

Externally Measured Condition Versus Internal Organ Mass in the Caecilian *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae)

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ABSTRACT—The relationship between externally measured condition ($\text{mass} \times \text{length}^{-3}$) and the mass of internal major organs in the caecilian *Gegeneophis ramaswamii* is investigated, based on a collection of 67 specimens from three southern Indian localities in the early and mid-monsoon. Condition in juveniles (< 90 mm total length) is higher than in subadults (90–170 mm) and adults (> 170 mm). The relationship between condition and total length is consistent in subadults, but variable in adults, and these differences indicate that the delimitation of these ontogenetic stages has some biological meaning. Adult females have fat bodies which fluctuate in mass, but not in relation to their body size. On average, adult females have heavier fat bodies and lighter gut contents than adult males, but there are no significant differences between subadult males and females. Gravid females are predicted to have a notably greater condition. There is no consistent relationship between condition and any major internal organ, but there is some significant variation among samples grouped by sampling time and locality. More sampling throughout the year is required to clarify the complex relationships between condition and internal organs, and before externally measured condition from ecological studies of living animals can be readily interpreted. However, its utility in helping to differentiate between ontogenetic classes may be of immediate use.

Key words: condition, fat bodies, India, reproduction, soil ecology, Western Ghats

INTRODUCTION

Some aspects of terrestrial caecilian ecology are now being gradually unearthed with the aid of a growing toolbox of techniques developed using the species *Gegeneophis ramaswamii* Taylor, a direct-developing, oviparous caeciliid from southern India (e.g. Seshachar, 1942). Oommen *et al.* (2000) found this species to be abundant in a variety of agricultural environments and suggested that it is therefore a potentially useful model system for establishing a quantitative ecology of caecilians. Information on diet indicates that *G. ramaswamii* is a subterranean generalist predator of soil ecosystem engineers (earthworms, termites and ants), and other invertebrate and even vertebrate prey (Presswell *et al.*, 2002; Measey *et al.*, 2004). Measey *et al.* (2004) also found a seasonal variation in the quantity of prey consumed, with more items present in guts of animals found in the mid-

monsoon than in the early monsoon period. The potential of several methods for permanently marking *G. ramaswamii* was demonstrated in a laboratory study (Measey *et al.*, 2001), and it was subsequently shown that animals can be marked and recaptured to yield population and life history information in field studies (Measey *et al.*, 2003a). The potential of this model is further demonstrated by results of trials of a survey technique for caecilians, utilising randomised quadrats dug within a 100 m² grid (Measey *et al.*, 2003b). These trials found densities of *G. ramaswamii* ranging from zero to 1.87 m⁻² per survey, with means of 0.51 and 0.63 m⁻² at early and mid-monsoon, respectively. These studies of *G. ramaswamii* concur in one important aspect, that more fieldwork, sampling, and quantitative analyses are necessary to gain a fuller understanding of caecilian ecology and how best to study it.

In amphibians, energy is stored chiefly as lipids in fat bodies, but also to some extent in the liver (e.g. Exbrayat, 1988; Jørgensen, 1992). Condition of an animal can be regarded as its well being, or more specifically in terms of energy storage levels, and hence in amphibians this can be studied by changes in fat-body and liver mass. Based largely on studies of anurans and urodeles, it is known that there is a functional (and often inverse size) relationship

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between gonads and fat bodies in amphibians (e.g. Jørgensen, 1992). Studies of Neotropical viviparous caecilians report seasonal cycles, including periods of sexual activity and inactivity, roughly aligned with wet and dry seasons respectively (Wake, 1980; Exbrayat and Delsol, 1985; Exbrayat, 1988). In these studies, fat bodies were found to be severely reduced in females during and after gestation (Exbrayat and Delsol, 1985; Exbrayat, 1988). Fat-body size is reported to generally increase proportionately with body size in caecilians, but with the largest fat bodies occurring in pregnant females, and being "proportionately much smaller in females with immature ova as in the condition reported by Noble (1931) for other amphibians" (Wake, 1968 p. 313). Thus, fat bodies in caecilians function as energy storage organs and have an important relationship with gonads (Wake, 1968). From these limited background data, it might be expected that fluctuations in fat-body mass may be observed during sexual cycles of other caecilians, including species that are not viviparous.

Examination of variation in repeated measures of live *Chthonerpeton indistinctum* (Typhlonectidae) demonstrates that variation in measures of total length (TL, using a fixed ruler) have an average deviation of 1.2%, but that variation in measures of mass is negligible (Measey *et al.*, 2003c). In the future, more studies of caecilian ecology may involve live animals (e.g. mark recapture, see Measey and Di-Bernardo, 2003; Measey *et al.*, 2003a), and so it is important that data are generated on the principle variants of internal mass and how they relate to total live mass. In this study, we use the condition factor, $M L^{-3}$, which is based on the geometric scaling relation $M \sim L^3$; i.e. the proportionately greater the mass of the animal, then the greater is its condition factor (May, 1991). The same index was used in a study of the aquatic, viviparous typhlonectid *Typhlonectes compressicauda* (Exbrayat, 1988). Here we test the hypothesis that, of the major internal organs, the greatest variations to total mass are correlated with changes in gonad maturity (especially in females), fat bodies, liver and gut contents. If corroborated, it is implicit that condition will differ between sexes, times of sampling and possibly between localities, and these subsidiary hypotheses are tested. Following Wake (1968), we also investigate the hypothesis that fat-body mass is correlated with individual size and gonad size/maturity. Our investigations are made using data obtained from dissections of the terrestrial, southern Indian caeciliid *Gegeneophis ramaswamii* collected in the randomised surveys reported by Measey *et al.* (2003b).

