Sexual dimorphism, reproductive biology, and food habits of two species of African filesnakes (*Mehelya*, Colubridae)

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(With 2 figures in the text)

The ecology and general biology of African snakes remains virtually unstudied, even in highly distinctive species such as the filesnakes (genera *Mehelya* and *Gonionotophis*). Our measurements and dissections of preserved specimens provided information on body sizes, sexual dimorphism in size and bodily proportions, clutch sizes, and food habits of two *Mehelya* species. In both *M. capensis* and *M. nyassae*, females attain sexual maturity at the same size as conspecific males, but grow to much larger sizes. *Mehelya capensis* displays extreme differences in body shape between males and females at the same body length: females have longer and wider heads, thicker bodies, and larger eyes (relative to both head length and head width) than do conspecific males. Dimorphism in body proportions is less marked in *M. nyassae*. Female reproductive cycles are seasonal in *M. capensis*, and clutch sizes are larger in this species than in its smaller congener (5–11 eggs in *M. capensis*, 2–6 eggs in *M. nyassae*).

Contrary to popular wisdom, *Mehelya* are not specialized ophiophages. *Mehelya nyassae* feeds primarily upon lygosomatine skinks, including many fossorial taxa. *Mehelya capensis* has a broader diet, feeding on a wide variety of terrestrial lizards (especially agamids and gerrhosaurids) and snakes. Toads are also common prey items. The diversity of prey types taken by *M. capensis* suggests that these snakes may use ambush predation as well as active foraging. *Mehelya* is strongly convergent with Asian elapids of the genus *Bungarus* in its morphology (triangular body shape; powerful jaws; visible interstitial skin), behaviour (nocturnality; reluctance to bite when harassed), and diet (feeding on elongate reptiles, including snakes). Observations of prey-handling and ingestion by captive snakes are needed to clarify possible selective forces for the evolution of the unusual traits shared by these taxa.

Introduction

Despite much recent interest in the ecology of snakes (Seigel & Collins, 1993), available data on this topic are heavily biased both taxonomically and zoogeographically. Current information is based primarily upon studies of the snakes of North America and Europe, continents that are dominated by a small number of phylogenetic lineages (Cadle, 1987). One major gap in our knowledge concerns the ecology of African snakes. Although Africa contains a diverse ophidian fauna, there are virtually no published studies that quantify ecological attributes of any component of that fauna. Because of their phylogenetic distinctiveness (Cadle, 1994), the African snakes offer an ideal opportunity for independent tests of ideas derived from studies of the ecological traits of snakes in other countries. For example, several African lineages show behavioural and morphological specializations that resemble those seen in distantly related taxa from other parts of the world (e.g. Shine, 1980; Henderson & Binder, 1980). Thus, the

African taxa are excellent study animals for tests of speculations on the evolutionary causes, consequences, and correlates of such modifications.

The filesnakes (genera *Mehelya* and *Gonionotophis*) of sub-Saharan Africa are of particular interest in this respect, because these colubrid snakes show a suite of ecological, morphological, and behavioural peculiarities strongly convergent with those displayed by some members of the Asian proteroglyphous (elapid) genus *Bungarus* (Savitsky, 1985 and pers. comm.). Both filesnakes and kraits are nocturnally active and are reputed to feed primarily on other snakes (Broadley, 1982; Slowinski, 1994). Both genera include species with a distinctive body shape: a subtriangular cross-section that results from hypertrophy of dorsal vertebral spines. The interstitial skin between the scales is exposed in both groups. Both genera are renowned for their reluctance to bite, even when harassed (Pope, 1935; Broadley, 1982; although note that *Bungarus* is responsible for many snakebite fatalities), and for the extraordinary power of their jaws when an object is seized (T. Madsen, pers. comm.). African filesnakes are non-venomous, lacking modified fangs for venom delivery (but with enlarged Duvernoy's glands: Taub, 1967; Kochva & Wollberg, 1970; McDowell, 1986), whereas Asian *Bungarus* have large venom glands, front fangs, and very toxic venoms. Independent evolution of the unusual morphological traits in both genera suggests some functional link between these peculiarities of ecology, morphology, and behaviour, unrelated to the possession of venom. In order to assess the nature of any such link, however, we first need detailed information on the species involved. The present paper provides data on the southern African species of *Mehelya*, based on measurement and dissection of preserved specimens. We also review published data on the ecology of other filesnake (*Mehelya* and *Gonionotophis*) species in Africa, to evaluate the degree to which the southern African species are typical of the group as a whole.

