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Ecology of the Worm-Lizard Amphisbaena alba in the Cerrado of Central Brazil

GUARINO R. COLLI AND DARIO S. ZAMBONI

Due to their secretive habits, very little is known about the ecology of amphisbaenians. Based on a large series of specimens from the Cerrado of central Brazil, the diet composition, reproduction, and sexual dimorphism of Amphisbaena alba are described. Amphisbaena alba displayed a relatively diverse diet, even ingesting vertebrates and plant material. Beetles, ants, and spiders dominated the diet numerically, whereas ants, insect larvae, and beetles were more important volumetrically. No association was observed between prey size and body dimensions. The smallest reproductive male was 422 mm SVL (snout-vent length), and the smallest reproductive female was 457 mm SVL. Clutch size ranged from 8–16, one of the largest known for amphisbaenians, and is possibly influenced by the large body size of A. alba. Reproduction is apparently seasonal and restricted to the dry season. No intersexual differences were observed, either in morphometric or meristic characters, presumably because of functional constraints related to fossoriality.

MPHISBAENIANS or worm-lizards comprise an array of approximately 150 species of highly specialized, fossorial squamates (Halliday and Adler, 1986; Zug, 1993). Due to their secretive habits, very little is known about the ecology of amphisbaenians. The diet consists primarily of arthropods, with some species being generalists, such as Amphisbaena gonavensis (Cusumano and Powell, 1991; White et al., 1992), whereas others have narrow diets, such as A. darwini heterozonata (Cabrera and Merlini, 1990), Cercolophia roberti and A. mertensi (Cruz Neto and Abe, 1993), and Blanus cinereus (Gil et al., 1993). The use of chemical cues for prey detection and identification was reported for B. cinereus (López and Salvador, 1992, 1994; López and Martin, 1994). The reproductive biology of amphisbaenians is poorly documented. For example, it was not until 1997 that the hatching of a clutch of amphisbaenian eggs was described in detail (Jared et al., 1997), and reviews of squamate reproductive patterns scarcely contain any data on amphisbaenians (Fitch, 1970, 1982; Dunham et al., 1988). There is apparently no sexual dimorphism in size (Fitch, 1981), but intersexual differences in head shape occur in B. cinereus (López et al., 1997a).

Amphisbaena alba ranges throughout most of South America east of the Andes, with perhaps the widest geographic distribution of any amphisbaenian (Gans, 1962; Peters and Orejas-Miranda, 1986). The species is distinctive from most congeners by the lack of caudal autotomy (Vanzolini, 1955; Gans, 1962). Despite its wide geographic distribution, the ecology of A. alba is poorly known. Preliminary diet data on very few individuals provided by Beebe (1945), Gans

(1962), Gorzula et al. (1977), and Riley et al. (1986) suggest that A. alba may be a food generalist. Riley et al. (1986) provided evidence that A. alba is a facultative inquiline of the leaf-cutting ant Atta cephalotes. The reproductive biology is unknown, except that A. alba may use nests of attine ants to deposit its eggs (Brandão and Vanzolini, 1985; Riley et al., 1986; Azevedo-Ramos and Moutinho, 1994) and that, apparently, there is no sexual dimorphism in SVL (Vanzolini, 1955; Fitch, 1981).

Herein we provide detailed information on the diet composition, reproduction, and sexual dimorphism of A. alba, based on a large series of individuals from the Cerrado. In addition, we compare our data with those available on other species of amphisbaenians.

MATERIALS AND METHODS

We analyzed 214 individuals deposited in the Coleção Herpetológica da Universidade de Brasília (CHUNB) and Centro de Estudos e Pesquisas Biológicas da Universidade Católica de Goiás. About 85% of the individuals (179) were collected at Minaçu, Goiás (13°38′S, 48°15′W), during the flooding of the Serra da Mesa hydroelectric dam, from November 1996 to March 1997. All other individuals came from Brasília, Distrito Federal (15°47′S, 47°55′W) and surroundings and were collected at different times, mostly from 1986 to 1997. Both sites are at the core region of the Cerrado biome and are located approximately 250 km apart.

