | 4.5 | 7.1 | 3.8 | 12.2 | 1.9 | | 156 | 31.6 |
| spring + fall | | | 7.9 | 9.4 | 10.8 | 10.8 | 12.9 | 7.9 | 7.9 | 22.3 | 7.9 | 0.7 | 1.4 | 139 | 42.9 |
| winter | | | 1.6 | 11.5 | 14.8 | 18.0 | 29.5 | 9.8 | 11.5 | 3.3 | | | | 61 | 25.5 |
| **M. occidentalis** | | | | | | | | | | | | | | | |
| summer | 0.7 | 11.8 | 25.7 | 17.6 | 11.8 | 2.9 | 2.9 | 7.4 | 3.7 | 4.4 | 5.1 | 5.9 | | 136 | 68.0 |
| spring + fall | | 1.6 | 4.8 | 16.1 | 33.9 | 11.3 | 8.1 | 6.5 | 3.2 | 9.7 | | 4.8 | | 62 | 32.0 |
| winter | | | | | | | | | | | | | | | |
| **M. variegata** | | | | | | | | | | | | | | | |
| summer | | 5.6 | 7.4 | 11.1 | 11.1 | 7.4 | | | | 1.9 | 5.6 | 16.7 | 33.3 | 54 | 49.5 |
| spring + fall | | | | 18.1 | 9.4 | 12.5 | 3.1 | 9.4 | | 12.5 | 9.4 | 12.5 | | 34 | 31.2 |
| winter | | | | 4.8 | 14.3 | 4.8 | 23.8 | 23.8 | 19.0 | 9.5 | | | | 21 | 19.3 |
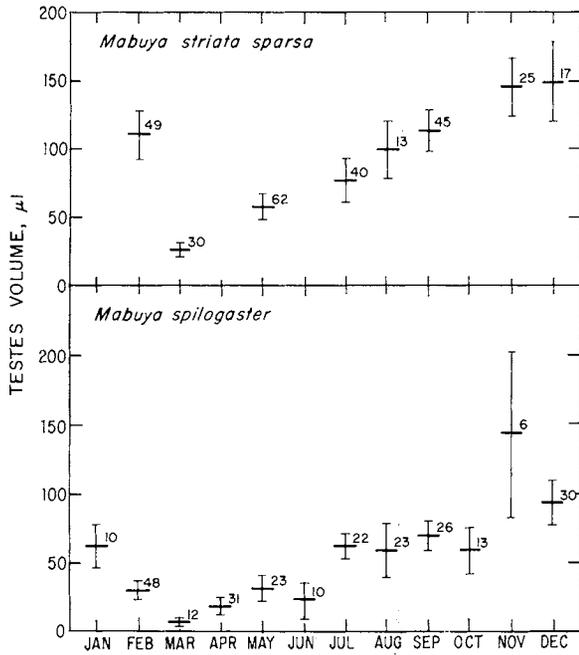
FIG. 2. Annual variation in testicular volumes of *Mabuya striata* and *M. spilogaster*. Mean ± SE and sample size. Allopatric and sympatric populations combined.

(.92). Overlaps for other species comparisons have a maximum of .78 (Table 5).

Prey size distributions (Table 10) show high overlap between the semiarboreal species (.98) and between the terrestrial species (.99), but low overlaps for other species combinations (maximum .76). Both semiarboreal species eat larger prey in sympatry (Kolmogorov-Smirnov tests, P values $< .001$). Mean head length of *Mabuya* is not significantly correlated with either mean prey size ($r_s = .627$, $P > .05$) or with prey-size niche breadth ($r_s = .314$, $P > .05$) (all six populations in Table 10 considered).

Reproduction

Males.—Length of smallest reproductive males (enlarged testes) are given in Table 9. In the semiarboreal species, testicular volumes are smallest in March and largest in November-December (Fig. 2).