MATERIALS AND METHODS

Detailed information on three localities, sites, and collection methods are presented elsewhere (Measey *et al.*, 2003b). All three localities surveyed are in the southernmost part of the Western Ghats of Kerala, India. The climate is monsoonal (Measey *et al.*, 2003b), and can be divided into a wet monsoon season (June to November) and a marked drier season (December to May). *G. ramaswamii* were collected by digging randomised 1 m² quadrats

in surveys conducted in early (end of June and early July 2000) and mid-monsoon (August 2000) periods. The survey site at the locality of Bonaccord (08°40' N 77°10' E; 593 m asl), a tea (*Camellia sinensis* (L.) Kuntze) plantation, is a flat, largely grassy clearing at the bottom of tea-planted slopes. Makki (08°40' N 77°10' E; 238 m asl) is dominated by rubber (*Hevea brasiliensis* (A. Juss.) Müll.-Arg.) cultivation, and although only 4.5 km direct, is 350 m below Bonaccord, separated, at least in part, by naturally forested steep slopes. The third site near Punalur (08°58' N 76°57' E; 70 m asl) is a low altitude rubber plantation crossed by a regular grid of drainage ditches.

Animals used in this study were anaesthetised in MS222 within two hours of capture, after which they were placed on paper towel along a fixed ruler for measurement of total length (to the nearest mm), and an electronic balance was used for measurement of mass (to the nearest 0.1 g). Animals were subsequently euthanased, fixed in formalin (10% of stock solution), and stored in 70% ethanol in the collection of the Zoology Department of the University of Kerala. Preserved specimens were dissected (altogether and in no particular order) using a stereo-zoom microscope. The body cavity was opened with a mid-ventral incision and the alimentary canal and closely associated organs removed from immediately posterior to the heart to the anterior end of the cloaca, and stored in 70% ethanol. The lungs, bladder and kidneys were left in place. The alimentary canal and its contents (hereafter gut), gonads and fat bodies were separated from the liver (and the liver from the gall bladder, pancreas, and spleen - GPS) and each weighed to the nearest 0.0001 g. Animals were sexed, where possible, by examination of gonads.

STATISTICA (v 5.5A, StatSoft, France) was used for statistical analyses of log (ln) normalised data. These were carried out using linear regression (R^2), correlation (r_{df}), two-tailed t-tests (t^2_{df}) and MANCOVA, with the mass of fat bodies, gut, liver, GPS and gonads as dependent variables in investigations of differences between sex, maturity, sampling time and locality as independent, between-group variables, with total length (TL) as a covariate. Juveniles were excluded from the MANCOVA analysis due to their very low numbers, presence at limited sites and absence of accurate gonad masses.

RESULTS

Of 70 *Gegeneophis ramaswamii* collected during surveys, 13% of specimens were damaged during collection. Dissection and data collection was made from all but three of the damaged individuals (Table 1). The 67 analysed *G. ramaswamii* were divided into three operational groups termed juveniles, subadults and adults. Juveniles were defined as small animals (TL < 90 mm) that were not possible to sex. Subadults and adults (> 90 mm) were all sexed by examination of gonads, and the cut-off between these two groups was set at a TL of 170 mm, based on the observation of the smallest female *G. ramaswamii* found with a clutch of eggs (172 mm, unpublished data). The condition ($M L^{-3}$) of the five juveniles was significantly greater than for all other animals combined ($t^2_{65}=1.997$; $P<0.001$). Subadults had a consistent relationship between L^3 and M ($R^2=0.943$, $P<0.001$), while for adults this relationship is significant but more variable ($R^2=0.723$, $P<0.001$; Fig. 1). Subsequent analyses of condition were carried out within each of these three groups, with membership of each determined by total length. Measey *et al.* (2003b) reported that sex ratios did not

Table 1. Pooled data for all 67 *Gegeneophis ramaswamii* analysed for condition. Mean values, (\pm Standard Error with ranges below) are given for live total length and mass, and percentage of live mass of preserved dissected organs. Juveniles are small (TL<90 mm) animals that could not be sexed, while subadults (s-a) are those 170 mm or shorter that could be sexed. GPS=pooled gall bladder, pancreas and spleen.