The Cerrado covers approximately 1,500,000 km² of the Brazilian territory (about 18%) and dominates the landscape in the center of the

country (Ferri, 1963). The region is characterized by the Aw climate, receiving annually 1500-2000 mm of a highly predictable and strongly seasonal precipitation, almost entirely restricted to the period from October to April (Nimer, 1977). Annual temperatures average 20-22 C, and minimum and maximum daily temperatures drop noticeably during the dry months (Nimer, 1977). The phytophysiognomy varies from extensive grasslands with few trees to grasslands with dense stands of stunted trees, forming in some areas a nearly closed canopy (Eiten, 1972: Ferri, 1977). Trees are tortuous, with thick barks, xeromorphic leaves, and deep root systems, apparently adapted to natural sporadic fires and soils that are poor in nutrients and rich in aluminum (Goodland, 1969).

Diet composition.—We removed stomachs by dissection and examined their contents under a stereoscope. To allow comparisons, we grouped prey items into the categories used by Pianka (1986), with a few modifications. Prey categories used by Pianka (1986) and in this paper are ants, beetles, grasshoppers and crickets, hemipterans, insect larvae, nonidentified arthropods, plant material, roaches, scorpions, spiders, termites, and vertebrates. We split insect eggs and pupae into separate categories and added pseudoscorpions, a category not identified by Pianka (1986).

We recorded the length and width (0.01 mm) of intact prey items, including seeds, with Mitutoyo® electronic calipers, and estimated prey volume (V) as an ellipsoid:

$$V=\frac{4}{3}\pi\bigg(\frac{w}{2}\bigg)^2\bigg(\frac{l}{2}\bigg),$$

where w = prey width and l = prey length. We calculated the numeric and volumetric percentages of each prey category for individual lizards and for the pooled individuals. The numeric and volumetric percentages were used to compute niche breadths (B) for each individual and for the pooled individuals, with the inverse of Simpson's diversity index (Simpson, 1949):

$$B=\frac{1}{\sum_{i=1}^{n}p_{i}^{2}},$$

where i stands for prey category, n for number of categories, and p for the numeric or volumetric proportion of prey category i. We also calculated the percentage of occurrence of each prey category (number of stomachs containing prey category i, divided by the total number of stomachs).

To investigate the relationship between prey dimensions and head dimensions, we conducted a canonical correlation analysis between two sets of variables: maximum prev length and maximum prev width versus head width, head height, and head length. Canonical correlation analysis finds a linear combination from each set of variables, called the first canonical variables, such that the correlation between the two canonical variables is the largest attainable. Next, successive sets of canonical variables are calculated, such that the correlation between the two canonical variables of each set is maximized and each successive pair is uncorrelated with all the preceding canonical variables (Johnson, 1998; Johnson and Wichern, 1998). The first canonical correlation is at least as large as the multiple correlation between any variable and the opposite set of variables. To determine how well prey dimensions can be predicted from the canonical variables of head dimensions, we performed a canonical redundancy analysis. PROC CANCORR of SAS (vers. 6.04 DOS, Statistical Analysis Systems Institute, Inc., Cary, NC, 1988, unpubl.) was used to implement canonical correlation analysis and canonical redundancy analysis.

Reproduction.—We sexed each individual by dissection and direct examination of the gonads. Females were considered reproductively active by the presence of vitellogenic follicles or oviductal eggs, whereas males were considered reproductively active by the presence of enlarged testes and convoluted epididymides. For reproductively active females, vitellogenic follicles or oviductal eggs were counted and measured for width (0.01 mm) and length (0.01 mm). We estimated size at maturity for females based on the smallest individual containing vitellogenic follicles or oviductal eggs and, for males, based on the smallest individual bearing enlarged testes and convoluted epididymides.

We analyzed the monthly distribution of mature individuals to determine the timing of reproduction. By pooling individuals collected during different years, we recognize that some error was introduced in the estimate of the reproductive cycle, due to annual variations in the amount and distribution of precipitation. However, we assumed that this error was small, since average annual deviations in precipitation from the normal are less than 15% in the Cerrado (Nimer, 1977). Further, we assumed that differences due to the geographic separation between the two regions sampled (Minaçu and Brasília, approximately 250 km) were unimportant.

