

**Ecological Comparisons between the Sympatric Lizards
Enyalius bilineatus and *Enyalius brasiliensis* (Iguanidae, Leiosaurinae)
 from an Atlantic Rain-Forest Area in Southeastern Brazil**

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ABSTRACT.—Aspects of the ecology of the semi-arboreal lizards *Enyalius bilineatus* and *Enyalius brasiliensis* were studied in a montane Atlantic forest region of Espírito Santo State, southeastern Brazil. Individuals of *E. bilineatus* were collected mainly in a coffee plantation, whereas *E. brasiliensis* was found only in the forest proper. *Enyalius brasiliensis* was significantly larger (up to 106 mm snout–vent length, SVL) than *E. bilineatus* (up to 90 mm SVL). Both species were sexually dimorphic in body size, with females larger than males. The two species consumed a broad spectrum of prey but differed quantitatively in their diet composition. Ants and orthopterans dominated the diet of *E. bilineatus*, whereas *E. brasiliensis* preyed mainly on cockroaches and caterpillars. Clutch size of *E. bilineatus* varied from 2–6 (mean = 4.4) and that of *E. brasiliensis* from 8–14 (mean = 11.5). Ecological differences between the two species may result in differential susceptibilities to habitat perturbation, with *E. bilineatus* being more tolerant of disturbed areas and perhaps even benefitting from anthropic action, unlike the forest-dependent *E. brasiliensis*.

Closely related lizard species living in sympatry tend to differ in one or more aspects of their ecology, which is presumably caused, maintained and/or reinforced by interspecific competition (e.g., Pianka, 1973). Much of the ecological knowledge on congeneric lizard species living in sympatry derive from studies carried out in deserts of North America and the Old World (see Pianka, 1986). In recent years, however, there has been an increase in ecological studies on pairs of sympatric congeners in South America (e.g., Nuñez et al., 1989; Colli et al., 1992; Vrcibradic and Rocha, 1996; Vitt et al., 2000, 2003; Dias and Rocha, 2004; Van Sluys et al., 2004b). Those studies, carried out in various different types of habitat, indicate that sympatric congeneric lizards usually differ in habitat/microhabitat use, food habits, and/or morphology.

Lizards of the genus *Enyalius* (Iguanidae, Leiosaurinae; sensu Schulte et al., 2003) are arboreal or semi-arboreal forest-dwellers that occur mostly within the Atlantic Forest biome in eastern Brazil, except for a single Amazonian species (Avila-Pires, 1995). Species in this genus typically have allopatric distributions (Jackson, 1978). Current knowledge on the ecology of such lizards is limited to a few studies (Vanzolini, 1972; Vitt et al., 1996; Zamprogno et al., 2001; Van Sluys et al., 2004a). In the present study, we examine some ecological traits of two species of *Enyalius* (*Enyalius bilineatus* and *Enyalius brasiliensis*) in an area where they occur in sympatry, assessing their similarities and differences in those traits. The population of *E. brasiliensis* treated in this study corresponds to the subspecies *Enyalius brasiliensis bouleengeri* (sensu Jackson, 1978).

MATERIALS AND METHODS

Lizards were collected by the senior author at Alto Rio Saltinho (19°55'S, 40°32'W; altitude 700–800 m), in

the municipality of Santa Teresa, Espírito Santo State, southeastern Brazil. The study area was adjacent to the Augusto Ruschi Biological Reserve, which comprises an extensive area (approximately 3600 ha) of preserved Atlantic forest. All fieldwork was carried out within a private property that totaled 14 ha, of which about 75% consisted of a coffee plantation; the remaining 25% was forest. The plantation/forest transition was abrupt, without a definable “edge” (i.e., the two habitats essentially blend). The region of Santa Teresa has a seasonal climate, with a warmer, wetter season from October to April and a cooler, drier season from May to September. Mean monthly temperature and mean annual rainfall at the region of Santa Teresa are 19.6°C and 1450 mm, respectively (data obtained at the 6th District of Meteorology, in Rio de Janeiro).

Lizards were collected between December 1997 and November 2000 during monthly surveys at the study area. Subjects were captured by hand during haphazard transects carried out during the day within the coffee plantation and the adjacent patch of Atlantic forest. The path traversed by the researcher during the transects was always similar, with collecting activity starting at about 0900–1000 h and continuing along the coffee plantation until about 1530–1600 h, when the researcher finally arrived at the forest, continuing the search within it until sunset (i.e., about 1730–1800 h). Thus, a much greater sampling effort occurred within the coffee plantation than within the forest, although this was not quantified or standardized. This sampling difference was mostly because of the forest area available for fieldwork being significantly reduced compared to the coffee plantation (most of the forest habitat in the general area is included within the limits of the Augusto Ruschi Biological Reserve, and we did not have permission to work inside the reserve).

All lizards captured were euthanized with ether, fixed in 10% formalin, and stored in 70% ethanol. Snout–vent length (SVL) of all lizards was taken (to the nearest 0.1 mm) with a caliper. Lizards were dissected

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TABLE 1. Mean, standard deviation, and range of body sizes (SVL) for males and females of *Enyalius bilineatus* and *Enyalius brasiliensis* in Santa Teresa, Brazil, and values of the one-way analysis of variance (ANOVA) used to test for size differences between sexes.

Species	Mean \pm SD SVL (range)	N	ANOVA
<i>E. bilineatus</i>			
males	70.9 \pm 4.3 (62.1–82.1) mm	33	$F_{1,66} = 24.12$; $P < 0.001$
females	77.7 \pm 6.8 (66.7–90.3) mm	35	
<i>E. brasiliensis</i>			
males	77.7 \pm 9.3 (64.1–94.3) mm	12	$F_{1,19} = 11.12$; $P < 0.005$
females	92.5 \pm 10.9 (70.3–106.1) mm	9	

for sex determination and examination of gonads (in females) and stomach contents. Mass of individual prey found in stomachs was determined (to the nearest 0.1 mg) with an electronic balance. All relatively intact prey found in stomachs were measured along their greater axis with a caliper. The importance of each prey category in the diet of the two lizard species was assessed by calculating their frequency of occurrence (i.e., proportion of stomachs containing a given category), numeric proportion (i.e., number of individual items of a given category divided by the total number of prey items consumed) and mass proportion (i.e., total mass of items belonging to a given category divided by the total mass of prey items consumed).

A Chi-square test (χ^2) was used to test whether the sex ratio deviated from 1:1 in each species. One-way analyses of variance (ANOVA; Zar, 1984) was used to test for differences in SVL (considering only individuals with SVL > 60 mm) between species and between sexes within species. Simple regression analyses were used to test for the influence of lizard SVL on prey size (based on the length of the largest prey item in each stomach) and on brood size. The dietary diversity (based on proportions of prey number and biomass) was estimated for each species using the inverse of Simpson's (1949) index of diversity:

$$B = 1 / \sum p_i^2,$$

where p is the proportional use of prey item i .

The similarity in diet composition between the two lizard species was estimated by performing a Spearman rank correlation (Zar, 1984), adjusted according to Fritz (1974).

Basic statistics given throughout the text and tables always represent means \pm 1 SD.