	n	Length (mm)	Mass (g)	$ML^{-3} 10^{-7}$	% fat bodies	% whole gut	% liver	% gonads	% GPS							
Juveniles	5	64	± 1.34	0.2	± 0.02	9.17	1.06	± 0.40	11.00	± 2.57	2.29	± 0.42	0.00	± 0.00	0.42 \pm	0.06
		59–67		0.2–0.3		0.1–1.9	6.1–20.7	1.5–3.9	0.00	0.2–0.5						
s-a males	19	135	± 4.69	1.7	± 0.16	6.37	1.55	± 0.20	9.60	± 0.81	3.16	± 0.11	0.16	± 0.03	0.39	± 0.03
		101–167		0.7–3.1		0.7–3.4	5.3–17.4	2.6–4.2	0.1–0.5	0.2–0.6						
s-a females	15	126	± 4.75	1.3	± 0.13	6.61	2.11	± 0.31	9.04	± 0.88	3.08	± 0.09	0.18	± 0.02	0.36	± 0.03
		100–168		0.6–2.6		0.8–4.8	5.6–16.2	2.6–3.6	0.1–0.4	0.2–0.5						
Males	13	203	± 4.98	5.2	± 0.43	6.06	1.51	± 0.19	8.97	± 0.96	3.19	± 0.11	0.54	± 0.07	0.33	± 0.02
		175–229		3.4–8.3		0.5–2.8	5.5–15.9	2.6–3.9	0.2–1.0	0.2–0.5						
Females	15	217	± 4.68	6.3	± 0.47	6.01	4.35	± 0.56	7.06	± 0.68	2.91	± 0.21	0.52	± 0.10	0.33	± 0.02
		195–252		4.5–11.4		0.4–7.4	4.0–11.4	1.5–4.0	0.1–1.6	0.2–0.5						

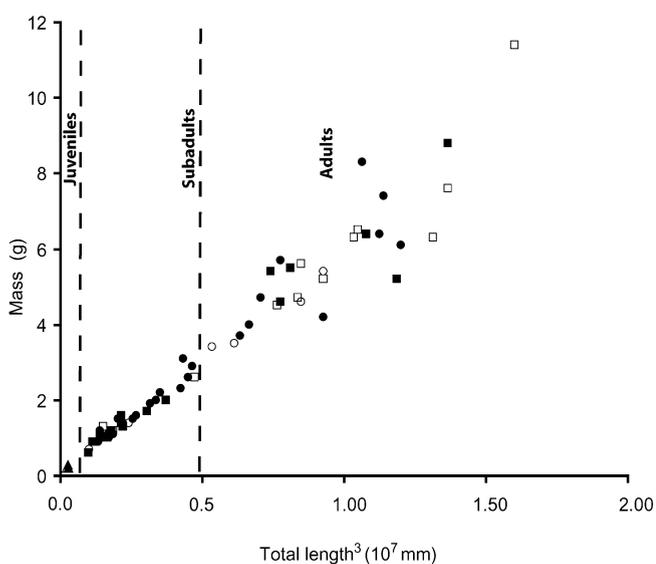


Fig. 1. Scattergram indicating the scaling ratio $M \sim L^3$ of *Gegeneophis ramaswamii* from surveys in Kerala, India. Females (circles), males (squares) and juveniles (triangles) are from collections at the beginning of the monsoon (open symbols), and mid-monsoon (solid symbols). The operational ontogenetic groups used in condition analyses, juveniles (< 90 mm TL), subadults (approximately 90 to 170 mm) and adults (> 170 mm), are shown with dotted lines.

differ significantly from 1:1, and here we add that numbers of adults were not significantly greater than numbers of subadults over the two sampling occasions ($\chi^2 > 0.05$), although proportions were found to be significantly different among sites ($\chi^2 < 0.05$); more adults were found at Bonaccord and more juveniles at Punalur.

Gut mass contributed the highest proportion to total body mass, up to 20% in juveniles and a maximum of around 17% in subadults and adult males, but only reaching a maximum of 11% in adult females (Table 1).

To further explore the condition factor ML^{-3} we individually investigated all those animals that fall outside one standard deviation ($SD = 1.22^{-7}$) of the mean ($\bar{x} = 6.49^{-7}$). Of the eight animals that fall above 1 SD (see Table 3), three of them are juveniles, and of the remaining five, four are

Table 2. Adjusted means for (a) sampling localities $F_{10,112} = 2.06$; $p < 0.034$ (b) sampling time $F_{5,56} = 1.79$; $p < 0.131$, and (c) the interaction between sampling time and locality $F_{10,112} = 3.01$; $p < 0.002$ for masses (in g) of internal organs of 67 *Gegeneophis ramaswamii* at three localities in early and mid-monsoon. GPS=pooled gall bladder, pancreas and spleen. * $P < 0.05$, ** $P < 0.01$.

