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Sexual Dimorphism, Reproductive Biology, and Dietary Habits of Psammophiine Snakes (Colubridae) from Southern Africa

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AND TERRI SHINE

Slender-bodied, diurnal “sand snakes” of the genus *Psammophis* are widespread and abundant through Africa, but the general biology of these animals remains poorly known. For example, sexual dimorphism is unstudied because it is difficult to determine the sex of live specimens (uniquely among snakes, the male hemipenis is vestigial). Our dissections of 700 preserved specimens provide detailed ecological information on ten psammophiine species from southern Africa. Males grow larger than females in most taxa, especially in species of large absolute body size. However, sex differences in body proportions (relative head size, relative tail length) are minor. Females produce small clutches (generally <10 eggs), with larger clutches in larger females in some but not all species. *Psammophylax tritaeniatus* differs from the nine *Psammophis* species studied in its higher fecundity and its primary reliance on mammalian rather than reptilian prey. Within *Psammophis*, five species (*P. brevirostris*, *P. jallae*, *P. leopardinus*, *P. subtaeniatus*, *P. trigrammus*) fed mostly on scincid lizards, two (*P. namibensis*, *P. notostictus*) fed mostly on lacertid lizards, and two (*P. trinassalis*, *P. mossambicus*) took approximately equal numbers of lizards and mammals. Although dietary composition thus varied with snake species and body size, conspecific males and females took similar prey types. Thus, despite reports of unusual mating systems in captive psammophiines, these snakes exhibit only minor sexual dimorphism in size, bodily proportions, and dietary habits.

OUR current understanding of snake ecology is derived disproportionately from a relatively small subset of taxa that occur in North America and Europe, with much less information on adaptive radiations in other parts of the world (e.g., Seigel and Ford, 1987). Although recent work has seen a significant reduction in this bias (Akani et al., 2002, 2003a, b), there remain many speciose groups for which available published data are fragmentary at best. One of the best examples involves the Psammophiinae, a lineage of about 40 to 50 species of slender-bodied snakes distributed through Africa, Madagascar, Asia, and Europe (Broadley, 1977, 2002; Branch, 1998; de Haan, 2003a). Most psammophiines are diurnal, fast-moving terrestrial snakes, although some are arboreal and others burrow in loose sand (Branch, 1998). Characteristic of relatively open habitats rather than thick forests, the psammophiines are active hunters that chase down their prey (Branch, 1998). In both general morphology (notably, slender body form) and foraging modes, these snakes are highly convergent with distantly-related lineages of “whip-snakes” in other parts of the world (e.g., the Australian elapid *Demansia*; the North American colubrid *Masticophis*; the South American colubrids *Leimadophis* and *Liophis*; the European *Coluber*: Stewart, 1971; Shine, 1980; Vitt and Vangilder, 1983).

The phylogenetic relationships of psammophiine snakes have been clarified only recently. Bogert (1940) first grouped the genera *Hemirhagerrhis*, *Cerastes* (= *Psammophylax*), *Malpolon*, *Dromophis*, *Psammophis*, and *Rhamphiophis*, based on the absence of hypapophyses on the posterior vertebrae, possession of small, unornamented, and fusiform hemipenes with an undivided sulcus, and grooved posterior maxillary teeth. Subsequently, Broadley (1990) revived *Dipsina* (Jan, 1863) to accommodate *D. multimaculata* (previously placed in *Rhamphiophis*), and the Madagascan genus *Mimophis* was shown to be allied to the group (Nagy et al., 2003). Although the monophyly of psammophiines is well-established (Kelly et al., 2003; Nagy et al., 2003, 2005), their familial relationships remain contentious, not least because of the lack of hemipenial features. Although Rasmussen (1985) included them within the Colubrinae, Cadle (1994) found significant albumin divergence between the two groups, suggesting an earlier divergence. Psammophiines share high chromosomal numbers (Branch, 1980) with other, mainly African, lineages such as the Lamprophiinae, Pseudoxyrhophiinae, Atractaspididae, and Elapidae, and this grouping is maintained in recent molecular colubroid phylogenies (Vidal and Hedges, 2002; Nagy et al., 2003, 2005). There is conflict over the taxonomic levels (families or subfamilies) cur-

rently afforded lineages within this clade, but for convenience we continue to treat sand snakes and their relatives as a subfamily within the artificial 'Colubridae,' although we note that Kelly (2005) has proposed familial status for the lineage, which probably had an Oligocene or early Miocene origin in northeastern Africa (Kelly, 2005).

Recent molecular studies (Kelly, 2005) have shown that existing generic boundaries within the psammophiines are confused. *Rhamphiophis* is polyphyletic, with '*R. acutus*' sister to *Psammophylax*, while *Dromophis lineatus* is nested within *Psammophis* (*D. praeornatus* was not assessed). *Rhamphiophis* and *Malpolon* together form the most basal psammophiine clade, while *Hemirhagerrhis* and *Mimophis* are sister taxa. There remains confusion over species boundaries within the *Psammophis phillipsi-mossambicus* complex, particularly in the western regions. Kelly (2005; unpubl. obs.) has noted no significant genetic divergence between typical *P. phillipsi* and *P. mossambicus*, and Hughes and Wade (2004) have revived *P. occidentalis* for West African populations (to which many previous studies on *P. phillipsi* are probably referable, e.g., Akani et al., 2002, 2003a). Butler's (1993) material is probably composite, possibly including species currently referred to *P. occidentalis*, *P. mossambicus*, and *P. sibilans*, and is here referred to as *P. 'phillipsi'*. We use the recent taxonomy of Broadley (2002), with additional updates (Hughes and Wade, 2004; Kelly, 2005) for analyses in the current paper.

Psammophiine snakes display a series of unusual features in their reproductive biology. For example, the hemipenes of males are virtually vestigial tubelike structures, in strong contrast to the large and elaborately spinous hemipenes of most snake taxa (Dowling and Savage, 1960; Broadley, 1977, 2002). Perhaps as a result, there are few overt morphological differences between male and female psammophiines and hence, the sex of living psammophiines is difficult to determine. Even relative tail lengths and ventral and subcaudal scale counts, sexually dimorphic in most snakes (King, 1989; Shine, 2000), generally display no significant sexual divergence within psammophiine species (Marx, 1988; Akani et al., 2002). However, sexual dimorphism can be manifested in other ways. For example, although sexual dichromatism is rare in snakes (Shine, 1993), male *Malpolon monspessulanus* are uniform in color, whereas females are spotted (de Haan, 1984). Reproductive modes also display unusual variation within this lineage. For example, of the four species within the genus *Psammophylax*, one is oviparous without parental care (*P. tritaenia-*

tus), two are oviparous but with maternal attendance of the clutch (*P. rhombeatus*, *P. multisquamis*), and one is viviparous (*P. variabilis*: Broadley, 1977; De Villiers, 1995; Branch, 1998). Lastly, observations of captive specimens suggest a uniquely complex social system in psammophiines (de Haan, 1984, 2003a, b).