RESULTS

Eighty-nine *E. bilineatus* (48 males and 41 females) and 27 *E. brasiliensis* (16 males and 11 females) were captured during field surveys. Eight (9%) of the *E. bilineatus* were collected at the forest patch, with the remaining 81 (91%) being collected at the coffee plantation, whereas all of the *E. brasiliensis* were

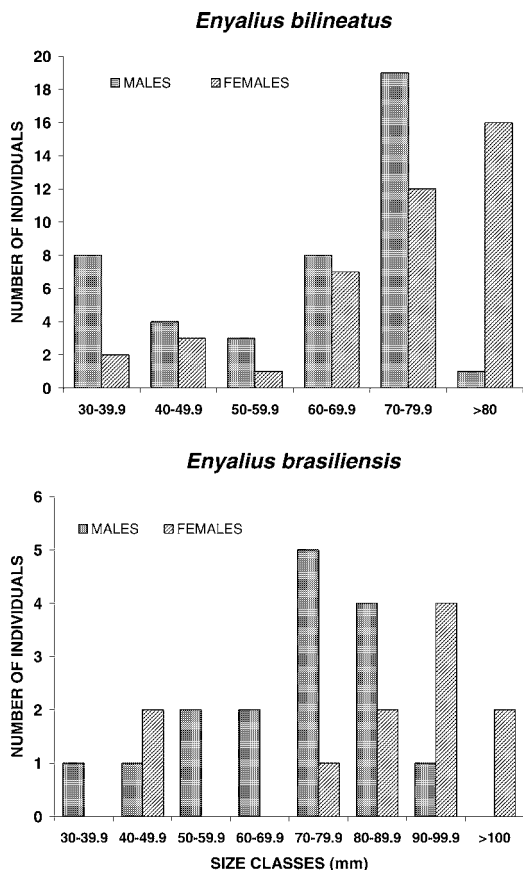


FIG. 1. Size distribution of *Enyalius bilineatus* and *Enyalius brasiliensis* collected between December 1997 and November 2000 in Santa Teresa, Brazil.

collected in the forest patch. *Enyalius bilineatus* was usually found among branches of coffee plants (*Coffea arabica*) and only very rarely on the ground (though such observations were not quantified), whereas *E. brasiliensis* was usually found perched on tree trunks and no individuals were found on the ground. The two species were never found together or in close proximity. The proportion of males and females in the sample did not differ for either *E. bilineatus* ($\chi^2 = 0.55$, $P = 0.46$) or *E. brasiliensis* ($\chi^2 = 0.90$, $P = 0.33$). Females were significantly larger than males in both species (Table 1). The two species differed significantly in body size (ANOVA: $F_{1,89} = 8.67$, $P < 0.05$), with *E. brasiliensis* being larger (Fig. 1).

Eighty-four *E. bilineatus* (94.4% of the sample) and 25 *E. brasiliensis* (92.6%) contained prey in their stomachs. Both species fed almost exclusively on arthropods and consumed no plant material (Table 2). The most frequent and numerically dominant prey of *E. bilineatus* were ants, with orthopterans constituting most of the prey biomass (Table 2). For *E. brasiliensis*, cockroaches (Blattodea) were the most frequent items and also comprised most of the prey biomass, whereas termites were the numerically dominant prey (Table 2). Mean prey size was 13.3 ± 7.4 mm (range 3.8–35.9 mm) for

TABLE 2. Frequency of occurrence (F), number (N), and mass (M, in mg) proportions (in absolute values and percentages) for each prey category in the diets of *Enyalius bilineatus* and *Enyalius brasiliensis* in Santa Teresa, Brazil.

Species	<i>Enyalius bilineatus</i>						<i>Enyalius brasiliensis</i>					
	F	%F	N	%N	M	%M	F	%F	N	%N	M	%M
INSECTA												
Blattodea	15	17.9	17	7.2	280.52	13.5	10	40.0	14	15.7	421.07	29.2
Coleoptera	11	13.1	17	7.2	131.75	6.3	3	12.0	4	4.5	103.4	7.2
Diptera	1	1.2	2	0.8	0.52	0.0						
Hemiptera	4	4.8	11	4.6	34.56	1.7	1	4.0	1	1.1	27.33	1.9
Hymenoptera (ants)	30	35.7	64	27.0	294.41	14.2						
Hymenoptera (non-ants)	1	1.2	1	0.4	7.95	0.4						
Isoptera	6	7.1	44	18.6	116.09	5.6	2	8.0	54	60.7	193.1	13.4
Odonata	1	1.2	1	0.4	10.1	0.5						
Orthoptera	23	27.4	25	10.5	827.78	39.8	2	8.0	2	2.2	103.31	7.2
Larvae												
Coleoptera	6	7.1	6	2.5	16.37	0.8						
Lepidoptera	11	13.1	14	5.9	153.26	7.4	7	28.0	7	7.9	238.48	16.5
Pupae	1	1.2	1	0.4	21.99	1.1						
Insect remains	2	2.4	—	—	9.26	0.4						
CRUSTACEA												
Isopoda	3	3.6	22	9.3	28.63	1.4	1	4.0	2	2.2	2.65	0.2
ARACHNIDA												
Araneae	9	10.7	9	3.8	87.53	4.2	2	8.0	2	2.2	214.99	14.9
MOLLUSCA												
Gastropoda	1	1.2	1	0.4	28.00	1.3						
MIRIAPODA												
Chilopoda	1	1.2	1	0.4	23.51	1.1						
Diplopoda	1	1.2	1	0.4	6.49	0.3	3	12.0	3	3.4	111.83	7.8
OTHER												
Shed skin							1	4.0	—	—	25.5	1.8
TOTAL			237	100.0	2078.72	100.0			89	100.0	1441.66	100.0

E. bilineatus and 15.0 ± 6.5 mm (range 6.2–32.4 mm) for *E. brasiliensis*. There was a positive and significant relationship between prey size and lizard SVL for *E. bilineatus* ($R = 0.41$, $P < 0.05$) but not for *E. brasiliensis* ($R = 0.23$, $P = 0.40$). Dietary diversity was higher for *E. bilineatus* ($B = 7.06$) than for *E. brasiliensis* ($B = 2.52$) when based on numeric proportions of prey, but slightly higher for the latter ($B = 5.91$) than for *E. bilineatus* ($B = 4.68$) when based on prey biomass (the low diversity value obtained for *E. brasiliensis* when based on numeric proportions was largely caused by the high number of termites consumed by two individuals). The similarity in diet composition between the two species was low, both in terms of prey number (Spearman rank correlation: $R_s = 0.04$, $t_s = 0.12$, $P = 0.91$) and in terms of prey biomass (Spearman rank correlation: $R_s = 0.31$, $t_s = 0.78$, $P = 0.45$).

Eighteen female *E. bilineatus* had oviductal eggs or enlarged vitellogenic follicles, with the smallest measuring 66.7 mm in SVL. Clutch size in this species varied from two to six eggs (mean = 4.4 ± 1.4) and was significantly influenced by female size (Fig. 2A). Six female *E. brasiliensis* contained oviductal eggs or enlarged vitellogenic follicles; the smallest female

measured 89.9 mm in SVL. Clutch size ranged from 8–14 (mean = 11.5 ± 2.5) and was also significantly correlated with female size (Fig. 2B). Clutch size was significantly greater in *E. brasiliensis* than in *E. bilineatus* (ANOVA: $F_{1,22} = 34.5$, $P < 0.01$). Females of *E. bilineatus* containing shelled oviductal eggs were collected in December 1997 (one), June (one), November (two), and December (two) 1998, May (one) and October (one) 2000. Juveniles (SVL < 40 mm) of *E. bilineatus* were found in December 1997 (one), June (two), October (four), and November (two) 1998 and October 2000 (one). Female *E. brasiliensis* with shelled oviductal eggs were collected in November 1998, October 1999 and January 2000 (one in each month), and the sole juvenile with SVL < 40 mm was collected in October 2000.

