

## ECOLOGICAL SHIFTS IN SYMPATRY: KALAHARI FOSSORIAL LIZARDS (*TYPHLOSAURUS*)<sup>1</sup>

RAYMOND B. HUEY,<sup>2</sup> ERIC R. PIANKA, MICHAEL E. EGAN, AND LARRY W. COONS  
*Department of Zoology, University of Texas, Austin, Texas 78712*

**Abstract.** Two species of legless, fossorial skinks (*Typhlosaurus*) are partially sympatric in the Kalahari Desert. *Typhlosaurus lineatus* occur both in the sandridge and flatland geographic provinces of the Kalahari, in dune streets and on sandridges microgeographically in sympatry, and primarily under log and leaf litter microhabitats. *Typhlosaurus gariensis*, always sympatric with *T. lineatus*, occur only in sandridge areas geographically, on sandridges microgeographically, and primarily in basal roots of bunch grass microhabitats. Microhabitat overlap in sympatry is low.

Morphologically, *T. lineatus* differ from *T. gariensis* in being longer and in having a longer and wider head. Snout-vent lengths, head dimensions, and proportional head lengths of sympatric *T. lineatus* are larger than those of allopatric *T. lineatus*; thus *T. lineatus* displace from *T. gariensis* in sympatry.

Both species are viviparous, have one brood per year, and give birth in summer after a 5-mo gestation period. Maturity is reached at minimum ages of one and two-thirds yr. Mean litter size of *T. lineatus* is 1.6, whereas *T. gariensis* have but one young. A response to competition between the two species is suggested by the facts that offspring of sympatric *T. lineatus* are significantly heavier than those of allopatric females, and that fewer sympatric *T. lineatus* females are reproductive than allopatric females.

Because *Typhlosaurus* are termite specialists (92.4% of diet by volume), termites in guts were identified to species and caste. Compared with sympatric *T. lineatus*, *T. gariensis* eat more *Psammotermes* workers, fewer *Allodotermes* major workers, and scarcely any *Hodotermes*. Sympatric *T. lineatus* eat fewer *Psammotermes* workers and more *Allodotermes* major workers than do allopatric *T. lineatus*. Prey size differences parallel lizard size differences. Because of dietary shifts by *T. lineatus* in sympatry, dietary overlap with *T. gariensis* is substantially reduced for females and immatures, although not for males.

Strong morphological and dietary evidence support, for *T. lineatus* females and immatures, the hypothesis that behavioral and morphological character displacement has occurred which reduces dietary overlap with *T. gariensis*. Dietary data for male *T. lineatus* are possibly conflicting.

**Key words:** Character displacement; competition; fossorial lizards; lizards; niche shifts; r- and K-selection; Scincidae; *Typhlosaurus*.

### INTRODUCTION

Sympatry is unusual in sand-swimming lizards and has not previously been studied. Pianka (1967) found no fossorial species on 10 study areas in the western North American deserts, and sympatric species on only one of 8 desert study areas in Western Australia (Pianka 1969), suggesting that interspecific competition may be keen in fossorial lizards.

During an investigation of lizard species diversity in the southern Kalahari Desert (Pianka 1971), we encountered two partially sympatric, legless, sand-swimming skinks of the genus *Typhlosaurus*. Here we describe the natural history of these fossorial skinks and examine niche shifts in sympatry. In particular, we focus on morphological and behavioral

character displacement which could possibly reduce dietary overlap.

*Typhlosaurus* are almost completely subterranean, but do not construct tunnels. They occasionally travel snake-like above ground for short distances, but normally move in a lateral sinuous path just beneath the sand. Travel occurs only at night. *Typhlosaurus* are much more abundant than the frequency of observed tracks would indicate, suggesting that they change positions rarely and localize their activities beneath cover.

Detailed descriptions of the southern Kalahari are given in Leistner (1967). The southwestern portion is covered by stabilized sandridges (Fig. 1). To the northeast, terrain is flat or gently undulating. Shifting barchanes are absent from both areas. Vegetation is predominantly grassy, with varying concentrations of shrubs and trees; and, in sandridge areas, it is distinctly zoned. Larger shrubs and trees are

<sup>1</sup> Received February 3, 1973; accepted August 14, 1973.

<sup>2</sup> Present address: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

normally restricted to dune slopes, while smaller shrubs occur in interdunal valleys (= streets).

#### METHODS

We collected over 500 *Typhlosaurus*<sup>3</sup> by digging under various cover objects on nine study areas and several additional localities from December 1969 through October 1970. Five study sites lie within the dune region as delineated by Leistner (1967); the other four are flatland habitats. Data and statistics on locations, vegetation, topography, climate, saurofauna, and avifauna of each of these areas are given by Pianka and Huey (1971) and Pianka (1971). Microhabitat location and habitat were recorded for each lizard collected. The term "microhabitat," indicating the object under which a *Typhlosaurus* was found, is preferable to "cover" since these sites are used for foraging as well as retreats. Dissection of preserved material provided information on gonadal conditions and stomach contents. Samples were augmented with specimens from the Transvaal and Um-tali Museums. During our study, 994 *T. lineatus* and 133 *T. garipeensis* were examined, of which we collected 454 and 125 specimens, respectively. Body weights and snout-vent lengths (SVL) were measured on freshly captured specimens in the field. Because of shrinkage due to preservation, we converted measurements of museum specimens (pSVL) to estimated fresh SVL's by the following empirically determined regression equation: estimated SVL = 0.06 + 1.02 pSVL. We measured head length to the nearest 0.1 mm as the distance between the posterior tip of the parietal scale and the tip of the snout, using a calibrated ocular micrometer; head width was similarly measured as the maximum width on a transverse line passing through the eyes.

We determined prey size by placing the contents of the entire gastrointestinal tract on mm-ruled graph paper on the stage of a dissecting microscope. For items other than termites, the area covered with a depth between .75 and 1.25 mm was recorded as the volume in  $\mu\text{L}$  (=  $\text{mm}^3$ ). Partially digested material and recognizable parts were recorded, but were not included in prey size frequency distributions unless the original size of the item could be estimated. Termites were counted individually. We measured lengths and widths of heads and abdomens of representative types with an optical micrometer, and estimated their volumes using the formula for the volume of a prolate spheroid ( $V = 4/3 \pi a b^2$ , where  $a$  and  $b$  are the major and minor semi-axes, respectively). Testes volumes were estimated similarly from their linear dimensions. We used the following formula to calculate overlap values:

$$D = 1 - 1/2 \sum_{i=1}^n |p_{x,i} - p_{y,i}|,$$

where  $p_{x,i}$  is the proportional utilization by species  $x$  of the  $i$ th resource category (Schoener 1969 discusses this overlap measure).

#### RESULTS

##### *Morphology*

*Typhlosaurus* are specialized morphologically to a subterranean existence. We first document their general fossorial adaptations and then examine specific morphological differences possibly important in ecological separation.

Reptilian adaptations to a subsand environment are often convergent. Since the adaptive responses have been detailed by Gans (1960) and Norris and Kavanau (1966), we merely list major adaptations of *Typhlosaurus*: shovel-shaped head, counter-sunk jaw, no external ears, brille over eye, nasal plug, depression of skull below longitudinal body axis, gular breathing in sand-free pocket behind mouth (deep-lung breathing above ground), legless body, "mushroom-cap" cross-sectional shape, and elongate embryos and testes.