Materials and methods

We examined preserved filesnakes in the collections of the Transvaal Museum, the Port Elizabeth Museum, and the Natural History Museum of Zimbabwe (Bulawayo). Measurements were taken of snout-vent length (SVL), tail length, head length (along the lower jaw, from the mandibular symphysis to the posterior projection of the quadrate), head width (across the eyes), eye diameter, body width (diameter at midbody), and body mass. The gonads and stomach were revealed by a midventral incision, and we recorded sex and reproductive status by visual inspection. Males were rated as mature if they had large turgid testes and/or thick, convoluted efferent ducts (indicating the presence of sperm). Females were classed as mature if they contained ovarian follicles > 5 mm, had thick muscular oviducts, or contained oviducal eggs. Clutch sizes were counted from eggs, or from enlarged vitellogenic follicles. Prey items were removed from the alimentary tract after the direction of ingestion had been recorded, and were later identified and measured. Reconstituted masses were estimated for prey items, based upon comparison with intact specimens of the same taxa. Dates and localities of collection were taken from museum registers.

Results

Morphology

Mehelya capensis

We examined 71 specimens, of which 21 were adult males, 24 were adult females, and 26 were juveniles. Extreme sexual dimorphism was evident in most of the traits we examined. Males and females matured at similar body lengths, but females grew much longer and heavier than did

males (Table I). Thus, females significantly exceeded males in mean values of most traits (head length, head width, body width, eye diameter), although not in tail length (Table I). Are all of these sex differences a direct consequence of the overall size dimorphism, or do males and females also differ in shape (i.e. relative body proportions) at the same snout-vent length? To answer this question, we used single-factor analysis of covariance, with sex as the factor and SVL as the covariate. At equivalent body lengths, female *M. capensis* had significantly larger heads than did males (for head length: heterogeneity of slopes $F_{1,28} = 0.19$, $P = 0.67$; ANCOVA $F_{1,29} = 11.66$, $P < 0.002$; for head width: heterogeneity of slopes $F_{1,28} = 2.02$, $P = 0.17$; ANCOVA $F_{1,29} = 10.73$, $P < 0.003$: see Fig. 1). Body width was also greater in females than in males at the same SVL (heterogeneity of slopes $F_{1,28} = 5.17$, $P < 0.03$), although mass relative to length did not differ between the sexes (using ln-transformed mass: heterogeneity of slopes $F_{1,28} = 1.44$, $P = 0.24$; ANCOVA $F_{1,29} = 0.17$, $P = 0.69$: see Fig. 1). The lack of a significant difference in mean tail length between adult males and females (see above) was due to two opposing factors: males are shorter than females, but have longer tails at any given SVL (heterogeneity of slopes $F_{1,28} = 2.62$, $P = 0.12$; ANCOVA $F_{1,29} = 4.93$, $P < 0.04$: see Fig. 1).

Possible sex differences in head shape and relative eye size were also examined by analysis of covariance, using head length as the covariate. Female *M. capensis* had heads of the same width as those of males at the same head length (heterogeneity of slopes $F_{1,33} = 3.00$, $P = 0.09$; ANCOVA $F_{1,34} = 2.70$, $P = 0.11$), but eye diameters were significantly larger in females than in males with same-sized heads, regardless of whether the covariate for this test was head length (heterogeneity of slopes $F_{1,33} = 1.71$, $P = 0.29$; ANCOVA $F_{1,34} = 8.65$, $P < 0.006$) or head width (heterogeneity of slopes $F_{1,33} = 0.24$, $P = 0.63$; ANCOVA $F_{1,34} = 6.32$, $P < 0.017$: see Fig. 1). Could this result be an artefact of nonlinearity in the relationship between eye diameter and head size, combined with the significant sex difference in absolute head size? We evaluated this possibility by restricting the range of the analysis to the area of overlap between the sexes, and the result was unchanged (for head length < 40 mm, heterogeneity of slopes $F_{1,26} = 0.02$, $P = 0.89$; ANCOVA $F_{1,27} = 5.63$, $P < 0.025$; for head width < 25 mm, heterogeneity of slopes $F_{1,25} = 0.55$, $P = 0.46$; ANCOVA $F_{1,26} = 5.22$, $P < 0.03$).

Mehelya nyassae

Our analyses are based on 19 adult males, 18 adult females, and 21 juveniles. As in *M. capensis*, females matured at the same size as conspecific males, but grew to much larger sizes (Table I). Thus, females exceeded males for mean values of snout-vent length, head dimensions (length and width), body mass, and body width, but not for tail length (Table I). ANCOVA analyses (as for *M. capensis* above) revealed significant sex differences in the relationship between body length and tail length (heterogeneity of slopes $F_{1,37} = 2.34$, $P = 0.13$; ANCOVA $F_{1,38} = 19.00$, $P < 0.0001$) and body length versus ln mass (heterogeneity of slopes $F_{1,37} = 0.19$, $P = 0.67$; ANCOVA $F_{1,38} = 15.63$, $P < 0.0004$), but not for any other traits (all $P > 0.30$).

