

Life history of an African caecilian: *Boulengerula taitanus* Loveridge 1935 (Amphibia Gymnophiona Caeciliidae)

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The life histories of amphibians are considered to be well recorded and are frequently regarded as the model complex life history for vertebrates. However, only the most basic information exists for caecilians. *Boulengerula taitanus* Loveridge 1935 is a direct developing terrestrial caecilian commonly found in agricultural settings of the Taita Hills, Kenya. During 12 monthly visits we collected 239 caecilians by digging into soil. Caecilians were captured on every visit, although increased searching time and low capture numbers coincided when soils were dry. The condition index (ML^{-3}) defines three ontogenetic stages, for which growth can be approximately followed over the sampling period through frequency histograms. Juveniles (< 140 mm) appear to become subadults (< 240 mm) around a year after hatching, while subadults mature into adults (> 240 mm) after a further year. Adult males are significantly longer than females. Mating occurs in the soil prior to egg laying at the beginning of the short rains. Females construct a chamber before laying eggs ($\bar{x} = 5$), and are found attending eggs during incubation and after hatching. Juveniles make up the smallest proportion of the population (maximum 24% in April and May). Information produced during this study is used to develop a tentative life-table for this species.

KEY WORDS: *Afrocaecilia taitana*, *Boulengerula taitanus*, caecilians, East Africa, Eastern Arc Mountains, ecology, life-table, parental care.

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INTRODUCTION

Amphibians have persistently drawn the attention of natural historians (e.g. DARWIN 1909-1914), perhaps due to their complex life histories and often large breeding congregations, especially in temperate regions. In the tropics, the natural history of very few of the many more species is recorded, and this is especially true of East Africa (HOWELL 2000). Although some tropical anuran species may have similar life history strategies to their holarctic counterparts, there exists another group of amphibians about which very little is known: the caecilians (Amphibia Gymnophiona). Along with salamanders (Caudata) and frogs (Anura), caecilians complete the three orders of living amphibians. Current taxonomy recognises approximately 160 nominate species in six families of caecilians (NUSSBAUM & 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.

Terrestrial caecilians are often considered to be rare, enigmatic components of tropical ecosystems (e.g. GUNDAPPA et al. 1981, DUELLMAN & TRUEB 1986, BHATTA 1997). This view is supported by the field experience of most 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, NUSSBAUM & PFRENDER 1998, OOMMEN et al. 2000, MEASEY & DI-BERNARDO 2003, MEASEY et al. 2003b). A recent review of the conservation biology of caecilians highlighted the lack of even basic information about most species, and the urgent need for ecological information from field studies (GOWER & WILKINSON 2005). The complete absence of regular year round collections, especially during tropical dry seasons, when caecilians are purportedly more difficult to find (MEASEY et al. 2003a), has also made caecilian life history information speculative at best.

Life history information exists for very few species of caecilians. WAKE (1980) first reported reproduction, growth and population structure for a common, Central American, terrestrial, viviparous, caeciliid caecilian: *Dermophis mexicanus* (Duméril & Bibron 1841). Subsequently, EXBRAYAT (2000 and references therein) reported on seasonal collections of a South American, aquatic, viviparous, typhlonectid caecilian: *Typhlonectes compressicaudus* (Duméril & Bibron 1841). Most recently, KUPFER et al. (2004b, 2005) made collections over 2 years to give detailed information on the life history of an Asian, terrestrial, oviparous, ichthyophilid caecilian: *Ichthyophis* cf. *kohtaoensis* Taylor 1960. Another species which has been reported to be relatively common is *Boulengerula taitanus* Loveridge 1935 (e.g. GLASER 1985). That *B. taitanus* is relatively easy to collect makes it possible to obtain valuable life history

information. Thus, this species could be used as a model for studies on terrestrial, direct developing, oviparous, caeciliid caecilians.

This study relates to 12 monthly collections over 1 year of *Boulengerula taitanus*, a Taita Hills endemic (NUSSBAUM & HINKEL 1994), is a dedicated subterranean burrower. Although presumably native to naturally occurring evergreen moist forest, it is also widespread in agricultural areas (GLASER 1985). Collected data and observations relate to areas of occurrence, microhabitat occupancy, size range, ontogenetic classification and sex ratio. We give particular attention to the ease or difficulty of finding specimens, using the semi-quantitative index of MEASEY (2004). MEASEY & GOWER (2005), proposed that condition (calculated from measurements of mass M and length L in the scaling ratio ML^{-3}) could be used to define ontogenetic groups in ecological studies. We examine the condition index of *B. taitanus* from four collections in order to ascertain its appropriateness for this species. Lastly, we use results from this study and other accounts to propose a tentative life-table for *B. taitanus*.

MATERIALS AND METHODS

Study site

The Taita Hills represent the northernmost range of forested ancient crystalline mountains in the Eastern Arc Mountains (LOVETT 1993). Although originally covered in forest, much of this area is now under cultivation, mostly as small scale low intensity agricultural units (NEWMARK 1998, WILDER et al. 1998). 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, with an annual rainfall above 1300 mm (Fig. 1).

