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Ecology and Life History of the Viviparous Lizard *Mabuya bistriata* (Scincidae) in the Brazilian Amazon

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The viviparous lizard *Mabuya bistriata* was studied in two lowland tropical forest sites in Amazonian Brazil with additional data taken on museum specimens. These diurnal lizards are active primarily during mid- to late morning on fallen logs or low on tree trunks. They are heliothermic averaging 32.9 ± 0.98 C in body temperatures. Prey include orthopterans, spiders, eruciform larvae, termites, and other invertebrates. Prey differences between the two sites most likely reflect differences in prey availability associated with tropical seasonality in rainfall.

***Mabuya bistriata* reach sexual maturity by the end of the first year of life, and females produce their first brood at an age of one yr. Females have larger body size than males, and males have larger head size than females. Females ovulate ova 1 mm in diameter and 0.47 mg dry mass. A chorioallantoic placenta forms through apposition of the chorioallantois to the uterine mucosa. During gestation, dry and wet mass increase by over 47,400% and 74,700%, respectively, with virtually all nutrients for development supplied by the female. Gestation lasts 9–12 months. Brood size varies from 2–9, and females with near-term embryos are heavier and wider than nongravid females suggesting a potential cost to reproduction related to the effect of clutch mass and volume on locomotor abilities.**

The extensive lowland tropical forest associated with greater Amazonia contains one of the most diverse herpetofaunas on earth (e.g., Duellman, 1978; Dixon and Soini, 1975, 1977). Although interest in these organisms has increased substantially over the past decade (Crump, 1971; Magnusson et al., 1985), ecologically they continue to remain among the poorest known reptiles and amphibians in the world.

Studies on mainland South American *Mabuya* are of particular interest because most, if not all, New World members of this genus are viviparous (e.g., Vanzolini and Rebouças-Spieker, 1976; Vanzolini et al., 1980), providing a major proportion of nutrients to developing embryos by means of a highly specialized chorioallantoic placenta (Blackburn et al., 1984; Vitt and Blackburn, 1983). In this paper, we describe the ecology and life history of one of the viviparous South American scincid lizards, *Mabuya bistriata*, which was studied in two areas in the Brazilian states of Rondonia and Para where rapid development is severely affecting all remaining wildlife (Fearnside, 1982, 1984a, 1984b, 1985). The only other lizard species at these sites for which ecological data have been published are the tropidurids (sensu Frost and Etheridge, 1989) *Plica plica* (Vitt, 1991a) and *Uranoscodon supercilliosum* (Howland et al., 1990).

METHODS

Field work took place from May through mid-Sept. 1985 (the dry season), in central Rondônia (10°S latitude), and Jan. through March 1987 (early wet season), near the Rio Xingu in Pará (<4°S latitude). These areas are considered part of equatorial Amazonia, consisting of tropical lowland rainforest (Ab'Saber, 1977). The habitat and microhabitat were recorded for 67 *M. bistriata* observed in the field. Habitat categories in Rondônia were (1) agricultural areas; (2) human dwellings; (3) primary (undisturbed) forest; and (4) secondary (regrown) forest. Microhabitat categories were (1) open ground; (2) ground under the overhang of vegetation; (3) leaf litter; (4) live tree trunk or branch; (5) dead tree trunk, log, or limb; (6) other green vegetation; and (7) rocks. In Pará, habitat categories included (1) river forest (floodplain); (2) primary forest; and (3) secondary forest. Microhabitats were (1) leaf litter; (2) live tree trunk or branch; (3) dead tree trunk, log, or limb; and (4) rocks. When lizards were observed above ground level, height off ground was estimated. In addition, time of day and type of activity (i.e., basking, foraging, social encounters) were recorded.

We captured lizards by hand or shot them with a BB rifle for diet and reproductive analyses. When possible, body temperatures (cloacal), air temperatures, and substrate temperatures were recorded with a rapid register thermometer. We also noted whether the lizard was in sun or shade at the time of capture. The following morphological data were recorded for each individual prior to fixation: snout–vent length to 1.0 mm; length of tail base and regenerated portion, if any, to 1.0 mm, head width; head height; head length; gape; body width; body height to 0.1 mm; and total mass to 0.1 g. We made linear measurements with either a meter rule or digital calipers, whereas mass measurements were taken with a Pesola® spring balance or an electronic balance. A similar set of morphological measurements was recorded for neonates born in the laboratory.

Embryos were removed from gravid females, the diameter of the implanted embryo was measured to 0.01 mm, and each embryo was preserved in Karnovsky's fixative or formalin for future examination. The entire complement of embryos was removed from several females containing term embryos, and each embryo was weighed to 0.01 g. Upon return from the field, fixed embryos, along with their attached extraembryonic membranes, yolk, and any visible pieces of shell membrane, carefully were dissected free of maternal tissues. These embryonic samples were weighed, dried to a constant mass at 45 C, and weighed to 0.01 mg to estimate embryonic dry mass. Tissue samples to be used for microscopic study were stored in 0.1 Moler cacodylate buffer or 70% ethanol.

For scanning electron microscopy, maternal and fetal portions of the placental membranes were carefully peeled apart and processed separately. Tissue samples were treated for one h in 1% osmium tetroxide in cacodylate buffer, dehydrated in ethanol, mounted on metal stubs, and coated with gold in a sputter coater. Samples were examined with a Hitachi S-500 scanning electron microscope at 20 kV. For light microscopy, intact samples were processed conventionally and stained with hematoxylin and eosin.

For males, testes were removed, measured (0.01 mm), and weighed (0.001 g). Abdominal fat bodies were removed from both sexes and weighed to 0.001 g. Lizards were then preserved in 10% formalin. Males were considered sexually mature if they possessed enlarged testes and convoluted epididymides. Females were considered sexually mature if they contained implanted embryos. Similar reproductive data were recorded for specimens from western Amazonian Brazil (states of Acre, Rondônia, and Amazonas) in the collections of the Museu Zoologia da Universidade de São Paulo (MZUSP).