Reproductive biology

Mehelya capensis

Reproductive females contained an average of 8.17 eggs or vitellogenic follicles (S.D. $= 2.04$, range $= 5-11$, $n = 6$). Clutch size tended to be higher in larger females, but the correlation fell
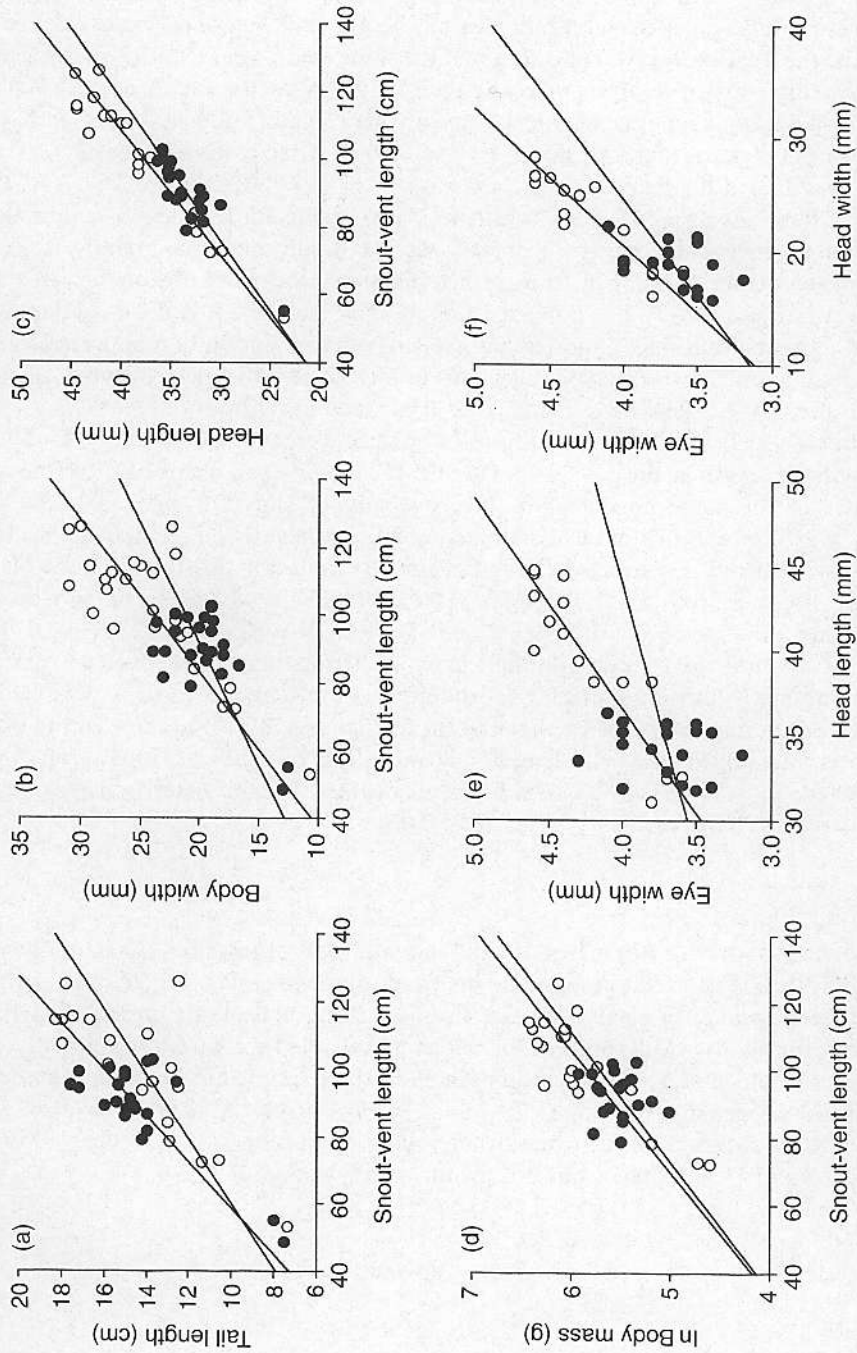
FIG. 1. Sexual dimorphism in Cape filesnakes. *Mehelya capensis*. Compared to conspecific males (●) at the same body length, female filesnakes (○) have shorter tails (a), wider bodies (b), and longer heads (c). However, the two sexes do not differ in mass (d). Females have larger eyes than do males at the same head size, regardless of whether the comparison is made against head length (e) or head width (f). See text for statistical analyses of all these trends.

TABLE I

*Morphology and sexual size dimorphism in filesnake (**Mehelya**) species of southern Africa. Table shows ranges and mean values, with S.D. in parentheses. See text for sample sizes. Last three columns show results from unpaired two-tailed t-tests for sexual dimorphism*