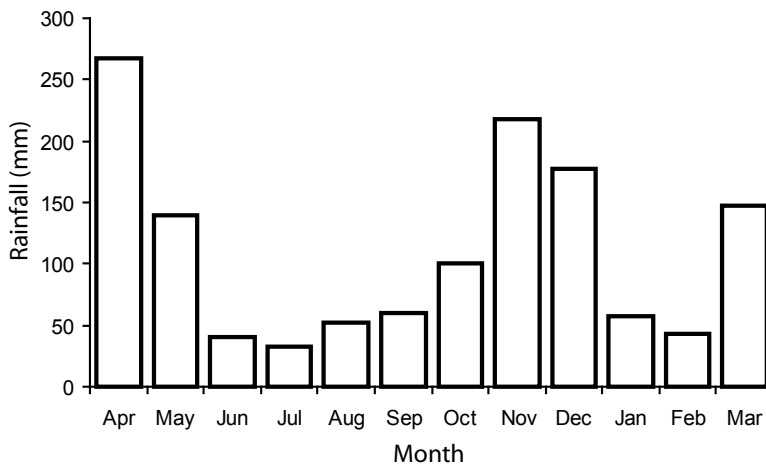


Fig. 1. — Rainfall histogram for monthly precipitation in Wundanyi, Taita Hills, Kenya. Total annual rainfall was 1331 mm. Data taken from VOGT & WIESENHÜTTER (2001).

We visited the town of Wundanyi (03°24'S 38°22'E, 1450 m a.s.l.) each month for 1 year to make regular samples of *Boulengerula taitanus*. The town is surrounded by small agricultural holdings, known locally as "shambas". Typically, these comprised mixed crops, including bananas (*Musa paradisiacal* L.), avocado (*Persea americana* Mill.), guava (*Psidium guajava* L.) sugar cane (*Saccharum officinarum* L.), yam (*Dioscorea* sp.), maize (*Zea mays* L.), and mango (*Mangifera indica* L.). Typical soil texture was a clay loam (sensu DUBBIN 2001) with a pH of 6.75. Soil penetrometer readings were taken at Kiwinda and Wurundu, the average reading being 2.6 kg cm⁻².

Field work

For the monthly samples, we dug at known shambas (where the proprietors were happy for us to turn their soil), aiming for a sample of around 20 animals (not including eggs or juveniles with adults). This sampling method was semi-quantified by recording both the amount of time taken digging and the number of active diggers, together with an approximation of the area searched (see MEASEY 2004). If the target of 20 animals was not reached at one shamba, we then travelled to another, and so on until a maximum of 48 hr had passed.

Within the shambas, the soil was turned manually with bladed hoes, known locally as "jembes". These consisted of a forged metal blade (around 0.3 × 0.2 m) set approximately perpendicular to a wooden handle. Jembes were used to excavate soil as deep as was practicable. Large obstacles such as tree roots and boulders were not disturbed. Particular attention was paid to the borders of water bodies (where available), the bases of banana plants, sugar cane, avocado trees and other plants with piles of decomposing organic material at their bases, terraces, fallen and decaying logs, alongside boulders, and in close proximity to any animal captured.

Animals were euthanased within 4 hr of capture (using the anaesthetic MS222), and measured (to the nearest mm) using a fixed ruler. Mass was measured with an electronic balance (to the nearest 0.1 g; CM 320-1, Kern, Germany) for four samples of freshly euthanased animals (9 April, 11 June, 17 November, and 2 December). Only samples from these dates were used for the condition index analysis. Each specimen was fixed (with 10% formalin from a ca 40% stock solution), washed in water, and then stored in 70% alcohol. Specimens are to be deposited in the collection of The National Museums of Kenya, Nairobi.

Sex was determined by examination of the gonads exposed by mid-ventral incisions of the body wall. Juveniles were defined as small animals that could not be sexed on the basis of inspection of the gonads (see MEASEY & GOWER 2005). The difference between adults and sub-adults was approximated through assessment of the condition index.

Data analyses

STATISTICA (v 5.5A, StatSoft, France) was used for the statistical analyses. Arithmetic means (\bar{x}) are given \pm standard error. One-way analysis of variance (ANOVA $F_{df} = F$ -test; P) and one tailed t-tests ($t_{df} = t$ -stat; P) were used to find differences in total length (on ln normalised data) of animals from different sites and between sexes of adults, respectively. Linear regression (R^2) was used to investigate the difference in condition index between different ontogenetic groups. Chi-square tests (χ^2 ; P) were used to test for bias between ontogenetic groups and sex in monthly samples. Size-frequency histograms were arranged following WAKE (1980) and EXBRAYAT (2000). The collections for 2 months were combined to give a bigger sample size, and the progression in ontogeny of size classes was approximated by eye.

