

Sexual selection vs ecological causation in a sexually dimorphic caecilian, *Schistometopum thomense* (Amphibia Gymnophiona Caeciliidae)

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Determination of the proximate cause of sexual dimorphism remains difficult, especially when trying to discriminate between sexual selection and ecological causation. A clear rejection of one of these hypotheses would advance the direction of future investigations, especially for cryptic and/or subterranean species. Sexual dimorphism in head size, but not body size, is confirmed for *Schistometopum thomense*, a fossorial caecilian from the island of São Tomé, in the Gulf of Guinea. However, a quantitative and qualitative study of diet reveals no significant difference between males and females sampled from three sites on the island. Females appear to take larger and heavier prey (principally earthworms) than males, despite having a significantly smaller head size. We tentatively reject the ecological causation hypothesis, and discuss several testable hypotheses for evidence of sexual selection.

KEY WORDS: diet, Gymnophiona, predation, resource partitioning, São Tomé, sexual dimorphism, sexual selection.

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INTRODUCTION

DARWIN (1871) first suggested the evolutionary mechanisms through which a sexual dimorphism may arise, and these have been further refined into three

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proximate causes: sexual selection, fecundity selection, and ecological causation (or resource partitioning). Fecundity selection is most commonly evidenced by a sexual size dimorphism (SSD) where females are larger to facilitate an increased fecundity (but see SHINE 1991). SLATKIN (1984) showed the theoretical possibility of the evolution of sex differences in body size and/or feeding structures and behaviour as a result of resource distributions. More recently, TEMELES et al. (2000) demonstrated ecological causation as the mechanism through which the purple-throated carib hummingbird (*Eulampis jugularis*) evolved a sexually dimorphic beak; the sexes have their resources partitioned through different species and/or morphs of *Heliconia*. Although DARWIN (1871) suggested that ecological causation should be associated with a dimorphic feeding apparatus, it is recognized that proving ecological causation over sexual selection is difficult as the former may be an epiphenomenon of the latter (SHINE et al. 2002). Birds are often considered the “model organisms” for studies of sexual dimorphism, but SHINE (1991) and SHINE et al. (1998) highlighted problems caused by the similarity of adult body sizes in birds, and suggested using animals which displayed a wide range of adult body sizes.

Caecilians are poorly known, soil dwelling tropical amphibians, whose ecology still remains largely unstudied probably due to their subterranean habits (MEASEY et al. 2003a). Some caecilians are known to be able to double in size after sexual maturation (e.g. KUPFER et al. 2004). Sexual dimorphism has been studied in very few caecilians, among the few known morphological variants are: a larger head size in males (*Schistometopum* spp., *Scolecophorus* spp. and *Hypogeophis rostratus*: NUSSBAUM & PFRENDER 1998, TEODECKI et al. 1998), differences in cloacal disk form (typhlonectids and ichthyophids: TAYLOR 1968, WILKINSON 1989, KRAMER et al. 2001), and annular and vertebral counts (*Scolecophorus* spp.: NUSSBAUM 1985). Although diet has been specifically studied for very few species (e.g. VERDADE et al. 2000, GABORIEAU & MEASEY 2004, MEASEY et al. 2004), it is known that some terrestrial caecilians are predators of soil macrofauna, and particularly of soil ecosystem engineers (SEE, sensu LAVELLE et al. 1998): earthworms, ants and termites.

Schistometopum thomense (Barboza du Bocage) is a bright yellow caeciliid caecilian, endemic to the island of São Tomé in the Gulf of Guinea. Its startling yellow colour and apparent high densities make it a well known animal on the island. NUSSBAUM & PFRENDER (1998) revised the genus *Schistometopum*, relegating several species to synonymy; one of which “*ephelè*” was described by TAYLOR (1965) on the basis of a proportionately smaller head size and difference in coloration. In their study, NUSSBAUM & PFRENDER (1998) described a microgeographic cline in colour and patterning, as well as describing the sexually dimorphic head morphology of *S. thomense* and its sister species *S. gregorii* from East Africa (see WILKINSON et al. 2003). However, no SSD was recorded for overall body size.

