Ecological Character Displacement in a Lizard

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SYNOPSIS. Two species of subterranean skinks (*Typhlosaurus*) are sympatric in part of the southern Kalahari Desert. The geographic range of the smaller species (*T. gariepensis*) is entirely included within that of the larger one (*T. lineatus*). Snout-vent lengths, head dimensions, proportional head lengths, and prey size of *T. lineatus* are larger in sympatry than in allopatry. Morphological and dietary evidence support the hypothesis that behavioral and morphological character displacement has occurred in female and immature *T. lineatus*, which reduces dietary overlap with *T. gariepensis*. Dietary data for male *T. lineatus* may be conflicting.

Character displacement has been a powerful contributor to ecological and evolutionary theory as a process for reinforcing reproductive and ecological isolation between species (Brown and Wilson, 1956; MacArthur and Levins, 1967; Schoener, 1969). We here discuss a probable case of character displacement in a legless, sand-swimming lizard (Scincidae: *Typhlosaurus*) from the Kalahari Desert of southern Africa. Our analysis supports the hypothesis that observed morphological and behavioral shifts reduce dietary overlap between the two species.

Typhlosaurus are almost completely sub-

terranean, 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.

Leistner (1967) describes the topography, climate, and vegetation of the southern Kalahari. 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 normally restricted to dune slopes, while smaller shrubs occur in interdunal valleys (streets).

Details of morphology, growth and reproduction, diet, and general natural history of these lizards were presented by Huey et al. (1974). Where appropriate we cite this previous publication here to minimize duplication.
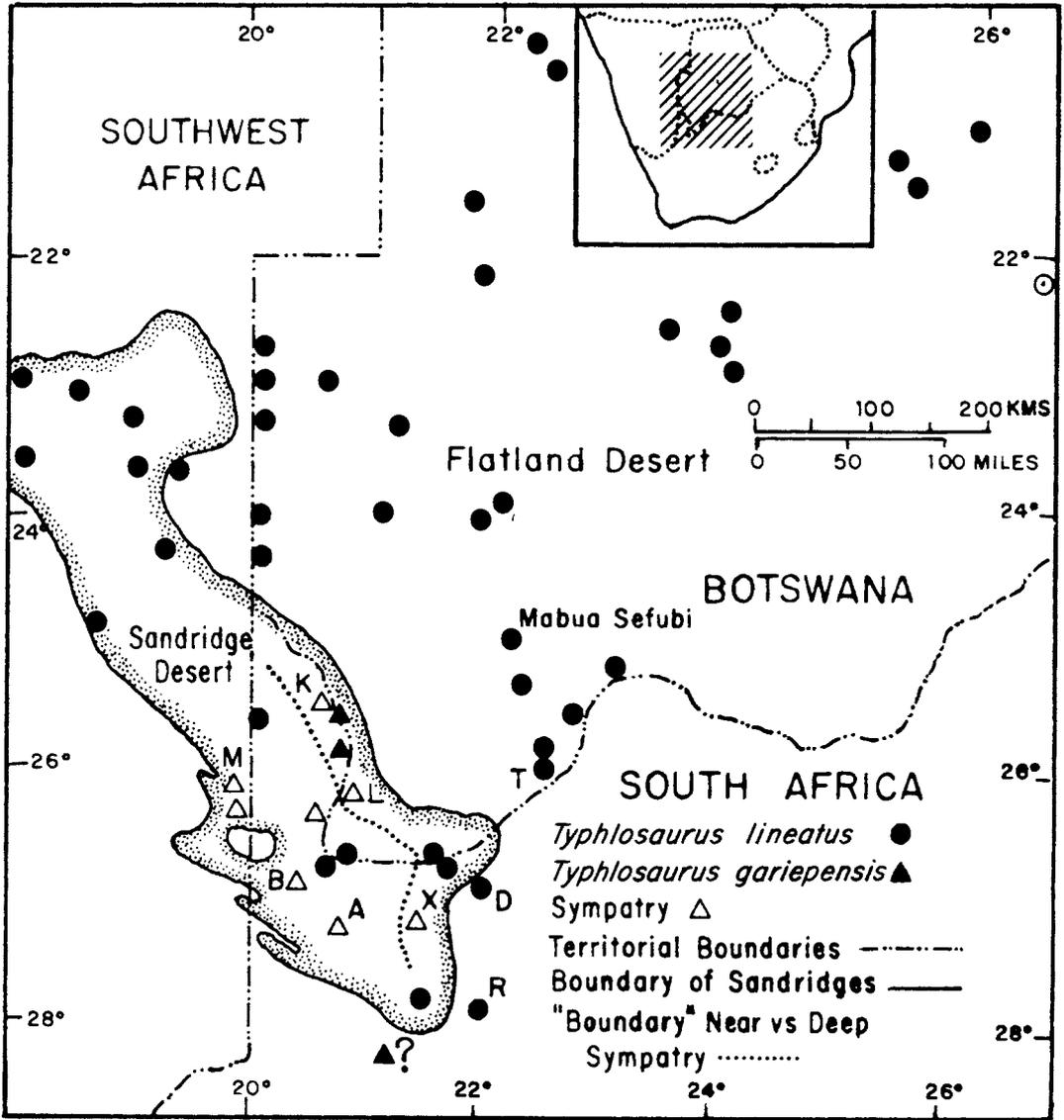
FIG 1. Map showing approximate localities of collection of *T. lineatus* and *T. gariepensis* in the Kalahari Desert. (There are a few extralimital records of *T. lineatus;* Broadley, 1968). They are sympatric on at least 8 sites within the dune region (outlined by line and stippling). Study areas indicated by letters. The type locality of *T. gariepensis*, indicated with a question mark, is probably in error (Huey et al., 1974).