Two of these adaptations require additional comment: the nasal plug and elongated embryos and testes. The nasal plug of *Typhlosaurus* protrudes into the naris from the posterior wall. Judging from live (W. D. Haacke, *personal communication*) and preserved specimens, this plug closes off the naris completely. The naris of *Anniella* is not protected by a plug or valve (Miller 1944), but the nasal vestibule may be partially constrictable (Stebbins 1948). *Chionactis* have a simple flap over the anterior part of the naris (Stickel 1941). The nasal plug of *Typhlosaurus* blocks the naris even during reverse motion, but the nasal valve of *Chionactis* is probably functional only during forward motion and rest (Norris and Kavanau 1966). Submerged *Typhlosaurus*, like *Chionactis*, breathe through their mouths in a sand-free pocket beneath the head; hence the nares are of little functional use (Pough 1969).

*Typhlosaurus* are viviparous, with the body axis of the embryo parallel to that of the mother rather than curled (Brain 1959); only the embryo's tail is folded. Since the force required to push a cylinder through a medium is a function of the diameter of the cylinder, parallel orientation of embryos results in female *Typhlosaurus* with a relatively uniform and narrow body, presumably minimizing energy expenditure on locomotion during pregnancy. Elongate testes confer similar advantages on males. Maturing *Anniella* embryos are folded 2-3 times, but are basically longitudinal (Klauber 1932, Miller 1944). Moreover, *Anniella* females have only a

<sup>3</sup> Deposited in the Los Angeles County Museum of Natural History.

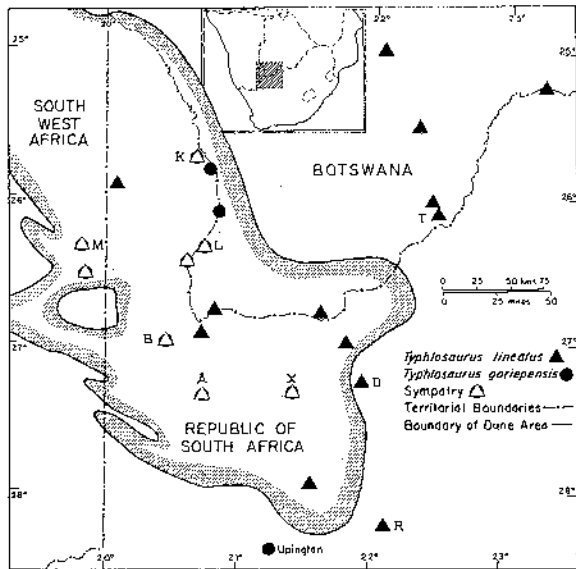


FIG. 1. Map showing approximate localities of collection of *T. lineatus* and *T. gariiepensis* in the southern part of the Kalahari Desert. They are sympatric on at least eight sites within the dune region (outlined by line and stippling). Tsane and Mabua Sefubi Pan are just off the map to the northeast. Study areas indicated by letters.

single functional (right) oviduct (Coe and Kunkel 1905, 1906).

#### Ecological Morphology and Character Shifts

*Typhlosaurus lineatus* and *T. gariiepensis* are partially sympatric in the Kalahari Desert (Fig. 1 and *Macrogeographic Distribution*, below). They differ considerably in snout-vent length (Fig. 2). Sympatric *T. lineatus* of both sexes are significantly longer (*t*-tests,  $P$ 's < .001) than adult *T. gariiepensis*. In maximum SVL *T. lineatus* is also longer (167 mm vs. 140 mm).

Data on allopatric *T. lineatus* were divided into two populations (Fig. 1 and 2): one is far from sympatry (Tsane and Mabua Sefubi Pan) while the other (T + D + R) is near sympatry. Sympatric *T. lineatus* were divided into two populations: deep sympatry (M + B + A + others) and near allopatry (K + L + X + others). Paired comparisons within sex classes show no significant differences (*t*-tests,  $P$ 's > .60) in SVL among either allopatric or sympatric populations. However, paired comparisons within sex classes show that both sympatric populations are significantly longer in SVL than any of the allopatric populations ( $P$ 's < .01) (Fig. 2). Thus *T. lineatus* exhibit a step-wise character shift (rather than a clinal shift) in SVL where sympatric with *T. gariiepensis*. (Whether or not this and other morphological shifts described below can properly be

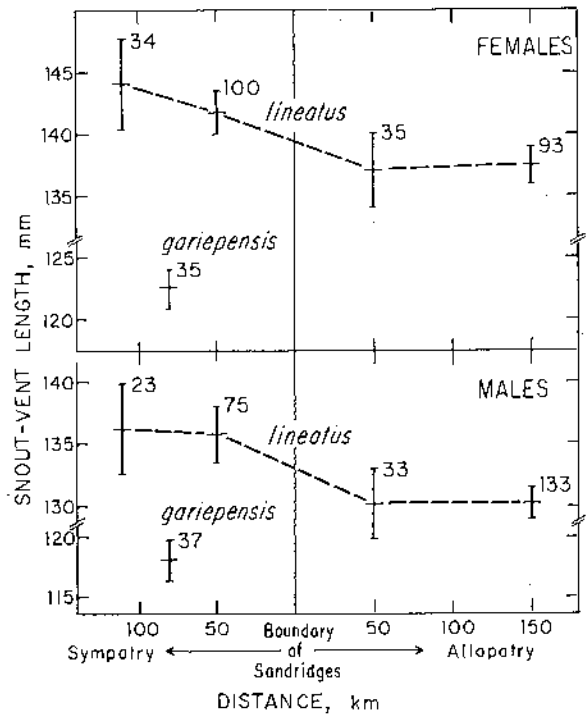


FIG. 2. Snout-vent lengths of male (below) and female (above) *Typhlosaurus* vs. approximate average distance of populations from boundary of sandridges. Means shown as horizontal lines; two SE of the mean on either side by vertical lines. Numbers inside graph are sample sizes (number of lizards).

called character displacement is considered in the Discussion). Because *T. gariiepensis* are always sympatric with *T. lineatus*, reciprocity cannot be directly observed. However, *T. gariiepensis* is the smallest of the eight species of *Typhlosaurus*, suggesting that its small size might reflect historical interaction with *T. lineatus* (Broadley 1968).

