

Burke and J. Feinberg made helpful editorial suggestions.

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Accepted: 17 February 2005.

Journal of Herpetology, Vol. 39, No. 2, pp. 312–315, 2005
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Sex Differences in Body Size and Ectoparasite Load in the Ball Python, *Python regius*

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ABSTRACT.—Sexual dimorphism in body size, body condition (body mass relative to body size), and relative head size was investigated on 1250 field-caught *Python regius* (Togo, western Africa). Sexual dimorphism was often undetectable in neonates. By contrast, sexual dimorphism was apparent for many traits in adults. Adult females were larger and had a higher body condition than males; they also had longer jaws relative to their body size. This suggests that females and males follow different growth trajectories from birth to adulthood. In support of this, neonate females had a higher postnatal growth rate than males. Fecundity was strongly correlated with body size in females; a larger body size may be favored by fecundity selection in this sex. Our data show that females mature at a large body size: 95 cm in snout–vent length (SVL). The estimated external parasite load (number of ticks) was higher in adult males than females, perhaps because males encounter more ticks during movements.

Sexual size dimorphism is widespread among animals, and its evolutionary interpretation has attracted considerable scientific attention (Darwin, 1871; Campbell, 1972; Wade, 1976; Shine, 1986). Sexual dimorphism is well documented in snakes, involving a variety of traits such as body size, body shape, head dimensions, tail length, size at maturity, coloration,

scalation, and body plan (Fitch, 1981; King, 1989; Shine, 1991, 1993, 1994; Bonnet et al., 1998). Sexual dimorphism in such traits may be generated by sexual selection (for instance, larger body size in males relative to females being favored by male–male combat; Shine, 1978, 1994); selection for fecundity (for example, large female's body size being favored because it provides more space to hold the clutch; Shine, 1989, 1993); ecological factors (such as dietary divergence between the sexes; Shine, 1986, 1989; Camilleri and Shine, 1990); or different combinations of these selective forces (Shine, 1989, 1993).

In reptiles, analysis of the evolutionary processes influencing sexual dimorphism and their ecological

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implications have focused primarily on adults (Weatherhead et al., 1995; Bishop et al., 1996; King et al., 1999; Bonnet et al., 2001), but few studies have investigated sexual dimorphism in neonates, and even fewer studies have investigated how and when sexual dimorphism is generated from birth to adulthood (i.e., the ontogeny and physiological basis of sexual dimorphism; Shine and Crews, 1988). The aim of this paper is to provide information about sexual dimorphism in neonate and adult wild Ball Pythons, *Python regius*, a species belonging to a taxonomic group (African Boidae), for which there is paucity of field data.

The Ball Python (*P. regius*) is common in the pet trade. Although Ball Pythons can be bred in captivity, most of the specimens used for commercial purpose originate from the wild. Paradoxically, despite such intensive use, there is virtually no published scientific information on this species. This study was conducted from January 1999 to June 2000, in Lomé (western Africa, Togo). Field evidence and personal observations indicate that Ball Pythons are abundant in anthropogenically disturbed habitats such as small fields (e.g., manioc, yam) in the secondary forest glades with high population densities being observed in the south of Togo. Rodents also occur in these fields, and they represent the major food source of the pythons. The Ball Python is essentially nocturnal and spends most of the daytime in rodent burrows or termite mounds that are also used by the reproductive females during incubation. This is where local snake hunters dig to find the pythons, just before oviposition, which occurs in early January to late February/early March (Aubret et al., 2003). Males and females of all age classes were found in the same habitat, frequently in the same burrow.