METHODS

We collected over 450 *T. lineatus* and over 100 *T. gariepensis* by digging under various cover objects on nine study areas and several additional localities from December 1969 through October 1970. Six study sites lie within the dune region as delineated by Leistner (1967); three others 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, 1973, 1975). Details on methods of taking body and head measurements, reproductive condition, prey vol-

ume, and prey taxa are given in Huey et al. (1974). Here we use the following formula to calculate overlap:

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

where $p_{x,i}$ is the proportional utilization by species x of the ith resource category (Schoener, 1968, discusses this overlap measure).

RESULTS

Geographic distributions

Known localities of *T. lineatus* and *T. gariepensis* are plotted in Figure 1 (data from Broadley, 1968; Haacke, 1970; Huey et al., 1974). *Typhlosaurus lineatus* is more widespread, occurring on Kalahari sands both in sandridge (outlined by stippling) and flatland areas, whereas *T. gariepensis* is restricted to sandridge areas (see Huey et al., 1974). Thus, the geographic range of *T. gariepensis* is entirely included within that of *T. lineatus*. We established actual sympatry on eight localities in sandridge areas of Botswana, South Africa, and Southwest Africa.

Microgeographic distribution in sympatry

We recognize four microgeographic subdivisions in sandridge areas, where *T. lineatus* and *T. gariepensis* are sympatric: street, dune base, dune slope, and dune crest. *Typhlosaurus lineatus* occur predominantly on dunes, but can also be found in interdunal streets (see Table 3 of Huey et al., 1974), whereas *T. gariepensis* is almost exclusively restricted to sandridges proper. Microgeographic distributions of the two species differ significantly in sympatry (G-test, $P < .001$) and neatly mirror their overall geographic distributions.

Microhabitat

Microhabitat associations among adult males, adult females, and immatures do not differ significantly for allopatric *T. lineatus*,

TABLE 1. *Microhabitat associations of* Typhlosaurus.

Microhabitat	Allopatric T. lineatus %	Sympatric T. lineatus %	T. gariepensis %
Leaf litter	64.8	42.8	3.2
Logs	22.4	19.7	6.4
Crotalaria	6.4	20.6	18.4
Bunch grasses	0.0 [a]	16.1	72.0
Miscellaneous	6.4	0.6	0.0
Sample size	125	329	125

[a] Microhabitat utilization on the basis of tracks only.

sympatric *T. lineatus*, or *T. gariepensis* (P's > .30). *Typhlosaurus* thus are unlike some nonfossorial lizards in which size and sex classes use different microhabitats (Schoener, 1968; Andrews, 1971).

