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Quantitative surveying of endogeic limbless vertebrates—a case study of *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India

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Abstract

Many subterranean, limbless reptiles and amphibians are predators of invertebrate soil ecosystem engineers. The potential importance of these predators in soil ecology partly rests on whether they occur in high densities, but their abundance has rarely been measured, and there are no standard methods. The mostly tropical and fossorial caecilians (Amphibia: Gymnophiona) are often considered rare, but there are very few quantitative data, and some species, including *Gegeneophis ramaswamii*, have been reported as abundant in some situations. Using simple and repeatable survey methods with randomised 1 m^2 quadrats, surveys of *G. ramaswamii* were conducted at five localities in southern India. Densities of 0–1.87 m^{-2} per survey were measured, with means of 0.51 and 0.63 m^{-2} at the beginning and middle of monsoon, respectively. These densities were far greater than for sympatric caecilians (ichthyophiids; uraeotyphlids) and fossorial snakes (typhlopids; colubrids). While ecological data remain very scant, establishing quantitative methods to assess the abundance of endogeic limbless vertebrates is an important step toward greater understanding of subterranean predator–prey relations, and of monitoring populations of these poorly known organisms.

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1. Introduction

Endogeic soil vertebrates display considerable taxonomic diversity. In addition to subterranean mammals, there are many reptilian and amphibian groups that live most of their life in soil. Adaptation to this habitat has, in most cases, resulted in the parallel evolution of elongate bodies with reduced or absent limbs. Several major lineages of squamate reptiles are predominantly elongate, limbless burrowers, including amphisbaenians, dibamids, some snakes, and several groups of 'lizards', and so are caecilian amphibians. All endogeic soil reptiles and amphibians are carnivorous, with many species preying on earthworms, termites and ants; the three invertebrate groups now widely recognised as soil ecosystem engineers (SEE, Lavelle et al., 1997). 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

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activities. However, no studies have addressed the potential impact of soil dwelling vertebrate predators of SEE.

Along with salamanders (order Caudata) and frogs (Anura), caecilians (Gymnophiona) complete the three orders of living amphibians. Current taxonomy recognises approximately 160 nominate species and six families of caecilians (Nussbaum and Wilkinson, 1989). These are distributed across the moist tropics, excluding Madagascar and Australasia. Except for one South American family of semi- and fully-aquatic species (Typhlonectidae), all caecilians are believed to be terrestrial burrowers in soil for all or a substantial part of their adult life. They are elongate and completely limbless animals with skin divided into annuli, giving many species a superficial similarity to earthworms. In association with their burrowing habit, most terrestrial species have sturdy, compact skulls, recessed mouths and reduced eyes sometimes covered by the bones of the skull roof. Although most adult terrestrial caecilians are in the range of 200–500 mm total length (TL), the known maximum adult size ranges from up to 112 mm in the Seychellean *Grandisonia brevis* (Boulenger) to 1520 mm in the South American *Caecilia thompsoni* Boulenger (Nussbaum, 1998).

Terrestrial caecilians are often considered to be rare, enigmatic components of tropical ecosystems (e.g. Gundappa et al., 1981; Duellman and Trueb, 1986; Bhatta, 1997). This view is supported by the field experience of most pedobiologists and herpetologists, and many of the caecilian species described are known from only a single or very few records (e.g. Taylor, 1968). Despite this, some publications have described some caecilian species as at least locally common or even abundant (e.g. Loveridge, 1936; Seshachar, 1942; Largen et al., 1972; Hebrard et al., 1992; Nussbaum and Pfrender, 1998; Oommen et al., 2000; Measey and Di-Bernardo, 2003). However, it appears that only three preliminary quantitative measures of caecilian density have been reported (Largen et al., 1972; Bhatta, 1997; Oommen et al., 2000). Clearly, terms such as common, rare or even, as recently claimed, declining and/or endangered (e.g. Wake, 1993; Wen, 1998; Pennisi, 2000) should be based on readily interpretable quantitative data.