	Fat bodies	Gut	Liver	Gonads	GPS
Bonaccord	0.111	0.334	0.118	0.018	0.012
Punalur	0.070	0.204	0.084	0.016	0.010
Makki	0.159	0.261	0.095	0.016	0.011
Effect	0.020	0.066	0.005	0.000	0.000
Error	0.010	0.018	0.001	0.000	0.000
$F_{2,60}$	1.899	3.640	4.810	0.038	1.222
P	0.159	0.032*	0.012*	0.963	0.302

	Fat bodies	Gut	Liver	Gonads	GPS
early monsoon	0.140	0.219	0.095	0.016	0.011
mid-monsoon	0.087	0.313	0.102	0.018	0.012
Effect	0.026	0.084	0.000	0.000	0.000
Error	0.010	0.018	0.001	0.000	0.000
$F_{1,60}$	2.526	4.666	0.421	0.144	0.565
P	0.117	0.035*	0.519	0.706	0.455

	Fat bodies	Gut	Liver	Gonads	GPS
Bonaccord early	0.107	0.187	0.099	0.008	0.009
Bonaccord mid	0.115	0.481	0.136	0.027	0.015
Punalur early	0.070	0.193	0.087	0.021	0.011
Punalur mid	0.070	0.214	0.080	0.011	0.010
Makki early	0.242	0.277	0.100	0.018	0.012
Makki mid	0.076	0.244	0.089	0.015	0.010
Effect	0.024	0.129	0.003	0.001	0.000
Error	0.010	0.018	0.001	0.000	0.000
$F_{2,60}$	2.288	7.150	3.073	3.946	5.982
P	0.110	0.002**	0.054	0.025*	0.004**

Table 3. Individual data for *Gegeneophis ramaswamii* found to have a condition index (ML^{-3}) greater or less than one standard deviation ($SD=1.22^{-7}$) of the mean ($\bar{\chi} = 6.49^{-7}$). Percentage of dissected organs were calculated from the proportion of live mass, and means (with Standard Errors) are given in Table 1. Those found to be the largest or smallest in their class (ontogeny and sex) are marked with a cross (+) or asterisk (*), respectively. GPS=pooled gall bladder, pancreas and spleen, A=adult, Sa=subadult

Tag Number	Locality	Monsoon period	sex	Ontogeny	Length (mm)	Mass (g)	Condition ML^{-3}	% fat bodies	% gut	% liver	% gonads	% GPS
MW01388	Punalur	mid	f	A	228	5.2	4.39^{-7}	0.42*	6.37	2.22	0.23	0.38
MW01395	Punalur	mid	m	A	210	4.2	4.54^{-7}	0.79	5.51*	2.62	0.35	0.29
MW01057	Bonaccord	mid	f	A	236	6.3	4.79^{-7}	3.01	5.41	2.72	0.36	0.27
MW01545	Bonaccord	mid	m	A	229	6.1	5.08^{-7}	1.10	6.80	3.85	0.50	0.50
MW01536	Bonaccord	mid	m	A	220	8.3	7.79^{-7}	2.80+	14.72	3.32	0.70	0.26
MW01548	Makki	mid	f	Sa	112	1.1	7.83^{-7}	1.17	12.17	3.27	0.15	0.16
MW01391	Punalur	mid	f	Sa	104	0.9	8.00^{-7}	1.99	9.96	3.29	0.14	0.41
MW01392	Punalur	mid	m	Sa	112	1.2	8.54^{-7}	1.53	16.98	2.95	0.05	0.27
MW01269	Punalur	early	f	Sa	115	1.3	8.55^{-7}	1.41	6.45	3.48	0.10	0.22

small subadults (104–115 mm). The last is an adult male (MW01536, Bonaccord mid-monsoon) with a combination of the heaviest of adult male fat bodies (2.8% of total mass) and a heavy gut (14% of total mass, see Tables 1 and 3). Four animals are below 1 SD, two adult females and two adult males. One of the adult females (MW01388, Punalur mid-monsoon) has the lightest proportionate fat bodies (0.4%) while one adult male (MW01395, Punalur mid-monsoon) has the lightest proportionate gut (0.8%). However, the remaining two can not be explained by the mass of any particular organ (Table 3).

The relationships between total mass and the mass of liver and of gonads do not vary among the operational ontogenetic grades, regardless of sex. Our data (Fig. 1, Table 1) suggest that there is little that total mass or length can inform about the state of major internal organs of *G. ramaswamii* of less than 170 mm. However, the variance in adult condition cannot be explained by sex, location or time sampled. Indeed, there seems to be no obvious, consistent relation between adult condition and the mass of any of the internal organs or their combined totals (Tables 1, 2).

Fat-body relationships

Table 1 and Fig. 2 show that adult females have a higher mass of fat bodies ($\bar{\chi}=0.28 \text{ g} \pm 0.19$) than adult males ($\bar{\chi}=0.08 \text{ g} \pm 0.06$), a difference that is significant ($t_{26}^2=2.055$, $P<0.001$). Adult females also have a greater range of fat-body mass, up to 7.4% of total body mass, compared to a maximum of only 2.8% in adult males (Table 1). There is no significant difference between the fat-body mass of subadult males and females ($t_{32}^2=2.037$, $P=0.790$), and the correlation with total mass is strong ($r_{32}=0.84$) and significant ($P<0.01$). Similarly, the correlation between fat-body and gonad mass for subadults is strong and significant for both males ($r_{17}=0.73$; $P<0.01$) and females ($r_{13}=0.93$; $P<0.01$). Subadult and adult males ($r_{11}=0.74$; $P<0.01$) have a very similar relationship between gonads and fat bodies.