In sympatry both species can be collected occasionally from under the same object. Nonetheless, they differ significantly (G-test, $P < .001$) in proportional microhabitat associations (Table 1, data on males, females and immatures pooled): *T. lineatus* are found chiefly in sand beneath logs and leaf litter of large shrubs and trees (*Acacia* spp. *Boscia* spp., *Grewia* spp.), whereas *T. gariepensis* associate predominantly with bunch grass stools. Allopatric and sympatric *T. lineatus* also differ significantly in microhabitats ($P < .001$), but this probably reflects only the greater variety of microhabitats available and examined in sandridge habitats (*Crotalaria* and bunch grass stools were rare in allopatry).

Morphological character displacement

Typhlosaurus lineatus and *T. gariepensis* differ considerably in snout-vent length (Table 2). Sympatric *T. lineatus* of both sexes are significantly longer (t-tests, P's < .001) than adult *T. gariepensis*. *T. lineatus* also have longer maximal SVL's (167 versus 140 mm in *T. gariepensis*).

Data on allopatric *T. lineatus* were divided into two populations (Fig. 1): one is far from sympatry (vicinity of Mabua Sefubi pan) while the other is near sympatry (T+D+R). Sympatric *T. lineatus* were divided into two populations: deep sympatry (M+B+A+others) and shallow

TABLE 2. *Snout-vent length statistics (mm) of adult* Typhlosaurus.

| Species | Males | | Females | |
	$\overline{X} \pm$ SE	n	$\overline{X} \pm$ SE	n
Allopatric *T. lineatus*				
vic. Mubua Sefubi Pan	130.5 ± 0.64	133	137.3 ± 0.75	93
T + D + R	130.3 ± 1.47	33	136.9 ± 1.52	35
Sympatric *T. lineatus*				
K + L + X + others	135.6 ± 1.16	75	141.6 ± 0.89	100
M + B + A + others	136.1 ± 1.81	23	144.0 ± 1.87	35
T. gariepensis (all)	116.1 ± 0.78	37	122.9 ± 0.77	35

Allopatric *T. lineatus* are subdivided by distance from sympatry; vicinity 14 mi N Mabua Sefubi Pan, Botswana is far from sympatry (about 150 km); T + D + R are study areas (Fig. 1) and are near sympatry (about 50 km). Sympatric *T. lineatus* are similarly divided into two populations: K + L + X and others are near allopatry (about 50 km) and M + B + A and others are in deep sympatry (about 115 km). $\overline{X} \pm$ SE = mean ± standard error of mean and n = sample size (number of lizards).

sympatry (K + L + X + others). Paired comparisons within sex classes (Table 2) show no significant differences (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 allopatric populations (P's < .01; see also Fig. 2 of Huey et al., 1974). Thus, *T. lineatus* exhibit a step-wise shift (rather than a clinal shift) to longer SVL's where sympatric with the smaller *T. gariepensis*. Because *T. gariepensis* is always sympatric with *T. lineatus*, reciprocity cannot be observed directly. However, *T. gariepensis* is the smallest of the eight species of *Typhlosaurus*, suggesting that its small size might reflect historical interaction with *T. lineatus* (Broadley, 1968).

Populations of adult sympatric *T. lineatus* have much longer heads than do adult *T. gariepensis* (Table 3). The two sympatric populations do not differ significantly (either sex class) in head length, but both have significantly longer heads (P's < .01) than do allopatric *T. lineatus* (we measured only the near allopatry specimens).

Head widths are also significantly greater in sympatric than in allopatric *T. lineatus* (see Table 1 of Huey et al., 1974).

Despite the fact that females have significantly longer SVL's (P's < .001) than males (Table 3) for all populations of *Typhlosaurus*, females and males do not differ significantly in head lengths (Table 3; P's > .10). Thus, males have proportionally longer heads than females.

