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Life history and reproduction of the neotropical caecilian *Siphonops annulatus* (Amphibia, Gymnophiona, Siphonopidae), with special emphasis on parental care

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Abstract

Due to their mainly fossorial way of life, caecilian amphibians are the least known order of terrestrial vertebrates. Here, we present new observations on the natural history and reproductive biology of the neotropical oviparous, siphonopid caecilian *Siphonops annulatus* from a long-term study of this species in the field and in captivity. In the studied population, mating occurs between the end of August and beginning of October, and oviposition between November and December, when rainfall peaks. Egg hatching occurs between the end of December and beginning of January. The complete cycle of maternal care, from oviposition to independent, self-sufficient offspring lasts about 3 months. After eclosion, the altricial young feed on the mother's specially modified skin (maternal dermatophagy) and are also supplied by a fluid released from coming from the maternal cloaca. Also presented are observations on the burrows, feeding and social behaviour of *S. annulatus*.

KEYWORDS

caecilians, dermatophagy, natural history, parental care, *Siphonops annulatus*, skin feeding

1 | INTRODUCTION

Caecilians are distinctive, mainly tropical, limbless, serpentiform amphibians, and the sister group of frogs and salamanders (Batrachia). Most are fossorial, and thus inconspicuous, and they rank among the most poorly known vertebrates (Wilkinson, 2012) with particularly scarce information on physiology, ecology, natural history and behaviour of these animals particularly scarce (e.g. Jared, Navas, & Toledo, 1999; Junqueira, Jared, & Antoniazzi, 1999; Kupfer, Nabhitabhata, & Himstedt, 2004, 2005). Similarly to other amphibians, the caecilians have glands in the skin that are responsible for the secretion of toxins for defence, but also mucus that, besides their use in respiration, have an important role in burrowing locomotion (Jared et al., 2018). Nonetheless, caecilians are noted for their diversity of reproductive modes (e.g. Parker, 1956; Taylor, 1968; Wake, 1977; Wilkinson & Nussbaum, 1998; Gomes, Antoniazzi, Navas, Moreira, & Jared, 2012; Kupfer, Maxwell, Reinhard, & Kuehnel, 2016). They may be oviparous, with an aquatic larval stage (Sarasin & Sarasin, 1887–1890), oviparous with direct development (Brauer, 1899) or viviparous (Peters, 1875). In oviparous species, parental care is, as far as is known, maternal and includes guarding of eggs until hatching with or without subsequent care of hatchlings. In the former case, initially, pigmentless, altricial young tear off and eat the outermost layer of the hypertrophied skin of their attending mother (maternal dermatophagy) within her nest chamber, using specialized vernal teeth

(Kupfer et al., 2006; Wilkinson et al., 2008; Wilkinson 2012; San Mauro et al. 2014).

The first Neotropical species in which maternal dermatophagy was reported is *Siphonops annulatus* Mikan 1820 (Wilkinson et al., 2008). This species inhabits many environments, from very dry regions (semi-arid) to tropical forests, and, perhaps consequently, has the broadest geographic distribution of any caecilian (Taylor, 1968). It is especially common in the cacao (*Theobroma cacao* L., Malvaceae) plantations of southern Bahia, Brazil (Jared, Antoniazzi, Wilkinson, & Delabie, 2015). Cacao plantations are important to the conservation of the Brazilian Atlantic Forest biome (Jared et al., 2015; Schroth et al., 2011), which is considered the most threatened biodiversity hotspot in South America (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). In the “cabruca” agroforestry system, cacao is planted in the shadow of selected large native trees after elimination of the undergrowth (Cassano, Schroth, Faria, Delabie, & Bede, 2009; Landau, Hirsch, & Musinsky, 2008). Besides preserving biodiversity, the cabruca also preserves many of the original soil characteristics of the Atlantic Rainforest (Johns, 1999).

