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Trophic ecology of East African caecilians (Amphibia: Gymnophiona), and their impact on forest soil invertebrates

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Abstract

Diets of the syntopic caecilian amphibians *Boulengerula boulengeri* and *Scolecomorphus vittatus* were studied from gut content analyses of 108 specimens collected from Nilo Forest Reserve, East Usambara Mountains, Tanzania. Head length and width relative to body length is greater in male *B. boulengeri* than in females, but no such dimorphism is apparent in *S. vittatus*. No differences, other than females consuming disproportionately more ants and invertebrate eggs and fewer termites than males, occur in the diets of *B. boulengeri*. The gut contents of *S. vittatus* are dominated by large, surface-active earthworms, in contrast to those of *B. boulengeri* which contained smaller, endogeic earthworms and a much greater number and diversity of soil arthropods (particularly termites, ants and Diptera larvae). These dietary characteristics underline differences in microhabitat use between these caecilian species and thus corroborate a previously proposed hypothesis of niche separation. The ecological impact of caecilians and other limbless endogeic vertebrates is little studied and poorly known. Approximations based on current knowledge are not clear, but are interpreted as indicating that predation by caecilians is unlikely to be among the most important factors influencing population densities of soil-dwelling termites and perhaps also ants: two groups recognized as soil ecosystem engineers.

Introduction

Soils are of critical importance because they facilitate essential ecosystem processes such as decomposition, nutrient cycling and primary productivity (Brussaard *et al.*, 1997; Laakso & Setälä, 1999) and because they support a huge proportion of terrestrial biodiversity (Giller, 1996). Yet, soils are one of the most poorly researched habitats on earth (Hall, 1996), and soil ecology is still poorly understood (Copley, 2000). To assess how organisms may influence soil processes, it is necessary to have some understanding of their autecology and their position within what are often very complex food webs (Bardgett, 2002). However, information on the biology of many groups of soil organisms is still sparse.

Caecilians are one such group of neglected soil animals. They are limbless, elongate amphibians (order Gymnophiona) with a predominantly subterranean, fossorial lifestyle as adults. The *c.* 170 known species are distributed widely throughout the humid tropics, with a few species found in subtropical regions (Taylor, 1968; Wilkinson & Nussbaum, 2006). Little is known about the natural history of the vast majority of these species (Himstedt, 2000; Gower & Wilkinson, 2005), and most published information on their trophic ecology has been obtained from opportunistic field observations or by examining the gut contents of preserved specimens. Despite the few detailed studies of caecilian diets (see O'Reilly, 2000; Measey *et al.*, 2004; Kupfer, Nabhitabhata & Himstedt, 2005*a*), it is generally assumed that terrestrial species are subterranean predators that feed mainly on soil invertebrates such as earthworms and termites (Wake, 1980; Nussbaum & Pfrender, 1998). There has been some debate over the degree to which caecilians are generalists or specialists in their diet (see Gaborieau & Measey, 2004).

Earthworms, termites and ants have been described as 'soil ecosystem engineers' (SEE) because of the impact they have on soil processes (Lavelle *et al.*, 1997). This impact arises from their feeding and building activities, combined with their high abundance in many tropical soils. Recent studies using randomized sampling methods have demonstrated that some caecilian species are locally abundant (e.g. Measey *et al.*, 2003). This has prompted some workers (e.g. Oommen *et al.*, 2000; Gower *et al.*, 2004; Measey *et al.*, 2004) to hypothesize that abundant caecilians may have an important impact on soil processes through their predation of invertebrate SEE.

To date, the small number of quantitative field-based studies of caecilian diet that have been carried out (e.g.

Delêtre & Measey, 2004; Gaborieau & Measey, 2004; Measey *et al*., 2004; Kupfer *et al*., 2005*a*) have all investigated single species, and mostly in agricultural habitats. In contrast, this paper is the first quantitative analysis of the diets of syntopic caecilian species in a forest habitat, and the first study to try and test the hypothesis that caecilians have a substantial impact on soil ecology through predation of invertebrate SEE. In this study two syntopic species, the caeciliid *Boulengerula boulengeri* Tornier and the scolecomorphid *Scolecomorphus vittatus* (Boulenger), were collected using three different sampling techniques in protected forest in the East Usambara Mountains of Tanzania. Some aspects of their morphologies and ecologies were presented in Gower *et al*. (2004). With a sample size of 108 specimens representing two species from a single site, this is one of the largest quantitative studies of caecilian ecology published to date.

In this paper we analyse the gut contents of these specimens to test the following hypotheses:

1. the diets of syntopic *B. boulengeri* and *S. vittatus* differ (Gower *et al*., 2004);
2. differences in diet between the two species reflect known differences in microhabitat use and, possibly, in morphology (Gower *et al*., 2004);
3. intraspecific dietary variation correlates with morphological variation, including sexual size dimorphism (see Delêtre & Measey, 2004);
4. species of *Boulengerula* are dietary specialists (Wake, 1986; O'Reilly, 2000) or generalists (Gaborieau & Measey, 2004);
5. terrestrial caecilian diets in natural habitats are dominated by invertebrate SEE (see Measey *et al*., 2004);
6. as predators of SEE, terrestrial caecilians may have a substantial impact on soil ecology (Oommen *et al*., 2000; Measey *et al*., 2003, 2004; Gaborieau & Measey, 2004; Gower *et al*., 2004);
7. sexual dimorphism in head size is less pronounced in those caecilians that are particularly endogeic and dedicated burrowers (Delêtre & Measey, 2004).