DISCUSSION

Our data indicate that the two species of *Enyalius* in the tropical montane rainforest region of Santa Teresa have marked ecological differences. They occupy different habitats within the area, with *E. brasiliensis* apparently being restricted to the forest patch and

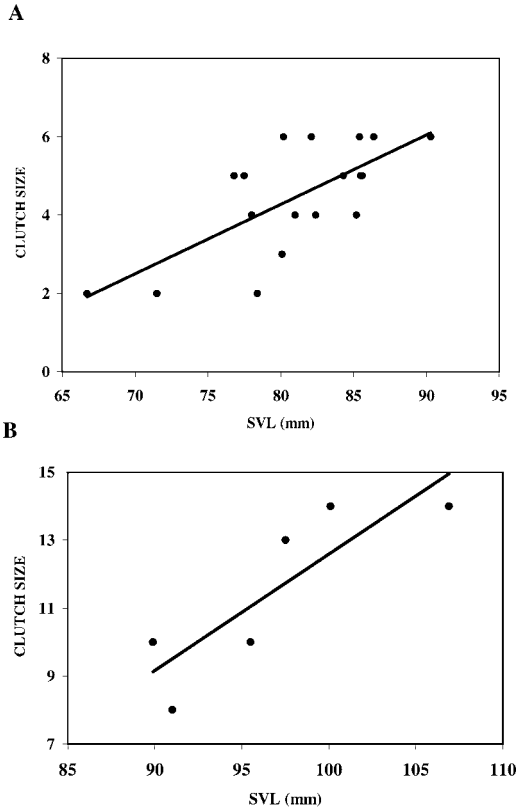


Fig. 2. Relationship between clutch size and female SVL for (A) *Enyalius bilineatus* ($y = 0.18x - 9.90$; $R^2 = 0.50$; $P < 0.01$; $N = 18$) and (B) *Enyalius brasiliensis* ($y = 0.34x - 21.61$; $R^2 = 0.72$; $P < 0.05$; $N = 6$) in Santa Teresa, Brazil.

E. bilineatus occurring mainly in the more open habitat of the coffee plantation but occasionally entering the forest. Jackson (1978) observed that *E. bilineatus* was common in second growth ("capoeira") and in coffee plantations in the region of Santa Teresa but was never seen in mature forest. He speculated that this species may have been originally absent from the hilly areas of Espírito Santo State but was able to colonize them after anthropogenic disturbances promoted the expansion of second-growth vegetation. In the present study, although *E. bilineatus* was found in greater numbers during fieldwork than *E. brasiliensis*, this may not necessarily reflect a markedly greater local abundance of the former species. *Enyalius brasiliensis* was found only in the forest patch where sampling effort was lower and the total area available for fieldwork was smaller. It may also be more difficult to visually locate lizards in the shaded, heterogeneous habitat of the forest where *E. brasiliensis* occurs. Additionally, animals perched high on tall trees in the forest may frequently escape detection. Indeed, Vitt et al. (2003) remarked that ground-level sampling of canopy animals is inevitably biased. This is less likely to happen at the coffee plantation, where individuals of *E. bilineatus* are usually perched lower, on coffee plants, within reach of

collectors. Preliminary data from Jackson (1978) suggested that *E. bilineatus* is a lower-perching and less arboreal species than *E. brasiliensis*. It is likely that the latter species may occur in relatively great densities within the large adjacent forest patch of the Augusto Ruschi Biological Reserve.

Both *E. bilineatus* and *E. brasiliensis* had reverse sexual size dimorphism, with females larger than males. Jackson (1978) and Vitt et al. (1996) also provided evidence that females tend to be the larger sex in members of the genus *Enyalius*. This is in contrast to what is normally observed in the family Iguanidae (sensu Schulte et al., 2003; see Fitch, 1981). The fact that clutch size tends to increase with female size in both *Enyalius* we studied here suggests that there has been selection for large female size in these species (or their common ancestor). Males tend to be the larger sex in lizard species in which males defend territories (Stamps, 1983). We do not know whether the two *Enyalius* we studied are territorial, but only rarely was more than one individual found sharing the same perch during the present study, and when this occurred they were usually of opposite sexes (RLT, pers. obs.). In any case, it seems that the selective forces favoring large body size have been more intense for females than for males during the evolutionary history of such lizards. Pianka and Vitt (2003), suggested that in some locally rare Iguanian lizards such as *E. leechi* and *Polychrus acutirostris*, which have reverse sexual dimorphism and size-influenced fecundity in females, the reduced local density of individuals may result in a low frequency of interactions among males, which would diminish the advantages of large male size.

Information on activity patterns of *Enyalius* are scant, and data are lacking on when these lizards start or resume their activity (Van Sluys et al., 2004a). All *E. brasiliensis* in the present study were collected during mid- to late afternoon and, thus, likely toward the end of their activity period. This would presumably increase the probability of finding individuals of this species with food in their stomachs, compared to *E. bilineatus* (assuming that the two species have similar activity patterns). Nevertheless, most individuals (>90%) of the two *Enyalius* species had food in their stomachs. Similarly high proportions of individuals with food in stomachs have been reported in studies of other populations of the same species (Zamprogno et al., 2001; Van Sluys et al., 2004a), indicating that these lizards tend to be in positive energy balance, as are most iguanids (Huey et al., 2001). Lizards of both species in our study fed exclusively on small invertebrates. They were generalist arthropod predators, consuming a wide variety of prey types and sizes, as has been reported in other dietary surveys of *Enyalius* (Vitt et al., 1996; Zamprogno et al., 2001; Van Sluys et al., 2004a). Nevertheless, there were quantitative differences in diet composition between the two species. *E. bilineatus* fed most frequently on ants, orthopterans and cockroaches, whereas *E. brasiliensis* ate mainly cockroaches and caterpillars. Hymenopterans (presumably including ants), orthopterans and cockroaches were also the dominant food items in the diet of an *E. bilineatus* population in another montane Atlantic forest area of Espírito Santo State (Zamprogno et al., 2001). However, Van Sluys et al. (2004a) found a large proportion of ants in the diet of *E. brasiliensis*

from an Atlantic forest area of Rio de Janeiro State (representing the nominal subspecies *E. b. brasiliensis* sensu Jackson, 1978), whereas no ants were found in the diet of *E. brasiliensis* in the present study (otherwise, however, the overall composition of the diet was practically the same). Given the generalist food habits of the two species of *Enyalius* studied here, it is probable that the observed dietary differences between them may reflect differential relative availability of prey types in the different habitats used by these species in the study area. In spite of their strongly scansorial habits, *Enyalius* appear to frequently forage on the ground (Jackson, 1978; Zamprogno et al., 2001; Van Sluys et al., 2004a), and this is supported by the abundance of typically ground-dwelling arthropods (e.g., cockroaches, orthopterans, isopods, myriapods) in the diets of *E. bilineatus* and *E. brasiliensis* observed in the present study.

It appears that oviposition and recruitment of both species occur primarily in the warmer, wetter months. Most of the females with shelled eggs and small juveniles of *E. bilineatus* were found during the October through December period. The fact that egg-bearing females and small juveniles of *E. bilineatus* were also found in dry season months (May and June), suggests, however, that this species may have extended or continuous reproductive activity, or that there may be two reproductive peaks per year. Data from *E. brasiliensis*, however, suggests reproductive activity in this species may be unimodal and concentrated in the spring–summer period. Van Sluys et al. (2004a) also suggested, albeit based on limited data, that the reproductive period of *E. brasiliensis* may be concentrated in the wet season.

