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Evidence of seasonal migration in a tropical subterranean vertebrate

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Abstract

Many animals undergo migrations that depend on a range of biotic or abiotic factors provoking daily, seasonal or annual movement of individuals and/or populations. Temperate amphibians frequently have their life cycles dominated by annual temperature fluctuations, but in the tropics it is often presumed that distinct rainy seasons will influence amphibians more than small changes in temperature. Here, we direct the seasonal changes in abundance hypothesis to a caecilian amphibian *Boulengerula boulengeri* found in monthly randomized quantitative surveys in the top 30 cm of soil. Meteorological data are used to interpret the significant changes found in relation to rainfall and temperature variables. Instead of the expected correlation of migration with rainfall, we find that frequency varies significantly and positively with temperature. In addition, data on the depth at which individual caecilians are collected suggest that animals undergo a vertical (rather than horizontal) migration within the soil. This is the first example of vertical migrations with temperature (as opposed to rainfall) of any tropical subterranean fauna. We discuss the possible influences that stimulate migration in this species (abiotic factors, feeding, reproduction and predation). The ecology of caecilians has lagged behind that of all other tetrapods, and this study has importance for future ecological studies, as well as biodiversity assessments and monitoring methodologies.

Introduction

Amphibian activities are regulated by a number of climatic influences, water availability, photoperiod and temperature being among the foremost abiotic factors (Denver, Boorse & Glennemeier, 2002). In temperate regions, drops in temperature may be so severe as to interrupt amphibian activity, whereas temperature increases may be used as cues for feeding and breeding activities (e.g. Blaustein *et al.*, 2001 and references therein). In the tropics, where variation in annual temperature and photoperiod can be very limited, rain may provide the stimulus for seasonal activities such as breeding, migration or diapause. However, some amphibian life histories are not dependent on standing or running water, and in these so-called terrestrial breeding species it has been found that seasonal activities are correlated with rainfall, especially when marked wet or dry periods change the availability or abundance of prey species (Watling & Donnelly, 2002 and references therein).

Of the different habitats in which amphibians reside, the soil can be considered as a relatively stable environment: soil moisture in tropical forests remains high year round, and fluctuations in temperature and pH are reduced (Lavelle & Spain, 2001). However, the soil imposes severe physical constraints on its dedicated subterranean inhabitants, such that any fossorial movements require enormous physical effort (e.g. Gans, 1973). In addition to subterranean mammals, there are many reptiles and amphibians that live most of their lives in the soil. All known subterranean reptiles and amphibians are carnivorous, preying on soil macrofauna (such as earthworms, termites and ants). Caecilian amphibians are largely soil-dwelling animals and have many remarkable adaptations to this habitat. For example, some have been shown to be unique among tetrapods in using hydrostatic locomotion, with which they can exert considerable burrowing force (O'Reilly, Ritter & Carrier, 1997).

For many years, study of the ecology of caecilian amphibians has lagged behind that of other lower vertebrates. Traditional reasons given for this lapse have been that caecilians are considered rare components of the terrestrial ecosystem (e.g. Duellman & Trueb, 1986; Bhatta, 1997). Logically, it follows that ecological studies of rare animals should be difficult, especially when the animals concerned live in an opaque, dense and complex medium: the soil. However, some authors suggest that some caecilians are not rare, and that these limbless mostly subterranean amphibians are common or even plentiful components of some tropical ecosystems (e.g. Loveridge, 1936; Glaser, 1984; Péfaur *et al*., 1987; Hebrard, Maloiy & Alliangana, 1992). Even when densities are low, ecological studies of caecilians are possible, as shown by the pioneering works of Kupfer, Nabhitabhata & Himstedt (2004*b*, 2005).

An ecological toolbox was developed by Measey *et al*. (2001, 2003*a,b*, 2004) for the southern Indian caeciliid *Gegeneophis ramaswamii* Taylor. A dedicated subterranean burrower, *G. ramaswamii* was found to be common in many types of low-intensity agricultural settings in the Western Ghats. Extremely high abundances (between 0.44 and 1.13 individuals m^{-2}) reported by Oommen *et al*. (2000) prompted Measey *et al*. (2003*b*) to design an unbiased quantitative method to measure the density for this species. Results using their randomized method demonstrated high densities with means of 0.51 and 0.63 individuals m^{-2} for the beginning and mid-monsoon periods, respectively. They suggested that this methodology might be used for comparative purposes in other caecilians and burrowing lower vertebrates.

