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Original article

Niche separation and comparative abundance of *Boulengerula boulengeri* and *Scolecomorphus vittatus* (Amphibia: Gymnophiona) in an East Usambara forest, Tanzania

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Abstract.—The ecology of the sympatric caecilians *Boulengerula boulengeri* and *Scolecomorphus vittatus* was studied in Nilo Forest Reserve in the East Usambara Mountains, Tanzania. Three sampling methods (timed digging, pitfall trapping and casual visual encounter surveys of the forest floor) yielded 85 *B. boulengeri*, found only by digging soil, and 23 *S. vittatus*, mostly collected above ground. The difference between these taxa in the proportions of captures above and below ground is statistically significant and is taken to indicate different ecologies. *B. boulengeri* is interpreted as predominantly a burrower in soil, and *S. vittatus* as an animal spending more time than *B. boulengeri* above ground. Niche separation appears to be correlated with some morphological differences. The vast majority of all vertebrate specimens dug from the top 300 mm of soil were *B. boulengeri*, and this species appears to be more abundant than *S. vittatus* in East Usambara forest soils. As an abundant endogeic animal, *B. boulengeri* may play an important role in the ecology of forest soils.

Key words.—caecilians, Eastern Arc, ecology, Caeciliidae, Scolecomorphidae, soil.

Caecilians are elongate, limbless, snake-like amphibians found mainly in the wet tropics. Little is known about caecilian ecology (Himstedt 2000). Most ecological information that has been published has been gleaned from examination of preserved specimens, and from piecemeal natural history observations made during the often opportunistic collection of caecilians. Recently, however, several largely field-based studies have made encouraging breakthroughs. These include quantitative estimates of abundance through surveys (Oommen *et al*. 2000; Measey *et al*. 2003a; Measey & Di-Bernardo 2003; Measey in press), testing and implementation of marking methods in recapture experiments (Measey *et al*. 2001, 2003b), investigations of diet and condition based on randomised sampling (Measey *et al*. 2004, Measey & Gower in press; Gaborieau & Measey 2004), growth (Kupfer *et al*. 2004a), and reproductive ecology (Kupfer *et al*. 2004b).

The majority of these studies have focussed upon autecology in agricultural or otherwise disturbed habitats. In this paper, we present a quantitative study of two sympatric caecilian species from a forest reserve in Tanzania - the caeciliid *Boulengerula boulengeri* Tornier and the scolecomorphid *Scolecomorphus vittatus* (Boulenger). These species are endemic to Tanzania, and *B. boulengeri* is endemic to the East Usambara Mountains (Taylor 1968; Nussbaum & Hinkel 1994; Nussbaum 1985). They are the only caecilian species thus far reported from the East Usambaras. Here we compare their ecology using quantitative field collection data, and relate comparisons to what is known of their morphology.

The East Usambara Mountains of Tanzania are one of the component blocks of the Eastern Arc of East Africa, a region of very high endemicity and a global biodiversity hotspot (e.g., Loveridge 1942; Lovett & Wasser 1993; Myers *et al*. 2000). The study site, Nilo Forest Reserve (FR), is in the northwestern part of the East Usambaras. It lies on hilly ground (400 - 1506 m a.s.l) and comprises submontane and lowland forest, some of which is under cultivation and some cleared for human settlement. At 6,025 hectares, it is the second largest protected block of forest in the East Usambaras.

Materials and Methods

This study was conducted as part of the East Usambara Biodiversity Surveys (EUBS), a collaboration between the East Usambara Conservation Area Management Programme (EUCAMP) and Frontier-Tanzania. The survey of Nilo FR was carried out between June 2000 and March 2001 (for details see Frontier-Tanzania 2002). This survey aimed to provide an inventory of selected plant, invertebrate and vertebrate taxa, and to quantify ecological parameters in the context of forest disturbance and regeneration. For the survey, Nilo FR was divided into a grid of 450 m (East - West) x 900 m (North - South) quadrats. The vast majority of these were surveyed in vegetation analyses, totalling 122 quadrats. All of the caecilian work reported here occurred in the forested areas within Nilo FR.