RESULTS

Caecilians were caught in every month from April 2003 to March 2004 with an average of 19.9 (\pm 2.64; maximum 34, minimum 3) *Boulengerula taitanus* from

shambas around Wundanyi, Taita Hills, Kenya (Table 1). Mean time between samples was 32 (± 2.2 ; maximum 44, minimum 15) days. Caecilians appeared to be most easily caught after heavy rains in the vicinity of the collection site (see Table 1), and the index of abundance suggests that animals are easily caught during most of the year: seven out of 12 months. Indeed, only a quarter of the collections fell well short of the desired 20 individuals (May, July and October; Table 1).

Condition index (ML^{-3})

Juveniles (< 140 mm) have the highest condition index, significantly greater than all other groups ($F_{4,81} = 28.355$; $P < 0.0001$; Table 2). In Fig. 2, demonstrating the relationship between total length cubed (L^3) and mass (M), juveniles stand out as the most uniform group. The next group has very little variation in their condition index, and are classified as subadults. Subadults have a consistent relationship between L^3 and M ($R^2 = 0.868$, $P < 0.001$), while for adults this relationship is significant but slightly more variable ($R^2 = 0.843$, $P < 0.001$; Fig. 2). The cut off between this group and the next falls at around 240 mm TL (Fig. 2). Lastly, the adults are divided into females, which have the largest variation in condition index ($\bar{x} = 2.64 \pm 0.080$ g mm $^{-3} \times 10^{-7}$), and males ($\bar{x} = 2.72 \pm 0.053$ g mm $^{-3} \times 10^{-7}$).

Hence, three operational ontogenetic groups were defined through analysis of the condition index data: (1) juveniles, from hatching to around 140 mm; (2) subadults, from around 140 mm to 240 mm; and (3) adults, from 240 mm. The largest individual was a male of 348 mm, while the largest female was 333 mm. Overall, males were found to be significantly longer ($\bar{x} = 252.2 \pm 4.01$ mm) than females ($\bar{x} = 241.8 \pm 3.79$ mm; ${}^1t_{216} = 1.77$; $P = 0.037$; Fig 2, Table 1).

Cohort chart

The consecutive monthly collections allow the charting of a single cohort (sensu WAKE 1980, EXBRAYAT 2000). The smallest juveniles were found with females in January, and this cohort is still evident in the February and March samples, although with greatly reduced numbers (Fig. 3). April and May has the largest number of non-adults, and the ratio of adults remains high from June to November (Fig. 3; Table 1). By taking the ontogenetic definition from the condition index (see above), it appears possible to chart a cohort of subadults. Those present in the first sample grow and appear to contribute to the adult population by the December sampling.

A combination of results from the analyses of condition index and the cohort chart are used, together with field observations, to make a tentative life-table for *Boulengerula taitanus*, presented in Appendix 1.

Sample bias

None of the monthly samples has a significant sex bias ($\chi^2 = 1.92$; $P = 0.999$; Table 1), the most different was the month of August (20 females and 10 males). The monthly proportion of subadults to adults (excluding juveniles) shows no significant difference throughout the year ($\chi^2 = 6.68$; $P = 0.8311$; Fig. 3), the mean

Table 1. Captures of *Boulengerula taitanus* from shambas around the town of Wundanyi in the Taita Hills, Kenya.

Dates visited	Rain notes	Sites visited	Location of animals	Digging time (hr)	Approximate area searched (m ²)	Index of abundance (animals h ⁻¹ m ⁻¹)	Total animals caught			
							females	males	juveniles total	
10-Apr-03		Kiwinda, Chomboke	adults in moist soil at base of trees. Juveniles in dry soil at base of sugar-cane	8.5	2050	0.055	6	7	8	21
15-May-03	no rain for 2 weeks	Mranju, Kiwinda	confined to areas of high soil moisture	2.5	600	0.212	6	7	0	13
11-Jun-03		Mwambwalo	terrace bases and/or within banana plants	2	300	0.808	12	14	0	26
10-Jul-03	no rain for 1 month	Shate	base of rock, next to permanent stream	2.75	1080	0.066	2	4	0	6
14-Aug-03	substantial rain 4 days before visit	Wurundu-Mwanda	base of rock, next to permanent stream; base of ficus tree	4.5	430	0.364	20	10	4	34
18-Sep-03	light showers during visit	Wurundu-Mwanda	deep soil amongst bananas and trees	1.33	400	0.714	9	12	0	21
16-Oct-03	no rain since last visit	Wurundu-Mwanda	base of rock, next to permanent stream, at > 30 cm depth	3.5	440	0.041	1	2	0	3
17-Nov-03	heavy rain during visit	Wurundu-Mwanda, Kiwinda	deep soil amongst bananas and trees	1.5	400	0.700	9	11	1	21*
2-Dec-03	no rain since last visit	Wurundu-Mwanda, Kiwinda	deep soil amongst bananas and trees	7.5	6300	0.032	8	9	2	19
15-Jan-04	unexpected heavy rains	Wasiyini	on terraces and within banana plants	1.25	800	0.820	15	17	(7)	32*
19-Feb-04	wet with light showers	Njovunyi	manured terraces and amongst bananas	1.42	625	0.592	11	9	1	21
25-Mar-04	moderately wet	Wurundu-Mwanda	deep soil amongst bananas and trees	1.5	350	0.784	13	9	0	22
Total				38.25	13775		112	111	23	239*

* Denotes totals without including eggs or juveniles found with females.

