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Comparative diet of three sympatric *Sceloporus* in the semiarid Zapotitlán Valley, Mexico

Comparación de la dieta de tres especies simpátricas de *Sceloporus* en el valle semiárido de Zapotitlán, Mexico

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Abstract. Ecology, morphology, and phylogeny contribute to the organization of lizard assemblages; however, the number of lizard assemblages for which detailed knowledge of closely related sympatric species is available is limited. We studied the diet of 3 sympatric species of lizards (*Sceloporus gadoviae*, *S. horridus*, and *S. jalapae*) from arid tropical scrub forest in Puebla, Mexico. These species prey primarily on arthropods, mostly termites, ants, and beetles. Spring and summer rains caused an increase in available prey biomass. However, lizards continued using the same resources throughout the study. These 3 species of *Sceloporus* are similar in their diet, especially the smaller bodied species, *S. gadoviae* and *S. jalapae*. Termites are a very important food for the 3 species throughout the year and are a major resource during the rainy season, which is not consistent with the hypothesis that many lizards eat termites only in the dry season.

Key words: diet, *Sceloporus gadoviae*, *S. horridus*, *S. jalapae*, Zapotitlán.

Resumen. La ecología, morfología y la filogenia contribuyen a la organización de los ensambles de lagartijas. Sin embargo, son pocos los estudios detallados sobre la organización de estos ensambles y más aún, con especies simpátricas. Estudiamos la dieta, reproducción y dimorfismo sexual de 3 especies simpátricas de lagartijas (*Sceloporus gadoviae*, *S. horridus*, and *S. jalapae*) de un matorral árido tropical en Puebla, México. Estas especies se alimentaron de artrópodos; principalmente de termitas, hormigas y escarabajos. Las lluvias de primavera y verano causaron un incremento en la biomasa de presas; sin embargo, las lagartijas continuaron usando los mismos recursos. Las lagartijas fueron especialistas consumiendo presas en relación a su abundancia. Las 3 especies fueron similares en su dieta, especialmente las especies pequeñas *S. gadoviae* y *S. jalapae*. Las termitas son un importante recurso para estas 3 especies durante el todo año y la principal fuente alimenticia en la estación lluviosa, lo cual no es consistente con la hipótesis de que muchas lagartijas comen termitas solamente en la estación seca.

Palabras clave: dieta, *Sceloporus gadoviae*, *S. horridus*, *S. jalapae*, Zapotitlán.

Introduction

Vitt and Pianka (2005) provided strong evidence for dramatic historical effects on contemporary ecological community structure of lizards, based on an unusually broadly sampled, ancient, and worldwide adaptive radiation (see also Losos, 1994; Vitt et al., 1999; Mesquita et al., 2006). Using phylogenies of lizards to reconstruct the evolutionary history of the included taxa and mean species body size as a covariate, these authors suggest that the

early history of squamate reptiles appears to have played a profound role in determining lizard diets and accounts for a large portion of putative ‘‘niche partitioning’’ observed in phylogenetically diverse lizard assemblages throughout the world (Gainsbury and Colli, 2003; Vitt and Pianka, 2005). However, it appears that local selective pressures have been very important in some lizard assemblages, even more than historical factors (e.g. Melville et al., 2006). The exploration of the relationships between historic and contemporary factors in structuring ecological communities, and future progress will depend in part on a wider range of empirical studies (Greene, 2005).

Ecology, morphology, and phylogeny contribute to the organization of lizard assemblages (Toft, 1985; Vitt and Pianka, 2005). Closer examination of ecological variation within taxa (e.g. family) on a broad geographic scale and comparisons among many communities in a historical context are needed to begin to understand the relative importance of phylogeny and local species interactions in structuring lizard assemblages (Vitt and Zani, 1996). Morphology in particular, which often reflects phylogeny, appears tied to numerous aspects of the ecology of lizards including prey and habitat use (Vitt and Zani, 1996). Previous studies on lizard assemblages have suggested that they can be structured with respect to microhabitat or habitat use (e.g. Vitt et al., 1999; James and M'Closkey, 2002; D'Cruze and Stafford, 2006; Attum et al., 2007; García-de la Peña et al., 2007a), diet (Vitt and Zani, 1998a, b; Gainsbury and Colli, 2003; D'Cruze and Stafford, 2006), or activity periods (Fuentes, 1976; Creusere and Whitford, 1982; García-de la Peña et al., 2007a, b; Rouag et al., 2007).

