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Bergmann's rule and the terrestrial caecilian *Schistometopum thomense* (Amphibia: Gymnophiona: Caeciliidae)

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ABSTRACT

Question: Do caecilians follow Bergmann's rule?

Hypothesis: Bergmann's rule explains the wide variation in body sizes found among populations of the terrestrial caecilian *Schistometopum thomense*.

Field site: This is a range-wide study incorporating most terrestrial habitats throughout the island of São Tomé in the Gulf of Guinea.

Methods: We performed morphological measurements on 95 museum specimens and 187 field-collected individuals and compared them with site data from 13 separate localities on the island.

Conclusions: This is the first example of a caecilian amphibian that follows Bergmann's rule. Total body mass doubles and length increases by nearly 50% up to 1050 m of altitude. This result is surprising as it occurs virtually on the equator, over a very small spatial scale (< 16 km horizontal), and within a relatively small temperature range (< 10°C).

Keywords: altitude, Bergmann's rule, burrowing, Gymnophiona.

INTRODUCTION

Trends for increasing body size have been hypothesized on macroevolutionary (i.e. Cope's rule) and macrogeographic scales (i.e. Bergmann's rule). Large body size usually confers a range of associated benefits, including defence against predators, predation success, intraspecific competition (including mating success), interspecific competition, and resistance to climatic variation. These benefits are generally thought to outweigh problems, such as increased developmental time and requirements for nutrients (see Hone and Benton, 2005). However, for certain organisms with extreme morphological adaptations for particular habitats, a larger size may result in a reduction of locomotory efficiency, thereby offsetting other potential advantages.

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Bergmann's rule predicts an increasing body size with latitudinal distance from the equator for endothermic vertebrate species, and the modern interpretation includes all situations where environmental temperatures decrease, such as those with altitude, potentially eliminating the macrogeographic scale of this rule (see Mayr, 1956). Bergmann's original explanation for increasing body size was heat conservation for endotherms at lower temperatures. However, it has been asserted that this adaptive explanation does not have to be proven for ectotherms to support the rule (Ashton, 2001). Increased growth rates as a result of directional selection have been shown when growing seasons are severely restricted for some larval amphibians (Ståhlberg *et al.*, 2001), and differences have even been demonstrated on a microgeographical scale (Skelly, 2004). When the stressors of short growing seasons and temperature-mediated mortality are sufficiently reduced, such as in equatorial contexts, we might expect that any remaining (presumably reduced) size differences are the result of the 'developmental temperature–size rule' (see Atkinson and Sibly, 1997).

Two reviews have both suggested a general compliance of amphibians to Bergmann's rule (Ashton, 2002a; Morrison and Hero, 2003). More recently, a detailed study showed that one of two congeneric frogs, occurring along the east coast of Australia, clearly demonstrated Bergmann's rule as well as identifying barriers that may have caused some of the larger morphometric differences observed (Schäuble, 2004). Another recent study has reported an apparent latitudinal limit to Bergmann's rule (Laugen *et al.*, 2005). It is noteworthy that Ashton (2002a) found slightly different trends between the orders Anura and Caudata such that the more sessile salamanders showed a much stronger trend in accordance with Bergmann's rule than the more vagile anurans (see Smith and Green, 2005). Similar differences have been noted between migratory and sedentary birds (Ashton, 2002b; Meiri and Dayan, 2003).

Caecilians are elongate, legless, mostly subterranean inhabitants of the wet or moist tropics (except Madagascar) east of the Wallace line (Himstedt, 1996). Previous investigations on microgeographic differences in morphology of caecilians have revealed surprisingly large inter-population variation in body size. Measey (2004) reported that populations of an East African caecilian, *Boulengerula taitanus*, from a high-altitude forest habitat were on average 30% longer than those from a lower-altitude population found in agricultural land. Nussbaum and Pfrender (1998) provided evidence of sexual dimorphism (males have larger heads), dramatic changes in mean total length between populations (of up to 30%), and north–south microgeographical clines in colour in *Schistometopum thomense* occurring on a small oceanic island, São Tomé in the Gulf of Guinea.