Since 1988, we have made multiple expeditions to Southern Bahia, Brazil, to study the local herpetofauna and its relationship with the cacao plantation, focusing especially on fossorial species, and making a range of field observations on caecilians (Jared et al., 2015). With the knowledge acquired from these field observations, we established a methodology for maintaining and breeding *Siphonops annulatus* in captivity, making this species an exceptionally good model for the study of caecilians (Jared et al., 1999; Junqueira et al., 1999). Although dermatophagy in *S. annulatus* has been known for a decade (Wilkinson et al., 2008) and its reproductive cycle has already been studied through a metabolic and endocrine approach (Gomes et al., 2012), direct observations on the history of life and behaviour of this species are still practically inexistent, especially those involving reproduction and parental care. Data on long-term studies, mainly in the field, about caecilians, in general, are inexistent. In this paper, we show many different aspects of the natural history and reproductive biology of *S. annulatus* collected along 10 years of fieldwork within the cacao plantations in Bahia, and in captivity. The results demonstrate the great effort expended to localize these fossorial animals in nature and to collect data about their cryptic life habits. We also present inedited data on the environment, microhabitat, fossorial life, copulation, oviposition and development of litters along the parental care.

2 | METHODS

2.1 | Locality of the study

Siphonops annulatus was observed in cacao plantations and in Atlantic Rainforest remnants belonging to the Experimental Farm of the CEPLAC-CEPEC (Brazilian Federal Government/Agricultural Ministry) located in the municipality of Ilhéus in the state of Bahia (BA). Cacao plantations, in the municipalities of Ilhéus and Itabuna, occupy 19.542 km^2 of the Brazilian Atlantic Forest, approximately between 39°00′W and 39°30′W, and 14°20′S and 15°00′S, elevation between 60 and 110 m, and bordered to the east by the Atlantic Ocean (Faria Filho & Araujo, 2003). The climate is typically humid or subhumid with annual average temperatures from 21 to 25°C, maxima between 26.1°C and 30.3°C, minima from 17.1 to 20.8°C and daily variation of not more than 10°C (Santana et al., 2003). Rainfall is regular, with abundant rains throughout the year particularly during the austral summer (December to March) and part of the austral winter (June to September). Close to the coast, an average annual rainfall of 1716.3 ± 408.1 (range 1199.5–2925.3) mm was observed (INMET, 2017; Table S1). The original vegetation of the region is perennial, broad-leaved, closed, moist forest, typical of the Atlantic Rainforest biome and characterized by an abundance of large trees and epiphytes with a great variety of lianas, ferns and palms (Velloso, Rangel Filho, & Lima, 1991). In the study area, cacao is traditionally cultivated beneath the canopy of large native trees in the cabruca system.

2.2 | Data collection

The data presented here were obtained in 10 expeditions from 2001 to 2017 covering the months of January, February, March, August, September and October. During these expeditions, specimens of *Siphonops annulatus* were collected in the cacao plantations by active search consisting in digging the soil, turning fallen vegetation such as epiphytes and decomposing trunks and branches or raking other sites rich in organic matter. Adults, hatchlings and young were maintained in the vivarium of the Cell Biology Laboratory at the Instituto Butantan (São Paulo) where observations on breeding, growth (from total length and body mass measurements) and behaviour in captivity were registered by daily notes and photography. As there is no obvious sex dimorphism in *S. annulatus* (Gomes et al., 2012), captive specimens were randomly maintained in numbers varying from 10 to 20 animals in plastic boxes (78 cm length × 56 cm width × 41 cm height) with soil, humidified daily and fed weekly with various food items including minced meat, chicken or fish, beef heart, earthworms, newborn mice and canned dog or cat food. Some studied specimens were fixed in formalin and were deposited in the MZUSP (Museu de Zoologia da Universidade de São Paulo), under MZUSP numbers 71276, 71277–71279, 71280–71284, 71285–71290, 135063–135065, 138852–13886, 139038–139042, 139045–139052. Rainfall data were furnished by the Instituto Nacional de Meteorologia

(INMET), from the meteorological station of Canavieiras, BA, within the region of cacao plantation (Table S1).

