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DIET AND ACTIVITY OF *MABUYA ACUTILABRIS* (REPTILIA: SCINCIDAE) IN NAMIBIA

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ABSTRACT

Mabuya acutilabris is a terrestrial African scincid lizard distributed from Little Namaqualand to the mouth of the Zaire (Congo) River. In the central portion of its range (near Kamanjab, Namibia) the species is active in early winter from 09.50 hr to 17.10 hr. These skinks spend much time basking, and 73% of their surface activity occurs within 30 cm of clumps of vegetation where they construct shallow burrows. Single day movements of the skinks are short in both duration and distance, yet long-term movement may be considerable. Density of the species at the study site was at least 106/ha. Across its geographic range *M. acutilabris* is a generalist insectivore, with hemipterans and a variety of insect larvae constituting the most important prey classes.

INTRODUCTION

Scincid lizards of the genus *Mabuya* comprise one of the most diverse elements in the saurian fauna of the Pronamib and northern Namibian savanna. Eleven species have been recorded from the region of the Great Escarpment near the Damaraland/Outjo District boundary in northern Namibia (Bauer, Branch & Haacke, in press). In addition to many species of "typical" skinks, at least two highly morphologically-specialized species occur. One of these, *Mabuya acutilabris*, is a terrestrial psammophile and bears a striking resemblance to a number of the sympatric species of lacertids. Like many other psammophiles, *M. acutilabris* has a flattened snout with a sharp, shovel-like upper lip and a partially counter-sunk jaw, attributes typically associated with sand burrowing (Pough, 1970).

Mabuya acutilabris ranges from Little Namaqualand in the northern Cape Province, South Africa, through Namibia and Angola to southern Zaire (Fig. 1). Throughout most of its range it occupies sandy habitats in desert and semi-desert (Mertens, 1937, 1955; FitzSimons, 1943; Hellmich, 1957; Poynton & Broadley, 1978; Branch, 1988), although in Zaire it occupies beach habitats and perhaps suitably sandy alluvial deposits (Schmidt, 1919) and in parts of Angola it may be found under fallen needles in coniferous forest (Laurent, 1954). Although *M. acutilabris* is broadly distributed and occurs in high densities, natural history data for the species has been limited to only a few comments in more general works (Schmidt, 1919; FitzSimons, 1943; Mertens, 1955; Branch, 1988). The goal of the present study was to establish base-line information on diet and activity of *Mabuya acutilabris* which might be applicable to broader studies of Namibian lizard ecology. The community relationships of this skink to sympatric scincids and lacertids are addressed elsewhere (Castanzo, 1991).

MATERIALS AND METHODS

FIELD STUDY

Data were collected over a six-week period during the dry, winter season (May-June) of 1990 near the village of Kamanjab, in the western Outjo District of northwestern Namibia (Fig. 1). The study site consisted of a 220 m section of a dry river bed (a small tributary of the Okatembo River) on Farm Franken. Lizard density appeared somewhat lower at this site than in surrounding areas, but the sparse vegetation of the river bed facilitated observation. Unusually heavy (405 mm vs. 300 mm rain/year average; Bauer *et al.*, in press) and late rainfall in 1989-90 supported relatively lush grass cover over much of the surrounding area well into the winter.