Lizards with SVL ≥77 mm were used for most morphological analyses. This approximates the minimum SVL individuals would attain during their first year. This was done to eliminate biases resulting from the inclusion of gravid, but juvenile-sized, females which are sexually mature by the above definition but would reach at least 77 mm SVL by the time parturition occurs (see Vitt and Blackburn, 1983).

Stomachs were removed from fresh or preserved animals and the contents were spread on a petri dish. Prey items were identified to the lowest taxon possible. Length and width of each prey item was measured, and prey volume was calculated with the formula for an ellipsoid:

$$V = 4/3\pi(\tfrac{1}{2}\text{ prey length})(\tfrac{1}{2}\text{ prey width})^2$$

Diet data from Rondônia were considered a dry season sample, and diet data from Pará were considered a wet season sample for comparison recognizing that geographic differences in prey may also exist.

Descriptive statistics include $\bar{x} \pm$ SE unless otherwise stated. Standard parametric statistical tests were performed unless the assumptions of those tests could not be met. Differences were considered significant at $P < 0.05$. All specimens were deposited at the MZUSP.

Results

Temporal and ecological distribution.—Individuals of *M. bistriata* (Fig. 1) were usually observed foraging or basking on fallen logs or low areas of tree trunks (Table 1) from midmorning through early afternoon (Fig. 2). Height off ground ranged from 0.1–2.1 m ($\bar{x} = 0.97 \pm 0.08$ m, n = 49). An individual observed at night appeared to be foraging in leaf litter. Of the 67 individuals observed, 26 (38.8%) were basking, and the remainder, 41 (51.2%), were foraging. Twenty-four (35.8%) were in direct sunlight, and 43 (64.2%) were in the shade. Body temperatures of 11 active individuals averaged 32.9 ± 0.98 (range 27.6–36.8) C. Spearman rank correlations revealed no significant relationship

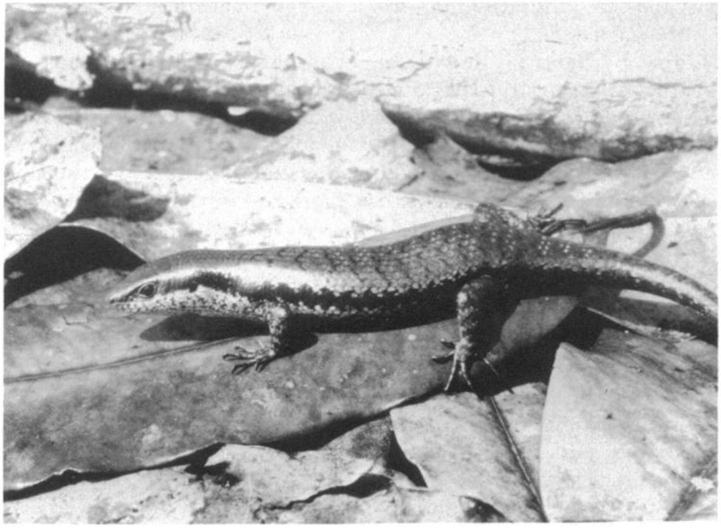

Fig. 1. Basking female of *M. bistriata* from Acampamento Jurua on the Rio Xingu, ParÁ, Brazil.

between body temperatures and air temperatures ($P = 0.12$) or body temperatures and substrate temperatures ($P = 0.12$). Body temperatures of individuals in the sun (34.1 ± 0.79 C, n = 7) and individuals in the shade (30.8 ± 2.07, n = 4) were not significantly different (Mann Whitney U test, $P = 0.18$).

Morphology and approximate growth rates.—Individual *M. bistriata* range in size from 35.8 mm SVL at birth to 109 mm as large adults (Fig. 3). Based on seasonal distribution of SVL (Fig. 3), it appears that neonates born in Aug. reach approximately 61 mm SVL by Nov. (8.4 mm/mo for the first three mo), approximately 77 mm SVL by Jan. (8.0 mm/mo for the next two mo), and approximately 87 mm SVL by June (2.0 mm/mo for the next five mo). Growth rate appears to fall off sharply after a size of about 77 mm SVL is reached.

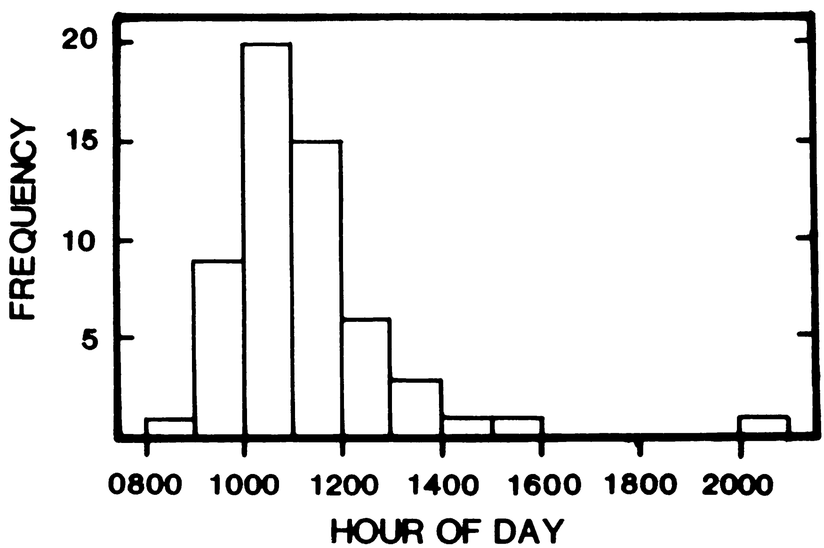

Fig. 2. Temporal distribution of hourly activity for *M. bistriata* from Amazonian Brazil.

