ARE CAECILIANS RARE? AN EAST AFRICAN PERSPECTIVE

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ABSTRACT

Despite increasing reports to the contrary, caecilians are often considered to be unusual components of tropical ecosystems, where they predate largely on soil ecosystem engineers. The status of two East African *Boulengerula* species is assessed using a quantitative randomised survey method and timed searches, in low-intensity agriculture and natural forested settings. Mean density of *B. boulengeri* was found to be greater in forest than agriculture (0.43 and 0.11 m^{-2}, respectively), but not significantly. *B. taitanus* were significantly more dense in agriculture (0.21 m^{-2}) than in forest (0.02 m^{-2}). Forest *B. taitanus* were found to be significantly longer ($\bar{x}$ 285.9 mm) than those found in agricultural settings ($\bar{x}$ 219.3 mm), and possible causes of this size bimodality is discussed. Results from quantitative surveys are found to be remarkably consistent, and significantly correlated with timed searches in the same habitats. Possible causes of over- and under-representation are identified. It is concluded that not all members of the order Gymnophiona in East Africa are rare, although more field studies are needed to redress herpetology's subterranean blind spot.

INTRODUCTION

Despite their near-pantropical distribution, the Gymnophiona (caecilian or apodan amphibians) probably remain the least known order of tetrapods. Caecilians are elongate and completely limbless amphibians with skin divided into annuli, giving many species a superficial similarity to earthworms (figure 1). Terrestrial caecilians are often considered to be rare (Gundappa, Balakrishna & Shakuntala, 1981; Duellman & Trueb, 1986; Bhatta, 1997), a view supported by the field experience of most herpetologists. Logically, this would explain why many of the caecilian species described are known from only a single or very few records (Taylor, 1968). However, some publications have described some caecilian species as locally common or even abundant (Loveridge, 1936; Largen, Morris & Yalden, 1972; Hebrard, Maloiy & Alliangana, 1992; Bhatta, 1997; Nussbaum & Pfrender, 1998; Oommen *et al.*, 2000; Measey & Di-Bernardo, 2003), while very few measurements of caecilian density have ever been reported (see Measey *et al.*, 2003b). Clearly, terms such as common, rare or, as recently claimed, declining and/or endangered (Wake, 1993; Wen, 1998; Pennisi, 1999; Wake, 2002) should preferably be based on readily interpretable quantitative data. To this end, Measey *et al.* (2003b) proposed a simple method for

Figure 1. A female Boulengerula boulengeri *with total length 176 mm and a total mass of 1.9 g. Despite having a distinctive head with recessed mouth (foreground), the skin which has distinctive folds, or annuli, together with their subterranean lifestyle, often lead local people to believe incorrectly that these and other Gymnophiona are earthworms.*

quantitative surveys of endogeic limbless vertebrates, finding that densities of a subterranean caeciliid reached as high as 1.87 animals per m^2.

Ecosystem engineers are organisms that modify, maintain or create habitats in ways that substantially affect other species (Jones, Lawton & Sachak, 1994). In tropical terrestrial ecosystems, earthworms, ants and termites are soil ecosystem engineers (SEE) because they greatly influence the physical structure and distribution of organic matter in the soil (Lavelle *et al.*, 1997). All caecilians are carnivorous, with many terrestrial species preying on soil ecosystem engineers (Measey *et al.*, 2004). Although predation of SEE by scarce predators is unlikely to have a large impact, common predators may have substantial effects on soil ecosystems through their predation of SEE and by their other activities. However, no studies have addressed the potential impact of soil dwelling vertebrate predators of SEE. The effects of anthropic disturbance of soil macrofauna are well documented in several groups (Fragoso & Lavelle, 1992; Lavelle *et al.*, 1997; Eggleton *et al.*, 2002). While there is a loss of

diversity in nearly all groups, earthworms have been found to increase in density in some agricultural systems (Lavelle, Brussaard & Hendrix, 1999). It is not clear whether traditional small scale agricultural practices should adversely affect SEE predators.

In East Africa, the distribution of caecilians is dominated by the Eastern Arc Mountains of Tanzania and southern Kenya (Nussbaum & Hinkel, 1994). The crystalline block-faulted mountains are comparatively very old within the region, with initiation of faulting dating from 290–180 million years before present. They are believed to have continuously acted as Indian Ocean condensers producing consistently high rainfall throughout the Pleistocene, and possibly the end of the Miocene (Lovett, 1993). Although archaeological evidence suggests that humans have inhabited the region for at least the past 2000 years (Rogers, 1993), major disturbance and in particular large scale clearing of forest is believed to have only occurred over the past 200 years with an estimated loss of as much as 77% of forest cover (Newmark, 1998). This has resulted in a severely fragmented forest, and concern that much of the endemic flora and fauna are already under threat (Newmark, 1998). Greatest loss has occurred in the Taita Hills (Kenya) with as much as 98% loss and only 6 km^2 of natural forest remaining (Newmark, 1998). Although an estimated loss of 57% of forest has been suffered in the East Usambaras (Tanzania), this constitutes some of the least disturbance for the Eastern Arc Mountains, with 413 km^2 of natural forest remaining.

Workers have found that it is often in agricultural areas in which caecilians can be easily found (see above). In contrast, several authors have remarked on the difficulty of finding the same species in adjacent natural forest (e.g. Hebrard *et al.*, 1992; Haft & Franzen, 1996). However, such commentaries lack quantitative assessments of density, and it is difficult to know whether comparisons can be made between taxa. Other authors have suggested that the agricultural practice of irrigation strongly favours caecilians, and that chemicals such as pesticides may explain their seemingly patchy distribution (Oommen *et al.*, 2000).

Two of the six families of caecilians have been recorded from East Africa: Caeciliidae Rafinesque-Schmaltz the most widely distributed globally, and Scolecomorphidae Taylor an African endemic (Nussbaum & Wilkinson, 1989; Wilkinson *et al.*, 2004). Two genera of caeciliids are known. The first, *Boulengerula* Tornier, with five currently recognised species, was synonymised from *Afrocaecilia* Taylor and *Boulengerula* by Nussbaum and Hinkel (1994)—although this may have been premature (Wilkinson *et al.*, 2003). The second genus, *Schistometopum* Parker is at present represented by two species, one of which occurs in East Africa. The scolecomorphids have three currently described species in East Africa, but their taxonomic status is in need of revision (Wilkinson *et al.*, 2003).

Baseline data on animal abundance is required for a great many types of study, including biodiversity, which is currently of special concern for amphibians (Houlahan *et al.*, 2000). Using standardised methods, it is possible to compare densities of species with both sympatric and allopatric distributions, although this has been hitherto unattempted for most caecilians or other lower subterranean vertebrates. By sampling animals from a range of habitats, both natural and within agroecosystems, it is possible to contrast natural and anthropogenically influenced populations.