MATERIALS AND METHODS

Data were collected on 1250 individual *P. regius*. Both adults ($N = 576$) and juveniles ($N = 69$) were captured in the wild in the vicinity of Lomé (maximal distance from Lomé was 40 km). Females were considered adults if they were 95 cm or more in snout-vent length (SVL), which corresponds to the size of the smallest gravid female we captured. Because there are no data on the minimal size for sexual maturity in males, we assumed they were mature at a similar body size to that at which females are mature to classify individuals as adults or juveniles. Neonates ($N = 605$), by contrast, were not measured directly in the field (for logistical reasons it is difficult to obtain neonates immediately after birth in the field). Instead, neonates were obtained from gravid wild females caught shortly before oviposition and kept in captivity in small wooden cages (50 × 50 × 30 cm) until laying (for details, see Aubret et al. 2003). Immediately after hatching, they were sampled randomly from approximately 1500 neonates obtained by incubating (with or without maternal attendance) clutches in a reptile farm in Lomé (Toganim®, SARL). Incubation temperatures were recorded using three automatic data loggers (Tinytag Ultra, -40 to 85°C; $N = 415$ measurements at 16.5-min intervals), with two attached to clutches and one in a potential natural nest site. The temperature experienced by the clutches, either maternally brooded or artificially incubated in boxes, is provided in Table 1. These records showed little variation in the mean temperature and range of

variation, as probably occurs in the field for successful clutches (Packard and Packard 1988; Shine and Harlow 1996). Almost all the neonates were apparently healthy with a low occurrence of scale abnormalities, further suggesting that the conditions for incubation were appropriate. We assumed that, although eggs were incubated in captivity, the resulting neonates were representative of wild neonates.

All snakes were measured for total length (± 0.5 cm), SVL (± 0.5 cm), body mass (BM; sensitivity 1 g, accuracy $\pm 0.2\%$), and tail length (± 0.5 cm). Head dimensions were measured to the nearest 0.1 mm using a digital caliper: jaw length (from the tip of the snout to the quadrato-articular); head width (HW, maximal width above the supra-oculars); skull length (from the tip of the snout to the base of the skull); and eye diameter. Sex was determined by eversion of the hemipenes. Ventral scales (excluding the tail) were also counted. The BM and SVL of a subset of neonates were measured at 10 days of age to estimate posthatching growth rate. Neonates were not fed during this period and maintained in individual plastic boxes with water provided ad libitum. Any growth would be supported by the postnatal body reserves (i.e., residual yolk; Ji and Sun, 2000; Ji et al., 1997). Body reserves were estimated using body mass scaled by SVL (body condition: using ANCOVA with sex as the factor, BM as the variable and SVL as covariate). Such an index provides accurate estimates of body reserves (chiefly fat and muscles in adults plus residual yolk in neonates) in snakes (Bonnet, 1996). Gravid females were not included in this calculation, because of the bias caused by clutch mass. During the oviposition period, snake hunters locate females by visiting potential oviposition sites, and they discard males and nonreproductive females. Consequently, this collecting technique increases the proportion of reproductive females captured. As such, gravid females collected before oviposition occurred were deleted from the data used to calculate sex ratio in adults.

As several reptile species are commonly infested by external parasites (Schneider et al., 1971; Keirans, 1972; Bull and Burzacott, 1993; Wikelski, 1999; Terenius et al., 2000; Burridge, 2001), field caught pythons were systematically checked for ticks at the time of capture. The total number of ticks was counted on each individual.

The distribution of the data deviated significantly from normality in approximately 50% of the variables (for example, for SVL, Shapiro-Wilk $W = 0.974$, $P = 0.00003$). Using log transformation did not solve this problem. However, visual inspection of the data suggested that the deviation from normality was caused by the relative low frequency of very large individuals, as we may expect in boids where few individuals reach a very large size. Consequently, despite a bell shape, the distribution curve was often asymmetrical. Although the F -test is very robust to departures from normality, especially when sample sizes are large, we confirmed our analyses using nonparametric tests; for simplicity we presented only the results of parametric tests. Growth trajectories of neonates were analyzed using multivariate analysis of variance with repeated measures of SVL and BM over time (O'Brien and Kaiser, 1985). Our sample sizes were large enough to provide results with reasonable confidence. This is important

TABLE 1. Temperature records ($N = 1929$ data for each data logger) from clutches incubated in this study and from a burrow (natural nest site).