Vyas (2003; see also Vyas, 2004) suggested a perennial horizontal migration of *Ichthyophis bombayensis* Taylor towards riparian habitats in the dry season, at the northern extent of the Western Ghats, India. Kupfer *et al*. (2005) also suggested seasonal horizontal and vertical migrations in another ichthyophid caecilian, from the seasonal tropics. In the dry season, they found animals concentrated around moist habitats, and significantly more animals were found closer to the surface during the rainy season. Loveridge (1936) speculated that specimens of *Schistometopum gregorii* Loveridge approach the surface soils during the heaviest rains in East Africa, and retreat deeper into the soil as the rains recede. A similar interpretation concerning soil moisture content was made by Malonza & Measey (2005) following their monthly samples of *Boulengerula taitanus* Loveridge in Kenya. Lastly, Measey, Majissa & Müller (2005) found *Boulengerula uluguruensis* Barbour & Loveridge to be deeper in sunlight-exposed soil with elevated temperatures, and higher up in the soil profile in cooler shaded areas, within the same agricultural plot in Tanzania.

This study was designed to address the hypotheses raised by the above studies for the East African caeciliid *Boulengerula boulengeri* Tornier: firstly, to determine the occurrence of changes in seasonal abundance of caecilians in the top 30 cm of soil using an unbiased randomized methodology, and further to determine whether changes in abundance are attributable to weather, specifically rainfall and temperature variation; secondly, given that densities do change during the year, to determine whether horizontal or vertical migrations (or their combination) are responsible. It follows that if horizontal migrations are being made by animals that are at least partly dependent on soil moisture content, these may be associated with permanent water bodies, as reported for ichthyophid caecilians (see above) and typical for many other amphibian species.

Materials and methods

Study site

The East Usambaras are a group of low crystalline block-faulted mountains 40 km west of the coast in north-eastern Tanzania. Rising steeply from the lowlands (around 250 m a.s.l.), the main range is about 40 km long and 10 km wide, with peaks ranging from 900 to 1500 m a.s.l. The area has bimodal rainy seasons: the 'Masika', which are long heavy rains from March to May, and the shorter lighter 'Vuli' from October to December (Fig. 1). The historically almost per-humid climate (all months with more than 100 mm precipitation) seems to have become disturbed in recent years with several more months a year receiving less than 100 mm of rain (B. Sanga, pers. comm.; Fig. 1). Whereas the June–September dry season coincides with the coolest time of the year, January and February are dry but with elevated temperatures (Fig. 1). This gives the region a distinct bimodal rain pattern, but a unimodal yearly temperature distribution, with a mean range of around 5 °C (Fig. 1).

The East Usambara Mountains were probably once more or less entirely forested (except the dry lowlands in the north). Today, much of the forest has been cleared, but large blocks have been preserved as forest reserves under the management of the East Usambara Conservation Area Management Programme (EUCAMP). As a result, the East Usambaras have suffered some of the least disturbance within the Eastern Arc Mountains, with an estimated loss of 57% and 413 km^2 of natural forest remaining (Newmark, 1998). Soils in the region are deep ferralsols.

Kwamkoro forest (S05°09′ E38°36′: 920 m a.s.l.) is part of the larger Amani Nature Reserve. Although intensively

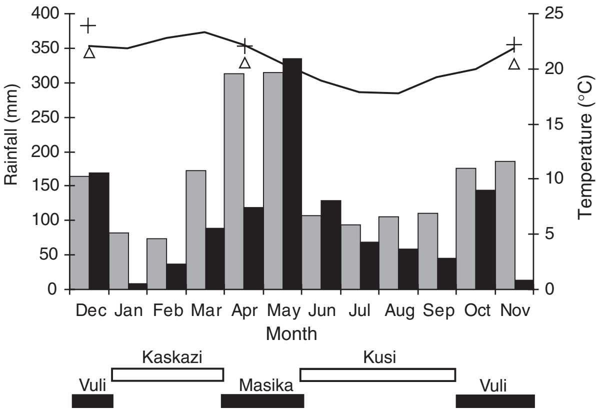

Figure 1 Mean air temperature (line and right ordinate) and rainfall (black bars and left ordinate) data from Marikatanda Tea Research Station for the time period from December 2002 to November 2003. Crosses and triangles indicate the air and soil temperature at the Kwamkoro sampling site, respectively. Grey bars show the monthly average precipitation from 783 months between 1922 and 1988 from the nearby Amani Malaria Unit, Tanzania (data derived from Global Historical Climatology Network).