Accordingly, this study describes the broad-scale geographic variation in body size of *S. thomense* from a series of museum specimens and individuals collected during recent fieldwork on São Tomé. We test for differences in body size by comparing total body length and mass of individuals from a number of populations chosen to represent a range of altitudes, habitats, and geographical locations from all over São Tomé. We hypothesize that differences relating to a general geographic cline (see Nussbaum and Pfrender, 1998) would be discernible over horizontal distances (e.g. north–south or east–west), whereas changes in size relating to altitude would not take any account of horizontal inter-site distances, but only collection site elevation. As the island represents the total known range of this species (Nussbaum and Pfrender, 1998), it can be considered to be a range-wide study.

METHODS AND MATERIALS

Study site

São Tomé is a small oceanic island [836 km^2, highest peak 2024 m above sea level (asl)] in the Gulf of Guinea lying immediately north of the equator, and 250 km from the coast of Gabon in continental Africa. It is one of four islands that form the offshore part of the Cameroon line and has been isolated from mainland Africa since its volcanic origin (Jones, 1994). The island lies within the wet tropical belt but has distinct seasonality, a short dry season from June to September, which is most pronounced at lower altitudes and towards the north of the island. Annual rainfall ranges from around 1000 mm in the northeast to more than 4000 mm in the southwest, and mean annual temperatures range from maxima of 30°C to 33°C and minima of 18°C to 21°C, with little seasonal variation and high humidity throughout the year (Gascoigne, 2004).

São Tomé has large forest reserves covering approximately a third of the island, most of which is inaccessible primary forest (Gascoigne, 2004). The remaining areas are predominantly agricultural: low-intensity private holdings, market gardens or plantations of cacao, oil palm, and coffee. Following independence (São Tomé e Príncipe) in 1975, many plantations were abandoned generating considerable areas of secondary forest (Gascoigne, 2004).

Study species

Schistometopum thomense (Bocage) is a bright yellow caeciliid caecilian, endemic to São Tomé. Its startling coloration makes it a well-known animal called 'cobra bobo' [locally meaning 'yellow snake', and not the literal translation 'silly or foolish snake' given by Nussbaum and Pfrender (1998, p. 31)] on the island, where many residents describe it as plentiful or abundant. Previous studies of *S. thomense* on São Tomé have remarked on its high abundance and cosmopolitan distribution (see Haft and Franzen, 1996; Nussbaum and Pfrender, 1998; Drewes and Stoelting, 2004), possibly explaining why it is a comparatively well-studied species (e.g. Greef, 1884; Haft, 1992; Ducey *et al.*, 1993; Teodecki *et al.*, 1998; Delêtre and Measey, 2004).

Fieldwork

São Tomé was visited in October 2002 and September 2003. Eleven sites were chosen to give a range of altitude, habitat, and geographical distribution (Table 1). Locality positions and altitude were measured with a Garmin 12XL GPS receiver (datum WGS 84) where possible. In cases where this was not possible (such as some forested areas with closed canopies), or where caecilians were collected over a large altitudinal range, an approximation was made using the nearest GPS waypoint (at the edge of the forest or a break in the canopy) and a digital map of the island (Wojciechowski and Gascoigne, 2004).

Material examined and measurements

Measurements of total length and mass were made from preserved animals before dissection against a fixed ruler to the nearest millimetre and on an electronic balance (CM 320-1, Kern, Germany) to the nearest 0.1 g, respectively. Repeatability for such measurements has already been shown to be high (Measey *et al.*, 2003). Sex was determined where possible by direct inspection of gonads through a small ventral incision.

Table 1. Site details for 13 localities on São Tomé Island, Gulf of Guinea, with raw morphological data for *Schistometopum thomense* from 13 sites on São Tomé