Materials and methods

Study site

Fieldwork was undertaken in Nilo Forest Reserve (6025 ha of protected forest), in the north-western part of the East Usambara Mountains of Tanzania. These mountains form part of the Eastern Arc of East Africa, a region of high endemicity (Lovett & Wasser, 1993) that is recognized as a global biodiversity hotspot (Myers *et al*., 2000). The study area (4°48′–4°13′S, 38°32′–38°48′E; 400–1506 m above sea level) comprises hilly terrain with lowland and submontane forest, some small patches of which are under low-intensity agriculture.

Caecilian sampling regime

Three methods (timed digging, pitfall trapping and opportunistic surface collecting) were used to sample caecilians in 38 representative plots (each 450 m × 900 m) within Nilo Forest Reserve. In the south-western corner of every plot, soil was dug to an approximate depth of 300 mm for 2 person hours (SPL plus one assistant digging concurrently for 1 h each), and all caecilians encountered were collected. At 10 locations, three unconnected drift fence lines of plastic sheeting were erected, each with 11 buckets (275 mm deep × 290 mm diameter at aperture) at 5 m intervals sunk to ground. The pitfall traps (330 in total) were emptied twice daily for 10 days. Visual searching for caecilians took place whenever fieldworkers moved about within the reserve, including outside the 38 plots. No sampling sites lay within patches under cultivation. Gower *et al*. (2004) give fuller details of the collecting methods.

Specimen analysis

All caecilians were anaesthetized (MS 222, Sandoz) and fixed in 4% formalin within 2 h of capture, and subsequently stored in 70% ethanol. Specimens were dissected under a stereo-microscope to expose the alimentary canal from immediately posterior of the heart to the anterior of the cloaca. This portion of the alimentary canal (hereafter referred to as the gut) was opened and all contents were removed for later examination. Before preservation and dissection, the fresh mass of each caecilian was recorded, and total body length was measured to the nearest 1 mm. The length of the lower jaw (from jaw angle of one side to tip of mandible) and transverse width at midbody, occiput (anteriormost nuchal collar groove) and jaw angle (approximately equivalent to gape) were all measured with vernier callipers to the nearest 0.1 mm. Where possible, sex was determined by examination of gonads. Specimens were deposited at the Department of Zoology, the Natural History Museum, London. Registration numbers for *B. boulengeri* are BMNH 2002.770-803, 805-852 and 854. Registration numbers for *S. vittatus* are BMNH 2002.855-61, 63 and 65-78.

Gut contents were examined under a stereo-microscope. Animals were assigned to prey categories (mostly to order or family level identifications), counted, and the maximum width and length of prey from each gut were measured to the nearest 0.01 mm with an eyepiece graticule. Where prey were partially digested and/or in fragments, the minimum possible number of individuals was recorded, based on unambiguous items such as head capsules. The maximum width and length measurements were of whole individuals when present, or were conservative estimates based on reassembled pieces of the largest individuals. Thus, some of the maximum lengths recorded, particularly of earthworms, were probably an underestimate of those individuals' length when intact.

Statistical analyses

The total body length within each caecilian species was compared using analysis of variance (ANOVA) with sex as the factor, whereas other morphological characteristics were compared using analysis of covariance (ANCOVA) with total body length as the covariate. The number and size of prey were compared using ANOVA, or using ANCOVA with total body length as the covariate. Numbers of prey per gut and maximum prey length were both log transformed because they varied greatly. Chi-squared tests of independence were used to detect potential significant differences between the numbers of prey ingested by male and female caecilians. Rarefaction was performed using the Biodiversity Pro software (McAleece *et al*., 1997).

Results

Eighty-five specimens of *B. boulengeri* were collected, three of which were damaged enough to be excluded from further consideration in this study. The remaining 82 *B. boulengeri* comprised 41 females, 31 males and 10 immatures (gonads insufficiently developed to identify sex). Four of these 82 specimens were less extensively damaged but could not be included in all analyses. Twenty-three specimens of *S. vittatus* were collected, with one damaged individual excluded from further consideration. The remaining 22 *S. vittatus* comprised 10 females, 10 males and two immatures.

Caecilian morphology

In our samples, *S. vittatus* is significantly larger than *B. boulengeri* (ANOVA for each of the six morphological characteristics recorded, $P<0.001$; see also Gower *et al*., 2004). There is no significant difference in total body length between males and females of *B. boulengeri* (Table 1). However, one-way ANCOVA using total body length as a covariate reveals that males have significantly wider and longer jaws, wider heads across the occiput, and are heavier than females of a similar length (Table 1). In the case of *S. vittatus*, sexual differences in size were not significant (Table 2), although the statistical power of these tests may be limited by the small sample size.