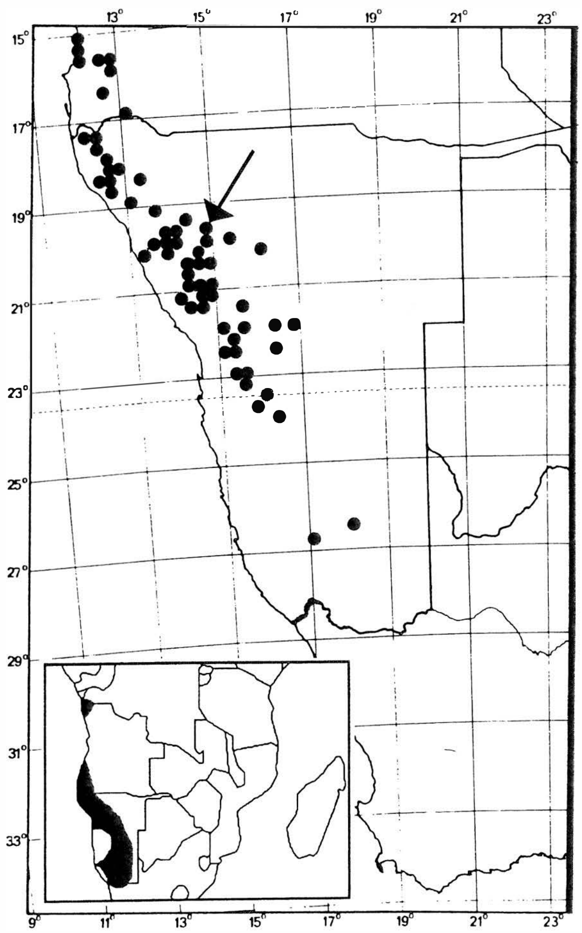

Fig. 1. Localities of specimens of *Mabuya acutilabris* examined in this study. The Kamanjab field site is indicated by the arrow. Inset map of Africa south of the equator shows the entire distributional range of the species. The disjunction between the northern and southern portions of the range may be a collecting artifact. If present in central Angola, *M. acutilabris* would be expected to occur in sandy coastal areas.

The river bed had dry, sandy soil that supported only a few plant species. The two dominant grass species were *Stipagrostis hirtigluma*, found in discrete clumps in the river bed, and *Cenchrus ciliaris*. Shrubs of several species of the Chenopodiaceae were also found in the river bed. The only reptiles otherthan *Mabuya acutilabris* that were observed in the study area were the lacertid species *Heliobolus lugubris* and *Pedioplanis undata*.

Other reptile species occurring in adjacent habitats on Farm Franken have been reported elsewhere (Bauer *et al.*, in press). Castanzo (1991) provided a list of potential predators present at the site. Environmental temperatures were measured hourly with a Fisher thermometer at 2 cm below the soil surface and 1 cm and 1.5 m above the substrate.

Lizards were observed for a total of 140 hr on 22 days during the study period. During this period 535 min of timed observations of behaviours exhibited and microhabitats utilized by individual lizards were recorded (mean $\pm$ SD=11.6 $\pm$ 2.2 min, n=46) using the focal-animal method (Altmann, 1974). Parameters recorded were: basking activity, distance moved, feeding behaviour, and escape behaviour (from humans, associated with collection for marking purposes). Microhabitat use data were placed into following categories: shrub/tuft, grass, and open. Time spent in each of these was further categorized into time spent in the sun and shade.

After data were collected for an individual for the first time, the lizard was captured, measured and marked uniquely by indelible paint pen markings and by toe clipping. Sighting and capture sites were determined relative to a marking grid of surveyors flags and plotted on a map of the study area. Lizards were always released at the point of the original sighting.

DIET

Specimens for dietary analyses were obtained from California Academy of Science, San Francisco (CAS), Field Museum of Natural History, Chicago (FMNH), Museum of Comparative Zoology, Cambridge (MCZ), Los Angeles County Museum of Natural History (LACM), Transvaal Museum, Pretoria (TM), and State Museum of Namibia, Windhoek (SMW). They included 174 individuals from 62 localities (Fig. 1), primarily from the central and southern portions of the species range. Specimens from the far north of the range, which seem to differ in at least some aspects of their ecology (Schmidt, 1919; Laurent, 1954), were not included in the study.

Stomach contents were removed and stored in 70% ethanol. Prey items were identified under a dissecting microscope and placed into food resource categories, chiefly those used by Pianka (1986). Percent of each prey type (by both item number and volume) were calculated. Volume was determined by measuring length (l) and width (w) of each item to the nearest 0.1 mm and approximating the prey body as a cylinder (Barbault & Maury, 1981). Body parts and partially digested material not associated with identifiable prey bodies (along with unidentified material) were recorded but excluded from dietary profiles (Huey *et al.*, 1974). Dietary niche breadth was determined using Shannon's Diversity Index (Pianka, 1966). Dietary niche overlap was calculated using Pianka's competition coefficient (Pianka, 1973). Because samples were obtained from many localities and during all seasons, no attempt was made to assess selectivity in diet. Statistical tests were performed primarily using Systat (Wilkinson, 1988).