	Adult males	Adult females	Significance of sexual dimorphism		
			d.f.	t	P
Mehelya capensis					
Snout-vent length (cm)	92.04 (7.17)	107.52 (11.21)	43	5.59	0.0001
SVL range	79.0–105.0	78.5–126.0	–	–	–
Tail length (cm)	15.08 (1.25)	15.61 (1.91)	34	1.00	0.33
Head length (mm)	34.05 (1.67)	40.61 (3.40)	34	7.58	0.0001
Head width (mm)	19.31 (1.77)	24.27 (2.86)	32	6.20	0.0001
Body width (mm)	20.09 (1.91)	25.38 (3.62)	40	5.92	0.0001
Body mass (g)	264.1 (49.5)	448.0 (111.5)	34	6.52	0.0001
Eye diameter (mm)	3.75 (0.28)	4.29 (0.28)	32	5.68	0.0001
Mehelya nyassae					
Snout-vent length (cm)	36.73 (2.41)	42.90 (4.70)	34	5.04	0.0001
SVL range	32.6–39.6	32.1–50.0	–	–	–
Tail length (cm)	10.05 (1.02)	10.69 (1.38)	33	1.55	0.13
Head length (mm)	15.73 (0.97)	18.10 (2.31)	35	4.12	0.0002
Head width (mm)	8.17 (0.92)	9.20 (1.25)	32	2.75	0.01
Body width (mm)	8.41 (1.32)	9.42 (1.21)	36	2.46	0.019
Body mass (g)	19.82 (5.72)	33.17 (15.82)	33	2.10	0.044
Eye diameter (mm)	1.68 (0.21)	1.76 (0.21)	34	1.07	0.29

short of statistical significance ($r = 0.62$, $n = 6$, $P = 0.19$). Oviducal eggs were covered by thick shells, confirming oviparity as the reproductive mode. Oviducal eggs ranged considerably in size, from 30×15 mm to 50×26 mm, and a clutch of newly-hatched young ranged in SVL from 26.5 to 30.5 cm (mean mass = 12 g). Ovarian follicles were <10 mm throughout late summer and autumn (Feb.–May), and vitellogenic in late winter through to spring and early summer (Aug.–Dec.: see Fig. 2). Gravid females were recorded in August (from the Caprivi Strip) and February (Transvaal).

Because reproductive biology might influence seasonal activity patterns (and thus, a snake's vulnerability to collection), we examined dates of collection of the museum specimens. The year was divided into four seasons: winter (Jun.–Aug.), spring (Sept.–Nov.), summer (Dec.–Feb.) and autumn (Mar.–May). For 50 snakes with known dates of collection, most came from spring (42%) or autumn (38%), and few from winter (6%) or summer (14%). These data enable rejection of the null hypothesis of equal numbers of snakes in each season ($d.f. = 3$, $\chi^2 = 18.80$, $P < 0.001$). However, we detected no seasonal shifts in the relative numbers of adult males versus females ($d.f. = 3$, $\chi^2 = 2.51$, $P = 0.47$) or adults versus juveniles ($d.f. = 3$, $\chi^2 = 0.05$, $P = 0.99$).

Mehelya nyassae

Clutch size averaged 3.00 (S.D. = 1.00, range = 2–6) in eight females, and was not significantly correlated with maternal body size ($r = 0.41$, $n = 8$, $P = 0.36$). A female from Maputo, Mozambique, contained two large, thick-shelled eggs (18×6 mm) when collected in December 1915. We have no records of size at hatching, but the smallest specimen we measured was 20.5 cm SVL, with four others < 25 cm. Of 38 specimens with known dates of collection, 45% came from
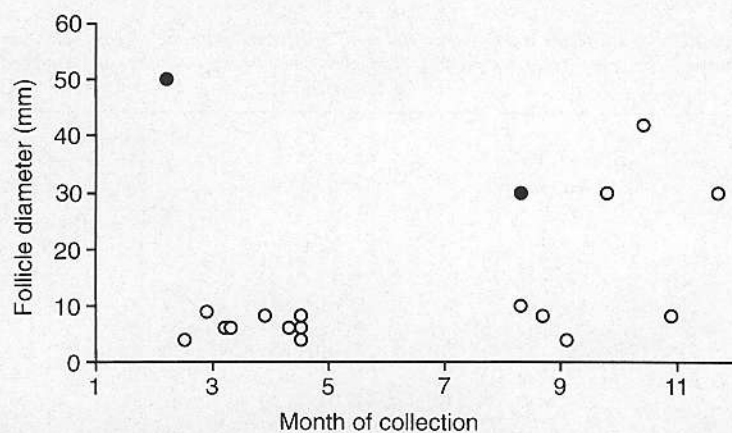
FIG. 2. Seasonal cycle of ovarian follicle diameters in Cape filesnakes, *Mehelya capensis*. Graph shows diameter of the largest ovarian follicles (O) or oviducal eggs (●) in adult females.

summer, 29% from spring, 26% from autumn, and none from winter. These data falsify the null expectation of equal numbers in each season ($d.f. = 3$, $\chi^2 = 9.08$, $P < 0.05$). There were no significant seasonal shifts in the relative numbers of adult males versus females ($d.f. = 3$, $\chi^2 = 3.10$, $P = 0.38$) or adults versus juveniles ($d.f. = 3$, $\chi^2 = 4.45$, $P = 0.22$).