Statistics in Table 1 show that sympatric *T. lineatus* (both populations combined) have significantly longer and wider heads than do *T. gariiepensis* (*t*-tests,  $P$ 's < .001). Sympatric *T. lineatus* also have significantly (*t*-tests,  $P$ 's < .001) longer and wider heads

TABLE 1. Head length and width statistics for *Typhlosaurus*.  $\bar{x}$  = mean, SE = standard error of mean, SD = standard deviation, and  $N$  = sample size. Text gives tests of significance

Species	Head length				Head width			
	$\bar{x}$	SE	SD	$N$	$\bar{x}$	SE	SD	$N$
Allopatric								
<i>T. lineatus</i>	4.39	.021	.203	94	3.25	.015	.142	94
Sympatric								
<i>T. lineatus</i>	4.65	.022	.215	93	3.40	.013	.129	93
<i>T. gariiepensis</i>	3.75	.017	.147	76	2.77	.010	.089	76

TABLE 2. Linear regressions of body length and head proportions. Parentheses following coefficients enclose one SE for that coefficient

Trunk length (TL) vs. head length (HL)	
Allopatric	
<i>T. lineatus</i> (N = 99)	HL = 2.166 (± .094) + .0204 (± .0008) TL
Sympatric	
<i>T. lineatus</i> (N = 93)	HL = 2.355 (± .097) + .0205 (± .0008) TL
<i>T. garipeensis</i> (N = 76)	HL = 1.992 (± .127) + .0163 (± .0012) TL
Snout-vent length (SVL) vs. head width (HW)	
Allopatric	
<i>T. lineatus</i> (N = 99)	HW = 1.398 (± .067) + .0163 (± .0006) SVL
Sympatric	
<i>T. lineatus</i> (N = 93)	HW = 1.440 (± .060) + .0168 (± .0005) SVL
<i>T. garipeensis</i> (N = 76)	HW = 1.284 (± .078) + .0133 (± .0007) SVL

than allopatric *T. lineatus* (near allopatry only were measured). Hence mean head length and mean head width of *T. lineatus* also shift in sympatry.

Character shifts in mean head sizes could be simple correlates of the larger SVL's of sympatric *T. lineatus*. To determine whether heads were proportionately longer and wider in sympatry, we computed linear regressions for head proportions of allopatric *T. lineatus*, sympatric *T. lineatus*, and *T. garipeensis* (Table 2). At any trunk or snout-vent length, there is no overlap in scatter diagrams between sympatric *T. lineatus* and *T. garipeensis* in either head length or head width: *T. lineatus* always have longer and wider heads. Slopes of regressions of head length on trunk length in allopatric and sympatric *T. lineatus* do not differ significantly, but the elevation of the regression for sympatric *T. lineatus* is significantly higher (*t*-test, *P* < .001; Zar 1973). Neither the slope nor the elevation of the head width vs. SVL regressions differ significantly between allopatric and sympatric *T. lineatus*. Overall, sympatric *T. lineatus* thus exhibit character shifts in SVL, head dimensions, and proportional head length.

*Macrogeographic distribution*

Known localities of *T. lineatus* and *T. garipeensis* in the southern Kalahari are plotted in Fig. 1; Broad-

TABLE 4. Microhabitat associations of *Typhlosaurus*

Microhabitat	Allopatric		Sympatric		<i>T. garipeensis</i>	
	<i>T. lineatus</i> N	%	<i>T. lineatus</i> N	%	N	%
Leaf litter	81	64.8	141	42.8	4	3.2
Logs	28	22.4	65	19.7	8	6.4
<i>Crotalaria</i>	8	6.4	68	20.6	23	18.4
Bunch grasses	1*	0.0	53	16.1	90	72.0
Miscellaneous	8	6.4	2	0.6	0	0.0
Totals	125		329		125	

\* Microhabitat utilization on the basis of tracks only.

ley (1968) lists extralimital records of *T. lineatus* which extend hundreds of miles northwards. This species is widespread, occurring on Kalahari sands both in sandridge and flatland areas, whereas *T. garipeensis* is restricted to sandridge regions. The single exception is the type locality of *T. garipeensis*, Upington (Fitzsimons 1941), with a gravel and rock substratum. The holotype probably came from one of several isolated dune patches within 3 to 13 miles of Upington.

We have established sympatry on eight localities in the sandridge areas of Botswana, South Africa, and Southwest Africa (Fig. 1); further collecting will almost certainly show that these two species are sympatric at most localities throughout most of the sandridge area of the southern Kalahari.

*Microgeographic distribution in sympatry*

We recognize four microgeographic subdivisions in the sandridge areas, where *T. lineatus* and *T. garipeensis* are sympatric: street, dune base, dune slope, and dune crest. The numbers of each species collected in each subdivision are presented in Table 3. *Typhlosaurus lineatus* occurs predominantly on dunes, but can also be found in interdunal streets. *Typhlosaurus garipeensis* is almost entirely restricted to sandridges proper; the two specimens listed for the dune street were on a very small dune less than 20 m from a major sandridge. Microgeographic distributions in sympatry differ significantly (*G*-test, *P* < .001).

On the basis of macrogeographic distributions, one might expect *T. lineatus* to be more abundant in the interdunal streets. This is not true, because (1) street

TABLE 3. Microgeographic distribution of sympatric *Typhlosaurus* on sandridges

Species	Total	Street		Base		Slope		Crest	
		N	%	N	%	N	%	N	%
<i>T. lineatus</i>	329	36	10.8	19	5.8	211	64.3	63	19.1
<i>T. garipeensis</i>	125	2	1.6	2	1.6	85	68.0	36	28.8

sands are generally compact and present locomotor difficulties for fossorial lizards, and (2) vegetational zonation affords more suitable microhabitats on sandridges. We therefore expended little effort digging for *Typhlosaurus* in the streets. Nonetheless, *T. lineatus* occurs in streets where suitable microhabitats exist, but *T. gariensis* does not. Microgeographic distributions of the two species thus neatly mirror their macrogeographic distributions.

#### Microhabitats

*Typhlosaurus lineatus* in sympatry are found chiefly (Table 4) in sand beneath logs and in leaf litter of large shrubs and trees (especially *Acacia giraffe*, *A. karoo*, *A. mellifera*, *A. haematoxylon*, *Boscia* spp., and *Grewia* spp.) *Typhlosaurus gariensis* associate predominantly with bunch grass stools. The two species differ significantly in microhabitat associations (*G*-test,  $P < .001$ ). Records for both species associated with bunch grass stools show that *T. gariensis* occur within the basal root complex significantly more often (77%,  $N = 64$ ) than *T. lineatus* (14%,  $N = 35$ ), which are usually found in underlying sand (*G*-test,  $P < .001$ ). Hence, despite co-occurrence on sandridges, these species differ considerably in microhabitat associations.

Solitary individuals of *T. gariensis* were found under individual microhabitats significantly more often than the more gregarious *T. lineatus* ( $\chi^2$ -test,  $P < .001$ ): 89% ( $N = 109$ ) of the former but only 54% ( $N = 404$ ) of the latter were alone.

We use the proportions in Table 4 as  $p_i$ 's in MacArthur's (1972) diversity equation ( $1/\sum p_i^2$ ) to estimate microhabitat niche breadth. We found *T. lineatus* under a greater diversity of microhabitats in sympatry (3.44) than either *T. gariensis* (1.79) or *T. lineatus* in allopatry (2.09). (The low diversity of microhabitats used by allopatric *T. lineatus* probably reflects only the greater variety of microhabitats available and examined in sandridge areas.)

#### Growth and reproduction

Both species are viviparous, and young are born in mid-January through early March (middle-late summer in the Southern Hemisphere). Two *T. gariensis* (Broadley 1968) gave birth to single young on 20 February (approximately 60 and 58 mm SVL). Two *T. lineatus* collected by W. D. Haacke (*personal communication*) on 10 January gave birth to young within 2 weeks. One *T. lineatus* we collected gave birth to a 57-mm SVL baby (0.35 gm) on 6 February.