In *S. thomense*, the lack of SSD suggests that fecundity selection be ruled out for this viviparous species, leaving the more difficult determination between sexual selection and ecological causation mechanisms. Defining a clear sexual role for the observed dimorphism may require extensive behavioral observations; difficult within the soil environment and as yet unavailable for any caecilian species. Even were such roles defined, pronounced differences in diet would not allow one hypothesis to be rejected over the other. Thus, whilst ecological causation is extremely difficult to prove, its rejection due to insignificant differences in diet between sexes would leave sexual selection, by elimination, the cause of head dimorphism in *S. thomense*.

In this study we address the alternative hypothesis, proposed by NUSSBAUM & PFRENDER (1998), that the sexually dimorphic head size in *Schistometopum*

thomense results from resource partitioning (ecological causation) or sexual selection. We use a recent collection of *S. thomense* from three localities on São Tomé. We first assess the collection with regard to overall size differences between the sexes, and the sexually dimorphic head size, both previously investigated (NUSSBAUM & PFRENDER 1998). We then use the mass, size and contents of the alimentary canal in a quantitative and qualitative investigation of sexual differences in diet.

MATERIALS AND METHODS

All animals were collected from the island of São Tomé during the months of October and November, 2002. Collections were made from three principle sites: a cacao plantation (Carnival — with bananas and native trees) in the north, natural forest in the centre (Largo Amelia), and small scale agriculture (Porto Alegre — bananas and yams) in the south of the island. Detailed information on localities, sites, and collection methods are presented elsewhere (G.J. MEASEY in prep.). Animals used in this study were euthanased (using the anesthetic MS 222) and fixed (with ca 4% formalin) within 4 hr of capture, and later stored in 70% ethanol. Measurements of total length (TL) and mass were made for preserved animals prior to dissection against a fixed ruler to the nearest mm, and on an electronic balance to the nearest 0.1 g, respectively. Measurements of head length and head width were made with vernier calipers, to the nearest 0.1 mm as described by NUSSBAUM & PFRENDER (1998). Sex was determined by direct inspection of gonads during dissections.

Dissections to remove the alimentary canal, from immediately posterior to the heart to the anterior of the cloaca, were made with the aid of a stereo-zoom microscope (as per MEASEY et al. 2004). This portion of the alimentary canal was weighed (to the nearest 0.0001 g), and the end of the stomach marked with a pin at the constriction and attachment point of the pancreas. The stomach was opened along its length and the contents removed and identified as morphospecies (rather than taxonomically). For earthworms, identification was made on the basis of observations of chetae distribution, general morphology, coloration and size, which occasionally allowed species identification, or otherwise to morphospecies (BOUCHÉ 1972, LAVELLE 1983). The frequency of each morphospecies was recorded, and their mass measured to the nearest 0.0001 g after blotting. The position of the items and their state of digestion were noted. Maximum diameter of the largest prey item in each stomach (where possible) was measured with vernier calipers, to the nearest 0.1 mm.

Data analyses

STATISTICA (v 5.5A, StatSoft, France) was used for statistical analyses of the data. Animals for which sex could not be determined through examination of the gonads (juveniles) were excluded from the following analyses. To test for SSD we made one-tailed t-tests (t_{df} = t-stat) on log converted TL. Following NUSSBAUM & PFRENDER (1998), we used analysis of covariance (ANCOVA) to test for morphometric differences in log converted head size between sexes, with log TL as the covariate, and a univariate (F) test for parallelism of regression lines between groups. Similarly, we used ANCOVA to test for differences between mass of stomach contents and maximum prey size between sexes, using TL as the covariate. Lastly, “between groups” discriminant analysis for sex, from a correlation principle component analysis (PCA) of prey morphospecies (excluding unidentified earthworm pieces), was used to test for frequency and mass differences in diet using the software ADE-4 (THIOULOUSE et al. 1997). Individuals without identifiable stomach contents were excluded from this analysis.

RESULTS

Numbers of males, females and juveniles found at each locality showed a heavy bias toward juveniles in the cacao plantation (Carnival) and no juveniles in natural forest (Table 1). Sex could not be determined for animals smaller than 130 mm, and these were classified as juveniles. Juveniles were equivalent to 29% of the sample, leaving 24 females and 15 males (Table 1). Preserved caecilians were placed into the collection of the Natural History Museum, London (BMNH 2000.301-347 inclusive).

Confirmation of known sexual dimorphism

Total length of females (\bar{x} 256.0 \pm 12.0 mm) was not significantly longer than that of males in this sample (\bar{x} 249.7 \pm 18.1 mm, $t_{37} = 0.408$, $P = 0.343$).

Table 1.