Sexual dimorphism.—From each individual, we recorded the following morphometric variables: snout-vent length (SVL: taken with a measuring tape, to the nearest 1 mm), body width (at its broadest point; this and the following measurements all taken with Mitutoyo® electronic calipers, to the nearest 0.01 mm), body height (at its highest point), head width (at its broadest point), head height (at its highest point), head length (from the tip of the snout to the commisure of the mouth), and tail length (from the cloaca to the tip of the tail). We log-transformed (base 10) each measurement prior to analyses. To partition the total morphometric variation between size and shape variation, we produced an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986): we calculated an isometric eigenvector, defined a priori with values equal to $p^{-0.5}$, where p is the number of variables (Iolicoeur, 1963), and obtained scores from this eigenvector, hereafter called body size. To obtain size-adjusted variables, we regressed each morphometric variable against body size and produced studentized residuals (Velleman and Welsch, 1981), hereafter called shape variables. To test the null hypothesis of no difference between sexes, we conducted separate analyses of variance on body size (ANOVA) and the shape variables (MANOVA).

We also recorded four meristic characters: body annuli (number of body annuli), tail annuli (number of tail annuli), segments around midbody (number of segments in annulus at midbody), and precloacal pores (total number on both sides). None of the meristic characters was correlated with body size (body annuli: r = 0.05, n = 213, P = 0.46; tail annuli: r = -0.12, n = 213, P = 0.08; segments around midbody: r = 0.06, n = 213, P = 0.41; precloacal pores: r = 0.02, n = 213, P = 0.76). Next, we conducted a multivariate analysis of variance (MANOVA) on the meristic data to test the null hypothesis of no difference between sexes.

Statistical analyses.—We carried out statistical analyses using SYSTAT 5.2.1 for Macintosh (vers. 5.2 ed. SYSTAT, Inc., Evanston, IL, 1992, unpubl.), except when indicated otherwise, and used a significance level of 5% to reject null hypotheses. Throughout the text, means appear ± 1 SD.

RESULTS

Diet composition.—A large proportion of the individuals examined (45.8%) had empty stomachs. The most frequent prey items were spiders, beetles, ants, and termites (Table 1). Based on the mean number of prey items per stomach, the diet consisted mainly of beetles, ants, spiders, termites, and nonidentified arthropods, whereas ants, beetles, insect larvae, and spiders dominated volumetrically (Table 1). The mean diversity index, calculated from numeric percentages of prey, was 1.31 ± 0.60 (n = 116). When using volumetric percentages of prey, the mean diversity index was 1.03 ± 0.11 (n = 23).

Based on the number of prey items of the pooled stomachs, the diet consisted mainly of termites, ants, beetles, and spiders, whereas grasshoppers and crickets, termites, beetles, insect larvae, insect pupae, ants, and spiders dominated volumetrically (Table 1). The diversity index, calculated from numeric percentages of prey, was 3.57 and, using volumetric percentages of prey, was 6.02.

The first canonical variable for the head measurements was a contrast between head width and head height, with more emphasis on head width, whereas the second was a contrast between head width and head length, with more emphasis on head length (Table 2). The first canonical variable for the prey measurements was a contrast between maximum prey width and maximum prey length, with more emphasis on the latter, whereas the second put more emphasis on the former. The first canonical correlation was 0.65, but the hypothesis that all canonical correlations are zero was not rejected, that is, no firm association between body dimensions and prey dimensions can be established. Indeed, the canonical redundancy analysis indicated that neither of the two canonical variables for the head measurements is a good predictor of the prey measurements, with only 18% of the variance in the latter being explained by the former.

Reproduction.—The smallest reproductive female measured 457 mm SVL, whereas the smallest reproductive male measured 422 mm SVL. However, only two reproductively active females were observed, which may have biased our estimate of size at sexual maturity for females. One of the pregnant females (457 mm SVL) contained eight vitellogenic follicles (length: $\bar{x}=7.00\pm2.31$, range 4.09–9.20; width: $\bar{x}=2.82\pm0.58$, range: 1.97–3.72), whereas the other female (654 mm SVL) contained 16 vitellogenic follicles (length: $\bar{x}=6.75\pm1.74$, range: 4.47–9.60; width: $\bar{x}=2.48\pm0.58$, range: 1.84–3.81).