Three methods were used to collect caecilians - timed digging, pitfall trapping, and visual encounter. Timed digging took place within 38 of the 450 m x 900 m quadrats in the central part of Nilo FR. Selected quadrats were contiguous along the North-South axis of the grid, but spaced every other quadrat along the East-West axis. Each timed dig comprised two person hours (SPL and assistant concurrently for one hour each) and took place adjacent to 50 m x 20 m vegetation plots situated in the southwest corner of each quadrat. Hoes were used to search leaf litter and dead wood, and to dig over approximately the top 300 mm of the soil.

Ten pitfall trap sites were set up in Nilo FR, with their location chosen to lie outside the vegetation plots and to cover differing environmental conditions (vegetation, altitude, slope etc) within the reserve. Six of these trap sites lay within the central region of Nilo FR that were chosen for timed dig sampling, and four lay elsewhere in the reserve. Each pitfall trap site consisted of three unconnected lines of 20-litre plastic buckets (275 mm deep, 290 mm diameter at opening) sunk to ground level. Along each line, 11 buckets were spaced approximately 5 m apart, with a drift fence formed by a continuous plastic sheet (1 m wide, of which 0.5 to 0.75 m was held perpendicular to the ground) extending across the centre of the buckets. Trap sites were checked each morning and afternoon for 10 days.

Searching by visual encounter took place casually and irregularly, mostly during daylight, whenever fieldworkers moved about in Nilo FR. This form of collecting was not systematic or randomised, in that areas between field camps and sampling sites were walked much more frequently than within quadrats. Digging took place between June and December 2000

Table 1. Numbers of individuals of two species of caecilian collected by three different methods in surveys of Nilo Forest Reserve, Tanzania. Visual encounter represents animals casually found above ground. For reasons unknown, Frontier-Tanzania (2002) report three *Scolecomorphus vittatus* collected by digging and do not mention pitfall captures.

Species	Collection method			Totals
	Timed digging	Pitfall	Visual encounter	
Boulengerula boulengeri	85	0	0	85
Scolecomorphus vittatus	2	2	19	23
Totals	87	2	19	108

but pitfall trapping and visual encounter were spread throughout the duration of the Nilo FR biodiversity survey.

Collected caecilians were killed using the anaesthetic MS222, Sandoz, individually tagged, fixed in formalin, and stored in ethanol. The position and method of capture of each specimen was recorded. Material is being deposited in the collection of the Department of Zoology, The Natural History Museum, London. Capture data were subject to a χ^2 test of the null hypothesis that the proportions of above and below ground captures are not different for each species, or alternatively that the proportions of the two species are not different for above and for below ground captures. Only one species was caught by pitfall trapping and visual encounter (see below) so that the captures for these two methods can safely be pooled without having to assume that they are equivalent. The test is based on proportions and so does not require us to assume that each capture above ground is equivalent to each below ground. Statistical analyses were performed by hand and with GenStat (2000).

RESULTS

The numbers of *B. boulengeri* and *S. vittatus* collected by the three methods are presented in Table 1. No caecilians were observed above the soil (including in litter) during digging. In total 108 caecilians, 85 *B. boulengeri* and 23 *S. vittatus*, were collected. *Boulengerula boulengeri* were found only during timed digging in soil, while *S. vittatus* were found using all three methods. Abundance within the soil was much higher for *B. boulengeri* than for *S. vittatus* (1.12 versus 0.03 individuals per person hour of digging). Categorising the data into subterranean (timed digging) and surface (pitfall plus visual encounter) collections, the relative proportions of each species found above and below ground are significantly different (Likelihood χ^2 = 92.81, df = 1, P < 0.001). Unsurprisingly, a Fisher exact test (sometimes recommended where expected values in contingency tables are low, as here) on the same data also yields a significant result (P < 0.001). The only *S. vittatus* captured by digging in soil were found in a single quadrat, which also yielded two *B. boulengeri*. *Scolecomorphus vittatus* collected by visual encounter were predominantly found after rain, mostly during daylight. Background demographic data for the two study species are lacking, but the frequency distributions of total length of individuals of the two species (Fig. 1) are not notably skewed, and are interpreted as being consistent with no obvious collecting bias toward especially small or large animals.