logged in the 1980s, this forest has been allowed to regenerate naturally from this time, apart from establishment of *Maesopsis eminii* Engler (an invasive tree from Uganda; see Binggeli & Hamilton, 1993). The 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, totalling nearly 2 ha. Three distinct subhabitat types were notable at the site: low flat areas with occasional flooding, higher undulating ground and steep slopes. Survey grids and quadrats were coded accordingly. Soil texture throughout the site was a sandy clay loam, with a pH of 6.24. The mean penetrometer measurement at a depth of 10 cm reflected the extremely dense and compact nature of the soil, 6.2 kg cm^{-2}.

Field work

The survey method described by Measey *et al.* (2003*b*) was followed because of its ease of use and reliance on widely available and durable materials. Five 1 m^2 quadrats were selected using random coordinates inside a 10×10 m grid. Three grids were laid, either side by side or at intervals of 10 m to avoid problems with micro-site selection and bias (see Measey, 2004); a total of 15 m^2 was dug per survey. Digging was conducted with local hoes to a depth of 0.3 m. An effort was made to disturb each quadrat as little as possible prior to digging, and each was dug rapidly and methodically from one side to the other.

Surveys were carried out on a monthly basis from 23 December 2002 until 22 November 2003. Periods between surveys were 1 month on average ($\bar{x}$ = 30.36 days), ranging between 18 and 42 days [standard error (SE) = 1.98 days]. To avoid redigging the same disturbed ground in quadrats, consecutive surveys were made without resampling the same areas. The distance from the first grid to the river, and the overall layout of all grids were noted. This enabled the calculation of the position, relative to the river, of all randomly placed quadrats inside each grid.

Boulengerula boulengeri are easily seen while digging, being blue against the red soil background, and hence the position of the animal in the soil was measured from the surface with a fixed ruler (30 cm). All caecilians seen during sampling were captured, placed into plastic bags with soil and labelled with date, site, survey grid, quadrat coordinates and depth (as appropriate). Excavated soil was replaced after sorting was completed. Each caecilian caught was euthanased by MS222 anaesthesia. All animals were given unique tags and were fixed in 10% formalin before thorough rinsing in water and storage in 70% ethanol. Sex was determined by examination of gonads exposed by mid-ventral incisions in the body wall of preserved specimens. For other equipment used and detailed methods, see Measey *et al.* (2003*b*) and Measey (2004).

Meteorological data

Weather data were obtained from the Marikatanda Tea Research Station for the time period over which sampling was carried out. This weather station is very close to the study site, being only 4.5 km direct.

The meteorological data used were daily (over 24 h) measurements of maximum and minimum temperatures (°C) and rainfall (mm). From these, the following variables were calculated: average daily temperature (the mean of maximum and minimum temperatures), Mean5max (i.e. the mean of maximum temperatures of the sampling day and the previous 4 days), MeanT5, MeanT10 and MeanT15 (i.e. the mean of maximum and minimum temperatures of the sampling day and the previous 4, 9 and 14 days, respectively) and SumR5, SumR10 and SumR15 (i.e. the sum of rainfall for the sampling day and the previous 4, 9 and 14 days, respectively).

Soil (10 cm below the surface) and air (1 m above the ground) temperatures were recorded at the sampling site on three occasions: 23 December 2002, 16 April and 22 November 2003.

Data analyses

The number of animals found in each quadrat was too low to consider it as a continuous variable. It was thus analysed through logistic regression models using the cumulative logit link function, with a global assessment of the model ($-2\log L$) as well as tests for individual effects (Wald χ^2) (Collett, 1991). To test the first hypothesis (changes in seasonal abundance), a non-parametric Kruskal–Wallis test was used on abundance data as this variable is non-Gaussian. In order to verify whether any meteorological data were associated with a significant change in abundance, a stepwise selection model using all meteorological data (see above) was constructed (i.e. abundance = all meteorological data). To assess whether monthly collections of caecilians were biased with regard to sex, χ^2 tests were performed on monthly sex data (sex and monthly distribution of the individuals found, excluding juveniles).