Frustratingly, little is known about the ecology of these animals in the field, despite their abundance over a wide region. Recent detailed autecological studies in Nigeria have clarified the biology of one species (Akani et al., 2002, 2003a), but our inability to determine the sex of living psammophiines poses a major logistical problem for investigation of sex differences in morphology and ecology. For this reason, dissection of preserved specimens in museum collections provides an ideal initial step for any investigation of psammophiine ecology and especially, sexual dimorphism.

MATERIALS AND METHODS

We measured and dissected preserved specimens of ten psammophiine species from southern Africa (south of 17°S latitude, corresponding to the northern borders of Namibia, Botswana, and Zimbabwe) in the collections of the Transvaal Museum and the Port Elizabeth Museum in the Republic of South Africa, and the State Museum of Namibia and the Directorate of Wildlife Conservation (both in Windhoek, Namibia). Identification of all specimens was verified (by WRB) at the time that we gathered ecological and morphological data, and has been updated with respect to subsequent taxonomic changes. For each animal we recorded snout-vent length (henceforth, SVL), tail length, head length (from the posterior margin of the lower jaw to the tip of the snout), head width (at the widest point), eye diameter, and body mass. The specimen was opened with a midventral incision, and any prey items in the alimentary canal (including the hindgut) were removed for later identification. Sex and reproductive status of the snakes were determined by visual inspection of the gonads. Males were considered mature if they had enlarged, turgid testes and/or white, thickened efferent ducts (indicating the presence of sperm). Females were classed as mature if they had thick muscular oviducts, vitellogenic ovarian follicles, and/or oviductal eggs. Frequent tail loss (Akani et al., 2003b) and damage to specimens during collection meant that our sample sizes varied among traits as well as among species; for example, we frequently were unable to obtain reliable measures of body mass or some head dimensions. Analyses of tail length were based

only upon complete (unbroken) tails. We also reviewed all available published literature on dietary habits and reproductive output of psammophiine species for comparison with our own data.

RESULTS

Sample sizes and sex-age composition.—Sample sizes varied from 23 (*P. brevirostris*) to 139 (*P. trinasalis*). The proportion of adult animals (based on gonadal appearance, see above) averaged 61.5% (SD = 11.1%), ranging from 43.8% in *P. trinasalis* to 77.4% in *Psammophylax tritaeniatius*. Although this data set thus shows significant interspecific variation in age structure ($\chi^2 = 32.25$, df = 9, $P = 0.002$), the result is highly influenced by *P. tritaeniatius*. If the data for this species are deleted (leaving the nine *Psammophis* species only), interspecific variation in the proportion of adult animals was no longer statistically significant ($\chi^2 = 13.92$, df = 8, $P = 0.08$). The proportion of adult animals within each species was not significantly related to mean adult body size in an interspecific comparison ($n = 10$, $r = 0.25$, $P = 0.49$).

Restricting analysis to adult animals only, sex ratios (% male) averaged close to equality (mean = 51.2%, SD = 11.2%) overall, but ranged from 33.3% in *P. brevirostris* to 70.4% in *Psammophylax tritaeniatius*. This interspecific variation was statistically significant overall ($\chi^2 = 21.05$, df = 9, $P = 0.01$) and also within the *Psammophis* species only ($\chi^2 = 20.95$, df = 8, $P = 0.01$), but was not associated with mean adult SVL ($n = 10$, $r = -0.27$, $P = 0.46$).

Body sizes and sexual dimorphism.—Because we have data on ten species and multiple variables, there is a risk of artifactually “significant” statistical results due to multiple testing. Hence, we first conducted a multivariate analysis of variance (MANOVA) with sex and species as factors and all morphological variables included as dependent variables. The MANOVA revealed significant differences in mean values of morphological traits among adult specimens of the ten species ($F_{54,1086} = 19.41$, Wilk’s Lambda = 0.80, $P < 0.0001$) as well as differences between males and females ($F_{6,212} = 2.96$, Wilk’s Lambda = 0.92, $P < 0.01$). The degree of sexual divergence in morphology did not differ significantly among the species (interaction between sex and species, $F_{54,1086} = 1.28$, Wilk’s Lambda = 0.73, $P = 0.09$).

The significant sex effect on morphology suggests that it is worthwhile examining dimorphism among adults within each species. Mean

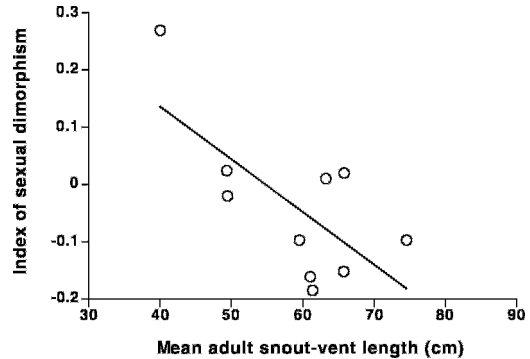


Fig. 1. Allometric trends of sexual size dimorphism in ten species of African snakes of the genera *Psammophis* and *Psammophylax*. The graph shows the index of sexual size dimorphism (SSD) calculated using Gibbons and Lovich’s (1990) method; negative values show species where males average larger than females in adult snout–vent length, whereas positive values indicate that females average larger.

adult snout–vent length (SVL) was used as the measure of absolute body size. A two-factor ANOVA with sex and species as factors, and mean adult SVL as the dependent variable, revealed a marginally non-significant interaction term ($F_{9,217} = 1.85$, $P = 0.06$); that is, the degree of sexual size dimorphism (SSD) did not vary significantly among species overall. Nonetheless, this result was so close to conventional statistical significance that we proceeded with individual species ANOVAs to examine patterns in more detail. As expected from the overall result, conspecific males and females differed significantly in mean adult SVL in only two taxa (*Psammophis jallae* and *Psammophylax tritaeniatius*). Nonetheless, the magnitude of SSD varied over a broad range across the ten species (from males averaging 19% longer in *P. jallae* to females averaging 27% longer in *P. tritaeniatius*). Within the genus *Psammophis*, SSD ranged from males 19% longer (*P. jallae*) to females 2% longer (*P. trinasalis*). Part of this divergence may relate to absolute body size; an interspecific regression of SSD against mean adult SVL (i.e., mean of male and female means) showed a significant trend for increasingly male-biased SSD in species with larger mean adult body sizes (Fig. 1; $n = 10$, $r = -0.73$, $P < 0.02$). However, this statistical significance is due primarily to the inclusion of the single *Psammophylax* species (*P. tritaeniatius*); if this species is omitted, the regression is no longer significant ($n = 9$, $r = -0.37$, $P = 0.33$). Reflecting the degree of SSD, mean values of most morphological traits were significantly higher in males than in females for *Psammophis jallae* (Table 1), and female *Psammophylax tritaeniatius*.

TABLE 1. SAMPLE SIZES AND MORPHOLOGICAL CHARACTERISTICS OF ADULT SPECIMENS OF THE TEN PSAMMOPHIINE SNAKE SPECIES EXAMINED IN OUR STUDY. The table gives values for adult snakes only; criteria for assessment of snakes as adult are given in the text. Some variables could not be measured reliably for some specimens, so sample sizes differ among traits. Data on body mass were log-transformed prior to analysis (to achieve equality of variances), but raw (untransformed) values are reported in the table. Asterisk refers to a significant ($P < 0.10$; see Quinn and Keough, 2003 for reasoning behind the use of 0.10 not 0.05 for this purpose) difference between mean values for adult males vs. females after sequential Bonferroni correction, based on results of one-factor ANOVA with sex as the factor. Table shows P -values prior to Bonferroni correction.