The two reproductive females observed were collected at Brasília on 29 April 1977 and 13 April 1982. If only the 179 specimens collected

TABLE 1. DIET COMPOSITION OF Amphisbaena alba. Data were obtained by pooling all stomachs; mean stomach data were obtained by averaging individual stomachs. Volume data are in mm³.

| | Occurrence (9,) | | Poole | Pooled stomachs | | | Mean stomach | tomach | |
|---------------------------|-----------------|--------|-------|-----------------|------|------------------|-----------------|-------------------|-----------------|
| Prey items | (n = 116) | Number | % | Volume | % | Number | % | Volume | % |
| Ants | 25.9 | 149 | 28.5 | 1,032.0 | 8.6 | 1.28 ± 4.13 | 19.0 ± 36.0 | 44.9 ± 125.7 | 31.8 ± 46.4 |
| Beetles | 25.9 | 37 | 7.1 | 1,446.3 | 12.0 | +1 | 20.8 ± 38.5 | 62.9 ± 153.6 | 17.4 ± 38.8 |
| Grasshoppers and crickets | 6.9 | œ | 1.5 | 3,145.2 | 26.1 | 0.07 ± 0.25 | 5.0 ± 20.7 | 136.8 ± 655.8 | 4.3 ± 20.7 |
| Hemipterans | 1.7 | 2 | 0.4 | 195.5 | 1.6 | 0.02 ± 0.13 | 0.6 ± 4.4 | 8.5 ± 40.8 | 3.9 ± 18.7 |
| Insect eggs | 6.0 | 15 | 5.9 | 1 | 1 | 0.13 ± 1.39 | 0.9 ± 9.3 | I | 1 |
| Insect larvae | 8.6 | 18 | 3.4 | 1,254.6 | 10.4 | 0.16 ± 0.65 | 5.1 ± 19.7 | 54.5 ± 217.2 | 17.4 ± 38.7 |
| Insect pupae | 6.0 | 1 | 0.5 | 1,132.7 | 9.4 | 0.01 ± 0.09 | 0.1 ± 1.3 | 49.2 ± 236.2 | 4.3 ± 20.9 |
| Nonidentified arthropods | 10.3 | 12 | 2.3 | ı | ı | 0.10 ± 0.31 | 9.9 ± 29.7 | ı | 1 |
| Plant material | 1.7 | 2 | 0.4 | 365.1 | 3.0 | 0.02 ± 0.13 | 0.1 ± 1.0 | 15.9 ± 76.1 | 3.4 ± 16.5 |
| Pseudoscorpions | 1.7 | 2 | 0.4 | I | I | 0.02 ± 0.13 | 0.6 ± 5.2 | 1 | 1 |
| Roaches | 6.9 | 6 | 1.7 | ı | ı | 0.08 ± 0.30 | 4.9 ± 19.8 | ı | 1 |
| Scorpions | 2.6 | 4 | 8.0 | ı | ı | 0.03 ± 0.23 | 1.3 ± 8.0 | I | 1 |
| Spiders | 26.7 | 35 | 6.7 | 759.0 | 6.3 | 0.30 ± 0.53 | 18.3 ± 34.6 | 33.0 ± 106.6 | 13.0 ± 34.4 |
| Termites | 15.5 | 225 | 43.1 | 2,727.9 | 22.6 | 1.93 ± 11.19 | 11.4 ± 28.9 | 118.6 ± 568.8 | 4.3 ± 20.9 |
| Vertebrates | 2.6 | 33 | 9.0 | 1 | ı | 0.03 ± 0.16 | 1.9 ± 13.2 | ı | 1 |