Jackson (1978) suggested that the largely allopatric distributions of most *Enyalius* species might result from an inability to niche partition, given their strong ecological similarities (except for *E. bilineatus*). Our results show that the two species of *Enyalius* inhabiting the region of Santa Teresa are sympatric but not syntopic, and also that they have some fundamental ecological differences. *Enyalius brasiliensis* is a larger-bodied, larger-clutched species than *E. bilineatus* and, unlike the latter, is apparently dependent on forested areas. *Enyalius bilineatus*, however, is more adaptable to open habitats and may actually benefit from deforestation and replacement of original forest cover with coffee plantations in the Santa Teresa region, as suggested by Jackson (1978). In their study on two closely related forest-dwelling species of *Anolis* in Amazonia, Vitt et al. (2003) observed that *A. punctatus* was more tolerant of open habitat conditions than *A. transversalis* but remarked that deforestation is likely to adversely affect both of them. In the case of the two *Enyalius* from Santa Teresa, habitat disturbance is likely to affect each species differently, with one being favored and the other not. Tolerance to open habitats may help *E. bilineatus* take advantage of anthropogenic alterations of the landscape in the area of Santa Teresa, maybe even expanding its area of occurrence, whereas the opposite may occur with its congener *E. brasiliensis*. Nevertheless, the presence of a large preserved patch of Atlantic rain forest in the area, protected within a conservation unit (the Augusto Ruschi Biological Reserve), may provide a relatively safe refuge for local *E. brasiliensis*.

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Ecology of the Common Barking Gecko (*Ptenopus garrulus*) in Southern Africa

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ABSTRACT.—We examined museum specimens of the Common Barking Gecko (*Ptenopus garrulus*) from the Kalahari and Namib Deserts to assess sexual size dimorphism, reproductive status, and diet. Males had significantly wider heads than females of the same body size; however, *P. garrulus* showed no sexual dimorphism in any other morphological character. The smallest mature male was 36 mm snout-vent length, whereas the smallest female was 31 mm. Peak reproductive activity for both sexes was in September and October. Clutch size was fixed at one large egg (average size = 5.9 × 4.4 mm); all eggs were in the right ovary, but more than one clutch may be laid in a single breeding season. *Ptenopus garrulus*, when compared with other geckos, produces very large offspring and thereby invest heavily in a single offspring. We recorded 15 arthropod orders in the diet of *P. garrulus*. Termites dominated their diet both numerically and volumetrically. Males and females ate prey of similar taxa and sizes, suggesting that trophic partitioning is absent. Therefore, the evidence suggests that the evolution of head width differences is driven by male contest competition.

Basic natural history data are fundamental to understanding and developing life-history theory. In this regard, squamate reptiles have been the focus of relatively intensive ecological study because unlike many other vertebrates, they are often easily sampled and identifiable prey items are readily recovered (e.g., Pianka, 1986; Huey et al., 2001; Vitt et al., 2003). Recently, Vitt et al. (2003) synthesized the global ecology of squamates to test the influence of phylogenetic history on current patterns of community assemblages. This analysis depended in part on life-history data. Future analyses will benefit from more extensive datasets that include more taxa from geographically disparate areas and possibly, more detailed natural history data.

Morphology is tightly linked to an organism's ecology (Miles, 1994). Sexual size dimorphism (SSD) is of special interest because the size difference between males and females potentially affects many aspects of their ecology (Andersson, 1994). The three most common explanations for SSD are (1) intersexual resource partitioning (Schoener, 1967); (2) sexual selection (usually male contest competition; Trivers, 1976); and (3) fecundity selection (Hedrick and Temeles, 1989; Shine, 1989; Stamps, 1995). When SSD has an ecological basis, one sex usually has an alternative feeding strategy in which different sized prey are selected caused by size-related functional constraints (Houston and Shine, 1993). This phenomenon may arise either because of competition for resources or as a by-product of sex-related selective pressures, such as sexual selection. Sexual selection is most commonly associated with situations where the male is larger than the female. Larger male size typically results from male-

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male interactions associated with competition for territories and/or access to mates (Vitt and Cooper, 1985; Olsson et al., 2002). Males may also be smaller than females in situations where the males have to search for widely scattered females and where a small-male advantage exists (e.g., horned lizards; Zamudio, 1998). Fecundity selection is the notion that larger females are capable of producing more (or larger) eggs or offspring (Fitch, 1981; Olsson et al., 2002). Basic ecological data on diet and reproduction are necessary to explain the evolution of SSD.

We studied the ecology of the Common Barking Gecko, *Ptenopus garrulus*, a small sized (max 60 mm SVL) lizard of the Kalahari and Namib Deserts of southern Africa. This species constructs burrows that are up to 38 cm deep in loose soils and usually have several branches (Haacke, 1975). Males have yellow throats and emit calls from the entrance of their burrows at dusk and dawn (Haacke, 1969). Pianka and Huey (1978) studied aspects of the ecology of several species of geckos in the southern Kalahari. They reported that *P. garrulus* had an invariant clutch size of one and that termites dominated their diet by volume. Our study had three main objectives: (1) to determine the extent of sexual size dimorphism; (2) to examine seasonal and sexual differences in diet; and (3) to examine the reproductive ecology of males and females and especially to examine offspring size relative to female size.

MATERIALS AND METHODS

We examined 150 specimens (Transvaal Museum) that had been collected in the following regions of Southern Africa: Northern Namibia, Southern Namibia, Central Botswana, Namaqualand, Kgalagadi Transfrontier Park, and Limpopo Province of South Africa. We examined an additional 490 specimens of *P. garrulus* collected in 1969 and 1970 in the Kalahari region of Botswana, Namibia, and South Africa by ERP and RBH. Diet and reproductive status from all specimens were analyzed. Methods used for these specimens are discussed in Pianka and Pianka (1976) and Pianka and Huey (1978).

Sexual Size Dimorphism.—We measured SVL (snout-vent length), tail length, head width, head depth, head length, torso length (axilla to groin), arm length (head of humerus to the end of the claw on the longest finger), humerus length, leg length (head of femur to the end of the claw on the longest toe), femur length, pes length, and fourth toe length of 150 preserved specimens (Transvaal Museum). All measurements were made to the nearest 0.01 mm using digital calipers. Characters were chosen based on studies of sexual selection and sexual dimorphism (head characters and torso length) and observations of *P. garrulus* breeding behavior (arm and leg characters). Sex of juveniles was verified by dissection. Prior to testing for sexual dimorphism, we log-transformed all variables and subjected each to an ANCOVA with log SVL as the covariate. A *t*-test for unequal variances was used on the raw SVL data. We used a reduced major axis (RMA) regression (Fairbairn, 1997) to investigate growth patterns of those characters, which were significantly different between the sexes.

Reproduction.—Growth patterns of characters were determined via dissection. Females were determined to be sexually mature when they contained oviductal eggs

or enlarged vitellogenic follicles. For gravid females, length and width of the egg was measured to the nearest 0.01 mm with digital calipers. Egg volume was estimated for each egg using the formula for a prolate spheroid (Vitt, 1991). Sexual maturity in males was determined by finding enlarged testes and convoluted epididymides. We measured the length and width of the left testis to the nearest 0.01 mm and estimated testes volume (formula for prolate spheroid). We used a Kruskal-Wallis test to determine differences in testes volume and egg length by month. Hatchlings were obtained during a field study of *P. garrulus* in 2003 and 2004 at Molopo Nature Reserve (25°50'S, 22°55'E) located in the eastern Kalahari, Northwest Province, South Africa, focusing on other aspects of their life history.