	Snout-vent length (cm)		Tail length (cm)		Head length (mm)		Head width (mm)		Eye diameter (mm)		Body mass (g)	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<i>Psammophis brevirostris</i>												
Sample size	4	6	3	4	4	6	4	6	4	6	4	6
Mean	62.7	67.0	30.5	32.7	30.7	32.7	13.1	15.0	5.0	5.1	100.3	137.8
Standard deviation	11.4	6.7	3.9	3.8	3.8	2.8	2.1	2.7	0.4	0.6	57.1	60.8
Minimum	54.5	58.5	28.2	27.5	28.3	30.0	10.9	12.4	4.6	4.5	63.0	84.0
Maximum	79.0	74.0	35.0	36.0	36.3	36.9	15.9	18.6	5.5	6.2	185.0	235.0
<i>Psammophis jallae</i>												
Sample size	26	11	22	10	25	9	24	9	24	8	24	10
Mean	66.3*	56.5*	31.8*	28.3*	23.9*	21.1*	9.8*	8.6*	4.5*	4.0*	85.9*	38.2*
Standard deviation	7.3	5.4	3.4	2.6	1.9	1.7	1.3	1.6	0.4	0.3	37.6	17.0
Minimum	55.5	46.0	26.0	23.8	20.9	18.5	8.0	6.5	3.7	3.5	34.0	14.0
Maximum	82.0	65.0	37.5	30.6	27.9	23.7	12.3	11.2	5.0	4.6	215.0	75.0
<i>Psammophis leopardinus</i>												
Sample size	9	6	6	3	9	6	9	6	8	6	8	6
Mean	72.2	68.5	33.4	29.2	31.0	31.9	14.2	14.8	5.1	5.3	117.3	173.0
Standard deviation	9.0	13.6	3.7	4.2	6.0	4.9	3.0	3.0	0.6	0.6	78.9	172.5
Minimum	58.2	54.2	29.5	24.4	23.8	27.1	10.2	11.2	4.4	4.8	10.0	50.0
Maximum	83.0	93.0	38.5	32.1	39.4	41.1	19.2	20.2	6.0	6.3	280.0	520.0
<i>Psammophis namibensis</i>												
Sample size	10	10	8	9	1	4	1	4	1	2	2	7
Mean	58.3	57.5	25.0	25.3	25.1	24.1	9.0	10.4	4.4	4.7	59.8	40.9
Standard deviation	6.1	6.5	2.2	3.8	—	2.2	—	1.2	—	0.3	14.5	19.3
Minimum	49.5	47.5	21.5	18.5	25.1	22.1	9.0	8.6	4.4	4.5	49.5	20.0
Maximum	66.0	68.0	29.0	32.0	25.1	27.0	9.0	11.1	4.4	4.9	70.0	70.0
<i>Psammophis notostictus</i>												
Sample size	31	35	27	29	29	33	29	33	27	33	29	32
Mean	48.8	48.9	22.4	21.2	20.8	20.4	9.1	9.5	3.6	3.6	31.7	27.9
Standard deviation	9.6	6.6	4.0	3.0	3.3	2.8	2.3	1.5	0.5	0.4	16.6	14.1
Minimum	27.0	38.0	15.5	15.5	15.1	15.1	6.4	6.5	2.7	2.9	10.0	15.0
Maximum	72.0	65.0	32.5	29.0	27.4	26.7	16.9	13.3	4.5	4.4	73.0	80.0
<i>Psammophis mossambicus</i>												
Sample size	27	10	21	7	26	9	24	9	25	8	25	8
Mean	81.7	75.7	33.2	31.3	35.5	33.5	16.3	15.1	5.9	6.0	258.1	169.8
Standard deviation	18.5	14.4	7.3	5.7	6.4	4.2	3.8	1.9	0.9	0.5	191.0	61.1
Minimum	41.7	44.5	17.6	22.0	21.5	24.8	9.0	12.1	4.4	5.2	30.0	78.0
Maximum	114.5	92.0	45.0	37.1	45.6	37.5	23.7	18.1	7.7	6.9	700.0	280.0
<i>Psammophis subtaeniatus</i>												
Sample size	21	16	16	13	18	14	18	12	19	14	18	15
Mean	61.9	57.7	33.4	31.8	25.7	25.0	10.9	10.8	4.5	4.3	78.1	58.2
Standard deviation	10.4	9.9	5.3	6.4	3.4	3.6	1.9	2.2	0.5	0.4	44.5	35.9
Minimum	46.5	40.3	23.5	21.5	21.9	18.1	8.2	7.5	3.7	3.7	27.0	17.0
Maximum	85.0	77.5	43.0	44.5	35.9	30.7	14.6	15.4	5.5	4.9	190.0	128.0

TABLE 1. CONTINUED.

	Snout-vent length (cm)		Tail length (cm)		Head length (mm)		Head width (mm)		Eye diameter (mm)		Body mass (g)	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
<i>Psammophis trigrammus</i>												
Sample size	11	3	9	2	10	3	10	3	10	3	10	3
Mean	67.8	61.7	40.0	34.1	24.0	23.4	10.3	9.9	4.0	3.8	55.5	47.0
Standard deviation	10.3	9.7	6.4	4.1	3.7	4.4	1.6	2.3	0.5	0.5	27.7	38.0
Minimum	51.2	50.5	30.7	31.2	17.6	18.8	8.1	7.7	3.3	3.3	12.0	15.0
Maximum	89.5	67.5	52.0	37.0	31.7	27.5	12.8	12.3	5.0	4.2	110.0	89.0
<i>Psammophis trinasalis</i>												
Sample size	69	18	60	15	47	13	47	13	43	12	59	15
Mean	52.4	49.9	24.1	23.2	20.4	22.0	8.7	9.0	3.9	4.0	45.2	38.0
Standard deviation	9.9	8.0	4.8	4.2	3.4	3.4	1.6	1.8	0.5	0.5	24.2	18.4
Minimum	35.0	38.9	14.3	14.7	15.2	18.2	6.0	7.3	2.8	3.5	13.0	17.0
Maximum	71.0	71.5	32.0	33.0	28.1	30.5	12.4	13.6	5.1	5.1	112.0	88.0
<i>Psammophylax tritaeniatus</i>												
Sample size	28	13	28	12	23	8	23	6	23	5	22	7
Mean	36.5*	44.5*	10.3	11.7	15.7*	18.3*	8.3*	10.2*	2.8	2.9	22.2	36.4
Standard deviation	9.5	6.4	2.4	2.6	2.4	2.3	1.2	0.7	0.5	0.4	17.2	21.9
Minimum	21.5	33.0	6.0	7.9	12.8	15.4	6.8	9.0	2.0	2.5	5.0	10.0
Maximum	60.6	52.0	16.0	16.0	21.1	22.0	11.3	10.7	4.0	3.4	75.0	75.0

natus had larger heads than did conspecific males (Table 1). However, we detected no statistically significant sexual dimorphism in any of the other species (Table 1).