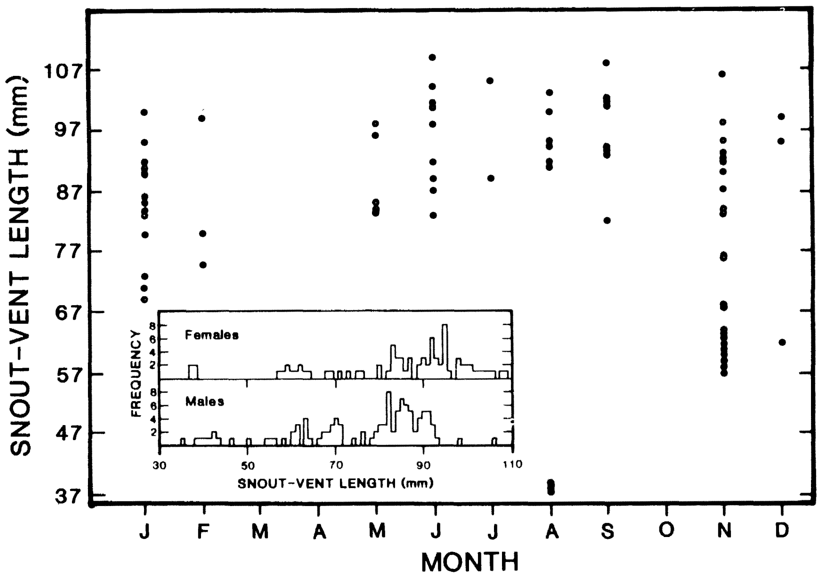

Fig. 3. Seasonal distributions of body sizes for *M. bistriata* (sexes pooled) from western Brazil. The insert shows body size distributions for male and female *M. bistriata* based on field captured and museum (MZUSP) specimens.

An examination of morphological data for individuals ≥77 mm revealed that females were larger than males in all morphological characteristics measured although only SVL and body mass were significantly different (Table 2). Analyses of covariance with SVL as the covariate revealed significant sexual differences in slopes and intercepts of regressions of three measures of head size (width, length, and height) but not gape or body mass with all lizards included. Restriction of this analysis to lizards ≥77 mm SVL produced similar results. This indicates that body mass differences reported above are a result of SVL differences between sexes.

TABLE 1. HABITAT AND MICROHABITAT DISTRIBUTION FOR *M. bistriata* IN RONDÔNIA AND PARÁ. Results are based on 67 individual observations of lizards in the field. The number in each category is given with percent of the total from each state represented by that category in parentheses.

Habitat	Frequency	Microhabitat	Frequency
Rondônia			
Agricultural	1 (1.79)	Open ground	3 (5.36)
Human dwelling	2 (3.57)	Under vegetation	2 (3.57)
Primary forest	31 (55.36)	Leaf litter	9 (16.07)
Secondary forest	22 (39.29)	Live tree trunk or branch	12 (21.43)
		Dead tree trunk, log, or limb	26 (46.43)
		Other green vegetation	2 (3.57)
		Rocks	2 (3.57)
Pará			
River forest	4 (36.36)	Leaf litter	2 (18.18)
Primary forest	1 (9.09)	Live tree trunk or branch	5 (45.45)
Secondary forest	6 (54.55)	Dead tree trunk, log, or limb	3 (27.27)
		Rocks	1 (9.09)

TABLE 2. MORPHOLOGICAL ATTRIBUTES OF ADULT MALE AND FEMALE *Mabuya bistriata* >77 mm SVL. Means are presented ±1 SE. Results of the Mann-Whitney two sample test comparing sexes appear in parentheses below data. The SVL sample labeled "all data pooled" includes measurements from museum specimens collected in western Brazil. NS indicates no significant differences between samples.

Characteristic	Males	N	Females	N
Snout–vent length (mm)				
Field sample only	87.2 ± 1.35 (77.0–106.0)	24	93.1 ± 1.48 (78.0–109.0)	36
		(Z = 2.42, P = 0.015)		
All data pooled	86.1 ± 0.60 (77.0–106.0)	70	92.2 ± 0.91 (78.0–109.0)	73
		(Z = 4.94, P < 0.001)		
Total mass (g)	14.22 ± 0.78 (10.0–27.6)	24	18.09 ± 0.94 (9.8–30.1)	36
		(Z = 2.86, P = 0.004)		
Head width (mm)	12.88 ± 0.22 (11.4–15.5)	24	12.71 ± 0.19 (11.0–14.7)	36
		(Z = 0.44, P = 0.66 NS)		
Head length (mm)	17.11 ± 0.29 (14.5–20.1)	24	16.87 ± 0.22 (14.5–19.2)	35
		(Z = 0.56, P = 0.58 NS)		
Head height (mm)	8.35 ± 0.15 (7.4–10.0)	24	8.16 ± 0.13 (6.3–9.6)	36
		(Z = −0.96, P = 0.34 NS)		
Gape, mm (Rondônia only)	18.12 ± 0.50 (14.5–20.8)	13	18.33 ± 0.47 (15.0–22.1)	19
		(Z = 0.15, P = 0.88 NS)		

The covariance analyses reveal that males have heads slightly larger than similar-sized females and that the lack of head-size differences based on the two sample test above was because of differences in SVL between sexes.

Prey utilization.—*Mabuya bistriata* feed primarily on small invertebrates, including insects and their larvae, spiders, harvesters, and snails (Table 3). They forage on tree trunks and large limbs, tangles of vines, and in leaf litter. The diversity of prey types in stomachs, including small vertebrates, indicates that *M. bistriata* most likely feed on any moving animal of the appropriate size with the exception of ants which appear to be eaten infrequently. Portions of shed skin were found in one stomach and placental membranes were found in the stomach of a female that had recently given birth.