For our samples, mean total length is significantly greater for *S. vittatus* (237.6 versus 158.7 mm, *t*-test, P < 0.001), with the largest *S. vittatus* 83% longer than the largest *B. boulengeri*. Of the specimens in which sex could be determined, there were more females than males for both *B. boulengeri* (41 : 31) and *S. vittatus* (10 : 9) but neither ratio is significantly different from unity (Likelihood $\chi^2 = 0.24$ and 0.82 for *B. boulengeri* and *S. vittatus* respectively, $P > 0.5$).

Some reptiles and other amphibians were also collected during searches for caecilians. Timed digging found one or two individuals each of the microhylid frog, *Probreviceps macrodactylus macrodactylus* (Nieden), and the skinks, *Leptosiaphos kilimensis* (Stejneger) and *Proscelotes eggeli* (Tornier). Thus, more than 90% of all vertebrate specimens found by digging were *B. boulengeri*. Many frogs (approximately ten species), lizards (four skink and one gecko species), snakes (two species) and small mammals were also collected in pitfall traps, but individuals were not counted for all taxa.

DISCUSSION

Of the three sampling techniques employed, only digging is likely to yield endogeic species, those that live and feed primarily within the soil (see also Measey *et al*. 2003b; Gower *et al*. 2004). Pitfall traps and visual encounter methods sample species that spend at least some time on the surface. We interpret differences in captures of *B. boulengeri* and *S. vittatus* when using different sampling techniques as indicative of a real difference in their ecologies. That *B. boulengeri* and *S. vittatus* occur in significantly different proportions above and below ground indicates a degree of niche separation across the sampled habitats. *Scolecomorphus vittatus* spend some time in soil and *B. boulengeri* rarely (though not in this study) are found in pitfall traps or on the surface, so the difference is not absolute.