Gut contents

When the gut contents of all specimens are combined, the prey of *B. boulengeri* is more diverse than that of *S. vittatus*. Excluding unidentified arthropod parts, the guts of sampled *B. boulengeri* contained prey from 16 categories, whereas the guts of sampled *S. vittatus* contained only six categories (Table 3). The maximum number of prey categories per specimen is five in *B. boulengeri* and only two in *S. vittatus* (Fig. 1). However, the frequency distributions of prey categories within the two species may have been the same if the sample sizes had been similar. Indeed, when the data are rarefied to 31 prey items (the total number of prey items in *S. vittatus*), the number of prey categories is very similar at 6.3 in *B. boulengeri* and 6.0 in *S. vittatus*.

Striking differences in the composition of the gut contents are apparent. The prey categories present most frequently in *B. boulengeri* are earthworms (found in 29.5% of specimens), Nematocera larvae (Diptera, 26.9%), termites (20.5%) and beetle larvae (10.3%). Other prey categories occurring in more than 5% of specimens are worker ants, geophilid centipedes, woodlice (terrestrial Isopoda), adult beetles and invertebrate eggs (all of which were unidentified, although they were not eggs of ants or termites). In contrast, earthworms are the only major prey category in the guts of *S. vittatus*, occurring in 55% of specimens. No termites, Nematocera, beetle larvae, centipedes or woodlice occurred in *S. vittatus* (Table 3). On the basis of the functional classification in Sims & Gerard (1999), four of the earthworms in the guts of *S. vittatus* are anecic species (large and heavily pigmented), whereas the remaining 11 earthworms are epigeic species (moderately large and pigmented). In the case of *B. boulengeri*, 22 of the earthworms in the guts are endogeic species (relatively small, non-pigmented) and the remaining specimen is a moderately large epigeic species.

Specimens of *B. boulengeri* contained significantly more individual prey items than specimens of *S. vittatus* ($F=5.69$, $P=0.020$). However, of the 1540 prey items found in the guts of *B. boulengeri*, 65.6% were invertebrate eggs, with a maximum of 624 in a single gut (Table 3). The vast majority of eggs were fused together into clusters, and each cluster was probably eaten as a single item. Even when all eggs from each specimen are treated as a single item of prey (i.e. $n=1$ rather than e.g. $n=624$), the number of prey per specimen is still significantly greater in *B. boulengeri* ($F=5.12$, $P=0.027$). In terms of the total number of prey found in all specimens, apart from eggs, the other dominant categories occurring in *B. boulengeri* are Nematocera larvae (15.1% of all prey), ants (7.6%) and termites (6.6%). In

Table 1 Morphological characteristics of the caecilian *Boulengerula boulengeri*, collected from East Usambara Mountains, Tanzania

	Males ($n=28$)	Females ($n=41$)	F
Total body length (mm)	170.7 ± 34.7 (117–234)	160.9 ± 22.6 (117–208)	1.96 NS
Width at jaw (mm)	2.9 ± 0.5 (2.0–4.0)	2.6 ± 0.3 (2.1–3.4)	20.43***
Width at occiput (mm)	3.2 ± 0.6 (2.3–4.4)	2.8 ± 0.3 (2.3–3.9)	22.21***
Width at midbody (mm)	3.6 ± 0.7 (2.5–5.0)	3.3 ± 0.5 (2.4–4.5)	1.97 NS
Length of lower jaw (mm)	3.2 ± 0.7 (2.2–5.0)	2.9 ± 0.4 (2.3–3.8)	11.25***
Mass (g)	2.1 ± 1.3 (0.5–4.7)	1.5 ± 0.6 (0.7–3.2)	6.58*

The values for males and females are the mean ± SD, and ranges are in parentheses. Total body length of males and females was compared using an analysis of variance, while the other variables were compared using an analysis of covariance with total body length as the covariate.
Levels of significance: NS, not significant; *<0.05; **<0.01; ***<0.001.

Table 2 Morphological characteristics of the caecilian *Scolecomorphus vittatus*, collected from East Usambara Mountains, Tanzania

	Males (n=10)	Females (n=10)	F
Total body length (mm)	248.0 ± 42.7 (184–306)	248.5 ± 79.9 (152–421)	0.001 NS
Width at jaw (mm)	4.5 ± 1.0 (2.8–5.9)	4.3 ± 1.3 (3.1–6.5)	0.204 NS
Width at occiput (mm)	4.7 ± 1.0 (3.1–6.0)	4.5 ± 1.3 (3.2–6.6)	0.390 NS
Width at midbody (mm)	6.6 ± 1.2 (5.1–8.5)	6.9 ± 2.5 (4.8–12.8)	0.834 NS
Length of lower jaw (mm)	5.1 ± 1.3 (3.7–7.3)	4.7 ± 1.4 (3.3–7.0)	1.22 NS
Mass (g)	8.1 ± 3.1 (3.4–12.4)	11.6 ± 13.7 (3.2–45.6)	3.55 NS

The values for males and females are the mean ± SD, and ranges are in parentheses. Total body length of males and females was compared using an ANOVA, whereas the other variables were compared using an ANCOVA with total body length as the covariate.

