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Peering into the unknown world of amphisbaenians (Squamata, Amphisbaenia): A summary of the life history of *Amphisbaena alba*

Carlos Jared¹ | José Duarte de Barros Filho² | Simone G. S. Jared¹ | César Alexandre¹ | Pedro Luiz Mailho-Fontana¹ | Selma M. Almeida-Santos³ | Marta Maria Antoniazzi¹

¹Laboratório de Biologia Estrutural e Funcional, Instituto Butantan, São Paulo, Brazil

²Departamento de Zoologia, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

³Laboratório de Ecologia e Evolução, Instituto Butantan, São Paulo, Brazil

Correspondence Carlos Jared, Instituto Butantan, São Paulo, Brazil. Email: carlos.jared@butantan.gov.br

Abstract

Capturing data on the life of fossorial vertebrates is difficult since access to the subterranean environment is made unfeasible by its density and opacity. Collecting specimens is only possible through excavation work, causing damage or even death to the specimens. Due to the obstacles of in situ studies, the scarce information comes from reports obtained indirectly, mainly through specimens preserved in museums. Considering the adaptations to fossoriality, investments in studying these groups could be very enlightening since they would contribute enormously to the knowledge of the evolutionary strategies developed throughout the colonisation of the subterranean world. *Amphisbaena alba* is the species of Amphisbaenia with the broadest geographic distribution in the world. It occupies virtually all countries in South America except for Chile and southern Argentina. This study, carried out over the last 36 years, aims to provide data on the biology and behaviour of *A. alba* in captivity and in the field. Our main objective is to provide subsidies to expand the knowledge of the life history of this species and, by extension, of amphisbaenians in general.

KEYWORDS

Amphisbaena alba, Amphisbaenia, captivity, fossoriality, life history, natural history

1 | INTRODUCTION

Amphisbaenia forms a monophyletic clade whose origins remain unclear (Gans, 1969; Kearney, 2003; Kearney & Stuart, 2004). Currently, this clade comprises six families, with 201 recognised species (Uetz & Hošek, 2023), about 30 fossil species and another ten *incertae sedis* (Charig & Gans, 1990; Estes, 1983; Fahlbusch, 2003; Scaferla et al., 2006). The possible early relative of the group is a full-legged fossil from the Late Cretaceous in Mongolia. Modern amphisbaenians likely originated in North America and dispersed via rafting during the Paleogene to Europe, Africa and South America (Longrich et al., 2015).

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The anatomical characteristics of fossil representatives are similar to those of current (Estes, 1983), suggesting a well-established and apparently stable degree of evolutionary adaptation. They are squamates typically adapted to fossorial life, having the ability to dig tunnels in compacted soils and move back and forth with equal ease in tunnels already excavated, which earned them the name of the clade (from the Greek amphis=double, baena=move) (Cameron & Gans, 1977). Although the infraorder Scolecophidia and the family Uropeltidae (Serpentes) (Gans, 1973) can also dig tunnels in compacted soils, and Dibamidae (Lacertilia) show marked, similar adaptations for fossoriality, they cannot move backwards inside their tunnels (Gans, 1969, 1978).

Controversies among taxonomists about the origin and evolution of Amphisbaenia come from the convergence (or homoplasy) of the several morphological characters for adaptation to life underground, posing difficulties to the interpretation of molecular findings and possible differences and similarities arising from geographic distribution (Gans, 1978; Kearney & Stuart, 2004; Mott & Vieites, 2009; Ribeiro et al., 2011). Due to the various anatomical peculiarities, Amphisbaenia has long been considered a suborder of Squamata (Bellairs & Gans, 1983; Gans, 1978). However, more recent studies indicate that the group is possibly part of the lizard clade Lacertoidea, which places it as a superfamily within the squamates (Streicher & Wiens, 2017; Vidal & Hedges, 2005).

The genus Amphisbaena, with 182 species, has the highest diversity among amphisbaenians (Uetz & Hošek, 2023). Amphisbaena alba was the second species of Amphisbaenia described by Linnaeus in 1758 (the first was A. fuliginosa in the same year) and shows the broadest worldwide distribution, with the most significant number of morphological, physiological and general biological studies (Barros-Filho & Valverde, 1996; Brehm, 1913; Colli & Zamboni, 1999; Crook & Parsons, 1980; Francis, 1977; Gans, 2005; Gorzula et al., 1977; Montero & Gans, 1999; Ruscaia et al., 1999; Vanzolini, 1968). Blanus cinereus (Blanidae), inhabiting southern Europe and northern Africa, similarly to A. alba, showed more aboveground activity and is probably the second-most cited species in terms of published articles (Gans, 2005).