Relatively little detailed information is known about the biology and ecology of many lizards in Mexico (Lemos-Espinal et al., 2003), especially from the tropical dry forest regions. Thus, conclusions regarding the ecology and life history characteristics of lizards from such habitats will not be known until considerably more data become available. To put existing data in a broader geographic and taxonomic context and to understand the combined influence of environment and history on lizards better, data describing patterns of species occurring sympatrically as well as closely related species living in different habitats are needed (Watling et al., 2005). Therefore, the goal of this paper is to present data that describe the diet of 3 sympatric species of lizards (genus *Sceloporus*) from the relatively understudied tropical dry forest of Mexico.

Materials and methods

The study was carried out at Valle de Zapotitlán de las Salinas, Puebla, Mexico. The area is located in the Tehuacán-Cuicatlán Valley system, located in the mountainous region of southeastern Puebla (18°20'N, 97°20'W; elevation 1 450 – 1 600 m), close to the northeastern limits of the state of Oaxaca. The climate is dry with a rainy season occurring between May and August (sometimes extending to September). Total annual precipitation is ca. 300-350 mm, and mean annual temperature is ca. 20°C (Valiente-Banuet, 1991). The major vegetation associations, with no clear ecotones in many parts, are: thorny scrub or matorral espinoso (with *Acacia cochliacantha*, *Cercidium praecox*, *Ipomoea pauciflora*, *Mimosa luisiana*, *Prosopis laevigata*,

tetechera (dominated by columnar cacti, *Cephalocereus hoppenstedtii* and *Neobuxbaumia tetetzo*), cardonal (dominated by cacti, *Cephalocereus hoppenstedtii*), izotal (dominated by *Yucca periculosa* (Agavaceae) and *Beaucarnea gracilis* (Nolinaceae)), and tropical dry forest (with *Bursera*, *Ceiba parviflora*, *Lysiloma microphylla*, *Plumeria rubra*). Approximately 290 species of flowering plants are known to occur in the area (Dávila et al., 1993).

The community of lizards of Zapotitlán consists of up to 13 species: *Anolis quercorum*, *Aspidoscelis parvisocia*, *Aspidoscelis sacki*, *Ctenosaura pectinata*, *Gerrhonotus liocephalus*, *Phrynosoma braconnieri*, *Phrynosoma taurus*, *Phyllodactylus bordai*, *Sceloporus gadoviae*, *Sceloporus horridus*, *Sceloporus jalapae*, *Urosaurus bicarinatus*, and *Xenosaurus rectocollaris* (Woolrich-Pina et al., 2005). We focused our work on 3 species of sceloporines (*Sceloporus gadoviae*, *Sceloporus horridus*, and *Sceloporus jalapae*) which live in syntopy and sympatry in the study area.

We established a 24 ha plot (800 x 300 m) that we visited 5 days per month. Random searches for lizards were conducted during the survey. We collected lizards by hand, noose, or rubber band monthly from February to December 2003. We obtained from each individual the following data: snout-vent length (SVL; to the nearest 1 mm), tail length (to the nearest 1 mm), and body mass (with an AVINET™ scale, to the nearest 0.2 g). All animals were killed by cardiac injection of 2% xylocaine, and fixed in 10% formalin, preserved in 70 % ethyl alcohol, labeled, and deposited in the herpetological collection of the UBIPRO, FES Iztacala, Universidad Nacional Autónoma de México.

We removed stomachs, examined their contents, and identified arthropods to order and occasionally to species in ants, using keys to ants (Bolton, 1994; Ríos-Casanova et al., 2004), termites (Constantino, 2002), and other arthropods (Borror et al., 1989). The presence of plant material was noted and classified into broad categories (e.g., fruit, seeds, leaves). We determined size of food items using fluid displacement to the nearest 0.1 mL (Milstead, 1957). To describe the importance of each prey category consumed (t), we calculated the index of relative importance (Pinkas et al., 1971) as $IRI_t = \%Ot (\%Nt + \%Vt)$, where $\%Ot$ is the occurrence percentage (i.e., the number of stomachs containing each t item), $\%Nt$ is the percentage of the number of t items in all stomachs, and $\%Vt$ is the percentage of the volume of t items in all stomachs.

