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Foraging Ecology of Rainbow Skinks (*Mabuya margaritifer*) in Southern Africa

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We determined group composition and foraging mode in a wild population of rupicolous rainbow skinks (*Mabuya margaritifer*) on rocky outcrops in a humid savannah of South Africa and examined diet, sexual dimorphism, and life-history traits in museum material. We also field-tested lizards for prey chemical discrimination. Males were larger than females in both body and head size. Both sexes reached maturity at 68 mm SVL, and females produced clutches of 2–9 eggs. Males excluded other males from their home range but shared overnight crevices with 1–4 females and 1–6 juveniles. *Mabuya margaritifer* were ambush foragers when only the amount of time spent moving (8%) was considered; however, other variables such as moves per minute (1.3) and average speed (0.01 m/s) suggest an intermediate foraging mode between active and ambush foraging for the population studied. Lizards spent most time on rock (81.5%) but also moved into vegetation (7.9%) and along the rock-vegetation interface (10.6%). Both sexes spent similar amounts of time in these microhabitats and were observed feeding in all three. Diet was dominated by termites, and overlap in prey types between sexes was high. In experimental tests for prey chemical discrimination, lizards tongue-flicked rarely, giving no indication of an ability to discriminate prey chemicals. Also, lizards observed in the field during focal observations performed few tongue-flicks. Based on these results, sexual dimorphism is best explained by sexual selection via male contest competition and not by ecological niche divergence.

SURVIVAL and reproduction depend on an individual's ability to successfully find and capture prey. In lizards, foraging mode is influenced by physiology, morphology, distribution, and abundance of prey, predators, and competitors (Eifler and Eifler, 1999). Foraging mode is also linked to a suite of coevolved traits. For example, active foragers are of slender body form and have a low relative clutch mass (RCM), whereas ambushers are stockier, with a high RCM (Huey and Pianka, 1981; Anderson and Karasov, 1988; Losos, 1990). The two major types of foraging mode in lizards are ambush (sit-and-wait) and active foraging (Huey and Pianka, 1981). Some authors (e.g., Perry, 1999) consider this division artificial and prefer to view them as merely two extremes of a continuum, whereas others label intermediate foraging modes ''cruising'' or ''mixed foraging'' (Regal, 1983; Cooper, 1994a). Active foragers move as they search for prey. They consume mainly patchily distributed prey of relatively small size, which may either be hidden or exposed (Huey and Pianka, 1981; Anderson, 1993). Ambush foragers also tend to move infrequently and capture prey detected visually. They consume larger prey that is visually exposed and dispersed (Regal, 1983; Cooper, 1994a). This results in quantitative differences between the two major foraging modes, with ambushers having low PTM (percent time moving), low MPM (moves per minute), low average speed of movement during a fixed time interval, but high average speed while actually moving (Anderson, 1993; Cooper, 1994a). Within lizard families, foraging mode is typically uniform (Cooper, 1994b; Cooper and Steele, 1999). However, exceptions to this rule occur, such as in the Lacertidae (Perry, 1999) and Scincidae (Cooper, 2000), and foraging mode can vary as a function of resource type and abundance (Greeff and Whiting, 2000). The genus *Mabuya* (Scincidae) exhibits a variety of foraging modes. Of 11 species studied, eight are active foragers, two ambushers, and one species shows a mixed strategy with the evolutionary polarity of foraging modes being uncertain (Cooper, 2000; Cooper and Whiting, 2000).

Foraging mode and chemical detection of prey are correlated in lizards (Cooper, 1995). For an ambush forager, tongue-flicking generally does not aid in prey detection (Cooper, 1994a). Ambushers therefore tongue-flick rarely or not at all while foraging, and if they tongue-flick in an experimental set up, they show no ability to detect prey chemical stimuli (e.g., Cooper and Van Wyk, 1994; Cooper and Steele, 1999; Mouton et al., 2000). In contrast, active foragers use tongue-flicking extensively while searching for prey, and several studies show that active foragers are able to detect and discriminate between odors, by tongue-flicking more frequently to prey odors than to odorless or pungency controls (Cooper and Vitt, 1989; Cooper et al., 1998; Cooper and Hartdegen, 1999). Because foraging mode is strongly linked to use of the vomeronasal system for prey chemical detection, a change in foraging mode may have consequences for prey chemical detection ability. A shift from ambush to active foraging should lead to acquisition of prey chemical detection, whereas a shift from active to ambush foraging may lead to its loss (Cooper, 1994b, 1995). Intermediate foraging modes may reflect a step between these two extreme forms of foraging.

Foraging mode also has an impact on strength of food competition. Group-living ambush foragers experience higher exploitative and interference competition for food than active foragers that are able to disperse and forage over larger areas (Mouton et al., 2000). Such high competition for food among group-living organisms may favor a shift from sedentary ''long-wait'' ambushing to more mobile ''short-wait'' ambushing or even to a cruising visual searcher, that is, a virtual active forager (R.A. Anderson, pers. comm.). However, shifts in foraging behavior may involve trade-offs, such as increased predation risk for lizards that normally forage close to refuges such as rock crevices. High intraspecific competition for food can also select for ecological niche divergence between sexes and result in sexual dimorphism (Shine, 1989, 1991; Butler et al., 2000). However, the evolution of sexual dimorphism can also be a consequence of sexual selection (Andersson, 1994). Larger body and head size may be an advantage in direct competition for territories and access to mates (Anderson and Vitt, 1991; Vitt and Cooper, 1985; Perry, 1996). And if mate preference occurs, it is often for larger members of the sexually selected sex (Ryan and Keddy-Hector, 1992). Large size may be used as an indicator of good health and/or survival ability (good genes hypothesis) or may be a more stimulating signal (sensory drive/exploitation hypothesis; Ryan, 1990; Tokarz, 1995; Jennions and Petrie, 1997). Fecundity in many female lizards strongly depends on size. Larger females can carry more eggs, or those with fixed clutch size may have larger eggs (Cooper and Vitt, 1993; Braña, 1996). Males may therefore use size as a direct cue to female fecundity (Olsson, 1992; Whiting and Bateman, 1999). Because of the diversity of factors implicated in each case, sexual dimorphism can occur in both directions. For example, males are larger than females in some species of Tropiduridae (Vitt, 1993), Xenosauridae (Smith et al., 1997) and Teiidae (Vitt and De Carvalho, 1995; Vitt et al., 1993); whereas no sexual dimorphism occurs in Amphisbaenia (Colli and Zamboni, 1999). In the Lacertidae, either males or females can be larger, or they may be of similar size (Olsson and Madsen, 1995; Braña, 1996). Because group living can enhance competition for mates and food, thereby influencing selection leading to sexual dimorphism, group composition should be considered in any study of lizards living in social aggregations in discrete habitats.