The focus of this paper, *Gegeneophis ramaswamii* Taylor, is a caeciliid caecilian endemic to the southern Western Ghats of peninsular India. The biology of *G. ramaswamii* is better known than for many other species of caecilian, with published data available on aspects of morphology, reproduction, chromosomes, and distribution (e.g. Ramaswami, 1942, 1947; Seshachar, 1942, 1944; Sesachar and Ramaswami, 1943). More recently, we encountered *G. ramaswamii* in varied agricultural habitats, where it is the most frequently encountered caecilian in terms of both localities and individuals, which led us to identify this species as a potential model system for pioneering quantitative ecological studies of caecilians (Oommen et al., 2000). Advances in marking caecilians (Measey et al., 2001) have made population estimates using mark-recapture possible, and one such attempt has been made (Measey et al., submitted for publication). However, the use of a non-random sampling method in that study means that caution is needed in interpreting the population estimates (60–216 individuals at 0.31–0.48 m^{-2}). Furthermore, mark-recapture is probably not feasible for large or multiple areas, or for conducting rapid assessments at previously unexplored localities.

Given the very meagre knowledge of caecilian ecology and evidence for population decline in at least some amphibians (Houlahan et al., 2000), there is a pressing need for methods to be developed that will enable caecilian populations to be assessed and monitored. The subterranean habit of terrestrial caecilians, and the overwhelming lack of even basic quantitative ecological data, demand that appropriate techniques must be devised and tested. The development of unbiased sampling techniques that will yield estimates of the most basic characteristic of any ecological population—its size, in terms of density—will facilitate spatially, temporally, and taxonomically comparative studies. To this end, we present results of a study focussing on *G. ramaswamii* and using a survey method developed to estimate caecilian density. This could be used in a variety of studies of elongate subterranean vertebrates including long-term population monitoring, rapid quantitative biodiversity assessments, and detailed comparative ecological investigations.

2. Materials and methods

Our survey method aimed to satisfy several desiderata, including ready availability, high durability and low expense of materials, as well as ease and reasonable duration of the field work. A 10 m × 10 m survey grid was effected by a 20 m length of coloured nylon rope with a loop halfway along, and contrasting markers tied at 1 m intervals (see below). A 1 m^2 quadrat was made by marking a 4 m loop of nylon rope with four pieces of contrasting coloured string tied at 1 m intervals. For digging, we used local hoes, each being an approximately 0.3 m × 0.25 m forged metal blade set approximately perpendicular to a wooden handle. Other equipment used included: plastic bags for collecting specimens, plastic sheets (1.5 m × 1.5 m) for searching through excavated soil, waterproof marker pens for labelling, a hand-held electronic pH meter and thermometer, a ruler, a portable electronic balance for measuring specimens, a 0.1% aqueous solution of 3-aminobenzoic acid ethyl ester methanesulfonate (MS222, Sandoz) for anaesthetising specimens, tags for labelling specimens, a 10% aqueous solution of formalin for fixing, and a 70% aqueous solution of ethanol for storing material.

At each site, three different areas were chosen to be roughly representative of any obvious variations in habitat, chiefly assessed in terms of vegetation. In each area, the survey grid was laid in a random fashion, so that the rope was not obstructed by trees, but did not consist of a 'chosen' area. The 20 m rope was anchored at the central loop and at each end, so that two 10 m lengths of rope lay at 90°. The one hundred 1 m^2 quadrats formed by this 10 m × 10 m grid were given co-ordinates, and five quadrats were selected randomly, such that no column or row was replicated in the sampling. Each quadrat was marked out using the 4 m loop of rope and dug to a depth of approximately 0.3 m, as far as was possible. For each site, three 100 m^2 grids were laid out in turn, making a total excavation of 15 m^2 per survey. For those sites surveyed twice, the grids and excavated quadrats of the second survey may have covered the same ground as those in the first survey, particularly at the smaller sites. 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. A note was made of any quadrat that included obstacles such as trees, drainage ditches or boulders. All excavated soil was turned onto a plastic sheet and roughly sifted by hand. All caecilians and any other fossorial vertebrates were placed into soil in plastic bags labelled with date, site, survey grid, and quadrat co-ordinates. Excavated soil was replaced after sifting was completed. Soil type was assessed using the ball method described by Dubbin (2001).

Each caecilian caught was euthanased by lethal anaesthesia, by placing into MS222 solution. Total mass (±0.05 g) and total length (TL to the nearest mm) were recorded for each freshly euthanased individual. All animals were given unique tags and were fixed in formalin (e.g. Simmons, 1987) before thorough rinsing in water and storage in 70% ethanol in the collection of the Zoology Department of the University of Kerala. Sex was determined by examination of gonads exposed by mid-ventral incisions of the body wall.