Amphisbaena alba inhabits all South American countries east of the Andes range, except for the coldest regions in Chile and southern Argentina (Gans, 2005; La Marca & Soriano, 2004; Montero & Terol, 1999). The species mainly distributes in forested areas and is particularly abundant in the biome Cerrado (Brazilian Savannah). It is also found in part of the Caribbean (Trinidad and Tobago), close to the Venezuelan coast (Sabiha, 2016). A. alba is among the most widely

distributed amphisbaenians, although the genetic data suggests it forms a complex rather than a single taxonomic unit (Mott & Vieites, 2009).

Due to its extensive distribution, A. alba is probably the most studied Amphisbaenia (Colli & Zamboni, 1999), but even so, its biology still needs to be better explored. Extending this statement to a broader view, the biology and natural history of fossorial vertebrates in general stand out due to the scarcity of data, including, together with Amphisbaenia, Scolecophidia (Squamata, Serpentes), Uropeltidae (Squamata, Serpentes) and, particularly, the caecilians (Amphibia, Gymnophiona). These reptiles and amphibians are undoubtedly the most neglected vertebrate groups in research (Kupfer et al., 2004; Measey & Herrel, 2006; Webb et al., 2000). Different from the terrestrial or aquatic environment, capturing animal life data in the subterranean environment is difficult since density and opacity make it inaccessible. In addition, the active collection of fossorial specimens is generally feasible only through the arduous work of manual excavation using bladed hoes, with almost no indication of more favourable sites to search for specimens. The bladed hoes often hurt or even kill subterranean herpetofauna if digging is carried out without caution and non-systematically. Occasionally, specimens are also collected by following tractors when cleaning and revolving the soil of natural habitats for buildings or farming. As a result, the little scientific knowledge about these animals generally comes from occasional observations obtained indirectly, mainly via natural history collections (e.g., Webb et al., 2000). For example, information on morphometry, ecology, geography etc. was gathered by Colli and Zamboni (1999) studying A.alba specimens exclusively from zoological collections. Large samples can be obtained mainly when new hydroelectric dams are abruptly filled, dislodging the animals from the galleries where they live. Therefore, most samples do not provide information about life history and behaviour.

Among people in general, A. alba is seen as a bizarre and dangerous animal known as the "two-headed snake" or "worm-lizard" generalist names for all amphisbaenians (Gadow, 1909). Moreover, the species is also popularly known as "blind-snake" (Freitas & Santos-Silva, 2004; Izecksohn & Carvalho-e-Silva, 2001), a name historically used for amphibian caecilians that, due to the apparent similarities, used to be classified as reptiles, close to amphisbaenians (Daudin, 1803). In rural areas and among South American indigenous peoples, A. alba is also called "ibijara" or "ymbyiára" ("lord of the land" in the Tupiguarani language) (Jared, Burman, et al., 1997) or even "mother of the ants" (Gadow, 1909), for its close relationship with ants of the genus Atta. Widespread reports of country people collected during fieldwork emphasise the

popular belief that *A*. *alba* is a very venomous species, injecting toxins through its tail.

Here, we summarised significant aspects of the life history of the amphisbaenian *A. alba* of the State of São Paulo (Brazil). We also reported observations made during several field expeditions but also from our extensive captive care program. We added results from some laboratory experiments aiming to understand aspects of amphisbaenian environmental perception. Finally, we also summarised some reproductive biology aspects. Our goal was to combine field observations with data obtained from captivity to expand the general knowledge of this stillenigmatic species' biology and natural history.

2 | MATERIALS AND METHODS

Since 1987, we have received around 60 live adults of *A. alba* Linnaeus 1758 (Figure 1a), originating primarily from the peripheral municipalities of São Paulo City but also from other neighbouring states in south-eastern Brazil were kept in the Vivarium of the Structural and Functional Biology Laboratory via the Animal Reception Sector of the Butantan Institute. The Government of the State of São Paulo (Brazil) officially recognises this vivarium as a maintenance and breeding place for Scientific Research Purposes (#0000051951/2021).

Some of the specimens in captivity (n=19) were weighted using a scale and measurements were taken from the long axis and from the perimeter of the middle region of the body using a string later stretched over a ruler.