Shifts in mean head sizes could be simple correlates of the larger SVL's of sympatric *T. lineatus*. To determine whether heads were proportionally longer and wider in sympatry, we computed linear regressions for head proportions of adult males and of adult females for allopatric *T. lineatus*, sympatric *T. lineatus*, and *T. gariepensis* (Table 4; see also head width regressions in Table 2 of Huey et al., 1974). At any trunk or snout-vent length, scatter diagrams between sympatric *T. lineatus* and *T. gariepensis* do not overlap in either head length or head width: *T. lineatus* always have longer and wider heads. In comparisons of regressions of head length on trunk length between allopatric and sympatric *T.*

TABLE 3. *Head lengths of adult* Typhlosaurus.

| | Males | | Females | |
	n	$\overline{X} \pm$ SE	n	$\overline{X} \pm$ SE
T. gariepensis	25	3.88 ± .027	27	3.87 ± .0328
T. lineatus				
near allopatry	35	5.49 ± .053	31	5.52 ± .041
near sympatry	58	5.73 ± .0467	73	5.72 ± .031
deep sympatry	26	5.75 ± .049	33	5.815 ± .048

n = sample size, $\overline{X}$ = mean, SE = standard error of mean.

TABLE 4. *Linear regressions of head length (HL) on trunk length (TL), by sex, for various populations of Typhlosaurus. Parentheses after the regression coefficients enclose one standard error for that coefficient.*

Males
    Allopatric *T. lineatus* (n = 33)
        HL = 2.068 (±.078) + .0275 (±.0006)TL
    Sympatric *T. lineatus* (n = 81)
        HL = 2.035 (±.029) + .0287 (±.0002)TL
    T. gariepensis (n = 25)
        HL = 2.481 (±.098) + .0125 (±.0008)TL
Females
    Allopatric *T. lineatus* (n = 36)
        HL = 2.842 (±.057) + .0203 (±.0004)TL
    Sympatric *T. lineatus* (n = 116)
        HL = 2.627 (±.017) + .0230 (±.0001)TL
    T. gariepensis (n = 30)
        HL = 2.298 (±.081) + .0133 (±.0007)TL

lineatus, variances around the lines are the same, the slopes are parallel, but the lines are not coincident (analysis of covariance: males $P < .01$, females $P < .001$). Therefore, head lengths of both male and female *T. lineatus* are proportionally longer in sympatry. Overall, sympatric *T. lineatus* exhibit morphological character shifts away from *T. gariepensis* in SVL, head dimensions (length and width), and proportional head lengths.

Prey size

Size distributions of prey from intestines of *Typhlosaurus* (Fig. 2) show that *T. gariepensis* of any age or sex class take significantly smaller prey than any corresponding class of either population of sympatric *T. lineatus* (χ^2-tests, $P < .001$) or than allopatric *T. lineatus* ($P < .001$). Interestingly, classes of both populations of sympatric *T. lineatus* eat significantly larger prey ($P < .001$) than do allopatric *T. lineatus*. This shift to larger prey by sympatric *T. lineatus* reduces overlap in prey size with *T. gariepensis* by an average of 12.1% (range 5.8 to 17.7%) for comparisons among males, females, or immatures.

Prey taxa

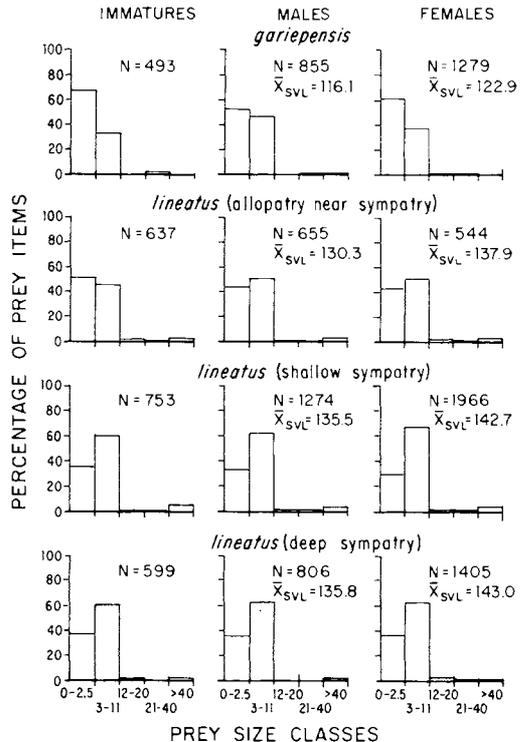Most lizard species eat a wide variety of prey taxa. Determination of prey items at

FIG. 2. Percentages of prey items in each of three prey size (volume) categories [S = small (0-2.5 μl), M = medium (3-11 μl), and 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 allopatric *T. lineatus*.