2.3 | Data analyses

The collecting effort required to find *Siphonops annulatus* was quantified as person-hours per animal (excluding clutches of eggs and broods of hatchlings), which is the total of hours worked in the different field expeditions multiplied by the number of collectors and divided by the number of animals found. A relationship between collecting effort and total rainfall for the specific month of each trip was assessed with the Spearman correlation test. The relationship between the mass and length of the mothers with the number of young per clutch, as well as young mass and length, was also analysed using the same statistical test. Results were presented as mean ± standard deviation (*SD*). Alpha was set at 0.05 in all tests. All statistical tests were conducted using SigmaStat 3.5.

3 | RESULTS

3.1 | Fieldwork

In 10 expeditions, a total 703 person-hours of active search by digging were expended, and 71 specimens (not including hatchlings) were collected (88.6 g ± 27.75 g/45.04 cm ± 3 .10 cm) of which 21 were females with clutches of hatchlings (48–109 g/38.7–48.2 cm; Table 1). Thus, the average collection effort was 10.5 person-hours per specimen of *Siphonops annulatus*. Effort varied across the different expeditions between 4 and 20 person-hours (Table 1). There was no significant relationship between rainfall and the rate of collection (rs = −0.3976, $p = .2552$).

3.2 | Environment

The outside appearance of the cabruca closely resembles a rainforest and does not indicate the existence of a plantation (Figure 1a). In the interior, fallen leaves of cacao are not removed and form a thick litter (Figure 1b). It is quite evident that the litter creates a barrier against soil desiccation, maintaining humidity and providing an environment rich organic matter, similar to that of the original Atlantic Rainforest.

Organically, rich soils provide suitable shelter mainly for invertebrates such as earthworms, centipedes, millipedes, spiders, cockroaches, insect larvae, but also for small mammals, squamate reptiles and anuran and caecilian amphibians, such as *Siphonops annulatus* (Jared et al., 2015). Additionally, *S. annulatus* are frequently found near the roots of large trees (Figure 1c) such as *Erythrina* spp. and *Ficus subtriplinervia* Mart, which also provide an extremely humid and nutrient-rich environment of accumulated humus. Another place preferred by *S. annulatus* is beneath large decomposing epiphytic bromeliads, mainly *Aechmea lingulata* L. that have fallen to the ground. The microhabitat below fallen bromeliads is rich in decomposing organic material and has a diverse and abundant fauna of invertebrates. The amphisbaenian *Leposternon infraorbitale* Berthold 1859 and the blindsnake *Amerotyphlops brongersmianus* (Vanzolini 1976) are also common under fallen bromeliads. *Siphonops annulatus* can also be found under piles of cut grass in the fields, but we have never found this caecilian in very sandy soil or very rocky places.

TABLE 1 Field work data

Month	Year	Rainfall (mm)	Field work (hr)	*N*	*N* Litter	*N* Young/litter	Man-hours/specimen[a]
January	2005	158.2	40	2	1	16	20
	2007	31.5	144	14	9	5, 10, 6, 14, 8, 7, 7, 9, 8	10
	2016	281.2	102.5	13	1	11	8
February	2006	20.8	132	10	7	12, 12, 8,14,16,14,10	13
	2017	145.3	16	4	3	15, 6, 5	4
March	2015	66.9	124	16[b]	0	–	8
May	2013	254.2	70.5	7	0	–	10
August	2001	130.6	20	1	0	–	20
September	2008	46.8	63	4	0	–	16
October	2009	256.9	32	0	0	–	–
Σ			744	71	21	213	–

hr, hours; mm, millimetres; *N*, number of animals.
[a]Adults/juveniles.
[b]Eight juveniles.

FIGURE 1 Characteristics of cacao plantation in the Cabruca system. (a) View from outside showing the forest-like canopy. (b) Interior view of the plantation showing the shady environment and the thick leaf litter. (c) Foot of a *Erythrina* sp., with large roots. (d) Part of a tunnel of *Siphonops annulatus* found during digging

3.3 | Fossorial life

In nature, well-constructed, sometimes ramifying tunnels are occasionally visible during digging (Figure 1d). *Siphonops annulatus* were found in quite superficial tunnels no deeper than 20 cm. These tunnels are characterized by smooth and shiny walls and are readily distinguished from those of the syntopic amphisbaenian *Leposternon infraorbitale* that can be recognized by the scale marks forming delicate rings and the v-shaped marks of the nostril tip that is actively used for tunnel excavation.