Diet.—Stomach contents were identified to order. Number and types of prey items were recorded for each individual. Measurements of length and width were made for complete prey items (to nearest 0.01 mm) and used to estimate volume (formula for prolate spheroid). We calculated correlations of prey size to SVL and head width, and prey size to head width with the effects of SVL removed. We tested for differences in diet between the sexes using Chi-square tests. We also tested for differences in prey size consumed between the sexes using ANCOVA with head width as a covariate and with a *t*-test assuming unequal variances. We used a Chi-square test to examine variation in diet by month. Dietary niche breadth was determined using Simpson's (1949) diversity index.

Foraging Mode.—A population of *P. garrulus* at Molopo Nature Reserve was studied to determine foraging mode. The substrate was sand throughout, and the vegetation was dominated by *Acacia mellifera* and *Acacia erioloba*, with very little ground cover. All focal observations were made between 1900 and 2200 h in November 2004.

Foraging mode is often determined from measurements of movements per minute (MPM) and percent time spent moving (PTM). A criterion of PTM = 10 was used by Perry (1995) to distinguish between ambush and active foraging, with ambush foragers falling below 10. We quantified foraging mode using 10-min focal observations of 11 adult *P. garrulus*. The observer sat about 4 m from the burrow using an artificial light source to view activity. Geckos appeared to act normally under these conditions. All observations were carried out on individuals that were visible at the entrance to their burrows. Any movement and prey capture attempts were recorded. Adult *P. garrulus* are solitary inhabitants of a burrow. The individuals observed were of known size and sex from an ongoing population study at the same site.

RESULTS

Sexual Size Dimorphism.—Males (mean \pm SE: 44.9 \pm 0.4) and females (45.2 \pm 0.4) did not differ significantly in SVL ($t_{628} = 0.519$, $P = 0.60$). However, males had significantly wider heads than females when controlling for SVL ($F_{133} = 8.5$, $P = 0.004$; Fig. 1). The sexes did not differ in any other morphological characters ($P > 0.05$). Head width of males grew isometrically with SVL ($r^2 = 0.89$, slope = 0.997, 95% CI = 0.807–1.071), whereas female head width grew less quickly than SVL ($r^2 = 0.87$, slope = 0.888, 95% CI = 0.807–0.970; Fig. 1).

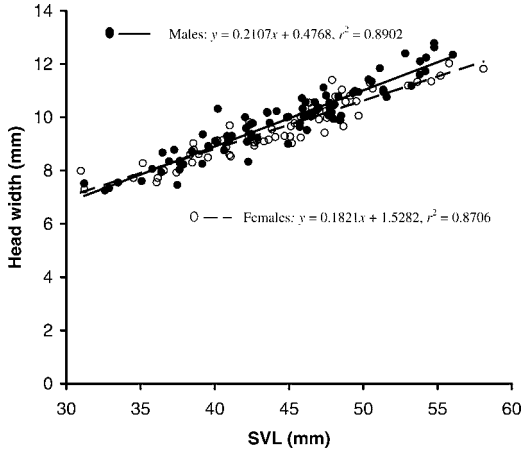


FIG. 1. Relationship between head width and snout-vent length of male and of female *Ptenopus garrulus*.

Reproduction.—Minimum size at sexual maturity for males was 36 mm SVL. Testicular volume peaked in September and October (Fig. 2), and these two months were significantly different than testicular volume in all other months ($H_{7,257} = 114.2, P < 0.001$). Minimum size at sexual maturity for females was 31 mm SVL. Egg volume was highest in September and October ($H_{7,56} = 17.6, P = 0.014$) and a similar statistical pattern to testicular volume existed, although not as strong. Eggs were present from August through April (Fig. 3). Clutch size was fixed at one; however, 8% of all females ($N = 4$) had two eggs at different stages of development suggesting that they lay a second clutch. All eggs were in the right oviduct, even when a second egg was developing.

Fifty-five *P. garrulus* less than 30 mm SVL were collected during fieldwork, with the two smallest individuals measuring 22 mm SVL. This size is also smaller than that reported for hatchlings by Haacke (1975). Minimum hatchling size was large relative to size at sexual maturity. Hatchling *P. garrulus* were also large relative to adult female size when compared to hatchling/female size in other gekkonids (Fig. 4). The regression line explained most of the variation ($r^2 = 0.95$), and *P. garrulus* was the only outlier.

Diet.—We identified 17 categories of prey (Table 1). Numerically, termites (51.1%) and ants (35.6%) dominated the diet. Volumetrically, termites were again the most important prey type (60%) followed by ants (8.9%) and beetles (8%). More gecko stomachs contained ants (46%) than any other food item, followed by termites (39%) and beetles (19%; Table 1). Eighteen percent ($N = 115$ out of 640) of all stomachs were empty and 17 geckos had eaten sloughed skins. The four most common prey types composed at least 90% of the diet in all months. Termites were most prevalent in December, composing 70% of the diet by number. Ants were eaten more commonly than termites in March and September and were most prevalent in September, making up 47% of the diet (by number) in that month. During all other months, termites were the most commonly eaten prey (Fig. 5). However, there were no significant differences between months ($\chi^2_7 = 0.15$;

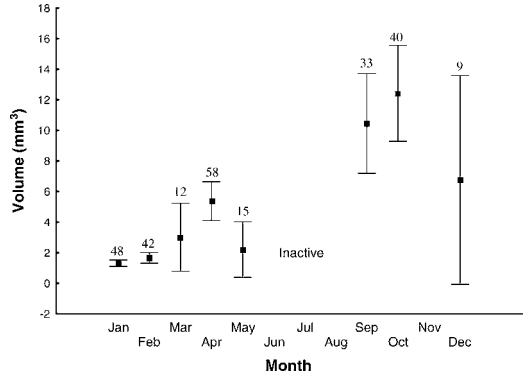


FIG. 2. Estimated testis volume by month. Mean (\pm SE) is displayed for each month. Sample size is listed above each error bar. Months with fewer than five males are excluded.

$P < 0.9$). *Ptenopus garrulus* are inactive in the winter months of June and July.

No differences existed between males and females in the numbers of the four most abundant prey groups and a group of all other prey items ($\chi^2_3 = 3.62; P < 0.5$). There was a significant correlation between prey size and SVL ($r = 0.39, P < 0.001$) and prey size and head width ($r = 0.4, P < 0.001$), but with the effects of SVL removed, there was no difference between prey size and head width ($r = 0.099, P = 0.44$). No difference between the sexes in relation to size of prey eaten was found when accounting for head width ($F_{59} = 0.287, P = 0.59$) or when not accounting for head width ($t_{170} = 0.158, P = 0.87$).

Foraging mode.—We determined MPM and PTM for six male and five female adult *P. garrulus*. All trials except one (8.6 min) were for the full 10 min: *P. garrulus* were classic ambush foragers. With the sexes pooled, adults moved infrequently (MPM = $0.4 \pm 1.9, 0-2.1$) and spent little time moving (PTM = 4.6 ± 1.9 sec, 0-16.7).

DISCUSSION

Males and females were sexually dimorphic only in relation to head width, with males having wider heads. Two major functions have been attributed to wider head width in one sex: ecological segregation in diet (Schoener, 1971; Camilleri and Shine, 1990; Shine, 1991)

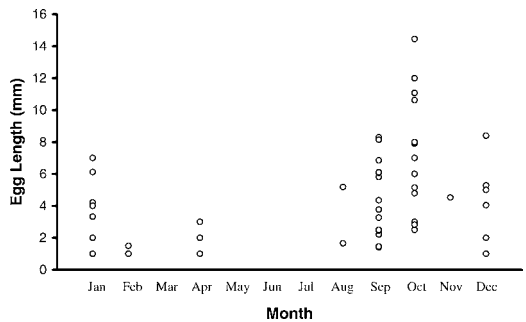


FIG. 3. Length of individual eggs in relation to month.