The diet of lizards from Rondônia was dominated numerically by beetles, spiders, and eruciform larvae and volumetrically by orthopterans, spiders, and eruciform larvae. The diet of lizards from Pará was dominated numerically by termites and orthopterans and volumetrically by orthopterans and spiders. Data on frequency of utilization of various prey items indicates that, in both areas, orthopterans are eaten by a majority of lizards. There was a small but significant difference (Z = 2.14, P = 0.03) in number of prey eaten by individual lizards from Rondônia ($\bar{x}$ = 1.58 ± 0.16) compared to Pará ($\bar{x}$ = 4.89 ± 1.96), but much of this difference is because of large numbers of termites in two Pará lizards (Table 3). Mean prey length, width, and volume were significantly larger in Rondônia lizards (12.262 ± 0.84 mm; 4.09 ± 0.15 mm; 0.124 ± 0.013 cc, respectively) compared to Pará lizards (6.28 ± 0.44 mm; 2.41 ± 0.15 mm; 0.055 ± 0.013 cc) (Mann-Whitney U test, all P values < 0.001). Overlaps (used as a measure of similarity) in numbers and volumes of prey from the two areas (using MacArthur and Levins, 1967 overlap measure) were 0.38 and 0.58, respectively. Regression analyses revealed no significant relationships between various measures of lizard head size (length, width, height, or gape) or body size (SVL) and various measures of mean or maximum prey size (length, width, and volume; all P values > 0.25) for the Rondônia samples. Similar analyses were not performed for the Pará samples.

Life history characteristics and fat cycling.—*Mabuya bistriata* is viviparous, ovulating tiny undeveloped ova from Aug. through Dec. (Fig. 4). All females exceeding 55 mm SVL contained implanted ova or vitellogenic follicles. Females ovulate at an age of approximately 2.5 mo. Very little growth of implanted ova occurs during the first 4–7 mo of gestation (Fig. 4). By the time embryonic growth takes place (approx. March),

TABLE 3. SUMMARY OF THE DIET OF *M. bistriata* FROM THE STATES OF RONDÔNIA (DRY SEASON) AND PARÁ (WET SEASON) IN AMAZONIAN BRAZIL. Prey volume is in cc. Frequency indicates the number of lizards containing a given item.

Prey category	Rondônia					Pará				
	N	% N	Vol.	% Vol.	Freq.	N	% N	Vol.	% Vol.	Freq.
Orthoptera										
Acrididae	3	5.08	0.67	9.10	3	2	1.60	0.11	1.64	2
Blattidae	5	8.47	0.97	13.18	5	14	11.20	3.26	48.73	11
Gryllidae	3	5.08	0.31	4.21	3	8	6.04	1.02	15.25	8
Tettigoniidae	4	6.78	0.53	7.20	4	—	—	—	—	—
Isoptera										
Termitidae	4	6.78	0.16	2.17	3	75	60.00	0.20	2.99	2
Coleoptera										
Buprestidae	1	1.69	0.24	3.26	1	—	—	—	—	—
Carabidae	1	1.69	0.08	1.01	1	1	0.80	0.23	3.44	1
Chrysomelidae	6	10.17	0.56	7.61	2	—	—	—	—	—
Erotylidae	1	1.69	0.23	3.13	1	—	—	—	—	—
Tenebrionidae	1	1.69	0.03	0.41	1	2	1.60	0.17	2.54	2
Hemiptera										
Reduviidae	1	1.69	0.11	1.49	1	—	—	—	—	—
Aradidae	1	1.69	0.03	0.40	1	—	—	—	—	—
Homoptera										
Cercopidae	1	1.69	0.02	0.27	1	1	0.80	0.01	0.14	1
Cicadellidae	1	1.69	0.05	0.68	1	—	—	—	—	—
Lepidoptera										
Noctuidae	1	1.69	0.22	3.00	1	—	—	—	—	—
Hymenoptera										
Formicidae	—	—	—	—	—	3	2.40	0.11	1.64	2
Ichneumonidae	1	1.69	0.09	1.22	1	3	2.40	0.06	0.90	1
Sphecidae	—	—	—	—	—	1	0.80	0.03	0.45	1
Megachillidae	2	3.39	0.12	1.63	1	2	1.60	0.04	0.60	2
Diptera										
Tiphiidae	1	1.69	0.42	5.70	1	—	—	—	—	—
Larvae										
Eruciform larvae	7	11.69	1.19	16.17	4	1	0.80	0.02	0.30	1
Vermiform larvae	—	—	—	—	—	2	1.60	0.04	0.60	1
Myrmeliontidae larvae	1	1.69	0.05	0.68	1	—	—	—	—	—
Araneae	7	11.86	0.83	11.28	7	5	3.40	1.00	14.95	2
Opiliones	3	5.08	0.29	3.94	3	—	—	—	—	—
Chilopoda	—	—	—	—	—	2	1.60	0.23	3.44	2
Diplopoda	—	—	—	—	—	2	1.60	0.05	0.75	2
Gastropoda	2	3.39	0.04	0.54	2	—	—	—	—	—
Reptilia										
Prionodactylus	1	1.69	0.12	1.63	1	—	—	—	—	—
Gonatodes (tail)	—	—	—	—	—	1	0.80	0.11	1.64	1
Shed skin	—	—	present	—	—	—	—	—	—	—
Placentae	—	—	present	—	—	—	—	—	—	—
Totals	59	100	7.36	100		125	100	6.69	100	