3.4 | Reproduction

In the field, we never encountered caecilians copulating, but twice in captivity, once in the end of August and another in the beginning of October, copulating couples were fleetingly observed at the laboratory (Figure 2a). In both cases, one of the individuals remained belly up with a visible increase in gular (ventilatory) movements (Figure 2a).

In captivity, females with egg litters ($n = 10$) were found between the second half of November and the first half of December (Figure 2a). Just after oviposition, the vitelline membranes of adjacent eggs form connecting strings (chalazae). After some time, this "bead necklace" appearance disappeared and the connections among eggs were typically tangled, with the clutch of eggs resembling a bunch of grapes (Figure 2b,c). Hatching occurred between the second half of December and the beginning of January.

In the field, offspring attended by a presumed mother were found in the months of January and February (Figure 3a). Numbers per brood ranged from 5 to 16 (mean 10 ± 4). We did not find any correlation between the clutch size and the mass (rs = 0.0195, $p = .9794$) and the clutch size and the length (rs = −0.2654, $p = .3808$) of the attending females and the number of offspring. In addition, there was no significant relationship between the mother's mass and that of the offspring (rs = −0.5330, $p = .0607$) or between the mother's length and offspring length (rs = −0.3200, $p = .2864$).

3.5 | Parental care

Parental care is divided into two distinct and obvious stages. During care of eggs, attending females remained shiny greyish-blue typical of the species (Figure 2b), but immediately after hatching, her colour changes to opaque whitish-blue (Figure 3a). Only during the period of posthatching, parental care is there an obvious external sexual dimorphism.

Nests are found in humid places with a high concentration of organic matter (Figure 3b) and always located in well-protected, but not deep (<15 cm), spots. The great

FIGURE 2 Aspects of reproduction and parental care of egg litter in *Siphonops annulatus*. (a) Copulation in captivity. Note that one of the animals remains belly up. (b) Mother and eggs (c) detail of the egg litter

majority of the nests (approximately 80%) were found at the bases of large trees (mainly *Erythrina sp*), among the roots, some of them serving as walls (Figure 3a,b). Other nests were located under decomposing tree stumps or trunks or among litter mounds. The nest consists of a rounded chamber just sufficient to contain the coiled mother's body and the young (about 10–15 cm), with loose and weak walls, quite dissimilar to their tunnel walls, and making it hard to discern all features during excavation (Figure 3a,b) and with one or more exits.

In captivity, egg clutches are usually surrounded by the coiled body of the attending mother and the egg mass is often gently displaced by the mother's head (Figure 2b). After hatchling, the gill-less, unpigmented, altricial hatchlings continue to receive maternal care in the nest until the beginning of March. Skin feeding occurs in short and intense bouts of seemingly frenzied, but coordinated (all young feeding simultaneously) activity, which must somehow be initiated through signals that the stratum corneum is ripe and ready to be removed with the aid of vernal teeth and ingested (Figure 3c). Young are more quiescent between bouts of skin feeding, but sometimes they aggregate at the posterior end of the attending mother with their heads close to the vent, where they seem to receive some maternal cloacal-derived fluid (Figure 3d). During this period of extended posthatching parental care, the young increase substantially in size and pigmentation (Figure 3e) and gradually acquire the appearance of the adults.

Monitoring the development of a litter obtained in captivity showed that after hatching, offspring grew quickly, increasing body mass by approximately 130% in the first week (Figure 4a and Table S2A). In the following 6 weeks, growth continued but was less notable compared with the first week. Just after the young acquire independence from the mother, they showed another pronounced growth peak (Figure 4a, Table S2A), followed by a brief period of weight loss (Figure 4b, Table S2B). Litters of hatchlings collected in the field that were subsequently followed in captivity ($N = 6$) presented a pattern of development similar to that of litters that hatched in captivity (Figure 4b, Table S2B). Captive young become self-sufficient in March, when, in nature, humidity is highest, and it is possible to find juveniles with

FIGURE 3 Aspects of reproduction and parental care of hatchlings in *Siphonops annulatus*. (a) Mother with altricial newborn young in a nest on the side of a tree root. Note the pale colour of the mother. (b) Unpigmented young in a nest. (c) Head of a young showing mandibular teeth used in skin feeding. (d) Aggregation of young around the posterior end of the attending mother. Note the vertical position of the female tail exposing the cloaca. (e) More developed, pigmented clutch aggregated with the attending mother

similar body mass and length. During the whole period of parental care, captive mothers were never observed to feed, resulting in weight loss of between 7.5 and 31.1% of body mass (mean 17.73 ± 8.43). After the young become independent, their mothers resume normal feeding.