The objective of this study is to determine the densities of two East African caecilians, *Boulengerula taitanus* Loveridge and *B. boulengeri* Tornier, endemic to the Taita Hills and the East Usambara Mountains, respectively. The methods of Measey *et al.* (2003b) are followed and contrasted with timed searches as a means of assessing abundance. Surveys were made in agricultural and naturally forested habitats, and these data are analysed together with population demographics (from length / mass data) to determine possible effects of low intensity agriculture on these subterranean predators.

LOCALITY AND SITE DESCRIPTIONS

All sites investigated here are at localities in the northernmost part of the Eastern Arc Mountains of Tanzania and Kenya. The Eastern Arc is a chain of mountains that lie close to the coastline of eastern Africa from southern Tanzania to southern Kenya, (located between 4°48' and 5°13' South; figure 2), and are a world biodiversity hotspot (Myers *et al.*, 2000). A wide variation in altitude exists from 200–300 m at the bases of the mountains to over 2000 m. The area is well known for its remarkable flora with high levels of specific and generic endemism, probably due to the long history of geographical and climatic stability; 25–30% of the *c*. 2000 Eastern Arc plant species are endemic, with a further 16 endemic or near-endemic genera (Lovett, 1993). Although originally covered in forest, much of this area is now under cultivation mostly as small-scale low-intensity agricultural units, shambas, but also as large-scale intensive plantations for crops such as tea (*Camellia sinensis* (L.) Kuntze).
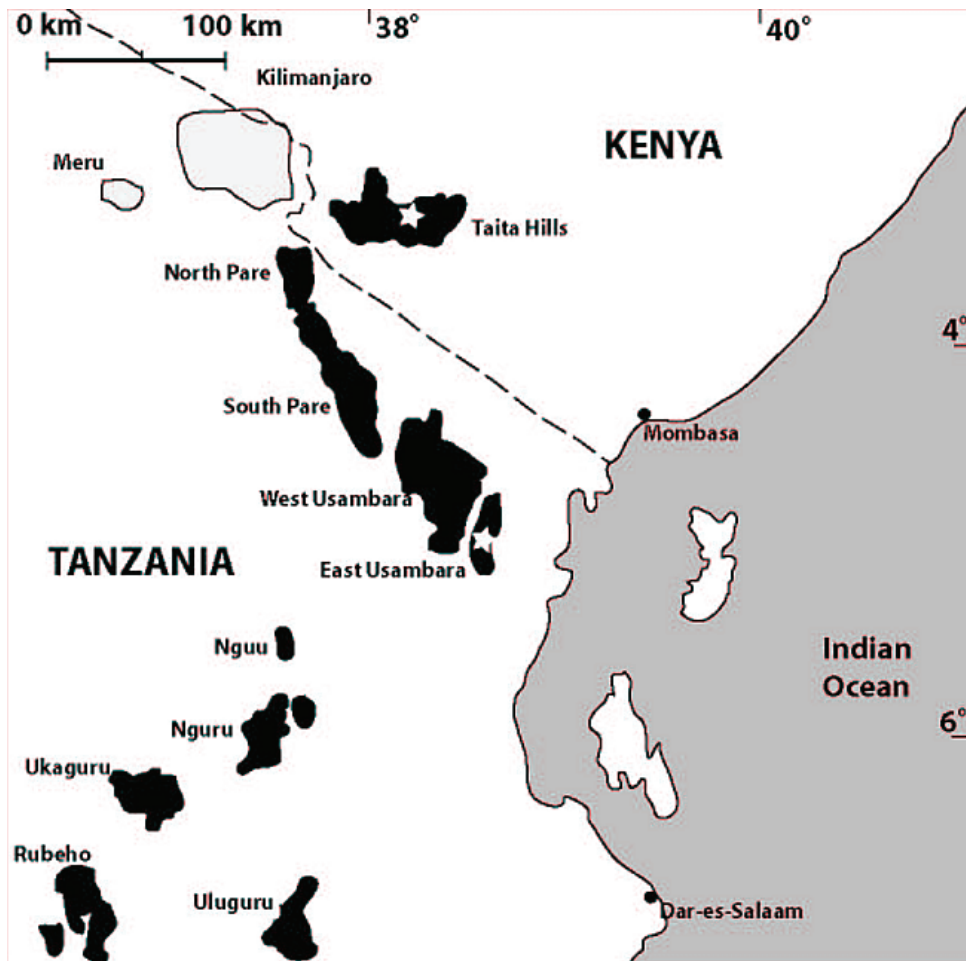

Figure 2. Mountains of northern Tanzania and southern Kenya (with dashed international boundary) supporting moist forest. Eastern Arc Mountains are shown in black. Sites visited for surveys and searches are shown with stars. Redrawn from Wasser and Lovett (1993).

The climate is characterised by strong seasonal variations in precipitation. Rainfall is monsoonal, with a wetter south-easterly monsoon from April to October and a drier north-easterly monsoon from November to March. This results in two distinct rainy periods: long rains, masika, from March to May, and short rains, vuli, from October to December. Rainfall generally increases with altitude.

Measurements at collection sites included soil texture (Dubbin, 2001), soil temperature using a temperature probe set 10 cm into the soil, and soil pH made by mixing approximately 1:2 volume with stream or well water (the pH of which was measured independently to avoid extreme acid or alkaline water). Temperature and pH were measured with an Acorn pH 6 pH meter (Forestry Suppliers, USA). Shade was estimated with regard to the total area searched or surveyed over a site, and attention was also paid to the amount of leaf litter covering the soil. In addition, in April 2003 soil penetration was measured using a soil penetrometer: a Pesola 2500 g (Dynatrac, France) fitted with a pressure adapter with a rounded tip of 30 mm^2 (results are expressed in kg.cm^{-2}). A mean of three horizontal measurements into a vertical soil profile at 10 cm depth are presented. Locality and altitude measurements were made with a Garmin 12XLS GPS (Garmin, USA).

Taita Hills (Kenya)
Boulengerula taitanus is the only caecilian known to occur in the Taita Hills of Kenya. Sites in the Taita Hills were visited in May and December 2002 and April 2003, with a range of sites studied to exemplify agriculture and forest. In the local language of Kitaita, *B. taitanus* are known as 'ming'ori', a word also used for earthworms; which presumably reflects an apparently common misconception that caecilians are a type of earthworm. Land owners reported that no chemical fertilizers or pesticides had been used for at least 15 years on their land, although a local store reported high sales of a diazinon pesticide and a dithane fungicide (see Harris *et al.*, 1998).