For the second hypothesis, to test whether change in abundance might be because of horizontal migration, the abundance in each quadrat and its recorded distance to the river were used. The hypothesis was tested with a logistic regression model to incorporate time, distance to the river and their interaction (i.e. abundance = month distance month × distance). Tests for vertical migration were performed using individual depths at which each animal was found, rather than quadrat data, with standard linear models (regression and covariance analyses): firstly, by a simple model relating depth of individuals found with time (i.e. depth = month); secondly, by two corresponding meteorological variables chosen to exemplify changes in temperature and rainfall: for example the mean temperature over 5 days and the total rainfall over 5 days (i.e. depth = MeanT5 SumR5).

Analyses on the three subhabitat groups defined within the forest site sampled (low flat areas, higher undulating ground and steep slopes) were carried out to see whether the subhabitat types had an effect on monthly abundance from quadrat data, and secondly on depth and distance from individual data. A non-parametric Kruskal–Wallis signed ranks test found no significant influence of subhabitat types on caecilian captures on either individual or quadrat data.

All statistical analyses were performed using the SAS statistical package (SAS, 1989).

Results

A total of 57 caecilians was captured during 12 monthly surveys in Kwamkoro, all of which were identified as *B. boulengeri*. Of these, 35% were males, 42% were females and 23% were juveniles (Table 1). Specimens of *B. boulengeri* were found in surveys on all occasions except during August (maximum 13, minimum 0; Table 1). The mean number of animals found in all quadrats ($n = 180$) was 0.32 (SE = 0.05). Of quadrats that contained animals ($n = 45$), the mean was 1.27 (SE = 0.09), with a maximum of four. The mean number of individuals found per month was 4.75, with a high variance of 14.75 (SE = 1.11). Changes in monthly abundance were found to be significant (Kruskal–Wallis $\chi^2 = 31.22$; d.f. = 11; $P<0.001$).

The vertical position of caecilians within the soil was determined in 93% of captures. It is noteworthy that no caecilians were found in vertical orientation. Many were removed from burrows that were not greater than their own diameter. Attempts were made to follow burrows, but these proved impossible after only a few centimetres, either because the soil was too hard or because too many burrows were present in the soil. Although some caecilians were found in looser soil (penetration between 5 and 6 kg cm^{-2}) within 10 cm of the surface, many were found deeper (>20 cm), and were removed from extremely compact soil (>8.3 kg cm^{-2}).

Air temperature at the site was within the maxima and minima recorded at the Marikatanda Tea Research Station, and close to the calculated mean (Fig. 1). The mean soil temperature was found to be 1.8° (SE = 0.30) below the air temperature at the site, and 1.1° (SE = 0.35) below the mean air temperature at the Marikatanda Tea Research Station.

The stepwise selection process (model 1) returned only one variable to explain monthly variations in abundance through a logistic regression, the mean of maximum temperatures over 5 days (Mean5max), which was found to be significant with a positive effect (PE, see Table 2). This signifies that the variable Mean5max best explains the variation in abundance (Fig. 2b). Plots of total abundance and different temperature variables show the same positive relationship of increasing abundance with increasing temperature (Fig. 2a–c), whereas those concerning rainfall show no discernable trend whatsoever (Fig. 2d–f).

Migrations

During the sampling, no caecilians were observed above ground, in or under leaf litter. The model concerning horizontal migration and testing for the effect of distance to the river, month and their interaction on the number of individuals found in each quadrat did not detect any significant effect (Table 2; model 2).

Table 1 Sampling dates, temperature, rainfall and abundance of *Boulengerula boulengeri* found during monthly randomized surveys in Kwamkoro forest, Tanzania

	23 Dec 02	30 Jan 03	1 Mar 03	29 Mar 03	16 Apr 03	28 May 03	1 Jul 03	3 Aug 03	2 Sep 03	1 Oct 03	30 Oct 03	22 Nov 03	Totals
Mean temperature over 5 days	22.4	22.0	22.7	23.5	22.6	20.3	18.2	18.0	17.6	20.1	20.0	21.8	
Total rainfall over 5 days	13.4	0.0	0.0	0.0	31.9	194.3	47.3	7.0	1.0	1.1	32.1	1.3	
Males	5	2	0	2	4	0	2	0	1	1	1	2	20
Females	3	6	0	4	1	1	1	0	2	0	3	3	24
Juveniles	5	1	1	2	2	0	0	0	0	2	0	0	13
Total caecilians captured	13	9	1	8	7	1	3	0	3	3	4	5	57
Density (m^2)	0.87	0.60	0.07	0.53	0.47	0.07	0.20	0.00	0.20	0.20	0.27	0.33	0.32