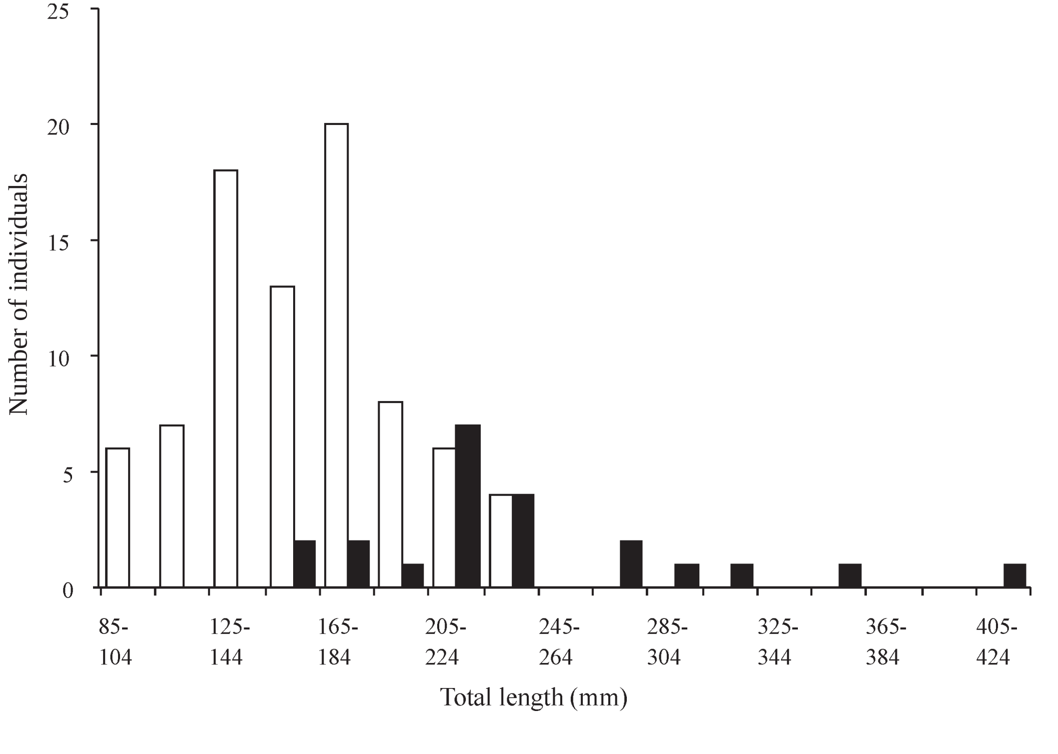

Figure 1. Frequency distributions of total length of complete caecilian specimens collected in Nilo FR, Tanzania. Open bars — *Boulengerula boulengeri* ($N = 82$); Black bars — *Scolecomorphus vittatus* ($N = 21$).

Table 2. Morphological differences between *Boulengerula boulengeri* and *Scolecomorphus vittatus*. Data from Taylor (1968), Wake (1985), Nussbaum and Hinkel (1994), Nussbaum (1985), Loader *et al*. (2003b), references cited therein, and personal observations. The *S. vittatus* sample collected from Nilo FR includes two apparent morphs. The taxonomic significance of these forms is under investigation, but the details do not affect this list of differences (except perhaps for maximum size) because most appear to hold at the generic level for *Scolecomorphus*. * G. J. Measey pers. comm.

Character	*Boulengerula boulengeri*	*Scolecomorphus vittatus*
Maximum length	< 280 mm*	> 400 mm
Body form	slender and subcylindrical	more tapered anteriorly
Head shape	subconical	slightly dorsoventrally compressed
Temporal region	strongly stegokrotaphic	zygokrotaphic
Nasal-premaxilla-septomaxilla	compound	unfused
Separate prefrontals	absent	present
Stapes	present	absent, and cheek less constrained
Eyes	covered by bone, strongly reduced	protrusible from cranium, less strongly reduced
Tentacles	short and globular	long and slender
Tentacle position	lateral, halfway along upper margin of mouth	underside of snout, level with or in front of margin of mouth
Tooth crowns	some bi-cusped	mono-cusped
Palatine teeth	substantial overlap with maxillary series	extend posteriorly from end of maxillary tooth row

Thus it is likely that there are opportunities for interspecific interactions, but our data suggest that intraspecific interactions are likely to dominate. With the exception of the aquatic and semiaquatic neotropical Typhlonectidae, adult caecilians are thought to be mostly terrestrial and soil dwelling. However, the literature suggests that some species differ in their soil-burrowing capability and propensity. Some species are dedicated soil dwellers (e.g., *Gegeneophis ramaswamii*, Measey *et al*. 2003b, c) while others (e.g., species of *Ichthyophis*, Ramaswamii 1941; Nussbaum & Gans, 1980) have been perceived to be relatively more frequently found in and under rotting vegetation. Through laboratory experiments, Ducey *et al*. (1993) demonstrated differing burrowing ability among some caecilian species. Arguments about burrowing ability have also been partly based on differences in morphology, with more loosely constructed crania and less cylindrical bodies thought to be associated with less adept burrowing (e.g., Nussbaum 1977, 1979).

Given that our data reveal real ecological differences, how do they match with what else is known of the biology of the study species? Although caecilians are often superficially considered to be rather morphologically uniform, *B. boulengeri* and *S. vittatus* are markedly different animals (see Table 2; Loader *et al*. 2003a). *Boulengerula* have bullet-shaped heads and near-cylindrical bodies, with relatively less mobile and more solid skulls. The skulls lack upper temporal fossae (stegokrotaphy), and they have markedly reduced eyes that are covered by bone. All these features might be expected to confer performance advantage in a predominantly burrowing, endogeic lifestyle.

Scolecomorphus also have the orbit covered by bone but the eye remains relatively well developed (Wake 1985). The eye migrates forward from the orbit with the tentacle during ontogeny. In adult *Scolecomorphus*, the eye lies in an open tentacular groove covered not by bone but only a relatively pigment-free and translucent patch of skin, and it can even be protruded with the tentacles (Taylor 1968; Nussbaum 1985; O'Reilly *et al*. 1996). The comparative morphology of these species is consistent with the visual system being more important for *S. vittatus* than for *B. boulengeri*, and thus with the former spending more time on or near the surface. *Scolecomorphus vittatus* have a less uniform body than *B. boulengeri*, with a more narrow anterior body and a highly zygokrotaphic skull, both of which we interpret as less well suited for burrowing in compact soil. The hypothesis that the two species have different burrowing abilities can be tested experimentally.