Food habits

Mehelya capensis

We recorded 32 identifiable prey items from alimentary tracts of this species, plus insect remains in another seven, and additional data on prey types in another 41 specimens were generously provided by D. G. Broadley and V. Wallach (Table II). All prey items for which we could determine direction of ingestion were ingested headfirst. The insect fragments were presumably secondarily ingested, probably from amphibian or lizard prey. The single record of feathers may also represent secondary ingestion from snake prey. The most important prey types from Table II were lizards (29 of 69 = 41%) and snakes (34 = 49%), with seven amphibians also (10%). Most of the ingested snakes were unidentifiable to species, but none had the heavily keeled scales typical of *Bitis*, and so were presumably colubrids or elapids. The snakes eaten by *Mehelya capensis* include both venomous (boigine, elapid, and viperid) and non-venomous species, and include diurnal as well as nocturnal taxa (Tables II and IV). None of the ophidian prey was of fossorial species, and all except the boomslang (*Dispholidus*) were terrestrial rather than arboreal species. At least six of the seven amphibians identified to species level were toads, but the lizards were taxonomically diverse. Agamids ($n = 15$ of 29 lizard records) and gerrhosaurids ($n = 14$ records) were the most important groups, but skinks and geckos were also recorded (Table II). Most of the lizards taken were terrestrial species, with the large agamid *Acanthocerus atricollis* being the only arboreal form (Table II). However, this species sometimes shelters under bark on fallen logs (W. R. Branch, pers. obs.), so may have been captured close to the ground also.

The relative numbers of anurans, lizards, and snakes did not differ between adult males and adult females ($d.f. = 2$, $\chi^2 = 2.20$, $P = 0.33$), or between juvenile and adult snakes ($d.f. = 2$,

TABLE II

*Prey items identified from alimentary tracts of Cape filesnakes, **Mehelya capensis**. The first data column shows the numbers of each prey type recorded in our study, whereas the second column provides unpublished data from other studies*

Prey type		Number of prey items	
		Present study	D. Broadley and V. Wallach (pers. comm.)
Amphibians			
	amphibian spp.		2
Bufonidae	*Bufo* spp.		2
	Bufo cf *gutturalis*	1	
	Schismaderma carens	1	1
Lizards			
	lizard sp.		1
Agamidae	*Acanthocerus atricollis*	2	5
	Agama sp.	3	1
	Agama aculeata		4
Gekkonidae	gecko sp.	1	
Gerrhosauridae	*Gerrhosaurus flavigularis*	2	1
	Gerrhosaurus nigrolineatus	2	5
	Gerrhosaurus sp.	4	
Scincidae	*Mabuya* sp.	1	
	Mabuya striata		1
Snakes			
	snake sp.	11	4
Colubridae	*Crotaphopeltis hotamboeia*	2	1
	Dasypeltis scabra		2
	Lamprophis fuliginosus		1
	Lycophidion capense		2
	Psammophis phillipsi		2
	Psammophis subtaeniatus		4
	Psammophylax tritaeniatus		1
Viperidae	*Causus rhombeatus*		1
Other			
	feathers		1
	insect remains	7	
	vegetation and soil	7	1

$\chi^2 = 1.67$, $P = 0.43$). Although females took larger prey than conspecific males (mean prey width $= 11.80$ mm [S.D. $= 3.49$] for adult males; vs. 20.50 mm [8.74] for adult females), this difference fell short of statistical significance (unpaired two-tailed t-test, 7 $d.f.$, $t = 2.06$, $P = 0.078$). The ratio of prey mass to predator mass averaged 0.13 (S.D. $= 0.11$, $n = 10$), ranged from 0.02 to 0.42, and was negatively correlated with predator size (vs. SVL: $r = -0.64$, $n = 10$, $P < 0.05$). This ratio did not differ significantly between males (mean $= 0.12$, $n = 6$) and females (mean $= 0.15$, $n = 4$: $t_8 = 0.29$, $P = 0.78$). The relative numbers of lizards versus snakes eaten did not vary significantly among the four seasons ($d.f. = 3$, $\chi^2 = 4.83$, $P = 0.18$).

Mehelya nyassae

Scincid lizards were the most important prey type for this taxon (26 of 31 records $= 84\%$: Table III), with the majority being terrestrial lygosomatine species. Most of the unidentified skinks are probably lygosomatines also (e.g. six skink records are from Zimbabwe, where

scincines are rare). However, we also found lacertid lizards and snakes in alimentary tracts of *M. nyassae* (Table III), and these taxa (plus a single amphibian prey item) have been reported previously also (Table IV). Note that two of our records (those for *Lygosoma sundevallii* and an unidentified snake: Table III) were the same items as previously reported by Haacke (1981). All prey items were ingested headfirst. The ratio of prey mass to predator mass averaged 0.15 (S.D. = 0.14, $n = 8$), ranged from 0.04 to 0.45, and was positively correlated with predator size (vs. SVL: $r = 0.69$, $n = 8$, $P = 0.058$). This ratio did not differ significantly between males (mean = 0.13, $n = 2$) and females (mean = 0.16, $n = 6$: $t_6 = 0.31$, $P = 0.77$).