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Of all specimens received, 30 were sacrificed and analysed in various research (e.g., Antoniazzi et al., 1993, 1994; Foureaux et al., 2010; Jared et al., 1995, 1999; Jared, Almeida-Santos, et al., 1998; Jared, Antoniazzi, et al., 1998; Spadacci-Morena et al., 1998).

Specimens were kept in closed wooden terraria (Figure 1b), with plenty of ventilation through a screened door, measuring 0.50 m (length) $\times 0.35 \text{ m}$ (width) $\times 0.25 \text{ m}$ (height). These terraria were enriched with ringed rubber tubes with a larger diameter than the animals' bodies. The environment was controlled, with temperatures maintained around 24°C. Water was provided in clay pots, in addition to daily spraying in the terraria.

The food, supplied weekly, consisted of a rotation among newborn mice (*Mus musculus*), ground beef or chicken meat, cockroaches (Blattoidea, *Picnocelus surinamensis*) and mealworm larvae (Coleoptera, *Tenebrium molitor*). The boxes were washed and sanitised monthly. During box cleaning, the animals were kept in individual plastic boxes measuring 0.70m (length) \times 0.50m (width) \times 0.40m (height), with a water film for hydration and hygiene. Soon after, they were transferred for a week



FIGURE 1 Amphisbaena alba (a) One specimen. (b) Usual terrarium used for the maintenance. (c) A larger terrarium.

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to larger terraria, $0.80 \text{ m} (\text{length}) \times 0.50 \text{ m} (\text{width}) \times 0.40 \text{ m}$ (height), with soil to provide an abrasive substrate (Figure 1c).

Over the past 36 years, studies on the behaviour of A. alba captive specimens have been carried out. Observations were also made in the field, particularly in regions of the Cerrado biome of the State of São Paulo. In addition, in the period between 2003 and 2013, Maria Celeste Costa Valverde, from the Laboratory of Vertebrate Morphology at the State University of Feira de Santana (State of Bahia, Brazil), also worked with A. alba, recording behaviour and biology. Moreover, one of the authors (JDBF), in 1991, while studying amphisbaenians, made several observations on A. alba specimens maintained in captivity at the Laboratory of Amphibians and Reptiles of the Federal University of Rio de Janeiro. We also gathered information provided by Edvaldo Antonio dos Santos (EAS), former technician of the Reptile Sector of the Zoological Park of the city of São Paulo, who for 30 years maintained and observed captive specimens of A. alba and, shortly after his retirement, made observations also in the field in the interior of Paraná State (Brazil).

Three adult specimens of *A. alba* were placed together in a terrarium (measures $700 \text{ mm} \times 530 \text{ mm} \times 400 \text{ mm}$) containing soil substrate, aiming experiments to investigate reproduction and territoriality in captivity in July (winter) and January (summer).

The records of defensive behaviour of *A. alba* against the opossum *Didelphis aurita* (Mammalia, Didelphimorphia) followed the methodology used in Jared, Almeida-Santos, et al. (1998) and Almeida-Santos et al. (2000) in predation studies of this marsupial against *Bothrops jararaca* and *Crotalus durissus* (Serpentes, Viperidae).

Some of the specimens used in the experiments are listed in the Alphonse Richard Hoge Herpetological Collection at the Butantan Institute under the numbers IBSPCR1501 (LBC-A672), IBSPCR1648 (LBC-A466), IBSPCR1697 (LBC-A757), IBSPCR1907 (LBC-A68), IBSPCR2231 (LBC-A304), IBSPCR2676 (LBC-A88), IBSPCR2703 (LBC-A81), IBSPCR2707 (LBC-A926).

3 | RESULTS

Amphisbaena alba has a long, serpentine and tubular body. Both head and tail are rounded and similarly thick (Figure 2a,b), which seems to be the origin of its popular name, "two-headed snake." The eyes are deep (Figure 2a), identified only by two dark spots below the ocular scale, possibly justifying the origin of the other common name, "blind snake" or "worm-lizard."

Amphisbaena alba has compact and robust body musculature surrounding the whole body. The size and age of animals kept in captivity were summarised in Table 1. We found a significant correlation between animal age and body length (Spearman's test, rs = 0.4785, t = 2.2468, p = .0382).

Amphisbaena alba was very active and voracious in captivity, rarely refusing food. As soon as they were introduced into captivity, they showed high aggressiveness, reacting and trying to bite at any touch. However, after getting used to captivity, they gradually decrease aggressiveness, although they continue with a sharp reaction to any slight touch.

