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Termitivore or detritivore? A quantitative investigation into the diet of the East African caecilian *Boulengerula taitanus* (Amphibia: Gymnophiona: Caeciliidae)

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Abstract—Most caecilians are thought to be generalist predators of soil ecosystem engineers (earthworms, termites and ants), but it has been suggested that members of the East African genus *Boulengerula* are specialist predators. Surprisingly, in the only detailed study of diet of any *Boulengerula*, the authors speculated that *B. taitanus* is partly detritivorous, based on the large amount of organic matter found in the alimentary canal. Here we test the conflicting hypotheses that *B. taitanus* is a termitivore or detritivore, using the stomach and gut contents of 47 specimens collected in the Taita Hills, Kenya. Termites and earthworms contribute most significantly to diet by number and mass, respectively. These constitute the major dietary items, together with dipteran larvae and other soil macrofauna. Contents of the intestine are mostly soil and organic matter originating from prey items. The mass content of the intestines averages 69% of total gut contents, and is significantly greater than identifiable stomach contents. The null hypotheses that *B. taitanus* is a generalist and a predator are not rejected.

Keywords: *Afrocaecilia taitanus*; predation; soil ecosystem engineers; subterranean predators; termites; vertebrates.

INTRODUCTION

Termites are an important prey item for many species of vertebrate and invertebrate predators (Sheppe, 1970; Abensperg-Traun and Steven, 1997). The benefits of specialising on these potentially rewarding food items relate to their occurrence in high densities, and the high energy content of individuals (Redford and Dorea, 1984). Myrmecophagy as an ecological strategy has led to physiological conver-

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gence in mammals (McNab, 1984) and is the modus operandi for many dedicated subterranean squamates (see Webb et al., 2000a, and references therein).

Most caecilian amphibians (Gymnophiona) are thought to be subterranean predators and are distributed throughout the humid tropics. Whilst detailed research on caecilian diet remains rare (Measey et al., 2004), several studies have mentioned the nature of food items in the course of addressing other aspects of caecilian biology. Such investigations have included general descriptions of frequently encountered food items such as earthworms (Nussbaum and Pfrender, 1998), termites (Barbour and Loveridge, 1928) or both (Wake, 1980), and these observations concur with general texts which describe diets of earthworms and termites (Taylor, 1968; Wake, 2002). Another group of literature has concentrated on infrequent and possibly unusual findings of vertebrate prey, particularly scolecophidian snakes, that also occur in caecilian gut contents (see Presswell et al., 2002, and references therein). In a quantitative study of seasonal changes in the diet of a subterranean caecilian, *Gegeneophis ramaswamii* Taylor, Measey et al., 2004 concluded that it was a generalist predator of soil macrofauna and, in particular, of soil ecosystem engineers: ants, termites and earthworms (sensu Lavelle et al., 1997).

The Taita Hills represent the northernmost range of forested ancient crystalline mountains in the Eastern Arc, an exceptionally rich area of biodiversity and endemicity in eastern Tanzania and south-east Kenya under the direct climatic influence of the Indian Ocean (Lovett, 1998). *Boulengerula taitanus* Loveridge is a dedicated subterranean burrower and Taita Hills endemic (Nussbaum and Hinkel, 1994). Although presumably native to naturally occurring forest, *B. taitanus* is now widespread in agricultural areas, and its ease of capture has resulted in several studies which include physiology (Wood et al., 1974), morphology (Maina and Maloiy, 1988) and diet (Hebrard et al., 1992). Hebrard et al. (1992: 513) stated that "the most frequent countable items in the guts were the head capsules of extremely small termites". Loveridge (1936: 378) also investigated stomach contents of *B. taitanus* found in presumably forested areas of the Taita Hills, finding them to be "so finely masticated as to be indeterminate".

In their study, Hebrard et al. (1992) commented on the large proportion of decaying plant material and unidentifiable organic matter that was present in the guts of all but one of the *B. taitanus* examined. That this occurred in the 43% of their sample without other identifiable prey, prompted Hebrard et al. (1992) to hypothesise that *B. taitanus* is partly detritivorous. Whilst soil, plant and organic matter have all been found previously in terrestrial and aquatic caecilian guts (Largen et al., 1972; Wake, 1978; Exbrayat and Delsol, 1985; Gudynas and Williams, 1986; Breckenridge et al., 1997; Nussbaum and Pfrender, 1998; Wilkinson et al., 1998; Measey et al., 2004), omnivory has not been suggested for these caecilian amphibians, although it is known in anurans (Das, 1996).