Mabuya margaritifer is a large, oviparous, sexually dimorphic skink in which males are territorial (Branch, 1998). Females and juveniles are dark olive-brown to black with three distinct bluish-white stripes on the back and a blue tail. Adult males are olive-brown with numerous pearly white spots on the dorsum and flanks and a yellowish-orange tail (Branch, 1998). They occur on granite, paragneiss and sandstone outcrops in mesic and arid savanna, with a distribution from southeastern Kenya south to KwaZulu-Natal in South Africa (Broadley and Bauer, 1998). We wanted to test the hypothesis that sexual dimorphism in *M. margaritifer* is the result of intrasexual niche divergence. We asked whether differences in body size could be attributed to trophic divergence in male and female *M. margaritifer.* To address this, we measured foraging mode and microhabitat use for males and females in the field and examined stomach contents of museum specimens. We also considered the influence of group composition and spatial overlap on foraging behavior, particularly because we saw individuals sharing crevices. Finally, to obtain a more complete picture of foraging ecology, we tested for prey chemical discrimination ability in the field.

MATERIALS AND METHODS

Study area.—We performed all observations and experiments on Pullen Farm (24°35′S, 31°11′E), 35 km east of Nelspruit, Mpumalanga Province, South Africa. The area is hilly, consisting of numerous granite exfoliation domes in moist savannah. These rocky outcrops are structurally simple and consist of loose, freestanding rocks or sheets of granite with horizontal cracks. Such sheets vary in size from a few meters to several hundred meters in length. They are ringed by thick surrounding vegetation. Distances between outcrops range from a few meters to several thousand meters.

Body size.—We measured and sexed 234 specimens housed in the Transvaal Museum, Pretoria. For each intact specimen, we measured snout–vent length (SVL) and tail length to the nearest millimeter with a ruler. Head width (widest portion of the head), height (deepest portion of the head) and length (from anterior edge of tympanum to the tip of the snout) were measured to the nearest 0.01 mm with digital calipers. All lizards were sexed by either body color or examination of their gonads. To determine minimum size at sexual maturity, females were examined for oviductal eggs or enlarged vitellogenic follicles. Males were considered sexually mature when they had convoluted epididymides and/or enlarged testes. Differences in SVL between adult males and females were tested with *t*-tests adjusted for unequal variances (Analytical Software, Tallahassee, FL, 1996). We used analysis of covariance to remove the effects of body size (covariate = SVL, sex = factor) when comparing head size and tail length between males and females. All means are reported ± 1 SE. Differences were considered significant at $a < 0.05$. All tests were two-tailed.

Diet.—To examine diet, we removed stomachs from 154 museum specimens. Date and location of capture were available for 126 individuals (58 females, 68 males). We identified prey items to family or the least inclusive taxon possible. We measured length and width of individual prey items with digital calipers to the nearest 0.01 mm and estimated volume of each prey item using a modified version of a formula for a prolate spheroid (Pianka, 1986):

$$\text{Volume} = \frac{4}{3}\pi \times \left(\frac{1}{2}\text{length}\right) \times \left(\frac{1}{2}\text{width}\right)^2$$

We calculated diet niche breadth using the formula

$$B = \frac{1}{\sum_{i=0}^{n} p_i^2}$$

where i is a resource category, p is the proportion of resource category i (either of frequency or volume), and n is the total number of categories (Pianka, 1986). Niche breadth overlap between sexes, within seasons, was calculated using the symmetric niche overlap formula (Pianka, 1986).

$$\Phi_{jk} = \frac{\sum_{i=0}^{n} p_{ij}p_{ik}}{\sqrt{\sum_{i=0}^{n} p_{ij}^2 \times \sum_{i=0}^{n} p_{ik}^2}}$$

where the symbols are the same as above but with j and k representing females and males, respectively. We tested for a correlation between the following morphological measures: gape-size (head length × head width), SVL, head width, head length and the following dietary variables: largest prey item consumed, total prey volume, and total number of prey consumed, using Spearman rank correlation coefficients.

Foraging mode and microhabitat use.—We conducted focal observations during the reproductive (October 2000) and postreproductive (February 2001) seasons. We observed lizards on warm, sunny days, starting when they were first seen active but at least 1 h after first appearance to allow lizards time to reach preferred body temperatures through thermoregulatory basking. We conducted observations until 1600 h with a noon break during the hottest part of the day. We slowly walked along the edges of granite exfoliation domes to detect lizards by unaided sight or with binoculars. We stopped moving as soon as we detected a lizard and categorized the animal as male, female, or juvenile. We started observations only if the lizard continued with its previous behavior (basking, moving, etc.) without looking at the observer or running away. Distance between observer and lizard was approximately 10 m. We performed observations with the aid of binoculars, and all foraging-related behaviors and social interactions were timed with a stopwatch and recorded on a dictaphone. Observations lasted for 10 min where possible, and recordings in which the focal animal moved from view during the first 2 min were discarded. For each focal observation, we recorded date, time of observation, sex/age class, microhabitat use (only during the postreproductive season), and behavior. Behaviors noted were duration and distance of movements, number of tongue-flicks, and feeding. Feeding was defined as observed consumption of prey. Postural adjustments were ignored. Movement bouts were defined as movement of at least 5 cm with an interval of at least 2 sec between separate movement bouts. To ensure that each lizard was observed not more than once per season, we visited each outcrop only once during the reproductive and postreproductive season and performed during that visit, focal observations on all lizards encountered being distinguishable by coloration and/or size.