Regarding the widespread knowledge of these animals, particularly among rural people, it is a recurrent report that specimens of *A. alba* are commonly found in beds of lettuce or buried vegetables (like potatoes or carrots) in the middle of roots, particularly during the summer, the wettest season of the year. They are also closely associated with coffee farming during the hot and rainy summer. On the other hand, when turning large areas of soil with tractors in soybean crops, they are often killed, being exposed on the surface, attracting several predatory birds (EAS, unpublished observations).

In the field, specimens of *A. alba* were observed three times moving on the surface: twice in the region of Araraquara (State of São Paulo, Brazil) and one time inside the campus of Butantan Institute, right after a heavy summer rain. Although the serpentine movement is observed, when on the surface, the predominant movement is straight and *in concertina* (Video S1), forming characteristic waves flowing along the body, both forward and backwards.

The number of pre-cloacal glands in A. alba (Figure 2b) varied from six to ten in both males and females. In captivity, as the animals were less mobile than those living in the wild, the pre-cloacal gland secretions in the form of plugs grew disproportionately and tended to deform. To avoid that, the animals were placed in larger terraria with a substrate of slightly moist soil enriched with rustic rubber tubes (see Figure 1c) every 2 weeks to abrade the plugs, keeping them functional.

At least in captivity, *A. alba* prefers to remain on the surface of the terrarium and rarely burrows. Some specimens lose the characteristic "horseshoe display" (described in Jared, Antoniazzi, et al., 1998). This defensive behaviour performed in confrontation with a predator/aggressor consists of widely opening the mouth while raising the head and the tail tip and simultaneously closing and opening the body laterally, forming a horseshoe arc (Figure 2c). During the body display, audible characteristic snorting sounds are emitted.

Moreover, another kind of vocalisation was noted during feeding, when *A. alba* approached its prey (especially neonate mice), consisting of wheezing, eventually FIGURE 2 Amphisbaena alba. (a) Head of a specimen showing the eyes covered by skin and the tongue. (b) Tail of *A. alba*. Note the presence of precloacal glands (arrow) close to cloaca (c). (c) Defensive "horseshoe display" of Amphisbaena alba.



associated with short, directed attacks. We also observed this kind of wheezing during the approach of a specimen to a water supply placed in the terrarium. As the sexing of *A. alba* proved very difficult, we assumed that the females' tail was narrower due to the absence of hemipenes. Based on this sexing methodology, we tried to set up a copulation experiment in captivity, also in different seasons of the year, but rather unsuccessfully, placing three adult individuals (two possible females and one possible male) together overnight in a large terrarium. Even the slightest contact between the animals resulted in intense bites, leaving evident scars and skin marks on the body.

Among the food items offered to *A. alba*, the preference for ground meat and new-born mice is evident. Specimens change behaviour, showing evident excitement as soon as the caretaker opens the terrarium door, offering, with the help of tweezers, pieces of meat or even crickets and cockroaches, which are quickly devoured. Unlike snakes and lizards, which protrude the tongue horizontally, flicking the bifid part, *A. alba* protruded the tongue down towards the substrate without touching it (Video S2). The tongue tips are smooth and show morphological characteristics distinct from the other lingual portions (Figure 2a). When capturing the prey or grasping the food, *A. alba* shows a potent bite that may persist for a long time on prey or dead animals (characteristics commonly reported by the country people). They need support to help capture the prey (or food) and facilitate ingestion (Figure 3a).

Following the behavioural experiments on the predation of viperid snakes *C. durissus* and *B. jararaca* by the ophiophagous opossum *D. aurita* (e.g., Almeida-Santos et al., 2000; Jared, Almeida-Santos, et al., 1998; Jared, Antoniazzi, et al., 1998), we also offered two specimens of *A. alba* to an opossum in two successive attempts. The immediate defensive horseshoe movement display

Animal	Years in captivity	Weight (g)	Length (mm)	Circumference (mm)
1	36	250	59	11
2	36	320	64	9
3	36	235	60	10
4	36	265	65	10
5	36	255	59	11
6	36	190	59	9
7	36	270	64	10
8	36	335	62	11
9	6	250	61	9
10	11	315	61	12
11	11	255	60	11
12	11	315	61	12
13	13	210	50	9
14	13	335	61	11
15	8	230	59	9
16	5	360	60	11
17	9	185	50	9
18	4	65	13	5
19	4	110	40	7
$Mean \pm SD$	20.16 ± 14.11	250 ± 76.17	562.10 ± 120.30	97.89 ± 17.18

TABLE 1Body dimensions of 19Amphisbaena alba specimens in captivity.

of *A. alba* did not avoid the attack by the skilled opossum that rapidly subdued and killed the amphisbaenians with bites directed to the entire body, particularly to the head and tail (Figure 3b,c). Differently from the snakes that were entirely consumed in about 10–15 min (Almeida-Santos et al., 2000), the opossum, in both cases, repeatedly chewed on the whole body but more intensively the tail and head but ended up quitting and abandoned both carcasses, found the following day in the experimental arena.