Oneway ANOVA was used to test for significant differences in density of *G. ramaswamii* between sites and dates. ANOVA was used to test for differences in log TL and log mass between sites, while two tailed *t*-tests assuming equal variances were used to test for differences between log TL and log mass of *G. ramaswamii* per site between sampling occasions. Means ($\bar{x}$) ± standard error are presented. Chi-squared (χ^2) tests were used to test for significant deviation from a 1:1 sex ratio.

2.1. Locality and site descriptions

All sites investigated here are at localities in the southernmost part of the Western Ghats, Kerala, India. The Western Ghats are a chain of mountains that lie close and approximately parallel to the southwest coastline of peninsular India, and they are a world biodiversity hotspot (Gadgil, 1996; Myers et al., 2000). Although originally covered in forest, much of this area is now under cultivation as rubber, teak, banana, coconut, cardamom, tea, and coffee plantations, and many small holdings of mixed agriculture. The climate is monsoonal, characterised by strong seasonal variations in temperature and precipitation (Fig. 1). The year can be divided into a wet monsoon season (June–November) and a drier season (December–May).

Five agricultural localities were selected from places where *G. ramaswamii* had been recently found (Oommen et al., 2000). Selected localities had areas of relatively flat and homogenous habitat that would facilitate field trials of our proposed method.

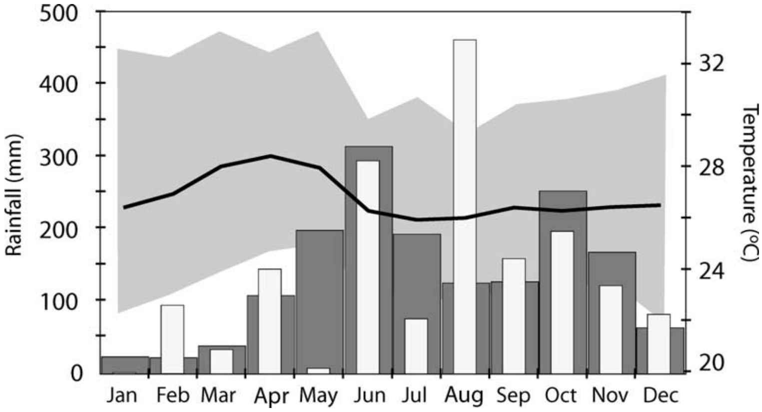

Fig. 1. Meteorological data for Thiruvananthapuram, Kerala (see Fig. 2) showing total monthly rainfall for 2000 (wide, dark bars), average monthly rainfall (narrow, light bars), maximum and minimum temperatures for 2000 (shaded area), and average monthly temperature (line).

All the localities lie within the state of Kerala and are on the western slopes or foothills of the Western Ghats (Fig. 2). Three sites (Bonaccord, Makki and Punalur) were visited early in the monsoon season, and the same three and a further two (Vanchuvam and Thekkada) were visited in mid-monsoon. Details of the sites, and the dates and times of surveys are given in Table 1.