Site	N	E	Altitude (m)	Soil temperature (°C)	*n*	Female TL (mm)	Male TL (mm)	Female mass (g)	Male mass (g)
Binda	0°13′	06°43′	150	23.5	22	185.4 ± 4.91 (15)	198.8 ± 6.94 (6)	6.7 ± 0.54 (15)	7.1 ± 0.76 (6)
Canivial	0°27′	06°39′	100	25	17	186.0 ± 24.06 (3)	216.0 ± 53.72 (3)	7.8 ± 2.63 (3)	14.1 ± 8.42 (3)
Java	0°15′	06°39′	600	#	36	204.6 ± 4.96 (21)	200.3 ± 7.74 (15)	8.1 ± 0.46 (21)	8.0 ± 0.83 (15)
Lagoa Amelia	0°20′	06°35′	1200	20	27	283.1 ± 11.08 (16)	290.0 ± 16.10 (11)	24.1 ± 2.19 (15)	26.5 ± 3.73 (11)
Macambrara	0°16′	06°36′	1360	18.3	8	275.8 ± 18.87 (4)	228.7 ± 46.58 (3)	16.9 ± 2.25 (4)	14.6 ± 6.51 (3)
Porto Alegre	0°02′	06°31′	45	26.1	22	227.9 ± 12.77 (9)	218.0 ± 20.23 (5)	12.2 ± 1.82 (9)	11.8 ± 2.54 (5)
Quisinda	0°18′	06°43′	55	25.1	16	229.9 ± 4.23 (7)	228.4 ± 7.56 (9)	9.2 ± 0.97 (7)	10.2 ± 1.72 (9)
Ribeira Peixe	0°06′	06°36′	76	24.5	20	203.8 ± 7.36 (13)	154.8 ± 3.75 (5)	9.7 ± 0.85 (13)	4.6 ± 0.45 (5)
Rio Maria Luisa	0°19′	06°30′	15	27.1	24	205.0 ± 8.57 (8)	211.1 ± 9.57 (11)	8.9 ± 0.99 (8)	8.9 ± 0.88 (11)
Santa Fe	0°17′	06°40′	408	23.5	21	213.8 ± 6.54 (18)	212.1 ± 4.94 (16)	9.6 ± 0.96 (17)	9.6 ± 0.71 (16)
Santa Luiza	0°16′	06°39′	400	#	20	200.7 ± 4.68 (9)	199.6 ± 8.82 (11)	7.5 ± 0.43 (9)	7.2 ± 0.80 (11)
Saudade	0°17′	06°38′	770	22.2	19	257.3 ± 27.57 (6)	227.6 ± 18.35 (9)	21.3 ± 6.08 (6)	13.1 ± 2.56 (9)
Zico	0°17′	06°34′	860	22.4	15	208.1 ± 8.71 (10)	252.6 ± 6.45 (5)	8.3 ± 0.92 (10)	11.1 ± 0.74 (5)

Note: Mean (±standard error) total length (TL) and mass for adults (no juveniles) together with sample sizes in parentheses. # = missing data.

Data analyses

As it is possible that differences in body length may arise from purely populational characteristics (disproportionate numbers of juveniles or adults), we used a general linear model (GLM) as implemented in PROC MIXED of the SAS statistical package (Littell *et al.*, 1996). Site was added as a random effect (to remove possible demographic differences between sites), as well as interactions between site and any other individual specific covariate used. All statistics were calculated with SAS (v 8.02), and details of other tests are given in the text.

RESULTS

A total of 187 animals were collected from 11 sites visited on São Tomé during October 2002 and November 2003 (Table 1). Together with 95 specimens from four sites collected for the Californian Academy of Sciences, this gave a total of 282 individuals for analysis. Individuals that were extensively damaged ($n = 2$) were not weighed.

More females than males were collected at most sites (Table 1). Overall, 56% (95% confidence interval = 51–61%) of individuals that could be sexed were found to be female, such that the sex ratio differed from the expected 1:1, a pattern consistent across the different sites ($\chi^2_{12} = 10.2$, $P = 0.60$). Overall adults had no sexual size dimorphism ($F_{1,12} = 1.05$, $P = 0.33$) (Table 1). Hence, we did not analyse the data for total length differently for the two sexes. Juveniles (animals that could not be sexed) were found at most sites (8/13) with one site (Canivial) having more juveniles than adults. This gave a substantial variation in size at most sites (Table 1, Fig. 1). However, to reduce potential bias in our results, we did not remove juveniles from the analyses unless specified.

The overall mean mass (9.99 ± 0.46 g) increases by 151.6% for animals collected from Lagoa Amelia (25.12 ± 1.99 g; 1200 m asl) and decreases by 34.2% at Binda (6.57 ± 0.46 g; 150 m asl) (Table 1). Thus, the mean change in mass between populations only 15.6 km (direct horizontal distance) and 1050 m (difference in altitude) apart is nearly double (186%). The corresponding measurements for mean body length indicate (206.2 ± 3.15 mm) an increase of 38.6% for Lagoa Amelia (285.9 ± 9.11 mm) and a decrease of 9.7% at Binda (186.3 ± 4.95 mm), with an overall change of nearly 50% (see Table 1). Regression analysis showed that elevation explained 46% of the variation in mean mass (data log-transformed and no juveniles) ($F_{1,11} = 9.33$, $P = 0.043$) and 56% of variation in mean total length ($F_{1,11} = 13.91$, $P = 0.004$).