4 | DISCUSSION

Starting from the name *A. alba* calls attention to the specific epithet used by Linnaeus (1758) (from Latin: alba, albus=very white), which is probably due to misunderstanding since the species has a markedly yellowish dorsal colour (Figure 1a). One possible explanation is that the original description was based on material with fading colours, a typical long-term storage condition in ethanol.

Since the beginning of the last century, farmers and country people from southeast and south Brazil have traditionally donated alive snakes to the Butantan Institute. The main objective of such donations has been to provide snakes for venom extraction and antivenom production. Along with the technical advancements for breeding and maintaining snakes in captivity for a long time and stricter environmental legislation in recent decades, there is a crescent tendency of venom supplying almost exclusively through snakes from the institution's breeding stock. However, the tradition of suppliers persists today, albeit on a much smaller scale. Due to a lack of knowledge and the usual human fear of snakes, along with actual snakes (both venomous and non-venomous), suppliers end up bringing other serpentine animals from other groups, such as Amphisbaenia, subterranean Lacertilia, scolecophidian snakes and Gymnophiona. Among the Amphisbaenia, the species A. alba is the most captured, closely followed by Leposternon microcephalum. Since the mid-1980s, the vivarium of the Structural and Functional Biology Laboratory has been stocked with these species. In recent years, however, possibly due to deforestation, the arrival of these animals to the Butantan Institute has been suffering a fast reduction.

According to Barbo and Sawaya (2008), *A. alba* lives in sympatry, at least in southeastern Brazil, with *L. microcephalum*, another amphisbaenian with wide distribution in Brazil and South America, inhabiting deeper in the soil. Due to the more evident fossoriality, the biology of *L. microcephalum* is even more inaccessible when compared with that of *A. alba*. Unlike *A. alba*, with a rounded snout and yellowish pigmented back, *L. microcephalum* has more specialised adaptations to the fossorial environment, such



FIGURE 3 *Amphisbaena alba* (a) Use of the terraria structure to facilitate predation and ingestion. (b, c) A specimen after opossum (*Didelphis aurita*) predation attempt. Note that the head and tail have been vigorously chewed off.

as a depigmented body and shovel-shaped snout, efficiently used in the construction of tunnel systems (Barros-Filho et al., 2008; Gans, 1968; Hohl et al., 2014, 2017; Navas et al., 2004). Such morphological and behavioural differences confirm the more generalist tendency of *A. alba* to occupy more superficial environments when compared with *L. microcephalum*, which explores deep layers of the soil (Barbo & Sawaya, 2008; Gans, 1969, 1974, 1978).

The similarity between the head and the tail, with diameters equivalent in thickness and round shape, and the serpentine body must have contributed to the spreading belief that *A. alba* is two-headed. The typical defensive display, with the horseshoe movement (Gorzula et al., 1977; Jared, Antoniazzi, et al., 1998), sharply lifting Zoologica

both extremities, demonstrates a highly aggressive attitude. Such characteristics justify why these animals became the protagonists of several legends (Jared, Burman, et al., 1997), which are still widespread today, reinforcing the belief among the people that they are poisonous and lethal "snakes" endowed with stinging tails (Mateus et al., 2011).

As in *Leposternon infraorbitale* (Jared, Antoniazzi, et al., 1997), neonates of *A. alba* (Sabiha, 2016) have an egg-tooth and positive geotropism at birth. When leaving the egg, they immediately dig into the soil head-first, looking for the fossorial environment. Sabiha (2016) also observed the horseshoe display in young, which is very similar to that of adults.

The rounded shape of the *A. alba* snout is associated with the way of digging the soil, which is suggestive of being less specialised when compared to species of the genus *Leposternon* (Gans, 1974). This fact and the frequent presence of *A. alba* on the surface suggest that it is not fully fossorial. Moreover, the dorsum's yellowish, beige, or brown tones (Gans, 1969) partially camouflage the animal against the superficial soil or fallen leaves (Figures 1a and 2c).