Table 3 Frequency and number of prey found in the guts of the caecilians *Boulengerula boulengeri* and *Scolecomorphus vittatus* collected from Nilo Forest Reserve, East Usambara Mountains, Tanzania

	B. boulengeri (n=78 specimens)							*S. vittatus* (n=20 specimens)						
	Frequency		Number of prey items					Frequency		Number of prey items				
Prey category	n	(%)	Total	Prey (%)	Mean	Min.	Max.	n	(%)	Total	Prey (%)	Mean	Min.	Max.
Oligochaeta[a]	23	29.5	23	1.5	1.0	1	1	11	55.0	15	48.4	1.4	1	3
Isoptera (workers and soldiers)	16	20.5	102	6.6	6.4	1	32	0		0				
Diptera Nematocera (larvae)	21	26.9	233	15.1	11.1	1	40	0		0				
Other Diptera (larvae)	2	2.6	2	0.1	1.0	1	1	0		0				
Hymenoptera Formicidae (workers)	5	6.4	53	3.4	10.6	1	44	3	15.0	3	9.7	1	1	1
Hymenoptera Formicidae (larvae)	2	2.6	64	4.2	32.0	2	62	0		0				
Coleoptera (adults)	4	5.1	4	0.3	1.0	1	1	1	5.0	1	3.2	1	1	1
Coleoptera (larvae)	8	10.3	11	0.7	1.4	1	3	0		0				
Lepidoptera Psychidae (larvae)	2	2.6	2	0.1	1.0	1	1	0		0				
Diplura Japygidae	1	1.3	2	0.1	2.0	2	2	0		0				
Chilopoda Geophilida	5	6.4	5	0.3	1.0	1	1	0		0				
Araneae	1	1.3	1	0.1	1.0	1	1	0		0				
Schizomida	1	1.3	1	0.1	1.0	1	1	1	5.0	1	3.2	1	1	1
Acari	3	3.8	3	0.2	1.0	1	1	2	10.0	2	6.5	1	1	1
Isopoda	5	6.4	5	0.3	1.0	1	1	0		0				
Indeterminate invertebrate eggs	5	6.4	1009	65.6	201.8	2	624	1	5.0	2	6.5	2	2	2
Indeterminate arthropod parts	20	25.6	20	1.3	1.0	1	1	5	25.0	7	22.6	1.4	1	2
Caecilian specimens with empty gut	11	14.1	0					4	20.0	0				
All caecilian specimens			1540		19.7	0	624			31		1.6	0	5

	Frequency		Number of parasites				Frequency		Number of parasites			
Parasite load	n	(%)	Total	Mean	Min.	Max.	n	(%)	Total	Mean	Min.	Max.
Nematodes	67	85.9	265	4.0	1	14	20	100	4111	206	7	798

[a] *B. boulengeri* contained 22 endogeic earthworms and one epigeic earthworm. *S. vittatus* contained 11 epigeic earthworms and four anecic earthworms.

contrast, 48% of the 31 individual prey items found in *S. vittatus* are earthworms (Table 3).

Nematodes

The occurrence and numbers of nematodes were high (Table 3), especially in *S. vittatus*. Except for a single specimen, the nematodes in *S. vittatus* represent two oxyurid species. There were also at least two species in *B. boulengeri* guts, including a probable pharyngodonid (cf. *Batracholandrus* spp.). Apart from an individual nematode from a specimen of *S. vittatus*, all nematodes from both species of caecilians appeared to be parasitic forms.

Diet and caecilian size

The maximum width of prey is significantly greater in *S. vittatus* ($F = 9.69$, $P = 0.0026$) than in *B. boulengeri* (Table 4). Similarly, log(maximum length + 1) of prey is also significantly greater in *S. vittatus* ($F = 5.71$, $P = 0.0192$). Earthworms were always the largest items found in the guts of *S. vittatus*. However, in the case of *B. boulengeri*, termites, woodlice and centipedes are often wider (and centipedes sometimes longer) than earthworms in the same gut.

In *B. boulengeri*, all the recorded morphological characteristics are significantly correlated with maximum prey width (Table 5). However, only total body length is significantly correlated with log(prey number), whereas log(maximum prey length + 1) is not significantly correlated with any morphological characteristics. In the case of *S. vittatus*, only body mass is significantly correlated with maximum prey width, only width at midbody and body mass are significantly correlated with log(maximum prey length + 1), and log(prey number) is not significantly correlated with any morphological characteristics (Table 5). No significant differences between males and females of *B. boulengeri* occur in maximum prey width, log(maximum prey length + 1) or log(prey number) using ANOVA, or using ANCOVA with total body length as the covariate (Table 6). Similarly, for *S. vittatus* no significant differences between the sexes occur (results not shown), although this test may have been limited by the relatively small sample size.

Sexual differences in dietary composition within *B. boulengeri* were considered by examining the six dominant categories of prey: earthworms, termites, Nematocera larvae, beetle larvae, ants (combining workers and larvae) and invertebrate eggs. There is no significant difference between male and female caecilians in their proportional representation of prey from the six categories (Fig. 2a; $\chi^2 = 1.78$, $P = 0.878$). In terms of the numbers of prey per specimen, there is a significant difference between males and females (Fig. 2b; $\chi^2 = 112$, $P < 0.001$). When all eggs from each specimen are treated as a single item of prey, there is still a significant difference between males and females in the number of prey per specimen (Fig. 2c; $\chi^2 = 65.7$, $P < 0.001$). Given the small sample size of *S. vittatus*, combined with the small number of prey, similar tests were not performed on this species.