During the postreproductive season, we scored microhabitat use, using the following categories: rock, rock-vegetation boundary, and vegetation. Rock-vegetation boundary was defined as the patchy interface between solid rock and vegetation. We tested for a difference in microhabitat use between females, males, and juveniles using a one-way ANOVA. We compared number of individuals catching prey in a microhabitat (excluding those who fed in more than one microhabitat) with the expected number of individuals from frequency of microhabitat use, using a Brandt-Snedcor chi-square test. We calculated MPM, PTM, average speed for the entire observation interval and average speed during motion to identify foraging mode. Time spent on social interactions (aggression, courtship) was excluded in the above calculations. Distribution of measurements did not display normality (Kolmogorov-Smirnov tests). Therefore, we used nonparametric tests. We tested each of these foraging variables for a difference between males, females, and juveniles within and between seasons using Kruskal-Wallis tests. If the main effect was significant, we assessed significance of differences between pairs with Tukey-Kramer tests.

Prey chemical discrimination and tongue-flicking.—We tested for prey chemical discrimination in *M. margaritifer* using an independent groups design in which 47 free-ranging lizards were presented once with one of three stimuli: odorless control, pungency control, and food chemicals. Integumentary chemicals of domestic crickets were used as a food stimulus, deionized water as the odorless control, and diluted men's aftershave (Fabergé Brut® by Elida Pond's, 1:10 diluted with deionized water) as a pungency control. Experiments were performed in early November (end of the reproductive season). We categorized lizards randomly encountered in the field as female, male, or juvenile. The first female encountered was tested with odorless control, the first male with cricket stimulus and the first juvenile with pungency control and from then on, alternately with one of the three stimuli types. We conducted observations on sunny days, starting when lizards were seen first active but at least 1 h after first appearance. Observations were conducted until 1600 h with a noon break when lizard activity declined during the hottest part of the day. Upon sighting a lizard, we prepared a fresh stimulus applicator. For food stimuli, we firmly rolled a moistened swab over the integuments of living crickets just seconds before presentation of the swab to the test individual. The pungency control was prepared by dipping the swab in diluted cologne. The prepared stimulus applicator was then fixed in a slightly upward angle to the thin end of a 3-m pole. Then we slowly extended the pole toward the lizard and carefully approached the animal. The cotton tip was maneuvered 1–3 cm anterior to the lizard's snout, and the tip of the pole slightly rested on the ground for stabilization. We recorded number of tongue-flicks and bites within 60 sec after placing the stimulus in front of its snout. If an animal bit the swab, either before or after tongue-flicking, we recorded its reactions for an additional 60 sec after the bite. If a lizard moved slowly away, we followed it with the cotton swab. But if a lizard ran away or otherwise seemed startled, we discarded the trial. Each swab was only used once and, if it touched vegetation or ground while being maneuvered, was replaced by a new one. To prevent testing a lizard more than once, we sampled each outcrop only once and tested all individuals encountered there that could be distinguished based on coloration and/or size.

We calculated tongue-flick frequency (TF), which is the number of tongue-flicks emitted during a trial until a bite occurred or the trial ended. Tongue-flick frequency is tightly linked to foraging mode and prey chemical discrimination ability (Cooper, 1995). Therefore, we used the tongue-flick data collected during focal sampling as an additional index of prey chemical discrimination ability. Because lizards also tongue-flick to obtain information on predators or social information, we recorded the context in which tongue-flicking occurred.

Spatial patterns and crevice use.—In November 2000 (end of reproductive season), we caught 27 males, 42 females, and 36 juveniles by noosing or with glue traps on 13 distinct outcrops (Whiting, 1998). We marked all lizards with nontoxic paint and immediately released them at the point of capture. Markings lasted until a lizard shed its skin, which happened within a couple of weeks. We mapped the outcrops and visited each of them once a day during a two-week period to record the position of all marked lizards. The sequence of visits to the different outcrops was altered each day to obtain data for all times of the day from each location. Based on these positional data we roughly calculated home-range size by taking a series of measurements (nearest 10 cm) with a 25-m tape between the marked points such that the enclosed area could be broken into geometric shapes for calculation of size (m^2). We determined age-sex spatial overlap to determine whether males were maintaining exclusive home ranges. Finally, we recorded which crevice was used as the overnight refuge by the resident male. Each of these (27 crevices distributed over 13 outcrops) was then monitored once in the evening from 1600 h to nightfall to determine

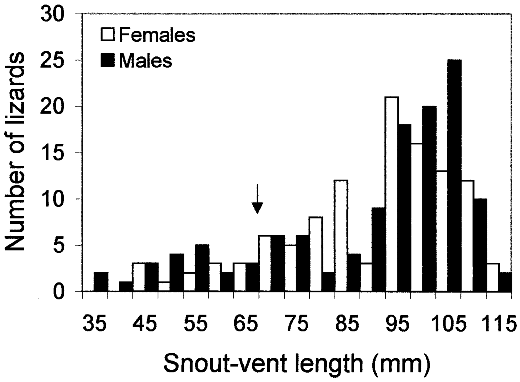

Fig. 1. Distribution of snout–vent lengths for male and female *Mabuya margaritifer.* Arrow indicates size at sexual maturity.

group-composition within crevices during the night.

Results

Body size.—The smallest male and female showing evidence of sexual maturity were 68 mm (SVL). Based on this criterion, 185 of the 234 specimens examined were classified as adult (93 females, 92 males). Twenty females collected between October and January contained clutches varying from 2–9 eggs (6.1 ± 1.1). Males were significantly larger than females in body (Fig. 1) and head size (Figs. 2–4) but not for tail length. When the effect of body size was removed, males were proportionally larger than females of the same body size for all morphological variables except tail length (Table 1).

Diet.—A total of 154 lizard stomachs examined contained 3292 prey items. Mean number of prey items per stomach was 21.4 (± 3.43, 0–248), and average volume of prey per stomach was 494 mm^3 (Fig. 5; ± 50.0, 0–3830). Of the 154 stomachs examined, 26 (17%) were empty. All identified prey are listed in Appendix 1. Date of capture for seasonal analysis was available for 126 adults (58 females, 68 males) and ranged from 1906–1997 (32% before 1950, 68% after 1950). Most museum specimens had been captured during spring (21 females, 25 males) and summer (19 females, 24 males), whereas the remaining had been collected during fall (nine females, 10 males) and winter (nine females, nine males). Numeric distribution of main prey categories for adults by season is presented in Figure 6. Frequency of adult males and females containing main prey categories is presented in Figure 7. Niche breadth for main prey categories was greatest in summer and lowest in winter (Table 2). Niche overlap between sexes was high for frequency over all seasons (Φ_{jk} = 1 for spring, summer, winter, Φ_{jk} = 0.9 for fall) but varied for volume in fall (Φ_{jk} = 0.4) and winter (Φ_{jk} = 0.6) but not for spring (Φ_{jk} = 1) and summer (Φ_{jk} = 1).