Weights of newly born and near-term embryos of allopatric *T. lineatus* ( $N = 20$ ) averaged  $0.32 \pm .01$  gm, sympatric *T. lineatus* ( $N = 4$ ) averaged  $0.39 \pm$

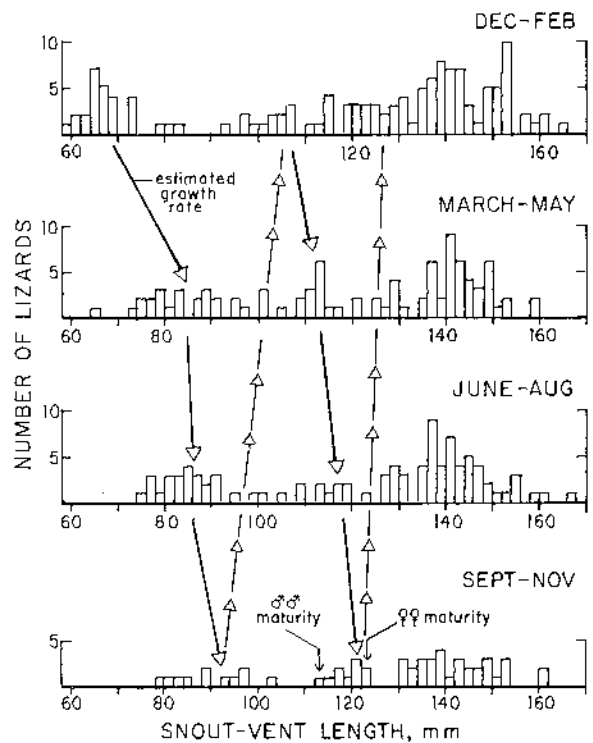


FIG. 3. Snout-vent length frequency distributions of sympatric *T. lineatus* by season, showing various size classes and estimated growth rates (beyond 1st year these are tenuous).

.03 gm, and *T. gariensis* ( $N = 2$ ) averaged 0.33 gm (weights of *T. gariensis* estimated by regression). Embryos and young of *T. lineatus* in sympatry are significantly heavier than in allopatry (Mann-Whitney *U*-test,  $P < .05$ ). Per progeny expenditure (weight of young as percent of total female weight) averaged 10.2% in *T. lineatus* and 17% in *T. gariensis*.

We grouped snout-vent lengths into 3-mo intervals (Fig. 3) to estimate seasonal growth. During their 1st year *Typhlosaurus* appear to grow rapidly except during winter; after the 1st year, their growth appears slowed.

With the criterion of enlarged testes, *T. lineatus* males in allopatry and sympatry reach sexual maturity at approximately 112 mm SVL; *T. gariensis* males mature at about 104 mm SVL.

Average monthly testes volumes of adult male *T. lineatus* are plotted in Fig. 4. Testes begin enlarging in midautumn and increase rapidly to a maximum volume in late winter. Testicular regression is complete by midsummer when the young are born. Male *T. gariensis* have a similar testicular cycle.

Using the presence of enlarged yolked follicles or embryos as criteria, we estimated that female *T. lineatus* mature at about 123 mm SVL in both

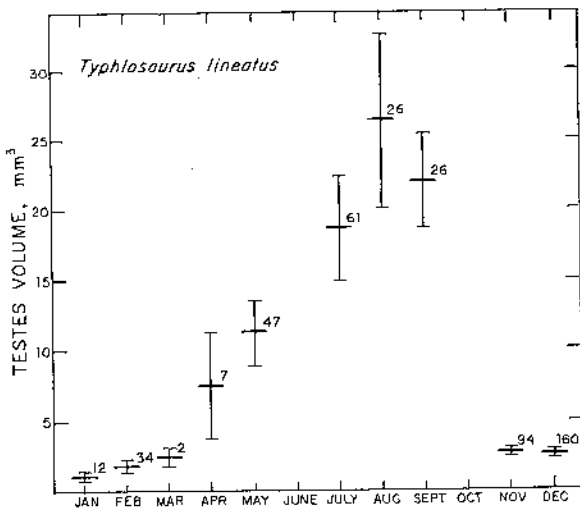


FIG. 4. Testicular cycle of *T. lineatus* by month, including both allopatric and sympatric lizards. Symbols as in Fig. 2. Numbers inside figure are sample sizes (= number of testes measured).

allopatry and sympatry, and female *T. gariensis* mature at about 118 mm SVL.

Histograms of follicle or embryo size for adult female *T. lineatus* are plotted bimonthly in Fig. 5. Follicular enlargement and vitellogenesis occur during late winter, at which time male testes volumes are beginning to decrease, implying that copulation takes place in August or September. We have the impression, based on frequency of encounters of tracks, that movements of *Typhlosaurus* are greatest during this time of year, despite stronger winds then (Leistner 1967), which suggests that *Typhlosaurus* are actively searching for mates at this time.

Embryo development continues until middle or late summer when young are born, the time of maximal rainfall and temperature in the Kalahari (Leistner 1967). Midsummer hatchings and births for many nonfossorial Kalahari lizards occur concurrently.

If copulation is in September and parturition in February, *Typhlosaurus* have a 5-mo gestation period, longer than any other low-altitude lizard (Tinkle 1967, Fitch 1970, Marion and Sexton 1971, Ballinger 1973). From these and other data presented earlier, we believe that *Typhlosaurus* females have a maximum of one brood per year.

The number of young per female, based on either the number of enlarged yolked eggs or embryos, is invariably one in *T. gariensis* ( $N = 11$ ), and from one to three ( $N = 208$ ) in *T. lineatus*. There is a slight tendency for larger *T. lineatus* to have larger broods ( $r = .378$ ,  $P < .01$ ) as is often the case in lizards (Tinkle et al. 1970). Mean litter size of *T. lineatus* in allopatry is 1.56, whereas in sympatry it is 1.66. Frequency distributions of females having

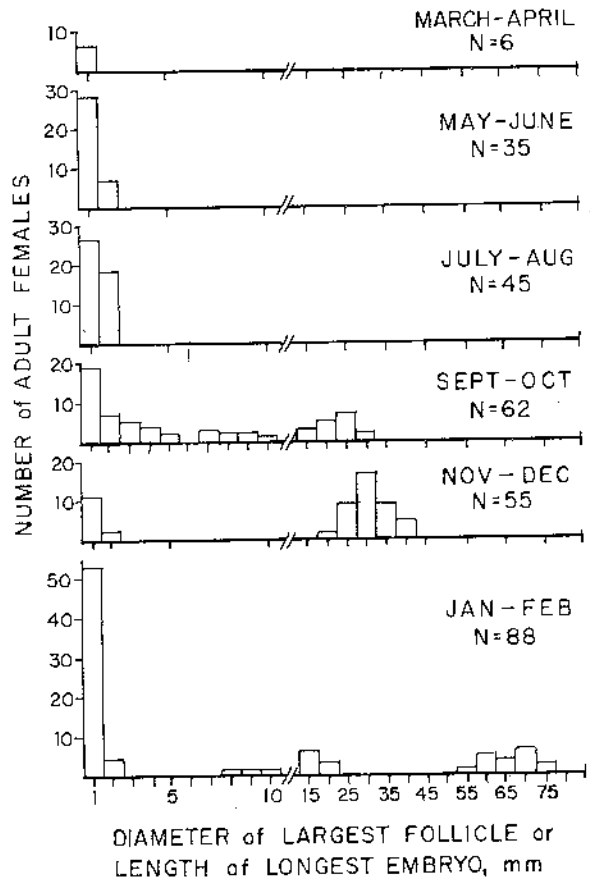


FIG. 5. Frequency distributions of the number of females with follicles and/or embryos of a given size at 2-mo intervals in *T. lineatus*. Both allopatric and sympatric specimens are plotted. Note the large numbers of nonreproductive females during January and February.

one versus two or more young do not differ significantly ( $\chi^2$ -test,  $P > .05$ ) between allopatry and sympatry.