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 rich (Coaton, 1963; Pianka, 1973, 1975), this methodology could conceal dietary differences and shifts. Hence, all isopterans were identified to distinct morphological types (species or castes). Other prey items were identified only to order or family.

Typhlosaurus eat at least ten species of termites but concentrate on only three species (Table 5): major and minor workers of *Allodontermes schultzei* (?), soldiers and workers of *Psammotermes allocerus*, and *Hodotermes mossambicus*. These three termites alone account for 93% to 96% of all prey items taken by *Typhlosaurus* (both

TABLE 5. *Percentage of prey items by number from intestinal contents of 117 allopatric T. lineatus, 324 sympatric T. lineatus, and 108 T. gariepensis. Data separated for males, females, and immatures within populations. Total number of prey at bottom.*

	Allopatric T. lineatus				Sympatric T. lineatus				T. gariepensis			
	Females	Imm.	Males	All	Females	Imm.	Males	All	Females	Imm.	Males	All
Psammotermes allocerus												
workers	20.1	16.8	7.7	14.2	2.8	4.4	8.2	4.8	35.2	39.7	25.1	32.8
soldiers	2.0	2.3	1.8	2.1	1.9	1.4	1.3	1.6	5.0	6.7	3.9	4.9
Allodontermes schultzei												
minor workers	28.0	31.7	34.4	31.8	28.5	29.0	25.0	27.6	23.7	25.3	24.4	24.2
major workers	34.3	42.1	46.2	41.7	62.0	54.1	59.8	59.7	29.9	24.7	42.2	33.0
Hodotermes mossambicus	4.3	1.9	3.0	2.9	1.4	2.9	2.5	2.0	—	—	0.2	0.1
Other termites and other prey	11.3	5.2	6.8	7.3	3.4	8.2	3.1	4.3	6.1	3.6	4.2	5.0
TOTAL NUMBER OF PREY	443	637	660	1740	3369	1393	2097	6859	1280	494	857	2631

lizards also occasionally eat spiders, ants, beetles, and insect larvae). Nests of all three species of termites are subterranean (Coaton, 1963). *Allodontermes* minor workers and *Psammotermes* workers are small (about 2 microliters), *Psammotermes* soldiers and major workers of *Allodontermes* are slightly larger (about 4 microliters), while *Hodotermes* are very large (about 60 microliters).

Allodontermes major workers are the chief food of both species. However, *T. gariepensis* (males, females or 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 (near and deep sympatry). Sympatric *T. lineatus* eat fewer *Psammotermes* workers than allopatric *T. lineatus* (females and immatures, P's $< .001$; but not males P's $> .40$) but more *Allodontermes* major workers (females, males, and immatures, P's $< .001$).

In an attempt to determine whether dietary differences result from gross differences in microhabitat associations or from active prey selection, we also summarized termites eaten by microhabitat site. 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 major termite types (data in Table 7 of Huey et al., 1974), occur in the intestines of *Typhlosaurus* from all four microhabitats (under logs, leaf litter, *Crotalaria*, and bunch grasses), but in different proportions primarily between species and populations rather than between microhabitats. For example, *T. gariepensis* 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 $< .001$) *Allodontermes* major workers than did sympatric *T. lineatus*. Sympatric *T. lineatus*, but not *T. gariepensis*, ate *Hodotermes* in all four microhabitats. Overall patterns described above thus hold within microhabitats, sug-

gesting that dietary differences are largely independent of microhabitats, which helps to justify treatment of food and place as separate niche dimensions (Pianka, 1973, 1975). Active prey selection may occur; nonetheless, subtle differences in use of space or time of activity cannot be discounted.