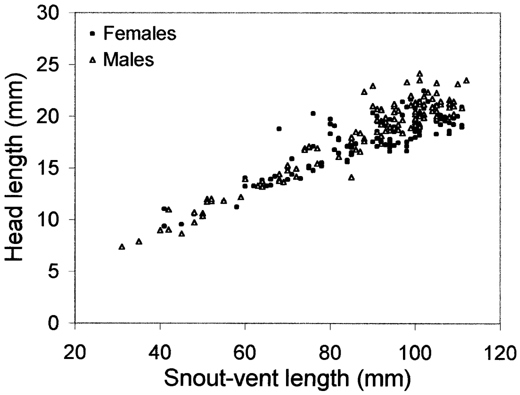

Fig. 3. Relationship between head length and SVL for male and female *Mabuya margaritifer.*

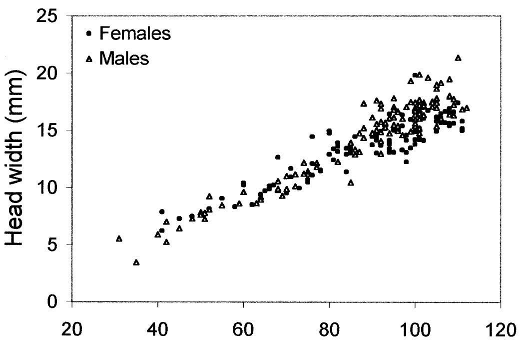

Fig. 2. Relationship between head width and SVL for male and female *Mabuya margaritifer.*

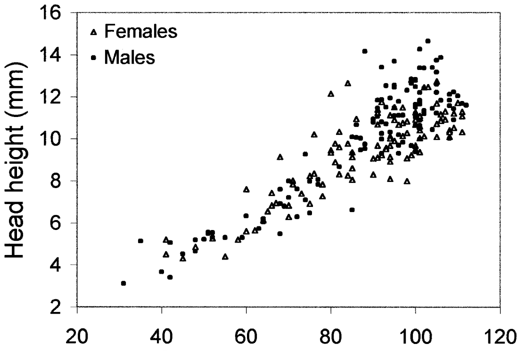

Fig. 4. Relationship between head height and SVL for male and female *Mabuya margaritifer.*

TABLE 1. MORPHOLOGICAL CHARACTERISTICS OF ADULT *Mabuya margaritifer*. Means are reported ± 1 SE; ranges are in parentheses. For tail length, only lizards with complete tails were included (n = 63 males, n = 61 females). T-tests were used to test for sexual size dimorphism. For snout–vent length, a t-test for unequal variance was used. A second analysis used one-way ANCOVA to control for body size, with sex as the factor and SVL as the covariate. All measurements are in millimeters.

Morphological trait	Males (n = 92)	Females (n = 93)	t-test			Effect of SVL removed					
						Slopes test			Intercepts test		
			df	t	P	df	F	P	df	F	P
Snout–vent length	96.9 ± 0.9 (68–112)	93.8 ± 1.1 (68–111)	176.7	2.13	0.03						
Tail length	142.1 ± 2.8 (92–181)	137.1 ± 2.6 (90–182)	122	1.29	0.20	1,12	1.07	0.30	1,12	1.21	0.27
Head length	20.0 ± 0.2 (14.4–24.2)	18.4 ± 0.2 (14.0–22.5)	183	6.02	<0.0001	1,23	1.29	0.26	1,23	5.29	0.02
Head width	16.1 ± 0.2 (10.5–21.4)	14.4 ± 0.2 (9.9–19.8)	183	6.51	<0.0001	1,23	4.02	0.05	1,23	6.95	0.01
Head height	11.3 ± 0.2 (7.1–14.7)	10.1 ± 0.1 (6.9–12.8)	183	5.85	<0.0001	1,23	4.39	0.04	1,23	5.65	0.02

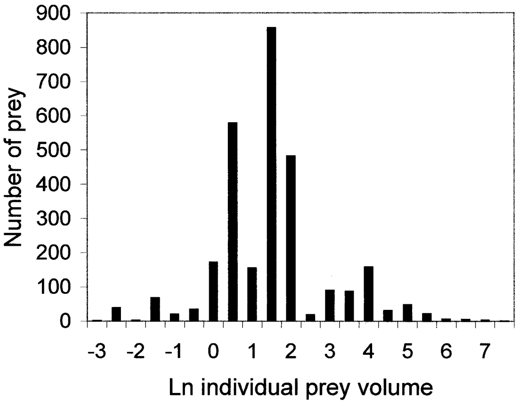

Fig. 5. Distribution of individual prey sizes consumed by *Mabuya margaritifer*.

Mabuya margaritifer consumed a wide variety of prey taxa (Appendix 1). Of the 128 stomachs with prey, 44.5% contained beetles, 43.8% ants/bees/wasps, 34.4% insect larvae, 32.0% termites, 32.0% crickets/grasshoppers, 22.7% bugs, 18.0% spiders and 15.6% millipedes. The greatest percentage of individual prey items consumed were termites (9.5% alates, 63.8% soldiers/workers, total 73.3%) which also constituted the greatest volume of stomach contents (16.9% alates, 15.7% soldiers/workers, total 32.6%). They were followed numerically by Hymenopterans, mainly ants (13.5%), and volumetrically by beetles (10.5%), crickets/grasshoppers (19.0%), and insect larvae (11.7%). Of the 111 insect larvae found 45 could be further identified either as Coleopteran larvae (42.3%), Lepidopteran larvae (55.5%) or Dipteran larvae (2.2%). Only four vertebrate prey (three lizards and one frog) were found of which one was a *Lygodactylus* sp. (Gekkonidae). Parasitic nematodes were found in 13% of all lizard stomachs.