Wundanyi Shambas
Wundanyi Shambas (03°24'S 38°22'E; 1450 m) are small private agricultural plots (hereafter 'shambas') around the central town of Wundanyi. General collections were made from two villages: Kiwinda and Chomboke. Both of these areas comprised mainly of shambas with various crops including bananas (*Musa* sp.), avocado (*Persea americana* Mill.), sugar cane (*Saccharum officinarum* L.), yams (*Dioscorea* sp.), tomatoes (*Lycopersicon esculentum* Mill.), beans (*Phaseolus vulgaris* L.), cassava (*Manihot esculenta* Crantz) and guavas (*Psidium guajava* L.). Sparse shade (around 40% from occasional trees) with little leaf litter covering the soil surface. At Kiwinda half of the shamba was a small banana plantation (total shade), and the other half open ground (no shade) with cabbages. At Chomboke the shamba contained mature silky oaks (*Grevillea robusta* A.Cunn., 80% shade) with various crops including yams, bananas and tomato trees (*Cyphomandra betacea* Sendt.) grown beneath. At all sites typical soil texture was a clay loam (Dubbin, 2000), with soil temperature 20.7° C, pH 6.75, and with typical penetrometer readings of 2.6 kg.cm^{-2}.

Mwabwalo Shambas
Mwabwalo Shambas (03°23'S 38°20'E; 1517 m) are similar to those around Wundanyi with major crops being bananas, sugar cane, yams, beans and cassava. These crops and occasional trees afforded sparse shade (around 30%) with little leaf litter. Much of the area surveyed had recently been dug over, although parts were still undisturbed since the previous year.

Soil texture was a sandy clay loam, with soil temperature 20.1° C and pH of 7.12, while penetrometer measurements averaged 0.8 kg.cm^{-2}.

Ngangao Forest
Ngangao Forest (03°22'S 38°20'E; 1910 m) is a small pocket (around 140 ha) of partly disturbed natural forest in the Taita Hills. Collections were made throughout the forest over several days, mostly by turning logs, digging in soft soil, or under palm trees. One site on a slope (around 25%) in the forest was quantitatively surveyed. Shade in the forest is near complete (around 95%) and leaf litter entirely covers the soil. The soil texture is a sandy loam, with a pH of 6.34 and temperature of 20.5° C.

Chawia Forest
Chawia Forest (03°27'S 38°21'E; 1706 m) is a highly disturbed linear stretch of natural forest following the crest of a hill (around 90 ha). Shade in the forest is almost complete, although there are many gaps in the canopy, and the edge of the forest is almost always visible from within. Collections were made in the forest and one site of level ground was quantitatively surveyed. The soil texture was a sandy loam, pH of 6.66 and temperature of 20.1° C, and penetrometer readings averaged 0.6 kg.cm^{-2}.

East Usambaras (Tanzania)
Two species of caecilians, *Boulengerula boulengeri* (figure 1) and *Scolecomorphus vittatus* (Boulenger) are known from the East Usambaras. Unlike the Taita Hills, a local name is given specifically for *B. boulengeri*, the Kisamba word 'mikudi', unlike earthworms, which are known as 'vyambo'. Many different names were offered for *S. vittatus*, although no consensus was reached. Shamba proprietors affirmed that no chemical fertilizers or pesticides had ever been used on their land.

Kwamkoro Shambas
Kwamkoro Shambas (05°09'S 38°36'E) are small holdings located within 250 m of the forest edge and have been established for around 30 years. Crops include sugar cane, avocado, bananas, yams and Napier grass (*Pennisetum purpureum* Schumach.). The soil is covered by little or no leaf litter, and shade is only from occasional trees (around 20%). Soil texture was sandy loam, soil temperature 18.4° C, and a pH of 5.82.

Emau Shambas
Emau Shambas (05°06'S 38°37'E) are small holdings close to the forest edge (within 500 m). Principle crops include bananas, yams and maize (*Zea mays* L.). Sparse shade (10%) and no litter. Soil texture was a sandy clay loam, soil temperature 24.8° C, and pH 6.24. The mean penetrometer measurement was 5.7 kg.cm^{-2}.

Shambangeda Village
Shambangeda Village (05°03'S 38°38'E) had crops of bananas, sugar cane, maize, cardamom (*Elettaria cardamomum* (L.) Maton), mangoes (*Mangifera indica* L.) and lemons (*Citrus limon* (L.) Burm.f.). Crops and trees provided a good covering of shade (70%) and the soil was covered with leaf litter. The area was around 200 m from the forest edge. Soil texture was sandy clay loam, temperature 24.8° C and pH 6.24. The mean penetrometer measurement was 6.3 kg.cm^{-2}.

Kwamkoro Forest
Kwamkoro Forest (05°09'S 38°36'E) is part of the larger Amani Nature Reserve. Although intensively logged in the 1980s, this forest has been allowed to regenerate naturally from this time, apart from establishment of *Maesopsis eminii* Engl. (see Binggeli & Hamilton, 1993). Remaining trees are small, but canopy cover is complete (around 95%), and the soil is covered by leaf litter. The selected site consists of a level area adjacent to the Kwamkoro River and a hill rising steeply (around 40%) away from it. Soil texture was a sandy clay loam, pH 6.24 and temperature 20.6° C. The mean penetrometer measurement was 6.2 kg.cm^{-2}.

Bom Bom Forest
Bom Bom Forest (05°06'S 38°38'E) is a protected area of primary forest. It has also been subjected to invasion by *Maesopsis eminii*, but to a more limited extent. The forest is used by local people for the sporadic collection of firewood, but is otherwise undisturbed. Canopy cover is complete with near 100% shade. The area of the forest surveyed was on a steep slope (around 40%) at the bottom of which (around 300 m) the Nanguruwe River flows. The soil is covered by a 10–15 cm of leaf litter. Soil texture was a silty clay loam, soil temperature 22.8° C and pH 5.25. The soil was too hard for a reading with the soil penetrometer ($>$ 8.3 kg.cm^{-2}).

METHODS

Collections of caecilians were made from the above sites using one or sometimes both of the methods presented below. When captured, animals were euthanased within four hours of capture (using the anaesthetic MS222), and measured (to the nearest mm) using a fixed ruler and their mass determined (to the nearest 0.1g) using an electronic balance (CM 320-1, Kern, Germany). Where indicated, sex was verified through direct examination of gonads of the preserved individual. Each specimen was fixed (with 10% formalin from a c. 40% stock solution), and Kenyan specimens were deposited in the collection of The National Museums of Kenya, Nairobi (NMKA/4007/1 to A/4010/3) and the Natural History Museum, London (BMNH 2002 103–126).