These inter-site differences were not solely due to differences in population structure, since the total length and body mass of *Schistometopum thomense* were positively related to altitude (total length: $F_{1,10} = 12.8$, $P = 0.005$; body mass: $F_{1,10} = 11.8$, $P = 0.007$) (Fig. 2). However, no north–south (total length: $F_{1,9} = 0.2$, $P = 0.68$; body mass: $F_{1,9} = 0.19$, $P = 0.67$) or east–west (total length: $F_{1,9} = 0.35$, $P = 0.56$; body mass: $F_{1,9} = 0.02$, $P = 0.89$) microgeographical clines were observed.

Given the established relationship of temperature with altitude (Barry and Chorley, 1992), we anticipated a significant relationship of *S. thomense* total length with recorded soil temperature, and this was the case ($F_{1,10} = 9.3$, $P = 0.01$).

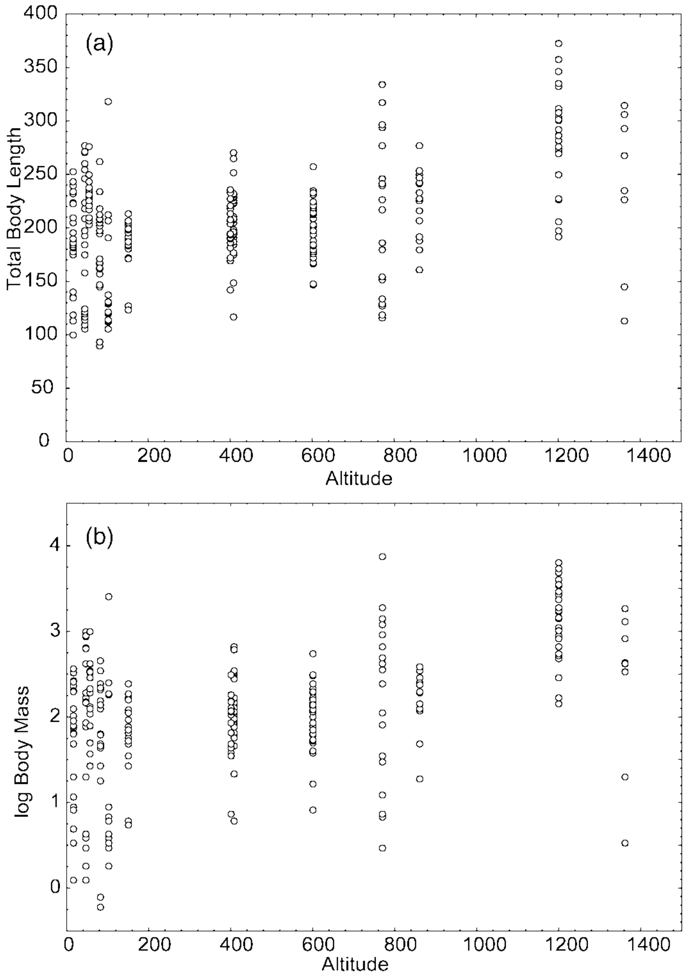

Fig. 1. Scatterplots showing the relationship of *Schistometopum thomense* total length in millimetres (a) and mass in grams (b) as a function of altitude in metres, from 13 sites on São Tomé.

DISCUSSION

Explaining Bergmann's rule in amphibians

Bergmann's rule has been shown to hold for certain Anura and Caudata (Ashton, 2002a), but this is the first example demonstrating Bergmann's rule in the Gymnophiona. This finding has important implications for the ongoing discussion on the validity of large-scale macroevolutionary rules. Here we consider our results in the light of previously proposed genetically mediated adaptive explanations and the 'developmental temperature–size rule' (see Atkinson and Sibly, 1997).