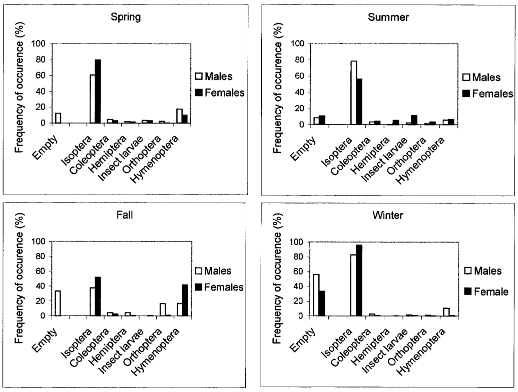

Fig. 6. Numerical frequency of main prey categories in *Mabuya margaritifer*, by sex and season.

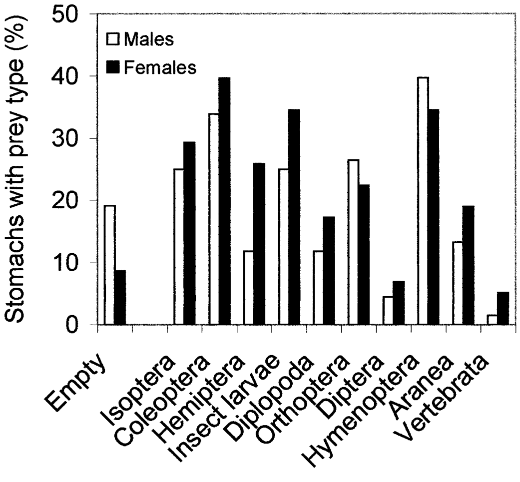

Fig. 7. Frequency of male and female *Mabuya margaritifer* containing main prey categories.

No significant relationship was found for number of prey and any body measurements (SVL: $r_s = 0.05$, $P = 0.58$; head width: $r_s = 0.09$, $P = 0.29$; head length: $r_s = 0.15$, $P = 0.06$; head height: $r_s = 0.12$, $P = 0.14$; gape size: $r_s = 0.09$, $P = 0.27$). Total prey volume was positively correlated with SVL ($r_s = 0.17$, $P = 0.04$), head height ($r_s = 0.17$, $P = 0.03$), and head width ($r_s = 0.16$, $P = 0.05$), but not with head length ($r_s = 0.14$, $P = 0.08$) or gape size ($r_s = 0.15$, $P = 0.06$). Largest individual prey volume was positively correlated with head height ($r_s = 0.16$, $P = 0.05$) but not with SVL ($r_s = 0.13$, $P = 0.13$), head width ($r_s = 0.15$, $P = 0.07$), head length ($r_s = 0.11$, $P = 0.17$), or gape size ($r_s = 0.14$, $P = 0.09$).

Foraging mode and microhabitat use.—Of 129 focal observations, 62 lasted for the full observation period (10 min), 40 for > 5 min, and 27 for 2–5 min. Shorter observations were caused by the disappearance of the focal animal in dense vegetation or under rocks. During the postreproductive season lizards spent 81.5% of their time on rock and the remainder along the rock-vegetation boundary (10.6%) or in vegetation (7.9%; Table 3). Lizards changed microhabitats on average 2.3 ± 0.6 (range: 0–8) times during observations. The amount of time lizards spent on rock was dependent on age-sex class ($F_{2,60} = 3.98$, $P = 0.023$). Adult males and females spent similar amounts of time on rock (Fisher's test, $P = 0.65$), whereas both males (Fisher's test, $P = 0.01$) and females (Fisher's test, $P = 0.03$) spent significantly more time in other microhabitats than juveniles. Time in vegetation was likely underestimated because focal animals

TABLE 2. MALE AND FEMALE NICHE BREADTH (PIANKA, 1986) FOR FREQUENCY B_{freq} AND VOLUME B_{vol} FOR ALL SEASONS, FOR *Mabuya margaritifer*. B_{max} = maximal niche breadth, n = number of prey categories.

Sex	Spring					Summer				
	n	B_{freq}	$[B_{freq}]/[B_{max}]$	B_{vol}	$[B_{vol}]/[B_{max}]$	n	B_{freq}	$[B_{freq}]/[B_{max}]$	B_{vol}	$[B_{vol}]/[B_{max}]$
Male	12	2.5	0.2	5.1	0.4	16	1.6	0.1	2.9	0.2
Female	11	1.6	0.1	4.6	0.4	12	2.9	0.2	4.8	0.3
Mean	11.5	2.0	0.2	4.9	0.4	14	2.3	0.1	3.8	0.2
	Fall					Winter				
Sex	n	B_{freq}	$[B_{freq}]/[B_{max}]$	B_{vol}	$[B_{vol}]/[B_{max}]$	n	B_{freq}	$[B_{freq}]/[B_{max}]$	B_{vol}	$[B_{vol}]/[B_{max}]$
Male	9	4.7	0.5	1.7	0.2	6	1.4	0.1	3.9	0.4
Female	10	2.3	0.2	4.8	0.5	11	1.1	0.01	3.7	0.3
Mean	9.5	3.5	0.4	3.2	0.3	8.5	1.3	0.1	3.8	0.4

TABLE 3. MICROHABITAT USE OF FEMALE, MALE, AND JUVENILE *Mabuya margaritifer*, OBTAINED DURING FOCAL ANIMAL OBSERVATIONS IN THE FIELD.

	Rock			Rock-vegetation interface			Vegetation		
	$\bar{x}$ (%)	SE	Range (%)	$\bar{x}$ (%)	SE	Range (%)	$\bar{x}$ (%)	SE	Range (%)
Male	91.5	2.2	67–100	2.7	1.3	0–20	5.8	2.0	0–32
Female	77.9	3.8	43–100	9.5	2.8	0–43	12.6	3.9	0–56
Juvenile	75.1	6.3	0–100	19.6	6.5	0–98	5.4	2.1	0–34
Total	81.5	2.7	0–100	10.6	2.5	0–98	7.9	1.6	0–56

moving in dense vegetation often disappeared from sight. During focal observations in February, 28 (44%) lizards (14 females, six males, and eight juveniles) consumed 1–5 prey items (mean 1.6 ± 0.2) resulting in a total of 44 feedings observed. Four (14%) individuals fed in vegetation (three females, zero males, and one juvenile), seven (25%) along the rock-vegetation boundary (three females, zero males, and four juveniles), 13 (47%) on rock (seven females, four males, and two juveniles), and four (14%) switched between rock and the rock-vegetation boundary during feeding (one female, two males, and one juvenile). Feeding per microhabitat was not significantly different from general microhabitat use ($\chi^2 = 1.03$, $P = 0.3$). Of the 44 prey consumed, five were flying insects, which were pursued from ambush positions (by three females, one male, one juvenile).