RESULTS

DAILY TEMPERATURES AND ACTIVITY

Daily temperature changes of the soil and of the air at 1 cm and 1.5 m are shown in Fig. 2. No linear change in average daytime temperature occurred over the course of the study (Pearson correlation, $P \leq 0.05$). Although no recordings were made outside of the period of lizard activity, night temperatures appeared to be typical for early winter, and approached freezing on several occasions.

Mabuya acutilabris was active from 09.50 hr to 17.10 hr. Lizard surface activity commenced approximately 2 hours after sun-up. Although sundown was not until approximately 18.30 hr, the river bed was almost entirely shaded by 17.30 hr, at which time lizard activity ceased. Soil temperature averaged 20.0°C at 09.50 hr (time of emergence from burrows) and the air temperature at 1 cm was 29.1 °C at 17.10 hr (time of retreat to burrows).

Unless approached by the observer or otherwise threatened, lizards remained above ground for most of their activity period. While surface active, *Mabuya acutilabris* spent the majority of their time (73%) within 30 cm of shrubs or tufts of grass (44.2% in shade, 28.8% in sun). The burrows of this species are made in the roots of these plants and serve as retreats for the lizards when they are threatened or otherwise stressed. Tufts were also used as hiding places from which lizards darted to capture prey. Four predation attempts by the lizards, as well as numerous putative prey investigatory movements, were observed during the study. In all cases lizards moved < 1 m from vegetation to capture prey. Only 19.7% and 7.3% (5.9% in sun, 1.4% in shade) of monitored activity periods were spent in open areas and sparse (unclumped) grass, respectively.

Basking was frequently observed in all types of sites used by *M. acutilabris* and occurred at all times of day, but especially during the early morning and late afternoon. Basking lizards faced away from the sun, assuming a stereotyped partially-elevated posture. Morning basking, which began immediately following emergence, lasted as long as 43 min, although periods of complete immobility rarely exceeded 10 min. Afternoon basking lasted as long as 1.5 hr, and was often characterized by a raising of the forebody and tilting of the head, again with the dorsum exposed to the sun.

LIZARD MOVEMENT AND DENSITY

Quantification of short-term movements of skinks was based on 535 mins of focal-animal observation, representing 46 observational sessions. *Mabuya acutilabris* were found to travel 0.54$\pm$0.13 m/movement at a rate of 0.29$\pm$0.04 moves/min or 0.16$\pm$0.05 m/min (means$\pm$SD). Minimal estimates of movements of lizards over the study period were derived from multiple sightings of individuals. Twenty-five individuals were observed in more than one focal-animal session. The period of time over which any individual lizard was monitored varied from 1 to 22 days (Table 1). The greatest distance between any two sightings of the same individual varied between 2 and 80