We also examined whether or not the sexes differed in body proportions at the same body length (i.e., after controlling for any differences in mean adult SVL between the sexes). We did this by including SVL as a covariate in our analyses. A two-factor ANCOVA with species and sex as factors revealed significant interaction terms between the main factors (and with SVL) in each case, so we proceeded to conduct ANCOVAs on data sets for each species separately. To avoid the consequent problem of multiple testing, we used sequential Bonferroni corrections and retained results with P -values < 0.10 as biologically significant (Quinn and Keough, 2003). Females had longer tails (relative to SVL) than did conspecific males in *P. leopardinus* (Table 2). At the same SVL, female *P. trinasalis* had longer heads but weighed less than did conspecific males. Head length increased more rapidly with increasing SVL in female *Psammophylax tritaeniatus* than in males, but the reverse was true in *Psammophis notostictus* (Table 2). Relative to head length, female *P. notostictus* had wider heads than their male counterparts. However, these are occasional exceptions to a general pattern of no significant sex-based divergence in body proportions among the psammophiine taxa that we examined, even in species with substantial divergence in mean values for adult body size (Table 2).

Fecundity.—Clutch sizes in dissected snakes ranged from 2–15 eggs, and mean values differed significantly among species (ANOVA, $F_{9,34} = 13.83$, $P < 0.0001$). However, inspection of the data suggested that much of this interspecific variation might be due to differing mean maternal body sizes among species (Fig. 2). Thus, we reanalyzed these data using one-factor ANCOVA with species as the factor and maternal SVL as the covariate. Slopes of this relationship differed among species ($F_{9,24} = 4.30$, $P < 0.002$); that is, clutch size increased rapidly with increasing SVL in some taxa but not at all in others. Much of this difference is due to high fecundity values in the single *Psammophylax* species (*P. tritaeniatus*; Fig. 2); but the interaction term remains significant even if we delete this taxon (i.e., restrict the analysis to *Psammophis* species only; $F_{8,22} = 3.93$, $P < 0.005$; Fig. 2).

Dietary composition.—Lizards and mammals were the most common prey taxa in guts of psammophiine snakes (Table 3). Multiple logistic regression with species, sex, and SVL of the predator as independent variables, and prey type (mammal vs. reptile) as the dependent variable, showed that dietary composition differed significantly among psammophiine species (likelihood ratio test, $\chi^2 = 32.12$, $df = 7$, $P < 0.0002$) and that larger snakes were more likely to take mammals rather than reptiles ($\chi^2 = 15.78$, $df = 1$, $P < 0.0001$). However, the sex of a snake did not influence its dietary composition at this level of analysis ($\chi^2 = 1.90$, $df = 1$, $P = 0.39$).

TABLE 2. SEX DIFFERENCES IN BODY PROPORTIONS IN THE PSAMMOPHIINE SNAKE SPECIES EXAMINED IN OUR STUDY. This table shows the results of tests for heterogeneity of slopes, followed by single-factor analysis of covariance if slopes did not differ significantly. Some variables could not be measured reliably for some specimens (due to damage, tail loss, etc.), so sample sizes differ among traits. Data on body mass were log-transformed prior to analysis (to achieve equality of variances). Asterisk and boldface font refer to a significant ($P < 0.10$; see Quinn and Keough, 2003) difference between adult males vs. females after sequential Bonferroni correction. Table shows P -values prior to Bonferroni correction. Sex was used as the factor in all analyses.

Trait	Covariate	Species	Heterogeneity of slopes test			Analysis of covariance		
			F	df	P	F	df	P
Tail length	Snout-vent length	<i>Psammophis brevirostris</i>	6.34	1,5	0.05	0.13	1,6	0.75
		<i>Psammophis jallae</i>	4.28	1,46	0.04	0.38	1,47	0.54
		<i>Psammophis leopardinus</i>	0.42	1,14	0.53	11.58*	1,15	0.004
		<i>Psammophis namibensis</i>	0.04	1,18	0.84	0.86	1,19	0.36
		<i>Psammophis notostictus</i>	2.25	1,70	0.14	0.68	1,71	0.41
		<i>Psammophis mossambicus</i>	0.56	1,39	0.46	0.97	1,40	0.33
		<i>Psammophis subtaeniatus</i>	0.01	1,37	0.93	0.0001	1,38	0.99
		<i>Psammophis trigrammus</i>	0.81	1,14	0.38	0.44	1,15	0.52
		<i>Psammophis trinasalis</i>	1.10	1,88	0.30	0.01	1,89	0.93
		<i>Psammophylax tritaeniatus</i>	0.16	1,82	0.69	3.15	1,83	0.08
Head length	Snout-vent length	<i>Psammophis brevirostris</i>	1.55	1,8	0.25	0.08	1,9	0.79
		<i>Psammophis jallae</i>	0.14	1,47	0.71	0.71	1,48	0.40
		<i>Psammophis leopardinus</i>	0.33	1,20	0.57	3.03	1,21	0.10
		<i>Psammophis namibensis</i>	6.87	1,3	0.42	0.21	1,4	0.67
		<i>Psammophis notostictus</i>	6.03*	1,77	0.02	—	—	—
		<i>Psammophis mossambicus</i>	0.05	1,42	0.83	0.90	1,43	0.35
		<i>Psammophis subtaeniatus</i>	0.01	1,38	0.94	0.29	1,39	0.59
		<i>Psammophis trigrammus</i>	0.45	1,17	0.51	1.49	1,18	0.24
		<i>Psammophis trinasalis</i>	0.68	1,73	0.41	6.85*	1,74	0.01
		<i>Psammophylax tritaeniatus</i>	6.12*	1,52	0.02	—	—	—
Head width	Head length	<i>Psammophis brevirostris</i>	1.59	1,8	0.24	0.48	1,9	0.51
		<i>Psammophis jallae</i>	0.001	1,47	0.97	1.59	1,48	0.21
		<i>Psammophis leopardinus</i>	3.35	1,21	0.08	0.43	1,22	0.52
		<i>Psammophis namibensis</i>	0.61	1,3	0.49	3.31	1,4	0.14
		<i>Psammophis notostictus</i>	1.00	1,77	0.32	6.85*	1,78	0.01
		<i>Psammophis mossambicus</i>	4.49	1,42	0.04	0.01	1,43	0.94
		<i>Psammophis subtaeniatus</i>	0.77	1,38	0.39	0.98	1,39	0.33
		<i>Psammophis trigrammus</i>	0.29	1,17	0.60	0.01	1,18	0.92
		<i>Psammophis trinasalis</i>	0.98	1,73	0.33	0.14	1,74	0.71
		<i>Psammophylax tritaeniatus</i>	1.74	1,52	0.19	0.07	1,53	0.80
Eye diameter	Head length	<i>Psammophis brevirostris</i>	0.34	1,8	0.52	0.59	1,9	0.46
		<i>Psammophis jallae</i>	1.64	1,45	0.21	0.10	1,46	0.75
		<i>Psammophis leopardinus</i>	0.01	1,20	0.92	0.05	1,21	0.83
		<i>Psammophis namibensis</i>	—	—	—	—	—	—
		<i>Psammophis notostictus</i>	0.37	1,75	0.55	0.17	1,76	0.69
		<i>Psammophis mossambicus</i>	0.09	1,42	0.77	2.24	1,43	0.14
		<i>Psammophis subtaeniatus</i>	0.97	1,40	0.33	0.41	1,41	0.53
		<i>Psammophis trigrammus</i>	0.29	1,16	0.60	0.80	1,17	0.34
		<i>Psammophis trinasalis</i>	0.52	1,68	0.47	2.62	1,69	0.11
		<i>Psammophylax tritaeniatus</i>	1.50	1,82	0.22	0.01	1,51	0.91

TABLE 2. CONTINUED.