Knowing prey taxa we can determine proximate reasons for differences in prey sizes previously described. Sympatric *T. lineatus* (females, immatures, and males) take larger prey than *T. gariepensis* because the former eat fewer *Psammotermes* workers (a small termite) and relatively more *Allodontermes* major workers (medium sized) and *Hodotermes* (large). Sympatric *T. lineatus* (females and immatures) take larger prey than allopatric *T. lineatus* because they eat fewer *Psammotermes* workers and relatively more *Allodontermes* major workers. Male sympatric *T. lineatus* also take larger prey, but do so only by taking more *Allodontermes* major workers, not by eating fewer *Psammotermes* workers (they eat fewer *Allodontermes* minor workers).

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. gariepensis* also finds substantial numbers of *Psammotermes*. Likewise, the increased number of *Allodontermes* 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 *Allodontermes* taken, we found that allopatric *T. lineatus* (males, females, and immatures lumped) eat 1:1.3 minor to major workers, *T. gariepensis* eat 1:1.4, and sympatric *T. lineatus* 1:2.1. Thus, sympatric *T. lineatus* appear to eat selectively more *Allodontermes* major workers than allopatric *T. lineatus* or *T. gariepensis* (G-tests, *P*'s < .001).

In all but one case (see Table 6 of Huey et al., 1974), *T. gariepensis* had greater dietary overlap with allopatric *T. lineatus* than with sympatric *T. lineatus,* demonstrating dietary displacement of *T. lineatus.* 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 from 5.8% to 12.1%. The discrepancy for males arises because males change dietary utilization primarily within a termite species (*Allodontermes*), rather than between prey species, so that only prey size overlaps are displaced.

DISCUSSION

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: (i) displacement in morphology or behavior related to species recognition which enforces reproductive isolation and (ii) displacement in morphology or behavior related to food acquisition which reduces ecological overlap. The latter can be subdivided into displacement 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, 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 involve changes in reproductive tactics.

While character displacement is intuitively appealing, biologists have 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 (Selander, 1971; Grant, 1972).

Are observed character shifts in body and head size of sympatric *T. lineatus* examples of character displacement reducing dietary overlap? To answer this question, we consider alternative hypotheses and their correlative evidence—recalling first that the morphological data show an apparent step-function change in SVL and head dimensions of *T. lineatus* between allopatry and sympatry (Tables 2 and 3); thus, these changes do not represent merely a clinal trend (Grant, 1972). Moreover, because the allopatric zone of *T. lineatus* is extensive (Fig. 1), allopatry probably preceded sympatry: thus *T. lineatus* in allopatry can serve as "controls" for comparison with conspecifics in sympatry (Grant, 1972, p. 44). (There is no "control" area for *T. gariepensis* since its geographic range is entirely included within that of *T. lineatus*.) Finally, note that *T. lineatus* show lower reproductive output (i.e., fewer young per female per year; see Huey et al., 1974) in sympatry than in allopatry, suggesting that competition may indeed be an important selective agent on *T. lineatus*.

Character shifts of *T. lineatus* could be responses, not to *T. gariepensis*, but to differences in the physical environment between allopatry (flatland desert) and sympatry (dunes). This non-competitive, non-reproductive isolation hypothesis, however, seems unlikely since the most obvious habitat change between allopatry and sympatry is that the flatland sands of allopatry are subjectively more compact and longer body lengths for *T. lineatus*, rather than shorter ones, would be more advantageous to increase propulsive forces for locomotion. Nonetheless, we cannot entirely discount this hypothesis.

A potential test might be to examine *T. lineatus* from the northwestern part of the sandridge desert (Fig. 1). If *T. lineatus* is allopatric in this area, snout-vent lengths could be used to distinguish between the influence of sandridge habitats and of *T. gariepensis*. This cannot presently be done because samples are very limited from this area (Broadley, 1968). Moreover, because of its specialized microhabitat, *T. gariepensis* might simply have been overlooked in these

areas (this species was known from only eight specimens prior to our study). Additional collections from this region would clearly be of interest.