Table 2.

Mean (\pm SE) measurements [with range] for total length, mass and condition index (ML^{-3}) of *Boulengerula taitanus* from small agricultural plots near Wundanyi, Taita Hills, Kenya. Measurements are taken from live animals collected in April, June, November and December 2003.

	n	Length (mm)	\pm SE	Mass (g)	\pm SE	$ML^{-3} 10^{-7}$	\pm SE
Juveniles	11	108.6 [93-134]	4.61	0.50 [0.3-0.9]	0.06	3.75 [3.39-4.82]	0.12
s-a males	13	219.0 [174-237]	4.87	2.95 [1.4-3.8]	0.18	2.76 [2.43-3.15]	0.06
s-a females	17	211.1 [182-238]	4.81	2.61 [1.7-3.5]	0.15	2.74 [2.37-3.39]	0.07
Males	27	276.4 [245-318]	3.84	5.82 [3.7-8.8]	0.25	2.72 [2.28-3.29]	0.05
Females	18	274.6 [244-333]	6.02	5.66 [3.4-10.6]	0.49	2.64 [1.89-3.20]	0.08
Total	86	233.0	6.37	4.04	0.25	2.85	0.05

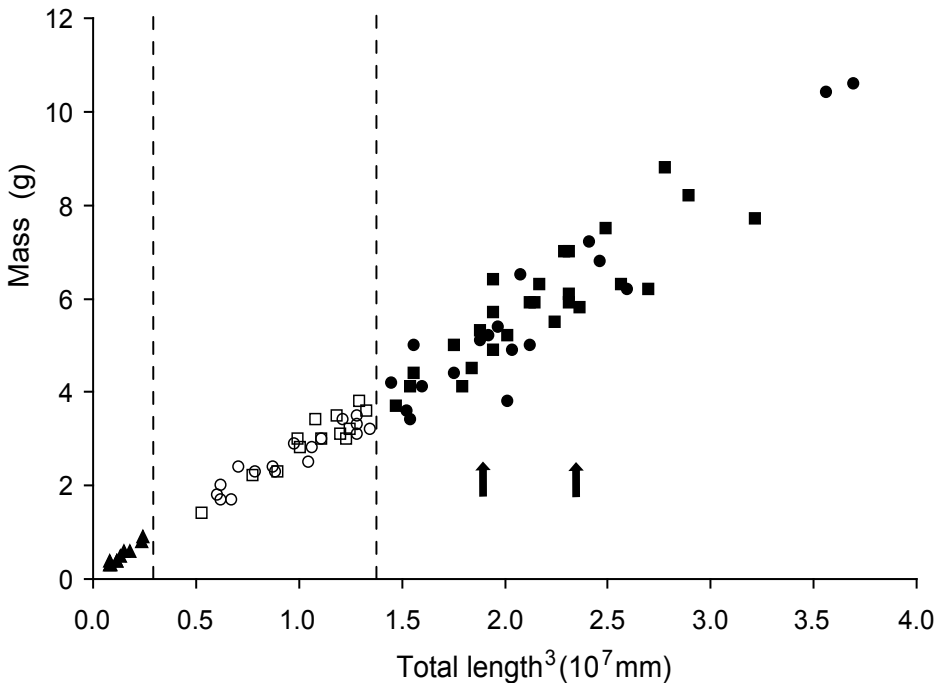


Fig. 2. — Scattergram indicating the scaling ratio ML^{-3} of *Boulengerula taitanus* from surveys in the Taita Hills, Kenya. Females (circles), males (squares) and juveniles (triangles). The operational ontogenetic groups used in subsequent analyses, juveniles (< 140 mm TL), subadults (approximately 140 to 240 mm) and adults (> 240 mm), are shown with dotted lines. The two females found brooding eggs are indicated with arrows.