Trait	Covariate	Species	Heterogeneity of slopes test			Analysis of covariance		
			F	df	P	F	df	P
Ln body mass	Snout-vent length	<i>Psammophis brevirostris</i>	0.08	1,8	0.78	3.31	1,48	0.08
		<i>Psammophis jallae</i>	0.60	1,49	0.44	4.99*	1,50	0.03
		<i>Psammophis leopardinus</i>	1.19	1,19	0.29	0.31	1,20	0.58
		<i>Psammophis namibensis</i>	2.18	1,3	0.24	3.51	1,4	0.13
		<i>Psammophis notostictus</i>	4.30	1,77	0.04	1.85	1,78	0.18
		<i>Psammophis mossambicus</i>	0.62	1,43	0.44	3.26	1,44	0.08
		<i>Psammophis subtaeniatus</i>	0.93	1,43	0.34	0.002	1,44	0.96
		<i>Psammophis trigrammus</i>	2.42	1,14	0.14	0.02	1,15	0.90
		<i>Psammophis trinasalis</i>	0.63	1,72	0.43	6.43*	1,73	0.01
		<i>Psammophylax tritaeniatus</i>	1.44	1,48	0.24	0.54	1,49	0.47

Restricting analysis to lizard prey items only, we used lizard familial category as our dependent variable and repeated the multiple logistic regression with the same independent variables as above. The relative numbers of each type of lizard consumed differed among psammophiine species ($\chi^2 = 87.09$, $df = 45$, $P < 0.0002$) and were significantly affected by the snake's body size (agamids tended to be consumed by larger snakes; $\chi^2 = 19.12$, $df = 5$, $P < 0.002$). However, male and female psammophiines did not differ in diets at this level of analysis ($\chi^2 = 2.09$, $df = 5$, $P = 0.84$). Overall, five of the *Psammophis* species fed mostly on scincid prey (*P. brevirostris*, *P. jallae*, *P. leopardinus*, *P. subtaeniatus*, *P. trigrammus*), two fed mostly on lacertid lizards (*P. namibensis*, *P. notostictus*) and the remaining taxa (*P. trinasalis*, *P. mossambicus*) took approximately equal numbers of lizards and mammals. In contrast, mammals predominated as prey items for *Psammophylax tritaeniatus* (Table 3).

DISCUSSION

Our dissections of 700 preserved specimens provide the first detailed information on these topics for ten psammophiine species from southern Africa. Importantly, previous researchers who have relied on measurements from living snakes have been unable to determine the sex of their specimens and, hence, have not been able to assess the degree of sexual divergence in traits such as body sizes, body shapes, and prey types (Akani et al., 2002). Our dissection data enables such an analysis.

Patterns of sexual dimorphism are of the most direct interest in this respect, because we might expect that a complex mating system including territorial defense (de Haan, 1984), pheromonally-mediated dominance hierarchies among members of both sexes (de Haan, 2003a), and

vestigial hemipenes in males (Broadley, 2002) would involve selective pressures different from those that operate on most other snakes. However, major features of sexual dimorphism in psammophiines appear to be broadly similar to those in other snakes. For example, males attained mean adult body sizes similar to or larger than those of conspecific females in all the *Psammophis* species, a genus in which male-male combat has been reported (Pitman, 1974, for *Psammophis punctulatus*; and de Haan, 2003a refers to combat bouts among captive *Psammophis*). In contrast, females attained larger mean body sizes than did conspecific males in the single species of *Psammophylax*, a genus in which combat has not been reported (Shine, 1994). Exactly the same correlation is evident in intergeneric comparisons among snakes overall, presumably reflecting advantages of larger body size in physical rivalry between males (Shine, 1994).

The degree of male size superiority tended to increase with mean absolute body size in an interspecific comparison among the psammophiines, again mirroring the overall pattern among snakes (Shine, 1994) as well as many other kinds of animals (Clutton-Brock et al., 1977; Harvey and Ralls, 1985; Reiss, 1989). Head sizes (especially width) tended to be greater in females than in conspecific males of similar body size in three species (*Psammophis notostictus*, *P. trinasalis*, *Psammophylax tritaeniatus*), with no significant sex divergence in this trait in the other seven taxa. Again, these relationships fit well with those of available data on other snakes. Shine (1991) reported significant sex-based divergence in relative head size in 47% of 114 species of snakes for which he obtained data, and in most of these cases (64%) it was females that were relatively larger-headed.

In keeping with Butler's (1993) report for *P. 'phillipsi'* (see comments above regarding no-