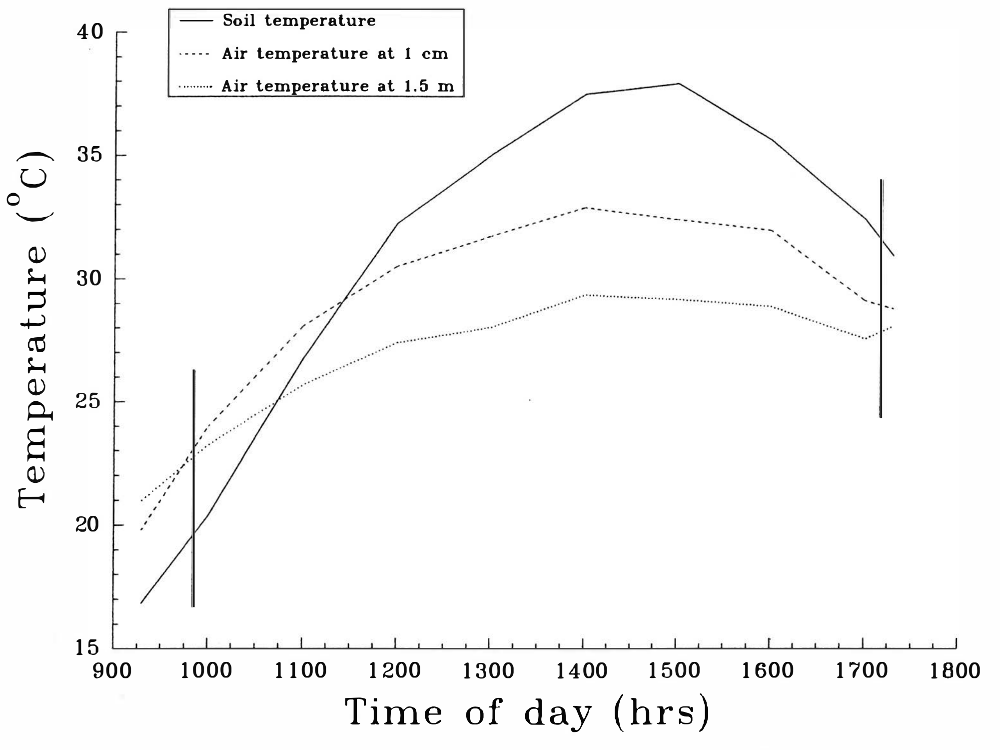

Fig. 2. Temperature (°C) vs. time of day (hrs) at the Kamanjab study site (hourly temperatures averaged over the period 30 May - 22 June, 1990). Mean soil temperature at a depth of 2 cm, air temperature at 1 cm, and air temperature at 1.5 m are given over the activity period of *Mabuya acutilabris* (bracketed with vertical bars).

No. observations	*N*	Max. distance between sightings (metres)	Time between first and last sightings (days)	Max. distance between two consecutive sightings (meters)	Time between maximally distant consecutive sightings (days)	Local lizard abundance (No./10 m radius)
8	1	22.0	22.0	12.0	6.0	2.0
6	4	6.0	20.0	3.0	3.0	6.0
4	6	17.2 (14.6)	17.5 (5.5)	14.8 (12.9)	5.5 (4.6)	5.2 (2.2)*
3	3	20.5 (10.9)	15.3 (9.8)	20.5 (10.9)	5.3 (5.1)	2.0 (1.0)
2	14	21.9 (19.8)	15.1 (8.3)	21.9 (19.8)	15.1 (8.3)	3.3 (2.1)**

TABLE 1. Movement and density of *Mabuya acutilabris* at the Kamanjab study site, based on multiple sightings of marked lizards.SD in parentheses for categories containing more than one individual. * sample size 5; not all individuals were recovered at end of study (see text). ** sample size 12 (see above).

Group	*N*	Total vol. (cm^3)	Iso	Ort	Col	Hem	Hym	Lep	Dip	For	Lar	Egg	Ara	Cru	Pla	Ver
			Food resource category													
All individuals	174	10.3	11.1	12.4	14.1	24.8	7.2	1.4	0.6	1.7	18.2	0.0	7.0	0.2	1.2	0.0.
	(146)	(1009)	(21.8)	(3.7)	(11.4)	(17.4)	(9.3)	(0.8)	(1.0)	(8.7)	(16.4)	(0.3)	(5.7)	(0.6)	(2.7)	(0.3)
Adult males	67	5.3	14.9	16.8	17.1	17.6	4.0	1.7	0.4	1.6	16.7	0.0	9.0	0.0	0.2	0.0
	(54)	(510)	(23.7)	(3.3)	(11.4)	(21.2)	(9.2)	(0.6)	(0.4)	(8.0)	(16.9)	(0.0)	(2.9)	(0.0)	(2.2)	(0.2)
Adult females	63	4.1	8.5	5.3	10.3	38.3	11.2	1.0	0.8	1.7	18.0	0.1	1.7	0.6	2.6	0.0
	(50)	(395)	(24.8)	(3.0)	(11.4)	(14.4)	(10.6)	(1.0)	(1.3)	(10.4)	(10.4)	(0.8)	(6.6)	(1.5)	(3.3)	(0.5)

TABLE 2. Diet of *Mabuya acutilabris*, with prey categories presented by percentage of total volume consumed, and percentage of total no. items consumed (in parentheses). *N*, total no. lizards examined with total no. lizards that contained prey of any kind in parentheses. "All individuals" includes 36 juveniles plus 8 adults in which sex could not be determined due to specimen damage. Iso, Isopoda; Ort, Orthoptera; Col, Coleoptera; Hem, Hemiptera; Hym, Hymenoptera (not including ants); Lep, Lepidoptera; Dip, Diptera; For, Formicidae; Lar, insect larvae; Egg, arthropod eggs; Ara, Arachnida; Cru, Crustacea; Pla, plant matter; Ver, vertebrate material (lizard scales).

m, whereas the greatest distance between consecutive sightings (for animals observed three or more times) ranged from 3 to 38 m.