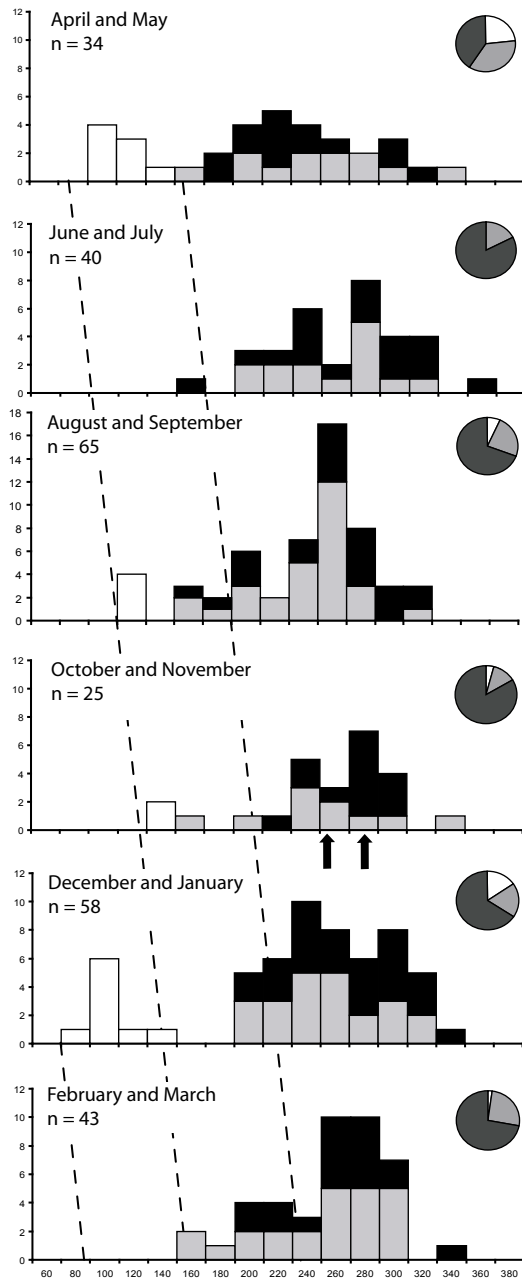


Fig. 3. — Length frequency bar-charts of total length for *Boulengerula taitanus* from around Wundanyi in monthly collections from April 2003 to March 2004. For histograms, males are shown by black bars, females by grey bars and juveniles by white bars. Data from 2 consecutive monthly samples are combined to increase sample sizes. The growth of two cohorts are shown with dotted lines. Pie-charts show the proportions of juveniles (white), sub-adults (grey), and adults (black) in combined samples. The sizes of two females found brooding eggs are indicated with arrows.

proportion being 34% subadults. Juveniles show significant changes ($\chi^2 = 3.12$; $P = 0.0101$) in proportion to adults and subadults (combined), with most being found around the short rains (see Figs 1 and 3).

Variations in total length of animals caught at the eight different sites around Wundanyi are significantly different ($F_{7,215} = 3.507$; $P = 0.0014$; juveniles excluded from analysis). For example, caecilians from Mranju ($\bar{x} = 210.8 \pm 15.06$ mm) were smaller than those caught at Chomboke ($\bar{x} = 267.7 \pm 20.00$ mm), despite the small distance between the sampling sites (see above and Table 1).

DISCUSSION

This is the first account of monthly collections of any caecilian species over a full year, and shows that it is always possible to find specimens of *Boulengerula taitanus*, even during dry periods. MEASEY et al. (2003b: 50) commented 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 southern India. Here we show semi-quantitatively that the amount of effort involved in finding animals increased during drier periods, and that the time and resources available (i.e. effort, see Table 1) did not always produce the desired number of individuals. Our observations also suggest that unseasonal weather (i.e. rainstorms during an otherwise dry period) makes it easier to find animals (Table 1). Thus it appears that the distribution of caecilians in surface soils may be rain or soil moisture dependent, at least as far as *B. taitanus* is concerned. However, during periods when soil was at its driest, animals were most easily found next to permanent water, or deeper in the soil profile (see Table 1).

VYAS (2003) and KUPFER et al. (2005) both suggest a perennial horizontal migration of ichthyophid caecilians towards riparian habitats in the dry season, while LOVERIDGE (1936) speculated that specimens of *Schistometopum gregorii* (Boulenger 1895) approach the surface soils during the heaviest part of the rains in East Africa and retreat deeper into the soil as the rains recede. MEASEY et al. (2004) also commented on the lack of data concerning caecilians outside of the rainy season, as well as the possibility of vertical migration. MEASEY et al. (2003a) suggested that *Gegeneophis ramaswamii* Taylor 1964 may have important vertical and/or horizontal migrations through the soil, which are reflected in their capture-recapture data. All of these studies agree that data on caecilians outside of monsoon or rainy seasons are badly needed in order to begin to understand the ecology of this neglected subterranean order. Two hypotheses appear to emerge from these observations:

(i) *Vertical migration*. Animals go deeper into the soil (becoming inaccessible to sampling) to be closer to the water table, but remain at a shallow depth where the soil is moist and the water table is higher (adjacent to a permanent stream).

(ii) *Horizontal migration*. Animals move closer to permanent water sources when the soil dries out, and move back when the soil is made moist by rainfall.