Females.—The semiarboreal species and *M. variegata* are viviparous, but the terrestrial *M. occidentalis* is oviparous. Clutch/litter sizes, correlation coefficients between SVL and clutch/litter size, and length of smallest reproductive female (yolked follicles, oviducal eggs, or embryos) are given in Table 9. Clutch sizes of allopatric and sympatric populations of the semiarboreal species do not differ significantly (t-tests, P values $> .05$). The apparent minimum length of females at maturity is greater in sympatric populations of both species (also of male *M. striata*): such differences probably result from smaller sample sizes in sympatry, but could also result from delayed maturity.

Fewer adult-sized females of both semiarboreal species were pregnant in sympatry than in allopatry (*M. spilogaster*, 33.0% [$N = 30$] vs. 58.9% [$N = 107$]; *M. striata*, 39.4% [$N = 33$] vs. 47.7% [$N = 128$]) between September and May, the period during which at least some females were pregnant, but the difference is significant only for *M. spilogaster* ($P < .001$). We cannot judge whether this difference reflects the impact of competition or relatively unfavorable environmental conditions at the sympatric study site.

DISCUSSION

The narrow zone of sympatry of the semiarboreal species could result from their adaptations to different aspects of the physical environment which abut geographically. Necessarily, *M. occidentalis* and *M. variegata* either would not share these adaptations or be unrestricted by them.

TABLE 7. Overall body and air temperature statistics for Kalahari *Mabuya*. All correlations significant at $P < .01$

| | Temperature (°C) | | | | |
| | Body | | Air | | |
Population	$\bar{x} \pm$ SE	N	$\bar{x} \pm$ SE	N	$r_{BT \cdot AT}$
M. spilogaster					
allopatry	34.5 ± .17	191	28.9 ± .28	216	.494
sympatry	33.9 ± .48	65	26.4 ± .64	76	.388
all	34.4 ± .18	256	28.2 ± .27	292	.456
M. striata					
sympatry	34.1 ± .23	70	26.5 ± .48	94	.554
allopatry	34.0 ± .24	194	28.0 ± .27	256	.463
all	34.0 ± .17	264	27.6 ± .24	350	.460
M. occidentalis	35.9 ± .23	133	29.9 ± .29	162	.536
M. variegata	33.6 ± .56	20	28.3 ± .81	72	.693

TABLE 8.   Dietary summaries (by volume) of various *Mabuya*

Prey category	M. striata Allopatric	M. striata Sympatric	M. spilogaster Sympatric	M. spilogaster Allopatric	M. occidentalis	M. variegata
Millepedes	.002	----	.001	.001	.002	.000
Centipedes	.000	.001	----	.001	.001	.000
Mites	.008	----	----	.000	.000	.000
Spiders	.054	.026	.034	.029	.022	.059
Other arachnids	.006	.041	.000	.012	.082	.003
Ants	.115	.100	.062	.009	.039	.012
Other Hymenoptera	.012	.015	.033	.011	.020	.007
Grasshoppers	.040	.015	.005	.118	.112	.154
Roaches	.009	.004	.013	.017	.000	.009
Phasmids and mantids	.005	----	----	----	.001	.029
Beetles	.328	.142	.260	.225	.369	.102
Termites						
Allodontermes (?)	.003	----	.000	.004	.003	.000
Allodontermes (major workers)	.098	.003	.028	.057	.104	.162
Allodontermes (minor workers)	.011	.001	.006	.008	.009	.041
Psammotermes allocerus (soldiers)	.001	.000	.002	.001	.003	.001
Psammotermes allocerus (workers)	.005	----	.000	.001	.000	.013
Hodotermes mossambicus	.016	.277	.228	.088	.080	.029
Trinervitermes spp.	.015	.151	.131	.073	.017	.012
Miscellaneous other termites	.017	.020	.033	.030	.017	.045
Homoptera–Hemiptera	.027	.028	.026	.034	.018	.123
Diptera	.013	.011	.001	.020	.007	.044
Lepidoptera (adults)	.060	.041	.003	.131	.009	.014
Larvae						
Coleoptera	.026	.019	.050	.008	.013	.013
Lepidoptera	.037	.015	.006	.052	.004	.000
Neuroptera	.002	.002	----	.004	.005	.000
Unidentified	.013	.024	.004	.030	.011	.024
Vertebrate material	.029	.014	.026	.011	.010	.000
Plant material	.006	.006	.002	.001	.010	.016
Miscellaneous unidentified insects	.022	.026	.030	.010	.034	.087
Total volume of food (cm³)	93.6	24.0	11.9	37.6	49.6	3.5
Food niche breadth	6.9	7.3	6.7	9.4	5.6	10.5