Surveys
The survey method described by Measey *et al*. (2003b) was followed due to its ease of use and reliance on widely available and durable materials. A 10 by 10 m survey grid was produced by a 20 m length of coloured nylon rope with a loop halfway along, and contrasting markers tied at 1 m intervals. Five 1 m^2 quadrats were selected using random co-ordinates inside the grid. Three grids were laid, either side by side or at intervals of 10 m to avoid problems with micro-site selection and bias, a total of 15 m^2 was dug per survey. Digging was done with local hoes, "jembes" to a depth of 0.3 m. For other equipment used and detailed methods see Measey *et al*. (2003b).

    In addition to the methods of Measey *et al*. (2003b), it was decided that surveys should only take place within habitats where caecilians were found on that occasion, and within 100 m of that occurrence. This meant that a period of searching in typical caecilian microhabitats (see below) was necessary prior to a survey, and that surveys were only carried out should a specimen be found.

Timed searches

Two types of timed searches were made: time limited searches (TLS), where a certain time (normally two hours) was given for as many animals as possible to be found in a approximated area. Secondly, time recorded searches (TRS), where the number of animals required (for other studies) was determined, and the time required to reach this number over an estimated area was recorded.

In timed searches, particular attention was paid to the borders of water bodies (where available), the bases of banana plants (in agriculture) or palms (in forest), fallen and decaying logs, and in close proximity to any animal captured.

Analysis of data

For analyses of timed survey data, a simple index was calculated, directly relating the number of animals caught with the area searched and person hours taken (i.e. individuals.person hour^{-1}.area^{-1}). The square root of the area searched was used to remove problems associated with comparing very large and very small areas. The intuitive logic of this data transformation is that searching can be considered as a linear process with respect to the path taken by the searcher. The resulting index produced gives an estimation of the number of animals which could be expected to be found per hour, per meter.

Statistica (v 5.5A, StatSoft, France) was used for statistical analyses of the data. Means ($\bar{x}$) of measurements are given with standard error ($\pm$SE). Two-tailed t-tests assuming equal variances ($^2t_{df}$ = t-statistic) were used to test for differences between log total length (TL) and log mass. A non-parametric Spearman rank correlation (Spearman R statistic) was used to test for a relationship between density using quantitative surveys and timed searches of caecilians. A Mann-Whitney U-test (Z statistic) was used to test for differences in densities between individual surveys in agriculture and forest, and between species. Numbers of individuals in each test included all ontogenic stages except eggs.

RESULTS

In shambas, *Boulengerula taitanus* and *B. boulengeri* were found most easily in soil around the base of banana plants and at the bases of solitary trees, especially where a large amount of leaf litter was gathered. This does not seem to be a prerequisite for these caecilians, as surveys in agricultural areas also revealed their presence in open areas (with no shade) both recently tilled and untilled. In more evenly shaded areas predictability of presence was less certain. One survey was carried out within 24 hours of an area being tilled (Kiwinda, December 2002, table 1), and one caecilian was found dead within one of the random quadrats. Another survey, undertaken within seven days of soil being tilled, found several live animals (Mwabwalo, April 2003, table 1). In most cases caecilians were found within the soil, and where this was not the case they were found at the bottom of deep piles of leaf litter in contact with the soil surface. No particular relationship was noted between presence of caecilians and irrigation ditches or natural streams.

In forest, *Boulengerula taitanus* was found in different circumstances to *B. boulengeri*. *B. boulengeri* were almost always within the soil, and the most efficient means of finding them was to dig in deep soil. While *B. boulengeri* appeared to be less frequent as the soil became drier, individuals were found at the maximum depth dug (0.3 m) in hard and compact soil (>8.3 kg.cm^{-2}). During a randomised survey (table 1), one *Scolecomorphus vittatus* was found alone in a quadrat at a depth of around 0.2 m. Conditions appeared to be identical to

Table 1. Density and mass of caecilians found in surveys in East Africa. For detailed site descriptions see text. For each survey, five 1 m² quadrats were randomly assigned and sampled in each of three 100 m² grids, giving a total of 15 m². * same survey, but numbers separated for the two species found. + female found with 2 eggs during survey (female but not eggs included in numbers).

Country	Species	Date	Site	Type	Numbers of individuals found	Numbers of empty quadrats	Density m⁻²	Mass g.m⁻²
Kenya	*Boulengerula taitanus*	3 May 2002	Kiwinda	Agriculture	2	13	0.13	1.01
Kenya	*Boulengerula taitanus*	4 May 2002	Chomboke	Agriculture	4	11	0.27	0.66
Kenya	*Boulengerula taitanus*	5 May 2002	Ngangao	Forest	0	15	0.00	0.00
Kenya	*Boulengerula taitanus*	18 December 2002	Kiwinda	Agriculture	4+	11	0.27	1.10
Kenya	*Boulengerula taitanus*	20 December 2002	Chomboke	Agriculture	4	12	0.27	0.97
Kenya	*Boulengerula taitanus*	19 December 2002	Ngangao	Forest	0	15	0.00	0.00
Kenya	*Boulengerula taitanus*	7 April 2003	Chawia	Forest	1	14	0.07	0.28
Kenya	*Boulengerula taitanus*	8 April 2003	Mwabwalo	Agriculture	2	13	0.13	0.21
Tanzania	*Boulengerula boulengeri*	28 April 2002	Kwamkoro	Agriculture	1	15	0.07	0.19
Tanzania	*Boulengerula boulengeri*	28 April 2002	Kwamkoro	Forest	9	9	0.60	0.67
Tanzania	*Boulengerula boulengeri*	24 December 2002	Kwamkoro	Agriculture	1	14	0.07	0.10
Tanzania	*Boulengerula boulengeri*	23 December 2002	Kwamkoro	Forest	13	6	0.87	1.46
Tanzania	*Scolecomorphus vittatus*	14 December 2002	Bom Bom*	Forest	1	14	0.07	0.27
Tanzania	*Boulengerula boulengeri*	14 December 2002	Bom Bom*	Forest	3	13	0.20	0.13
Tanzania	*Boulengerula boulengeri*	13 April 2003	Bom Bom	Forest	1	14	0.07	0.19
Tanzania	*Boulengerula boulengeri*	14 April 2003	Kwamkoro	Forest	7	9	0.47	0.59
Tanzania	*Boulengerula boulengeri*	15 April 2003	Emau	Agriculture	3	12	0.20	0.42

those in which *B. boulengeri* were being found. *B. taitanus* were most easily found in the first few centimetres of soil under rotting logs, and in soil built up around large rocks. Finding animals by simply rolling logs was uncommon, although one individual was found inside a rotting log. Only one *B. taitanus* was found during a forest survey (table 1), and this reflects the rarity that animals were found within undisturbed soil. In contrast, animals were found in loose soil, against rocks, between the buttresses of large trees, associated with the soil around a tree fall, or the deep litter accumulated under some palm trees. After the second survey at Ngangao (December, 2002, table 1), two animals were found whilst digging in soil that had been dug during the first survey, although these quadrats had been empty in April (table 1).