Discussion

There are few published ecological studies on African snakes (particularly species from West and Central Africa), and no previous detailed studies of reproduction or diet for any filesnake species. Because ecological traits (especially feeding habits) often show extreme phylogenetic conservatism in reptiles (e.g. Greene, 1983), it is difficult to interpret the adaptive significance of characters (such as the bizarre morphology of filesnakes) without reference to the attributes of related species. Thus, we first summarize diversity and phylogenetic affinities of the African filesnakes, before we consider specific results from our own study. The most recent revision of the genus *Mehelya* (Loveridge, 1939) recognized seven species including (in addition to the two species studied here) *M. poensis*, *M. crossii*, *M. stenophthalmus*, *M. guirali*, and *M. riggenbachi*. Three additional species have been described subsequently: *M. vernayi* (Bogert, 1940), *M. laurenti* (de Witte, 1959) and *M. egbensis* (Dunger, 1966). The two latter species remain poorly-known, with no further specimens recorded since the type descriptions. The main distribution of the genus is centred on Cameroon (four species) and Nigeria (five species), although *M. capensis* is more widely distributed, occurring from southern Africa to Cameroon

TABLE III

*Prey items identified from alimentary tracts of black filesnakes, **Mehelya nyassae**. Items marked with an asterisk are personal communications from D. G. Broadley*

Prey type		Number of prey items
Lizards		
Lacertidae	lacertid sp.	1
	Nucras taeniolata ornata	1
Scincidae	skink sp.	8
	Lygosomatinae sp.	6
	Lygosoma sundevalli	3
	Mabuya sp.	1
	Mabuya striata wahlbergi	1
	Mabuya varia	1
	Panaspis sp.	3*
	Panaspis wahlbergii	2
	Scelotes arenicola	1
	Scelotes bidigittatus	2
	Scelotes mossambicanus	2
Snakes		
	snake sp.	1
Leptotyphlopidae	*Leptotyphlops distanti*	1

and Somalia. Most *Mehelya* species are large (1–2 m), with the smallest being *M. stenophthalmus* (maximum SVL 70 cm) and *M. nyassae* (maximum SVL 57.6 cm). The type of *M. egbensis* (SVL 23.5 cm) is immature. Loveridge (1939) recognized only three species of lesser filesnakes (*Gonionotophis*)—*G. klingi*, *G. grantii*, and *G. brussauxi*. Rare and poorly-known, they inhabit rainforest and savannah habitats from Togo to Zaire.

The phylogenetic affinites of African filesnakes remain obscure. Bogert (1940) informally grouped *Mehelya* (in his Group 2) with the other African snake genera *Hormonotus*, *Gonionotophis*, *Lycophidion*, and *Chamaelycus*. Dowling (1969, 1975) suggested that this group was closely related to another of Bogert's (1940) groups (Group 1: *Lycodonomorphus*, *Lamprophis*, *Bothrophthalmus*, *Pseudoboodon*, and *Bothrolycus*), and hence allocated them as separate tribes (Boaedontini and Lycophidini) within the subfamily Lycodontinae. Cadle (1994) found no significant cross-reaction between the albumin of *Mehelya* and that of any other African colubrid, including representatives of *Lycophidion* and *Gonionotophis*. None the less, a phylogenetic tree based on his immunological data did group *Mehelya* with *Lycodonomorphus* and *Lamprophis* (the only genera of Bogert's groups 1 and 2 for which Cadle had antisera). The lack of cross-reaction between the sera of *Mehelya* and *Gonionotophis* is surprising, because the two genera share numerous scutellation 'abnormalities' and other morphological similarities. In fact, the two genera are diagnosed from each other only by the presence (*Gonionotophis*) or absence (*Mehelya*) of a diastema in the maxillary teeth series. The distinctiveness of the two genera was questioned by Loveridge (1939), and is further blurred by Dunger's (1966) description of *M. egbensis*. Because Cadle's (1994) immunological data did not associate *Mehelya* with any other African or Madagascan genera, these snakes may be related only distantly to other living taxa.