Table 2 Logistic regression analysis for quadrat data on the abundance of *Boulengerula boulengeri* found during monthly randomized surveys in Kwamkoro forest, Tanzania

Model number	Model name	Individual effects: Variable	PE	Wald χ^2	Model global assessment: $-2\log L$	P
1	Abundance = all meteorological data	Mean5max	0.2234	8.89***	214.33	0.0021
2	Abundance = month distance month × distance	Month	NS	0.0002	259.78	0.0001
		Distance	NS	14.2182		
		Distance × month	NS	16.2733		

The logit link function was used. PE is the estimated value for the parameter corresponding to the tested effect. NS, not significant. For an explanation of other terms in the models, see text.
***$P<0.001$.

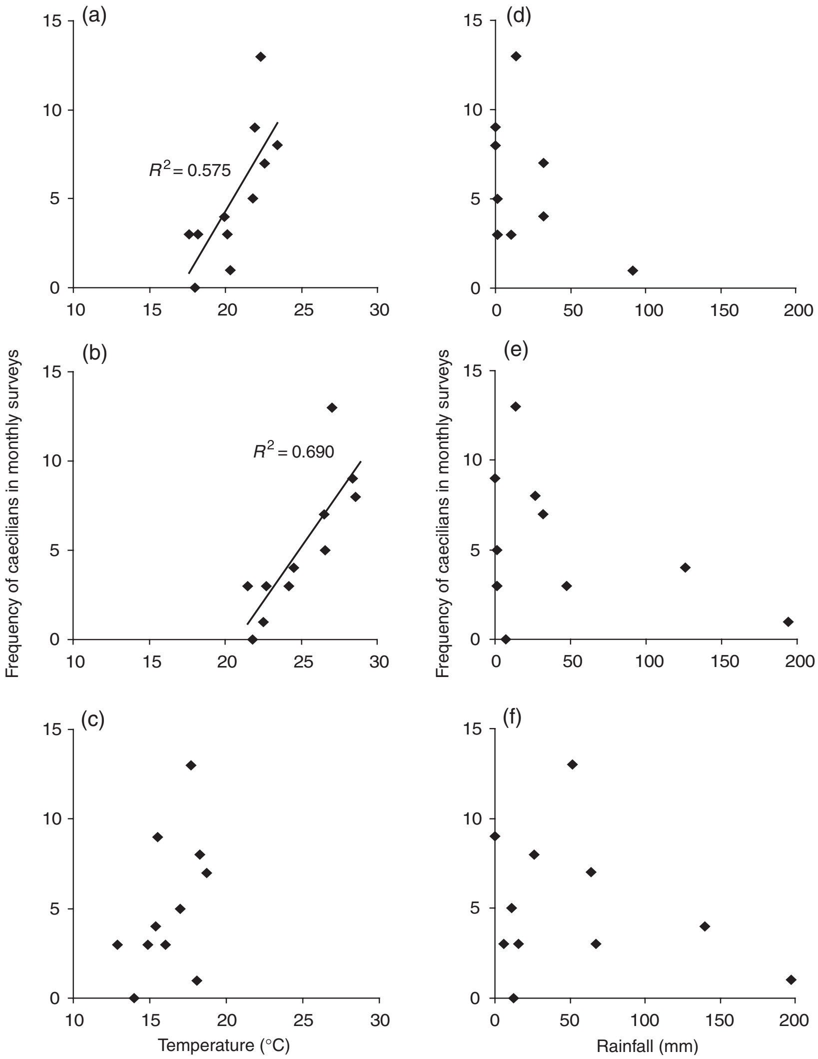

Figure 2 Scattergrams showing change in frequency of *Boulengerula boulengeri* found in monthly surveys with abiotic factors: (a–c) temperature [(a) mean temperature over the previous 5 days; (b) mean maximum temperature over the previous 5 days; (c) mean minimum temperature over the previous 5 days] and (d–f) total rainfall over the previous (d) 5, (e) 10 and (f) 15 days. Regression lines and R^2 (shown when regressions are significant; $P<0.05$) are calculated from the same data (see text for detailed explanation).