	Mean	SD	Minimum	Maximum	Range
Brooded clutch	30.5	0.8	28.1	32.2	4.1
Artificial incubator	29.5	1.2	26.3	31.8	5.5
Natural nest-site (burrow)	28.8	0.9	25.9	31.1	5.2

because the relative measurement error may have differed among the different age categories of snakes (e.g., if jaw length is more difficult to measure accurately in neonates than adults) and may be a confounding factor in our analyses. Subtle differences between categories of neonates have been found in snakes, notably pythons (Shine et al., 1997, and references therein), suggesting that the small size of neonates does not preclude the possibility of detecting significant effects. Means are provided, ± 1 SD. All statistical analyses were performed using the program STATISTICA 6.0.

RESULTS

Sex Ratio.—Sex ratio was not biased at birth (301 males vs. 304 females, $\chi^2 = 0.01$, $P = 0.92$), nor in randomly field-collected juveniles (39 males vs. 30 females, $\chi^2 = 0.54$; $P = 0.46$) or adults (115 females vs. 108 males, $\chi^2 = 0.15$; $P = 0.70$).

Morphological Traits.—For most traits, female and male neonates were statistically indistinguishable (Table 2). There was a weak, but not significant, trend in neonates for females to be in better body condition than males (Table 2). Females had a greater developmental rate than did males (higher postnatal growth rate in SVL; see Table 2). Except for this characteristic, sexual dimorphism was undetectable in neonates and juveniles for any of the other traits investigated (Table 2). However, adult females were longer than males (Table 2) and reached a greater maximal body size (SVL = 170 cm, BM = 3224 g in females vs. 140 cm and 2460 g in males). When gravid females were deleted from analyses, the mean body condition was similar between adult males and females (Table 2). Adult females had more ventral scales than males (Table 2). The number of ventral scales was also higher in females relative to SVL (Ancova, $F_{1, 90} = 8.53$; $P < 0.004$). This indicates that scales were wider in males than in females. We did not count the number of ventral scales in neonates and juveniles; however, such number is fixed at birth, and it is likely that females have more ventral scales than males in all the age categories.

Head Size.—The relationship between jaw length and SVL differed significantly between males and females (see Table 2). Although in both neonates and juveniles, we found no sex difference in jaw length relative to SVL; adult females exhibited a relatively larger jaw length than adult males (Table 2). However, we may imagine that in very large females the jaw length/SVL

TABLE 2. Morphological comparison between male and female Ball Pythons. Several traits (i.e., ventral scale count in neonates) were not measured in all three age categories. Values presented are means \pm SD. * Statistical comparison was performed relative to SVL; ** relative to jaw length; *** relative to BM at birth; ^s gravid females not included.

	Females	Males	N	F	P
Neonates					
Snout-vent length (cm)	38.3 \pm 2.7	38.3 \pm 3.04	603	0.001	0.97
Tail length (cm)*	3.4 \pm 0.5	3.4 \pm 0.4	603	0.23	0.62
Body mass (g)	59.5 \pm 9.7	58.4 \pm 10.6	603	1.67	0.20
Body condition*	59.5 \pm 8.2	58.3 \pm 8.2	603	3.0	0.08
Jaw length (mm)*	27.6 \pm 1.2	27.5 \pm 1.3	487	2.5	0.11
Head width (mm)**	9.9 \pm 0.5	9.8 \pm 0.5	489	1.02	0.32
Skull length (mm)**	26.5 \pm 1.2	26.4 \pm 1.3	63	0.79	0.37
Eye diameter (mm)**	3.7 \pm 0.2	3.8 \pm 0.5	422	1.0	0.32
Growth in SVL (cm)*	5.7 \pm 1.7	5.1 \pm 1.5	106	4.0	0.048
Gain in BM (g)***	2.6 \pm 2.8	1.7 \pm 3.4	106	1.76	0.19
Juveniles					
Snout-vent length (cm)	72.0 \pm 18.0	73.4 \pm 18.4	69	0.10	0.75
Tail length (cm)*	5.7 \pm 1.7	5.7 \pm 1.6	68	0.09	0.76
Body mass (g)	380.4 \pm 285.6	394.4 \pm 276.6	67	0.04	0.84
Body condition (g)*	389.7 \pm 285.6	385.59 \pm 276.6	64	0.05	0.81
Jaw length (mm)*	32.8 \pm 4.5	33.1 \pm 5.4	43	0.54	0.47
Number of ticks*	8.1 \pm 13.9	4.3 \pm 8.1	55	1.98	0.16
Adults					
Snout-vent length (cm)	116.2 \pm 10.3	111.3 \pm 10.3	576	24.73	<0.0001
Tail length (cm)*	8.7 \pm 1.1	8.6 \pm 1.1	288	0.54	0.46
Body mass (g) ^s	1275.7 \pm 359.0	1181.5 \pm 333.2	327	5.93	<0.015
Body condition (g) ^s	1229.4 \pm 359.0	1227.8 \pm 333.2	324	0.01	0.95
Jaw length (mm)*	44.3 \pm 3.4	43.6 \pm 3.1	286	6.68	0.01
Ventral scales	204.8 \pm 3.3	201.4 \pm 5.1	193	13.8	<0.001
Number of ticks*	6.7 \pm 7.1	10.4 \pm 10.6	267	11.3	< 0.001