During time limited /recorded searches, shambas were much easier habitats in which to find caecilians. Most importantly, the presence of certain crops (see above) often indicated where to begin a search, and once the first animal in a microhabitat was located, it was usually possible to find more within the immediate area. Animals were not infrequently found together. Often it was difficult to assess the relationship between individuals when they were found in successive hoes lifted, but there were instances where more than one animal appeared in the same hoe of soil already entwined. In *B. taitanus* this included a large adult with a single seemingly dependent juvenile (68 mm), and in *B. taitanus* and *B. boulengeri* pairs of adults in very close proximity. In forest, it was not uncommon to find more than one *B. taitanus* in soil under the same log, but seemingly unassociated, there being sometimes several meters between them. An adult female *B. taitanus* was found curled around a clutch of two eggs 5 cm under the soil surface in a survey (see table 1). Burrow dimensions were measured as $50 \times 40 \times 30$ mm. During time limited digging on 24 December in Kwamkoro Forest, a female *B. boulengeri* was found with a clutch of three eggs within 10 cm of the soil surface (table 2). The burrow was destroyed whilst digging, so that no further measurements could be made.

No site selected for a survey was abandoned because caecilians could not be found. Table 1 shows the range of densities and masses found in all surveys of caecilians. The maximum density within any single quadrat was 4 m^{-2} in Kwamkoro Forest (23 December 2002), while all sites recorded the minimum of zero for at least a third of quadrats dug ($\bar{x}$ 12.6 $\pm$0.62; table 1). No significant difference was found between overall densities of *B. taitanus* ($\bar{x}$ 0.14 $\pm$0.04 individuals.m^{-2}) and *B. boulengeri* ($\bar{x}$ 0.30 $\pm$0.12 individuals.m^{-2}; Z = 0.64; P = 0.524).

Figure 3 shows opposite trends in densities between forest and agriculture for *B. boulengeri* and *B. taitanus*. For *B. taitanus*, densities in the forest ($\bar{x}$ 0.02 $\pm$0.02 individuals.m^{-2}) were significantly less than in agriculture ($\bar{x}$ 0.21 $\pm$0.03 individuals.m^{-2} Z = 2.24; P = 0.025), while differences between forest ($\bar{x}$ 0.43 $\pm$0.18 individuals.m^{-2}) and agriculture ($\bar{x}$ 0.11 $\pm$0.04 individuals.m^{-2}) in *B. boulengeri* were not significant (Z = 1.23; P = 0.216; table 1). The same trend was observed for time recorded/limited searches with more *B. boulengeri* than *B. taitanus* found in forests ($\bar{x}$ 0.041 $\pm$0.010 and $\bar{x}$ 0.002 $\pm$0.001 individuals.m^{-1}·h^{-1}, respectively) and less in agriculture ($\bar{x}$ 0.011 $\pm$0.003 and $\bar{x}$ 0.015 $\pm$0.004 individuals.m^{-1}.h^{-1}, respectively; figure 3). A significant relationship was found between randomised quadrat surveys and time recorded/limited searches carried out at the same localities and occasions (tables 1 and 2; Spearman R = 0.991; P < 0.0001). Normally, where randomised quadrat surveys failed to find any caecilians, time recorded searches provided substantial sample sizes. However, the reverse situation was recorded: a time

Table 2. Results of time recorded searches (TRS) and time limited searches (TLS) for caecilians in agricultural and forested habitats in East Africa. For detailed site descriptions, and a description of calculating the density index, see text. Boulengerula boulengeri is sympatric with Scolecomorphus vittatus, but none of the latter species were found in TRS or TLS. + female found with 3 eggs during survey (female but not eggs included in numbers).

Country	Species	Date	Site	Type	TLS / TRS	Number of animals found	Estimated area searched (m²)	Time taken (person hours)	Density Index (Animals. h⁻¹.m⁻¹)
Kenya	Boulengerula taitanus	4 May 2002	Chomboke	Agriculture	TRS	3	42 000	4	0.004
Kenya	Boulengerula taitanus	8 May 2002	Mwoburi	Agriculture	TLS	11	60 000	2	0.022
Kenya	Boulengerula taitanus	5 May 2002	Ngangao	Forest	TRS	21	500 000	20	0.001
Kenya	Boulengerula taitanus	20 December 2002	Chomboke	Agriculture	TLS	0	60 000	2	0.000
Kenya	Boulengerula taitanus	20 December 2002	Njumwa	Agriculture	TLS	12	80 000	3	0.014
Kenya	Boulengerula taitanus	19 December 2002	Ngangao	Forest	TRS	23	300 000	12	0.003
Kenya	Boulengerula taitanus	7 April 2003	Chawia	Forest	TRS	17	300 000	16	0.002
Kenya	Boulengerula taitanus	9 April 2003	Mwabwalo	Agriculture	TRS	19	45 000	3	0.030
Kenya	Boulengerula taitanus	9 April 2003	Kivvinda	Agriculture	TRS	28	80 000	4.5	0.022
Kenya	Boulengerula taitanus	10 April 2003	Chomboke	Agriculture	TLS	9	40 000	3	0.015
Tanzania	Boulengerula boulengeri	28 April 2002	Kwamkoro	Agriculture	TLS	6	60 000	2	0.012
Tanzania	Boulengerula boulengeri	27 April 2002	Kwamkoro	Forest	TLS	10	2 000	4	0.056
Tanzania	Boulengerula boulengeri	24 December 2002	Kwamkoro	Forest	TRS	24+	8 000	6	0.045
Tanzania	Boulengerula boulengeri	16 April 2003	Kwamkoro	Forest	TRS	15	50 000	3	0.022
Tanzania	Boulengerula boulengeri	14 April 2003	Emau Shambangeda	Agriculture	TLS	5	45 000	4	0.006
Tanzania	Boulengerula boulengeri	15 April 2003	Village	Agriculture	TRS	22	65 000	5.5	0.016