The horseshoe display of A. alba, probably directed to terrestrial predators of medium or large size, also seems to reinforce the hypothesis that the species is not fully fossorial, as this defensive behaviour would not be effective, or even possible, in the subterranean environment. Our observations in captivity showed that A. alba specimens seemed comfortable on the surface and did not dig when exposed. In contrast, Leposternon ssp. (e.g., L. infraorbitale, L. microcephalum and L. scutigerum, pers. obs.) usually desperately sought a shelter, indicating negative phototaxis. Moreover, Leposternon is much more specialised in digging with its shovel-shaped head (Gans, 1974). Several coral snakes (genus Micrurus, Elapidae), which also show fossorial or semi-fossorial habits, are their more frequent predators (Cineros-Heredia, 2005). Besides A. alba, the better-studied amphisbaenians are the species of the genus Blanus (Gans, 2005), which are also characterised as semi-fossorial, although much smaller in size, measuring about 220 mm in total length (Gil et al., 1993).

The tail scars of *A. alba* were assumed to be remnants of unsuccessful attacks by aggressors or potential predators and are probably associated with the horseshoe display used to lure the predator, keeping bites away from the head. The robust body musculature is involved by a resistant integument that is a kind of elastic armour, constituted by a resistant net of collagen fibres, which are even thicker in the tail (Jared, Antoniazzi, et al., 1998). The tail is also less vascularised, which explains its use for luring and offering it to the predator. The frequent caudal scars were first noted by Vanzolini (1955) and later cited by * WILEY- Zologia

Gans (1962) and Gorzula et al. (1977), but they can serve as individual recognition in captivity, which may constitute a handy tool in the study of their biology, including behavioural experiments.

Regarding the predation test we have conducted, the ingestion of *A. alba*, even by an ophiophagus animal such as the opossum *D. aurita*, was impracticable due to the very resistant amphisbaenian skin, endowed with unconventionally thick and resistant collagen fibres (Jared, Antoniazzi, et al., 1998). The marsupial repeatedly chewed on the entire amphisbaenian body, mainly on the extremities, but eventually abandoned the carcass, usually after a few minutes, in contrast to snake predation (e.g., Almeida-Santos et al., 2000).

Despite A. alba being often associated with termite mounds or anthills (Gorzula et al., 1977), we have never found these animals in such locations during fieldwork. The occurrence of amphisbaenians in ant nests is reported for some species (Brandão & Vanzolini, 1985; Vaz-Ferreira et al., 1973), and the association of A. alba with ants (genus Atta) in Trinidad-Tobago is well described (Riley et al., 1985, 1986). Despite the indigenous belief and popular name "mãe-de- saúva" (leaf-cut ants' mother, genus Atta) for A. alba, the authors have never found or heard reliable reports on A. alba in association with termite or ant nests in Southeast and Southern Brazil. It may be that such mutualism does not occur, and the idea is just a folkloric remnant. In any case, the clarification of this lifestyle aspect still needs detailed observational data from the field.

The diet of A. alba consisted mainly of invertebrates (especially ants and beetles), but there were also dietary records of vertebrates, indicating a generalist diet (e.g., Colli & Zamboni, 1999). In captivity, it became evident that A. alba fed efficiently on raw meat, that is mainly preferring minced beef or chicken, as well as neonate mice (see Figure 3a). We observed an increased tongue-flicking frequency right after the food was placed in the terrarium. The immediate interest and the subsequent capture suggested that, under natural conditions, A. alba must also feed on subterranean rodent litter in their underground nests. In addition, using a rotational feeding mode (e.g., Measey & Herrel, 2006), they may be able to devour dead animal carcasses on the surface. An effective bite able to cut and punch pieces of prey larger than their mouth width seemed to be an essential adaptation towards successful prey capture since amphisbaenians do not have any degree of jaw progression easing prey ingestion as known for some lizards or most snakes (Gans & Montero, 2008; Hohl et al., 2014).

Observations carried out in an open arena with five specimens suggest that tong-flick frequency increased as soon as prey or food was detected. The recurrent approach consists of moving around, sweeping the area with lateral head movements and decreasing head angulation as they approach the prey or food.