The two hypotheses are not mutually exclusive. Individuals in the vicinity of standing water or streams may move horizontally into the wetter hydric zones associated with such water bodies. MEASEY (2004) commented that *B. taitanus* were found under rotting logs and in deep litter in forests, and such animals may indicate that horizontal movements are made in an epigeic fashion. Most soil mac-

rofauna is found within the first 15 cm of the soil (LAVELLE & SPAIN 2001). If *B. taitanus* is dependent on a minimum soil moisture content, this would restrict them to deeper soils (or soils adjacent to water bodies) during dry periods; they migrating back towards the surface soil in order to feed on their macroinvertebrate prey items (GABORIEAU & MEASEY 2004). Hypotheses relating to soil moisture content and migration could be explored experimentally.

MEASEY & GOWER (2005) found the mean condition index for *G. ramaswamii* adults to be 6.0^{-7} , and that of juveniles to be significantly greater than both adults and subadults. However, the condition index could not be explained by the mass of any major internal organ, making it difficult to explain exactly how this index relates to individual "well being". The mean condition index for adult *B. taitanus* was 2.7^{-7} , about half that of *G. ramaswamii*, reflecting the difference in body form between these two species; *B. taitanus* are longer and thinner. This difference in body form may be responsible for the reduction in variation of the condition index of adult *B. taitanus*, compared to the large variation noted for adult *G. ramaswamii* and *T. compressicaudus* (EXBRAYAT 1988, MEASEY & GOWER 2005). Despite this large difference in body form, it appears as if the method proposed by MEASEY & GOWER (2005) to differentiate between subadult and adult *G. ramaswamii* is also applicable to *B. taitanus*. However, this needs to be confirmed through a detailed examination of the gonads of all individuals in this study.

The year-round nature of the data also provides valuable insights into the annual demographic changes in populations of *B. taitanus*. That animals caught in different sites were not of a uniform size within the areas around Wundanyi is important, as it suggests that population structures differ over small distances, although it is as yet unclear whether these represent discrete populations or metapopulations, typical of many amphibian species (MARSH & TRENHAM 2000). MEASEY (2004) found that animals from the forest were significantly larger than animals found in agricultural soil. Here we note that within agricultural landscapes, the smaller size differences in populations persist. Importantly, in this study, the problems associated with the different sample sites limit the amount of interpretation of the data. Nevertheless, important insights into the natural history of *Boulengerula taitanus* can be made, and we continue by highlighting the most important ones.

Clutch size in caecilians has been stated to be between 20 and 50 eggs (EXBRAYAT & DELSOL 1988), although smaller clutches are known for other caeciliids (e.g. *Idiocranium russeli* Parker 1936 down to six, see WAKE 1977). The mean clutch size reported here for *B. taitanus* ($\bar{x} = 5$) is the smallest recorded for any caecilian. MEASEY (2004) reported a similar clutch size for *B. boulengeri*, another thin caecilian from the neighbouring East Usambara Mountains in Tanzania. Small clutch sizes may enable gravid females to continue to burrow and predate within hard substrates without overly swelling their rather thin body form. MEASEY & GOWER (2005) suggested that gravid *G. ramaswamii* females would be easy to separate from non-gravid females by their highly elevated condition index. In this study, no females appear to have a greatly elevated condition index commensurate with a gravid condition (Fig. 2), perhaps because female *B. taitanus* lay relatively few eggs (see above).

The proportion of the first generation of *Dermophis mexicanus* compared to the total captured reported by WAKE (1980) was 40, 45, 27 and 13% in August, January, March and June, respectively (figures calculated from WAKE 1980: fig. 1). In this study the highest proportion of juveniles was 24%, in April and May (Fig. 3), corresponding to the period of juvenile independence (see Appendix 1). The considerably smaller proportion of juveniles may result from a combination of larger

clutch size (mean given as seven by WAKE 1980) in *D. mexicanus* and the presumed increased survivorship of a viviparous species. That juveniles and subadults were always inferior in proportion to adults may reflect unequal catchability or the vulnerability of these smaller size classes, particularly to invertebrate predators (see discussion in MEASEY 2004).

While it is not possible to draw a definitive conclusion from our data, it appears that the ontogenetic development from juvenile to subadult to adult takes around 2 years in *B. taitanus*. Clarification, through detailed examination of gonads or by laboratory studies, is needed to determine whether males and females have different ages at maturity (as proposed by WAKE 1980, EXBRAYAT 2000) or growth trajectories (as found by KUPFER et al. 2004a). Juveniles (defined as individuals whose sex could not be determined by direct examination of the gonads) may undergo a form of parental care far in advance of simple egg guarding (Appendix 1). The possibility that juveniles feed on skin from their mother (see Appendix 1) needs to be investigated to ascertain exactly what is being provided, and for how long this period of dependency continues.

Sexual dimorphism has been studied in very few caecilians. Among the few known morphological variants are a larger head size in males, paired anal glands, differences in cloacal form, and annular and vertebral counts (see DELÉTRE & MEASEY 2004 and references therein). DELÉTRE & MEASEY (2004) suggested that male *Schistometopum thomense* (Bocage 1873) use their larger heads to attach to females during mating. This was not observed in *B. taitanus*, and obvious bite marks were not observed on the trunks of individuals caught (as reported by TEODECKI et al. 1998, MEASEY et al. 2001). A larger body size may confer advantages to males defending a territory, or potential egg deposition sites, as is known with other terrestrial amphibians (HALLIDAY & TEJEDO 1995, MATHIS et al. 1995) and has been suggested for caecilians (MEASEY et al. 2003a).