limited search for *B. taitanus* found no animals in a Wundanyi shamba (Chomboke, December 2002, table 2), but the following randomised quadrat survey revealed a density of 0.27 animals.m^{-2} (table 1). This shamba was noticeably different from others sampled as it was relatively heavily shaded from tall trees under which the usual crops were grown (see site description).
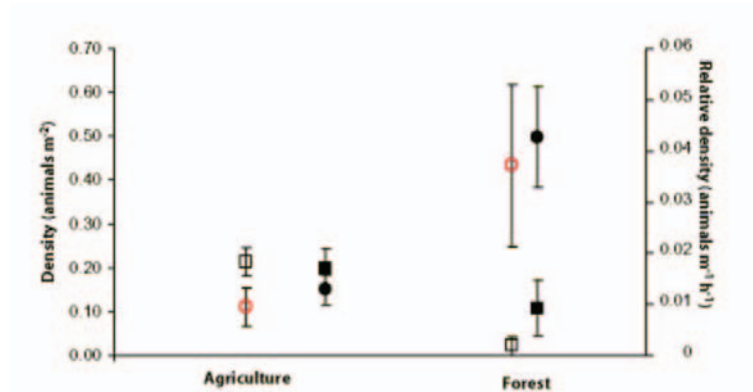

Figure 3. The density of Boulengerula taitanus *(squares) and* Boulengerula boulengeri *(circles) found in agricultural areas is very similar, but opposite trends are seen in forest (significantly for* B. taitanus *see text). Randomised survey methods (open symbols, left ordinate) give similar results to time recorded / limited searches (closed symbols, right ordinate). Standard errors (bars) are shown around arithmetic means (symbols).*

Total length of adult *B. taitanus* collected from shambas was found to be significantly shorter ($\bar{x}$ 219.3 $\pm$7.93 mm; n = 86) than animals found in forest ($\bar{x}$ 285.9 $\pm$5.79 mm, n = 61: ^{2}t$_{145}$ = 5.743; P < 0.0001; figure 4a). However, no significant difference in condition (*WL^{-3}*) was found between the same animals from shamba ($\bar{x}$ 3.14^{-7} $\pm$5.48^{-15} g.mm^{-3}) and from forest ($\bar{x}$ 2.98^{-7} $\pm$1.55^{-14} g.mm^{-3}: ^{2}t$_{145}$ = 0.976, P = 0.331).

For *B. boulengeri* collected from shambas ($\bar{x}$ 165.1 $\pm$6.55 mm; n = 55), there was no significant difference to the size of those collected from forest ($\bar{x}$ 158.1 $\pm$4.03 mm; n = 81: ^{2}t$_{134}$ = 0.429, P = 0.669; figure 4b). Nor was there any difference in condition (shambas $\bar{x}$ 3.30^{-7} $\pm$1.10^{-8} g.mm^{-3}; forest $\bar{x}$ 3.81^{-7} $\pm$3.19^{-8} g.mm^{-3}; ^{2}t$_{134}$ = 1.276, P = 0.204).

DISCUSSION

This study clearly demonstrates that neither *Boulengerula taitanus* nor *B. boulengeri* can be considered to qualify for IUCN categories "Critically Endangered, Endangered, Vulnerable or Near Threatened" within their range of occurrence (IUCN, 2001). Indeed, despite the small area of occurrence, both species have high abundance in agriculture suggesting that they should be considered "Least Concern". The highest densities shown in table 1 are similar to those found for *Gegeneophis ramaswamii* Taylor by Measey *et al*. (2003b), and once again demand further investigation of the influence of these subterranean predators on their soil ecosystem engineer prey. Other recent field work in East Africa has also found caecilians in abundance. Gower *et al*. (20041), commented that large numbers of

Boulengerula uluguruensis Barbour and Loveridge were easily collected in agricultural areas of the Uluguru Mountains (but that none were found in forest). *Schistometopum gregorii* (Boulenger) have also been found in large numbers on the Ruvu floodplain (M. Wilkinson, pers. com.; pers. obs.). This data suggests that all Gymnophiona in East African should not be considered rare. Instead their biomass may be more important than previously appreciated in tropical agricultural and forest ecosystems.
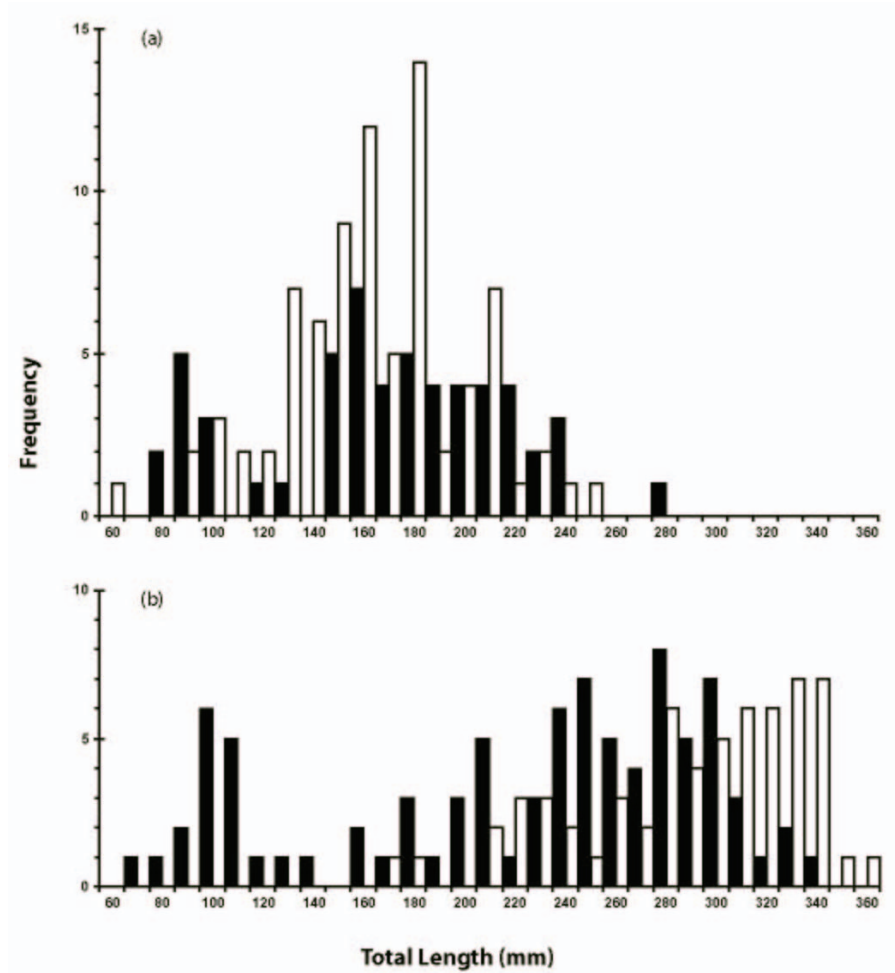