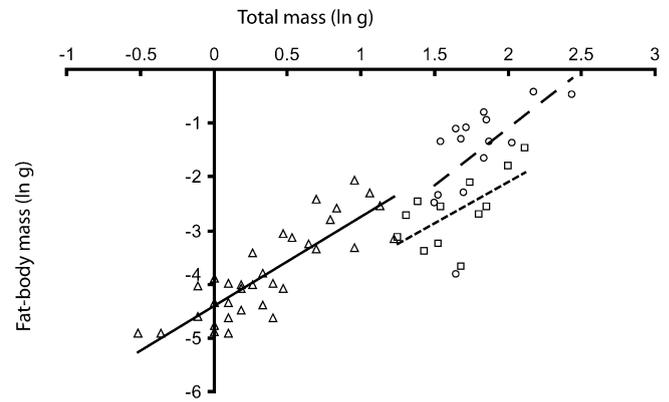


Fig. 2. Regression of fat-body mass on total mass for males (squares, dotted line), females (circles, dashed line) and subadults (triangles, solid line) of pooled data for *Gegeneophis ramaswamii* from surveys in Kerala, India. Adult males have significantly lower fat-body mass than adult females.

The ovaries of most female *G. ramaswamii* contained only very small ova, less than 1.5 mm maximum diameter. Their mass is not significantly different from that of male testes ($t_{60}^2=2.00$, $P=0.498$; Table 1). A single specimen (MW01537) with numerous large, yolky ovarian ova (3.7 mm) was collected in the mid-monsoon survey at Bonaccord. The gonads of this specimen are more than twice the absolute mass of other female specimens. The following calculations regarding fat-body and gonad mass were thus made with and without this singleton. Given that juveniles lacked identifiable gonads, these were removed from consideration.

Adult females have a weak but significant relationship between fat-body and gonad mass ($r_{13}=0.66$; $P<0.01$). However, if the single female with yolky ova is removed from the analysis, the correlation is weaker and no longer significant ($r_{12}=0.45$; $P>0.05$). Fig. 3 shows the relationship of fat-body and gonad masses to be roughly linear, but with a large dif-

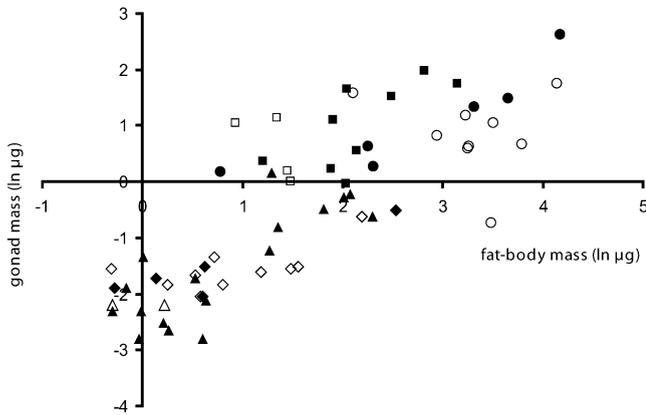


Fig. 3. Correlation of fat-body and gonad mass for *Gegeneophis ramaswamii* collected in early monsoon (open symbols) and mid-monsoon (solid symbols) periods in Kerala, India. Adult males (squares), subadult males (triangles) and subadult females (diamonds) show a clear linear relationship, while that for adult females (circles) is ambiguous.

ference in gonad mass for animals sampled in early monsoon from those in mid-monsoon. While numbers of animals from each category are not sufficient to make meaningful statistical tests, the figure suggests an increase of gonad size for adult animals independent of fat-body mass, while no such interpretation can be made for subadults.

Influences of Season and Locality

The results of MANCOVA analyses show that the effects of locality on internal organs are significant, as well as the interaction between locality and sampling time (Table 2). Univariate tests show that the interaction between time and locality is significant with respect to gut, gonads and the composite group of gall bladder, pancreas, and spleen (GPS). The gut is significantly heavier in the second sampling in mid-monsoon (except Makki), and notably so at Bonaccord ($F_{1,60}=4.66$; $P=0.035$, Table 2c). Among sites, animals from Bonaccord have significantly heavier guts and livers.

Although interactions with time and site are not significant for fat-body mass, Table 2b shows that fat bodies of early monsoon animals are heavier than those collected in mid-monsoon. Furthermore, fat-body mass has a negative relationship with gut mass. This negative relationship is also shown in Table 2c, except for at Punalur where fat-body mass does not differ between samplings. For subadults, there is a clear and significant relationship between total mass and mass of fat bodies ($R^2=0.71$; $F_{1,33}=80.58$; $P<0.001$, Fig. 2). The greater gut mass of mid-monsoon animals with respect to early monsoon animals is correlated with a greater number of gut-content items (for data see Measey *et al.*, 2003b).