The life history and population structure of *Boulengerula taitanus* bears some similarities and differences to those of other caecilians studied thus far. For example, reproduction appears to be dependent on the rainy season, with eggs being laid and brooded in underground chambers, as reported for ichthyophids (KUPFER et al. 2004b). Many authors have speculated that reproductive cycles of caecilians are tied to rainy seasons (e.g. WAKE 1980, BALAKRISHNA et al. 1982, EXBRAYAT 2000, MEASEY & DI-BERNARDO 2003). Unlike ichthyophids, the small clutches of *B. taitanus* eggs develop directly, hatching as juveniles with no larval stage (NUSSBAUM & HINKEL 1994). Like *Siphonops* and *Geotrypetes* there seems to be an altricial stage in development (suggested by JARED et al. as reported by PENNISI 1999, see also O'REILLY et al. 1998), where newly hatched juveniles are dependent on their mother within the brooding chamber (see Appendix 1). These observations are potentially exciting and important (PENNISI 1999), but need to be better studied with field observations to better define the relationship between mothers and offspring.

CONCLUSION

Adults make up the largest proportion of *Boulengerula taitanus* populations, and can be found together with subadults year round in low intensity agriculture in the Taita Hills. The data suggest that juveniles mature to subadults in around 1 year, and subadults to adults in another year. Populations appear to be very

localised, and individuals may undergo a vertical migration in the soil depending on soil moisture, which affects their catchability during the drier months of the year. Males are longer than female *B. taitanus*, although it is not clear why this is so. Like other caecilians, the reproductive period appears to be linked to the onset of the rainy season (the short “masika” rains) in the Taita Hills. Ease of field collection and the existence of (comparatively) numerous studies make *B. taitanus* a possible future model for terrestrial, oviparous, direct developing caecilians.

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APPENDIX 1

Life History

In Table 3 we present a tentative life history table from data and observations made during this study, interpreted with the aid of literature on *Boulengerula taitanus* and other caecilians. Interpretations of some observations are necessarily speculative, although we aim to produce hypotheses which may be useful in future studies. Conventional life-tables are made either by following the progress of a cohort (horizontal life-tables) or by taking a single large sample representative of the entire population (vertical life-tables). While we have not strictly followed either of these strategies, but a mixture of the two, we attempt to provide a “diagonal life-table”. Rather than attempting a regular age-class analysis, we concentrate on what we recognise as important life history stages. The choice of each stage and the generalisations described in the table are discussed below:

Copulation. One observation was made of a mating during November 2003 at Kiwinda. Two animals were unearthed, intertwined together, from within the top 20 cm of soil. Upon examination, one animal (a male TL 295 mm) was seen to have the phallus everted, while the other (a female TL 266 mm) lay in the same orientation. Observations of mating terrestrial caecilians are extremely infrequent, and we know of no other report in the literature concerning terrestrial caecilians. Observations of the mating of aquatic *Typhlonectes compressicaudus* (Duméril & Bibron 1841) suggest that there may be a considerable amount of courtship behaviour involved, and that the copulation period may be prolonged for several hours or days (e.g. WAKE 2002). While it is possible that mating occurs year round, EXBRAYAT (2000) found changes in the morphology of the female cloaca during reproductive periods in *T. compressicaudus*. We suggest that there may be a similar period of sexual activity for *B. taitanus*, but further studies are needed for its demarcation.

Chamber construction. Individual *B. taitanus* were observed coiled inside the soil in November, although no direct observations of brooding chambers were made. Digging through soil to find animals easily destroys such structures. We presume that the construction of a brooding chamber involves finding an appropriate site (see MEASEY et al. 2003a), in the upper region of loose soil (top 15 cm), where the coiled female may turn repeatedly to produce a smooth sided chamber. Soil penetrometer readings made at brooding chamber sites were constantly below those generally recorded at sites (e.g. 1.3 and 1.6 kg cm⁻², see site description). Brooding chamber shapes are typically flattened spheres around 50 mm in diameter, and half this in height, with very smooth interior walls (MEASEY 2004 and G.J. MEASEY unpublished data). This suggests that one individual constructs the chamber, as a pair of animals would presumably produce a far bigger structure.

Egg-laying. One female was captured in November with three eggs trailing by the ‘string’ which links eggs from the cloacal opening. A fourth egg was discernable inside the female by feeling the posterior portion with thumb and forefinger. However, the female had not produced the fourth egg between collection and preservation (approximately 2 hr later). Laying a clutch may take several days (as has been reported for *Ichthyophis* cf. *kohtaoensis*, see KUPFER 2002).