Figure 4. Histograms showing the total length frequency of total numbers of (a) Boulengerula boulengeri *and (b)* Boulengerula taitanus *caught during all surveys and searches in agriculture (closed bars) and forest (open bars).*

Do survey results represent true densities?
Measey *et al* (2003b) discussed the possible mis-representation of survey results, especially that the highest densities may represent within patch sampling of caecilians. This discussion will not be repeated here, instead critical discussion is confined to the possibilities of over or under representation of these surveys:

Over representation?
In this study, the deliberate sampling of patches was avoided by regular spatial relation between sampling grids, and by using previously unknown collecting sites. Experience from time limited and time recorded searching both suggest that patches may exist. If patchiness occurred, it could be expected that surveys that include free digging would over-represent the densities of animals, as human searchers, like animals, are pre-disposed to exploit patches (see MacArthur & Pianka, 1966). Random sampling would therefore be expected to yield lower (truer) densities as patches are sampled with the same intensity as areas outside patches. Obviously, this only holds true if surveys span patches. Data presented here are not sufficient to test presence of patchiness in caecilians, and the hypothesis that caecilians occur in patches remains to be tested.

Under representation?
The degree to which caecilians are associated with plants, be it bananas in a shamba or trees in a forest, is difficult to judge. The observations made here may reflect the greater shade afforded by such plants, as well as the increased humidity of the soil resulting from both shade and the channelling of rainwater toward the base of the plants (particularly for bananas). It is likely that such areas harbour larger amounts of soil macrofauna on which caecilians prey. However, surveys in shambas must respect the proprietors desire to retain yield from crops, and likewise in forest reserves it is not possible to fell and remove trees. Measey *et al* (2003a) suggested that the Indian caecilian, *Gegeneophis ramaswamii*, was difficult to recapture as it was using micro-refuges not available for sampling within an agricultural situation in Kerala, India. Their results indicated that the population of animals within a small area (around 100 m^2) was nearly double that found on any occasion. This study does not go any further to revealing possible refugia. Measey *et al*. (2003b) commented that they considered few animals escaped while they dug quadrats, however this remains unknown and to be tested. Hence, it is clear that surveys may under represent the true densities of caecilians within the areas studied. Testing the extent to which animals are under-represented would require fast, destructive and random sampling, such as by using a mechanical digger.

Despite the possibilities for over or under representation listed above, the survey results presented here are remarkably consistent at the same sites over several sampling occasions (table 1). This suggests that while there may be problems associated with some assumptions of this survey technique, it may be tentatively accepted that the method is repeatable and therefore can be used in comparative studies. Measey *et al*. (2004) have already demonstrated the values of dietary studies from animals sampled in randomly designed surveys. Time recorded/limited searches appear less consistent (table 2), despite giving similar relationships between species and land cover types (figure 3). However, their usefulness as a stand-alone technique to assess density and/or abundance may be questioned. An important factor is expected to be operator experience, which is almost certainly responsible for some of the large variance reported. Obviously, these techniques can be used together and given that the appropriate data is recorded at the time of collection, may provide valuable comparative information for future studies. Here it is shown that while surveys may provide sufficient data to compute densities in most habitats, additional timed searches are necessary to provide sufficient animals for further (especially statistical) analyses, such as the differences in size observed for *B. taitanus*.

Agricultural effects

Boulengerula boulengeri and *B. taitanus* are not sympatric, and hence it is not known whether distributions are influenced by species, habitat or a combined effect. For the discussion of agricultural effects, species differences are largely ignored (although these almost certainly exist, see above), instead the discussion concentrates on differences found between different habitats, specifically agriculture and forest. Agricultural practices are almost certainly different between the two distributions. For example, shambas in the Eastern Usambaras are often relatively 'new' as they are cut from secondary forest that has been allowed to regrow over older agricultural sites (J. Mtango, pers. com.). However, in the Taita Hills, deforestation is much more advanced (see Newmark, 1998), and shambas are unlikely to regenerate forest if left fallow, even for a period of years (pers. obs.).

A significant increase in the density of *B. taitanus* was observed within shambas, compared to that in forest. Animals were not easy to find in forest (with only a single animal occurring in a survey), and this corroborates with the findings of Hebrard *et al*. (1992: 513) "Although we made some efforts to collect at Ngangao, no specimens were found in indigenous forest." It is possible that this represents sampling error, and that more animals were present in forest, in an unsampled micro-refuge (such as within the roots of large trees). However, such micro-refuges are also believed to occur in agricultural landscapes (see above). It is possible that different ontogenic stages may have different or more highly aggregated distributions that were not sampled; these aggregations could be associated with breeding or feeding. The occurrence of a discrete breeding site has been previously suggested for an oviparous caecilian (Measey *et al*., 2003a). If this were true, it would suggest that habitat utilisation was different within forest compared to agriculture where animals of all sizes were found in soil during surveys. Results from only time-limited or time-recorded searches may reflect more the greater ease of finding caecilians in agricultural settings. It would be interesting to know whether particular crops, such as bananas, actually increase the density of caecilians, or merely make them easier to find. Again, such hypotheses are difficult to test without the use of more destructive rapid sampling methods (see above). The nature of the quantitative surveys performed here suggests that densities in forest and agricultural habitats are in reality significantly different for *B. taitanus*. The contrasting results for *B. boulengeri* support this (with the above caveats). Although average density of *B. boulengeri* was found to be greater in the forest, the difference was not significant. There was also no significant difference between sizes of *B. boulengeri* caught in shambas and forest.

The results presented here provide evidence that these caecilians inhabit exposed soils without shade, and that tilling results in mortality. Measey *et al*. (2001), suggested that mortality from agricultural practices (and also through sampling) would not have a significant impact on the populations of *Gegeneophis ramaswamii*. It should be emphasised that all of these studies have been carried out in low intensity agricultural settings, and that the effects of mechanised agricultural methods on caecilian populations remain unknown. In their surveys of *G. ramaswamii*, Measey *et al*. (2003b) suggested that constant high densities indicated that populations were not harmed by sampling. A similar inference may be drawn from the results presented here. While it is possible that a higher agriculturally mediated mortality may produce a different population structure, as larger animals are more likely to be struck by a jembe, it is not clear why this would have such a pronounced effect on *B. taitanus* and not *B. boulengeri* (see below).