Wake (1986) appears to have first proposed that species of the genus *Boulengerula* are specialists of termites, presumably following the comments of Barbour and Loveridge (1928). In a recent review of caecilian feeding, O'Reilly (2000) (without reference to Wake, 1986) remarked on previous studies and his own experience of feeding captive *Boulengerula*. He also suggested that species of this genus are specialised, and he contrasted them with other species which are apparently opportunistic predators. In this quantitative investigation of caecilian diet, we use the contents of *B. taitanus* guts from animals collected in natural forest and low intensity agriculture to test the conflicting hypotheses that caecilians of the genus *Boulengerula* are specialist predators (Wake, 1986; O'Reilly, 2000), and that *B. taitanus* is partly detritivorous (Hebrard et al., 1992).

MATERIAL AND METHODS

Material used in this study was collected as part of an investigation into density and abundance of caecilians in East Africa using the randomised survey methods of Measey et al. (2003) and additional timed searches. Detailed information on localities, sites and collection methods, together with morphological data on animals captured, is presented elsewhere (Measey, subm.).

Two sites were chosen to sample animals representative of agriculture and forest; low intensity small holdings ('shambas') around Wundanyi and N'Gan'Gao Forest Reserve, respectively. The shambas, with various crops including bananas, maize, cassava and sugar cane, were visited from 3-5 May 2002. At all shambas, typical soil texture (sensu Dubbin, 2001) was a clay loam, with a temperature of 20.7°C and pH 6.75 (measurements made with an Acorn pH 6, Forestry Suppliers, USA). N'Gan'Gao Forest Reserve is a small pocket of natural forest; collections were made throughout the forest on 6 and 7 May 2002. The soil consistency was a sandy loam, with a pH of 6.34 and temperature of 20.5°C.

All caecilians were killed via anaesthesia (MS222) within 4 h of capture, and subsequently fixed in formalin (10% from a stock solution ca 40%), and stored in 70% ethanol. Total preserved length was measured to the nearest 1 mm with a ruler. Laboratory dissections were made with the aid of a stereo-zoom microscope to remove the alimentary canal from immediately posterior to the heart to the anterior of the cloaca (Measey et al., 2004). This portion of the alimentary canal was weighed (to the nearest 0.0001 g), and the end of the stomach (defined by a constriction and opening of pancreatic ducts) marked with a pin. Thereafter, the two portions, stomach and intestine, were treated separately:

Stomach

This was opened along its length and the contents removed and identified as morphospecies or sorted into ecological groupings (Lavelle, 1981; Eggleton et al., 2002), and Diptera identified to family (Foote, 1991) with the aid of a stereo-zoom microscope. Each morphospecies was enumerated and its total mass determined, after blotting, for each stomach (to the nearest 0.0001 g); any debris found was similarly treated. For termites, attention was paid to numbers and mass of castes as well as between ecological groups. Enumeration of arthropod groups was made with reference to unique pieces (such as head capsules in termites) such that no individual prey item was recounted due to fractionation of an individual. Notes were taken on the position and state of digestion of prey items.

Intestine

The intestine was opened and the contents put into 5 ml of water which was then agitated and allowed to stand until all coarse elements had settled (between 30 and 60 s). Three aliquots of 1 ml were then taken from the remaining suspension using a pipette. They were placed separately into a Petri dish, and the contents searched for earthworm setae using low angle light against a black background with a stereo-zoom microscope at ×30. Viewed in this way, earthworm setae are visible as small, translucent, yellow, curved spines. The mean and variance were calculated for these three sub-samples for each animal dissected. Mass of the empty gut was determined to the nearest 0.0001 g. The remaining sediment was then examined for pieces of identifiable material, and its mass determined by subtracting the sum of empty gut and total stomach contents from the total gut mass.

Preserved caecilians were placed into the collections of the National Museums of Kenya (NMK A/4007/1 to A/4010/3 inclusive) and the Natural History Museum, London (BMNH 2002 103-126 inclusive).

Data analyses

STATISTICA (v 5.5A, StatSoft, France) was used for statistical analyses of the data. To assess the importance of dietary items, morphospecies were grouped together into broad taxonomic categories (termites, earthworms, dipteran larvae and others). One-way analysis of variance (ANOVA $F_{\mathrm{df}} = F$-test; P) was used to find differences in mass and frequency (on log transformed data) of these broad taxonomic groups. Analysis of covariance (ANCOVA) was used on the mass of detritus in stomach and intestine and identifiable food items, with total preserved length as the covariate, and their adjusted means used for figures.