Table 3.

Life history table for *Boulengerula taitanus* from data and observations of 246 individuals caught in agricultural settings around Wundanyi, Taita Hills, Kenya. The proportion of animals relates specifically to the period mentioned and sex (where applicable). Data on diet comes from GABORIEAU & MEASEY (2004).

	Approximate size of individuals (mm)	Approximate period	Micro-habitat	Comments	Proportion of animals
Copulation	> 240	November	within the soil	as all caecilians have internal fertilisation, this could potentially occur year round	13%
Brood chamber building	females > 240	November	within top 15 cm of soil	only single females have been observed inside brooding chambers	11%
Egg-laying	females > 240	November	within brooding chambers	egg-laying may take a number of days to complete	20%
Brooding	females > 240	November to January	within brooding chambers	the exact period of brooding is unknown, but could be up to 2 months	22%
Hatching	females > 240 and hatchling juveniles at 83	January	within brooding chambers	females were found coiled around juveniles and were notably lighter in colour, whilst their juveniles appeared pink and helpless	20%
Independence	> 70 to 140	February to December	within friable organic matter	juveniles become pigmented and can be found in deep accumulations of organic matter. They are not found near to or in association with adults	5.5%
Subadults	140 to 240	all year	within soil	subadults can be found in the same localities as adults, apparently feeding on the same types of prey items	23%
Adults	> 240	all year	within soil and under surface debris	adults feed mostly on termites and earthworms, but seem to be generalist and opportunistic predators	68%

Egg attendance. Two females were found attending clutches of eggs at Wurundu and Kiwinda in November 2003 (Table 1). Clutch sizes were 4 and 7 from females 266 and 289 mm total length, respectively. NUSSBAUM (1985) suggested that parental care of eggs in salamanders helped in facilitating gas exchange, preventing fungal growth, desiccation and predation. It is likely that similar interpretations can be made for egg attendance in caecilians (NUSSBAUM 1992).

Altricial juveniles. The smallest seven caecilians found were from 80 mm ($\bar{x} = 83.1 \pm 1.26$) total length, all of them found with females (presumably the mothers). The females were coiled, in chambers similar to those described above. The juveniles were both in the centre of the coiled female and between her coils, so that each was in contact with the female. The attending females had a markedly changed skin colour: they had become a milky grey all over, almost obscuring both the dorsal and lateral black patterning, as well as the ventral and lateral blue normally associated with this species (NUSSBAUM & HINKEL 1994). Numbers of juveniles were from two to five ($\bar{x} = 2.3$) from three females. We had the impression that these pigmentless juveniles were helpless, specifically that they were not able to burrow in soil. Such observations have been previously made for other caeciliid caecilians (see O'REILLY et al. 1998, JARED et al. 1999), and PENNISI (1999) reported on observations by O'Reilly, Nussbaum and Wilkinson on viviparous *Geotrypetes seraphini* (Duméril 1859), suggesting that these apparently helpless young underwent a fivefold increase in weight over a few weeks by feeding on their mothers' skin secretions. The size of newly hatched juveniles is unknown.

Independent juveniles. The smallest independent caecilian was 93 mm (April 2003), while the largest juvenile was 134 mm (November 2003). We do not know the size at which juveniles are able to become independent of the attending female, or if size is the only factor. The smallest independent juveniles have the beginnings of black pigmentation along their dorsum, and more pronounced from the anterior, while the venter remains an unpigmented pink. In the largest juveniles, it is possible to determine the same patterning described for adults. The diet of these independent juveniles may differ from that of adults, i.e. consisting solely of small earthworms (GABORIEAU & MEASEY 2004), although the sample size ($n = 4$) was not large enough to draw firm conclusions.

Subadults. Gonads were visible, and hence sex was determined, from 142 mm. Fig. 3 suggests that this stage is reached around 1 year after eggs are laid, although we recognise that there may be a wide variation in this. Given that subadults are not sexually active, and that our finding of a discrete breeding period in *B. taitanus* is correct, it would seem that animals pass approximately 1 year as subadults, during which time they increase in size by about 100 mm. In a laboratory study, KUPFER et al. (2004a) found *Ichthyophis* cf. *kohtaoensis* terrestrial juveniles to increase by an average of 25 mm between the 1st and 2nd year, with both sexes maturing at around 4 years. Growth patterns were not the same for the two sexes and this may also be the case for *B. taitanus*.

Adults. Sexually active adults appear to be larger than ca 240 mm in total length. The Gymnophiona have been presumed to exhibit indeterminate growth patterns (e.g. KUPFER et al. 2004a), as are known from Caudata and Anura (HALLIDAY & VERRELL 1988, SMIRINA 1994). The largest adult captured during this study was a

male (348 mm), although HEBRARD et al. (1992) found larger individuals (i.e. 355 mm in HEBRARD et al. 1992: 514; Table 1) and MEASEY (2004) found that individuals from the forest were significantly longer than those found in agricultural soil.