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A mark–recapture study of the caecilian amphibian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India

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Abstract

The potentially important ecology of subterranean predators of soil ecosystem engineers is poorly understood. This is especially true of caecilian amphibians (Gymnophiona) for which there are virtually no quantitative data. Results of the first field trials of permanent marking in caecilians are presented. A preliminary assessment is made of the efficacy of mark–recapture studies for estimating population size of *Gegeneophis ramaswamii* Taylor in 100 m^2 of low intensity agriculture in Kerala, India. Over three sampling occasions spanning 58 days of the monsoon season, 114 individuals were captured, 104 marked and released, and 21 recaptured. Models estimate an open population of 60 individuals (95% confidence interval of 45.2 to 151.3), and a closed population of 236 (95% confidence interval of 174 to 351). A census interpretation of the raw capture data gives densities of about 0.31 to 0.48 m^{-2}. Results suggest large movement in and out of the sampled area during the study. Despite caveats associated with these data, progress is made in identifying potential limitations and improvements in the methods used. This study highlights the paucity of knowledge of caecilian ecology, and the need for long-term studies to elucidate further ecological information and to monitor populations.

Key words: population, monitoring, soil, ecology, census, vertebrates, *Gegeneophis ramaswamii*

INTRODUCTION

Emphasis has often been placed on the importance of soil in terrestrial ecosystems and contrasted with our relative ignorance of those organisms that inhabit this environment, recently dubbed 'ecology's subterranean blind spot' (Copley, 2000). This lack of understanding is particularly true for soil vertebrates, with studies largely restricted to mammals that inhabit permanent or semi-permanent burrow systems and that can be relatively easily monitored (see Lacey, Patton & Cameron, 2000). 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 because they greatly influence the physical structure and distribution of organic matter in the soil (Lavelle *et al*., 1997). However, the ecology and potential importance of their natural predators has been largely overlooked.

Most caecilian amphibians (order Gymnophiona) are soil-dwelling predators of the wet tropics. Little is known of the ecology of any caecilian species, and there are virtually no quantitative data. The sketchy information on diet indicates that soil ecosystem engineers are among the prey of at least some species (see review by O'Reilly, 2000). *Gegeneophis ramaswamii* Taylor is a direct-developing, oviparous caecilian from southern India (Seshachar, 1942). Oommen *et al*. (2000) found this species to be abundant in a variety of agricultural environments and suggested that this made it a potentially useful model system for investigating caecilian ecology. Measey *et al*. (2001) demonstrated the potential of several methods for permanently marking *G. ramaswamii* in a laboratory study, and emphasized the need for field trials of these techniques. In this paper, one such field trial is reported in the context of a mark–recapture study of *G. ramaswamii* in Kerala, southern India, the first for any species of caecilian.

The main aim of this study was to carry out field trials of marking, and to assess the feasibility of recapturing marked caecilians. A preliminary assessment was also made of the potential of mark–recapture techniques to estimate for caecilians the most basic quantitative characteristic of any population, its size. Several previous studies have reported numbers of caecilians collected (e.g. Loveridge, 1936; Péfaur *et al*., 1987; Hebrard, Maloiy & Alliangana, 1992), and five have related such

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numbers to quantified areas of sampled habitat (Smith, 1916; Largen, Morris & Yalden, 1972; Bhatta, 1997; Oommen *et al*., 2000; Measey & Di-Bernardo, 2003). No previous studies, however, have attempted to establish population parameters for any caecilian species using methods that would facilitate comparative studies and long-term population monitoring.