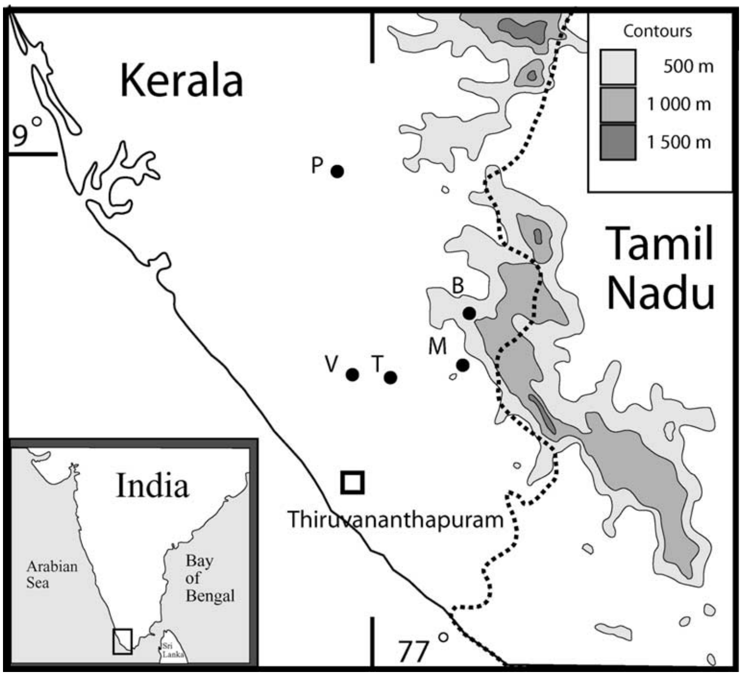

Fig. 2. Map showing the position of survey localities (black dots) in southern India close to the state capital of Kerala, Thiruvananthapuram. B: Bonaccord, M: Makki, P: near Punalur, T: Thekkada, V: Vanchuvam.

Table 1
Site descriptions for five agricultural localities in Kerala, southern India (see Fig. 2), surveyed in the 2000 monsoons

	Bonaccord	Makki	Punalur	Vanchuvam	Thekkada
Co-ordinates	08°40′N 77°10′E	08°40′N 77°10′E	08°58′N 76°57′E	08°39′N 77°01′E	08°37′N 76°57′E
Altitude (m asl)	593	238	70	80	60
Area of site (m^2)	1000	3000	1500	800	800
Habitat	Grassy clearing in plantation next to vegetable garden and tea-planted slopes	Sparse grass and taro in flat rubber plantation	Flat area with grass and taro in largely terraced rubber plantation	Mixed plantation with banana, arecanut, coconut, and taro	Flat area with sparse grass, in rubber plantation
Shade	Little shade	Near total shade	Near total shade	Almost no shade	Almost no shade
Water	Loose grid of irrigation ditches plus small stream	Grid of drainage ditches	Grid of drainage ditches	Site bordered by well canalised stream	Site bordered by well canalised stream
Soil texture	Sandy loam	Silty clay	Loam		
pH	7.9	8.0	7.6		
Soil temperature °C	21.0	23.9	24.0	26.2	24.7
Other caecilian species	None	*Ichthyophis* cf. *tricolor*	*Ichthyophis* cf. *tricolor*	*Ichthyophis* cf. *tricolor*, *Uraeotyphlus* cf. *narayani*	*Ichthyophis* cf. *tricolor*
Survey dates	27/06/00 and 25/08/00	27/06/00 and 25/08/00	03/07/00 and 17/08/00	21/08/00	21/08/00

For those sites surveyed twice, soil pH and temperature data are for the second survey date. Data on caecilian species other than *Gegeneophis ramaswamii* occurring at each locality are taken from Oommen et al. (2000).

3. Results

Overall, surveys were easy to conduct and not too time consuming, averaging 1.5 h of digging and collecting for four people. The presence of trees, roots, boulders or irrigation ditches meant that only partial excavation was possible in 6% of all quadrats, and that no digging was possible in a further 5%. No caecilians observed during the digging of quadrats went uncaptured.

A total of 72 caecilians were captured during the surveys, 71 *G. ramaswamii* (one of which was an egg) and one *Ichthyophis* cf. *tricolor*. Of these, nine of the *G. ramaswamii* (13%) were injured during collection. The single *I.* cf. *tricolor* was collected at Vanchuvam ($0.07\,m^{-2}$). *G. ramaswamii* were captured in all surveys except at Vanchuvam and Thekkada, where they were nonetheless found on the same date within 100 m of the survey sites. Apart from caecilians, the only other fossorial vertebrates found during surveys were snakes. Single individuals ($0.07\,m^{-2}$) of the endemic colubrid *Xylophis stenorhynchus* (Günther) and the more cosmopolitan typhlopid *Ramphotyphlops braminus* (Daudin) were found at Punalur (17 August) and Thekkada (25 August), respectively.