Table 3 Analysis of variance (model 3) and regression (model 4) of data from individual *Boulengerula boulengeri* found during randomized surveys in Kwamkoro forest, Tanzania

Model				d.f.		Sum of squares			
number	Model name	Variable	R^2	Model	Error	Model	Error	*F*	*P*
3	Depth = month		0.426	10	42	1534.09	2067.19	3.12	0.0047**
4	For example depth = MeanT5 SumR5		0.066	2	50	238.48	3362.80		
		MeanT5		1		183.84		2.73	0.1045
		SumR5		1		54.64		0.81	0.3717

For an explanation of the terms in the models, see text.
$^{**}P<0.01$.

In most cases (93%), the depth of caecilians could be recorded to within 5 cm, as the animal (being blue) contrasted with the red soil. When this was not the case, missing data were entered into the model. The ANOVA exploring the relationship between month and depth was found to be significant, with more animals being found deeper in the soil from May to September (Table 3). No significant relationship was found between depth and meteorological data. However, the relationships between depth- and temperature-based variables were consistently found to be more significant than rain (Table 3), suggesting that a larger data set may have rejected the null hypothesis.

Sex

Sex could be determined for individuals greater than 130 mm in total length. The maximum number of juveniles found was in December (Table 1), and this sample also contained the smallest individual (total length = 57 mm). The numbers of juveniles were not sufficient to perform a test, but their temporal distribution clearly suggests that females lay and guard eggs during December. No females were found brooding eggs during the surveys (but see Measey, 2004). χ^2 tests on sex ratios were not found to be significant ($\chi^2 = 9.174$; $P = 0.421$, Table 1), indicating that there was no month with a significant bias towards either males or females.

Discussion

The strong correlation of seasonal activities with rainfall for amphibians in tropical habitats is not surprising, even when peaks occur during dry periods, as prey items may also peak and trough with wet/dry climatic fluctuations (Watling & Donnelly, 2002). Indeed, the influence of the abundance of potential prey items on predator populations may be considered a classical cornerstone of ecology (Begon, Townsend & Harper, 1998). However, biotic factors are not always those that are limiting, either for predators or for prey. Abiotic factors define the distribution, and hence niche, of many species, often in advance of limiting biotic factors (Begon *et al*., 1998). Whereas most tropical terrestrial breeding amphibians are known to be predators of predominantly invertebrate prey, the constraints of the soil habitat on those that are subterranean may invoke seasonal activities that are not in accord with their taxonomically close relatives with similar life-history traits.

This study clearly indicates that the abundance of *B. boulengeri* in the top 30 cm of soil undergoes significant seasonal fluctuations; thus, the null hypothesis (that there are no seasonal changes) is rejected. It is also demonstrated that for this species, these fluctuations are significantly related to temperature changes, rather than rainfall, as speculated previously for other caecilian species (Loveridge, 1936; Measey *et al*., 2003*b*; Malonza & Measey, 2005). It is important to note that we do not suggest that our results show population fluctuations or even changes in density. The results specifically show that more animals were found in the upper 30 cm of soil when higher maximum air temperatures were recorded over 5 days. Other temperature-based variables yielded less significant results, although no soil temperatures were used in tests and we suggest that these (when available) may better explain the observed data. Although the effect of temperature seems certain for this species, and air temperatures used are similar to air and soil temperatures measured at the site (Fig. 1), the relationship between maximum and minimum daily air temperatures (in Marikatanda) and soil temperatures in Kwamkoro remains to be firmly established.

No support could be found for the existence of horizontal migrations in relation to the permanent river running through the study site. This does not prove that there is no horizontal movement, but given that this species was not seen over ground, and the extreme demands that any horizontal migratory movement through soil would make (see Gans, 1973; Ducey *et al*., 1993), it is not surprising that the null hypothesis (that there is no horizontal migration to the river) can be accepted. However, long-distance horizontal migration may be possible when in another medium, for example during flooding, under leaf litter or in the presence of underground aquifers (see Measey *et al*., 2003*a*).