Numbers of male, female and juvenile *Schistometopum thomense* found at three sites on the island of São Tomé in the Gulf of Guinea. Juveniles were animals that could not be sexed, and all were < 130 mm total length.

	Collection dates	Site type	Site position	Males	Females	Juveniles
Carnival	30-31 October 2002	Cacao plantation	00°22'N 06°39'E	3	3	11
Largoa Amelia	14-16 & 24 October 2002	Natural forest	00°17'N 06°38'E	7	12	0
Porto Alegre	2 November 2002	Small scale agriculture	00°02'N 06°32'E	5	9	8

Table 2.

Analyses of covariance of morphometric measurements of male (m) and female (f) *Schistometopum thomense* and their prey. Adjusted means are converted from log results, and only presented when the test for parallelism is not significant.

Character	Sex	n	Adjusted means (mm)	F-test (P) parallelism	R^2
Head length	f	24	8.5	0.549	0.821***
	m	15	9.3		
Head width	f	24	5.6	0.103	0.766***
	m	15	6.3		
Maximum prey diameter	f	14		0.02	0.039
	m	12			
Mass of stomach contents	f	14		0.039	0.228*
	m	12			

* $P < 0.05$; *** $P < 0.001$.

Fig. 1 shows the significantly greater head width (ANCOVA $F_{1,36} = 14.02$, $P = 0.0006$) and head length (ANCOVA $F_{1,36} = 14.79$, $P < 0.0005$) of male *S. thomense*. Unlike NUSSBAUM & PFRENDER (1998), we found that univariate tests show the regression lines are parallel. Hence, from adjusted means male heads are 0.7 mm wider and 0.8 mm longer than those of females (Table 2).

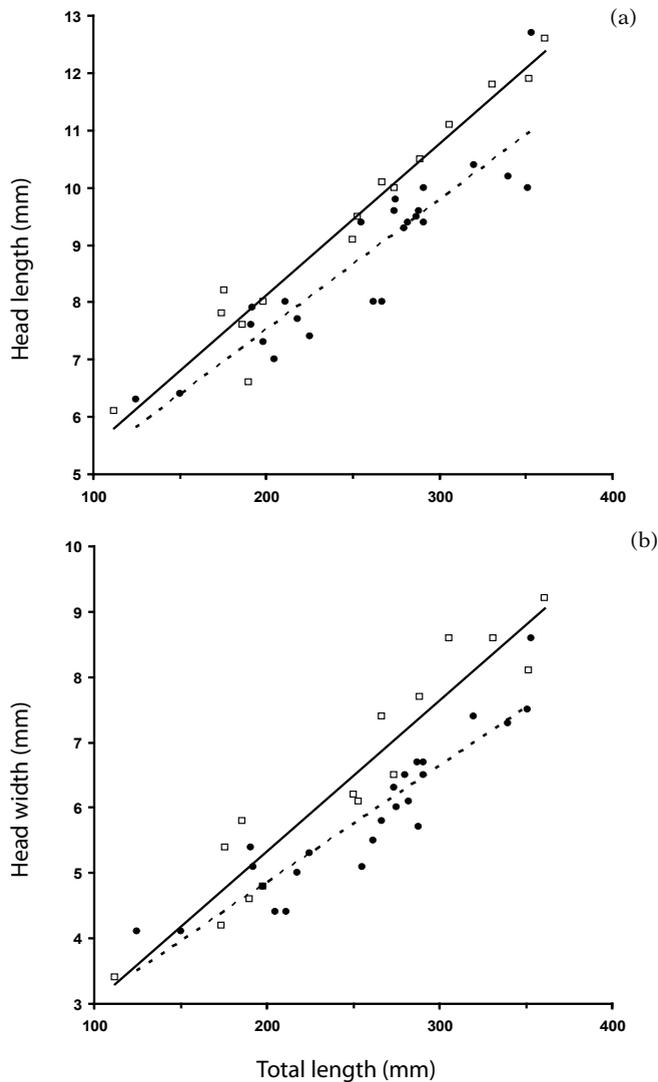


Fig. 1. — Regression of (a) head length and total body length for female (filled circles; dashed line $y = 0.023x + 2.996$ $R^2 = 0.8298$) and male *Schistometopum thomense* (empty squares and solid line $y = 0.026x + 2.851$ $R^2 = 0.9512$); (b) head width and total body length for females (filled circles; $y = 0.017x + 1.268$ $R^2 = 0.8536$) and males (open squares; $y = 0.023x + 0.7194$ $R^2 = 0.9084$) for raw (untransformed) data. N.B. Two black squares represent a male and female that fall on the same point.