Shift in body size might also be related to changes in reproductive tactics. However, litter sizes between allopatric and sympatric *T. lineatus* do not differ significantly (Huey et al., 1974). Nonetheless, weights of embryos of sympatric *T. lineatus* are significantly heavier, suggesting that larger body size of adult females might relate to increasing weight of progeny as a response to greater *K*-selection in sympatry (Pianka, 1970, 1972). However, altered reproductive tactics do not account for shifts in male SVL's, proportional head lengths, or in diets of females, males, and immatures; so this is at best a partial explanation.

Character shifts are unlikely to indicate simply an older average age of sympatric *T. lineatus* as a result of *K*-selection (Grant, personal communication). If only mean sizes 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 (males, 9 and 12 mm shorter; females, 10 and 11 mm shorter). Additionally, this hypothesis does not account for shifts in diet or in proportional head lengths.

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

Finally, are morphological shifts related to reducing overlap in diet (ecological character displacement)? Morphological shifts themselves (Tables 2 and 3), particularly the proportional changes in head length

(Table 4), are consistent with and suggest this hypothesis. Moreover, parallel changes in prey size (Fig. 2) of *T. lineatus* plus reductions in dietary overlap (both prey taxa and prey size) provide strong correlative support at least for females and immatures (males discussed below).

There is an interesting sidelight. First, different size and sex classes within a population have significantly greater dietary overlaps (*P*'s < .001) by prey type ($\overline{X}$ = .887, see Table 6, Huey et al., 1974) or by prey volume ($\overline{X}$ = .938) than interpopulational overlaps ($\overline{X}$ = .727, $\overline{X}$ = .816, respectively). For example, female *T. lineatus* in allopatry overlap much more in prey taxa with immatures (.916) and with males (.833) in allopatry than with females in sympatry (.719). This pattern suggests that behavioral character displacement probably preceded and overrides morphological character displacement in the evolution of dietary pattern of *Typhlosaurus*.

Male data require resolution. While male *T. lineatus* eat significantly larger prey in sympatry (Fig. 2), their overlap in prey taxa with *T. gariepensis* is not reduced. Rather than shifting diet between prey taxa as do females and immatures, males shift diet within a prey taxon (*Allodontermes*). Nonetheless, because overlap in prey taxa between sympatric male *T. lineatus* and all *T. gariepensis* (.700) is essentially the same as that for sympatric immatures and females with *T. gariepensis* (.693), males may not experience relatively greater overlap in diet with *T. gariepensis*.

A recent discussion of exceptions to the notion that there can be no more species in a habitat than kinds of resources on which they depend may be relevant. Haigh and Maynard Smith (1972) argue that 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 separate resources: ". . . if x_1 is functionally dependent on x_2, so that a knowledge of the 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 ratio of minor to major workers of *Allodontermes* in the diets of *Typhlosaurus* is 1:1.3 for male allopatric *T. lineatus*, 1:1.4 for all *T. gariepensis*, and 1:2.4 for sympatric male *T. lineatus*. The shift by *T. lineatus* is highly significant (*G*-test, *P* < .001) and does reduce overlap with *T. gariepensis* when only this species of termite is considered. The shift from minor to major workers of *Allodontermes* by male *T. lineatus* in sympatry could thus indeed reduce competition and enforce isolation in consonance with the hypothesis of ecological character displacement.

FINAL REMARKS

The occurrence of ecological character displacement in a lizard is somewhat surprising. Most lizards are generalists with respect to food type and therefore might well exhibit convergence rather than divergence in sympatry (Schoener, 1969). *Typhlosaurus* could conflict with these theoretical expectations for several reasons. Termites in the Kalahari are an abundant food resource available year round (Coaton, 1963; Pianka, 1973, 1975; Huey et al., 1974); this may have permitted evolution of dietary specialization in *Typhlosaurus* (MacArthur and Pianka, 1966) to an extent unparalleled in insectivorous lizards except for ant-eating *Moloch* and *Phrynosoma* (Pianka and Pianka, 1970; Pianka and Parker, 1975). Indeed divergent character displacement might even be expected because *Typhlosaurus* are so specialized on abundant and predictable foods.

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