The significant variations in depths at which caecilians were found in the top 30 cm of soil over 12 months suggest the probable existence of seasonal vertical migrations of *B. boulengeri*. That these could not be found to regress significantly with temperature is not surprising, given the limitations of the data (see above). However, the difference in fit between the rainfall and temperature variables does suggest that rainfall is not as influential as temperature for this species in Kwamkoro forest.

The interpretation of results from this study critically depends on the meaning of finding a caecilian in the top 30 cm of soil. For the purpose of defining the limits of discussion, some of the least likely scenarios are briefly discussed here. (1) *Boulengerula boulengeri* could be a very short-lived species, whose fluctuations in abundance are a result of short-lived individuals. However, other caecilians have been maintained for long periods in laboratory conditions (e.g. Kupfer, Kramer & Himstedt, 2004*a*), and the maximum longevity for the caecilian *Dermophis mexicanus* (Duméril and Bibron) is given as 14 years (Wake, 2002). In addition, *B. boulengeri* have been maintained in enclosures near the study site for 1 year (G. J. Measey, unpubl. data). Hence, although it cannot be ruled out, there is no reason to suspect that *B. boulengeri* is so short lived that it could influence the interpretation of this study. (2) The forest habitat sampled may not be the natural habitat for *B. boulengeri*, and their changes in abundance represent displacement to and from other sites by, for example, flooding. This species has been recorded from the Amani region for over 100 years (Tornier, 1897), and has apparently always been easy to find, judging by the numbers determined in collections (e.g. 57 specimens collected by Barbour & Loveridge, 1928). The densities reported here are similar to those observed by Measey (2004) in this and other sites. Although the area studied is a secondary forest, it is likely that some deforestation would occur naturally within the area following catastrophic meteorological events (e.g. unusually large floods or storms). (3) Individuals may be faster to avoid capture at certain times than at others. Although this is possible (see 'Discussion' in Measey, 2004), for an ectothermic animal, it would be more likely that less animals would be found when conditions are warmer, contrary to the findings here. (4) Migrations may be diel, or influenced by some unmeasured variable (e.g. photoperiod). Caecilians have been shown to avoid strong light and exhibit nocturnal behaviour patterns (Himstedt, 1996), but as all sampling was carried out during the daytime (typically around midday), and the study site is nearly equatorial, we do not consider this likely.

Despite caveats (above), this appears to be the first suggestion of an example of seasonal vertical migration correlated with temperature in a soil-dwelling animal. It may be expedient to first summarize how a typical tropical forest soil habitat changes with depth. Most soil macrofauna can be found in the top 10 cm of soil (a horizon), together with most of the organic matter and soil moisture (Lavelle & Spain, 2001). Generally, the soil becomes drier (less water in interstitial spaces), cooler (with reduced fluctuations in diel temperature at around 50 cm depth, although seasonal temperature may vary year round), more compact (reduced air spaces), increasingly hypercarbic (and thus increasingly hypoxic) and coarser (increasing ped size) with increasing depth (Lavelle & Spain, 2001). This may change depending on the depth of the soil, which could quickly reach the water table (reaching a stony shingle saturated with water) or bedrock.

Terrestrial caecilians have been shown to be generalist predators of soil macrofauna (Delêtre & Measey, 2004; Gaborieau & Measey, 2004; Measey *et al*., 2004), a number of which are known to make vertical migrations in the soil. Earthworms are known to retreat further into the soil during the dry season (e.g. Jiménez *et al*., 1998, 2000; Lavelle & Spain, 2001 and references therein; Leon *et al*., 2003). Social insects, ants and termites, can increase their activities in the dry season, preparing alates for the first rains (Rouland *et al*., 2003). Termites in East Africa have been shown to be able to produce two broods, corresponding with the two rainy seasons (Nutting, 1969). Predatory caecilians may find that the abundance of prey fluctuates throughout the year, although if their activities are correlated with rainfall, it does not explain the findings here.