Masses of liver and GPS did not differ significantly between early and mid-monsoon samples, but liver mass was significantly greater at Bonaccord. There was a significant interaction of GPS with time and site (Table 2c),

although this is not evident at the level of either sites or sampling time independently (Table 2a, b).

DISCUSSION

Although the exact length at which *G. ramaswamii* achieve sexual maturity is not clear from our data (Fig. 1), and in all probability is variable, we defined three operational groups based on maturity of gonads and extrinsic data on minimum observed TL of reproducing ('adult') females. Although somewhat arbitrary, the division of subadults from adults receives support from differences in condition between the two groups, specifically in the mass of fat bodies (in females) and gonads (Table 1). Additionally, the condition of juveniles is higher than in the other groups. The main differences found within the pooled data for adult *G. ramaswamii* are that fat bodies were of greater mass in females than males, and gut-content mass of males was heavier and with a higher maximum than in females. No significant differences were found between subadult males and females, but it can be seen that, on average, even subadult females have a greater mass of fat bodies (Table 1). The differences between adults and non-adults shown in Fig. 1 suggest that reproductive biology has an important impact on length-weight relationships.

That adult males have a slightly higher liver mass and females a higher fat-body mass (Table 1) may relate to differences in the speed and/or timing at which energy reserves are mobilised by each sex. Males also have a greater maximum gut mass, which may be a reflection of their reliance on a more labile energy source. A similar interpretation was given by Exbrayat (1988) for seasonal cycling of liver and fat-body mass in *T. compressicauda*. He found greatest variations in gestating females, and a lag between augmentation of fat-body and liver mass, although he found males to have a lower liver mass during periods of peak activity. Despite significant differences in gut mass, Measey *et al.* (2004) found no sexual differences in *G. ramaswamii* diet. It should be noted that Measey *et al.* (2004) considered only masses of identifiable items in gut contents, while this study concerns the whole gut including often notable amounts of soil and detritus.

Both sampling time and locality are significant properties for this data set, and this is perhaps not surprising given the profound influence of the monsoon season on the region and range of altitudes and habitat covered by the study sites. Similarly, Measey *et al.* (2004) found significant differences in diet of the same sample of *G. ramaswamii* between sampling times. *G. ramaswamii* from Bonaccord had the highest masses of liver and gonads. Measey *et al.* (2003b) commented on the consistent nature of density of *G. ramaswamii* caught at this site, and their greater mass per meter squared, which this study suggests may be explained by their heavier livers and gonads. Liver mass of starved frogs decreases sharply in the initial phase of starvation, as a result of metabolised glycogen and lost water (Merkle and

Hanke, 1988). Exbrayat (1988) found that liver mass peaked in male and female *T. compressicauda* during the reproductive season, and it may be that reproductive periods are not the same at all sites (see Table 2c). The single female with yolky ovarian ova was collected in the mid-monsoon survey at Bonaccord (but see below). However, it might be that the consistently higher liver mass of *G. ramaswamii* from this higher altitude locality relates to their increased condition compared to other localities, which may differ in the timing and magnitude of seasonal fluctuations. Bonaccord *G. ramaswamii* had the highest occurrences of a possibly parasitic gut nematode (Measey *et al.*, 2004), but this seems to have had no noticeable effect on condition.

Except for possibly one specimen, females in this study were not found to be reproducing within the surveyed area. We predict that gravid females would be easy to identify from a much higher condition caused by an increased egg mass, and if corroborated this may be useful in future studies. Otherwise, we are unable to reject the null hypothesis that there is no consistent relationship between condition and the masses of fat bodies, liver and guts. Condition indices have been widely used in amphibian ecology, following the seminal work of Pough (1980) in which he described the relationship between mass and snout-vent length in anurans to be:

$$\text{Mass} = 6.0 \times 10^{-2} \text{ SVL}^{3.24} \text{ cm}$$

as a way of combining live length and mass measurements to give an indication of animal well-being independent of overall size. This is especially useful where it is not feasible to dissect animals during an ongoing study. We had hoped that condition of *G. ramaswamii* in this study would be found to be related to the mass of organs such as fat bodies, liver or the amount of gut contents, or some combination of these. The null hypothesis that there is no variation in the mass of internal organs in relation to maturity, sex, site and time can be rejected, but the relation between condition and internal organs is complex and requires further study.

Individuals outside one standard deviation from the mean condition index demonstrate well the complex relations among internal organ mass in *G. ramaswamii*. Clearly there is some ambiguity in the division between juveniles and subadults, and by choosing fixed lengths to demarcate ontogenetic stages we do not account for the possibility that there are differences in sizes at hatching. The clear difference in condition between juveniles and subadults suggests that this index may be used to better describe ontogenic progression than reliance on length alone. Similarly, changes in condition between subadults and adults seem to better reflect developmental changes than does length alone. Variation in fat bodies and a high gut mass (presumably resulting from a larger intake of food) seem to be the main factors influencing the condition of the remaining individuals, although two individuals seemed to have no remarkably low organ masses to explain their presence below 1 SD of the mean.