RESULTS

Of the 47 *Boulengerula taitanus* stomachs examined, four (8.5%) were empty, and three more had no contents which could be identified, other than as very small quantities (<0.005 g) of detritus; hence they were treated as empty. Twenty eight (61.7%) stomachs contained earthworms, and 15 (38%) termites (table 1). In addition, ten stomachs (21.3%) had dipteran larvae, and other occasional prey included centipedes, ants, antlions, thrips and slugs. Table 1 shows that termites are the most frequently ingested prey, followed by dipteran larvae and earthworms; a difference which was found to be significant ($F_{3,184} = 5.02$; $P = 0.002$). However,

Table 1.
Morphospecies found in the stomachs of *Boulengerula taitanus* (J, juveniles, F, females and M, males) collected from the Taita Hills, Kenya. Prey items are ordered by soil macrofaunal groups, with frequency of occurrence and total mass in g (0.00 indicates presence at <0.005 g). Soil ecosystem engineers (SEE) are shown in bold.

	Frequencies			Masses			Total Freq.	Total Mass
Sex	J	F	M	J	F	M		
Sample Size	4	16	27	4	16	27	47	47
Earthworms								
Polyhumics	3	8	7	0.00	0.02	0.01	18	0.03
Mesohumics	4	19	9	0.02	0.19	0.40	32	0.61
Epigeics	0	9	0		0.22		9	0.22
Unidentified	1	9	8	0.02	0.41	0.70	18	1.13
Sub-total	**8**	**45**	**24**	**0.04**	**0.84**	**1.10**	**77**	**1.98**
Termites								
Small xylophageous	0	33	11		0.04	0.02	44	0.06
Large xylophageous	0	52	27		0.10	0.07	79	0.17
Small humivorous	0	17	41		0.04	0.05	58	0.09
Large humivorous	0	8	61		0.04	0.20	69	0.24
Small workers	0	5	103		0.04	0.13	108	0.17
Large workers	0	40	38		0.02	0.05	78	0.07
Sub-total	**0**	**155**	**281**		**0.27**	**0.53**	**436**	**0.80**
Fly larvae (Tipulidae)								
A	0	0	102			0.32	102	0.32
B	0	0	5			0.06	5	0.06
C	0	2	0		0.00		2	0.00
Sub-total	0	2	107		0.00	0.38	109	0.38
Others								
Antlion larvae	0	0	2			0.08	2	0.08
Centipede	0	1	2		0.01	0.42	3	0.43
Ants	**0**	**1**	**1**		**0.00**	**0.00**	**2**	**0.00**
Thrips	0	0	2			0.01	2	0.01
Slugs	0	0	1			0.11	1	0.11
Sub-total	0	2	8		0.01	0.61	10	0.62
Total SEE	**8**	**201**	**306**	**0.04**	**1.12**	**1.63**	**515**	**2.79**
Total Others	0	3	114		0.01	0.99	117	1.00
Total	8	204	420	0.04	1.12	2.62	632	3.79

table 1 also shows that earthworms account for a greater mass than termites, and this comparison is illustrated in the summary of adjusted mean masses of broad taxonomic groups (fig. 1).

Precise taxonomic determination of termites proved problematic as many were only represented by their head capsules. We therefore emphasised identification of ecological groups. This was only possible when examples of individuals whose abdomen was not completely digested were present (table 1). Of a total of 434

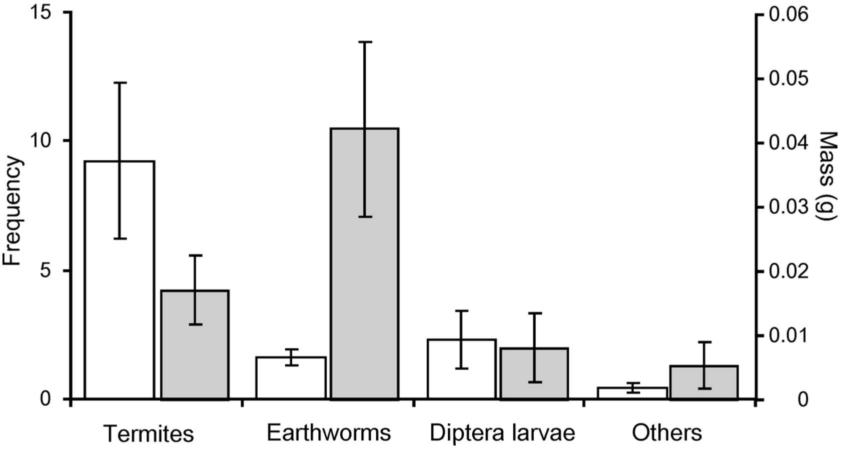

Figure 1. A bar chart showing that termites have the greatest mean frequency (white bars, left ordinate) of large taxonomic groups of prey items in stomachs of *Boulengerula taitanus* from the Taita Hills, Kenya, while earthworms contribute the greatest mean mass (grey bars, right ordinate). Error bars are ± standard error of the mean.