Table 2. Canonical Correlation Analysis and Canonical Redundancy Analysis of Prey Dimensions versus Head Dimensions

| | Standardized canonical coefficients for head measurements | | | |
|-------------|---|------------------------------|--|--|
| | First canonical variable | Second canonical variable | | |
| Head width | -1.68 | -1.35 | | |
| Head height | 0.62 | 0.08 | | |
| Head length | 0.24 | 1.70 | | |
| | | | | |

| Standardized | l canonica | l coefficient |
|--------------|------------|---------------|
| for pre | ey measure | ements |

| | | for prey mea | isurements | | |
|------------------------|--------------------------|-----------------------------|--------------|------------------------------|--|
| | | First canonical variable | | Second canonical variable | |
| Maximum prey width | | .09 | 1 | .03 | |
| Maximum prey length | | .50 | -0 | .04 | |
| Canonical variables | Canonical correlation | | F approx. | P | |
| I II | 0.65 0.32 | 0.58 0.29 | 2.30 1.11 | 0.06 0.35 | |

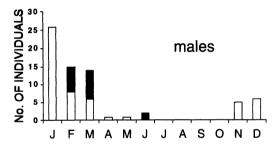
Wilks' Lambda = 0.52, P = 0.06 (H₀: all canonical correlations are zero)

Standardized variance of prey measurements explained by canonical variable of head measurements

| variable of nead measurements | | | |
|-------------------------------|-----------------------|--|--|
| Proportion | Cumulative proportion | | |
| 0.10 | 0.10 | | |
| 0.08 | 0.18 | | |
| | Proportion 0.10 | | |

at Minacu from November 1996 to March 1997 are used, then no reproductive females were observed, and reproductive males occurred only in February (6) and March (7). Even though almost all individuals were sampled during the rainy season (Oct. to April), the monthly distribution of sexually mature individuals suggests that reproduction is seasonal, being mostly restricted to the end of the rainy season and presumably entering into the dry season. This view is supported by the fact that no adult individuals sampled from November to January were reproductive (Fig. 1). Further, in February and March, no females were reproductive, whereas more than 50% of the males were reproductive during the same period, indicating that males seemingly have a longer period of reproductive activity than females.

Sexual dimorphism.—The smallest individual examined was a male measuring 245 mm SVL, whereas the largest individual was a female measuring 810 mm SVL (Fig. 2). To the best of our knowledge, this is the largest SVL ever recorded for A. alba. The largest male measured 780 mm



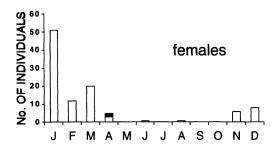


Fig. 1. Monthly distribution of sexually mature *Amphisbaena alba* from the Cerrado. Shaded bars indicate reproductive individuals, whereas empty bars indicate nonreproductive individuals.

SVL. There was a significant difference between the sexes in body size, with females being larger than males (females: $\bar{x} = 4.05 \pm 0.02$, n = 117; males: $\bar{x} = 3.98 \pm 0.02$, n = 96; F = 5.56, P = 0.02). This difference clearly resulted from a larger number of juvenile males in the sample (see Fig. 2), since no intersexual difference in body size was observed when only adult individuals (SVL \geq 422 mm, see above) were considered (females: $\bar{x} = 4.07 \pm 0.01$, n = 113; males: $\bar{x} = 4.08 \pm 0.02$, n = 80; F = 0.20, P = 0.66). Moreover, no sexual dimorphism was observed

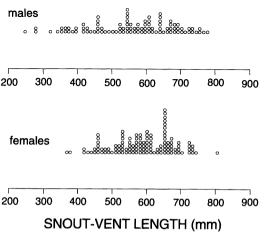


Fig. 2. Size distribution of $Amphisbaena\ alba$ from the Cerrado.

| TABLE | 3. | SUMMARY | STATISTICS | OF | MORPHO! | METRIC |
|-----------------------------------|-------|------------|------------|-------|------------|--------|
| AND M | ERIST | ΓΙC CHARAC | TERS OF Am | bhisb | aena alba. | Values |
| indicate mean \pm SD and range. | | | | | | |