MATERIALS AND METHODS

The study was conducted at Cheranikara, (08°39′N, 76°58′E, 180 m a.s.l.) a known caecilian locality (Oommen *et al*., 2000) in the south-western foothills of the Western Ghats, Thiruvananthapuram District, Kerala, India. The climate here is strongly seasonal (see Measey, 2003) and the year can be divided roughly into monsoon (June–November) and dry seasons (December–May). The small study site is in an area of low-intensity, mixed agriculture and housing (4 houses are within 50 m of the site). The major crop is rubber *Hevea brasiliensis* (A. Juss.) Müll.-Arg., with coconut *Cocos nucifera* L., banana *Musa* sp., areca nut *Areca catechu* L., coffee *Coffea arabica* L. and *C. canephora* Pierre ex A. Froehner, and pepper *Piper nigrum* L. also grown. The area is hilly (typical slopes 1:4) with extensive terracing supported by dry stone walls.

The site (Fig. 1; an area of *c*. 100 m^2) is delimited by an access track above, and walls at the sides and bottom. Shade was estimated by eye to be 75%. A spring-fed pool lies immediately above the access track, and is reported to be permanent by residents who use it daily for washing. Water from this pool feeds subterranean seepages, occasionally rising as shallow streams, that course through the site, at least in the monsoon season. Close to the study site are outcrops of high-grade metamorphic garnet–kspar–pyroxene granulite. Outcrops immediately above the site (around the pool) consist of iron-rich (ferruginous) sandstones containing haematite and goethite. Clasts of this same rock were found within the locality, both in the terrace walls and occasional isolated examples littered on the surface and within the soil. Soil temperature and pH at the site ranged on the sampling occasions from 22.8 to 23.6 °C and from 7.62 to 7.82, respectively. Soil texture, assessed by the ball technique (Dubbin, 2001), was sandy clay. Decaying leaf litter was present throughout much of the site, and had been placed around the bases of the larger trees.

The study site was visited 3 times over a 58-day period: 30 June, 12 and 27 August 2000. On each occasion the soil was turned manually with bladed hoes as deep as was practicable (from 0.05 to 0.4 m depending on the heterogeneous substrate). Large obstacles such as tree roots and boulders were not disturbed. Thus, the total surface area and volume of soil dug was <100 m^2 and 40 m^3, respectively. The *G. ramaswamii* encountered were either isolated individuals or clutches of eggs and/or hatchlings associated with a single adult. All clutches and any individuals injured during collection were killed (by anaesthesia), fixed, and accessioned into the collection of the Department of Zoology, University of Kerala. All other individuals were marked and released as described below. The presence of clutches of eggs and/or hatchlings of *G. ramaswamii* indicated that the area was used as a breeding site during the sampling period. *Gegeneophis ramaswamii* attend their egg clutches, as is apparently true for all oviparous caecilians, and it is presumed that this parental care is essential for their successful development. In this study, clutches were removed because as nest sites were disturbed, it was possible that replaced clutches would not survive. Furthermore, little is known of caecilian ontogeny so the preserved clutches provide valuable material for developmental studies (e.g. Wilkinson *et al*., 2002).