During fieldwork in February 2006, we found a solitary female with the opaque whitish colour, characteristic of attending mothers, but without young. A few days later, in a different location, we found a group of entangled unpigmented hatchlings but no mother in the nest or in the vicinity. In an attempt to test whether the solitary female would adopt the mother-less litter, we placed female and hatchlings together in the same box. Immediately, the female and litter aggregated and subsequently skin feeding and normal development ensued. The adoptive relationship continued until the young were self-sufficient. During our studies, two other successful attempts at adoption were made (for similar reasons). In one of them, adopted young were visibly smaller when compared to individuals of similar age developed in normal conditions (Figure 4c, Table S2C).

During parental care, if young animals were put apart from their attending mother for a short time (for example, during cleaning of their enclosure), they would subsequently return to her side. Reaggregation seems to depend entirely upon the young moving towards the mother and not vice versa. The mode of locomotion of the altricial young involves flexion between the head and vertebral column with the anterior part of the head being pushed down and anchoring against the substrate, and the body being pulled forward with dorsal displacement of the craniovertebral joint. The head is then lifted and extended forward to complete one cycle of this “head-pulling” or “maggotiform” locomotion.

The entire reproductive cycle of *Siphonops annulatus* is represented in Figure 5 together with the monthly average rainfall of the cacao region.

3.6 | Additional observations in captivity

The variation on substrates used during these several years of captive maintenance of *Siphonops annulatus* indicated that when the terrarium contained non-friable clay-rich substrate, they construct permanent tunnel systems, with diameters closely corresponding to those of the animals, similar to those reported for other captive caecilians by Himstedt (1996). Within the terraria, the caecilians spend much of their time in these tunnels or under surface shelters, such as half coconut shells (Figure 2a). When inside the tunnels, they are frequently observed with their heads slightly emerging from the tunnel opening on the surface. In community terraria, they are frequently found in tightly aggregated small groups, in particular preferred places such as under coconut shells and inside pieces of bamboo. In contrast, most mothers, while using the same type of environment, are generally found alone with their offspring, probably