Comparing growth and reproductive data (Fig. 3), we estimate that male *T. lineatus* and *T. gariensis* reach maturity at a minimum age of 1½ yr. Unless females grow faster than males, some female *T. lineatus* may not reach sexual maturity until 2½ yr and hence be 3 yr old when their first young are born. In either case, *Typhlosaurus* definitely have delayed maturity compared with most lizards (Tinkle et al. 1970).

A large fraction of adult female *T. lineatus* are nonreproductive during the reproductive season from September through February. Significantly fewer ( $\chi^2$ -test,  $P < .001$ ) sympatric *T. lineatus* (31.4%,  $N = 71$ ) were pregnant than allopatric *T. lineatus* (65.7%,  $N = 139$ ) during these months. Although some of these may be females that have already given

TABLE 5. Summaries of the intestinal contents of 117 allopatric *T. lineatus*, 324 sympatric *T. lineatus*, and 108 *T. garipeensis*. No. = total number of prey items in a category, Vol. = total of prey in a given category (in  $\mu$ l), %N = percentage composition of diet by number, %V = percentage composition by volume, and F = frequency of occurrence in the guts examined (percentages). tr = trace (less than .1%)

Prey Categories	Allopatric <i>T. lineatus</i>					Sympatric <i>T. lineatus</i>					<i>T. garipeensis</i>				
	No.	Vol.	%N	%V	F	No.	Vol.	%N	%V	F	No.	Vol.	%N	%V	F
<b>ISOPTERA</b>															
<i>Allodermes (schultzei?)</i>															
Minor workers	528	1164	31.3	12.4	53.8	1858	3706	27.6	11.6	56.2	686	1372	24.6	14.5	66.7
Major workers	822	3699	44.2	39.5	53.0	4007	18031	59.4	56.2	61.9	928	4176	33.2	44.0	64.8
<i>Psammotermes allocerus</i>															
Workers	268	670	14.4	7.1	15.4	337	842	5.0	2.6	11.4	949	2872	34.0	30.3	63.0
Soldiers	41	164	2.2	1.8	16.2	106	424	1.6	1.3	17.3	118	472	4.2	5.0	43.5
<i>Microtermes</i> sp.	6	12	0.3	0.1	2.6	2	4	tr	tr	0.6	64	128	2.3	1.4	8.3
<i>Trinervitermes</i> sp.	—	—	—	—	—	4	16	0.1	0.1	1.0	—	—	—	—	—
( <i>Odontotermes</i> sp.?)	5	55	0.3	0.6	2.6	4	44	0.1	0.1	1.2	3	33	0.1	0.3	2.8
<i>Microcerotermes</i> sp.	—	—	—	—	—	5	7	0.1	tr	1.0	—	—	—	—	—
( <i>Trinervitermes</i> sp.?)	—	—	—	—	—	12	48	0.2	0.1	0.3	—	—	—	—	—
( <i>Microtermes</i> sp.?)	—	—	—	—	—	1	11	tr	0.1	0.3	—	—	—	—	—
<i>Trinervitermes</i> sp.	—	—	—	—	—	11	550	0.2	1.7	1.0	—	—	—	—	—
<i>Hodotermes mossambicus</i>	47	2820	2.5	30.1	17.1	107	6420	1.6	20.0	13.6	2	120	0.1	1.3	0.9
<b>COLEOPTERA</b>															
Adults	34	230	1.8	2.5	24.8	69	750	1.0	2.3	17.9	2	2	0.1	tr	0.9
Larvae	25	339	1.4	3.6	15.4	51	830	0.7	2.6	13.6	13	162	0.4	1.7	12.0
Other Insect Larvae	5	72	0.3	0.8	4.3	16	187	0.2	0.6	5.2	4	22	0.1	0.2	3.7
Insect Eggs	1	10	0.1	0.1	0.9	13	17	0.2	0.1	0.9	3	6	0.1	0.1	0.9
Hymenoptera: Formicidae	17	12	0.9	0.1	6.0	131	87	1.9	0.3	7.7	11	36	0.4	0.4	3.7
Miscellaneous and/or Unidentified Insects		45		0.5	2.6										
<b>ARACHNIDS</b>															
Araneae	4	28	0.2	0.3	1.7	6	103	0.1	0.3	1.9	11	73	0.4	0.8	—
Scorpionidae	—	—	—	—	—	1	3	tr	tr	0.3	—	—	—	—	—
Solpugidae	1	50	0.1	0.5	0.9	—	—	—	—	—	—	—	—	—	—
<b>TOTALS</b>	<b>1858</b>	<b>9370</b>	<b>100.0</b>	<b>100.0</b>	<b>—</b>	<b>6741</b>	<b>32080</b>	<b>100.0</b>	<b>100.0</b>	<b>—</b>	<b>2794</b>	<b>9474</b>	<b>100.0</b>	<b>100.0</b>	<b>—</b>

birth to young, the proportions of reproductive females suggest that about two-thirds of all allopatric *T. lineatus* females breed each year but only about one-third of all sympatric adult female *T. lineatus* reproduce.

If these differences of frequency of litters are real, one should find a higher ratio of newborn to adult females in allopatry than in sympatry. To test this we counted the number of newborn in our January and February collections and added the number of fully developed embryos in gravid females; this number was then compared to the actual number of adult females collected. In allopatry there were 30 embryos and young versus 32 adult females. In sympatry we found 30 embryos and young versus 49 adult females. Although these data are not significantly different ( $\chi^2$ -test,  $P < .15$ ), they do not contradict the expectation that female *T. lineatus* in sympatry reproduce less frequently than females in allopatry. Moreover, if one multiplies the numbers of females (32 allopatry, 49 sympatry) times the average litter sizes (1.56 allopatry, 1.66 sympatry) times the estimated frequencies of reproduction (.33 allopatry, .66 sympatry), one obtains expected numbers of embryos and young of 32 (allopatry) and 27 (sympatry), very close to observed values of 30

and 30, again suggesting that allopatric *T. lineatus* have a higher reproductive rate than do sympatric *T. lineatus*.

Delayed maturity, small brood size, and non-annual reproduction, coupled with the low frequency of juveniles, all indicate that these lizards have a long life expectancy and an extremely low reproductive potential. Tinkle (1967, 1969) noted that viviparity in lizards is often associated with low reproductive potential and long life expectancy.