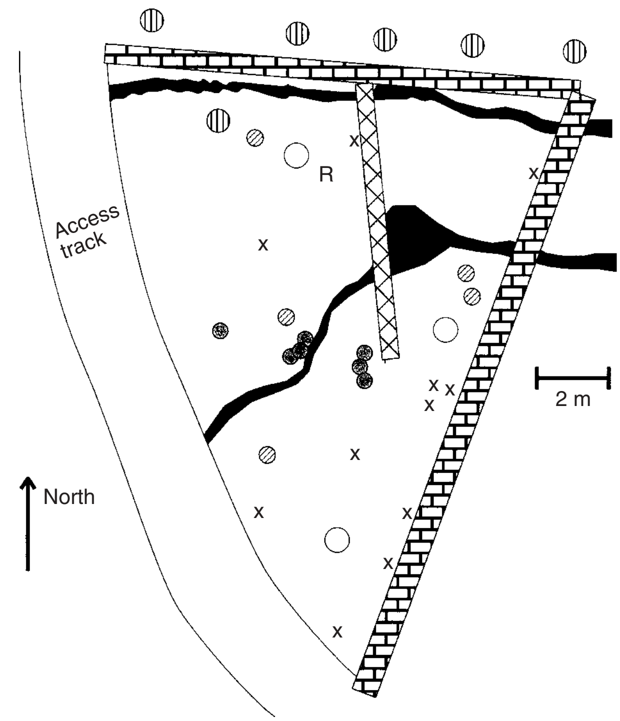

Fig. 1. Plan of field site, indicating position of: dry stone walls (brick), terrace step (cross-hatch), coffee (x), coconut (open circles), areca nut (horizontal line filled circles), rubber (vertical line filled circles), banana trees (shaded circles), seepages (shaded), release point (R) of marked *Gegeneophis ramaswamii.* Site slopes west to east, with base of terrace step and base of easternmost wall 1.3 m and 3.1 below access track, respectively.

On each visit, *G. ramaswamii* were batch marked with a Panjet needleless tattoo gun (Wright Health Group Ltd, Dundee), loaded with a 2% solution of alcian blue (Measey *et al*., 2001). On the second and third visits, animals were anaesthetized by immersion in 0.1% aqueous MS222 (Sandoz) and total length measured to the nearest mm. On the second visit, a subsample ($n = 15$) of *G. ramaswamii* were also marked with VIAlpha tags (Northwest Marine Technology, Salisbury) injected subcutaneously (Measey *et al*., 2001). On the second and third visits, animals were inspected for Panjet marks, and on the third visit, animals with Panjet marks were examined for VIAlpha tags. VIAlpha tags were independently read by 3 observers to check for possible ambiguity. Additional Panjet marks were given to all recaptured animals. After recovery from anaesthesia, all animals were simultaneously released into a single shallow excavation towards the middle of the site (Fig. 1), from which they burrowed into the soil. The excavation was then filled with soil and the release point was covered with leaf litter. The distance from the point of release of subsequently recaptured marked animals was recorded with a tape measure.

Mark–recapture data were analysed using the triple catch method (a modification of the Jolly–Seber method, see Begon (1979), with 95% confidence limits obtained using equations given by Manly, 1984), and the CAPTURE program (V 05/95; Otis *et al.*, 1978) with best fit model option selected, and any animals not released in the first or second sampling removed from analysis. Each method was used under assumptions that the measured populations were either open or closed respectively. Means ($\bar{x}$) are presented ± SE.

RESULTS

Sampling, marking, and release took about 7 person h on the first occasion and 18 person h on the second and third occasions, with animals being examined for marks and anaesthetized for the application of VIAlpha tags on the latter two occasions. In total, 104 *Gegeneophis ramaswamii* were collected, marked and released at the site. An additional 10 animals were injured, and were killed and fixed, along with 25 clutches of eggs and/or hatchlings. The size range of *G. ramaswamii* found was not significantly different between those captured once (90–270 mm, $\bar{x} = 173.2 \pm 5.7$) and those recaptured (103–265 mm, $\bar{x} = 192.8 \pm 11.42$; one-way ANOVA on log length data $F_{1,90} = 1.935$, $P = 0.168$). Panjet marks and VIAlpha tags were easily recognized on each of the 21 recaptured individuals. Table 1 shows that similar numbers of *G. ramaswamii* captured, released and recaptured on each visit, and population parameters were estimated from these data.

Using the triple-catch method, the estimated open population of *G. ramaswamii* (excluding eggs and hatchlings) on the second sampling occasion was 60 (± 18.4) with a 95% confidence interval of 45.2 to 151.3. The estimated survival rate (i.e. proportion of the population that was not lost) between first and second sampling occasions was 0.3 (± 0.5); and their estimated gain rate (i.e. proportion of dilution from animals not previously present) between second and third visits was 0.7. If survival and gain are presumed to be constant, the population size is calculated as 60 and 59 on the first and third visits, respectively. Using the CAPTURE program, the best fit model was with constant capture probabilities, with estimated probability of capture of 0.17 and a closed population estimate of 236 with a 95% confidence interval of 174 to 351.