Table 3.

Frequency and means with standard error (\pm SE) of stomach contents of *Schistometopum thomense* from São Tomé.

Prey type	Females (n = 24)		Males (n = 15)		Juveniles (n = 19)	
	Frequency	Mean \pm SE	Frequency	Mean \pm SE	Frequency	Mean \pm SE
Earthworm pieces	18	0.75 \pm 0.30	15	1.00 \pm 0.49	17	0.89 \pm 0.45
Earthworm A	0	0 \pm 0.00	3	0.2 \pm 0.11	0	0 \pm 0.00
<i>Amyntas corticis</i>	13	0.54 \pm 0.29	4	0.27 \pm 0.15	0	0 \pm 0.00
<i>Dichogaster greeffi</i>	3	0.13 \pm 0.07	1	0.07 \pm 0.07	0	0 \pm 0.00
<i>Dichogaster</i> sp. D	7	0.29 \pm 0.21	3	0.20 \pm 0.11	4	0.21 \pm 0.10
<i>Dichogaster</i> sp. E	1	0.04 \pm 0.04	3	0.20 \pm 0.14	0	0 \pm 0.00
Earthworm F	0	0 \pm 0.00	2	0.13 \pm 0.09	0	0 \pm 0.00
Earthworm G	2	0.08 \pm 0.08	0	0 \pm 0.00	7	0.37 \pm 0.23
Eurdrilidae	4	0.17 \pm 0.13	4	0.26 \pm 0.21	5	0.26 \pm 0.18
Earthworm I	0	0 \pm 0.00	1	0.07 \pm 0.07	0	0 \pm 0.00
Mean earthworms*	30	1.25 \pm 0.52	21	1.40 \pm 0.47	16	0.84 \pm 0.39
Centipede	0	0 \pm 0.00	2	0.13 \pm 0.09	0	0 \pm 0.00
<i>Wasmannia</i> sp.	1	0.04 \pm 0.04	1	0.07 \pm 0.07	0	0 \pm 0.00
Acariens	2	0.08 \pm 0.06	2	0.13 \pm 0.09	0	0 \pm 0.00
Unidentified larvae	1	0.04 \pm 0.04	0	0 \pm 0.00	0	0 \pm 0.00
Total others	4	0.17 \pm 0.08	5	0.33 \pm 0.16	0	0
Total items	34	1.42 \pm 0.51	26	1.73 \pm 0.53	16	0.84 \pm 0.39

* Earthworm totals and means do not include earthworm pieces.

Table 4.

Discriminant analysis "between test" of sex on correlation Principle Components Analysis results, 9999 replications. The ratio of total inertia and between class inertia gives the amount of variation in the data explained by the class (sex). A significant result ($P < 0.05$) would indicate that diets of males and females were different.

	Males:Females	Total inertia	Between class inertia	Ratio (% explained by sex)	<i>P</i>
Frequency	9:13	13	90.72	7.0	0.907
Mass	9:13	13	76.83	5.9	0.768

Comparison of stomach contents

Empty stomachs were found to account for 39% of males and 40% of females, a chi-squared test shows no significant difference ($\chi^2 = 0.0002$, $P = 0.9899$). Data from these animals were removed from subsequent analyses.

Earthworms were by far the major prey item in terms of mass and frequency, accounting for 98.3% of all prey items identified in stomachs. However, nine mor-

phospecies of earthworms were identified as either epigeic (those that live close to the soil surface and amongst leaf litter) or endogeic (those that live deeper in the