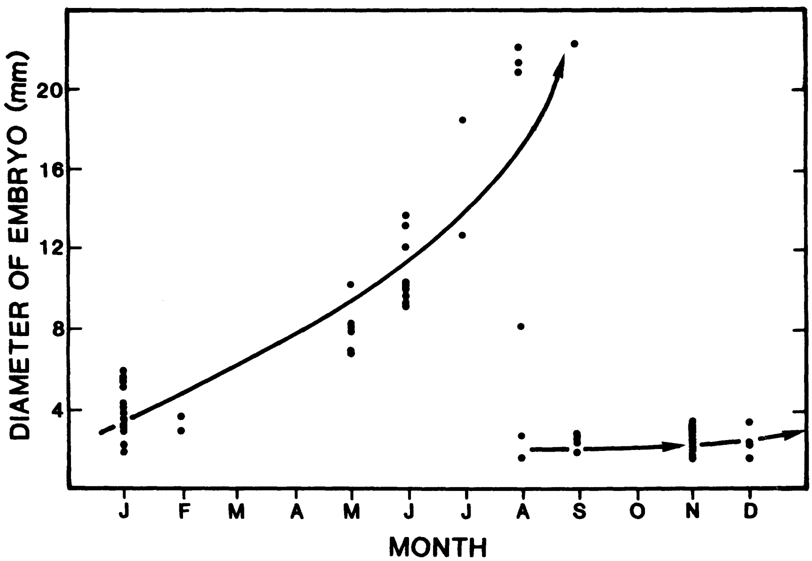

Fig. 4. Seasonal distribution of sizes of embryos taken from *M. bistriata*. Diameter of the embryo is taken as the distance across the embryo sac with the embryo coiled inside. The lines approximate the increase in diameter of the embryo sac, estimating relative growth of the embryos.

most yearling females have reached at least 77 mm SVL (Fig. 3) and thus are capable of accommodating the enlarging embryos. The overall gestation period extends from 10–12 months.

Development and placentation.—*Mabuya bistriata* ovulates between Aug. and Nov., and parturition occurs in the following Aug.–Sept.; thus gestation lasts about 9–12 months. At ovulation, eggs are approximately 1 mm in diameter, 0.47 mg in dry mass (n = 14), and 1.78 mg in wet mass (n = 13). Late stage fetuses (Stage 40: Dufaure and Hubert, 1961) averaged 222.42 mg (n = 7) in dry mass and 1332.05 mg (n = 7) in wet mass. These data suggest that during gestation, dry mass and wet mass of the conceptuses increase by over 47,400% and 74,700%, respectively.

Following ovulation and fertilization, a thin shell membrane is deposited, and the eggs lodge in the uterine portion of the oviduct where development proceeds. The eggs undergo very little growth in diameter and mass during the first 4–7 months of gestation (Fig. 4). Most of the increase in size and dry mass occurs during the final four months of gestation, following establishment of the chorioallantois.

A chorioallantoic placenta forms through apposition of the chorioallantois to the uterine muscosa. The shell membrane has degenerated by mid- to late gestation, leaving maternal and uterine tissue in direct contact. The entire surface of the chorionic vesicle is given over to chorioallantoic placenta, and no trace of a yolk sac placenta or omphalallantoic placenta is apparent. The placenta is epitheliochorial throughout; no areas of epithelial cell erosion are evident. In unspecialized regions, uterine and chorionic tissues interdigitate, and uterine and chorionic epithelia are present as thin squamous cells interposed between the uterine and allantoic vasculature.

Two types of morphological specialization indicative of nutrient transfer develop in the mature chorioallantoic placenta—chorionic crypts and the placentome. Chorionic crypts are invaginated pits lined by tall, columnar cells that bear microvilli. The crypts lie apposed to openings of uterine glands, within which secretory material often is evident. Cytoplasm of the crypt epithelium contains inclusions that stain identically to the uterine secretions.

Lying mesometrially, the placentome is formed by enlarged uterine villi that protrude into a deep invagination into the external surface of the chorion. Fetal and maternal tissues tightly interlock in this region and are difficult to separate. The chorionic epithelium consists of two cell populations: "giant cells," and thin,

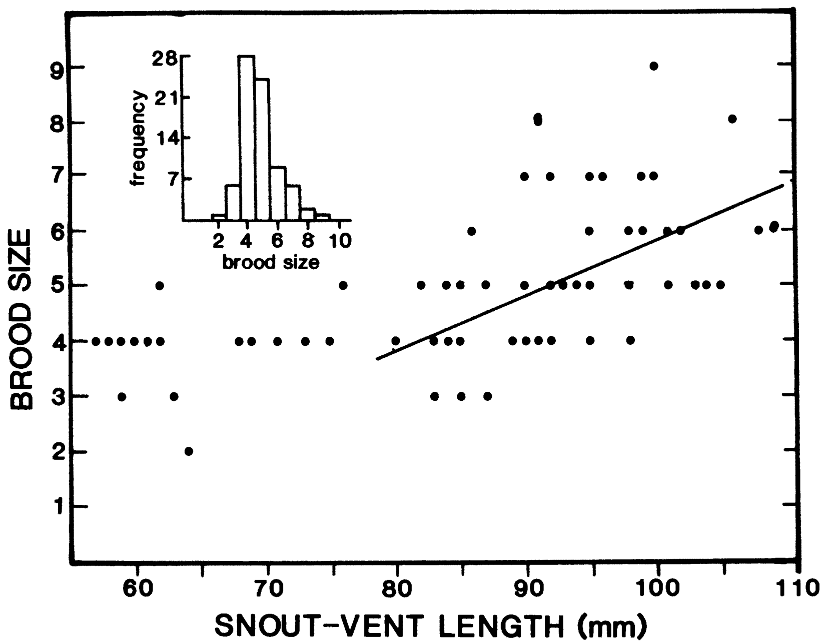

Fig. 5. Relationship between female size (snout–vent length) and brood size in *M. bistriata.*

columnar "interstitial cells." The giant cells are enormously enlarged binucleated cells with prominent apical borders of microvilli that protrude toward the maternal interface. The interstitial cells are thin, columnar cells that surround the giant cells laterally and appear attached to them apically through tight junctions. On the maternal side of the placentome, the uterine epithelium is represented by a syncytium of simple cuboidal epithelium overlying an extensive capillary network. Histologically, the chorionic and uterine epithelia are tightly apposed and often appear fused to one another at their apical borders.