Marked animals were found up to 4.5 m away from the point of release ($\bar{x} = 1.68 \pm 0.296$). Two Panjet-marked animals were found guarding eggs upon recapture. The injection wound on the single VIAlpha tagged animal that was recaptured had fully healed, and the tag was read without ambiguity. At the second sampling, this animal was 223 mm and 4.9 g, and then 229 mm 4.7 g at the third sampling.

Table 1. Numbers of marked and unmarked *Gegeneophis ramaswamii* captured (excluding clutches of eggs and/or hatchlings) on three sampling occasions at the study site in 2000

	30 June	12 August	27 August
Day	1	43	58
Captured	31	45	48
Day 1, marked		6	1
Day 43, marked			14
Released	30	43	41

DISCUSSION

Concern for amphibians has prompted increased quantitative monitoring of anurans and urodeles, providing evidence that some populations are in decline (e.g. Houlahan *et al.*, 2000). In stark and alarming contrast, no quantitative monitoring of any caecilians has been carried out, so that it is not possible to evaluate claims that some species are rare or declining (e.g. Gundappa *et al.*, 1981; Wake, 1993; Wen, 1998; Pennisi, 2000). Several factors potentially complicate the use of mark–recapture methods, but long-term monitoring of individually marked caecilians would greatly increase understanding of their ecology, and may help to determine properly their conservation status.

This study demonstrates the applicability of the two marking techniques recommended by Measey *et al.* (2001). As in the laboratory (Measey *et al.*, 2001), applying VIAlpha tags took much longer than Panjet tattoos. No special difficulties were encountered in applying, recognizing or reading marks in this first field trial. Recaptured animals showed no deleterious effects caused by marking, and the recapture of two Panjet-marked animals in attendance of egg clutches suggests that this technique does not interfere with normal activity. The insertion point of VIAlpha tags heals rapidly, within 15 days in the field. The small change in length of the recaptured VIAlpha marked animal might be explained by measurement error (Measey, 2003). Recapture of caecilians has never previously been attempted. This study confirms its feasibility and thus the potential for marking methods to generate data on basic demographic and life-history parameters.

Available ecological data for caecilians lack baseline information on their three-dimensional distribution in the soil, movement and home range, making experimental design and assessment of assumption violations difficult. Pitfall traps can occasionally catch caecilians (pers. obs.), but are unlikely to be effective for sampling an apparently dedicated subterranean burrower such as *G. ramaswamii*.

Of the assumptions made for mark–recapture estimates of population size (e.g. Begon, 1979), it seems unlikely that permanence and recognition of marks were violated. Equal catchability, the Achilles' heel of mark–recapture studies (Krebs, 1999), would have been violated if caecilians were non-randomly distributed through the soil profile, including in relation to undisturbed obstacles. The size range of animals caught (and recaptured) indicates no obvious bias in this aspect of sampling. The absence of any effect of marking and release on recapture might have been violated if site disturbance impacts on migration in and out of the area. Breeding sites dominate population studies of non-caecilian amphibians (e.g. Gittins, Parker & Slater, 1980; Elmberg, 1990; Miaud, Guyétant & Elmberg, 1999). However, caecilians are unusual among amphibians in practising internal fertilization via copulation (e.g. Taylor, 1968). How this might affect demographics at an egg-laying site is thus far completely unknown, but it is conceivable that copulation and oviposition are temporally and spatially decoupled. Selection of a breeding site might lead to assumption violations. For example, brooding *G. ramaswamii* may be inclined to leave the site after being released without their clutches, and caecilian populations at breeding sites might not accurately represent their populations as a whole. Assumptions of mark–recapture studies are often violated to some degree and ecologists have to be pragmatic in working with imperfect conditions (e.g. Begon, 1979). For *G. ramaswamii*, future work should assess potential assumption violations more rigorously, but the prime aim of the following discussion of our preliminary results is to assess the efficacy of mark–recapture techniques rather than draw firm conclusions about the size of the study population.