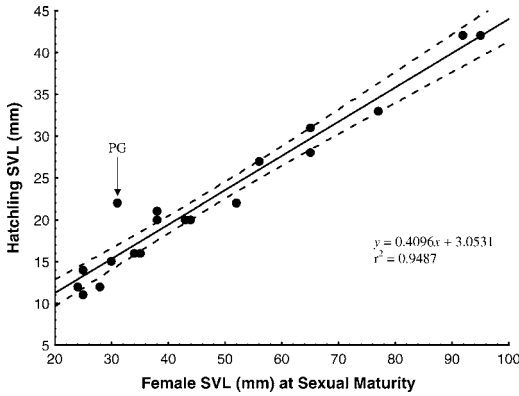


FIG. 4. Comparison of minimum hatchling size to female SVL at sexual maturity in 19 gekkonid species (Inger and Greenburg, 1966, *Cyrtodactylus malayanus*; Vitt, 1986; and references therein, *Phyllopezus pollicaris*, *Hemidactylus mabouia*, *Lygodactylus klugei*, *Gymnodactylus geckoides*, *Pseudogonatodes guianensis*, *Lygodactylus somalicus*, *Lygodactylus picturatus*, *Gonatodes concinnatus*, *Lepidodactylus lugubris*, *Hemidactylus frenatus*, *Gehyra mutilata*; Marquet et al., 1990, *Garthia gaudichaudi*; Doughty and Shine, 1995, *Phyllurus platurus*; Vitt and Zani, 1997, *Thecadactylus rapicauda*; Okada et al., 2002, *Gekko hokouensis*; Colli et al., 2003, *Gymnodactylus amarali*). Arrow marks *Ptenopus garrulus*.

and sexual selection (male contest competition; Vitt and Cooper, 1985; Saenz and Conner, 1996; Kratochvíl and Frynta, 2002; Reaney and Whiting, 2002). To determine whether head shape dimorphism is related to sexual selection, experiments must be conducted that deal with either mate choice or male-male interactions (Tokarz, 1995). However, ecological segregation in diet can be addressed by analyzing the diet of each sex. Increased head width should increase gape size allowing the sex with the wider head to eat larger prey items (Schoener, 1971; Camilleri and Shine, 1990). We found no difference in the diet of males and females. Termites and ants were the dominant prey of both sexes and the size of prey items eaten by males and females did not differ significantly. Thus, the dimorphism in head size seems unrelated to food niche segregation. The other explanation for SSD in head size in *P. garrulus* is sexual selection. Males have two traits that are likely "ornaments" for sexual selection. They vocalize from the mouth of their burrow and will defend an area within a radius of 1 m (TJH, pers. obs.); and males also have yellow throat patches, which are absent in females. We also observed frequent bite mark scars on males in the field (TJH, pers. obs.). Larger male head width is, therefore, best explained by male contest competition, though fights between males have not been witnessed.

Males attained sexual maturity at 36 mm and females at 31 mm. In gekkonids, males typically attain sexual maturity at smaller or similar sizes to females (Inger and Greenburg, 1966; Vitt and Zani, 1997; Vitt et al., 1997; Okada et al., 2002). These sizes can be reached in less than a year. The greater size of maturity for male *Ptenopus* may be caused by some form of reproductive suppression by rival males. Male *P. garrulus* have an

TABLE 1. Summary of the diet of *Ptenopus garrulus*. Total number and percent number categories include 640 specimens. Volume and percent volume categories are from 150 specimens dissected by TJH. Volumetric data for the other 490 stomachs are presented in Pianka and Huey (1978). Volumes for the 490 specimens were not combined with the other 150 specimens because different methods of volume estimation were used. Frequency is the number of stomachs containing the particular food item.

Prey Type	N	N%	Freq.	V (mm ³)	V%
Myriopoda					
Centipedes	2	0.06	2	—	—
Arachnida					
Acarina	2	0.06	2	—	—
Aranea	67	2.2	54	82.6	0.8
Solpugidae	6	0.2	6	—	—
Pseudoscorpiones	2	0.06	2	4.7	<0.1
Hexapoda					
Blattoidea	7	0.2	5	421.1	4.3
Coleoptera	191	6.2	120	788.4	8.0
Diptera	10	0.3	9	10.3	0.1
Hemiptera	60	1.9	35	709.3	7.2
Hymenoptera					
Formicinae	1100	35.6	294	875.9	8.9
Other	14	0.5	12	346.4	3.5
Isoptera	1578	51.1	247	5883.3	60.0
Neuroptera	4	0.1	2	50	0.5
Lepidoptera	8	0.3	7	316.9	3.2
Orthoptera	16	0.6	16	303.2	3.1
Thysanoptera	7	0.2	6	13	0.1
Larvae	12	0.4	12	17	0.2
Total	3086	100.0		9822.1	100.0
Niche Breadth				2.5	2.6

advertisement call, and the pitch of that call is negatively correlated with body size (TJH, pers. obs.). If a small male calls too close to a larger resident male, the smaller male might be physically challenged by the larger male and could suffer an injury. Males observed in the field frequently bore bite mark scars (TJH, pers. obs.). Small males are unlikely to secure matings in this scenario, and sexual maturity may be delayed to reduce conflict with larger males. Alternatively, males may grow at a more rapid rate than females and mature at the same age or females may choose larger males for copulations causing the evolution of later maturation.

Breeding is restricted to early summer months with peak testicular volume and largest egg size in October. Rainfall in the Kalahari can be quite erratic but hatchlings of eggs laid in October will likely emerge after significant summer rains when insect prey is expected to peak (late December to early January).

Females have an invariant clutch size of one, but four individuals had a second egg at an earlier developmental stage. Too few individuals with two eggs were found to test for a correlation between female size and number of clutches. All gekkonids have an invariant clutch size; however most produce two eggs with one egg produced in each ovary (Fitch, 1970). A growing

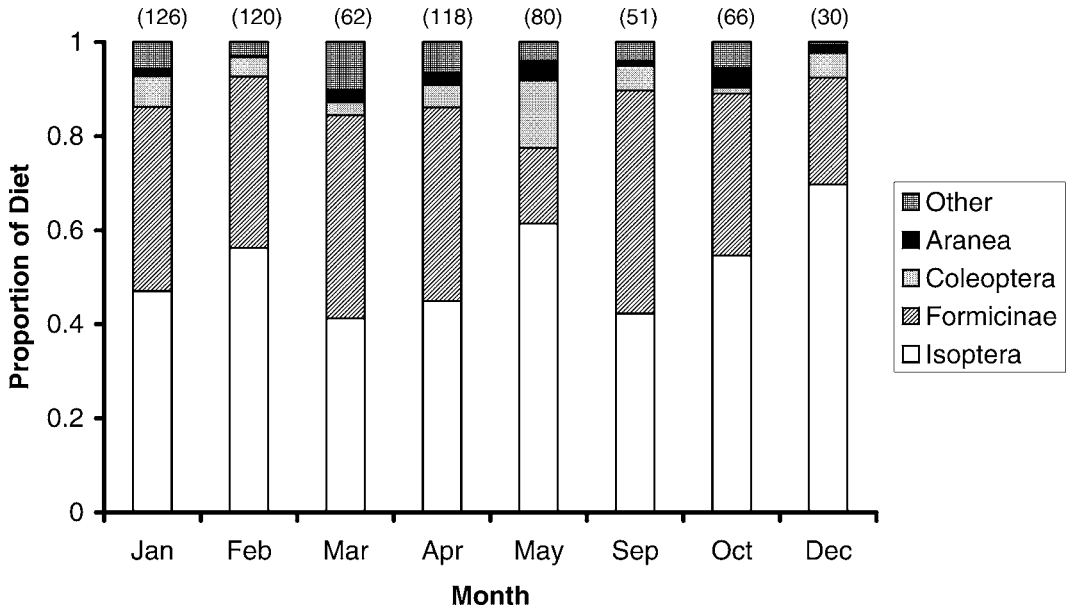


FIG. 5. Seasonal representation of the four most abundant prey types by prey number found in gut contents of *Ptenopus garrulus*. Number of guts examined is listed in parentheses.