The lack of a well-corroborated phylogenetic hypothesis for *Mehelya* and its allies makes it difficult to interpret our data in a phylogenetic framework. None the less, filesnakes appear to be similar in their ecology to their probable closest relatives, the other genera in Bogert's groups 1 and 2. All of the species within these groups are primarily nocturnal, although their foraging habits and diets are diverse. For example, the semi-aquatic *Lycodonomorphus* forages actively for frogs, tadpoles, and fishes (Branch, 1988; Madsen & Ostercamp, 1982), whereas the terrestrial *Lamprophis* (including *Boaedon*) ambushes lizards and small mammals. The dwarf wolf snake, *L. nanum* (previously placed in a monotypic genus *Cryptolycus*: Broadley, 1995) is a specialist feeder on burrowing amphisbaenians (Branch, 1988). Other wolf snakes (*Lycophidion*) specialize mainly on diurnally-active lizards, particularly skinks, probably capturing the lizards whilst they are asleep in their nocturnal retreats (Branch, 1976, 1988). Similar behaviour may be utilized by filesnakes, with *M. nyassae* specializing on sleeping skinks and lacertids, while *M. capensis* takes larger gerrhosaurids and agamas, which are too large and heavily armoured for *M. nyassae* or any *Lycophidion* species. The three smallest *Mehelya* (*M. nyassae*, *M. stenophthalmus,* and *M. egbensis*) all have reduced keeling and small eyes, whilst *M. egbensis* also has an enlarged rostral. These traits suggest adaptation for burrowing in the smaller filesnakes, a possibility consistent with the dietary records of fossorial prey. *Mehelya stenophthalmus* has been recorded to eat the fossorial lizard *Feylinia* (Table IV), and V. Wallach (pers. comm.) has two records of predation by this species on *Typhlops*. Similarly, prey records from the *M. nyassae* that we examined included the highly fossorial *Scelotes* and *Leptotyphlops* (Table III).

The prey consumed by *M. capensis* includes a much wider array, ecologically as well as taxonomically, than for *M. nyassae*, suggesting a more diverse array of foraging tactics in the larger species. For example, as *M. capensis* is active nocturnally, it presumably captures

TABLE IV

Published records of prey items from alimentary tracts of African filesnakes of the genera **Mehelya** *and* **Gonionotophis**

	Prey item	Authority
Mehelya capensis		
Amphibians		
	Bufo regularis (2)	Wilson, 1965
	Shismaderma carens	Broadley, 1974
Lizards		
Agamidae	*Agama* sp.	Wilson, 1965
	Acanthocerus atricollis	Broadley, 1959
Gerrhosauridae	*Gerrhosaurus nigrolineatus*	Loveridge, 1951
Scincidae	*Mabuya striata*	Broadley, 1959
Snakes		
Colubridae	*Crotaphopeltis hotamboeia*	Broadley, 1974
	Dispholidus typus	Wilson, 1965
	Lamprophis fuliginosus	Pakenham, 1983
	Lycodomorphus rufulus	Pienaar *et al.*, 1983
	Natriciteres olivaceus	Loveridge, 1953
	Philothamnus irregularis	Quartau, 1971
	Psammophis sp.	Pitman, 1974
	Psammophis phillipsi	Pienaar *et al.*, 1983
	Psammophis sibilans	Wilson, 1965
	Psammophis subtaeniatus	Loveridge, 1953
Elapidae	*Naja mossambica*	Pienaar *et al.*, 1983
Pythonidae	*Python sebae*	Pienaar *et al.*, 1983
Viperidae	*Causus rhombeatus*	Loveridge, 1939
Mehela nyassae		
Amphibians		
Hyperoliidae	*Kassina senegalensis*	Wilson, 1965
Lizards		
Lacertidae	*Ichnotropis capensis*	Jacobsen, 1982
Scincidae	*Lygosoma sundevallii*	Haacke, 1981
	Panaspis wahlbergii	Broadley, 1962
Mehelya vernayi		
Amphibians		
Bufonidae	*Bufo garmani*	Haacke, 1981
Lizards		
Gerrhosauridae	*Gerrhosaurus* sp.	Bogert, 1940
Mehelya riggenbachi		
Snakes		
Colubridae	*Dromophis lineatus*	Loveridge, 1939
Mehelya poensis		
Lizards		
Agamidae	*Agama* sp.	Dunger, 1971
	Agama agama	Loveridge, 1938; Leston & Hughes, 1968
Scincidae	*Mabuya blandingii*	Loveridge, 1938, 1939
	M. maculilabris	Laurent, 1956
Mehelya stenophthalmus		
Lizards		
Feylinidae	*Feylinia currori*	Laurent, 1956
Snakes		
Colubridae	*Mehelya stenophthalmus*	Loveridge, 1939
	Natriciteres sp.	Lawson, 1993

TABLE IV
(cont.)

	Prey item	Authority
Mehelya guirali		
Snakes		
Colubridae	*Aparallactus* (?)	Dunger, 1971
	Boiga pulverulenta	Dunger, 1971
Mehelya crossi		
Lizards		
Scincidae	*Mabuya perrotetii*	Dunger, 1971
Gonionotophis brussauxi		
Amphibians		
Bufonidae	*Schoutedenella* sp.	Laurent, 1956
Gonionotophis granti		
Amphibians	unidentified frog	Leston & Hughes, 1968

nocturnal prey (e.g. bufonids, *Crotaphopeltis*) while they are active, and diurnal prey (e.g. agamids, gerrhosaurids) while they are sleeping. Thus, *M. capensis* may use a combination of active searching and ambush foraging to obtain prey.