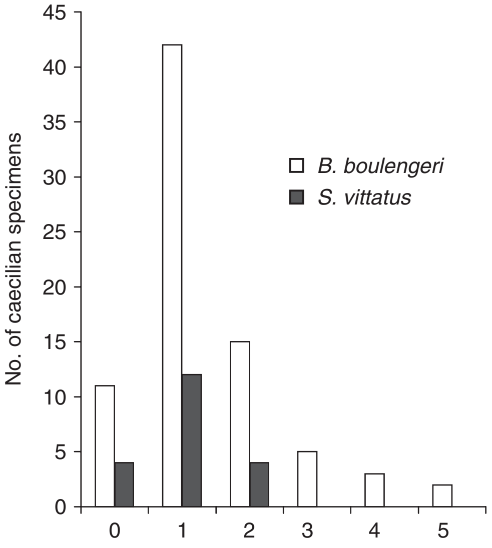

Figure 1 Frequency distributions of the number of prey categories found in the guts of caecilians collected in Nilo Forest Reserve, Tanzania. Open bars, *Boulengerula boulengeri* ($n = 78$); black bars, *Scolecomorphus vittatus* ($n = 20$).

Discussion

The following interpretations carry the caveat that sampling was undertaken only once in a single area. *Scolecomorphus vittatus* in our sample fed predominantly on earthworms. These are the first data published on the diet of any scolecomorphid species, and along with the caeciliid *Schistometopum thomense* (see Delêtre & Measey, 2004), it is the greatest degree of dietary specialization recorded for caecilians (see Gaborieau & Measey, 2004), albeit based on a small sample of individuals. In contrast, *B. boulengeri* is a dietary generalist, feeding on a wider range of soil invertebrates, a high proportion of which are earthworms, Nematocera larvae, termites, beetle larvae and ants. Although *S. vittatus* also feeds on soil arthropods, the mean number consumed per individual is significantly lower than in *B. boulengeri*. It is important to note that all but one of the earthworms (96%) eaten by *B. boulengeri* are small endogeic species, whereas all earthworms eaten by *S. vittatus* are moderate to large epigeic (73%) and anecic (27%) species. Epigeic and anecic species are mainly active on or in the leaf litter, whereas endogenic species usually remain in the soil below the litter layer (Sims & Gerard, 1999).

In contrast to our results for *B. boulengeri*, Gaborieau & Measey (2004) found that 12% of the earthworms eaten by *Boulengerula taitanus* were epigeic forms. Delêtre & Measey (2004) also distinguished epigeic and endogeic earthworm prey in the at least occasionally surface-active *Schistometopum thomense*, but they presented no data on the numbers of these prey categories. Most of the earthworm prey reported by Delêtre & Measey (2004) can be classified as either endogeic (*Dichogaster* sp. D, E; Eurdrilidae; taxon G) or epigeic (*D. greeffi*, *Amynthas cortocis*, taxon A) taxa

Table 4 Maximum width and length of prey items from the guts of two syntopic species of East African caecilians

	Boulengerula boulengeri ($n = 67$)		*Scolecomorphus vittatus* ($n = 16$)			
	Mean (SD)	Range	Mean (SD)	Range	*F*	*P*
Maximum prey width (mm)	1.36 (0.65)	0.19–3.45	2.15 (1.63)	0.27–5.21	9.69	0.0026
Maximum prey length (mm)	6.68 (1.44)*	0.61–64.51	15.01 (4.85)*	0.41–167.5	5.71	0.0192

The values (*) given for the mean and standard deviation (SD) were back-transformed from log(maximum prey length + 1).

Table 5 Correlation coefficient (*r*) between morphological variables of two syntopic species of East African caecilians, and their gut contents

	Boulengerula boulengeri (*n*=67)			*Scolecomorphus vittatus* (*n*=16)		
	Log(prey number)	Maximum prey width	Maximum log (prey length)	Log(prey number)	Maximum prey width	Maximum log (prey length)
Total body length	0.236*	0.400***	0.219 NS	0.218 NS	0.306 NS	0.254 NS
Width at jaw	0.178 NS	0.382**	0.147 NS	0.126 NS	0.389 NS	0.237 NS
Width at occiput	0.164 NS	0.383**	0.146 NS	0.116 NS	0.393 NS	0.219 NS
Width at midbody	0.156 NS	0.344*	0.110 NS	0.326 NS	0.420 NS	0.455*
Length of lower jaw	0.208 NS	0.399***	0.194 NS	0.103 NS	0.288 NS	0.133 NS
Body mass	0.194 NS	0.402***	0.210 NS	0.317 NS	0.496*	0.448*

Specimens with an empty gut were excluded.
Levels of significance: NS, not significant; $^{*}<0.05$; $^{**}<0.01$; $^{***}<0.001$.

Table 6 Testing for dietary differences between males and females of the East African caecilian *Boulengerula boulengeri*

Variable	ANOVA or ANCOVA	*F*	*P*
Maximum prey width	ANOVA	1.17	0.283
Maximum prey width	ANCOVA	0.34	0.565
Log(maximum prey length + 1)	ANOVA	0.06	0.816
Log(maximum prey length + 1)	ANCOVA	0.02	0.871
Log(number of prey)	ANOVA	2.01	0.163
Log(number of prey)	ANCOVA	2.04	0.163

The number of prey, and the maximum width and maximum length of prey in each caecilian gut were compared between the sexes using analysis of variance (ANOVA) or analysis of covariance (ANCOVA) using caecilian body length as the co-variable.