number of species have been reported to have a clutch size of only one (see Werner, 1989, *Cyrtodactylus amictophilis*, *Tropicolotes steudneri*, and *Gehyra variegata*; Marquet et al., 1990, *Garthia gaudichaudi*; Vitt and Zani, 1997, *Thecadactylus rapicauda*). Interestingly, all *P. garrulus* eggs ($N = 56$) were in the right ovary, suggesting that the left ovary may be nonfunctional. *Thecadactylus rapicauda* is a large gecko (up to 126 mm SVL) that also lays one egg but produces eggs in both ovaries (Vitt and Zani, 1997). Most single-egg gekkonids are small (< 35 mm SVL and weigh < 1 g), which may explain why they have one egg clutches (Fitch, 1970). But adult *Ptenopus* can exceed 55 mm SVL and weigh more than 4 g, which is as large as many geckos that produce two-egg clutches. The reason for a single-egg clutch is unknown. A plausible adaptive explanation is that larger juveniles have a survival advantage; however, phylogenetic history may also be an explanation through similar juvenile size in close relatives. Hatchling *P. garrulus* are very large in relation to adult female size, and this ratio is much larger than for any other gecko reported (Fig. 4). One factor limiting egg size is the size of the pelvic aperture (Vitt, 1986; Sinervo and Licht, 1991). The hard-shelled eggs producing relatively large juveniles in *P. garrulus* suggest that an adaptation in the size of the pelvic aperture may have occurred, permitting a larger than expected egg to be laid.

Diet of *P. garrulus* consisted mainly of termites, both numerically and volumetrically. However, these lizards should not be considered termite specialists. In arid areas of southern Africa, termites are patchily distributed both spatially and temporally (Lepage and Darlington, 2000; Traniello and Leuthold, 2000). Some of the sampled geckos had eaten more than 30 *Hodotermes* termites, indicating that the resource is patchy.

Ptenopus are normally sit-and-wait foragers, waiting at the mouth of their burrow to ambush prey; confirmed by the observed low values for MPM and PTM. When termites swarm, however, *P. garrulus* come out of their burrows, even during the day, and become transient wide foragers (Huey and Pianka, 1981) and at these times they are often killed by shrikes (Huey and Pianka, 1981). *Ptenopus garrulus* may gain significant amounts of their nourishment while actively foraging during termite swarms and or termite foraging aggregations.

A broad survey of diets of many ($N \approx 200$) lizard species revealed differences among three major clades (Pianka and Vitt, 2003; Vitt et al., 2003). Iguanians tend to consume more ants than gekkotans or autarchoglossans. *Ptenopus garrulus* is unusual among gekkotans in consuming ants. Among the diets of desert geckos listed by Pianka (1986), only the diurnal Kalahari gecko *Lygodactylus capensis* consumes more ants than does *P. garrulus*.

In conclusion, we found that males become sexually mature at a larger size than females. *Ptenopus garrulus* have single egg clutches that are always produced in the right ovary. And, in relation to size, they have larger offspring than other geckos. Finally, *P. garrulus* are among a relatively small number of geckos to consume ants. These findings along with their use of a self-constructed burrow and calling behavior make the ecology of *P. garrulus* unique among other known gekkonids.

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Incubation Temperature and Sex Ratio of the Veiled Chameleon (*Chamaeleo calypttratus*)

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ABSTRACT.—Eggs from five clutches of *Chamaeleo calypttratus* were incubated at 25, 28, and 30°C during the period of sex determination. Sex ratios were slightly biased toward females at all temperatures but did not differ statistically from the expected 1:1 ratio of males and females. Egg survival was sufficiently high that sex-biased temperature-induced mortality cannot account for the lack of departure from 1:1 sex ratios. I conclude that the veiled chameleon has genetic sex determination (GSD) and that anecdotal accounts of temperature-dependent sex determination (TSD) for this species, and other chameleons are likely to reflect reporting or statistical bias.

For crocodylians, tuatara, some turtles, and some lizards, temperatures experienced by embryos during incubation affect their sex (Janzen and Paukstis, 1991; Valenzuela and Lance, 2004). For lizards, temperature-dependent sex determination (TSD) is well documented for some species of agamids, scincids and gekkotans (Harlow, 2004). TSD may occur in other families of lizards as well, but reports to date are anecdotal (Harlow, 2004). The problem is that temperature-related sex-ratio bias occurs for reasons other than TSD (Valenzuela et al., 2003). For example, temperature-induced sex-biased mortality during incubation could incorrectly give the appearance of TSD. Reports of TSD could also be statistical artifacts: by chance alone a small

number of temperature-biased sex ratios will occur. These apparent sex ratio anomalies (for a GSD species) would be more likely to be noticed and reported than sex ratios not differing from the expected 1:1 ratio of females and males.

The family Chamaeleonidae is one of the taxa for which TSD has been suggested on the basis of anecdotal accounts (Harlow, 2004). The objective of this paper is to report results of incubation experiments on the veiled chameleon *Chamaeleo calypttratus*. Although the study was conducted for purposes other than assessing TSD (unpubl.), results pertinent to TSD are reported here because they (1) document convincingly that incubation temperature does not affect sex

and (2) support a null hypothesis that is likely to be correct for *C. calypttratus* and perhaps the family as well.

MATERIALS AND METHODS

Eggs were obtained from a breeding colony in my laboratory. Clutch size in captivity is typically 30–40 eggs or more but likely less in nature (Necas, 1999). The five clutches used for this study were laid between 3 and 25 April 2004. Eggs from each clutch were weighed and numbered sequentially with a fine India ink pen within 24 h of oviposition and placed in a plastic “shoe box” container. Eggs were incubated in moistened ecopeat (High Sierra Exotics, P. O. Box 1996, Quincy, CA 95971) at a water potential of -280kPa (150 g H_2O per 100 g ecopeat) based on a standard curve established by vapor pressure psychrometry that related water content to water potential (unpubl. data). Eggs were buried leaving roughly one-third of their top surface exposed so that they could be monitored without disturbance. Water was added to the containers once or twice a week to return the water content to 150%. Eggs were incubated at 25, 28, or 30°C in three Percival incubators. Temperature within an egg container in each of the three incubators was checked daily; temperatures were adjusted if necessary to maintain the targeted temperature. Means recorded within the egg containers during the incubation period averaged 24.8, 28.0, and 29.9°C. Containers were rotated within each chamber several times a week to minimize the effect on development of temperature gradients within the chamber.