individual termite remains from 15 *B. taitanus*, 50.5% were humivorous taxa (feeding group III, see Eggleton et al., 2002), 7.1% xylophagous (feeding group II), and 42.4% workers of unidentified origin. Each group had roughly equal numbers of large and small working casts (table 1), their head capsule size varying from 1.1 to 1.7 mm maximum width. When present, the average number of termites found in a stomach was 28.9 (±7.31), although the range was large (1-99). No termites of soldier cast were found in stomachs, and only the remains of two soldiers were found in the intestine. No evidence of termite nymphs or eggs was found in stomachs or intestines.

Of the 75 earthworm pieces found in stomachs, 21.6% were unidentifiable due to their advanced state of digestion. In such cases only the anteriormost portion in the stomach was recognisable as earthworm tissue, and the posterior part of the stomach contained only soil and humic matter. Two earthworms were found to be completely distorted, with soil from their intestines embedded around the remains which were twisted throughout their length. The tissue was not in an advanced state of digestion, and was recognisable as earthworm tissue with setae still protruding from the integument. The remaining 58 identifiable earthworms were placed into three ecological categories (Lavelle, 1981): polyhumic (31.0%), mesohumic (53.4%), and epigeic (15.5%). Of the mesohumic species, 29% were identified as *Pontoscolex corethrurus*, a South American geophagous invasive earthworm, now found pantropically (Hallaire et al., 2000). Numbers of earthworms found in stomachs were small ($\bar{x} = 2.7 \pm 0.42$), and ranged from one to four individuals (sometimes broken into numerous pieces). However, mass of earthworms found in stomachs was found to be significantly greater than that of other groups (fig. 1; $F_{3,184} = 4.369$; $P = 0.005$). Of the stomachs which contained

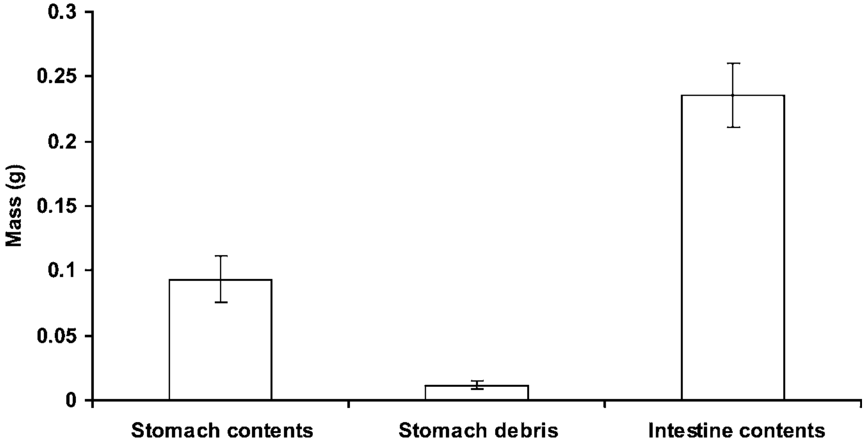

Figure 2. Corrected means (with total length as a covariate) for the masses of identified stomach contents, unidentified stomach debris, and intestine contents from *Boulengerula taitanus*. Error bars are ± standard error of the mean.

earthworms, 25% also had termites, but of those without earthworms, 67% had termites (not including empty stomachs).

Dipteran larvae made up a large proportion of numbers of prey items ($\bar{x} = 10.9 \pm 4.37$; fig. 1, table 1), although analysis of raw data shows that 80% were from three individuals. All larvae showed a longitudinally excised head capsule and a metapneustic respiratory system, both characteristic of Tipulidae (Foote, 1991); and these were further divided into three distinct morphotypes. Most of the remaining prey items were of small size and found in small numbers (table 1). Also present in the stomach were organic matter and soil which made up 12.5% of stomach contents mass ($\bar{x} = 0.012 \pm 0.003$ g), and in three animals this material was equal to the total stomach contents (see above).