#### Diet

Most lizard species are opportunistic feeders and eat a wide variety of prey taxa. Determination of prey items at the ordinal or familial levels is often sufficient to demonstrate dietary patterns and differences between species. However, since both species of *Typhlosaurus* are termite specialists and since the Kalahari termite fauna is very rich (Coaton 1963), this methodology could conceal both dietary differences and dietary shifts. Hence we identified all isopterans to distinct morphological types (species or castes). Other prey items were identified only to the ordinal or familial level.

In our original analysis, we separated data on *T. lineatus* into three populations (allopatry [T + D + R],

TABLE 6. Dietary overlaps for *Typhlosaurus*. gar = *T. garipeensis*, allo = allopatric *T. lineatus*, near = near sympatric *T. lineatus*, far = far sympatric *T. lineatus*, imm = immature. Asterisks refer to significance levels of R × C contingency tests, not to overlap values: \* = < .05, \*\* = < .01, \*\*\* = < .001

	D (prey taxa)	D (prey size)
<b>Intrapopulational</b>		
♀ gar × ♂ gar	.855***	.907***
♀ gar × imm gar	.941	.947
♂ gar × imm gar	.823***	.855***
♀ allo × ♂ allo	.833***	.981
♀ allo × imm allo	.916***	.929*
♂ allo × imm allo	.897***	.936
♀ near × ♂ near	.928***	.967*
♀ near × imm near	.853***	.907***
♂ near × imm near	.867***	.939*
♀ far × ♂ far	.895***	.982*
♀ far × imm far	.933*	.969**
♂ far × imm far	.898***	.939***
<b>Interpopulational</b>		
♀ gar × ♀ allo	.816***	.819***
♀ gar × ♀ near	.610***	.679***
♀ gar × ♀ far	.587***	.756***
♂ gar × ♂ allo	.789***	.919***
♂ gar × ♂ near	.761***	.798***
♂ gar × ♂ far	.789***	.861***
imm gar × imm allo	.712***	.837***
imm gar × imm near	.590***	.707***
imm gar × imm far	.538***	.660***
♀ allo × ♀ near	.702***	.836***
♀ allo × ♀ far	.689***	.891***
♂ allo × ♂ near	.837***	.879***
♂ allo × ♂ far	.865***	.908***
imm allo × imm near	.836***	.869***
imm allo × imm far	.783***	.819***

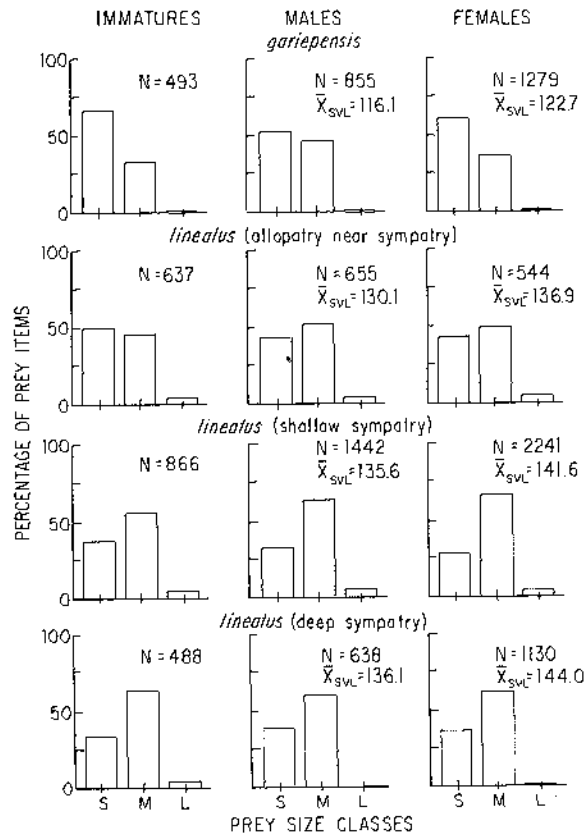


FIG. 6. Percentage of prey items in each of three prey size (volume) categories [S = small (0–2.5 μl), M = medium (3–11 μl), L = large (over 11 μl)]. Total number of prey items and mean snout-vent lengths included for adults. Note that sympatric *T. lineatus* eat more larger prey than do allopatric *T. lineatus*.

near sympatry [K + L + X + others], and deep sympatry [M + B + A + others]) and distinguished among adult males, adult females, and immatures for all populations. However, to save space, we pool data from sympatric populations and for size and sex classes for presentation here (Table 5). The essence of the original data is preserved, however, in the overlap values of Table 6.

Table 5 summarizes results of stomach content analysis for *T. lineatus* and *T. garipeensis*. Isopterans comprise from 84.4% to 96.5% ( $\bar{x}$  = 92.4) of the intestinal contents by volume among the various populations. Although 12 isopteran types were found in the 554 intestines examined, only 5 termite types comprised the bulk of prey of *Typhlosaurus*: major and minor workers of *Allodontermes* (probably *schultzei*), soldiers and workers of *Psammotermes allocerus*, and *Hodotermes mossambicus*. Nests of all these termites are subterranean (Coaton 1963). *Allodontermes* minor workers and *Psammotermes*

workers are small (about 2–2.5 μl), *Psammotermes* soldiers and major workers of *Allodontermes* are medium sized (about 4–4.5 μl), while *Hodotermes* are very large (about 60 μl). Both species of *Typhlosaurus* occasionally eat spiders, ants, beetles, beetle larvae, and other larvae.

*Allodontermes* major workers are the chief food of both species. However, *T. garipeensis* (males, females, immatures: *t*-tests, *P*'s < .001) take far more *Psammotermes* workers, fewer *Allodontermes* major workers (*P*'s < .001), and scarcely any *Hodotermes* compared with sympatric *T. lineatus* populations. Sympatric *T. lineatus* eat fewer *Psammotermes* workers (females and immatures, *P*'s < .001; but not males, *P*'s > .40) but more *Allodontermes* major workers (females, immatures, and males, *P*'s < .001) than do allopatric *T. lineatus*.

Intrapopulational dietary overlaps ( $\bar{x}$  = .887) by prey type in Table 6 are significantly greater (Mann-Whitney *U* test, *P* < .001) than interpopulational overlaps ( $\bar{x}$  = .727). The overall diversity of prey



TABLE 7. Percent, number, and diversity of prey items (by number) eaten by *Typhlosaurus* under specific microhabitats. (No allopatric *T. lineatus* were captured under grasses)