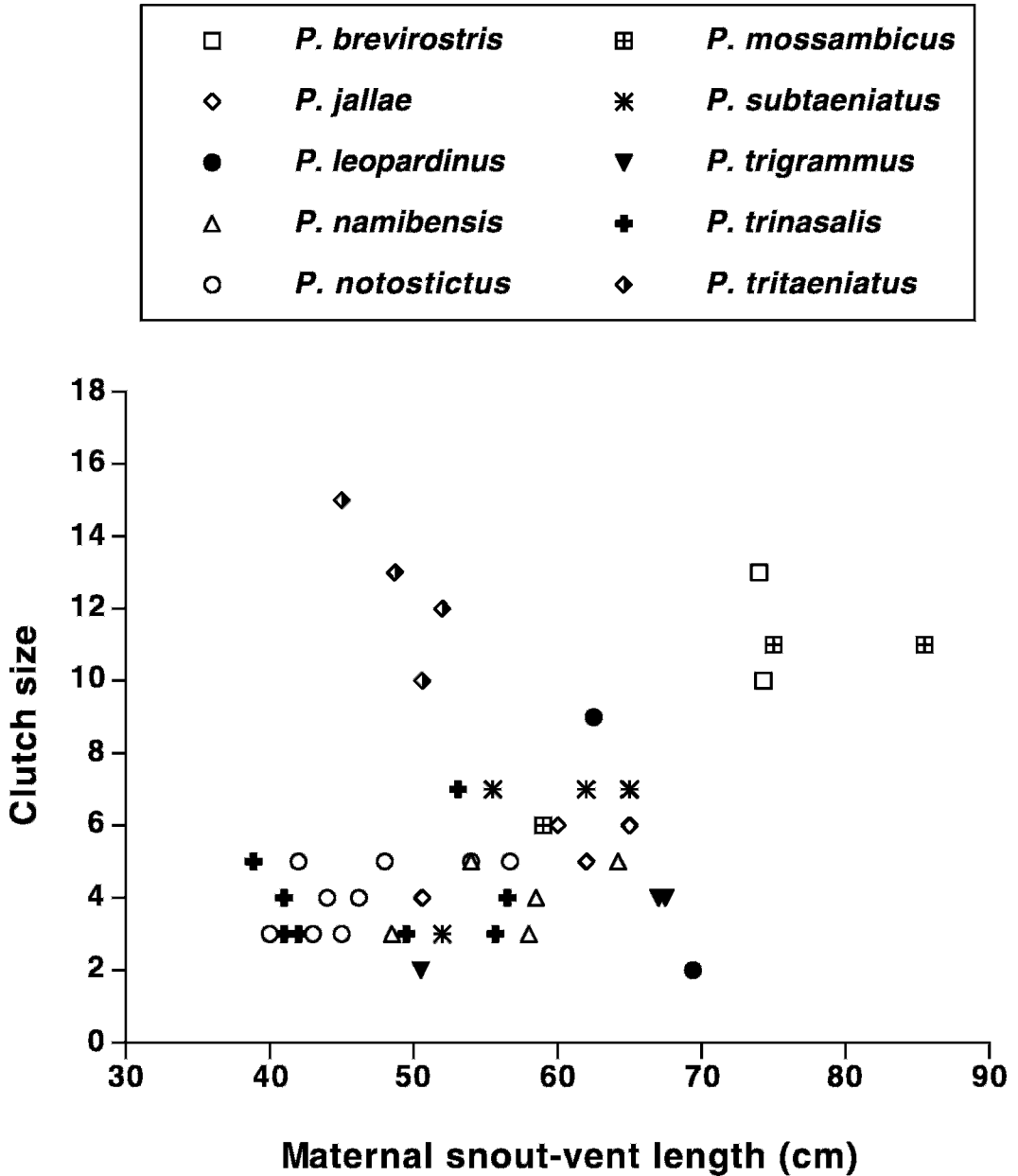


Fig. 2. Clutch sizes relative to maternal body size (snout-vent length) in ten species of African snakes of the genera *Psammophis* and *Psammophylax*. All species belong to the genus *Psammophis* except for *Psammophylax tritaeniatus*.

menclature) from tropical Africa, we found no significant sexual dimorphism in relative tail length in most psammophiine species that we examined. However, in the sole exception (*P. leopardinus*), tails of males were actually shorter relative to SVL than were those of conspecific females. To our knowledge, this is the first report of this “reverse” dimorphism. Extensive reviews

confirm that relative to SVL, male snakes generally have longer tails than conspecific females, although the disparity is often small (King, 1989; Shine, 2000).

Given that the lack of sex differences in tail length of psammophiines may be functionally linked to their unusually small hemipenes (King, 1989), what selective advantages drove the re-

TABLE 3. PREY ITEMS RECORDED FROM ALIMENTARY TRACTS OF PRESERVED SPECIMENS OF *Psammophis* AND *Psammophylax* SPECIES IN MUSEUM COLLECTIONS FROM SOUTHERN AFRICA. The table shows the number of snakes of each species containing each prey type.

Prey type	<i>Psammophis breviostris</i>	<i>Psammophis jallae</i>	<i>Psammophis leopardinus</i>	<i>Psammophis namibensis</i>	<i>Psammophis notostictus</i>	<i>Psammophis mossambicus</i>	<i>Psammophis subtaeniatus</i>	<i>Psammophis trigrammus</i>	<i>Psammophis trinasis</i>	<i>Psammophylax tritaeniatus</i>
Lizards										
Lizard spp.			1			3	2	5		2
Agamidae		1			1					
<i>Agama</i> sp.							1			
<i>Agama aculeata</i>							1			
Gekkonidae							1	1	1	
<i>Pachydactylus</i> sp.						1			1	
<i>Ptenopus kochi</i>				1						
Lacertidae	1	3		8	9		2	1	10	1
Scincidae		4	2	1	2	7	2	1		1
<i>Trachylepis</i> sp.	2		2	1	2	3		5	6	1
<i>Trachylepis striata</i>							2			
<i>Trachylepis variegata</i>	1							1	1	
Snakes										
Colubridae										
<i>Aparallactus capensis</i>						1				
Typhlopidae										
Typhlopidae						1				
Mammals	1		1		2	9			5	4
Neonatal rodent										1

duction in hemipenis size within psammophiines or their ancestors? These vestigial hemipenes may facilitate rapid disengagement for mating pairs likely to encounter predators in open habitats (de Haan, 2003a). However, the spinous morphology of snake hemipenes also may have evolved to prevent female escape, especially if insemination is forcible (Shine et al., 2003). The complex pheromonal marking of conspecific animals by psammophiines suggests that male-female interactions may be mediated differently than in most other snakes, perhaps reducing or eliminating this battle between the sexes. In turn, such a change could favor (or allow, for locomotor advantages?) reduction in the size of the hemipenis, and thus a reduction in the degree of sexual dimorphism in relative tail length.

Our data on reproductive output in psammophiines support earlier statements that the study taxa are oviparous and produce relatively small clutches of eggs (generally <10). Previous studies have described reproduction of *P. breviostris* and *P. crucifer* in South Africa (Haagner, 1988), *P. elegans* in Ghana (Spawls, 1980), *P. 'phillipsi'* in tropical Africa (Butler, 1993) and Nigeria (Akani et al., 2002), and *P. leightoni*, *P. crucifer*, and *P.*

notostictus in South Africa (Haagner, 1988; Flemming, 1994). Data are more extensive for *Psammophylax* species, especially *P. rhombeatus* (Broadley, 1977; De Villiers, 1995; Flemming and Douglas, 1997), but also *P. tritaeniatus* (Broadley, 1977), *P. multisquamis* (Loveridge, 1942; Spawls in Broadley, 1977), and *P. variabilis* (Broadley et al., 2003). Other psammophiine genera have attracted less attention, although Haagner (1988) reported a clutch of four eggs in a *Dipsina multimaculata* and Broadley and Hughes (2000) noted three eggs in a specimen of *Hemirhagerhis kelleri*. Most previous work has not involved large enough sample sizes to examine allometry of reproductive output, but the trend for increasing fecundity with increasing maternal body size in our own data (albeit non-uniform among species and weak or absent intraspecifically) aligns with general patterns among snakes (Fitch, 1970; Seigel and Ford, 1987; see Akani et al., 2002 for *Psammophis*). One study on *P. 'phillipsi'* reported no significant correlation between maternal body size and output, but attributed this result to combining samples from different regions (Butler, 1993; and also perhaps different taxa, see above).

The small clutch sizes of *Psammophis* species fit well with a general trend for slender-bodied snake species to exhibit relatively low relative clutch masses, perhaps simply reflecting physical restrictions (limited abdominal space) for accommodating the clutch (Seigel and Fitch, 1984; Shine, 1992; Du et al., 2005). Consistent with this hypothesis, the more heavy-bodied species *Psammophylax tritaeniatus* (like its congeners: Broadley, 1977; De Villiers, 1995) produces a much larger number of eggs per clutch (despite its smaller body length). Reproductive investment in the slender *Psammophis* species also may be constrained by costs to maternal mobility while carrying the clutch, because these animals rely upon speed to forage and to escape predators, and gravid females continue to feed (at least in *P. phillipsi* [occidentalis]: Akani et al., 2003a). As noted above, there is interesting diversity in maternal investment within *Psammophylax*. Although egg-guarding has not been recorded in *P. tritaeniatus* (Sweeney, 1971; Broadley, 1978), this species lays eggs with well-developed embryos (Sweeney, 1971) and the incubation period of eggs (43–45 days; Haagner, 1988) is consequently relatively brief. *Psammophylax tritaeniatus* differs from *Psammophis* species but resembles its congener *P. rhombatus* not only in its high fecundity (above) but also in its concentration on mammalian rather than reptilian prey (Appendix 1). *Psammophylax rhombatus* also feeds primarily upon mammals (Van Wyk, 1988; Douglas, 1992; Appendix 1).