Bernardo (1994) suggests that small body size has an adaptive value in warmer areas, reducing daily maintenance costs for low-altitude populations of salamanders in his study. He argues that because of the positive relationship between metabolism and temperature/

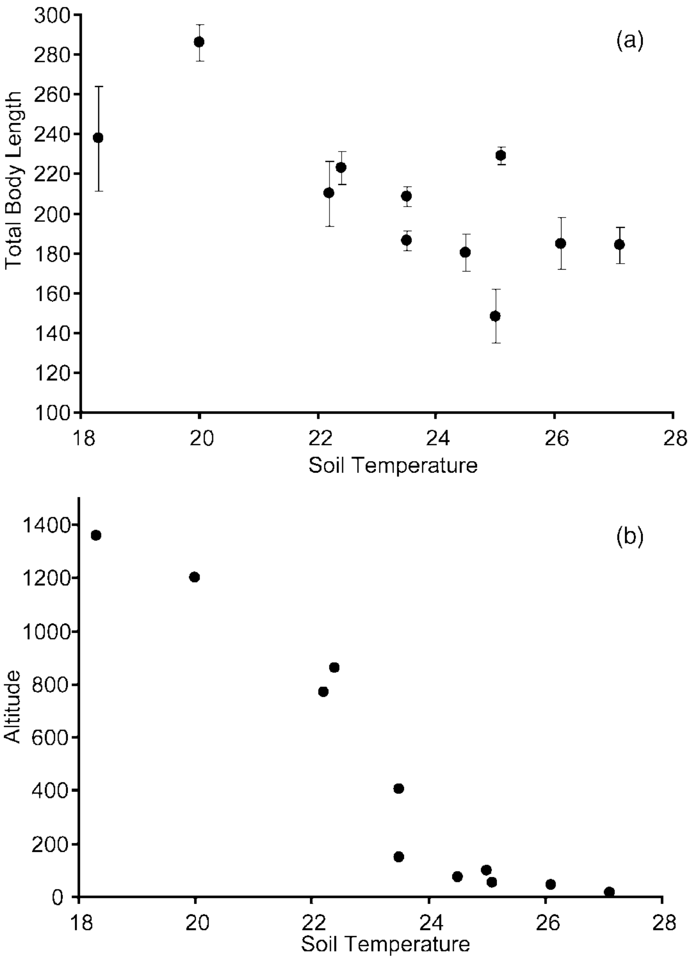

Fig. 2. (a) Mean total body length of *Schistometopum thomense* in millimetres (standard error shown with bars) and (b) altitude in metres as a function of soil temperature in degrees centigrade (at a depth of 10 cm), from 11 sites on São Tomé.

body size, larger size is less costly at higher sites where the active season is shorter. Ashton (2002a) favours this explanation as he reasons that larger body size confers fasting endurance to amphibians in cooler, more seasonal environments as larger animals can store more fat. This adaptive explanation could be considered as an ectothermic equivalent to Bergmann's original heat conservation mechanism for endotherms.

Another explanation given for altitudinal differences in size is climate-induced demographically differential survivorship. Rosso *et al.* (2005) report that populations of Italian tree frogs were younger (and hence smaller) in colder climates, surmising that climate has a substantial impact on demography. In their study, this factor worked against Bergmann's rule, although an age bias associated with climatic features could potentially produce data that resemble this rule (see also Monnet and Cherry, 2002). Similarly, Ashton (2002a) draws attention to climatic changes in humidity and precipitation as a major determinant of amphibian body size. This simple adaptive explanation provides an advantage for larger individuals which have greater desiccation tolerance because of the relative decrease in surface area. Atkinson and Sibly (1997) consider this to be a resource-limiting factor, whereby reduced size at maturity is an adaptation before growth rate is curtailed, in this case by moisture. Although Ashton gives several examples of amphibians that are larger in drier climates (see Ashton, 2002a and references therein), this mechanism is presumably a confounding effect when rainfall or humidity increases with altitude or decreasing latitude (see also Laugen *et al.*, 2005).

The 'developmental temperature–size rule' is based on differences in the growth coefficient from the von Bertalanffy equation for growth curves (see Atkinson and Sibly, 1997; Angilletta and Dunham, 2003). Although von Bertalanffy growth curves were conceived to explain determinate growth of endotherms, they are also employed for indeterminate growth of ectotherms (Angilletta and Dunham, 2003), including amphibians (e.g. Hota, 1994). During development, some processes are sensitive and others insensitive to temperature. Inequalities between temperature-insensitive diffusion rates (governing protein synthesis) and temperature-sensitive enzyme reactions (responsible for DNA replication) produce rapid cell division but limit cell growth. A lower growth coefficient is equivalent to slower initial growth rates at cool temperatures, but an asymptote at a larger adult size. Conversely, at higher temperatures faster initial growth results in a lower asymptote and smaller adult size (see Atkinson and Sibly, 1997).