Statistical analyses were undertaken only for the *G. ramaswamii* data and excluding the single egg. The TL of *G. ramaswamii* captured in the surveys shows an approximately continuous distribution of individuals that could be sexed from 100 to 252 mm (Fig. 3). Another group of indeterminate sex (juveniles, TL 59–67 mm) were found at Makki and Punalur. The largest individual encountered was a 252 mm female caught at Makki on 27 June. *G. ramaswamii* are oviparous (Seshachar, 1942), and one female *G. ramaswamii* was found in association with a single egg at Makki on 16 June. Additionally, within the surveyed areas, clusters of juveniles were sometimes found in close association with an adult female (e.g. $n = 3$; $\bar{x}$, TL 64.7 ± 0.33 mm, $\bar{x}$, mass $= 0.27 \pm 0.03$ g, found with a female TL 228 mm, mass 5.2 g). On occasion, several similar sized juvenile *G. ramaswamii* were found in close proximity to one another without any associated adult, but within a single quadrat (e.g. $n = 8$, $\bar{x}$, TL 131.3 ± 3.25 mm, $\bar{x}$, mass $= 1.44 \pm 0.10$ g). Both of these examples were found in the same quadrat

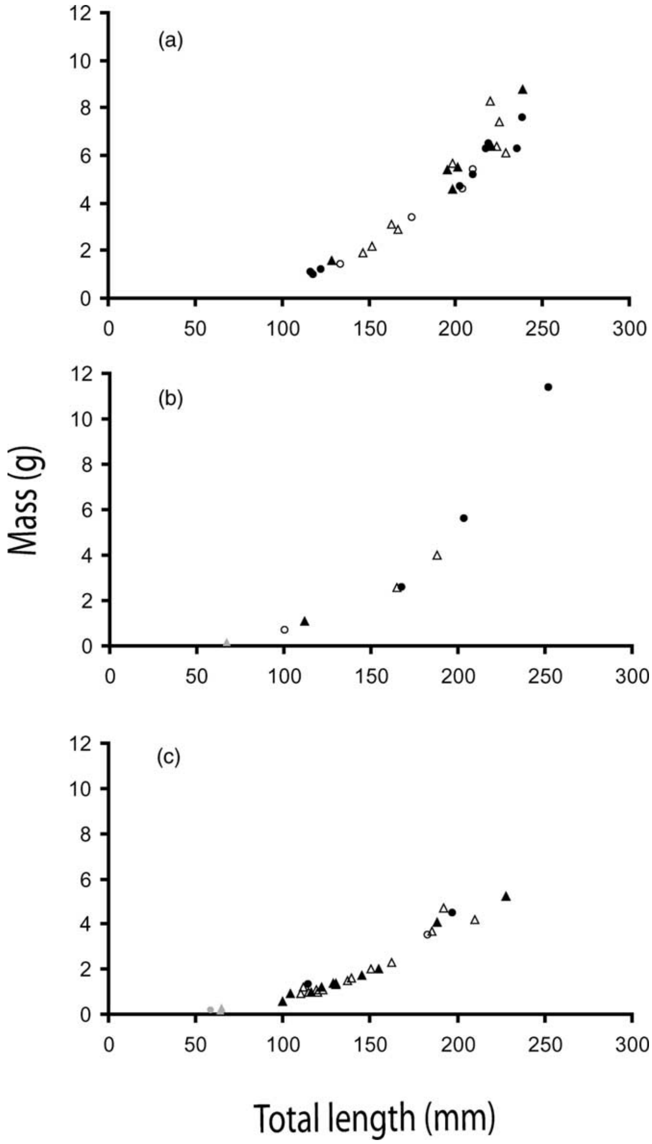

Fig. 3. The distribution of total length and mass for *Gegeneophis ramaswamii* from three sites, (a) Bonaccord, (b) Punalur and (c) Makki, in Kerala, southern India. Circles represent animals collected at the beginning of the monsoon season, and triangles those collected in the second, middle of the monsoon sampling period. Open symbols are males, closed are females, and shaded are juveniles (<100 mm).

in Punalur on 17 August. A χ^2-test on sex ratios showed no significant differences from 1:1 on all occasions and sites, and between dates ($\chi^2 > 0.05$, see Table 2).

The density and mass of *G. ramaswamii* recorded for each survey are shown in Table 2. Maximum density within any single quadrat was as high as $12\,\mathrm{m}^{-2}$ at Punalur (17 August, see earlier), while in all sites the minimum of zero was recorded for at least one quadrat. The mean density and mass of *G. ramaswamii* at all sites surveyed in late June/early July (early in the monsoon season) was $0.51\,\mathrm{m}^{-2}$ (± 0.17, $n = 45$ quadrats) and $1.97\,\mathrm{g\,m}^{-2}$ (± 0.83, $n = 43$), and in late August 2000 (the middle of the monsoon season) was

Table 2
Density and mass of *Gegeneophis ramaswamii* found in surveys at five localities in southern India