Clutch characteristics.—Brood size varied from 2–9 ($\bar{x}$ = 4.7 ± 0.14, n = 94) among all females ($\bar{x}$ SVL = 86.3 ± 1.4) containing vitellogenic follicles or implanted embryos. For females >77 mm SVL ($\bar{x}$ SVL = 92.2 ± 0.91, n = 73) brood size averaged 5.1 ± 0.15 ranging from 3–9. Analysis of covariance revealed significant differences in slopes ($P < 0.05$) among various regressions of log brood size on log SVL (best fit). The six regressions compared were (1) all females containing vitellogenic follicles or implanted embryos; (2) all females containing only vitellogenic follicles; (3) all females containing only implanted embryos; (4) females >77 mm SVL containing vitellogenic follicles or implanted embryos; (5) females >77 mm SVL containing only vitellogenic follicles; and (6) females containing only implanted embryos. Pairwise analyses of covariance revealed that most of the variation was associated with the inclusion of small females early in the reproductive season, i.e., those which would reach at least 77 mm SVL prior to parturition. Thus the model we present for the regression of brood size with SVL is based on females ≥77 mm containing oviductal embryos or vitellogenic follicles (Fig. 5).

We attempted to indirectly estimate the cost to females of carrying large broods by comparing body mass and body width of three groups of females: nongravid females, those with well-developed but not term embryos (2–4 mo prior to parturition), and those with term embryos. For this comparison, we used only females from Rondônia. Our analysis shows that females with term embryos weigh more and have wider bodies than either of the other groups, and these results are supported with results of analyses of covariance (Table 4). Three females with term embryos weighed prior to and after removing the embryos averaged 101.7 ± 0.88 mm SVL, 28.5 ± 0.10 g total mass, and 18.17 ± 0.88 g body mass (without embryos). Their broods av-

TABLE 4. SUMMARY STATISTICS ($\bar{x}$ ± SE) COMPARING MORPHOLOGICAL CHARACTERISTICS OF TERM, LATE GRAVID, AND NONGRAVID FEMALES OF *M. bistriata*. Analysis of covariance results are indicated for comparisons with term females by superscripts. SVL was the covariate in the body width comparisons, and log SVL was the covariate with log body mass. Differences are considered significant at $P < 0.05$. Significantly different slopes and intercepts were higher for term females.

Category	SVL (mm)	Body mass (g)	Body width (mm)
Term (5)	97.0 ± 2.9	24.30 ± 2.59	23.82 ± 1.36
Late gravid (13)	93.0 ± 2.4	[a]18.03 ± 1.64	[a]18.53 ± 0.90
Nongravid (5)	93.0 ± 3.1	[b]15.62 ± 0.67	[a]16.92 ± 0.91

[a] Indicates similar slope but significantly different intercept.
[b] Indicates significant difference in slope and intercept.

eraged 10.33 ± 1.16 g, brood mass/total mass averaged 0.362 ± 0.039, and brood mass/body mass averaged 0.581 ± 0.103. Thus females containing term embryos carry broods constituting more than 50% of their nongravid body mass.

Considerable variation in size of abdominal fat bodies exists among females during any one month, but a slight decrease in the amount of abdominal fat is apparent as the dry season progresses (July--Sept.). This is followed by an increase following the onset of the wet season (Oct.–Nov. in Rondônia), coincident with final embryonic growth and parturition (analysis restricted to animals from western Brazil).

DISCUSSION

Ecology.—Based on habitat and microhabitat data, *M. bistriata* can be characterized as a diurnal, forest dwelling species. It is terrestrial and arboreal occurring primarily on tree trunks and large limbs as well as in leaf litter. Most activity, including basking and foraging occurs in late morning and early afternoon when sun is available. Body temperatures as well as behavioral observations indicate that *M. bistriata* is a heliotherm. It maintains relatively high body temperatures by shuttling between patches of sunlight filtering through the tropical forest canopy and shade.

The diet of *M. bistriata* is typical of most diurnal lizards of its size, consisting of a variety of invertebrates as well as small vertebrates. *Mabuya bistriata* apparently eats its shed skin, and females eat the placental membranes during parturition as reported in certain other South American *Mabuya* (Rebouças-Spieker and Vanzolini, 1978). Lizards from Rondônia during the dry season ate consistently larger prey than wet season lizards from Pará reflecting either prey size differences associated with seasonality of rainfall or, alternatively, prey size differences associated with different localities. It is most likely that the low diet similarities between Rondônia and Pará lizards are associated with dry versus wet season differences in prey availability (Janzen and Schoener, 1968).

Apparent sexual dimorphism in body size exists (females larger) as well as sexual dimorphism in relative head size (males larger). Because brood size is associated with female body size, there should be a selective advantage to large female body size because of its immediate reproductive consequences. It is possible that potential increased risk to the female during pregnancy as a consequence of increased mass, is offset by behavioral changes as demonstrated in other lizards (Shine, 1980; Cooper et al., 1990). Although nothing is known of the social system in this species of skink, larger relative head size in other skinks (e.g., *Eumeces laticeps*, Vitt and Cooper, 1985) appears associated with advantages it accrues individual males in intrasexual interactions affecting mating success. Males of a closely related species (*M. heathi*) have been observed aggressively interacting (Vitt, pers. obs.), and presumably this occurs in *M. bistriata* as well. Thus relatively large head size in male *M. bistriata* may be a result of sexual selection.

Development and placentation.—The enormous gestational increase in dry mass of the conceptus of *M. bistriata* indicates that virtually all of the nutrients for development are supplied by the pregnant female following ovulation. A similar mass increase occurs in *M. heathi* (Blackburn et al., 1984; Vitt and Blackburn, 1983), and other South American *Mabuya* that have been studied (see Vanzolini and Rebouças Spieker, 1976; Vitt, 1991b). In sharp contrast, a substantial postovulatory nutrient contribution is exceedingly rare among viviparous squamates of other genera (Yaron, 1985). In all viviparous squamates for which nutrient provision has been quantified in detail, the yolk provides most of the organic nutrients for development, and dry mass of the conceptus decreases during gestation (Stewart, 1989; Stewart and Castillo, 1984; Stewart et al., 1990).