Externally measured condition in *G. ramaswamii* does not provide a good indicator of energy reserves in the form of fat-body mass (Fig. 4), and a clear correlation of these

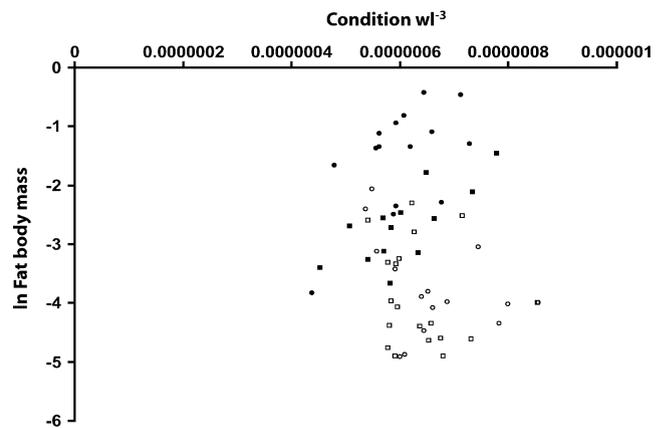


Fig. 4. The overall relationship between fat-body mass and condition in *Gegeneophis ramaswamii*. Females (circles), males (squares) adults (solid symbols), and subadults (open symbols).

variables is not apparent for *T. compressicauda* (Exbrayat, 1988). For *G. ramaswamii*, despite the wide variation found in gut contents (see above and Measey *et al.*, 2004), exclusion of gut-content mass from consideration does not substantially improve the correlation.

Few details are known about reproduction in *G. ramaswamii*, including whether females reproduce annually or less or more frequently. The build up of energy reserves in the form of fat bodies may be important not only for the development of eggs, but also in the maintenance of the adult while guarding egg clutches (see Measey *et al.*, 2003b). If it is only females that guard eggs, and if this activity restricts their ability to feed, storage of energy in fat bodies can be expected to be of even greater importance. This may make these oviparous animals prone to larger fluctuations than the viviparous model studied by Exbrayat (1988). Males may use more labile energy stores, thus reducing the ceolomic space required for fat bodies.

Clearly our data are incompatible with the hypothesis (see Introduction) that adult female fat-body and total mass have a simple linear relationship. It is difficult to determine the nature of the complex relationships within this data set. Other workers have examined this relationship in anurans and urodeles finding fat-body cycles to have strong seasonal rhythms in temperate regions (Jørgensen, 1992 and references therein). However, seasonal rhythms are absent in the fat bodies of tropical *Bufo melanostictus*, where fat-body size varies widely and unpredictably (Jørgensen *et al.*, 1986). Similarly, the distinct relations between reproduction and fat bodies found in temperate snakes is reported to be absent in tropical species (Seigel and Ford, 1987: 221), suggesting that reduced or absent seasonality may lessen the importance of fat reserves. Despite living in the tropics, *G. ramaswamii* is exposed to a highly seasonal climate (see

Materials and Methods). Jørgensen (1992) suggested two factors which may relate to fat-body mass, local environmental conditions and breeding status. *G. ramaswamii* may have dedicated breeding sites (Measey *et al.*, 2003a) which might explain the absence of actively breeding females in these samples. Breeding females were found outside the survey areas at each of the sites during the survey period (Measey *et al.*, 2003b), and this raises questions (beyond the scope of this work) about the presence of non-breeding females in our sample and the periodicity of reproduction in this oviparous, direct developing species.

In general, early monsoon *G. ramaswamii* have relatively heavy fat bodies and light gut contents. While many possible scenarios may explain these data, we forward the following contrasting, but testable hypotheses. First, that fat bodies are reduced in mid-monsoon when there is plenty of food available, liberating coelomic space for other needs. Second, that fat-body reserves are used up early in the monsoon, perhaps by a burst of activity (such as breeding or dispersal) and that by mid-monsoon, more food is required to replace energy reserves. Breeding drastically reduces fat-body size in the aquatic viviparous caecilian *T. compressicauda* (Exbrayat and Delsol, 1985; Exbrayat, 1988), and it is postulated that small fat-body size in captive *Typhlonectes* is attributable to inadequate feeding over an extended period (Wake, 1968), and these observations are consistent with the second hypothesis. Greater fat-body mass in female *G. ramaswamii* also supports the association between energy reserves and egg development, laying, and guarding. Testing these hypotheses requires further sampling both at the end of the monsoon period, and perhaps more importantly outside of the monsoon period. The animals collected here were not actively breeding, and more data are also needed on the reproductive biology of *G. ramaswamii*. This information would undoubtedly greatly increase our understanding of the ecology of caecilians through the model species *G. ramaswamii*.