Distributions of the semiarboreal *Mabuya* parallel sandridge and flatland habitats in the south (Fig. 1A), and these contiguous habitat zones seemingly affect distributions of Kalahari subterranean lizards (*Typhlosaurus*, Huey and Pianka 1974), terrestrial geckos (*Colopus*, Haacke 1976), and perhaps certain terrestrial lacertid lizards (*Nucras*, see Broadley 1972; *Ichnotropis squamulosa*, Pianka et al. 1977). However, zones of sympatry and habitat changes are only similar, not congruent. For example, *M. spilogaster*, while normally associated with flatland habitats, replaces *M. striata* in the northern sandridges of South West Africa; moreover, *M. striata* occurs in some southern flatland localities (Fig. 1A). Therefore, the narrow zone of sympatry is probably not directly related to the relatively abrupt change between sandridge and flatland habitats, per se, at least in the north.

However, other environmental features also change near the sandridge-flatland junction. Published rainfall isohyets (Leistner 1967, Wellington 1955), though of questionable accuracy for many parts of the Kalahari, seemingly parallel the border (*M. spilogaster* is found in areas with slightly higher annual rainfall). Trees are somewhat more abundant in high rainfall areas, and some replacement of tree

species occurs as well (Leistner 1967, Werger 1973). For example, *Acacia reficiens* and *Terminalia* trees are apparently restricted to high rainfall areas, while *A. giraffae* is the dominant large *Acacia* in low rainfall areas (Leistner 1967). Yet, because of the patchy distribution of the vegetation, detailed quantitative observations of possible associations of lizards

TABLE 9.   Clutch/litter sizes, correlation coefficients between SVL and clutch/litter size, and length of smallest reproductive ♂ and ♀ in Kalahari *Mabuya*

Population	Clutch/litter size $\bar{x} \pm SE$	N	r	Length at maturity (mm) ♂♂	♀♀
M. spilogaster					
allopatry	5.3 ± .21	61	----	55	55
sympatry	5.5 ± .46	13	----	55	63
combined	5.4 ± .19	74	.59	55	55
M. striata					
allopatry	4.4 ± .15	64	----	63	73
sympatry	4.2 ± .49	10	----	67	79
combined	4.4 ± .18	74	.60	63	73
M. occidentalis	6.7 ± .28	32	.32	72	78
M. variegata	2.1 ± .23	15	.08	35	39

TABLE 10. Prey size (in microlitres) distributions (percentages)

Prey size category	M. spilogaster		M. striata		M. occidentalis	M. variegata
	allopatry	sympatry	sympatry	allopatry		
<1	0.0	2.7	----	1.2	---	----
1–5	65.6	32.7	30.6	78.2	69.7	85.0
6–14	8.5	18.6	31.8	6.5	5.2	5.4
15–24	10.1	34.0	30.1	5.1	9.5	5.2
25–34	7.8	7.9	3.4	2.1	4.8	1.7
35–44	1.7	1.1	0.3	0.6	2.3	1.3
45–54	1.9	1.6	1.0	1.5	4.4	0.8
55–64	0.2	----	0.1	0.8	1.1	0.2
65–74	0.2	----	0.2	0.8	0.6	----
75–84	1.1	----	0.9	1.8	0.4	----
85–94	0.2	----	0.1	0.0	0.1	----
>94	2.9	1.4	1.7	1.3	1.9	0.4
Mean prey size	14	15	17	10	15	6
Total prey items (n)	1848	559	1250	6293	2713	479
Mean head length (mm)	13.1	13.8	16.6	15.1	14.8	7.7
Prey size niche breadth	2.2	3.8	3.5	1.6	2.0	1.4