At the time of the increase in dry mass of the conceptus of *M. bistriata,* the chorioallantoic placenta is the only organ available for maternal-fetal nutrient transfer. Neither a true omphaloplacenta nor an omphalallantoic placenta (*sensu* Stewart and Blackburn, 1988) is apparent by mid- to late gestation. The chorioallantoic placenta exhibits two structural specializations suggestive of histotrophic nutrient transfer—chorionic crypts and a placentome. Morphology of the chorionic epithelium of both these regions is typical of absorptive epithelia; the cells are tall and columnar with long microvilli and apical tight junctions. The chorionic crypts lie apposed to the openings of the uterine glands, and their epithelial cells contain material very similar in appearance to uterine secretions. Confirmation of an absorptive role, as well as specific functions of the crypts relative to the placentome, will require experimental investigation.

Structure of the mature placenta in *M. bistriata* is similar to that of *M. heathi* (Blackburn et al., 1984; Blackburn and Vitt, 1986), and thus conforms to the recently recognized Type IV placental morphotype (Blackburn, 1988). Diagnostic features of this morphotype include chorionic crypts, as well as a placentome with two differentiated populations of chorionic epithelial cells. Neither feature has ever been discovered among other viviparous squamates. Although a placentome is present in a European scincid, *Chalcides chalcides* (ten Cate-Hoedemaker, 1933), in which it may function in nutrient transfer, this placentome bears only superficial resemblance to that of Brazilian *Mabuya* (Blackburn, 1988).

Life-history characteristics.—Reproductive characteristics of *M. bistriata* are strikingly similar to those of *M. heathi* studied in northeast Brazil (Vitt and Blackburn, 1983), and *M. caissara* and *M. macrorhyncha* studied in the state of São Paulo, Brazil (Vanzolini and Rebouças-Spieker, 1976). These species ovulate tiny ova which increase little in size during the first 4–6 months of gestation. During the seventh to ninth months, rapid embryonic growth occurs followed by parturition during the tenth to twelfth month. Thus, the gestation period is extended, and females are more or less synchronous in reproductive activities. More variation in reproductive stage occurs among females in *M. bistriata* compared with *M. heathi.* This variation may be a consequence of reduced environmental seasonality in Amazonia compared to caatinga of northeast Brazil (see Vitt and Goldberg, 1983). The reproductive season for *M. bistriata* begins earlier and is more extended than that of *M. heathi.* Both species, however, produce their young during the dry season. Seasonality of reproduction for the two species studied by Vanzolini and Rebouças-Spieker (1976) appears more complex and may be complicated by the interaction between two climatic zones.

The large mass of the brood (>50% of non-gravid female body mass) and the brood's effect on female morphology suggest a high potential cost to reproduction in females (Shine, 1980). Early in the breeding season (Jan. through Mar.), females appear to be more active than females during the time period when parturition occurs (Aug. through Oct.). Preparturition females are most often observed basking near crevices in tree trunks or other refugia which can be entered rapidly with little movement. Thus the potential high cost to extended gestation may be at least partially offset by behavioral adjustments in gravid females as in another skink, *Eumeces laticeps* (Cooper et al., 1990).

In terms of its ecology and life history, Amazonian *M. bistriata* is more similar to other species of South American *Mabuya* than to sympatric species in the families of the Iguania (Frost and Ethridge, 1989), and other families such as the Gymnophthalmidae, Teiidae, and Gekkonidae. This suggests that the evolutionary history of New World *Mabuya* contributes more to aspects of the ecology of *M. bistriata* than adaptation at the local level. This is consistent with the observation by Dunham and Miles (1985) that phylogeny is one of the most important determinants of life-history characteristics in squamate reptiles. Nevertheless, some of the differences between populations in west Amazonia and Pará suggest that, within the framework of historical constraints, there is local adaptation. Numerous detailed studies on temperate zone lizards have demonstrated the influence of the local environment on lizard life histories (e.g., Ballinger, 1983; Dunham, 1982; Tinkle and Ballinger, 1972).

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Literature Cited

Ab'Saber, A. N. 1977. Os dominios morphoclimáticos na America do Sul. Primeira aproximacão. Geomorfologia (Inst. Geogr. Univ. São Paulo) 52: 1–21.

Ballinger, R. E. 1983. On the nature of life history variation in lizards, p. 241–260. *In:* Lizard ecology: studies on a model organism. R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Harvard Univ. Press, Cambridge, Massachusetts.

Blackburn, D. G. 1988. Late-stage placentation in the matrotrophic viviparous lizard *Chalicides chalcides.* Amer. Zool. 28:196A.

———, and L. J. Vitt. 1986. Eutherian-like placentation and fetal nutrition in a viviparous reptile. Biol. Reprod. 34, Suppl. 1:69.

———, ———, and C. A. Beuchat. 1984. Eutherian-like reproductive specializations in a viviparous reptile. Proc. Natl. Acad. Sci. 81:4860–4863.

ten Cate-Hoedemaker, N. J. 1933. Beitrage zur Kenntnis der Plazentation bei Haien und Reptilien. Z. Zellforsch. mikrosk. Anat. 18:299–345.

Cooper, W. E., Jr., L. J. Vitt, R. Hedges, and R. B. Huey. 1990. Locomotor impairment and defense in gravid lizards (*Eumecas laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. Behav. Ecol. Sociobio. 27:153–157.

Crump, M. L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occ. Pap. Mus. Nat. Hist. Univ. Kansas 3:1–62.

Dixon, J. R., and P. Soini. 1975. The reptiles of the upper Amazon Basin, Iquitos region, Peru. I. Lizards and amphisbaenians. Contr. Biol. Geol. Milwaukee Publ. Mus. 4:1–58.

———, and ———. 1977. The reptiles of the upper Amazon Basin, Iquitos region, Peru. II. Crocodilians, turtles and snakes. *Ibid.* 12:1–91.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publ. Univ. Kansas Mus. Nat. Hist. 65:1–352.