In the ongoing debate over whether large body size is adaptive or the unavoidable consequence of a physiological constraint (Angilletta and Dunham, 2003), our example of a subterranean ectotherm appears both pertinent and revealing. We report a near two-fold increase in body mass and a 50% increase in body length over a very small geographic distance and temperature change. This size change is larger than any reported by Ashton (2002a) and is, to our knowledge, the greatest reported for any amphibian. However, it should be noted that due to the substantial difference in morphology between Anura, Caudata, and Gymnophiona, it is inappropriate to compare slopes of change in body length as reviewed by Ashton (2002a). Data on changes in mass are comparable but infrequently reported.

Environmental or genetic determination of body size trends?

The adaptive explanations for Bergmann's rule outlined by Ashton (2002a) are not congruent with our example. For example, although cooler, what passes for seasonal change in this equatorial island is (if anything) reduced at higher altitudes where rainfall is greater and spread more evenly throughout the year (Gascoigne, 2004). In addition, given the relatively small changes in environmental temperature (especially the lack of freezing), we do not consider that this would produce differential survivorship (see Rosso *et al.*, 2005) for *S. thomense* on São Tomé. This also responds to Ashton's (2002a) suggestion for the strong influence of another environmental factor, rainfall. Some evidence indicates that caecilians are dependent on soil moisture content (e.g. Kupfer *et al.*, 2005; Measey *et al.*, 2006); if implicated we would expect this to produce a north–south size difference (see above). However, to completely rule out other proximate or adaptive causes, reciprocal transplant studies and/or 'common garden' experiments are needed.

We know of no incidents where larger body size would be advantageous to populations of *S. thomense* at higher altitudes, although it might be a disadvantage. An increase in head size may impact on the ability of an individual to construct tunnels due to the exponential relationship between body diameter and work required for burrowing (Navas *et al.*, 2004). Previous studies of *S. thomense* and other caecilians have shown that increasing body size reduces burrowing performance (Ducey *et al.*, 1993; Teodecki *et al.*, 1998). Therefore, rather than conferring an adaptive advantage, large size associated with lower developmental temperatures may represent a disadvantage for organisms specialized for a burrowing lifestyle.

Ashton (2002a, p. 714) proposes that the direct effects of temperature on body size 'may at least partially explain why most amphibians have a larger body size in cooler areas'. However, we believe that the 'developmental temperature–size rule' is the only hypothesis that explains the variation in body size with climate of *S. thomense* on São Tomé. While terrestrial and aquatic amphibians may be able to optimize developmental temperatures of their offspring through behaviour or choice of microhabitats (Freidenburg and Skelly, 2004), we believe that the subterranean caecilians do not have similar possibilities.

Soil is a complex, dense medium that not only restricts movement of its inhabitants, but also buffers abiotic factors. Generally, the soil becomes cooler with reduced fluctuations in diel temperature as depth increases; typically at around 50 cm depth, only slight seasonal temperature fluctuations occur (see Lavelle and Spain, 2001 and references therein). Thus, as a habitat, soil provides its inhabitants with reduced fluctuations in temperature compared with terrestrial and aquatic habitats, although the extent of this will depend on the soil depth at which animals inhabit. Despite these buffering effects, we show here that an altitudinal cline in soil temperature measured at a depth of 10 cm (Table 1, Fig. 2b) corresponds to known altitudinal changes in air temperature (see Barry and Chorley, 1992). Hence, with the reduction in variation of environmental microclimates and the decreased mobility of subterranean burrowers, caecilians may have limited behavioural control of their body temperature (see Measey and Barot, 2006). In addition, *S. thomense* is a live-bearing caecilian (Haft and Franzen, 1996), suggesting that temperature during development is similar to that experienced by adults, thereby removing conflicting or confounding ontogenetic temperature influences.

It should be stressed that we know very little of the ecology of caecilian amphibians; in particular, the concept of a caecilian home range has yet to be explored (Measey and Di-Bernardo, 2003). However, their relatively sessile and subterranean lifestyle may mean that changes in temperature with altitude have a larger effect on caecilians than on other sympatric amphibians. Certainly, more studies of the change of caecilian morphology with environment are welcome, making an important contribution to the ongoing debate on Bergmann's rule.

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