Associations of *A. alba* with "saúva" or "tanajura" ants (attine leaf-cut ants) of the genera *Atta, Acromyrmex* and *Cornitermes*, using their anthills both for feeding and laying eggs, were reported by different authors (Azevedo-Ramos & Moutinho, 1994; Duleba & Ferreira, 2014; Riley et al., 1985, 1986; Tschudi, 1867). Anthills seem to offer protection and constant temperatures, suitable for reproduction (Duleba & Ferreira, 2014), not only for several amphisbaenians but also for lizards and snakes (Brandão & Vanzolini, 1985; Vaz-Ferreira et al., 1970, 1973).

Colli and Zamboni (1999) recorded an average snoutvent length (SVL) of 550mm for males and 580mm for female A. alba (with a maximum male SVL of 780 mm and 810mm for females). Although maximum female SVL exceeded male SVL, the available size data did not indicate sexual size dimorphism yet (e.g., Vanzolini, 1955). The same lack of sexual size dimorphism is observed when analysing female tail width, although the tail was slightly narrower than that of males due to the absence of hemipenes. In our sample (see Table 1), regardless of the sex, the measurements of live animals resembled those by Vanzolini (1955) made on ethanol-preserved specimens. An interesting finding was the positive correlation between specimen length and age, indicating indeterminate growth, also known from caecilian amphibians (see Kupfer et al., 2004). Among living amphisbaenians, A. alba undoubtedly reaches the most significant size, with more than 500 mm in snout-vent length and 25 mm in body diameter (e.g., Vanzolini, 1955), as confirmed by our data here. The closest species to A. alba in terms of body size seemed to be A. fuliginosa, a typical fauna element of the Amazon region, distributed across northern South America (e.g., Casey-Deaven, 2015; Vanzolini, 1951, 2002a, 2002b).

body length, Regarding A. alba Colli and Zamboni (1999) record an average of 55 cm for males and 58 cm for females, with a registered record of 78 cm for males and 81 cm for females. Although females reach greater absolute lengths when compared to males, currently, the available data on size do not provide true sexual dimorphism (Vanzolini, 1955). The same happens when analysing the measurements of the female's tail, which although slightly narrower than those of males due to the absence of a hemipenis, do not provide reliable information concerning sexual dimorphism. In our sample, regardless of the sex of the animals, the measurements of live animals are much like those pointed out by Vanzolini (1955). In this context, an interesting finding was the positive correlation between specimen length and age, which indicates that these animals continue to

grow throughout their lives. Among all current amphisbaenians, *A. alba* is the species that undoubtedly reaches the most significant proportions, with more than 50 cm in length and 2.5 cm in diameter (Vanzolini, 1955), as confirmed by our data. Concerning size, the closest species to *A. alba* seems to be *A. fuliginosa*, typical of the Amazon region, distributed across northern South America (Casey-Deaven, 2015; Vanzolini, 1951, 2002a, 2002b).

The aggressiveness observed in *A. alba* is likely related to marked territoriality, making it impossible to keep specimens in the same terraria. Territoriality is primarily connected to the high energy each individual expends in constructing its own exclusive tunnel system, protecting it most probably during periods underground.

Data on the reproductive biology of Amphisbaenia are rare and sparse; for example, the birth of a litter of *L. infraorbitale* was described in detail only by the end of the 20th century (Jared, Antoniazzi, et al., 1997). Studies by Andrade et al. (2006), Barros-Filho and Nascimento (2003) and Colli and Zamboni (1999), suggested that *A. alba* reproduction is seasonal and probably restricted to the end of the rainy season (October to April), possibly entering the dry season (Colli & Zamboni, 1999), with males having a more extended reproductive period than females (Andrade et al., 2006; Colli & Zamboni, 1999). The oviductal clutch size varied between 6 and 16 eggs (e.g., Colli & Zamboni, 1999), and Barros-Filho and Nascimento (2003) reported an oviposition of eight elongated, white and leathery eggs measuring around 31×15 mm on average.

To confirm experimentally the reproductive season of A. alba, specimens in captivity were placed together in terraria at different periods of the year. Our breeding attempts, although unsuccessful, allowed us to observe aggressive behaviour involving biting, leaving evident skin marks on the individuals. Mating, egg-laying and other reproductive aspects of A. alba remained unregistered (Andrade et al., 2006). Any reproductive biology study would depend on the investment in extensive captivity for better chances of observations. It seems quite evident that the continuous displacement of A. alba, both in tunnels and on the soil surface, caused a constant erosion of precloacal plugs involved in the dispersion of pheromones (described in Antoniazzi et al., 1993; Jared et al., 1999). Conversely, pre-cloacal plugs tended to grow disproportionately in captivity due to reduced friction with the substrate. As animals moved through the tunnels, these solid pre-cloacal plugs left trails containing the pheromones (Antoniazzi et al., 1993; Jared et al., 1999). In captivity, using larger terraria with a slightly moistened substrate and an environmental enrichment with tubes to serve as "tunnels" helped to monitor pre-cloacal plug size to a normal condition, keeping them at the level of the body