Sampling caecilians by digging constitutes a census of the dug soil. Thus the raw capture data presented in Table 1 could be translated into precise densities had the dimensions of the soil dug been measured, which would have been easier at a less heterogeneous site. Given that its surface area was $<100\ m^2$ (see Methods), population densities were $> 0.31\ m^{-2}$, $0.43\ m^{-2}$, and $0.48\ m^{-2}$ on the three sampling occasions.

Ignoring eggs and hatchlings, the three sampling occasions found similar numbers of animals, but the raw recapture data demonstrate that turnover was high. For example, between the first and second samplings, 24 marked animals moved out of the area sampled and 39 unmarked animals moved in. Given the relatively short study duration, and the removal of clutches, loss and gain are best explained largely by immigration and emigration rather than birth and death. These migrations can probably be best explained by (1) animals moving a short distance in/out of the soil sampled from/to the immediately adjacent areas not dug, and/or (2) animals migrating greater distances and/or for a longer time. These are testable with future work, but the second hypothesis is more plausible considering that recaptures of animals marked at the first sampling occasion fell to one animal by the third occasion. These interpretations must be with the caveat that clutch removal might have increased the probability of attending adults leaving the site.

The open population triple-catch estimate of about 60 individuals is less than twice as many as were captured on each occasion. It corresponds to a density of about $0.6\ m^{-2}$ for this arbitrarily bound open population. The accuracy of this value is subject to the caveats and confidence limits outlined above, and other variables not considered (e.g. size of the boundary strip). The triple-catch results also indicate high loss and gain of individuals over the study duration.

Although there was clear loss and gain during the study, the strict operational division between open and closed models is often overly restrictive, and a consideration of timescales is important (Pollock *et al*., 1990). Thus we interpret the closed population model estimate of 236 to be an indication of the number of animals associated with the site over the relatively short study period. This closed population occupies some unknown area so that this estimate cannot be converted into a density. The accuracy of the closed population estimate might be affected by assumption violation through the permanent removal of 10 individuals.

The estimates from the open model and the censuses are not dissimilar. Thus, despite the caveats associated with the former, it might be concluded that the sampling for the mark–recapture estimate was not too inappropriate. All the estimated densities seem high for a subterranean vertebrate predator. At three other localities, Oommen *et al*. (2000) reported densities of *G. ramaswamii* of 0.64 and $1.13\ m^{-2}$, and Measey, Silva & Di-Bernardo (2003) densities of $0–1.87\ m^{-2}$ (means $0.51–0.63\ m^{-2}$). The present study confirms that *G. ramaswamii* occurs at high densities in at least some places at some times, and thus its candidacy as a potentially significant predator of soil ecosystem engineers.

Future mark–recapture estimations of population size in terrestrial caecilians would benefit from random sampling and more background information on natural history. Data are required for perhaps 10+ years to estimate the size of a real biological population without undue influence of stochastic factors (Marsh, 2001). Future studies should ascertain whether mark–recapture is a workable method for measuring population size, or whether its greatest value will instead be in revealing sorely needed individual life-history data. For density estimates, the randomised survey method presented by Measey (2003) is probably more efficient than mark–recapture techniques, especially for larger areas. This study emphasizes some special considerations in investigating the ecology of terrestrial caecilians and perhaps other similarly endogeic soil vertebrates. Field ecology is usually intrusive to some degree, with disturbance of abiotic and biotic ecosystem components often unavoidable. Neither short- nor long-term effects of the digging required to find caecilians effectively are known, nor how these differ from the 'normal' changes that agricultural ecosystems may undergo. Digging might be expected to have a greater impact than in studies of more readily accessible organisms. Providing a platform on which to build quantitative caecilian ecology justifies what, we hope, will be seen in the future as a 'heavy handed' approach.

This study demonstrates that caecilian mark–recapture is feasible and identifies some important limitations and areas needing future work. Most importantly, mark–recapture studies and censuses are recognized as only two ways in which population parameters can be measured and monitored, and each has associated problems. Further work needs to be carried out to assess the efficacy of alternative methods for estimating population parameters in terrestrial caecilians.

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