and vegetation in and near the zone of sympatry will be necessary to examine these patterns rigorously. A correspondence between distributions of vegetation and lizards might relate to color matching: for example, M. spilogaster may be better camouflaged on A. reficiens (?) than on A. giraffae. Moreover, the terrestrial Mabuya would probably be unaffected by changes in tree species. In any case, because potentially important environmental factors change in approximate correspondence with the zone of sympatry, basic distributional patterns of the semiarboreal species probably reflect adaptations to different environments. Certainly it is presently impossible and probably unwise to discount this hypothesis.

Nonetheless, why is the zone of sympatry relatively narrow? We suspect that environmental transitions are too gradual and too patchy to provide a complete answer. Interspecific competition might play a role. Mabuya striata and M. spilogaster are nearly idenitcal in all niche parameters examined (position on sandridges, microhabitat associations, structural niche, time and season of activity, body temperatures, and types and sizes of prey), whereas M. occidentalis and M. variegata generally overlap

little with each other and with the semiarboreal species (Tables 2–8, and estimates of overall overlap in Table 11). Thus the narrowly sympatric species pair has high niche overlap while broadly sympatric pairs have much lower overlaps (Tables 5 and 11). This trend is paralleled in Greater Antillean Anolis: a greater percentage of parapatric pairs have high structural-habitat overlaps than do sympatric pairs; and, where structural-habitat overlap is high, parapatric pairs are less different in size than are sympatric pairs (Schoener 1970).

Overlap is not necessarily proportional to intensity of competition, nor does high niche overlap necessarily imply strong competition. Nonetheless, given the relative magnitudes of overlaps here, competition is almost certainly greater between the semiarboreal species than among all other species pairs. Whether competition is intense for this pair is problematical because we have no direct information on resource depression in sympatry. Also, our circumstantial evidence relevant to intensity of competition is inconsistent (reproduction is depressed only in sympatric M. spilogaster) and possibly contradictory (next paragraph). Therefore, we argue that our overlap

TABLE 11. Estimates of overall overlap along the six niche dimensions of Table 5. Multiplicative values above the diagonal, and summation values below (the latter represent upper bounds on true multidimensional niche overlap—see May 1975)

	M. striata	M. spilogaster	M. occidentalis	M. variegata
M. striata	1.000	0.760	0.039	0.005
M. spilogaster	0.956	1.000	0.130	0.004
M. occidentalis	0.646	0.759	1.000	0.074
M. variegata	0.558	0.585	0.715	1.000

values are only consistent with the hypothesis that relatively strong interspecific competition between the semiarboreal species may help restrict the zone of coexistence.

Brown (1971), Cody (1974), and Nevo et al. (1975) have noted that narrowly sympatric species are often interspecifically territorial or aggressive. Given a stable environment, selection would favor such aggression only if competition is potentially severe. However, several individuals of both semiarboreal *Mabuya* commonly occur on the same log or tree in sympatry, and we noted little or no interspecific aggression (a few tethering experiments also failed to elicit aggression).

The apparent lack of interspecific aggression does not necessarily invalidate the hypothesis that competition is intense. These *Mabuya*, particularly *M. striata* (Brain 1969), are social lizards and frequently occur in large numbers on the same log or tree. Evolution of interspecific aggression might be difficult or impossible in such gregarious species, even in the absence of gene flow from nearby allopatric populations.

To summarize, our evidence supports two nonexclusive explanations for distributional patterns of *Mabuya* in the Kalahari. First, the narrow zone of sympatry probably reflects in part adaptations of these species to geographically discontinuous aspects of the physical environment. Second, more intense competition between the semiarboreal species, inferred from high niche overlap, may restrict the zone of sympatry. While the first explanation could entirely account for the narrow zone of sympatry, the nearly identical niches of the semiarboreal species nonetheless suggests that the second explanation is also important.

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