The amount of movement varied among individuals (Table 4). Significant differences in foraging parameters occurred between season and sex/age classes (Table 4). Post hoc comparisons showed that the significant main effect in MPM was caused by females moving less often during the reproductive season than during the postreproductive season ($P = 0.03$) and less often than juveniles ($P = 0.01$) during the postreproductive season. The significant main effect in average speed was caused by males moving faster in the postreproductive season than during the reproductive season ($P = 0.005$); by males moving faster in the postreproductive season than females ($P = 0.004$) or juveniles ($P = 0.007$) during the reproductive season; and by males moving faster than juveniles during the postreproductive season ($P = 0.03$). The main effect in PTM was because of females moving less during the reproductive season than juveniles moved during the reproductive season ($P = 0.02$).

Prey chemical discrimination and tongue-flicking.— In all treatments, the number of tongue-flicks was generally low (Table 5). Only 11 of 47 individuals tongue-flicked, of which three did so only after a first bite. No statistical analysis for prey chemical discrimination was performed because of the low number of tongue-flicks emitted. Most bites (seven of 10) occurred without prior chemical investigation by tongue-flicks. Of these, six individuals bit the cricket stimulus, four bit the water stimulus, and no individual

TABLE 4. MEASURES OF MOVEMENT PARAMETERS FOR MALE, FEMALE, AND JUVENILE *Mabuya margaritifer* FOR THE REPRODUCTIVE SEASON (OCTOBER) AND POSTREPRODUCTIVE SEASON (FEBRUARY). Means are reported ± 1 SE, ranges are in parentheses. MPM = moves per minute, PTM = proportion of time spent moving, MS = average speed while moving (m/s) and AS = average speed over entire observation interval (m/s). A Kruskal-Wallis test was used to test for significant differences between adult males, adult females, and juveniles, between and within seasons; posthoc comparisons are given in the text.

	Reproductive season			
	Males ($n = 26$)	Females ($n = 21$)	Juveniles ($n = 19$)	Combined ($n = 66$)
MPM	1.5 ± 0.2	0.7 ± 0.1	1.3 ± 0.2	1.2 ± 0.1
	(0.2–2.8)	(0–1.9)	(0.1–3.3)	(0–3.3)
PTM	11.0 ± 1.6	4.5 ± 1.0	9.7 ± 1.6	8.4 ± 0.9
	(0.3–24.6)	(0–20.4)	(0.5–31.0)	(0–31.0)
MS	0.1 ± 0.01	0.11 ± 0.02	0.12 ± 0.01	0.11 ± 0.01
	(0.04–0.19)	(0–0.39)	(0.04–0.24)	(0–0.39)
AS	0.010 ± 0.002	0.007 ± 0.002	0.010 ± 0.002	0.009 ± 0.001
	(0.0005–0.02)	(0–0.04)	(0.0003–0.03)	(0–0.04)

bit the cologne stimulus. Two lizards bit the cricket stimulus twice, whereas three lizards tongue-flicked the cricket stimulus after biting it. During $>$ 15 h of focal observations, only 6.2% (eight of 129) of lizards were observed to tongue-flick and only during the reproductive season. Two of these tongue-flicked at lizard feces, two males investigated conspecific females, and four directed tongue-flicks toward the substrate.

Spatial patterns and crevice use.—Mean number of sightings for individuals in which spatial overlap was examined was 7.5 ± 0.25 (range: 1–12) (females: mean = 7.3 ± 0.36; males: mean = 9.2 ± 0.35; juveniles: mean = 6.4 ± 0.45). Up to four males were observed on large outcrops with several crevices. Each male ($n = 27$) maintained an exclusive area (zero overlap with other males) containing one crevice used during the night, several other crevices and at least one termite mound. Male home ranges overlapped with those of 1–4 females (mean = 1.7 ± 0.16) and 0–6 juveniles (mean = 1.8 ± 0.24). Three of 42 females overlapped adjoining male home ranges, whereas the remainder were associated with only one male. Six of 36 juveniles moved freely between adjoining male home ranges. Home-range size was estimated for individuals with a minimum of five observations. The average male home range size was 63 m^2 (SE = 6.3, range: 28–170 m^2, $n = 27$). Juveniles had home-range sizes similar to males (mean: 54 m^2 ± 7.2, range: 21–140 m^2, $n = 29$). Females had significantly smaller home ranges (27 m^2 ± 1.8, range: 9–55, $n = 38$) than either males (Mann-Whitney U-test, $P < 0.0001$) or juveniles (Mann-Whitney U-test, $P < 0.0001$). Skinks generally shared a communal overnight crevice within each male's home range (mean = 4.52 ± 0.35, 2–9 skinks per crevice).

DISCUSSION

Diet.—The stomachs we examined were from museum specimens collected over both a broad time span (90 yr), and a large geographical area within South Africa (Northern, Mpumalanga, Kwa-Zulu Natal and Gauteng provinces) and should therefore be representative of dietary preference. Skinks consumed a wide variety of insects. The bulk of gut contents were termites, which dominated numerically over the whole year. Volumetric dominance of termites in spring and summer was caused by the seasonal flush of large alates from October to February. Termites are an important dietary source for numerous southern African lizards (Pianka, 1986; Bauer et al., 1989; Mouton et al., 2000), including other *Mabuya* (Pianka, 1986; Castanzo and Bauer, 1993). Other dominant insect groups included beetles, true bugs, hymenopterans, and orthopterans. About half of the insect larvae consumed were Lepidopteran larvae, which can be easily seen moving by lizards that ambush prey. The other half were mainly Coleopteran larvae which require more active search. *Mabuya margaritifer* also consumed spiders ($n = 23$ lizards). One individual contained five small, fleshy fruits, which were likely ingested intentionally. The remainder of the plant material was probably ingested secondarily.