| Character | Males $(n = 97)$ | Females (n = 117) |
|------------------|-------------------|-------------------|
| SVL | 556.5 ± 126.1 | 587.6 ± 87.7 |
| | (245-780) | (370-810) |
| Tail length | 36.1 ± 7.2 | 37.4 ± 5.9 |
| - | (16.2-57.0) | (23.8-58.0) |
| Body width | 21.0 ± 4.9 | 21.7 ± 3.1 |
| | (8.2-31.8) | (14.1-33.3) |
| Body height | 19.3 ± 4.5 | 20.0 ± 3.5 |
| | (6.7-28.2) | (12.0-30.5) |
| Head width | 18.1 ± 4.3 | 19.0 ± 3.0 |
| | (8.3-26.2) | (11.3-25.8) |
| Head height | 15.5 ± 3.5 | 16.5 ± 2.8 |
| | (6.7-21.6) | (9.8-24.9) |
| Head length | 18.5 ± 4.3 | 19.2 ± 2.4 |
| | (9.3-40.0) | (12.0-26.2) |
| Precloacal pores | 7.7 ± 0.8 | 7.6 ± 0.8 |
| | (6-10) | (5-10) |
| Body annuli | 216.9 ± 11.4 | 219.5 ± 4.4 |
| | (117-240) | (207-234) |
| Tail annuli | 13.5 ± 1.1 | 13.2 ± 1.6 |
| | (11-16) | (3-16) |
| Segments around | 71.4 ± 6.4 | 71.6 ± 6.7 |
| midbody | (49–84) | (50–83) |

in the shape variables (Wilks' Lambda = 0.97, P = 0.57) or in the meristic characters (Wilks' Lambda = 0.17, P = 0.17). Summary statistics of morphometric and meristic characters appear in Table 3.

DISCUSSION

Amphisbaena alba consumed a wide variety of prey, even including plant material and vertebrates in its diet, indicating that it is a generalist feeder. The ingestion of plant material by A. alba was also observed by Riley et al. (1986) and has been reported in other amphisbaenians as well (Cabrera and Merlini, 1990). We presume that the ingestion of plant material by amphisbaenians is accidental. Some studies have shown that amphisbaenians occasionally take vertebrate prey (Gans, 1966; Cusumano and Powell, 1991; Sazima and Haddad, 1992). In this study. we found the hind limb of a Tropidurus (Squamata, Tropiduridae) in one individual, a whole Liotyphlops (Squamata, Anomalepididae) in another, and hair, possibly from a rodent, in a third individual. In addition, we have successfully fed A. alba with neonate mice in the lab.

Numerically, beetles, ants, spiders, and termites, in this order, are favorite prey for A. alba, all of them being abundant and diverse ele-

ments of the Cerrado arthropod fauna. The very high numeric percentage of termites (43.1%), when using data from the pooled stomachs, resulted from the ingestion of large numbers of termites by a few individuals since. on the average, each individual A. alba ingested 11.4 ± 28.9% of termites (Table 1). Volumetrically, ants, beetles, insect larvae, and spiders are the most important dietary items. Again, the high volumetric percentage of grasshoppers and crickets (26.1%) and termites (22.6%). when using data from the pooled stomachs, resulted from the ingestion of large volumes of these items by a small number of individuals since, on the average, each individual A. alba ingested $4.3 \pm 20.7\%$ of grasshoppers and crickets and $4.3 \pm 20.9\%$ of termites. These results suggest that the use of data from pooled stomachs is less adequate than using stomach means, because the former are more susceptible to the influence of a few, deviant individuals.

Fossorial squamates in general exhibit low values of prey diversity, presumably because of morphological limitations to handle large prev (Andrews et al., 1987). For example, Bachia bresslaui, a fossorial gymnophthalmid from the Cerrado, has a narrow diet composition (Colli et al., 1998). Likewise, among the desert lizards studied by Pianka (1986), the highly fossorial species of Typhlosaurus had very low food diversity values. On the contrary, the diversity of prev ingested by A. alba is within the range recorded for many terrestrial and arboreal lizard species from the Cerrado (Vitt, 1991; Vitt and Colli, 1994). Still, the numeric diversity of prey based on the pooled stomachs was higher than that observed by Vitt (1991) for three species of tropidurids and two species of teilds from the Cerrado. The high dietary diversity values of A. alba may be partially expalined by the large body size of this species. Indeed, A. alba is one of the largest species of amphisbaenians, reaching 735 mm SVL (Cunha, 1961).