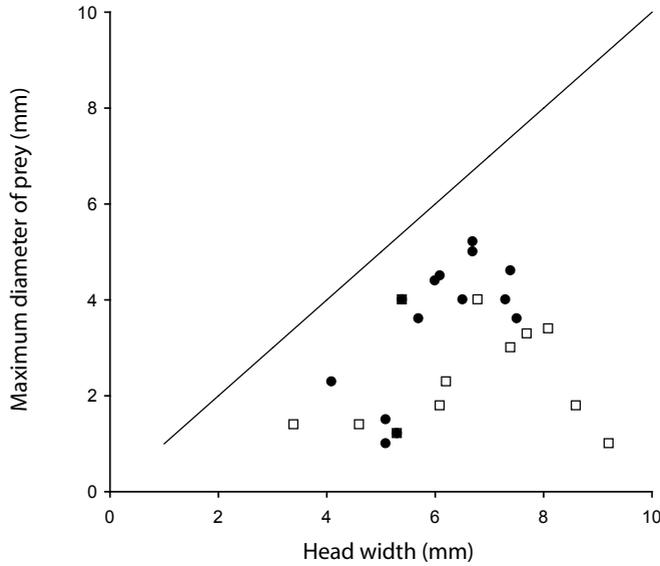


Fig. 2. — The positive relationship between head width and maximum diameter of prey is clear for female (filled circles), but not consistent for male (open squares) *Schistometopum thomense*. The solid line represents parity between head width and maximum diameter of prey. N.B. Two black squares represent a male and female that fall on the same point.

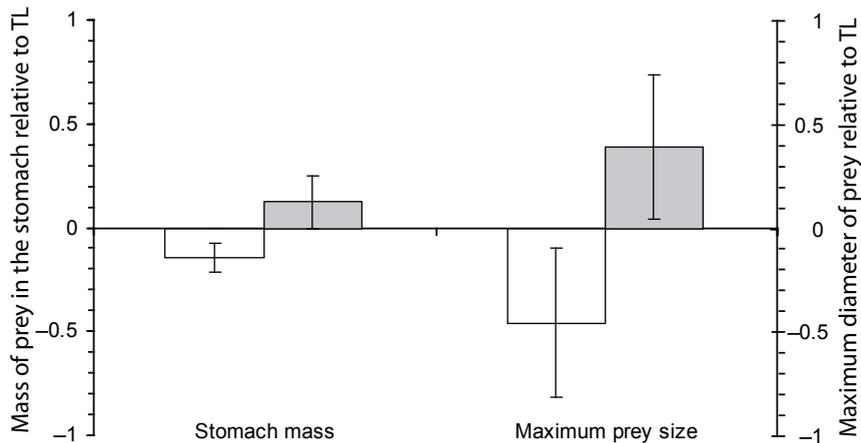


Fig. 3. — The relationship between mass of prey (g, left ordinate) and maximum diameter of prey (mm, right ordinate) relative to total length of *Schistometopum thomense*, males (open bars) and female (shaded bars), using means and standard errors (vertical bars) taken from residuals of linear regression.

soil profile). Other contents included centipedes, an unidentified insect larvae, very small oribatid mites and worker ants (*Wasmannia* sp.) (Table 3). The intestine contained mostly soil and organic matter.

Principle components analysis gave eight and nine important eigenvalues for frequency and mass of prey items, respectively. The between tests discriminant analyses gave one important eigenvalue for each test, and did not find any significant effect between male and female diets (Table 4). Sex only accounted for 7% and 6% of the variation in the dietary data (ratio of total and between class inertia) for frequency and mass, respectively.

Prey size and head size

Average maximum prey size for males was smaller than for females, but the difference was not significant ($F_{1,23} = 2.787$, $P = 0.109$; Figs 2-3). Univariate F tests show that the regression lines for the sexes were not parallel, for maximum prey size and total mass of stomach contents, therefore neither means nor adjusted means can be given (Table 2). Regression of maximum prey size on head width was significant for females ($R^2 = 0.458$, $P = 0.0078$), but not for males ($R^2 = 0.2030$, $P = 0.1644$; Fig. 2). Mean deviations from a regression on all data show that it is males which take smaller prey than females (Fig. 3). Similarly while the total mass of prey items found in stomachs showed no significant difference ($F_{1,23} = 1.37$, $P = 0.2545$) between sexes, it is the females which on average have the heavier stomach contents (Fig. 3).

DISCUSSION

No differences were found between the sexes for the numbers of empty stomachs, diet (by frequency or mass), or total mass of contents (Fig. 3). This data alone would be sufficient to reject the alternative hypothesis that there is resource partitioning between sexes in *Schistometopum thomense*. However this study further demonstrates, that for females, there is a significant relation between the size of the head and the maximum diameter of prey eaten, but this is not true for males (Table 2, Fig. 2); showing that, for males in our sample, a larger head size is not being used to catch larger prey. Moreover, while there is no significant difference between males and females, proportionately it is the females that have the prey with the largest diameter and heavier stomach contents (Fig. 3). Although this result does not seem parsimonious with respect to head size, when the greater relative reproductive investment of females is considered, it is easy to understand why females might be expected to consume more and larger prey items than males, especially in a viviparous species such as *S. thomense*.