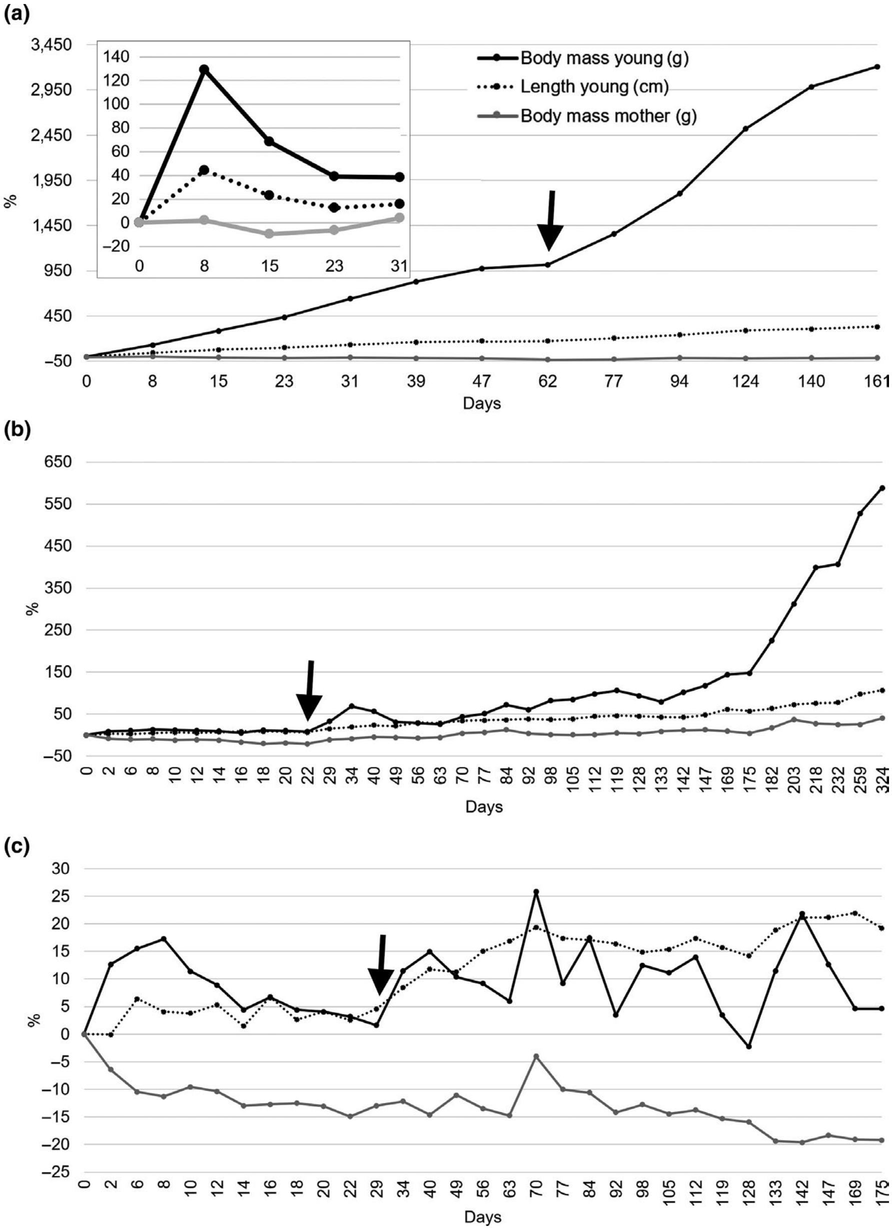

FIGURE 4 Growth of young in captivity expressed by cumulative percentages of mass and length. (a) Clutch born in captivity and followed since hatching. The insert shows the same data, but expressed by non-cumulative percentage of growth, highlighting the high growth rate during the first weeks. (b) Newborn clutch collected in the field. In this case, it is not possible to establish the exact age of the young. Note the lower growth rate when compared to (a). (c) Adoptive young. Growth rate is even lower than that observed in (b). The arrows indicate the time when young acquire self-sufficiency

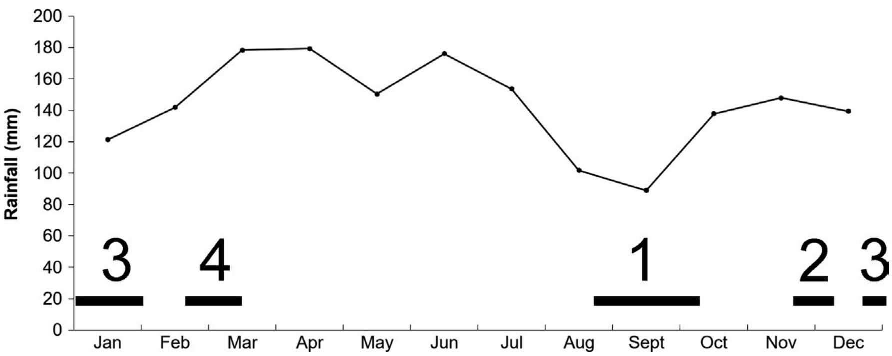

FIGURE 5 Reproductive cycle of *Siphonops annulatus* and monthly average rainfall in the cacao region. (1) mating, (2) oviposition, (3) hatching, (4) independent young

avoiding any disturbance caused by other individuals. So far, we have found no evidence of antagonistic interactions between individuals of *S. annulatus*. Similarly, despite many egg litters been laid in the communal terraria, we have never had any evidence of cannibalism or aggressive behaviour among individuals.