The limited dietary information available for other *Mehelya* species suggests that lizards and snakes are the major prey types, but with occasional amphibians also taken (Table IV). All feeding records for *M. poensis* suggest that it is a specialist feeder on lizards, and we have been able to discover only two feeding records for the genus *Gonionotophis*, both small amphibians (Table IV). Although *Mehelya* is renowned as a specialist ophiophage, the available data suggest that lizards are as important as snakes in the diet of *M. capensis*, and are the major prey of *M. nyassae*. The oft-repeated suggestion that *M. capensis* prefers night adders as prey (FitzSimons, 1912, 1962, 1970; Rose, 1950; Bruton & Haacke, 1980) is not supported by the information that we have assembled (Tables II and IV).

Our records of clutch sizes, reproductive seasonality, and offspring sizes are consistent with earlier reports on these topics (Barbour & Loveridge, 1928; Haacke 1981; Broadley, 1982; Krzystyniak & Pewtress, 1983; Branch, 1988). Like most temperate-zone snakes, African filesnakes produce eggs in the warmest part of the year (Shine, 1985; Flemming, 1994). The long period over which female gonads were active (Aug.–Feb.: see Fig. 2) is consistent with records of double-clutching in captivity (Krzystyniak & Pewtress, 1983). The strong seasonality in dates of collection of the museum specimens may reflect a trend for activity to be depressed during drier months (Haacke, 1981). The proportion of males among the adult *M. capensis* was highest in spring (11 of 17 = 65%; vs. 36% autumn, 40% winter, 56% summer), suggesting that mate-searching behaviour may explain the higher capture rates of filesnakes at this time of year.

Although Fitzsimons (1962) noted that female *M. capensis* attain larger body sizes than do conspecific males, our data provide the first detailed examination of sexual dimorphism in *Mehelya*. The degree of dimorphism in *M. capensis* is greater than that seen in most other snakes (Shine, 1994). Not only do females attain larger body sizes (almost 70% greater mean body mass in adult females than in adult males), but bodily proportions differ considerably also. Differences in head size relative to body length are widespread among snakes, and may reflect sex-specific adaptations to minor divergences in foraging habits or dietary composition (Shine, 1991, 1993).

Our data do not enable us to evaluate this hypothesis: diets of male and female *M. capensis* appear to be similar, although (not surprisingly) prey sizes tend to be larger in the larger sex (females). Sexual dimorphism in tail length is widespread in snakes, and may be due to several selective pressures (e.g. King, 1989). Dimorphism in midbody width may reflect fecundity selection on females, to accommodate the eggs more easily (Shine, 1993). However, the sexual dimorphism in eye size relative to head size (Fig. 1) is more perplexing. Analogous differences have been reported in an Asian colubrid (*Dendrelaphis picta*—Kopstein, 1941) and a South American viperid (*Bothrops moojeni*—Leloup, 1975). In both of these species, males were the sex with the larger eyes. We have no plausible explanation for this dimorphism in *Mehelya*, and can only suggest that careful studies of captive specimens of this taxon would be worthwhile. In particular, we need more detailed information on foraging habits and activity cycles (especially, the relative importance of diurnal versus nocturnal activity in the two sexes).

Lastly, we consider the ecological, morphological, and behavioural convergence of *Mehelya* with the Asian elapid genus *Bungarus*, as noted in the **Introduction**. The apparent correlation between morphology and diet (ophiophagy) is weakened by our data. Snakes are an important prey type in both *Mehelya* and *Bungarus*, but both genera contain species (e.g. *M. nyassae*, *B. multicinctus*) that possess the distinctive triangular body shape but feed primarily on taxa other than snakes (for diets of kraits, see Slowinski, 1994). Indeed, there is no evidence that the lesser filesnakes (*Gonionotophis*) feed on snakes at all (Table IV). None the less, it remains possible that this morphology evolved in ophiophagous ancestors and is retained in present-day, less ophiophagous species. Evaluation of this hypothesis must await data on intrageneric relationships within these two groups.

The distinctive morphology of African filesnakes has given them the local name of 'saw cobras', in the belief that these snakes use their rough scales and triangular shape to saw through people's legs as they pass by (W. Haacke, pers. comm.). Although the suggestion is ludicrous, the functional significance of the constellation of traits shared by *Mehelya* and *Bungarus* remains obscure. The powerful jaws of these snakes may relate to the difficulty of holding a writhing reptilian prey item. Because of the elongate shape of most squamates, a gape-limited predator that specializes on this type of prey can none the less ingest prey that is very large relative to predator size. The subtriangular body shape may function as a defence mechanism, by protrusion of the hypertrophied vertebral spines through the snake's mid-dorsal surface (Savitsky, 1985 and pers. comm.). Alternatively, the modified body shape may make it more difficult for a gape-limited prey item (such as a snake or a lizard) to seize the predator, because the prey is faced with a relatively flat surface and an increased body diameter. Ideas on the adaptive significance of *Mehelya* morphology and behaviour, as well as of the sexually dimorphic features we have documented, could be usefully explored with behavioural observations on captive animals. Filesnakes settle well and feed readily in captivity (W. Haacke, pers. comm.), so that it should be feasible to investigate prey-handling 'tactics' and general activity cycles in these unusual snakes.

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