There remains the possibility of a Type I statistical error ($\alpha = 0.05$), and we remain critical of the low number of individuals and the single sampling period used in this study. However, we feel that our analyses are robust as we have conducted independent tests on quantity and quality of diet, finding that it is females (although not significantly) that consume the larger prey, both by size and mass. Thus we conclude that for *Schistometopum thomense* in our study there is no suggestion of resource partitioning, the so called "ecological causation" hypothesis.

Rejection of the alternative “ecological causation” hypothesis in this study, does not discount further alternative hypotheses. For example, we cannot know whether the ancestors of *S. thomense*, prior to their arrival on São Tomé, existed in a habitat where male and female resources were partitioned. Evidence that this head dimorphism also occurs in *S. gregorii* might be interpreted as its presence in an ancestral condition (see NUSSBAUM & PFRENDER 1998, WILKINSON et al. 2003).

Intraspecific biting is known to occur in caecilians, with both males and females being bitten (NUSSBAUM & PFRENDER 1998, MEASEY et al. 2001). TEODECKI et al. (1998) have previously discussed possible reasons for such biting in *S. thomense*, including male defense of females, males stimulating females, and lastly communication, which they favoured as an explanation.

TEODECKI et al. (1998) demonstrated that larger head size incurs the penalty of decreased burrowing efficiency. Thus, we would predict that species with a highly subterranean lifestyle would have a less pronounced sexually dimorphic head size. Many caecilians have a complete covering of bone in their skull, others retain an orbit, and the eye is clearly visible under unpigmented skin; as found in *S. thomense*. Both larger head sizes and retention of an orbit suggest a more surface active lifestyle. Some collection sites in this study (Carnival and Larga Amélia) were characterized by hard mineral soils with many animals being found under leaf litter or rotten logs. However, all caecilians from the third site (Porto Alegre), were found within the softer soil there.

Despite previous studies, many factors relating to the sexually dimorphic head size in *S. thomense* remain open to question. For example, NUSSBAUM & PFRENDER (1998) found that the extent of head dimorphism varied between collection sites from North to South of the island coinciding with a change in skin coloration and patterning. That the extents to which head dimorphism and colour differences vary genetically, could be tested using molecular data. Secondly, in animals with an acute sense of smell and highly sensitive tentacles (HIMSTEDT & SIMON 1995), it is not clear why biting would be necessary for obtaining sexual cues.

While we have a clear reason for linking the sexually dimorphic head size in *S. thomense* with sexual selection, we cannot yet be certain that there are enlarged male heads. If, as stated by TEODECKI et al. (1998), sexually receptive females are a scarce resource, males may increase their chances of successful copulation by holding females with their mouths, and not simply relying on their everted copulatory phallus locked inside the female cloaca (see GOWER & WILKINSON 2002). This would explain the bite marks found predominantly toward the head of female *S. thomense* by TEODECKI et al. (1998). For animals that are primarily surface living, shelter (such as rotting logs or dense litter with a good food supply) may have a higher resource value and this may be defended by territorial interactions between males. Field observations suggest that appropriate shelters may be limited as it is not unusual to find more than one animal beneath a large rotting log or within the litter under a large palm (G.J. MEASEY personal observation). Additionally, males might interrupt copulation by biting both copulating male and female in order to force a release. In the scenarios proposed above, a larger head size would have a clear advantage for a male in being able to hold a larger female, as well as increasing success of defending territories or attacking other males.

An important variable in this scenario is the availability of receptive females. *Schistometopum thomense* is reported as being common on São Tomé but with various densities in different habitats (HAFT & FRANZEN 1996, NUSSBAUM & PFRENDER 1998), and as yet, no quantitative assessments of abundance have been made. MEA-

SEY et al. (2003b) found a large variation in densities of *Gegeneophis ramaswamii* in Kerala, southern India, from 0 to 1.87 animals per m². Factors such as territoriality may change in relation to density, as has been reported for plethodontid salamanders (MARVIN 1998). It is clear that more studies, and in particular more field work and collections of *Schistometopum thomense* and other caecilians, are needed to help resolve some of the hypotheses raised in this study. It is also evident that much more remains to be revealed about the Gymnophiona, their lifestyles, behaviours and morphological adaptations.

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