We used analysis of covariance (ANCOVA) with body size (SVL) as the covariate to examine differences in size of ingested prey between males and females. Food niche breadth was calculated using Levins standardized formula (Hurlbert, 1978): $B_A = [(1 / \sum p_i^2) - 1] / (n - 1)$; where

p_i = proportion of occurrence of each prey species in each age-sex category of diet; n = number of prey species in the lizards diet. B_A ranges from 0 to 1, a value of 1 for B_A means that all of prey were used in equal proportions, whereas a value near 0 for B_A means that only 1 or a few categories were used with high frequency and that most prey were used in low frequencies.

We also used an analysis of similarity (ANOSIM; Clarke, 1993) to examine differences in diet among the 3 species. We pooled samples from March to July because they were the months that had the most diet data available (Fig. 1). To assess compositional differences between the diets of the 3 species, a matrix of similarity among species was developed using a Bray-Curtis index based on the percentage of each prey taxon detected in the diet of each species. The data matrices were standardized and transformed ($\log[x+1]$). This nonparametric permutation based procedure compares mean ranks of dissimilarities of samples within and among groups. When groups of samples are distinct from each other, the compositional dissimilarities between samples within a group are smaller than dissimilarities between samples from different groups. The ANOSIM test statistic, R , varies between -1 and 1, reaching its maximum value when all between group dissimilarities are greater than all within-group dissimilarities. Statistical significance is determined by comparing the sample R with those produced by randomly assigning samples to groups. The proportion of random arrangements with R -values higher than the sample value is the significance level of the test (Clarke and Gorley, 2001).

The SIMPER (Similarity percentage) procedure was used to identify those prey species contributing most to the similarity within species, and the dissimilarity between groups. Both the ANOSIM and SIMPER procedures were conducted using the PRIMER Software package (Clarke and Warwick, 1994).

We surveyed 1 transect of 100 m to sample arthropods with pitfall trapping (PT). The PT method used plastic cups (450 ml) containing a salt and soap solution. Two traps were placed every 10 meters along the transect for a total of 20 traps. Traps were open for 24 hours every month. Samples was dried at 60°C for 7 days and then weighed with an analytical scale to the nearest 0.0001 g. The samples served as a reference collection and to estimate the availability of food resources (mg dry mass/m^2).

We also used an analysis of variance to examine differences in food resources among months. We used a Spearman's correlation to evaluate if there was a relationship between volume of prey with rainfall.