Adult caecilians have been shown to have morphological and physiological adaptations to abiotic factors (e.g. hypercarbic and hypoxic conditions) in the subterranean habitat. The blood has a low pH sensitivity (Wood *et al*., 1975), and the structure of the lung is highly compartmentalized, considerably increasing the surface area (Maina & Maloiy, 1988). However, it is not known whether their eggs are able to withstand the same environmental conditions. Most caecilians are oviparous, with a free-living larval stage or through direct development (Wilkinson & Nussbaum, 1998). In species with aquatic larvae, horizontal migration may be an obligatory aspect of breeding activity (cf. Vyas, 2003; Kupfer *et al*., 2005). *Boulengerula boulengeri* has been found brooding eggs away from water in the top 30 cm of the soil (Measey, 2004), and is presumably oviparous with direct development like other members of the genus (Nussbaum & Hinkel, 1994). The egg jelly must act as a respiratory surface, providing the growing embryo with oxygen and removing carbon dioxide. In caecilians, like plethodontid salamanders, this process is believed to be aided through parental care (e.g. Kupfer *et al*., 2004*b*; Malonza & Measey, 2005). Mothers coil around their eggs and periodically move them, facilitating gas exchange (aeration and hydration), as well as preventing fungal growth and predation (see Crump, 1995). Females with eggs or young are presumably unable to move the location of their chamber throughout the duration of guarding (see Malonza & Measey, 2005). There is a suggestion that some caecilians may have preferred breeding sites (Measey *et al*., 2003*a*), and this may explain why no brooding females were found in this study. Such sites might be characterized by well-aerated (e.g. recently disturbed), warm or well-oxygenated (e.g. through seepages) soil. If lateral movement to breeding sites were necessary, then surface soils would offer least resistance for burrowing (see above).

Higher temperatures and elevated oxygen concentrations in the upper layers of the soil, combined with higher seasonal temperatures, may provide optimal conditions for incubating eggs in this species. In this case, a combination of migration to upper layers of the soil and oviposition of eggs would be expected to coincide with the start of a period of elevated temperatures. This study suggests a peak of migration to the top 30 cm of soil in November and December, and Measey (2004) reported finding eggs in December. Another real problem within a three-dimensional complex medium such as the soil is finding a mate. Hence, a synchronized movement of all sexually active animals to the soil surface would make mate finding more two dimensional, and hence easier.

Many snakes are predators of amphibians, including Gymnophiona (Gower *et al*., 2004*b*). For example, it has been suggested that the Usambara garter snake *Elapsoides nigra* (Gunther) predates solely upon caecilians (Spawls *et al*., 2002), and Barbour & Loveridge (1928) report finding *B. boulengeri* in the stomachs of *E. nigra* (see Broadley, 1971). However, Measey (2004) suggested that invertebrate predators, such as ants, spiders and centipedes, may be more important. If these predators were more active in the surface soils (which is certainly true of snakes, ants and spiders), then spending a period deeper in the soil would mean that *B. boulengeri* would reduce predation risk for at least part of the year. That this period coincides with a reduction in overall invertebrate food availability (see above) may mean that otherwise predation risks at the surface are further elevated.

Available evidence suggests a synergistic explanation with a combination of abiotic (temperature and oxygen gradients) and biotic (mate finding and predator avoidance) factors that prompt *B. boulengeri* to migrate to the top 30 cm of soil during the warmest period of the year. At other times, adults and juveniles may be safer from the risk of predation deeper in the soil.

It has been suggested that vertical migrations occur in other caecilian taxa, but in relation to rainfall and soil moisture content rather than temperature (see above). Measey *et al*. (2005) found differences in the vertical distribution of the cogeneric *B. ulugurensis* between agricultural microhabitats. Ecological data are unknown for the vast majority of caecilian taxa, and it is not yet possible to generalize the findings in this study for different habitats (such as agriculture) or across taxonomic groupings.

The importance of understanding apparent changes in abundance of subterranean lower vertebrate species, and their causative factors, has ramifications not only for the study of their ecology but especially for workers who attempt to describe the biodiversity of preserved or threatened habitats. Previous studies have highlighted the misconceptions that all caecilians are rare (Measey, 2004), whereas others have shown that they are not the only subterranean lower vertebrate species that can be misrepresented in biodiversity assessments (Gower, Loader & Wilkinson, 2004*a*). In this study, it is shown that there are significant changes in seasonal abundance if the top 30 cm of soil is sampled, and that this may correspond with a vertical migration. Hence, biodiversity assessments that attempt sampling at inappropriate times, or even those that are conducted during the rainy season, may yield inaccurate presence/absence data. It is clear that a re-appraisal of the methods generally used to detect and study subterranean lower vertebrate species is urgently needed.

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