The general objectives of the experiment were to assess the effect of incubation temperature on the phenotypes of hatchlings and to determine whether the time of exposure to relatively low and relatively high temperature would modify these effects. Embryos of *C. calypttratus* are gastrulae at oviposition and their development arrested (in diapause) for 60–80 days following oviposition (Andrews and Donoghue, 2004). Eggs were thus incubated at 28°C for 70–72 days at which time a single egg from each clutch was opened and its stage checked using criteria of Dufaure and Hubert (1961). All embryos had initiated development (Stages 11–23) and experimental temperatures were thus imposed at this time (Table 1). One egg from the 28°C treatment from each clutch was also checked at 100 days to determine whether embryos had reached stage 35. Sex is fixed by this stage and, thus, is not influenced by any further change to incubation temperature. Embryos from three of the clutches were at stage 35 at 100 days; thus, some eggs were switched to experimental treatments (Table 1). Embryos from two of the clutches were at Stage 33.5, and these were switched after 3–4 more days based on developmental rates observed in previous studies (Andrews and Donoghue, 2004; Andrews 2004). Embryos that were staged were preserved for other studies.

Incubation temperatures were selected that were known to result in high survival of eggs of *C. calypttratus* in captivity (Necas, 1999; Schmidt, 2001). These observations indicated that 25, 28, and 30°C would represent relatively low, moderate, and high incubation temperatures, respectively. This temperature range also matches the range of mean nest temperatures of *Chamaeleo chamaeleon* during its summer incubation period in nature (C. Díaz-Paniagua, pers. comm.). For

TABLE 1. Incubation temperatures experienced by eggs of *Chamaeleo calypttratus* after incubation at 28°C for 70–72 days. Treatments are indicated as, for example, 28/25 for eggs incubated at 28°C through Stage 35 and at 25°C thereafter. Eggs from each clutch were randomly allocated to the five temperature treatments. Incubation temperature during the sex determining period (Stages 11–35) is the relevant temperature for assessing the effect of temperature on sex ratio.

Treatment designation	Temperature during Stages 11–35	Temperature during Stages 36 to hatching
25/25	25	25
28/25	28	25
28/28	28	28
28/30	28	30
30/30	30	30

lizards with TSD, a range of 25–30°C is sufficiently wide to produce female dominated and male dominated sex ratios (Harlow, 2004).

Eggs from each clutch were randomly allocated to five treatments once development resumed (day 70–72): (1) eggs continued to be incubated at 28°C with no change in temperature during incubation (28/28); (2) change to 25°C for the remainder of incubation (25/25); (3) change to 30°C for the remainder of incubation (30/30); (4) no change in temperature until embryos reached stage 35, then a change to 25°C (28/25); (5) no change in temperature until embryos reached stage 35, then a change to 30°C (28/30; Table 1).

Sex determination in reptiles is associated with gonadogenesis (Bull, 1987). For the lizard *Sceloporus undulatus*, gonads are undifferentiated at Stage 30 but distinguishable as ovaries or testes by stage 35 (Austin, 1988). Only the incubation temperatures that embryos experienced from 70–100 days (stages 11–35) are, thus, assumed to be relevant for assessing sex ratio. Analyses thus contrast the combined 28/25, 28/28, and 28/30 treatments (incubation at 28°C during the sex determining period) with the 25/25 and 30/30 treatments (incubation at 25 and 30°C, respectively, during the sex determining period), although for heuristic purposes observations from all five treatments are reported.

Containers were checked daily for hatchlings from 25 September when the first egg hatched to 3 December when the last egg hatched. At hatching, lizards were identified individually with numbers written on their sides with a “Sharpie” marker and weighed. They were sexed on the basis of a sexually dimorphic character; males have a conspicuous heel spur, females do not. The association between the presence or absence of the heel spur and sex was confirmed by dissecting 13 individuals at about one month of age; in all cases gonadal sex corresponded to the presence or absence of a heel spur. Moreover, all individuals remained the sex initially assigned as they grew.

RESULTS AND DISCUSSION

Results reported here do not support the suggestion that sex ratios of *C. calypttratus* are affected by incubation temperature (Schmidt, 2001). Overall, 98 of

TABLE 2. Percent of eggs surviving incubation and sex ratio at three incubation temperatures for five clutches of *Chamaeleo calypttratus*. See Table 1 for temperature treatment designations. Deaths represent the number of eggs that died prior to allocation to the experimental treatments and Sampled represents the number of eggs used to determine embryo stage. Two hatchlings from the D4 clutch and one from the T6 clutch escaped and thus were not sexed.

	Clutch (clutch size)					% Surviving
	E7 (38)	D4 (57)	T6 (35)	S3 (50)	C5 (54)	
Deaths, sampled	0, 3	2, 3	2, 2	1, 5	9, 6	
Hatched, not hatched						
25/25	12/0	19, 0	10, 0	14, 1	6, 0	98.4
28/25	4, 0	5, 0	3, 0	4, 0	9, 1	96.1
28/28	4, 0	5, 0	4, 0	4, 2	5, 0	91.7
28/30	2, 2	4, 1	3, 0	4, 0	7, 1	83.3
30/30	7, 4	16, 2	10, 1	16, 0	8, 2	86.4
%Surviving	82.9	94.2	96.8	93.3	89.7	
Females, Males						% Female
25/25	6, 6	12, 5	5, 4	3, 11	4, 2	51.7
28/25	3, 1	2, 3	1, 2	2, 2	2, 7	40.0
28/28	2, 2	3, 2	2, 2	4, 0	3, 2	63.6
28/30	1, 1	2, 2	2, 1	3, 1	4, 3	60.0
30/30	3, 4	11, 5	6, 4	7, 9	5, 3	56.1
% Female	51.7	54.0	55.2	45.2	51.4	

the 182 hatchlings in this study were females, and 84 were males (Table 2). Although these numbers reflect a slight female bias, they did not differ from the expected equal numbers of females and males ($\chi^2 = 2.9$, $P > 0.05$). Sex ratios favored females at all incubation temperatures as well with 51.7, 53.7, and 56.1% females from the 25, 28, and 30°C treatments, respectively, and did not differ among treatments ($\chi^2 = 1.0$, $P > 0.05$).

High egg survival, 92% overall, indicates that any sex ratio bias due to differential mortality would be negligible. For example, the slight overall female bias at all temperatures could be explained by higher mortality of male embryos. However, assuming all mortality to have been incurred by female embryos at 25°C ($N = 1$) and all mortality to have been incurred by male embryos at 28°C ($N = 7$; given that TSD produces males at 25°C and females at 28°C as illustrated in figure 5.1 in Harlow, 2004), resultant sex ratios would not differ from 1:1 (25°C; 30 females, 28 males; 28°C: 36 females, 31 males, $\chi^2 = 0.8$, $P > 0.05$). Finally, inspection of the sex ratios from the five clutches does not indicate any clutch-specific bias in sex ratio that could obscure TSD.

Anecdotal suggestions of temperature-related sex ratio bias in *Furcifer lateralis*, *Chamaeleo chamaeleon*, and *C. calypttratus* (Schmidt et al., 1994a,b; Necas, 1999) likely reflect reporting or statistical bias rather than TSD. Results of this study and the observation that sex

ratios of *Furcifer pardalis* hatchlings did not differ from 1:1 when eggs were incubated at either 23 or 28°C (pers. comm. from G. Ferguson in Viets et al., 1994) support the conclusion that sex of chameleons is genetically determined. The Chamaeleonidae includes a large number of species and represents several major adaptive radiations (Townsend and Larson, 2001; Raxworthy et al., 2002), however, and carefully controlled tests for TSD could be made systematically for species in different lineages to determine if TSD actually occurs in the family.

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