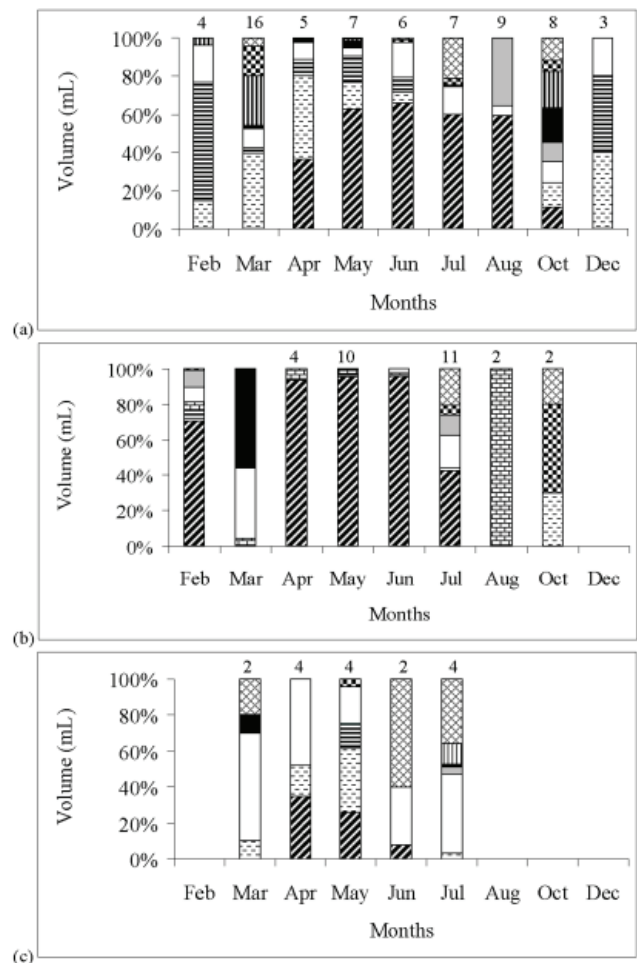


Figure 1. Monthly distributions of diet of (A) *Sceloporus gadoviae*, (B) *S. jalapae*, and (C) *S. horridus*. Symbols: Larvae Lepidoptera \square , Araneae \square , Apidae \square , Hymenoptera \square , Acrididae \square , Coleoptera \square , *Pogonomyrmex barbatus* \square , *Camponotus rubrithorax* \square , *Tenuirostritermes* sp. \square , *Solenopsis* sp. \square , Larvae Coleoptera \square . Numbers above each bar give sample sizes.

Results

The alimentary tracts of *S. gadoviae* ($n_{\text{females}} = 27$, $n_{\text{males}} = 28$) all contained identifiable food items. Dietary index of relative importance (IRI) indicate that termites (*Tenuirostritermes*), ants (*Camponotus rubrithorax*), and coleopterans were the most important prey in the diet of *S. gadoviae* (Table 1). Termites were present in the diet from April to October (Fig. 1a). The ants, *Camponotus rubrithorax* and *Pogonomyrmex barbatus*, were also an important resource, because of its high volume and frequency in the stomachs (Fig. 1a). Some individuals (10.16%) were found to contain plant material (e.g.

flowers). Analysis of covariance (ANCOVA) with SVL as the covariate, revealed that the sexes did not differ in length of ingested prey in *S. gadoviae* ($F_{1,44} = 0.01$, $P = 0.98$). Dietary niche breadth of *S. gadoviae* was $B_A = 0.075$.

The alimentary tracts of 2 of the 47 individuals of *S. jalapae* were empty ($n_{\text{females}} = 15$, $n_{\text{males}} = 32$). In *S. jalapae*, termites, coleopterans, and ants (*Solenopsis*) were important prey items based on the IRI (Table 1). Termites were present in the diet in more than 40% of *S. jalapae* in the first 5 months (Fig. 1b). Analysis of covariance (ANCOVA) with SVL as the covariate, revealed that the sexes did not differ in length of ingested prey in *S. jalapae* ($F_{1,39} = 3.2$, $P = 0.051$). Dietary niche breadth of *S. jalapae* was $B_A = 0.03$.

The alimentary tracts of all of the *S. horridus* contained identifiable food items ($n_{\text{females}} = 6$, $n_{\text{males}} = 10$). Ants (*Camponotus rubrithorax*), coleopterans, termites (*Tenuirostritermes*) and larval Lepidoptera were important prey items, based on the IRI, for *S. horridus* (Table 1). We observed coleopterans in the diet of *S. horridus* from March to July. Termites and ants (*C. rubrithorax*) were also important items in the diet of this species (Fig. 1c). Analysis of covariance (ANCOVA) with SVL as the covariate, revealed that the sexes did not differ in length of ingested prey in *S. horridus* ($F_{1,13} = 0.15$, $P = 0.69$). Dietary niche breadth of *S. horridus* was $B_A = 0.084$.

ANOSIM test confirmed differences in diets of the 3 species (ANOSIM, global $R = 0.288$, $P = 0.015$). We found *S. gadoviae* significantly differed from *S. horridus* (ANOSIM, $R = 0.596$, $P = 0.008$), but no differences between *S. gadoviae* and *S. jalapae* (ANOSIM, $R = 0.062$, $P = 0.238$) and between *S. jalapae* and *S. horridus* (ANOSIM, $R = 0.24$, $P = 0.087$) were detected. The abundance of *Tenuirostritermes*, *C. rubrithorax*, *P. barbatus*, Coleoptera, Lepidoptera larvae, and plant material contributed the most (63.7%) to pairwise dissimilarities between the diet of *S. gadoviae* and *S. horridus* (SIMPER analysis). Although both species consume the same prey species, they do so in different quantities (Fig. 1).