(M. Delêtre, pers. comm.). Adult *Schistometopum thomense* sampled by Delêtre & Measey (2004) fed on both types in equal proportions, whereas juveniles had only endogeic worms in their guts.

The significant correlation between the morphology of *B. boulengeri* and maximum prey width suggests that the size of the head of individual caecilians limits the width of prey ingested. The same trend is not evident in *S. vittatus*. Delêtre & Measey (2004) found a significant positive correlation between prey and predator head size only in females of *Schistometopum thomense*. Gape is known to be a factor in the size of prey taken by some frogs and salamanders (e.g. Duellman & Trueb, 1994).

Earlier results from this study (Gower *et al*., 2004) demonstrated differences in microhabitat use between these two syntopic caecilian species. The smaller *B. boulengeri* is predominantly a soil burrower captured almost only by digging, whereas the larger *S. vittatus* is rarely found by digging soil and spends more time at the surface than *B. boulengeri*. Differences in morphology appear to match interspecific differences in behaviour. For example, *B. boulengeri* have bullet-shaped heads, near-cylindrical bodies and markedly reduced eyes that are covered by bone: these are thought to be adaptations to a predominantly burrowing lifestyle (see Gower *et al*., 2004). In *S. vittatus*, however, the better developed eye is more exposed, consistent with the visual system being more important in this species, in agreement with the understanding that it spends more time near or on the surface. One of the *S. vittatus* collected for this study was found on the surface ingesting an earthworm. The more mobile cheek region of *S. vittatus* (see Gower *et al*., 2004) is perhaps an advantage in handling predominantly large, soft-bodied prey. It is unknown to what extent *S. vittatus* feeds deeper in the soil (one of the two specimens dug from soil had an empty gut; the other had indeterminate arthropod fragments), but a combination of all these results provides further strong evidence of niche separation between these syntopic species. *Boulengerula boulengeri* are dedicated burrowers feeding opportunistically on a wide range of soil invertebrates, whereas *S. vittatus* spend more time than *B. boulengeri* at or near the surface and feed predominantly on larger, surface-active earthworms.

All the ants found in the guts of both caecilian species are of the Myrmicinae subfamily. The presence of ant larvae in two specimens of *B. boulengeri* indicates that these two caecilians were likely to have fed within subterranean ant nests. Sixteen specimens of *B. boulengeri* had eaten termites but only soldiers and workers were found in the gut, suggesting that these caecilians had been feeding on foraging parties and had not penetrated brood chambers within termite nests. The termites are mostly species of *Microtermes* and *Odontotermes*, of the Macrotermitinae subfamily (Termitidae). This is not surprising, given that this subfamily is a dominant part of the soil-dwelling termite assemblage in the nearby mid-elevation forests of the Taita Hills, Kenya (P. Eggleton, unpubl. data), and the Nyika plateau, Malawi (Donovan, Eggleton & Martin, 2002).

Heavily sclerotized chitinous arthropod exoskeletons are relatively resistant to degradation. Fragments of exoskeleton are always present in soil, and are ingested with soil into the guts of soil-feeding termites and earthworms (Donovan, Eggleton & Bignell, 2001). Thus, some of the unidentifiable arthropod fragments found in caecilian guts may have come from the guts of their soil-feeding prey.

The generalist diet of *B. boulengeri* is similar to that of two other caeciliid species that have been subject to dietary analysis based on randomized samples. *B. taitanus* from both agricultural and forest habitats in the Kenyan Taita

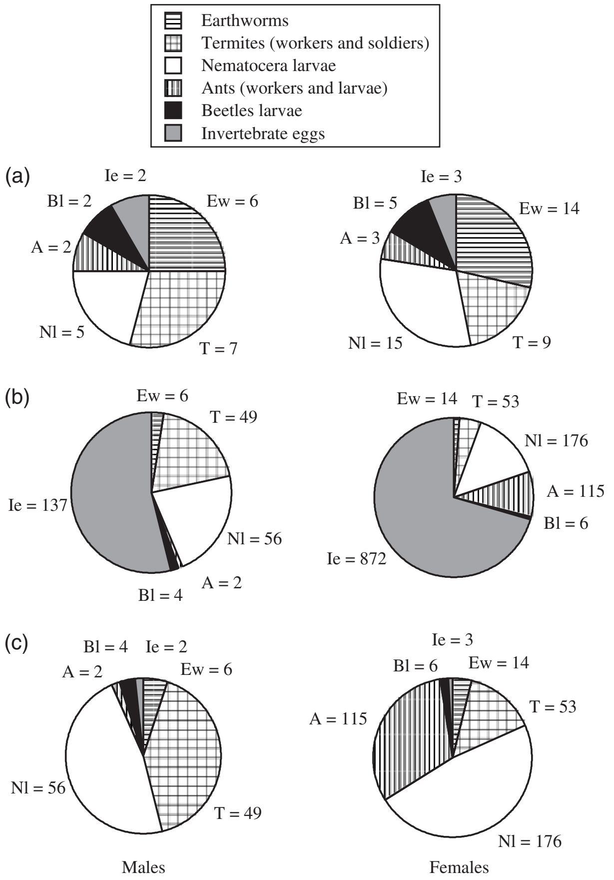

Figure 2 Pie charts of the six dominant prey categories found in the guts of male (left; n=24) and female (right; n=49) specimens of the caecilian *Boulengerula boulengeri* collected from Nilo Forest Reserve, Tanzania. (a) Proportion of specimens containing prey from each category; (b) Proportion of prey in each category; (c) Proportion of prey from each category when all invertebrate eggs from each gut are treated as a single item of prey. Absolute numbers are given for prey. Ew, earthworms; T, termites (workers and soldiers); Nl, Nematocera larvae; A, ants (workers and larvae); Bl, beetle larvae; Ie, indeterminate invertebrate eggs.