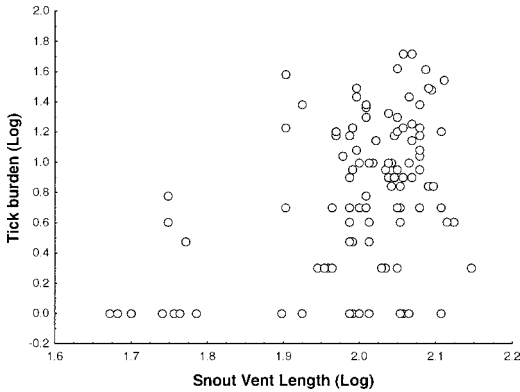


FIG. 1. Relationship between the amount of ticks and SVL in male ball pythons.

relationship is modified and is the source of the sex difference we observed. The larger adult males sampled reached 140 cm in SVL; therefore, we removed from the analysis all females exceeding 140 cm in SVL, allowing us to directly compare similar sized animals. Using that restricted dataset, the results remained unchanged (ANCOVA; $F_{1, 282} = 6.52$; $P < 0.011$), reinforcing the conclusion that females possess a larger jaw relative to their body than conspecific males.

Reproduction.—Mean clutch size of pythons was 7.7 ± 1.8 eggs. Clutch size was highly correlated with maternal SVL ($F_{1, 137} = 50.71$; $P < 0.0001$; $r = 0.52$; for details see Aubret et al., 2003).

Tick Burden.—Neonates were free from tick parasitism as they were observed immediately after hatching. Adults and juveniles were caught after a potentially long period of exposure to ticks in the wild (ranging from months to years), and they were often parasitized (approximately 30% of the snakes). Tick burden did not follow a normal distribution (Shapiro-Wilk W test; $N = 356$, $W = 0.74$, $P < 0.00001$). In juveniles, the number of ticks was not significantly different between males and females. In adults, however, the tick burden was significantly higher in males than in females (these analyses were also performed using a Kruskal Wallis ANOVA with sex as factor and the residual values of the regression between log SVL and log tick burden as dependent variable, without changing the results presented in Table 2). In males (juveniles and adults pooled), the number of ticks and SVL were strongly correlated ($r = 0.36$; $P < 0.0001$; Fig. 1), whereas this was not the case in females ($r = 0.03$; $P = 0.70$).

DISCUSSION

In snakes, females are often larger than males (> 60% of species; Shine, 1978, 1986; Fitch, 1981). Such dimorphism has often been interpreted in terms of the fitness consequences of different body sizes (Andrews, 1982). Several proximate causes have been invoked, including sex differences in growth rate, age at maturity, and adult survivorship (Shine, 1993; Stamps, 1993). Our study showed that, in Ball Pythons, sexual size dimorphism is absent at birth (or at least very weak and, therefore, statistically undetectable despite large

sample sizes) for most traits except postnatal food-independent growth and probably number of ventral scales. Because the sex ratio was not biased, different survivorship patterns are not likely to be responsible for the marked sexual size dimorphism observed in adults. Females exhibited a higher initial food-independent growth rate in comparison to males, and this effect was observed over a short (10-day) period, suggesting that this sex difference was strong. We acknowledge that more data are needed to determine whether the initial difference in growth rate is maintained and may somehow be responsible for the sexual size dimorphism observed during adulthood. Nonetheless, this study provides the first report of such "physiological" sexual dimorphism.