Clutch size in A. alba is higher than in several other amphisbaenians: for example, Amphisbaena dubia, four (Gans, 1964); Chirindia ewerbecki, one (Fitch, 1970); Leposternon infraorbitale, six (Jared et al., 1997); L. microcephalum, two, four, eight (Gans, 1971); Rhineura floridana, two (Carr, 1949); Tomuropeltis pistillum, four (Fitch, 1970). This pattern results presumably from the effects of body size on life-history traits (Dunham and Miles, 1985; Dunham et al., 1988; Roff, 1992), but other factors may likewise influence clutch size, such as lineage-specific effects (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Stearns, 1992). Untangling the effects of historical and ecological factors upon life-his-

tory traits requires the consideration of phylogeny, information that is currently lacking for amphisbaenians.

Amphisbaenians may be less susceptible to the vagaries of climate than other squamates that live above ground, because the subterranean habitat may act as a buffer (Withers, 1981). If we regard precipitation, photoperiod, and temperature fluctuations as major correlates of the reproductive cycles of squamates (Licht and Gorman, 1970; Fitch, 1982; Andrews and Wright, 1994; Censky, 1995), amphisbaenians should therefore have relatively prolonged reproductive seasons. Nevertheless, A. alba most likely has a seasonal reproductive cycle in the Cerrado, and that seems to be characteristic of the few amphisbaenians studied to date (Fitch, 1970; Gil et al., 1994), suggesting a phylogenetic effect. Several other squamates that inhabit open landscapes in Brazil, such as the Cerrado (Colli, 1991; Van Sluys, 1993), Caatinga (Vitt, 1992), Restingas (Rocha, 1992), and Amazonian Savannas (Magnusson, 1987) have seasonal reproductive cycles. A comprehensive explanation for the seasonality in reproduction of tropical squamates, however, is still lacking (Colli et al., 1997). The observation that sympatric tropical squamates may show a remarkable diversity of reproductive cycles (James and Shine, 1988; Vitt, 1992) suggests that lineage-specific effects may supplant responses to present-day, local environmental conditions.

Unlike many species of squamates (Shine, 1978; Fitch, 1981; Stamps, 1983), A. alba are not sexually dimorphic. Sexual differences in body size and shape in squamates are usually attributed to sexual selection, which produces males often larger and/or with proportionally larger heads than females (Carothers, 1984; Vitt and Cooper, 1985; Anderson and Vitt, 1990). The strictly fossorial habits of amphisbaenians, however, may impose severe constraints on any intersexual divergence in morphology, superseding reproductive benefits males may possibly obtain by being larger and/or having proportionally larger heads. Nevertheless, López et al. (1997a) report on the sexual dimorphism in head shape in Blanus cinereus and speculate that sexual dimorphism may be present in primitive (less specialized) amphisbaenians and secondarily lost in more derived (specialized) species. This explanation is attractive, but crucial data for its testing, such as phylogenetic relationship hypotheses and information on sexual dimorphism for a variety of amphisbaenians, are still lacking.

The femoral and precloacal glands of squamates allow conspecific recognition (Alberts,

1991; Cooper et al., 1994; López et al., 1997b) and are usually more developed in males than in females (Cole, 1966; Gans, 1978). We observed, however, no intersexual difference in the presence or the number of precloacal pores in *A. alba*. Further, Antoniazzi et al. (1994) found no difference between sexes in the ultrastructure of precloacal glands of *A. alba*. The exact social role played by the secretions of precloacal glands is unknown, but their use by amphisbaenians may be higly advantageous, due to the limits imposed by fossoriality on visual cues (Gans, 1975; López et al., 1997b).

Amphisbaenians are an important element of the Cerrado herpetofauna and, with the exception of widespread forms such as A. alba and A. fuliginosa (Vanzolini, 1951), most species have spotty distributions and are known from few specimens (Vanzolini, 1991, 1992). Nothing is known on the ecology of most Cerrado amphisbaenians, and, with the accelerated pace of development of the biome (Dias, 1994; Alho and Martins, 1995; Ratter, 1995), it is likely that some species of this highly derived group of squamates will face extinction before we can adequately know where and how they lived.

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