Hills (also part of the Eastern Arc) feed mainly on termites, earthworms and Diptera larvae but also consume other arthropods including ants and centipedes (Gaborieau & Measey, 2004). For *Gegeneophis ramaswamii*, collected from agricultural sites in Kerala, southern India, ants, termites and earthworms are the major dietary constituents, together with low numbers of other groups including spiders, Coleoptera and Diptera larvae (Measey *et al.*, 2004). The presence of ant brood in their guts suggests that *G. ramaswamii* also feeds within ant nests. Ants have also been recorded in the diet of the ichthyophiid *Ichthyophis* cf. *kohtaoensis* from Thailand (Kupfer *et al.*, 2005*a*).

Of the 21 specimens of *B. boulengeri* that had fed on Nematocera larvae (total = 233 larvae), nine contained 90% of the total, with relatively large numbers in three individuals (n = 33, 38 and 40). The guts of small numbers of individual *B. taitanus* also contain large numbers of tipulid dipteran larvae (Gaborieau & Measey, 2004). If dipteran eggs are deposited in clusters in the soil, then the distribution of hatched larvae may be very heterogeneous. Thus, individual caecilians encountering this prey would have the opportunity to feed upon large numbers of larvae and eggs.

Sexual size dimorphism has not been reported for many caecilians and head size dimorphism only previously published for the caeciliids *Schistometopum thomense, Schistometopum gregorii* and *Hypogeophis rostratus* and the scolecomorphids *Scolecomorphus kirkii* and *Scolecomorphus uluguruensis* (Nussbaum, 1985; Nussbaum & Pfrender, 1998; Teodecki *et al.*, 1998). In agreement with Nussbaum (1985), we found no head size dimorphism in *S. vittatus*. Contrary to Delêtre & Measey's (2004, p. 251) prediction, the dedicated burrower *B. boulengeri* has a pronounced sexual dimorphism in head size. Although both sexes of *B. boulengeri* feed on the same categories of prey, the females in our sample consumed disproportionately more ants and invertebrate eggs, and disproportionately fewer termites than males. If ant larvae and invertebrate eggs have a higher nutritional value than later life stages, one possible explanation for this may be that female *B. boulengeri* have a greater tendency to actively seek these types of prey in order to benefit their reproductive effort. However, it is not possible to state whether this is a general trend for *B. boulengeri* because the numbers of specimens found to contain ants and invertebrate eggs is relatively small, and our statistical results are thus not compelling. In *G. ramaswamii* there is no evidence for significant differences between male and female diet (Measey *et al.*, 2004). Delêtre & Measey (2004) claim that males and females of the sexually dimorphic *Schistometopum thomense* do not have significantly different diets. However, their conclusion is based on tests conducted on small numbers of prey items (mean <2 per caecilian) from caecilians pooled from three subsamples collected from very different habitats at one time of the year, and we do not find their statistical results compelling.

Caecilian impact on SEE

The density of caecilians and their prey has not been measured at our study site, so that, at present, the impact of caecilian predation on invertebrate SEE populations can only be approximated using density data from other locations. In surveys of caecilians from forest sites in northern Tanzania (Measey, 2004), the mean density of *B. boulengeri* was $0.44\,\mathrm{m}^{-2}$ (range: 0.07–0.87) and that of *S. vittatus* was $0.014\,\mathrm{m}^{-2}$ (0.00–0.07). There are very few data available on the density of earthworms, termites and ants in East African forest soils, and so we considered data from forests in other areas of tropical Africa (Table 7).

To gauge the possible impact of caecilians on invertebrate SEE populations, we considered mean population densities of caecilians and the mean number of prey in the gut. For caecilians, there are no published data on the passage time of prey from ingestion to defecation (Duellman & Trueb,

Table 7 Density (m^{-2}) of earthworms, termites and ants in African forest soil and litter

Location	Habitat	Altitude	Source	Earthworms	Termites	Ants
Nigeria	Tropical forest	Lowland	Edwards & Bohlen (1996)	34	–	–
Nigeria	Tropical forest	Lowland	Edwards & Bohlen (1996)	61.7	–	–
Nigeria	Semi-deciduous forest	Lowland	Wood *et al.* (1982)	–	3163	–
Nigeria	Riverine forest	Lowland	Wood *et al.* (1982)	–	2646	–
Ivory Coast	Tropical rainforest	Lowland	Fragoso & Lavelle (1992)	35	–	–
Ivory Coast	Riverine forest	*c.* 300 m	P. Eggleton, unpubl. data	38	–	171
Ivory Coast	Rainforest	*c.* 200 m	P. Eggleton, unpubl. data	55.5	–	162
Congo	Riverine forest	Lowland	Maldague (1964)	–	1000	–
Congo	Tropical rain forest	Lowland	Fragoso & Lavelle (1992)	44	–	–
Kenya	Highland equatorial forest	1936 m	Lee (1983)	157	–	–
Gabon	Primary rainforest	Lowland	B. Bolton unpubl. data	–	–	48.4
Ghana	Moist semi-deciduous forest	Lowland	B. Bolton unpubl. data	–	–	139.1
Cameroon	Semi-deciduous forest	650 m	Watt, Stork & Bolton (2002)	–	–	49.1
Cameroon	Semi-deciduous forest	650 m	Eggleton *et al.* (1996)	–	4620	–
			Mean	60.7	2857	114

–, density not determined.