Food resources varied significant among the months of study. Arthropod biomass (mg/m^2) was highest in June and July (ANOVA-one way; $F_{9,59} = 29.06$ $P < 0.001$) (Fig. 2). We found a positive relationship between arthropod availability and monthly mean precipitation (Spearman Rank Correlation, $r_s = 0.84$, $P = 0.002$). In the study area we observed many termites under rocks and leaf litter during the months we sampled lizards, but we were not able to quantify this resource because termites did not fall into pitfall traps.

Discussion

The diets of the 3 species of *Sceloporus* in this study differed in both taxonomic and volumetric composition from those reported for Iguania by Vitt et al. (2003), primarily because of the importance of termites in all 3 species. However, termites have been shown to be significant components in the diets of other *Sceloporus* from Mexico. Feria-Ortiz and Pérez-Malvárez (2001) found that termites were a significant component of the diet of *S. gadoviae* from southwestern Puebla, with ants, coleopterans, and lepidopteran larvae also being important. In a comparative study of trophic niches on an assemblage of diurnal insectivorous lizards in the Chihuahuan Desert, Gadsden and Palacios-Orona (1997a) found that Formicidae and Isoptera were the most important prey in *Cnemidophorus tigris*, *Uma paraphygas*, and *Uta stansburiana*. Termites also make up a substantial portion of the diets of *S. clarkii* and *S. nelsoni* from Sonora (Brooks and Mitchell, 1989). The degree of vertebrate termitivory is highest in semi-arid and arid biomes (Abensperg-Traun, 1994). In the dry season, many insectivorous vertebrates rely on termites as staple prey (James, 1991). Reduced termite biomass at this time has more severe consequences than during the rainy season when alternative prey is available (Whitford and Creusere, 1977; Abensperg-Traun, 1994). Gadsden and Palacios-Orona (1995) found that termites were an important item for the diet of *Sceloporus undulatus consobrinus*, and that ingestion of termites varies seasonally. We found the termites were a very important food for the 3 species throughout the year and were more important during the rainy season, which is not consistent with this hypothesis. Termites are diverse and abundant, suggesting that they may act as a keystone species in the assemblage of lizards we studied (Redford, 1984; Colli et al., 2006). Given the abundance of termites observed in Zapotitlán (V.H. Serrano-Cardozo, pers. observ.), it is not surprising that these 3 species of *Sceloporus* might include large numbers and volumes of termites in their diet. Indeed, Abensperg-Traun and Steven (1997) found that specialization on termites by lizards is very frequent in the arid zones of Australia (Abensperg-Traun, 1994). Likewise, Barbaut and Maury (1981), and Gadsden and Palacios-Orona (1995, 1997a) have reported the importance of termites and dietary specialization of lizards in the Chichuahuan Desert. The abundance of termite prey in many different microhabitats and at different times may be 1 of the key elements contributing to the relatively fine-scale microhabitat separation of the 3 species *Sceloporus* and the overall high alpha-diversity of lizards in the Zapotitlán area (V.H. Serrano-Cardozo and J. Lemos-Espinal, unpubl. data). Likewise, Colli et al. (2006) found

Table 1. Food item in stomachs of *S. gadoviae* (N = 59), *S. horridus* (N = 16), and *S. jalapae* (N = 45). N = Number, V = Volume (mL), F = Frequency, DIV = Dietary Index Value