Locality	Time (date) visited	Density (g/m^2)	Mass (g)	Number of individuals				Time (date) visited	Density (g/m^2)	Mass (g)	Number of individuals			
				T	*f*	*m*	*j*				*T*	*f*	*m*	*j*
Bonaccord	12:00 h (27/6/00)	0.90	3.65	14	9	4	0	11:00 h (25/8/00)	1.00	5.09	15	5	10	0
Punalur	11:00 h (3/7/00)	0.27	0.63	4	2	1	1	10:00 h (17/8/00)	1.87	3.29	28	10	15	3
Makki	16:00 h (27/6/00)	0.33	1.93	5	3	2	0	13:00 h (25/8/00)	0.27	0.53	4	1	2	1
Thekkada								10:00 h (21/8/00)	0.0	0.0	0	0	0	0
Vanchuvam								12:00 h (21/8/00)	0.0	0.0	0	0	0	0

For each survey, five $1\,m^2$ quadrats were sampled in each of three $100\,m^2$ grids, giving a total of $15\,m^2$. Numbers of individuals are given for totals (*T*), females only (*f*), males only (*m*), and small individuals of indeterminate sex (*j*).

$0.63\,m^{-2}$ (±0.19, $n = 75$) and $1.78\,g\,m^{-2}$ (±0.48, $n = 75$).

Three sites were sampled twice, with intervening periods of 58 (Bonaccord and Makki) and 45 days (Punalur). For the first survey at these sites, there is no significant difference in log TL of *G. ramaswamii* caught at Bonaccord ($\bar{x}$, 185.08 ± 12.75), Makki ($\bar{x}$, 185.80 ± 25.05) or Punalur ($\bar{x}$, 138.50 ± 31.98; $F_{2,19} = 1.721$, $P = 0.2055$). This difference remained non-significant when the single juvenile caught at Punalur (see Fig. 3) was removed from the analysis. For the second surveys at these sites, *G. ramaswamii* caught at Bonaccord ($\bar{x}$, 193.87 ± 8.86) were significantly longer than those at Makki ($\bar{x}$, 133.00 ± 27.15) and Punalur ($\bar{x}$, 133.64 ± 7.64; $F_{2,44} = 9.564$, $P < 0.0001$). This length difference is significant even when the juveniles caught at Punalur and Makki are removed from consideration.

At both Bonaccord and Makki, the density of *G. ramaswamii* was very similar across the two surveys. At Punalur, the second survey recorded a notably higher density (Table 2). Despite the similar densities, the mass m^{-2} of *G. ramaswamii* at Bonaccord was notably higher for the second survey (Table 2). However, there are no significant differences in numbers and total mass of *G. ramaswamii* for the two surveys at any of the three sites. Differences in log TL and individual log mass of *G. ramaswamii* captured during the first and second surveys at each site are not significant for Bonaccord ($t_{26} = 2.055$, $P = 0.481$; $t_{26} = 2.055$, $P = 0.260$, TL and mass, respectively), Makki ($t_6 = 2.447$, $P = 0.318$; $t_6 = 2.447$, $P = 0.313$) or Punalur ($t_{29} = 2.045$, $P = 0.977$; $t_{29} = 2.045$, $P = 0.825$).

4. Discussion

The method described here is a stratified approach to sampling subterranean vertebrates, incorporating workable site selection procedures as well as a randomised method that reduces sampling bias and allows the application of inferential statistics. The method meets our aims of being 'low tech.' in approach, requiring little time or specialised equipment in the field, and it yields random samples of individuals that can be used for a wide range of further studies. We issue several caveats associated with interpreting the results gained from using this method. Our $1\,m^2$ quadrats appeared suitable in terms of the size of Western Ghats caecilians, amount of land disturbed and time taken to dig, although we made no tests for optimal quadrat size or shape. Concern may be raised over the disturbance and possible escape behaviour of caecilians during excavation, as well as the edge effect of animals up to 252 mm TL in $1\,m^2$ quadrats. However, we gained the impression that *G. ramaswamii* did not escape capture, in contrast to some other soil fauna such as large megascolecid earthworms, and that edge effect was not substantial. Digging with bladed hoes is not the ideal way to sample subterranean vertebrates in relation to habitat disturbance and animal injury if non-destructive sampling is desired (see also Measey et al., 2001, and above), although it will not have affected the results of this study. Possible confounding effects for this study include sampling inconsistency caused by multiple diggers, and habitat heterogeneity where it limited access to randomly selected quadrats in some grids. While these caveats relate to ways in which the resulting densities may have been influenced in a non-random fashion, we suggest that the generation of data, together with awareness of these caveats, is currently of greater benefit than a less practical but perhaps more robust method.