The last two days of the study period (June 20-21, 1990) were spent collecting all lizards seen on the study site. A total of 54 *Mabuya acutilabris*, four *Heliobolus lugubris*, and four *Pedioplanis undata* were captured, yielding a density of *M. acutilabris* of 106/ha and a total lizard density of 122/ha. These estimates are not based on standard density estimation techniques and are empirically-derived minimal estimates of density. For each site where a lizard was captured during this censusing period, local abundance was recorded as the total number of additional lizards within a 10 m radius (approximately one-half the average distance between consecutive sightings of the same lizard). This value varied from 1 to 8 (Table 1). Both the greatest distance between any two sightings and the distance between consecutive sightings of the same individual were negatively correlated with local lizard density, although not significantly so (Pearson correlations, $P=0.099$ and 0.114 respectively).

Throughout the study period, lizards entered the site from more heavily vegetated areas bordering the river bed. Other individuals disappeared from the site. A total of 41 *M. acutilabris* were marked during the study, of which 23 were recovered on the last two days of collecting. An additional 31 unmarked lizards were also collected during the removal census, yielding a minimum of 72 individuals present on the site sometime during the study period. Thirteen of the 18 marked individuals not recovered were only seen during the first five days of observation. One individual marked on day two of the study was not seen again for 21 days. Losses from the site probably involve both emigration and predation. No predation attempts on *M. acutilabris* were observed, but evidence of digging at likely burrow sites by nocturnal carnivores was seen on several occasions.

DIET

Mabuya acutilabris is predominantly insectivorous, and takes only small percentages of terrestrial isopods and arachnids. Measurable amounts of plant material appear to reflect accidental ingestion associated with insect prey capture, or in some cases may be derived from the rupture of the guts of ingested herbivorous insects. Vertebrate remains consisted solely of scales, probably the animal's own ecdysed skin, and constituted a non-measurable element of the total ingested material examined. For the adult skinks the five most important prey categories accounted for over 80% of the prey consumed by volume and over 70% by prey item number (Table 2). Hemipterans and homopterans as a single combined category comprised the largest single resource category and constituted 24.8% of prey by volume. Other important elements in the diet were termites, orthopterans and insect larvae (18.2% by volume).

Adult males and females consume similar prey (Table 2) and have similar dietary niche breadths (2.009 and 1.876, respectively). Some sexual differences in the relative volume of prey types occur. Males consume significantly greater percentages of termites, orthopterans, coleopterans, and arachnids, whereas females consume greater volumes of hemipterans and hymenopterans. Dietary overlap between the sexes was 0.802.

DISCUSSION

Mabuya acutilabris is an exclusively terrestrial, psammophilous skink (Horton, 1973; Poynton & Broadley, 1978; Visser, 1984; Branch, 1988). At the study site, *M. acutilabris* focused their activity around grass clumps or shrubs near the lizards' burrows, as it does elsewhere in the range of the species (Schmidt, 1919; FitzSimons, 1943). The size and extent of *M. acutilabris* burrows was not investigated, but they are probably comparable to those of *Heliobolus* and *Pedioplanis*, which are under 13 cm in depth (Nagy, Huey & Bennett, 1984).

At Kamanjab *Mabuya acutilabris* were active from 09.50 hr to 17.10 hr Comparable fall-winter activity times have been reported for other southern African diurnal lizards, including congeners (Huey & Pianka, 1977). Factors initiating daily activity in lizards have not been adequately addressed. It is generally assumed that activity is largely temperature dependent (Cowles & Bogert, 1944; Bradshaw, 1986), although endogenous circadian patterns may also be significant (Mitchell *et al.*, 1987; Seely *et al.*, 1988) and seasonally variable threshold activity temperatures may modulate the lizard's response to environmental cues (Porter & Tracy, 1983). At Kamanjab, *M. acutilabris* activity began at approximately the time that soil temperature reached 20°C and air temperature at 1 cm was 23°C. Soil temperature probably is of greater significance to the lizards at this time of day because lizard burrow temperature is largely dependent on soil rather than air temperature (van Wyk, 1992). The end of the activity period was more likely to be related to ground level air temperatures. By the time of last retreat to the burrows, air temperature had dropped to 29.1°C, 3.8°C below its highest point. In addition, large portions of river bed were shaded by this time and the loss of direct sunlight on the site at this time may have contributed to the cessation of surface activity. At the relatively low temperatures encountered, observed thermoregulatory behaviour consisted chiefly of postural adjustments during basking. Mertens (1955), however, reported that *Mabuya acutilabris* exhibits physiologically controlled colour-change in response to temperature, but only at ambient temperatures exceeding those encountered during the study.