It is commonly reported that caecilians favour loose friable soil, especially that which is rich in organic matter (e.g. Gundappa *et al*., 1981; Jared, Navas & Toledo, 1999; O'Reilly,

2000). With the exception of one animal found in a forest survey, the results for *B. taitanus* are consistent with such statements. However, results presented for *B. boulengeri* (and a single *S. vittatus*) indicate that this caecilian can be regularly found in hard and compact substrates in its naturally forested habitat. Such reports are previously unknown for this order, and put previous experimental studies (Ducey *et al.*, 1993; O'Reilly *et al.*, 1997; Teodecki *et al.*, 1998) in a new light. It should be noted however, that it is not known whether caecilians are constructing their own burrows in this medium, or enlarging pre-existing excavations (*e.g.* earthworm galleries).

Although animals were not found in association with water in either shambas or forest during searches or surveys, this does not rule out that natural subterranean or surface watercourses or irrigation is a factor affecting distributions during the dry season. However, given the distribution of animals in forest and their distance to streams, this seems unlikely. Almost nothing is known of caecilian distributions during dry seasons, and this should become a priority for caecilian ecologists (Measey *et al.*, 2003a).

What causes size bimodality and density differences observed for *Boulengerula taitanus*? It is possible that observed differences result entirely from sampling error. Discussion of causes of sampling error have already been given (above and in Measey *et al.*, 2003b), thus here the alternative hypotheses, that there was no sampling error or that sampling error was insignificant, are examined. Huston and DeAngelis (1987: 662) gave four biological mechanisms through which size bimodality can arise:

- *Spatial heterogeneity*: That the populations were separated spatially is implicit in the methods and sites. Forest and agriculture differ spatially and presumably provide different habitats for *B. taitanus*. Studies of soil macrofauna have shown a gradient of abundance and diversity from natural forests and low intensity agricultural systems (Fragoso & Lavelle, 1992; Lavelle *et al.*, 1997; Eggleton *et al.*, 2002). A different diet may afford a change in the growth rates of animals producing faster growing and hence larger individuals. If reproduction is stimulated by rainfall onto soil, this may cause higher fecundity in agriculture, where effects of even occasional rain are more immediately felt.

- *Temporal heterogeneity:* Forest and agricultural habitats may produce some differences in temporal heterogeneity especially with regard to dry periods. Forests may provide a sheltered habitat, in terms of shade and leaf litter covering the soil, where the extremes of the dry season are not felt to the same extent as in agriculture where animals are harder to find after prolonged periods without rain (pers. obs.). The reduction of seasonal impacts may have a similar effect on potential prey items. Extended active seasons should allow animals to attain a larger size, such as those displayed here by *B. taitanus*. However, this hypothesis alone would not explain the differences in density of animals found between forest and agriculture.

- *Genetic:* Genetic differences between populations found in forest and shambas are possible, and this hypothesis may be testable using molecular data analysis. However, it seems that this theory would be unlikely to explain how populations in isolated patches of forest produce larger animals than the shambas that surround them.

- *Mortality:* A selective mortality, such as through predation, on smaller rather than larger individuals would produce differences in both size and density. It is possible that forests, where the soil is densely covered with leaf litter, may harbour greater populations of potential predators of caecilians, such as snakes. Barbour and Loveridge (1928) report finding *B. boulengeri* in the stomachs of the Usambara Garter Snake *Elapsoidea nigra* (Gunther) (see Broadley, 1971), and it has been suggested that this species predates solely

upon caecilians (Spawls *et al.*, 2002). As gape limited predators (see Shine, 1991), snakes may predate on smaller rather than larger caecilians, making juveniles particularly vulnerable to predation and thus impacting on population densities as well as size distributions. Snakes are often persecuted in agricultural settings, which may effectively decrease predation. Similarly, smaller caecilians may be more vulnerable to invertebrate predators such as spiders and centipedes. Safari ants (genus *Dorylus*) have been seen carrying caecilians (J. Mwandoe pers.com.), and may be the cause of significant levels of predation. Forest reserves also have bush pigs (*Potamochoerus porcus* (L.)), which are reported to eat caecilians.

As stated by Huston and DeAngelis (1987), a bimodal population need not have a single cause, but a number of synergistic factors. The lack of significant difference found for *B. boulengeri* is intriguing. One substantial difference between the localities sampled is the degree of forest fragmentation. The spatial separation between shambas and forest in the Eastern Usambaras was certainly smaller than that in the Taita Hills. Similarly climatic differences may be reduced and the effects of predators more equal when forest is closer. Hypotheses concerning the effects of forest fragmentation, densities and differences in sizes between caecilians found in forests and agriculture deserve more investigations, and could also be tested with other caecilian taxa, such as *Gegeneophis ramaswamii* in India.

Given the above evidence of high densities and abundances, two immediate questions arise: (1) Why are caecilians so often considered rare? (2) If caecilians are not rare in East Africa, why are certain species, such as *Boulengerula changamwensis* Loveridge, *B. denharti* Nieden and *B. ficheri* Nussbaum and Hinkel, known from so few specimens?

Caecilians are not alone amongst subterranean lower vertebrates in being considered rare. Many scolocophidian snakes are known from very few specimens and they may be given an inappropriate status when insufficient investigations, rather than actual abundance, are responsible for low numbers in collections (e.g. Gower *et al.*, 2004). Similarly, amphisbaenians (worm lizards), another dedicated subterranean group, have been described as the least known reptiles in East Africa (Spawls *et al.*, 2002). Field work specifically orientated to finding caecilians appears to be more rare than the animals themselves. While some general herpetological techniques may occasionally find caecilians (e.g. log rolling, pit fall trapping, leaf litter sorting), because they are principally subterranean, investigators who fail to dig into the soil may erroneously conclude that caecilians are rare or absent. A digging implement, such as a jembe, is essential for this work. Failure to look into the soil has left us ignorant about the biology of many amphibians that construct subterranean burrows, producing a herpetological subterranean blind spot.

There does seem to be evidence of differences in densities between taxa. Measey *et al.* (2003b) reported a single *Ichthyophis tricolor* Annandale in their surveys of *G. ramaswamii*, despite it being sympatric with both *I. tricolor* and *Uraeotyphlus narayani* Seshachar. This resembles the results presented here, with the single *Scolecomorphus vittatus* found in this study. Although, unlike Measey *et al.* (2003b), the single *S. vittatus* was found in the same survey, and within 2 m of a *B. boulengeri*. Interspecific niche differentiation has never been studied in caecilians, and we are ignorant of the factors that may favour one species over another. Undoubtedly, like other amphibians, caecilians are vulnerable to habitat loss, although low intensity agriculture does not seem to have a negative effect on all species. It is hoped that evidence of caecilian abundance provided in this study will generate enthusiasm for research into the biology of caecilians—the not so rare subterranean predators.

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