Examination of the intestine revealed a larger assortment of prey items based primarily on the chitinised integuments of arthropods. Here again termites dominated numerically and were present in 49% of intestines, of which more than half (13) also had termites in the stomach. Other recognisable items included beetle elytra, centipedes, and other arthropod parts. Mass of intestine contents was on average found to contribute 69% of alimentary canal contents (adjusted $\bar{x} = 0.271 \pm 0.003$ g) and its mass was significantly greater than that of stomach contents (ANCOVA $F_{2,90} = 42.303$; $P < 0.0001$). Stomach contents made up the remaining 31%, with only 4% being detritus (fig. 2).

Only three intestines (6%) were empty but, of the rest, all sub-samples of suspended matter were found to have earthworm setae ($\bar{x} = 68.1 \pm 23.5$), although the range was very high (1-833). We observed that the size of setae was inversely related to their frequency.

Nematodes were found in both the stomach and intestine of *B. taitanus*. Two examples of Mermithidae (a family of insect parasites) were found in the stomach (around 10 mm long, thin, translucent brown nematodes), and occasionally numerous small white nematodes (around 1 mm), thought to be free-living soil nematodes which are regularly found in earthworm digestive tracts (Dash et al., 1980). Intestines always contained more nematodes, the most numerous being the same small translucent form found in the stomach, but here also a third form was found, *Cosmocerca* sp. (identification by J. Mariaux), with a size distribution extending to 5 mm.

DISCUSSION

The Taita Hills have two distinct rainy seasons: long rains ‘masika’ from March to May, and short rains ‘vuli’ from October to December. Here we present the results of an investigation into the diet of animals sampled during the ‘masika’ rainy season. Loveridge (1935) also sampled during the ‘masika’ rainy season, and found 30 specimens from Mount Mbololo over 10 days in April, 1934. Hebrard et al. (1992) mention collecting animals in July and February, although they do not state from which sampling came the 14 animals that they dissected.

It is possible that a shift in season was responsible for the absence of earthworms from the intestinal tract of *B. taitanus* collected by Hebrard et al. (1992). Measey et al., 2004 noted that the numbers of earthworms in guts of *Gegeneophis ramswamii* were reduced during the progression of the monsoon season in southern India, and that this followed the natural fluctuations in soil fauna. Hebrard et al. (1992) did not claim that *B. taitanus* was a specialist, and they noted that a number of other categories of prey occurred in the intestinal tract, although it seems that these were not in large numbers. This conforms to our data (excluding the three animals that ate large numbers of tipulid larvae) which show that, apart from earthworms and termites, other soil macrofauna taxa are consumed in small quantities. Measey et al., 2004 found that if they had analysed diet from a small number of individuals all collected from the same place at the same time, they would have been misled into thinking that *G. ramaswamii* was a specialist termitivore. It is possible that a similar situation occurred during the study of Hebrard et al. (1992); i.e., that a realised, and not the fundamental, niche of *B. taitanus* was reported (sensu Futuyma and Moreno, 1988).

The specialist hypothesis presented by Wake (1986, 2002) and O’Reilly (2000) is not unreasonable considering that existing studies on fossorial squamate diets often show specialist tendencies (Webb et al., 2000a), and that social insects represent rewarding food items in soil environments (see above). Our results show conclusively that not only are earthworms present in the diet of *Boulengerula taitanus*, but that they make up a large proportion of ingested prey items by number, and the significantly greatest mass during the ‘masika’ rains (table 1; fig. 1). The presence of earthworm setae in contents of all intestines further demonstrates that this prey item is widely utilised by populations of *B. taitanus* although it may not always be present or recognisable in stomachs (also see Largen et al., 1972). We conclude that *B. taitanus* is not a specialist termitivore. We further predict that other members of this genus will (if studied) be shown to eat earthworms, termites and occasionally other soil macrofauna.

Figure 2 demonstrates the large mass of debris inside *B. taitanus* intestines, which was found to be significantly heavier than the meagre amount of identifiable stomach contents. Within the intestine, no parts of earthworms could be identified without our procedure of taking aliquots of resuspended matter and examining it with good illumination under a microscope (see above). The amount of debris occurring in stomachs was relatively small (fig. 2), and our observations on the state of digestion of stomach contents suggest that all of this debris was derived from the alimentary tracts of earthworms and/or termites. Hebrard et al. (1992: 513) stated that they "dissected the alimentary canal of each specimen" finding "masses of decaying plant material and unidentifiable organic matter" (p. 514); which is somewhat reminiscent of comments made by Loveridge (1936, see above) and Barbour and Loveridge (1928). This is consistent with our findings, except that, in a novel approach to the study of caecilian diet, we differentiated the contents of stomach from intestine of each animal. Termite workers have large abdomens which are quickly digested leaving only a head capsule and a residue of organic matter, which is characteristic of its ecological group (see above). Similarly, the gut contents of earthworms may either appear as soil, decaying plant material or organic matter, depending on the trophic niche of the prey species (see above).