Most data on psammophiine diets are anecdotal, except the reports by Akani et al. (2003a) and Luiselli et al. (2004) on *P. phillipsi* from Nigeria. These snakes took mainly lizards (especially *Agama* and *Trachylepis* [formerly *Mabuya*]), resembling our study taxa in this respect. Akani et al. (2003a) reported a trend for larger snakes to take larger prey and, hence, (although non-significantly) to take mammalian rather than reptilian prey. A similar shift from reptiles to mammals with increasing predator size attains statistical significance in our own sample. Moreover, the large psammophiines eat a wide variety of prey classes, with ophidian prey mainly taken by the larger species such as *Psammophis phillipsi* (Akani et al., 2003a) and *P. mossambicus* (this study). The largest psammophiine, *Malpolon monspessulanus* (maximum size 2.17 m), has a wide prey spectrum, with juveniles taking mainly lizards, but adults taking mammals (including small rabbits), birds, snakes (five species), and even tortoises (Vericad and Escarre, 1976; Schleich et al., 1996). This increase in prey diversity also appears to be reflected in venom toxicity, where clinically important symptoms

have been associated with bites from *P. mossambicus* (Spawls and Branch, 1995) and *Malpolon monspessulanus* (Gonzales, 1979).

The interspecific divergence in types of lizards consumed may involve either habitat-associated differences in prey availability or some shift in snake foraging habits. Whether the prevalence of lacertids in the diet of both *Psammophis notostictus* and *P. namibensis* reflects the abundance of these diurnal lizards in arid regions of southwestern Africa (Branch, 1998), or limitations imposed by their extremely elongate body form, remains unknown. A combination of our own data with that published by other authors reveals clear dietary differences at the generic as well as specific level (Appendix 1). For example, the bark snakes (*Hemirhagerrhis*) represent a specialized group of psammophiines adapted for living under tree bark and in rock cracks and feeding on small lizards and their eggs. Species of the genus *Psammophis* primarily take lizards, whereas the more heavy-bodied *Psammophylax* specialize on frogs and mammals.

Available data reveal extensive interspecific variation in morphology and ecology among psammophiines, but sexual dimorphism appears to be relatively limited. Given the unusual social systems reported in captive psammophiines, plus the abundance of these animals over such a broad geographic range, there is considerable potential for field studies to expand our understanding of the diversity of mating systems in snakes. However, we need reliable methods to determine the sex of living psammophiines before such studies can be conducted. Although we have found that male and female psammophiine snakes diverge only slightly in traits such as adult body sizes and body shapes, detailed studies on other kinds of animals often have revealed reliable means of non-destructive sex determination (Bonnet et al., 2001; Bermudez-Humaran et al., 2002; Gilgenkrantz, 2004). It would be worthwhile exploring such methods with these snakes to facilitate behavioral research on this intriguing lineage.

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APPENDIX 1. PUBLISHED RECORDS OF DIETARY ITEMS FOR PSAMMOPHINE SNAKES. Numbers in parentheses refer to the number of snakes containing each prey type.

Snake species	Prey type	Prey species	Authority
<i>Dromophis lineatus</i>	Frog	<i>Ptychadena mascareniensis</i>	Loveridge, 1933
<i>Dromophis lineatus</i>	Lizard	spp.	Haagner et al., 2000
<i>Hemirhagerrhis hildebrandtii</i>	Lizard	<i>Hemidactylus platycephalus</i> eggs	Hoegers and Johnston, 1982
<i>Hemirhagerrhis kelleri</i>	Lizard	<i>Holodactylus africanus</i>	Broadley and Hughes, 2000
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Hemidactylus mabouia</i>	Broadley, 1997
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Lygodactylus capensis</i>	Broadley, 1997
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Lygodactylus angolensis</i>	Loveridge, 1933
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Lygodactylus picturatus</i>	Pitman, 1974
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Pachydactylus punctatus</i>	Broadley, 1997
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Panaspis wahlbergi</i>	Broadley and Hughes, 2000
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Trachylepis striata</i>	Broadley, 1997
<i>Hemirhagerrhis nototaenia</i>	Lizard	<i>Trachylepis varia</i>	Broadley and Hughes, 2000
<i>Hemirhagerrhis viperina</i>	Lizard	<i>Trachylepis laevis</i>	Bogert, 1940 (see Broadley, 1997)
<i>Psammophis angolensis</i>	Lizard	<i>Panaspis</i> sp.	Broadley et al., 2003
<i>Psammophis biseriatus</i>	Lizard	<i>Chamaeleo dilepis</i> (2)	Loveridge, 1936
<i>Psammophis biseriatus</i>	Lizard	<i>Latastia longicauda revuili</i>	Loveridge, 1936
<i>Psammophis biseriatus</i>	Lizard	<i>Lygosoma sundevallii</i> (2)	Loveridge, 1933
<i>Psammophis biseriatus</i>	Lizard	<i>Trachylepis planifrons</i>	Loveridge, 1936
<i>Psammophis brevirostris</i>	Lizard	<i>Acontias</i> sp.	Branch and Haagner, 1999
<i>Psammophis brevirostris</i>	Mammal	<i>Rhodomys pumilio</i>	Marais, 1993
<i>Psammophis crucifer</i>	Lizard	<i>Chamaesaura anguina</i>	Branch and Bauer, 1995
<i>Psammophis mossambicus</i>	Bird	<i>Merops breweri</i> eggs	Schmidt and Branch, 2005
<i>Psammophis mossambicus</i>	Frog	<i>Phrynobatrachus minutus</i>	Loveridge, 1933
<i>Psammophis mossambicus</i>	Frog	<i>Ptychadena mascareniensis</i>	Loveridge, 1933
<i>Psammophis mossambicus</i>	Lizard	<i>Acanthocercus atricollis</i>	Loveridge, 1936
<i>Psammophis mossambicus</i>	Lizard	<i>Lygosoma sundevallii</i>	Loveridge, 1942
<i>Psammophis mossambicus</i>	Lizard	<i>Trachylepis maculilabris</i>	Loveridge, 1933
<i>Psammophis mossambicus</i>	Lizard	<i>Trachylepis varia</i>	Loveridge, 1942
<i>Psammophis mossambicus</i>	Mammal	<i>Lemniscomys striatus massaicus</i>	Loveridge, 1936
<i>Psammophis mossambicus</i>	Mammal	<i>Oenomys bacchante editus</i>	Loveridge, 1936
<i>Psammophis mossambicus</i>	Mammal	rodent fur	Loveridge, 1942
<i>Psammophis mossambicus</i>	Mammal	rodent fur	Loveridge, 1936

APPENDIX I. CONTINUED.