Interestingly, 20 lizards (15.6%) contained millipedes, a group that secretes noxious compounds from repugnatory glands (Vitt, 1992) and which are avoided by certain lizard taxa (Pianka, 1986; Vitt and Cooper, 1986). However, millipedes are eaten by at least two other south-

TABLE 4. EXTENDED

Postreproductive season				Both seasons total (n = 129)	Test for differences		
Males (n = 21)	Females (n = 21)	Juveniles (n = 21)	Combined (n = 63)		H	df	P
1.7 ± 0.2 (0.2–3.8)	1.5 ± 0.2 (0.1–4.1)	1.0 ± 0.2 (0.2–3.7)	1.4 ± 0.1 (0.1–4.1)	1.3 ± 0.1 (0–4.07)	15.12	5	0.01
8.6 ± 1.2 (0.5–15.7)	8.7 ± 1.3 (0.3–22.1)	6.5 ± 1.3 (0.3–23.1)	7.9 ± 0.7 (0.3–23.1)	8.2 ± 0.6 (0–31.0)	16.68	5	0.005
0.13 ± 0.01 (0.06–0.28)	0.14 ± 0.01 (0.05–0.24)	0.24 ± 0.05 (0.05–0.45)	0.17 ± 0.02 (0.05–0.45)	0.14 ± 0.001 (0–0.45)	9.8	5	0.081
0.012 ± 0.002 (0.0005–0.04)	0.014 ± 0.003 (0.0002–0.05)	0.014 ± 0.004 (0.0003–0.03)	0.014 ± 0.002 (0.0002–0.05)	0.011 ± 0.001 (0–0.05)	15.35	5	0.009

TABLE 5. TONGUE-FLICK FREQUENCY (TF) OF MALE, FEMALE, AND JUVENILE *Mabuya margaritifer* IN RESPONSE TO CRICKET, WATER, AND PUNGENCY CONTROL (COLOGNE) STIMULI.

	Stimulus								
	Cricket			Cologne			Water		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Males	1.25	0.75	0–3	0.33	0.33	0–1	0.33	0.33	0–1
Females	0.57	0.43	0–3	0.14	0.14	0–1	0.00	0.00	0
Juveniles	0.00	0.00	0	0.17	0.17	0–1	0.00	0.00	0
Combined	0.56	0.27	0–3	0.19	0.10	0–1	0.07	0.07	0–1

ern African lizards (*Cordylus cataphractus*: Mouton et al., 2000; *Cordylus giganteus*: Van Wyk, 2000). Investigation into toxicity of southern African millipedes ingested by *Mabuya* and other lizard taxa and possible adaptations by lizards to deal with any such toxins could be rewarding.

Small and large lizards were found to eat similar numbers of prey, but small lizards contained a smaller total volume of prey in their stomachs than large lizards, as predicted for a smaller stomach size. The prediction that smaller lizards consume smaller individual prey was not confirmed. The only predictive parameter for largest individual prey volume consumed was head height. Neither SVL nor gape size, which are normally important factors determining prey handling capacity, correlated with prey size.

Foraging mode and microhabitat use.—Cooper and Whiting (2000) reported intrageneric variation in foraging mode in *Mabuya*, such that three southern African taxa were active foragers, and two were ambush foragers. The average value for PTM for *M. margaritifer* was slightly lower than the arbitrary upper limit for ambush foraging of 10% (Perry, 1999). Large variation in PTM occurred and mean PTM (8.17%) was higher than that reported for two ambush foraging *Mabuya* (*M. acutilabris* 1.4%; *M. spilogaster* 2.9%) but lower than that reported for three active foraging *Mabuya* (*M. striata sparsa* 41.4%; *M. sulcata* 49.2%; *M. variegata* 28.8%; Cooper and Whiting, 2000). *Mabuya margaritifer* moved more frequently (mean = 1.29) compared to two ambushing congenerics (*M. acutilabris*: 0.37; *M. spilogaster*: 0.31) and had an MPM value similar to that of active foraging *Mabuya* (*M. striata sparsa* 1.67; *M. sulcata* 1.35; *M. variegata* 1.19; Cooper and Whiting, 2000). Average speed while moving was faster than three active foraging *Mabuya* for which there are data but similar to values reported for two ambushing *Mabuya* (Cooper and Whiting, 2000). The intermediate character of foraging behavior in this species is reflected in attacks on prey observed in the field. Both attacks from ambush positions (mostly on flying insects) as well as active searches for prey were common. Feeding occurred in all three microhabitats. No significant difference in time spent in each microhabitat or time spent feeding per microhabitat was found. However, consumption of prey in vegetation was difficult to observe and very likely underestimated. Therefore, we presume that lizards visited vegetation for foraging.

Prey chemical discrimination and tongue-flicking.—Lizards rarely tongue-flicked, both during normal activity observed in focal observations in the field as well as in the experimental testing for prey chemical discrimination with cotton applicators. Tongue-flicking observed in the field occurred only during the reproductive season, indicating a social and not foraging related use. This result is typical for ambush foragers, which with few exceptions lack prey chemical discrimination ability (Cooper, 1999). However, tongue-flicking by active foragers may be difficult to observe in the field (W. E. Cooper, pers. comm.). Most bites occurred without prior tongue-flicks and are, therefore, not based on information collected through the vomeronasal system. Lizards were likely driven by the visual system in response to movement. Typically, lizards closely followed the cotton applicator with their eyes, and their attacks closely resembled their attacks on flying insects. In one instance, while moving the applicator toward a test individual, a second lizard pursued it from several meters and bit it. However, bites following tongue-flicking are less likely to be caused by movement. Foraging mode and prey chemical discrimination ability are tightly coupled such that ambushers lack prey chemical discrimination and active foragers can discriminate prey chemicals (Cooper, 1994a). Indeed, this is the case for two other southern African *Mabuya*, one of which (*M. acutilabris*) is an ambusher and cannot detect prey chemicals the other (*M. striata sparsa*) forages actively and can detect prey chemicals (Cooper, 2000). *Mabuya margaritifer* with its rather intermediate foraging mode appears not to use prey chemical discrimination. This species may therefore represent an incipient evolutionary stage from ambush to active foraging, but the ancestral mode of foraging is uncertain in *Mabuya.*

Spatial patterns and crevice use.—Lizards approached by a potential predator (a human) retreated to the safety of a crevice. However, crevices that are deep and narrow enough for protection may be a limited resource. Our examination of spatial distribution in relation to retreat sites showed that adult males excluded other males but shared overnight crevices with females and juveniles. Up to nine individuals were observed sharing a crevice, suggesting that suitable crevices may be limited. These crevices are also used by other lizard species, increasing potential competition for food near the crevice. Foraging distance from crevices may reflect a trade-off between energetic gains and predation risk. If competition were high but predation pressure relatively low, lizards would be predicted to forage further from the crevice. We did not measure this directly, but high variation in PTM values among individual *M. margaritifer* may reflect an attempt to reduce competition between group members by using a larger area for foraging. Estimates for home-range sizes also varied considerably among individuals and may indicate different quality of habitat. We found that females had a significantly smaller home range than males and juveniles. Spatial locations were obtained at the end of the reproductive season when females are normally gravid. Other studies have shown that gravidity influences endurance and thereby escape capabilities (Miles et al., 2000). Smaller home-range size of females at the end of the reproductive season may, therefore, reflect a behavioral change to reduce escape distance during late gestation. This is supported by the observation that females were usually in close proximity to the main crevice.