We found no evidence of significant amounts of soil or detritus associated with prey items in the stomach (other than with distorted earthworms), as suggested by Breckenridge et al. (1972). Large myrmecophagous mammals regularly ingest soil and detritus due to their indiscriminate feeding behaviour, but the proportion of substrate diminishes with decreasing predator size, presumably as a result of individual prey selection (McNab, 1984). We found no evidence that *B. taitanus* is a detritivore as proposed by Hebrard et al. (1992), nor that it ingests large quantities of substrate with prey as proposed by Breckenridge et al. (1972). Instead we suggest that the organic matter and soil found originated from the alimentary tracts of ingested prey taxa. Similar suggestions have been made for other caecilians (see above).

Loveridge (1935) mentioned finding parasitic nematodes (*Oxyurus* sp.) in the intestines of *B. taitanus*, and Hebrard et al. (1992: 514) stated that "all but three individuals had light to heavy infestations of gut nematodes." We also found large numbers of nematodes, especially (but not exclusively) in the intestine of *B. taitanus* examined. Whilst certain nematodes seem to be related to ingested prey (insects and earthworms), it is not clear whether any of those encountered were parasitic, and we do not present any further analyses here.

As Measey et al., 2004 reported for *G. ramaswamii*, diet analyses suggest that *B. taitanus* is feeding on macrofauna within the soil. However, our data also provide further information about the feeding ecology of *Boulengerula taitanus*. Bemis et al. (1983) described prey capture in captive *Dermophis mexicanus* (Duméril and Bibron), and speculated that in nature animals break off pieces of oversized prey by rotating on their longitudinal axes as they retreat into burrows. Breckenridge et al. (1987) questioned whether the same mechanism would be utilised once both caecilian and earthworm were within the soil. Tanner (1971) found that ichthyophids he studied only ate within their burrows, with repeated cycles of simultaneous rotation and ingestion, until the entire earthworm was eaten. He also noted that none of the earthworms were torn apart. In this study, the majority of earthworms appear to have been ingested whole apart from the twisted remains found in the stomachs of two individuals, which appears to correspond with previous observations. We know of no evidence that suggests caecilians masticate: what Loveridge (1936) may have found, as here, were the semi-digested remains of earthworm prey.

Myrmecophagous mammals avoid aggressive species of ants that sting in defence (McNab, 1984), and similar explanations have been suggested for amphisbaenian avoidance of ant prey (Webb et al., 2000b), but Measey et al., 2004 found that the diet of Indian caecilian *G. ramaswamii* included the brood of such ants. In this study no termite or ant brood were found in stomachs of *B. taitanus*, only two adult driver ants (subfamily Dorylinae). Certain of these ants are known to hunt below ground, flushing earthworms from their burrows (A. Dejean and P. Lavelle, pers. comm.). Termite soldiers, found in the diet of *G. ramaswamii*, were also absent from stomach content of *B. taitanus*, with only the remains of two individuals found in intestines. It therefore seems unlikely that *B. taitanus* enters ant or termite nests (but see Hebrard et al., 1992), and that they feed instead in their underground foraging trails; and further, that termite soldiers defending workers under caecilian attack are avoided rather than eaten. Foote (1991: 710) notes that tipulid larvae are characteristic of “wet earth or decaying wood”, corresponding to the microhabitats in which some animals were found (Measey, subm.).

In conclusion, we find that *Boulengerula taitanus* is not a specialised predator of termites, but that earthworms contribute a significant mass of items ingested in the ‘masika’ rains. We find no evidence that *B. taitanus* is a detritivore, but that detritus found in the alimentary tracts is derived from its prey. Further study is needed on these caecilians to obtain information about how diet may change throughout the year, and especially in the dry season for which virtually no data are available for caecilians. Oommen et al. (2000) and Measey et al. (2003) commented on the potential impact of subterranean predators on their largely soil ecosystem engineer prey. At high densities, *B. taitanus*, like *G. ramaswamii*, has the potential to significantly impact upon soil ecosystem engineer populations.

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