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surface. The observation of pre-cloacal plug growth corroborated our data on pheromone dispersion, confirming the decisive role of a glandular holocrine mode in pheromone dispersal (Antoniazzi et al., 1993; Jared et al., 1999). Pheromone composition may vary seasonally since the precloacal glands' secretion seems important in reproduction and territorial demarcation (Sabiha, 2016). However, in *A. alba.* no signal of glandular sexual dimorphism has

in *A. alba*, no signal of glandular sexual dimorphism has been observed in pore numbers (Colli & Zamboni, 1999) nor in glandular histological or ultrastructural morphology (Antoniazzi et al., 1994).

Concerning longevity, Gans (1975) pointed out that at the Bronx Zoo in New York, USA, one *A. alba* specimen and one *L. microcephalum* were kept "for a long time." To the best of our knowledge, it is the best-documented record of the lifespan of *A. alba* or any other amphisbaenian so far. Based on our data, it is possible to estimate that *A. alba* can reach 40 years old or more, at least in captivity. The data provided by EAS, working with reptiles at the São Paulo Zoological Park, reinforces our observations on their longevity. These animals significantly increase their life expectancy without predatory pressures or feeding difficulties, as Stark et al. (2018) pointed out.

On January 8, 1992, during a hot and rainy summer, a specimen of A. alba was taken from the vivarium by one of the authors (CJ) to be photographed in an external, wide, open area adjacent to the Structural and Functional Biology Laboratory building at the Butantan Institute. During this activity, the specimen was left in place for a few minutes while the photographer ran to the laboratory to take a macro lens. In this time-lapse, the animal escaped, disappearing in a tangle of roots and damp leaves inside a bamboo grove rich in organic matter. Surprisingly, on January 21, 1993, after a heavy summer rain, the specimen reappeared, crossing the street surrounding the bamboo grove and was promptly recognised by the scars on the tail, registered in photographs taken before the escape. This specimen died in 2018, with no apparent signs of illness, after 31 years of captivity, where it arrived already as an adult specimen in 1987.

Regarding sound emission, vocalisation in Amphisbaenia was known only in the European *B. cinereus* (Durán, 1985). In Neotropical amphisbaenians, spontaneous sound emission had never been reported. Our data showed that *A. alba* vocalisation seems to be associated with both offensive (wheezing) and defensive (snorting) behaviour. It is possible that, inside the tunnels, these sounds can also serve for intraspecific recognition or to use as echoes helping displacement through the galleries (Durán, 1985).

An analysis, albeit superficial, shows that, at least among the different groups of vertebrates, the most adapted to the fossorial environment are the less

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species-rich. For example, Amphisbaenia currently comprises 201 species (Uetz & Hošek, 2023), compared to almost 4000 species of snakes, excluding the fossorial Uropeltidae and Scolecophidia (Uetz & Hošek, 2023). There are 221 species among Gymnophiona, compared to the 8430 anurans and caudates. Considering these numbers, the fossorial environment, with its stable characteristics, seems to impose resistance to speciation. In almost all of South America, A. alba has remained an abundant vertebrate group since the first record of its ancestors in the Cretaceous (Estes, 1983).

Stability imposed by the fossorial microenvironment, with few changeable conditions, possibly disfavours specific diversification and eventual dispersal of well-adapted populations. However, the difficulty of accessing these animals in nature and observing them in loco may be masking a greater diversity. The cause of differences in each group's speciation is essentially an unknown topic. In summary, the mechanisms acting in the speciation of subterranean animals remain a mystery, and we are still far from knowing the barriers imposed on the diversity of these vertebrate groups.

Even in view of the rapid loss of the environment due to the advance of deforestation, the conservation status of A. alba seems not to be compromised. According to the IUCN Red List of Threatened Species (IUCN, 2022), its status remains "Least Concern." With its wide distribution throughout South America and a reasonable degree of conservation, it is still possible to study the various aspects of its life history associated with its morphological and physiological transformations to adapt to the fossorial environment.

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ORCID

Carlos Jared **b** https://orcid.org/0000-0002-9117-6276

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