In captivity, *Siphonops annulatus* are voracious carnivores or scavengers and are sometimes observed spinning around the long axis of the body when handling large food items as reported in some other caecilians. When large carcasses are left on the surface of the terraria, they may be penetrated from below by the animals emerging from the soil, with body spinning being used to break of pieces of the carcass.

4 | DISCUSSION

The effort required to find a specimen of *Siphonops annulatus* varied throughout the different years/months of the year, showing no relation to the rainfall indexes of each collection expedition. On the other hand, when analyzing the historical pluviometric means, it was observed that in the driest months (August to October), a larger sample effort is usually required to find *S. annulatus*. It is important to reinforce that we are here discussing about digging effort for the collection of fossorial animals, what cannot be compared with usual methods of terrestrial amphibian collection, such as pitfalls or visual active search, requiring lower levels of energy investment. We believe that such difficulty in collection is probably one of the reasons why caecilians remain the less studied group among all vertebrates.

In relation to reproduction, our observations show that mating occurs within the driest months, during the austral winter. Analysis of captive specimens shows that gonads are best developed during winter months, when vitelogenic oocytes are present in females and mature spermatozoa are found in male testes, in contrast with other seasons in which both female and male germinative cells are absent (Gomes et al., 2013). Egg laying is dissociated from mating, occurring about 1 month after copulation, by the end of the winter. Hatching, posthatching parental care and the eventual self-sufficiency of young coincide with the rainiest months, greatest humidity and availability of food resources.

Maternal care begins immediately after egg laying. Periodic displacement of eggs by the head of the attending mother may serve to aerate the eggs and, at the same time, to cover them with skin secretion, conferring protection against microorganisms. Some such protection is expected given that cutaneous bioactive substances, usually including antimicrobials, appear ubiquitous in amphibians (Rollins-Smith, 2009; Toledo & Jared, 1995).

About 1 month after oviposition, the fragile hatchlings emerge from the eggs and climb onto their mothers' body. Hatchlings are initially altricial, with incompletely ossified vertebral systems, and seem poorly suited to either the internal concertina or serpentiform modes of locomotion employed by adults in their tunnels and on the surface, respectively. Thus, they are reliant upon the distinctive head-pulling or maggotiform mode of locomotion that, as far as we are aware, is unique among vertebrates. Aggregation of young with their mother seems to be an obligate behaviour for the young since they feed exclusively on their mother's skin in their first months of life (Wilkinson et al., 2008).

In *Siphonops annulatus*, skin feeding persists for about 3 months. Eating the mother's skin, however, is probably not the only feeding mode of the young, which may also receive fluid from the mother's cloaca (Wilkinson et al., 2008). This fluid needs to be investigated further, but taking into account the rapid development of the hatchlings, more than doubling their mass during their first week after hatching, it seems likely that cloacal fluid has an additional nutritive function. According to Kupfer et al. (2016), the reproductive modes of only 25% of all known living caecilians are available, and maternal dermatophagy was first reported only very recently (Wilkinson et al., 2008). Thus, it seems reasonable to expect as yet undiscovered reproductive strategies to exist within the group.

Encounter of nests in the field together with observations in captivity indicates that the number of hatchlings varies from 5 to 16 and usually corresponds to the number of laid eggs. From the laying of eggs to the independence of the young, the mothers spend around 5 months attending their offspring. If copulation and nest construction are added to this period, the complete reproductive cycle of *Siphonops annulatus* is estimated around 6 months. The small size of the litter and the long-term brood care define *S. annulatus* as an amphibian with extremely high reproductive investment, producing high-quality offspring that, for example, may be able to access a greater variety of prey and be less vulnerable to predation (Kupfer et al., 2016).

Positive correlations between reproductive traits such as clutch size and female body length are commonly found in frogs and salamanders, particularly in species with terrestrial litters (Kupfer et al., 2004; Salthe, 1969). In *Siphonops annulatus*, however, we found no significant correlation. Similarly, there is no definitive evidence of a positive correlation in number of oviductal foetuses and female body length in viviparous caecilians (Exbrayat & Delsol, 1985; Wake, 1980). According to Kupfer et al. (2016), several caecilian lineages have reduced clutch and egg size, but produce large, high-quality offspring using alternative means of parental investment such as maternal dermatophagy.