The two species also differ substantially in their sensory tentacles. In *B. boulengeri*, the tentacle lies in a lateral position close to the eye, where the head is almost as wide as the body. It is small and cannot be strongly protruded. Such an arrangement seems adequate for life in soil where the substrate is close to the sides of the head. The more protrusible tentacles of *S. vittatus* are much closer to the snout tip and more ventrally oriented when protruded, and we suggest this may provide a performance advantage in accessing sensory cues on the surface and in litter.

Other notable differences in the biology of these two species include maximum length, reproductive mode (Wilkinson & Nussbaum 1998; Loader *et al*. 2003b) and colour. These are less obviously related to propensity and/or ability to spend more or less time within soil, but are consistent with different autecologies. The probability that *B. boulengeri* and *S. vittatus* have different niches, combined with differences in their dentition and probable cranial mobility (Table 2), prompts the hypothesis that their diets also differ.

An alternative explanation for our data is that they are biased or otherwise atypical due to sampling error. For example, it might be hypothesised that *S. vittatus* are better able to escape collection by digging or that they are more patchily distributed and occur in areas of soil not sampled, or that *B. boulengeri* are less conspicuous when on the surface, avoid or escape from pitfalls, and/or only emerge at times when casual visual encounter was less likely (e.g., at night). However, biases would have to be strong to account for the magnitude of the differences observed. Additionally our interpretation is consistent with other (unpublished) field observations, including the extremely rare collection (< 10) of *B. boulengeri* in pitfall traps or on the surface in other Frontier Tanzania surveys in the East Usambaras over eight years.

Taken at face value, the collection data suggest that *B. boulengeri* is more abundant than *S. vittatus* in Nilo FR (at least within the top 300 mm of soil), with nearly four times as many specimens being collected during this study. This is with the strong caveat that we do not know the relative efficiencies of the different habitat-specific sampling regimes. That the greater abundance of *B. boulengeri* applies elsewhere receives support from additional fieldwork in Amani Nature Reserve forest in the southern part of the East Usambara. During twelve days (February-March, 2000) of dedicated caecilian sampling by digging soil and searching through leaf litter and dead wood, 124 *B. boulengeri* (approximately 1.5 per person hour of digging) and one *S. vittatus* (approximately 0.1 per hour) were found (DJG,SPL, MW unpublished data). In surveys conducted by digging randomised quadrats, Measey (in press) also found *B. boulengeri* to be much more abundant than *S. vittatus* in both forest and agricultural habitats in the southern part of the East Usambaras.

Oommen *et al*. (2000) and Measey *et al*. (2003a, b, c) commented on the high abundance of the caeciliid *Gegeneophis ramaswamii* in agricultural habitats in India, reported that they appeared to be the most abundant vertebrate in these habitats, and suggested they may have an impact on soil ecology through predation of invertebrate groups considered to be soil ecosystem engineers. In this study, *B. boulengeri* was the most abundant vertebrate dug from the surface 300 mm of the soil, so that we expect this species to have a significant role in forest soil ecology in the East Usambaras.

Standard methods for sampling terrestrial caecilians have yet to become established (Measey *et al*. 2003a, b) and this is usually attributed to the apparent rarity of these animals (e.g., Lips *et al*. 2001). However, caecilians can be abundant in tropical soils, and this makes ecological hypotheses amenable to testing in some situations. *Scolecomorphus* and *Boulengerula* are not sympatric across the whole of their ranges. For example, only species of *Boulengerula* are known from Kenya, and only *Scolecomorphus* are known from the Pare Mountains of Tanzania. This mixture of sympatry and allopatry might be exploited to investigate the degree to which ecological differences result from interspecific competition.

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