We stress that our data were collected from only a short period of the year. Data from throughout the year should be gathered before further conclusions are made. For example, differences between adult males and females may not hold true across the year as a whole. Dismissal of the utility of an external condition index for *G. ramaswamii* also requires additional data. Caecilians are diverse, and we caution against generalising findings for *G. ramaswamii* to other taxa in the absence of further studies.

CONCLUSION

In *Gegeneophis ramaswamii*, externally measured condition does not consistently correlate with the mass of viscera, but there is interesting variation with respect to sampling time and locality. Significant differences occur between *a priori* ontogenic groupings, but possible allometric variation among these groups make within group differences more readily interpretable. The greatest variations occur in

adults. Adult females have heavier fat bodies than adult males, and an inconsistent relationship with gonad mass, suggesting a more complicated relationship than that proposed for other amphibians (Noble, 1931) and other caecilians (Wake, 1968; Exbrayat, 1988). Adult males have heavier gut contents with a wide range of masses. The complex relations between condition and internal organs will be best clarified by increased sampling throughout the year, at several localities. Gravid females should be readily identifiable by a greatly inflated condition index. Currently, the condition index might be best used for assisting differentiation between ontogenic classes in ecological studies.

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REFERENCES

- Exbrayat J-M (1988) Variations ponderales des organes de reserve (corps adipeux et foie) chez *Typhlonectes compressicaudus*, amphibien apode vivipare, au cours des alternances saisonnieres et des cycles de reproduction. *Annales des Sciences Naturelles Zoologie et Biologie Animale* 9: 45–53
- Exbrayat J-M, Delsol M (1985) Reproduction and growth of *Typhlonectes compressicaudus* - a viviparous gymnophione. *Copeia* 1985: 950–955
- Jørgensen C (1992) Growth and reproduction. In "Environmental Physiology of the Amphibians" Ed by M Feder, W Burggren, University of Chicago Press, Chicago, pp 439–466
- Jørgensen C, Shakuntala K, Vijayakumar S (1986) Body size, reproduction, and growth in a tropical toad, *Bufo melanostictus*, with a comparison of ovarian cycles in tropical and temperate zone anurans. *Oikos* 46: 379–389
- May R (1989) How many species? In "The Fragile Environment" Ed by LE Friday, RA Laskey, Cambridge University Press, Cambridge, pp 61–81
- Measey GJ, Di-Bernardo M (2003) Estimating juvenile abundance in a population of the semiaquatic caecilian, *Chthonerpeton indistinctum* (Amphibia : Gymnophiona : Typhlonectidae), in southern Brazil. *J Herpetol* 37: 371–373
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M (2001) Permanent marking of a fossorial caecilian, *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae). *J South Asian Nat Hist* 5: 109–115
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M (2003a) A mark-recapture study of the caecilian amphibian *Gegeneophis ramaswamii* (Amphibia : Gymnophiona : Caeciliidae) in southern India. *J Zool* 261: 129–133
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M (2003b) Quantitative surveying of endogeic limbless vertebrates - a case study of *Gegeneophis ramaswamii* (Amphibia : Gymnophiona : Caeciliidae) in southern India. *Appl Soil Ecol* 23: 43–53
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M (2004) Diet of

- the fossorial caecilian *Gegeneophis ramaswamii* (Amphibia; Gymnophiona; Caeciliidae) in southern India. *C R Biol* 327: 65–76
- Measey GJ, Silva J, Di-Bernardo M (2003c) Testing for repeatability in measurements of length and mass in *Chthonerpeton indistinctum* (Amphibia: Gymnophiona), including a novel method of calculating total length of live caecilians. *Herpetol Rev* 34: 35–39
- Merkle S, Hanke W (1988) Long-term starvation in *Xenopus laevis* Daudin II. Effects on several organs. *Comp Biochem Physiol A Physiol* 90: 491–495
- Noble A (1931) *The Biology of Amphibia*. McGraw-Hill, New York
- Oommen OV, Measey GJ, Gower DJ, Wilkinson M (2000) Distribution and abundance of the caecilian *Gegeneophis ramaswamii* (Amphibia : Gymnophiona) in southern Kerala. *Curr Sci* 79: 1386–1389
- Pough F (1980) The advantages of ectothermy for tetrapods. *Am Nat* 115: 92–112
- Presswell B, Gower DJ, Oomen [sic] OV, Measey GJ, Wilkinson M (2002) Scolecophidian snakes in the diets of south Asian caecilian amphibians. *Herpetol J* 12: 123–126
- Seshachar B (1942) The eggs and embryos of *Gegenophis* [sic] *carinosus* Bedd. *Curr Sci* 11: 439–441
- Wake M (1968) Evolutionary morphology of the caecilian urogenital system. I. The gonads and the fat bodies. *J Morphol* 126: 291–331
- Wake M (1980) Reproduction, growth and population structure of the Central American caecilian *Dermophis mexicanus*. *Herpetologica* 36: 244–256

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