Although limited, the data from this field trial of the sampling method presented do provide insights into caecilian abundance, and are important in suggesting directions of future research. In this study, overall densities of *G. ramaswamii* were found to be about 0.5 m^{-2} early in the wet season and 0.6 m^{-2} in the middle of this season. The absolute value of these combined data should be interpreted with care because they do not represent mean density throughout the known range of *G. ramaswamii*. These results say nothing about densities at sites not visited, or at different times of the year for those sites surveyed. We have scant, qualitative data that *G. ramaswamii* are more difficult to find (lower densities, at least in the surface 0.3 m of soil) outside of the monsoon season. In order to obtain a fuller understanding of *G. ramaswamii* density, it would be necessary to randomly select sites from within its entire range (yet to be established), as well as making samples throughout the year. Hence, here we confine the discussion to the sites studied in relation to the method used, rather than taking a landscape view of *G. ramaswamii* density, something that must await future studies.

Densities of *G. ramaswamii* calculated for each site cover a wide range from 0 to 1.87 m^{-2}, the latter being, to the best of our knowledge, the highest density ever reported for any species of caecilian. This highest value is from a survey in which one of the quadrats, contained 11 small animals (see above, Fig. 3b and Table 2) that accounted for approximately two thirds of the individuals found in the survey at Punalur on 17 August. However, even when such dense assemblages within a single quadrat are ignored, there were high densities (about 1 m^{-2}) at Punalur and Bonaccord.

Oommen et al. (2000) dug multiple measured plots at Bonaccord and Punalur toward the end of the 1999 monsoon season (October), with average densities of *G. ramaswamii* recorded as 1.13 and 0.64 m^{-2}, respectively. These figures are very similar to those found in this study, providing support for the reality of very high densities in some places. In both studies, and at each sampling, all animals captured were permanently removed. That numbers were not substantially lower in this later study, suggests that removals of this magnitude may not have been sufficient to detrimentally affect density. This partly allays the concerns of Measey et al. (2001) that fatal injury of 8% (and here 13%) of *G. ramaswamii* during collection might have an adverse effect on populations, at least for relatively small areas. Furthermore, digging and associated mortality undoubtedly occur 'naturally' in cultivated land (Measey et al., 2001).

In contrast to those at Makki and Bonaccord, the two surveys at Punalur recorded markedly different densities. This suggests that caution should be exercised in interpreting the zero densities recorded at Vanchuvam and Thekkada, where similar fluctuations might also occur. Further investigations of the specimens preserved during this study may help explain some of the observed differences in size, particularly at Bonaccord (Table 2).

During this study, clutches accompanied by attending adults were found outside the surveyed areas at two sites: Punalur (3 July) and Bonaccord (27 June). Although breeding occurred at these times and at these sites, the occurrence of only a single egg suggests that little breeding was occurring within the survey areas at these times. Although virtually nothing is known about sex ratios in caecilians, the lack of a significant bias in the sex ratio in the surveys carried out for this study is perhaps consistent with the view that the density data are not greatly inflated by breeding aggregations. We have also studied a known breeding site where the proportion of adults (presumably females) captured in association with clutches was 22% (Measey et al., submitted for publication). This figure was not approached in any of the sites surveyed here, suggesting that they were not harbouring breeding assemblages at much higher than background densities at this time. Knowledge of caecilian biology, such as normal population sex ratios and whether breeding aggregations occur, is insufficient to allow further conclusions, emphasising the need for further quantitative study.