Body size and evolution of sexual dimorphism.—Males were larger than females in both body and head size. Sexual dimorphism is traditionally explained by sexual selection (male contest competition in particular; Andersson, 1994) or intrasexual niche divergence (Shine, 1989, 1991; Censky, 1996). The food niche overlap for males and females was extensive, and males and females foraged in similar microhabitats. Intrasexual competition as an explanation for the evolution of sexual dimorphism in *M. margaritifer* was therefore not supported. However, aggression between males was observed, mainly during the reproductive season. Also, males are territorial (Branch, 1998), and in our field study, males had nonoverlapping home ranges and were never found sharing crevices with other adult males. This suggests that male contest competition could influence access to mates and that observed sexual size dimorphism is a consequence of sexual selection.

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Appendix 1. Prey Items Obtained from Stomach Contents of 128 Preserved *Mabuya margaritifer*. We report the number of individual prey (*n*), percent of total prey ingested (% *n*), volume (mm^3) of individual prey types, the percentage of total prey by volume (% volume), the number of lizards containing individual prey types (Frequency), and the percentage of lizards containing individual prey types (% frequency).

Prey type	*n*	% *n*	Volume	% volume	Frequency	% frequency
Coleoptera	113	3.43	7978.0	10.49	57	44.53
Buprestidae	2	0.06	110.4	0.15	2	1.56
Carabidae	11	0.33	1000.1	1.32	10	7.81
Cerambycidae	1	0.03	126.1	0.17	1	0.78
Chrysomelidae	4	0.12	275.2	0.36	2	1.56
Coccinellidae	1	0.03	83.9	0.11	1	0.78
Curculionidae	16	0.49	557.1	0.73	10	7.81
Discolomidae	1	0.03	41.8	0.05	1	0.78
Elateridae	1	0.03	71.0	0.09	1	0.78
Scarabaeidae	33	1.00	2795.6	3.68	24	18.75
Unidentified	43	1.31	2916.8	3.84	31	24.22
Diptera	12	0.36	486.3	0.64	9	7.03
Muscidae	3	0.09	111.8	0.15	2	1.56
Unidentified	9	0.27	374.5	0.49	7	5.47
Hemiptera	37	1.12	6144.1	8.08	29	22.66
Aradidae	2	0.06	176.7	0.23	2	1.56
Coreidae	1	0.03	48.0	0.06	1	0.78
Cydnidae	1	0.03	234.1	0.31	1	0.78
Delphacidae	1	0.03	10.9	0.01	1	0.78
Lygaeidae	3	0.09	101.7	0.13	2	1.56
Reduviidae	1	0.03	2291.0	3.01	1	0.78
Unidentified	28	0.85	3281.7	4.32	23	15.63
Hymenoptera	445	13.52	2901.6	3.82	56	43.75
Braconidae	1	0.03	51.4	0.07	1	0.78
Eumenidae	1	0.03	7.3	0.01	1	0.78
Formicidae	430	13.06	1744.4	2.29	50	39.06
Melittidae	1	0.03	839.5	1.10	1	0.78
Tenthredinidae	1	0.03	28.2	0.04	1	0.78
Vespidae	1	0.03	38.8	0.05	1	0.78
Unidentified	10	0.30	192.0	0.25	10	7.81
Isoptera	2413	73.30	24804.4	32.63	41	32.03
Hodotermitidae	501	15.22	4163.6	5.48	5	3.91
Kalotermitidae	1	0.03	66.0	0.09	1	0.78
Termitidae	825	25.06	13815.9	18.17	17	13.28
Unidentified	1086	32.99	6758.9	8.89	20	15.63
Lepidoptera	14	0.43	2178.1	2.86	9	7.03
Unidentified	14	0.43	2178.1	2.86	9	7.03
Mecoptera	2	0.06	49.4	0.06	2	1.56
Bittacidae	2	0.06	49.4	0.06	2	1.56
Orthoptera	48	1.46	14432.6	18.98	41	32.03
Blattidae	1	0.03	453.3	0.60	1	0.78
Blattelidae	1	0.03	32.7	0.04	1	0.78
Mantidae	2	0.06	516.3	0.68	2	1.56
Empusidae	1	0.03	12.9	0.02	1	0.78
Acrididae	5	0.15	1715.0	2.26	2	1.56
Gryllidae	2	0.06	824.8	1.08	2	1.56
Lentulidae	1	0.03	195.7	0.26	1	0.78
Phasmatidae	2	0.06	73.8	0.10	2	1.56
Unidentified	33	1.00	10608.1	13.95	30	23.44
Insect larvae	111	3.37	8910.4	11.72	44	34.38
Araneae	30	0.91	2941.6	3.87	23	17.97

Appendix 1. Continued.

Prey type	n	% n	Volume	% volume	Frequency	% frequency
Chilopoda	3	0.09	231.4	0.30	3	2.34
Diplopoda	23	0.70	845.6	1.11	20	15.63
Vertebrata	4	0.12	3878.9	5.10	4	3.13
Frogs	1	0.03	1474.3	1.92	1	0.78
Lizards	3	0.09	2404.6	3.15	3	1.95
Plant material	32	0.97	219.3	0.29	7	5.47
Flowers	1	0.03	10.4	0.01	1	0.78
Fruits	5	0.15	119.3	0.16	1	0.78
Seeds	21	0.62	89.6	0.12	1	0.78
Leaves	5	0.15	—	—	5	3.25
Annelidae	1	0.03	1.9	0.00	1	0.78
Eggs	4	0.12	22.4	0.03	2	1.56
Totals	3292	100.00	76026.0	100.00		