Table 8 Estimates of the consumption of earthworms, termites and ants by two caecilian species, *Boulengerula boulengeri* and *Scolecomorphus vittatus*, in Nilo Forest Reserve, Tanzania (see text for explanation)

	B. boulengeri			*S. vittatus*		
	Earthworms	Termites	Ants	Earthworms	Termites	Ants
Number of prey in gut	0.29	1.37	1.15	0.75	0.00	0.15
Caecilian density (m^{-2})[a]	0.44	0.44	0.44	0.07	0.07	0.07
Number of prey in gut (m^{-2})	0.13	0.60	0.51	0.05	0.00	0.01
Invertebrate density (m^{-2})	60.7	2857	114	60.7	2857	114
Percentage of invertebrate population in gut	0.21	0.02	0.44	0.09	0.00	0.01
Passage time through gut (days)	1.5	1.5	1.5	1.5		1.5
Number of days to consume 10%	71.4	711	33.8	173		1629

[a] Data from Measey (2004).

1994), but several species of wild-caught terrestrial caecilians kept in captivity without food stop producing faeces after about 2 days (A. Kupfer, pers. comm.). For our two study species, we assumed a constant passage time of 1.5 days. This is similar to many measures of passage time in frogs and salamanders (e.g. Larsen, 1992), but is perhaps on the rapid side for a constant mean when considering the seasonality of the East Usambara region, and evidence that density of caecilians, and their dietary composition and intake, fluctuate in seasonal environments (e.g. Measey *et al.*, 2004; Kupfer *et al.*, 2005*a*; Kupfer, Nabhitabhata & Himstedt, 2005*b*).

At the time of sampling, the percentage of the estimated standing crop of earthworms, termites and ants found in the guts of *B. boulengeri* was 0.21, 0.02 and 0.44%, respectively (Table 8). Thus, it would take *c.* 71, 711 and 34 days for the *B. boulengeri* population to consume 10% of the standing crop of earthworms, termites and ants, respectively (Table 8). The estimated impact of *S. vittatus* is much less because of its lower population density (Table 8).

Our approach includes several assumptions and sources of possible error, so that the impact estimates must be treated with caution. Although uncertain, the estimated proportion of the termite standing crop consumed by caecilians at our study site is unlikely to be among the most important factors impacting population densities of the local termite assemblage over ecological time. This is particularly true given that Macrotermitinae queens can produce thousands of eggs per day (Nielsen & Josens, 1978), and the fact that there is no evidence that caecilians are entering termite nests and consuming brood. The potential effect on ant populations appears to be much greater, especially given that some caecilians occasionally feed within ant nests. However, all the ant densities presented in Table 8 are likely to be underestimates because they are based on Winkler bag sampling, unlike the termite estimates, which are all from hand-sorting of soil and litter, and therefore likely to be more accurate. Data from 200 hand-sorted soil samples from mostly tropical regions suggest that ants represent *c.* 29% of the soil and litter macrofaunal abundance compared with 49% for termites (Lavelle & Fragoso, 2000), suggesting that the ant densities in Table 8 are perhaps up to an order of magnitude too low.

Our data suggest that the two caecilian species found in Nilo FR use earthworms, termites and ants as a dietary resource, at least at the time of sampling. Although caecilian predation may have an impact on these SEE, it is perhaps unlikely that this is among the most important factors controlling ant and termite populations over ecological time. It is more difficult to assess the impact of caecilian predation on the earthworm community because the abundance and life histories of the prey species are unknown.

Some other endogeic vertebrates do prey on large numbers of invertebrate SEE (e.g. scolecophidian snakes on termites and ants, Webb *et al*., 2000; Webb, Branch & Shine, 2001), but few quantitative measures of their abundance exist, and only four scolecophidian snakes (*Rhinotyphlops gierrai*) were found in Nilo Forest Reserve during our sampling. SEE are preyed upon by many invertebrates and vertebrates, but there is no evidence thus far that caecilians stand out in their predatory impact. Although contributing to nutrient turnover, it may be that caecilians also impact soil ecology through alterations to soil drainage, aeration and physicochemical properties caused by burrowing (Oommen *et al*., 2000). Additionally, caecilians may impact invertebrate SEE by exerting selective pressures on them over evolutionary time. Our aim here was to move the field forward by beginning to use quantitative data to test the general hypothesis that abundant caecilians impact soil ecology. We have provided one preliminary 'test' of a specific part of this hypothesis. Further progress requires the formulation of more precise hypotheses, and use of appropriate data and experimental designs, probably including lab- or field-based manipulations such as exclusion experiments.

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