The relatively little information available on adult caecilian diet suggests they are mostly generalist predators feeding mainly on invertebrate and occasionally vertebrate prey (e.g. Kupfer et al., 2005; Measey, Gower, Oommen, & Wilkinson, 2004; Presswell, Gower, Oommen, Measey, & Wilkinson, 2002). It is possible that in nature, they are also opportunistic scavengers. When feeding on the surface, *Siphonops annulatus* will often drag food into their burrows and probably use the resistance provided by burrow walls to help them in prey manipulation and ingestion. The ability to process food by spinning around the long axis of the body has been reported in some other caecilians (Measey & Herrel, 2006; Tanner, 1971).

Records of predation of *Siphonops annulatus* are rare. It seems likely that they are more vulnerable to predation at times of the year when they leave their flooded burrows and crawl on the ground surface or under the litter. On the other hand, we have never seen predation events in the field. Remains of *S. annulatus* have been found in stomachs of the colubrid snake *Clelia clelia* (Sawaya, 1937) and coral snakes (Marques, 2002; Marques & Sazima, 1997). It is probable that the sympatric coral snake *Micrurus ibiboboca* Merrem 1820 is an important subterranean predator of this caecilian. Presumed bite marks (scars) have been are reported on the dermophiid caecilian *Schistometopum thomense* (Bocage 1873) as a result of antagonistic interactions with conspecifics (Teodecki, Brodie, Formanowicz, & Nussbaum, 1998) and are seen in many other species (M. Wilkinson, personal observation.). We also observed marks on the body of *S. annulatus* in the wild but, due to its gregarious and inoffensive behaviour, we consider it more probable that they result from attempted predation than from antagonistic interactions.

Soil-dwelling caecilians are head-first burrowers. Numerous cutaneous mucous glands spread across the entire surface of *Siphonops annulatus* presumably provide lubrication during burrowing, reducing friction (Gabe, 1971) and enabling these animals to "dive" underground (Jared et al., 1999, 2018). Additionally, mucous gland secretions lubricate the walls of established tunnels contributing to their smooth, shiny and sometimes moist surface. Similar to earthworms, movement of caecilians inside their tunnels must pump large volumes of air into, out of and around the burrow system and probably plays a significant role in the macro-aeration, drainage and leaching of the soil, at least in places, such as cacao plantations, where they are common.

Besides the intense mucous skin secretion, *Siphonops annulatus* has long been known to possess toxic and repellent cutaneous secretions that presumably provide protection against potential predators (Jared et al., 1999; Sawaya, 1940). In one of the few existing studies on the bioactivity of caecilian skin secretions, Schwartz et al. (1999) demonstrated cardiotoxic and haemolytic activity in the skin of *S. paulensis* Boettger 1892, the likely sister species of *S. annulatus* (San Mauro, Gower, Zardoya, & Wilkinson, 2006) that might also be expected in *S. annulatus*. In our experience, skin secretions of *S. annulatus* can irritate open cuts, abrasions or mucosa and may induce sneezing in some people. What happens to defensive skin secretions of attending mothers during parental care and whether young have any toxin resistance is unknown and in need of study. In addition to toxic substances, attending *S. annulatus* may produce semiochemicals (pheromones) to control the aggregation of their and signal the readiness of the stratum corneum for harvesting. The cases of adoption reported are an indication that aggregation pheromones do not have significant individual variation that would allow parents to identify their own offspring.

The integrative study on *Siphonops annulatus* combining data extracted from observations both in the field and in captivity demonstrates the potential of this type of approach for the elucidation of the natural history and biology of cryptic animals such as caecilians. According to the IUCN (2017), among the entire taxa, only six species are considered as "endangered," four species as "vulnerable" and yet the majority of species are classified as "deficient data" (66%), indicating a high level of ignorance about these animals. Maintenance of caecilians in captivity may represent an alternative way to access their biology, especially the reproductive cycle, contributing to the design of conservation strategies for the different species of this interesting and still unknown group of amphibians.

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