The activity patterns of *Mabuya acutilabris* suggest that the species may be classed as a typical sit-and-wait predator (Pianka, 1966, 1971), in contrast to the majority of scincid lizards examined previously (Pianka, 1986). *M. acutilabris* spend the majority of their time near their burrows and only a small proportion of time in the open spaces between vegetation. Daily movements are few and both distance/min and distance/move are significantly lower than in the lacertids *Heliobolus lugubris* (a wide forager) and *Pedioplanis lineoocellata* (a nominal sit-and-wait predator) (Huey & Pianka, 1981), with which *M. acutilabris* is broadly sympatric. However, the lacertid data were collected in the Kalahari (Huey & Pianka, 1981), at a site with less vegetation than Kamanjab, and may not be strictly comparable. Movement may increase as the amount of abundant cover decreases. This appears to be the case for *H. lugubris*, which, at the Kamanjab site does not move as far or as often per unit time as in the Kalahari (Castanzo, 1991).

Although *M. acutilabris* remained stationary for most of each day, individuals moved as much as 80 m over the course of the study period. The total density of *M. acutilabris* on the site (106/ha) is more than twice as high as the average value for other small lizards (Turner, 1977). Local abundance, however, varied greatly. Many lizards inhabited the eastern area of the site where grass tufts and shrubs were numerous, whereas few animals were observed in the sparsely vegetated western part of the study area.

Previous statements regarding the diet of the species reported that prey included beetles and ants (FitzSimons, 1943) and beetles, ant-lions and wasps (Branch, 1988). All of these prey items were taken by the animals examined, but only beetles accounted for more than 10% of the prey intake by volume and number. In this study hemipterans (+ homopterans), larvae (of all insect groups), coleopterans, isopterans and orthopterans were found to comprise the bulk of the diet, both with respect to volume and prey item number (Table 2). This is consistent with what is known of the foraging behaviour of *M. acutilabris*. This species' reliance primarily on relatively mobile prey (orthopterans, coleopterans, and hemipterans/homopterans) plus larvae (found in the same vegetation clumps as the lizards' burrows) seems to support its characterization as a sit-and-wait predator. The diets of Kalahari species of *Mabuya* contain high percentages of termites (up to 45% by volume in *M. striata*) (Huey & Pianka, 1977). Termites, a clumped resource, which typically predominate in the diets of widely foraging lizards (Pianka 1986), are present in the diet of *M. acutilabris*, but account for only 11.7% by volume of the prey consumed. The low level of utilization of this resource corroborates the aforementioned interpretation of the foraging mode of *M. acutilabris*.

Male and female *Mabuya acutilabris* consume similar types of prey and the relative importance of the prey types taken are in general agreement with the overall species dietary profile presented (Table 2). However, when volumes of prey are considered, greater sexual divergence is evident. The majority of female's diet is comprised of bugs, while males consumed considerably greater volumes of termites, spiders, orthopterans, and coleopterans. The significance of these difference, if any, is unclear, however, because the overall similarity of the diets, as measured by niche overlap (0.802), is high relative to interspecific overlap between sympatric congeners (Castanzo, 1991).

The ecology of *Mabuya acutilabris* would appear to be atypical in some regards with respect to that of other southern African skinks that have been examined (Huey & Pianka, 1977; Pianka, 1986). Both the limited daily movements and dietary profile of this lizard suggest that it is primarily a sit-and-wait predator. In this aspect the species may be convergent with syntopic lacertids (Castanzo, 1991). The differences observed between scincids from different arid regions, however, are likely to be influenced by both local prey availability and vegetational characteristics, and as such are not strictly comparable. In addition, the realized niche of each species will be heavily influenced by interactions with other taxa. While such interactions have been documented by community studies of Kalahari lizards (Pianka, 1986), these remain to be elucidated in the case of the lizard fauna of the northern Namibian savanna.

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