The density of other caecilian species and of fossorial snakes was zero or very low in all our surveys. Presswell et al. (2002) reported on a single *G. ramaswamii* feeding on one individual of the scolecophidian snake *Ramphotyphlops braminus*, and the apparent rarity of this is consistent with the relatively low density of this snake we recorded in those areas where the snake and caecilian co-occur. Although *Ichthyophis* cf. *tricolor* and *Uraeotyphlus* cf. *narayani* are known to occur at least at some of the surveyed localities (Oommen et al., 2000), the collection of only a single individual of *Ichthyophis* and no *Uraeotyphlus* suggests that these caecilians occur at much lower densities in these sampled habitats, at this time of the year, and in this part of their ranges. Whether this is generally true for these species across their ranges is unknown, but is worthy of future investigation. The survey results, especially for taxa other than *G. ramaswamii*, suggest that the method is not guaranteed to find even a single individual at localities where/when densities are low. In such cases, the method could be modified for less abundant species by increasing the number of quadrats dug per grid, or augmented with time limited searches.

Non-caecilian, non-fossorial amphibians can occur in very dense assemblages, sometimes associated with breeding (e.g. Gittins et al., 1980; Elmberg, 1990; Miaud et al., 1999), but also as the most numerous vertebrate in some habitats (e.g. Burton and Likens, 1975). Some frogs and salamanders occasionally burrow in soil. The North American salamander *Plethodon cinereus* Green is a surface-cryptic, terrestrial amphibian that burrows in litter and soil and is considered to occur in very high densities (e.g. 0.21 m^{-2}, Klein, 1960). A density estimate of 0.26 m^{-2} made *P. cinereus* the most abundant vertebrate in one forest habitat sampled (Burton and Likens, 1975). Pooley et al. (1973) reported ranges of densities of the fossorial frog *Hemisus marmoratus* (Peters) of 0–0.1 m^{-2} in censuses of non-randomly selected areas (total of 438 m^2 in areas of 1.67–414.66 m^2) within different habitats in South Africa. There have been very few studies of the density of fossorial squamates, but in the same study in South Africa, Pooley et al. (1973) found, using non-random digging, three species of scincid lizards, one amphisbaenian “worm lizard”, and two atractaspidid snakes. The most abundant of these were found in densities of 0–0.42 m^{-2} (the scincid *Scelotes bidigittatus* Fitzsimons) and 0–0.9 m^{-2} (the amphisbaenian *Zygaspis violacea* (Peters)) in the various censuses. That fossorial squamates can occur in high densities is also demonstrated by Burger’s (1993) report of 154 specimens of the fossorial scolecophidian snake *Leptotyphlops nigricans* (Schlegel) at a density of 0.62 m^{-2} in South Africa, and Papenfuss’ (1982) report of thousands of amphisbaenians collected by digging at localities in Mexico over several years. Relative to birds and mammals, reptiles and amphibians “have low rates of energy flow and high efficiencies of biomass conversion” (Pough, 1983, p. 142) and thus ecosystems can support them in greater abundances.

Oommen et al. (2000, p. 1388) reported that *Gegeneophis ramaswamii* “was highly abundant at some sites”, but conclusions concerning its absence from other localities were difficult to draw. If these and other ‘common’ caecilians exist throughout their range at the high levels of density reported here, it would probably make them a more recognised and relatively frequently encountered component of the tropical soil fauna than they appear to be. Given that this is not the case, it seems sensible to work with the hypothesis that caecilians have a patchy distribution, as Largen et al. (1972) concluded for the Ethiopian caeciliid *Sylvacaecilia grandisonae* (Taylor). Patchy distributions are known for representatives of the other orders of amphibians (e.g. Marsh and Trenham, 2001), and for other soil organisms (e.g. Ettema and Wardle, 2002).

Considering the entire range of *G. ramaswamii*, this study has only sampled in localities of known occurrence. In order to assess spatial characteristics of the species across its range, further work is necessary. For analyses of patchiness, both within and among sites, the powerful methods of Perry et al. (1999) may be employed, but these require precise determination of the relative position of grids. This was not undertaken for this study, but simple modifications of our method have the potential to successfully quantify general population parameters as well as to tackle specific questions, such as how large and for how long any possible patches occur? Spatially explicit approaches will help to understand the natural history of caecilians and how best to monitor their populations, and also the ecology of the communities they live in.

5. Conclusions

The method proposed and investigated here would seem to be appropriate for the rapid assessment of densities of relatively abundant soil-dwelling caecilians. It has confirmed that *G. ramaswamii* can occur at very high densities in some habitats in southern India, raising important questions about its impact on soil ecosystems (Oommen et al., 2000). Simple modifications could enhance the utility of the method for surveying less common caecilians and other subterranean lower vertebrates.

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