	LOGS			LEAF LITTER			<i>Crotalaria</i>			GRASS	
	Allo- patric <i>T.</i> <i>lineatus</i>	Sym- patric <i>T.</i> <i>lineatus</i>	<i>T.</i> <i>gari-</i> <i>epensis</i>	Allo- patric <i>T.</i> <i>lineatus</i>	Sym- patric <i>T.</i> <i>lineatus</i>	<i>T.</i> <i>gari-</i> <i>epensis</i>	Allo- patric <i>T.</i> <i>lineatus</i>	Sym- patric <i>T.</i> <i>lineatus</i>	<i>T.</i> <i>gari-</i> <i>epensis</i>	Sym- patric <i>T.</i> <i>lineatus</i>	<i>T.</i> <i>gari-</i> <i>epensis</i>
<i>Allodoterms (schultzei?)</i>											
Minor workers	32.3	34.2	15.4	34.4	21.9	14.6	29.2	30.2	35.2	40.7	23.2
Major workers	24.5	52.7	10.8	48.0	74.1	21.9	42.3	64.5	31.9	54.8	36.4
<i>Psammotermes allocerus</i>											
Workers	36.5	7.1	56.9	7.3	1.8	56.9	24.6	1.9	27.0	1.6	33.7
Soldiers	1.0	3.9	14.6	3.0	1.4	3.6	3.2	1.4	2.6	1.8	4.1
<i>Hodotermes mossambicus</i>											
Other termites	5.5	1.8	—	6.0	0.6	—	0.7	1.1	—	0.7	—
Number termites, total	2385	4214	380	2500	4746	397	1037	3386	927	2620	4604
Diversity ( $1/\Sigma p_i^2$ )	3.33	2.49	2.62	2.79	1.67	2.53	3.07	1.97	3.32	2.14	3.31

eaten, with proportional representation by volume of prey categories (age and sex classes of *Typhlosaurus* lumped, both sympatric *T. lineatus* populations lumped) as  $p_i$ 's in MacArthur's (1972) diversity equation is 3.23 for *T. gariensis*, 2.69 for sympatric *T. lineatus*, and 3.71 for allopatric *T. lineatus*; thus, the diet of *T. lineatus* is more restricted in sympatry.

Prey size distributions (Fig. 6) show that *T. gariensis* of any age or sex class take significantly smaller prey than does any corresponding class of either population of sympatric *T. lineatus* ( $\chi^2$ -tests in Table 6,  $P$ 's < .001) or than allopatric *T. lineatus* ( $P$ 's < .001). Classes of both populations of sympatric *T. lineatus* eat significantly larger prey ( $P$ 's < .001) than do allopatric *T. lineatus*. Intrapopulation dietary overlaps by prey size ( $\bar{x} = .938$ ) in Table 6 are significantly greater (Mann-Whitney  $U$  test,  $P < .001$ ) than interpopulational overlaps ( $\bar{x} = .816$ ).

Percentages of various prey types and prey size categories fluctuate somewhat monthly; but, since there are no apparent repeatable seasonal patterns, these fluctuations may merely reflect sampling error and small sample sizes.

In an attempt to determine whether dietary differences result from differences in microhabitat associations or from active selection of different isopteran types, we also summarized diets by the microhabitat where lizards were collected (only termites were considered). Here we assume that a lizard's gut contains prey captured in that microhabitat (since *Typhlosaurus* apparently change microhabitats infrequently, this assumption seems reasonable). All five major termite types (Table 7) occur in the intestines of *Typhlosaurus* from all four microhabitats (under logs, leaf litter, *Crotalaria*, and bunch grasses), but differ in proportion primarily between species

and populations rather than between microhabitats. For example, *T. gariensis* ate significantly more ( $t_s$ -tests,  $P$ 's < .001) *Psammotermes* workers than did sympatric *T. lineatus* under each of the four microhabitats. Similarly, allopatric *T. lineatus* ate significantly more ( $P$ 's < .001) *Psammotermes* and significantly fewer ( $P$ 's < .001) *Allodoterms* major workers than did sympatric *T. lineatus*. Sympatric *T. lineatus*, but not *T. gariensis*, ate *Hodotermes* in all four microhabitats. The overall patterns previously described thus hold within microhabitats, indicating that active prey selection is probably occurring. Nonetheless, we cannot discount the possible influence of subtle differences in times of activity or in the use of space (perhaps like those shown earlier for bunch grass).

Patterns of diversities of prey items taken (Table 7) under the four microhabitats are also consistent with overall diversities previously given. Allopatric *T. lineatus* always ate a greater diversity of termites than did sympatric *T. lineatus*, and *T. gariensis* always ate a greater diversity than did sympatric *T. lineatus*. This last result is somewhat surprising, for *T. gariensis* is relatively specialized in microhabitat associations compared to sympatric *T. lineatus* (see *Microhabitats*). Moreover these observations further emphasize the apparent independence of prey taxa and microhabitat and help to justify treatment of food and place as separate niche dimensions (Pianka 1973).

Sympatric *T. lineatus* (females and immatures) take larger prey than allopatric *T. lineatus* because the former eat fewer *Psammotermes* workers (a small termite), and relatively more *Allodoterms* major workers. Male sympatric *T. lineatus* also take larger prey, but do so only by taking more *Allodoterms* workers, not by eating fewer *Psammotermes*.

The reduction in numbers of *Psammotermes* workers taken by sympatric *T. lineatus* is not due to decreased absolute abundance of this termite in sympatry, for *T. gariensis* finds substantial numbers of *Psammotermes*. Likewise, the increased number of *Allodotermes* major workers taken by *T. lineatus* does not stem from a greater absolute abundance of this caste in sympatry. Comparing the relative proportions of minor and major workers of *Allodotermes* taken, we found that allopatric *T. lineatus* (males, females and immatures lumped) eat 1:1.3 minor to major workers, *T. gariensis* eat 1:1.4, shallow sympatric *T. lineatus* 1:2.0, and deep sympatric *T. lineatus* eat 1:1.8. Thus, sympatric *T. lineatus* eat selectively more *Allodotermes* major workers than do allopatric *T. lineatus* or *T. gariensis* ( $G$ -tests,  $P$ 's < .001).

In all but one case (Table 6), *T. gariensis* has greater dietary overlap with allopatric *T. lineatus* than with sympatric *T. lineatus*, demonstrating dietary displacement by *T. lineatus*. The reductions in dietary overlap by prey taxa for female and immature *T. lineatus* range from 12.2% to 24.9% ( $N = 4$ ,  $\bar{x} = 18.8\%$ ), but only 0.0% to 2.8% for the two male comparisons. Reductions in dietary overlap by prey size for females and immatures range from 6.3% to 17.7% ( $\bar{x} = 12.7\%$ ), and for males 5.8% to 12.1%. The discrepancy for males arises because males change dietary utilization primarily within a species (*Allodotermes*), rather than between prey species, so only prey size overlaps are displaced.

#### DISCUSSION

After summarizing ecological differences and shifts in these two species of *Typhlosaurus*, we speculate on apparent reproductive shifts in the context of  $r$ - and  $K$ -selection (MacArthur and Wilson 1967, Pianka 1970, 1972) and evaluate the possibility of divergent character displacement by sympatric *T. lineatus* (Grant 1972).

We considered three aspects of the use of space by *Typhlosaurus*: macrogeographic distributions, microgeographic distributions in sympatry, and microhabitats in allopatry and sympatry. *Typhlosaurus lineatus* occur both in the sandridge and flatland geographic provinces of the Kalahari, in dune streets and on sandridges microgeographically in sympatry, and primarily under log and leaf litter microhabitats. *Typhlosaurus gariensis* occur only in sandridge areas geographically, on sandridges microgeographically, and primarily in the basal roots of bunch grass microhabitats. The low overlap in the use of space because of these differences could result directly from interference competition for space (terminology of Park 1962), indirectly from exploitative competition for food, or directly from

morphological or behavioral adaptations of the two species to different subsand environments. Exploitative competition is an unlikely explanation since prey taxa differences between the lizards are chiefly independent of microhabitats. Discrimination between the two other alternatives is impossible; indeed, they are not necessarily mutually exclusive.