Dufaure, J. P., and J. Hubert. 1961. Table de developpement de lezard vivipare: *Lacerta (Zootoca) vivipara* Jacquin. Arch. Anat. micr. Morphol. exp. 50:309–328.

Dunham, A. E. 1982. Demographic and life history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life history phenomena in lizards. Herpetologica 38: 208–221.

———, and D. B. Miles. 1985. Patterns of covariation in life history traits of squamate reptiles: the effect of size and phylogeny reconsidered. Am. Nat. 126:231–257.

Fearnside, P. M. 1982. Deforestation in the Brazilian Amazon: how fast is it occurring. Interciencia 7:82–88.

———. 1984a. Land clearing behaviour in small farmer settlement schemes in theBrazilian Amazon and its relation to human carrying capacity, p. 255–271. *In:* Tropical rain-forest: the Leeds Symposium. A. C. Chadwick and S. L. Sutton (eds). Leeds Philosophical and Literary Society, Leeds, England.

———. 1984b. Roads in Rondônia: highway construction and the farce of unprotected reserves in Brazil's Amazonian forest. Environ. Cons. 11:358–360.

———. 1985. Rondônia: sem florestas na proxima decada? Ciencia Hoje 4:92–94.

Frost, D. R., and R. Ethridge. 1989. A phylogenetic analysis and taxonomy of Iguanian lizards (Reptilia: Squamata). Univ. Kansas Mus. Nat. Hist. Misc. Publ. No. 81:1–65.

Howland, J. M., L. J. Vitt, and P. T. Lopez. 1990. Life on the edge: the ecology and life history of the tropidurine iguanid lizard *Uranoscodon supercilliosum.* Can. J. Zool. 68:1367–1373.

Janzen, D. H., and T. W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49:96–110.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. Amer. Nat. 101:377–385.

Magnusson, W. E., L. J. Paiva, R. M. Rocha, C. R. Franke, L. A. Kasper, and A. P. Lima. 1985. The correlates of foraging mode in a community of Brazilian lizards. Herpetologica 41:324–332.

Rebouças-Spieker, R., and P. E. Vanzolini. 1978. Parturition in *Mabuya macrorhyncha* Hoge, 1946 (Sauria, Scincidae), with a note on the distribution of maternal behavior in lizards. Papeis Avulsos Zool. (São Paulo) 32:95–99.

SHINE, R. 1990. Costs of reproduction in reptiles. Oecologia (Berl.) 46:92–100.

STEWART, J. R. 1989. Facultative placentotrophy and the evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula*. Amer. Natur. 133:111–137.

———, AND R. E. CASTILLO. 1984. Nutritional provision of the yolk of two species of viviparous reptiles. Physiol. Zool. 57:377–383.

———, AND D. G. BLACKBURN. 1988. Reptilian placentation: structural diversity and terminology. Copeia 1988:838–851.

———, ———, D. C. BAXTER, AND L. H. HOFFMAN. 1990. Nutritional provision to the embryos in a predominantly lecithotrophic placental reptile, *Thamnophis ordinoides* (Squamata: Serpentes). Physiol. Zool. 63:722–734.

TINKLE, D. W., AND R. E. BALLINGER. 1972. *Sceloporus undulatus*: a study of the comparative intraspecific demography of a lizard. Ecology 53:570–584.

VANZOLINI, P. E., AND R. REBOUÇAS-SPIEKER. 1976. Distribution and differentiation of animals along the coast and on continental islands of the state of São Paulo, Brasil. 3. Reproductive differences between and within *Mabuya caissara* and *M. macrorhyncha* (Sauria, Scincidae). Papeis Avulsos Zool. (São Paulo) 29:95–109.

———, A.M.M. RAMOS-COSTA, AND L. J. VITT. 1980. Repteis das caatingas. Academia Brasileira de Ciencis, Rio de Janeiro, Brazil.

VITT, L. J. 1991a. Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. Can. J. Zool. 68:1366–1373.

———. 1991b. An introduction to the ecology of cerrado lizards. J. Herpetol. 25:79–90.

———, AND D. G. BLACKBURN. 1983. Reproduction in the lizard *Mabuya heathi* (Scincidae): a commentary on viviparity in New World *Mabuya*. Can. J. Zool. 61:2798–2806.

———, AND S. R. GOLDBERG. 1983. 1983. Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. Copeia 1983:131–141.

———, AND W. E. COOPER, JR. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Can. J. Zool. 63: 995–1002.

YARON, Z. 1985. Reptilian placentation and gestation: structure, function and endocrine control, p. 527–603. *In:* Biology of the Reptilia, Vol. 15. C. Gans and F. Billett (eds.), John Wiley & Sons, New York, New York.

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Phylogenetic Relationships of the Crystal Darter, *Crystallaria asprella* (Teleostei: Percidae)

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Evidence is presented to support the hypothesis that the North American darters form a monophyletic group and that *Crystallaria asprella* is the sister taxon to a clade consisting of *Percina* plus *Etheostoma*. *Crystallaria* Jordan and Gilbert is resurrected for *C. asprella* thus maintaining a classification of darters that is consistent with their hypothesized phylogeny.

THE crystal darter, *Crystallaria asprella*, is known from the Missouri, Ohio, Mississippi, and Gulf Coast drainages although it appears to have been extirpated from much of its former range (Page, 1980). This fish requires open stretches of large streams with a sand or gravel substrate (Pflieger, 1971). The translucent body of *C. asprella*, together with its ability to bury itself in sand (based on aquarium observations, Miller and Robison, 1973), has led previous investigators to place *Crystallaria*, together with the sand darters, in the genus *Ammocrypta*. The genus *Ammocrypta*, however, is a polyphyletic assemblage. Members of the subgenus *Ammocrypta* are more closely related to members of the *Boleosoma* group of the genus *Etheostoma* than to *C. asprella* (Simons, 1989). Based on morphological evidence, *Crystallaria*