Snake species	Prey type	Prey species	Authority
<i>Psammophis mossambicus</i>	Snake	<i>Dendroaspis polylepis</i>	Broadley et al., 2003
<i>Psammophis mossambicus</i>	Snake	<i>Naja annulifera</i>	Haagner, 1990
<i>Psammophis mossambicus</i>	Snake	<i>Philothamnus semivariegatus</i>	Bruton and Haacke, 1980
<i>Psammophis mossambicus</i>	Snake	<i>Thelornis capensis</i>	Bruton and Haacke, 1980
<i>Psammophis notostictus</i>	Lizard	<i>Chamaesaura anguina</i>	Branch and Bauer, 1995
<i>Psammophis notostictus</i>	Lizard	<i>Merops suborbitalis</i>	Mertens, 1954
<i>Psammophis notostictus</i>	Lizard	<i>Trachylepis acutilabris</i>	Mertens, 1954
<i>Psammophis orientalis</i>	Frog	<i>Arthroleptis stenodactylus</i> (2)	Loveridge, 1942
<i>Psammophis orientalis</i>	Frog	<i>Pyxicephalus edulis</i>	Loveridge, 1936
<i>Psammophis orientalis</i>	Lizard	<i>Heliobolus spekii</i>	Loveridge, 1933
<i>Psammophis orientalis</i>	Lizard	<i>Nucras boulengeri</i> (2)	Loveridge, 1933
<i>Psammophis orientalis</i>	Mammal	<i>Rattus rattus</i>	Loveridge, 1933
<i>Psammophis phillipsi</i>	Insect	Orthopteran	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Insect	Mantid (2)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Mammal	<i>Crocidura</i> sp. (7)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Mammal	<i>Rattus rattus</i> (5)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Mammal	<i>Mus musculoides</i> (19)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Mammal	Mice (31)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Snake	<i>Psammophis phillipsi</i>	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Snake	<i>Natriceres</i> sp.	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Snake	sp.	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Lizard	<i>Trachylepis maculilabris</i> (6)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Lizard	<i>Trachylepis</i> sp. (26)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Lizard	<i>Mochlus fernandi</i> (3)	Luiselli et al., 2004
<i>Psammophis phillipsi</i>	Lizard	<i>Agama agama</i> (81)	Luiselli et al., 2004
<i>Psammophis punctulatus</i>	Lizard	<i>Latastia longicauda revoili</i>	Loveridge, 1936
<i>Psammophis subtaeniatus</i>	Frog	<i>Afrana angolensis</i>	Schmidt, 2002
<i>Psammophis subtaeniatus</i>	Lizard	<i>Trachylepis sulcata</i>	Mertens, 1954
<i>Psammophis trigrammus</i>	Lizard	<i>Pachydactylus rugosus</i>	Mertens, 1954
<i>Psammophis zambiensis</i>	Frog	spp.	Haagner et al., 2000
<i>Psammophis zambiensis</i>	Lizard	<i>Eumecia anchietae</i>	Broadley et al., 2003
<i>Psammophylax multisquamis</i>	Mammal	mice (3)	Bogert, 1940
<i>Psammophylax multisquamis</i>	Snake	<i>Philothamnus battersbyi</i>	Broadley, 1977
<i>Psammophylax rhombeatus</i>	Frog	<i>Strongylopus grayii</i>	Broadley, 1977
<i>Psammophylax rhombeatus</i>	Lizard	<i>Pachydactylus geitje</i>	Branch and Bauer, 1995
<i>Psammophylax tritaeniatus</i>	Frog	<i>Afrana</i> sp.	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Frog	<i>Breviceps mossambicus</i>	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Frog	<i>Breviceps poweri</i>	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Frog	<i>Kassina senegalensis</i>	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Frog	<i>Tomopterna</i> sp.	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Lizard	<i>Trachylepis varia</i>	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Mammal	<i>Lemniscomys griselda</i>	Broadley, 1977
<i>Psammophylax tritaeniatus</i>	Mammal	<i>Rhabdomys pumilio</i>	Broadley, 1977
<i>Psammophylax variabilis</i>	Bird	spp. (fledgling)	Bogert, 1940
<i>Psammophylax variabilis</i>	Fish	spp.	Broadley, 1977
<i>Psammophylax variabilis</i>	Frog	<i>Afrana angolensis</i> (2)	Loveridge, 1933
<i>Psammophylax variabilis</i>	Frog	<i>Afrana</i> sp.	Stewart and Wilson, 1966
<i>Psammophylax variabilis</i>	Frog	<i>Afrana</i> sp.	Broadley, 1977
<i>Psammophylax variabilis</i>	Frog	<i>Bufo loennbergi</i>	Loveridge, 1953
<i>Psammophylax variabilis</i>	Frog	<i>Hyperolius</i> sp.	Loveridge, 1953
<i>Psammophylax variabilis</i>	Lizard	<i>Proscelotes mlanjensis</i>	Broadley, 1977
<i>Psammophylax variabilis</i>	Lizard	<i>Trachylepis mlanjensis</i>	Loveridge, 1953
<i>Psammophylax variabilis</i>	Lizard	<i>Trachylepis varia</i> (5)	Loveridge, 1933
<i>Psammophylax variabilis</i>	Lizard	<i>Trachylepis varia</i>	Loveridge, 1953

APPENDIX 1. CONTINUED.

Snake species	Prey type	Prey species	Authority
<i>Psammophylax variabilis</i>	Mammal	<i>Crocidura occidentalis</i>	Loveridge, 1933
<i>Psammophylax variabilis</i>	Mammal	<i>Lophuromys</i> sp.	Loveridge, 1953
<i>Psammophylax variabilis</i>	Mammal	<i>Mus triton</i> (3)	Broadley, 1977
<i>Psammophylax variabilis</i>	Mammal	mouse	Bogert, 1940
<i>Psammophylax variabilis</i>	Mammal	rodent	Loveridge, 1953
<i>Psammophylax variabilis</i>	Mammal	rodent fur	Loveridge, 1933
<i>Psammophylax variabilis</i>	Mammal	rodent fur	Laurent, 1956
<i>Rhamphiophis acutus</i>	Mammal	rodent hair	Haagner et al., 2000
<i>Rhamphiophis acutus jappi</i>	Mammal	mouse	Broadley et al., 2003
<i>Rhamphiophis acutus jappi</i>	Lizard	amphisbaenian	Broadley et al., 2003
<i>Rhamphiophis rostratus</i>	Frog	<i>Arthroleptis stenodactylus</i> (3)	Loveridge, 1933
<i>Rhamphiophis rostratus</i>	Frog	<i>Kassina senegalensis</i> ?	Loveridge, 1936
<i>Rhamphiophis rostratus</i>	Lizard	<i>Heliobolus spekii</i>	Loveridge, 1933
<i>Rhamphiophis rostratus</i>	Lizard	<i>Lygosoma sundevallii</i>	Loveridge, 1933
<i>Rhamphiophis rostratus</i>	Mammal	small mammal	Loveridge, 1942