Reproductive outputs of *Typhlosaurus* per individual per year are extremely low, the lowest of any known lizard (c.f. Tinkle et al. 1970). Female *T. lineatus* are at least 2 and possibly 3 yr old when their first young are born. Litter size of *T. gariensis* is always 1, and about 1.5 to 1.7 in *T. lineatus*. Both species produce only one brood per year. Moreover, the average expenditures per progeny by females (about 10% for *T. lineatus* and 17% for *T. gariensis*) are the highest of any of 73 species of lizards in 10 families examined by Pianka (*in prep.*) suggesting that juvenile *Typhlosaurus* encounter keen competition soon after birth (Pianka 1972).

These reproductive characteristics plus certain others (high densities, presumably near saturation; long lives; and the stability of a subsand existence) all suggest that *Typhlosaurus* are strongly  $K$ -selected (correlates of  $K$ -selection in Pianka 1970). Indeed, comparisons with data of Tinkle et al. (1970) and our own subjective comparisons with lizards from desert systems of North America, Australia, Peru, and Africa lead us to conclude that *Typhlosaurus* are probably the most  $K$ -selected lizards yet studied.

Because sympatric *T. lineatus* experience inter-specific competition from *T. gariensis*, greater  $K$ -selection may ensue and lead to reduced expenditures of energy on reproduction but more energy for factors related to competition. Our evidence, though neither precise nor conclusive, suggests that sympatric *T. lineatus* do indeed produce fewer young per female per year than do allopatric *T. lineatus*. How is the expected additional energy utilized? The significantly greater weight of embryos and young of sympatric *T. lineatus* suggests that at least part of this energy is channeled into increased energy investment per progeny, as is also the case in the semiarboreal Kalahari skink, *Mabuya punctitissimus spilogaster*.

The reduced reproductive output of sympatric *T. lineatus* could, however, also be due to short-term competition with *T. gariensis* or to a lower absolute abundance of food in sympatry. Should either reduce the availability of food resources, an accompanying decrease in energy for all energy demands, including reproduction, would ensue. The greater weight of embryos and young of sympatric *T. lineatus* is, however, inconsistent with this hypothesis. Nonetheless, demonstration of increased  $K$ -selection

would require that available energy resources be identical or, in experimental conditions, that reduced reproductive frequency is genetic and not phenotypic. Our data are thus inconclusive, but they are consistent with theoretical predictions.

Character displacement (Brown and Wilson 1956) has recently been redefined (Grant 1972) as the process by which a "... character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively." Two basic types of divergent (as opposed to convergent) character displacement exist: (1) displacement in morphology or behavior related to species recognition which enforces reproductive isolation and (2) displacement in morphology or behavior related to food acquisition which reduces ecological overlap. The latter can be subdivided into displacements of characters directly related to food capture (for example, head size affecting prey size) or to those related to foraging method or place of foraging (for example, a displacement in leg length affecting foraging speed). For animals like lizards and fish where size of clutch or young is a function of body size, displacement in size might also require changes in reproductive tactics.

While character displacement is an intuitively appealing concept, biologists have for a variety of reasons had difficulty finding concrete field examples (Grant 1972). First, displacement probably occurs less frequently than originally thought (MacArthur and Wilson 1967). Second, falsification of all but one of the possible causes of displacement is usually difficult or impossible (Schoener 1969) and often neglected. Third, character displacement has been invoked in the absence of substantive and correlative data (Grant 1972, Selander 1971).

Are the observed character shifts in body and head size of sympatric *T. lineatus* legitimate examples of character displacement reducing dietary overlap? To answer this question, we first consider alternative hypotheses and their correlative evidence—recalling, however, that the morphological data show an apparent stepfunction change in SVL of *T. lineatus* between allopatry and sympatry (Fig. 2); thus, these changes are not merely representative of a clinal trend (Grant 1972). Also, not only are SVL's larger in sympatry, but heads are proportionately longer as well.

The character shifts probably are not related to differences in habitats between allopatry (flatland desert) and sympatry (dunes), because the major habitat change is that flatland sands are more compact (Leistner 1967), and longer lengths would seem to be more advantageous in allopatry to increase propulsive forces for locomotion.

Neither, probably, are the character shifts related to altered reproductive tactics, since litter sizes between allopatry and sympatry do not differ significantly. Larger size might permit females to increase progeny size in response to *K*-selection. However, altered reproductive tactics do not account for shifts in head proportions, male SVL's, or diet.

It is unlikely that the character shifts are simply indicative of an older average age of sympatric *T. lineatus* as a result of *K*-selection (P. R. Grant, *personal communication*). If only the mean sizes were shifted because of predominantly older ages, some allopatric *T. lineatus* should be as large as the largest sympatric *T. lineatus*. However, the largest male and female in allopatry are considerably shorter than their counterparts in the two sympatric populations (male 9 and 12 mm shorter; female 10 and 11 mm shorter). Additionally, this hypothesis does not account for shifts in head proportions or diet.

The character shifts cannot be related to maintaining reproductive isolation (reproductive character displacement). SVL's overlap broadly (16 mm between male *T. lineatus* and *T. garipeensis*, 17 mm between females) so some hybridization would result if *Typhlosaurus* recognized conspecific individuals using body length alone. However, neither Broadley (1968) nor we found any evidence of hybridization. Also, we believe that fossorial lizards rely more on chemoreception than on size for species and sexual recognition.

Finally, then, we must consider whether character shifts are related to reducing ecological overlap in diet (ecological character displacement). The morphological shifts themselves (Fig. 2, Table 1), particularly the proportional changes in head length (Table 2), are consistent with and suggestive of this hypothesis. Moreover, the parallel changes in prey size (Fig. 6) of *T. lineatus* plus the reductions in dietary overlap (both taxa and size) provide strong correlative support, at least for females and immatures.

There are complications, however. First, different size and sex classes within a population overlap more in prey taxa or size (Table 6) than do similar size or sex classes between populations. Behavior thus overrides purely mechanical considerations in prey selection, suggesting both that behavioral character displacement preceded morphological displacement in the evolution of dietary patterns of *Typhlosaurus*, and that morphology displaced only to reduce the resultant mechanical disadvantages of eating larger prey. Second, while female, male, and immature *T. lineatus* eat larger prey in sympatry and thus overlap less in prey size with *T. garipeensis*, dietary shifts, when analyzed by prey taxa, are not substantial for males. Our correlative data, therefore, support the

hypothesis of behavioral and morphological character displacement reducing dietary overlap for females and immatures only.

A recent discussion of exceptions to the notion that there can be no more species in a habitat than the kinds of resources on which they depend may be relevant. Haigh and Maynard Smith (1972) argue that the roots and leaves of the same tree can be regarded as different resources to herbivores. By analogy, different castes ( $x_1$  and  $x_2$ ) of the same species of termite might serve as two separate resources: ". . . if  $x_1$  is functionally dependent on  $x_2$ , so that a knowledge of one value at any time specifies the other, then they are the same resource, but . . . otherwise they can act as different resources, even if they are highly correlated" (Haigh and Maynard Smith 1972). The shift from minor to major workers of *Allodotermites* by male *T. lineatus* in sympatry may thus indeed reduce competition and enforce isolation in consonance with the hypothesis of ecological character displacement.

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