Adult females have longer jaws (adjusted to body size) relative to males. In Ball Pythons that are typical gape-limited predators, longer jaws may improve female's foraging success by increasing their swallowing capacities (Shine, 1977, 1986, 1989, 1991; Voris and Voris, 1983; Camilleri and Shine, 1990; Forsman and Shine, 1997). This might at least partially explain why females grow larger than males. However, many alternative, and not necessarily exclusive, hypotheses such as the hormonal influences on growth trajectories (e.g., androgen-induced inhibition in the rate of growth of the head; Shine and Crews, 1988; King and Turmo, 1997) may play a significant role as well. Whatever the proximate factor causing the sexual size dimorphism, our data suggest that a higher growth rate in females is important, rather than a sex difference in survival. Large body size could be under stronger selection in females relative to males. Clutch size was highly correlated with SVL, as observed in many other snake species (Shine, 1986; Seigel and Ford, 1987); this relationship is probably important to better understand sex differences in growth rate and/or age at maturity (Andrews, 1982).

Our study also showed that the tick burden was higher in adult males than in females. Differential parasitism between the sexes has been documented in many vertebrates (Bundy, 1988; Zuk, 1990; Poulin, 1996 for review), but not yet in snakes. Shine et al. (1998) indicated an absence of a difference in gut nematode burden between male and female reticulated pythons. Such sex-biased parasitism may result from differences in immunocompetence resulting from unequal costs of reproduction, or from natural selection favoring ecological divergence which results in differential exposure to infectious agents (Selander, 1966; Trivers, 1976; Reimchen, 1980; Hamilton and Zuk, 1982; Slatkin, 1984; Tinsley, 1989; Houston and Shine, 1993; Perry, 1996). For instance, elevated levels of testosterone can lead to immuno-suppression which increases susceptibility of infection or disease (Folstad et al., 1989; Folstad and Karter, 1992). Proximate differences in parasitic infection between genders might arise from ecological rather than sexual selection. For example, niche partitioning involving habitat or diet (Selander, 1966; Grant, 1975; Reimchen, 1980; Grant, 1985; Shine, 1989; Houston and Shine, 1993) can result in differential exposure to parasites unrelated to the unequal costs of reproduction (Tinsley, 1989). However, the relative importance of niche partitioning as a general explanation for gender differences in parasitism has not been well established (Reimchen and Nosil, 2001).

In our study, all field-caught pythons were collected in the same sites, as males and females commonly share burrows. Thus, the difference in tick burden is unlikely to be caused by differences in habitat use. Different reproductive roles between the sexes may provide a simple alternative explanation. In many snake species (Slip and Shine, 1988; King and Duvall, 1990; Plummer and Mills, 1996; Bonnet et al., 1999), reproductive males exhibit intensive mate-searching behavior during the breeding season. It is possible that male Ball Pythons move intensively to maximize encounters with conspecific females. In contrast, females frequently remain immobile for prolonged periods, particularly during the two months of incubation while they brood their clutch. Consequently, adult males may be more exposed to ticks during their movements than are females. Although preliminary, this result is the first report to date of sex differences in parasitism rates in snakes.

Acknowledgments.—We wish to thank all the snake hunters who helped us in Togo, Talawash, Antoine, and Tatiana Ganne beh damme. We also thank R. Cambag and J. Hunt for help at various stages of the study and especially E. Fouchard who holds the reptile farm (Toganim) in Togo. Two reviewers provided constructive comments on previous version of the manuscript. Financial support was provided by the CNRS, and the IUCN (World Conservation Union-Project cc31053a/75645, Status assessment of reptiles in Togo, IUCN Species-Survival Commission Wildlife Trade Programme, U.K. Darwin Initiative for the Survival of Species, and the Commission of the European Union). Finally, we are grateful to the Togo wildlife authorities who enabled us to conduct this study. All the experiments conducted in Togo complied with the current laws of the country and were approved by the local committee for conservation and land management.

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Accepted: 18 February 2005.