Food item	<i>S. gadoviae</i>				<i>S. horridus</i>				<i>S. jalapae</i>			
	N	V	F	DIV	N	V	F	DIV	N	V	F	DIV
Araneae	13	0.68	9	71.9	2	0.09	1	7.8	8	0.12	6	18.9
Coleoptera												
Larvae					6	1.33	2	136.7	1	0.08	1	0.42
Adults	54	1.59	30	586.9	32	4.9	14	3797.2	37	0.46	21	305.3
Hymenoptera												
Apidae	14	1.37	8	113.5	4	0.6	1	33.4				
Formicidae												
<i>Solenopsis</i>	22	0.15	6	28.8	4	0.02	1	8.7	24	0.18	9	84.5
<i>Pheidole</i>	10	0.1	2	4.8	3	0.02	1	6.8	15	0.2	1	5.9
<i>Tetramorium</i>	11	0.05	3	6.5					11	0.03	4	17.1
<i>Atta</i>	13	0.25	3	12.7					3	0.03	1	1.2
<i>Odontomachus clarus</i>	22	0.3	5	30.5	10	0.16	2	52.6				
<i>Dorymyrmex flavus</i>	6	0.04	1	1.3					7	0.02	3	8.2
<i>Crematogaster opaca</i>	4	0.02	2	0.4					20	0.06	4	7.8
<i>C. rubrithorax</i>	207	3.05	24	1348.8	89	1.4	11	2582	9	0.08	5	17.6
<i>Pogonomyrmex barbatus</i>	45	1.31	11	203.8	3	0.28	1	17.9	11	0.08	4	10.6
Other	9	0.74	7	55.2	8	0.2	2	48.1	4	0.06	3	4.7
Isoptera												
Termitidae												
<i>Tenuirostritermes</i>	551	5.46	17	2283.3	138	1.37	3	991.1	409	3.93	25	4007.8
Lepidoptera larvae	8	0.71	5	37.3	13	3.01	5	767.4	11	0.34	8	35.2
Orthoptera												
Acrididae	8	0.88	3	26.9	1	0.23	1	11.5	6	0.17	4	9.6
Phasmidae					3	0.88	1	43.3	1	0.13	1	0.4
Unidentified arthropods		0.06	1			0.15	1			0.02	1	
Plant material	9	0.7	6	45.2					1	0.02	1	0.4

that a rich and abundant termite fauna may moderate local extinction of lizards.

That flowers were found in nearly 10.20% of the examined lizards suggests that ingestion is not accidental and that flowers are a common food item. We found flowers in 6 lizards (5 males and 1 female) among February and June. Gadsden and Palacios-Orona (1997b) and Gansden et al. (2001) found that the ingestion of plant parts in stomachs of *Uma exsul* and *U. paraphygas* respectively were greater than 50% and that the ingestion was not accidental. These authors found that males ingest more plants than females. The role of plants in the diet of lizards is unclear, but it is possible that in desert lizards the ingestion of flowers can constitute an additional source of water.

Rain during the summer and spring caused an increase

in the abundance of prey, and an overall increase in prey biomass available for lizards, but the lizards continued using the same resources. The 3 species of *Sceloporus* appear to be specialists in their diet, as evidenced by the relatively small food niche breadths (*S. gadoviae*, $B_A = 0.075$; *S. jalapae*, $B_A = 0.03$; *S. horridus*, $B_A = 0.084$). Seasonal variation in diet composition of lizards has been reported in several studies in different regions (e.g. Chapman and Chapman, 1964; Pianka, 1970; Fleming and Hooker, 1975; Best and Gennaro, 1984; Burquez et al., 1986; Maya and Malone, 1989; Rocha, 1996; Whitfield and Donnelly, 2006). These variations have been attributed mainly to seasonal changes in prey availability (Maury, 1995). However, we did not find seasonal variation in diet composition in our 3 species, only variation in the volume

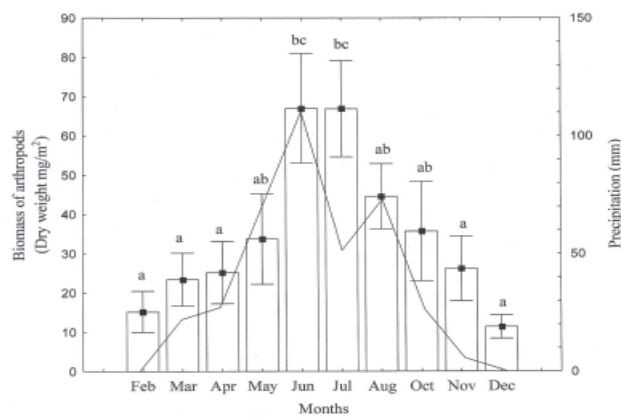


Fig. 2. Food abundance of arthropods (principally insects) collected for square meter. Bars: biomass of arthropods (dry weights mg/m²). Line: rainfall (mm) data compiled by the Instituto Meteorológico Nacional de México. Values represented are means for 25 years of precipitation data. Different letters denote significant pairwise differences between months (ANOVA, Tukey postcomparation test). The whiskers show the mean and standard deviation.

of consumed prey (i.e. the amount consumed).

In conclusion, the 3 studied species of *Sceloporus* have relatively similar diets, with the most dissimilar diets being *S. gadoviae* and *S. horridus*. The general similarity arises from the extensive use of termites in their diets.

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