Spatial Ecology of a Cottonmouth (*Agkistrodon piscivorus*) Population in East Texas

ERIC D. ROTH[1]

*Department of Zoology, and Sam Noble Oklahoma Museum of Natural History, University of Oklahoma,
Norman, Oklahoma 73019, USA; E-mail: eric.d.roth-1@ou.edu*

ABSTRACT.—Radio-telemetry was used to study spatial ecology of a Cottonmouth (*Agkistrodon piscivorus*) population in eastern Texas. I examined effects of sex, reproductive state, and body size on spatial use within a riparian habitat. Snakes inhabited a relatively linear environment, restricting movements to the vicinity of the stream. Males occupied larger home ranges than both gravid and nongravid females. Gravid females exhibited marginally larger home ranges than nongravid females, but any effects attributable to reproductive state were relatively small when compared to sex differences in spatial use. Body size was positively correlated with home-range size but did not account for observed home-range differences among population subunits.

To further understand the spatial ecology of snakes, it is important to first define general patterns of spatial use and then determine what factors are influencing spatial patterns. Within snakes, spatial use differences in relation to sex and reproductive state are commonly reported (e.g., Macartney et al., 1988; Webb and Shine, 1997; Whitaker and Shine, 2003). However, these relationships are often variable and mechanisms driving divergent spatial patterns in relation to sex and reproductive state remain unclear.

Another factor influencing spatial use is body size. An animal with greater energetic requirements may require a larger area to satisfy its energetic needs (McNab, 1963). Harestad and Bunnell's (1979) theoretical model defines minimum home range as, ''the minimum area that can sustain the individual's energetic requirements.'' Although this model may oversimplify some factors (e.g., factors relating to reproductive success) influencing home range area, it suggests that body size and other measures of metabolic requirements can likely explain some variance in home-range size (e.g., Mace and Harvey, 1983; Kelt and Van Vuren, 1999; Perry and Garland, 2002). In snakes, some intraspecific studies are suggestive of a relationship between body size and home range (e.g., Clark, 1974; Shine, 1987; Whitaker and Shine, 2003), but data are yet too limited for detailed interspecific analyses. Furthermore, it is evident that spatial patterns often vary within and between individuals, populations, species, seasons, and years (e.g., Shine, 1987; Tiebout and Cary, 1987; Slip and Shine 1988). Attaining a greater understanding of snake spatial ecology will require additional comparative studies that consider the influence of sex, reproductive state, body size, and other ecological interactions.

I explored patterns of spatial use within a population of *A. piscivorus* in east Texas. *Agkistrodon piscivorus* is a semiaquatic snake that occurs throughout much of the southeastern United States. Aspects of natural history and ecology have been examined for the snake (Burkett, 1966; Gloyd and Conant, 1990; Ford, 2002), but very little is known about its spatial ecology.

Previous studies on spatial use in *A. piscivorus* (Tinkle, 1959; Wharton, 1969; Martin, 1982) will provide a comparative template for this investigation, which examines patterns of spatial use in relation to sex, reproductive state, and body size.

MATERIALS AND METHODS

Study Site.—I conducted this study from May 2000 to January 2002 at Sam Houston State University's Center for Biological Field Studies (CBFS). This site was adjacent to the Sam Houston National Forest and consisted of a stream system within a pine woodlands habitat. For a detailed description of the study site, see Dent and Lutterschmidt (2001). *Agkistrodon piscivorus* were collected from the study site at the beginning (April to June) of each radio-tracking season. Over the duration of the study, I monitored 17 adult snakes using radio-telemetry. Each snake weighed greater than 160 g, and each 5.5 g transmitter represented less than 5% of total body weight. During the first summer (May to August 2000), I radio-tracked six females and one male. During the second summer (May to August 2001), I radio-tracked six females and four males.

In the summer of 2000, one female died 15 days after being released, and another female dislodged her transmitter from the body cavity. Observations and home-range calculations on these individuals were discarded. Thus, results are reported for 15 adult *A. piscivorus* (five gravid females, five nongravid females, five males).

Surgical Procedures.—Holohil Systems, Inc., SB-2 transmitters were coated with a 1:1 mixture of paraffin and beeswax and surgically implanted into the body cavity using methods described by Reinert and Cundall (1982). Prior to surgery, I administered isoflurane (inhalation gas) until subjects were unresponsive to touch. After surgery, I maintained snakes in the laboratory for approximately one week. Water was provided ad libitum during this observational period until snakes were released at original capture locations.

Data Collection and Analysis.—Radio-tagged snakes were usually located every other day during the early morning and afternoon hours (0500–1500). Upon location of each snake, geographic coordinates were recorded with a global positioning system receiver (Magellan GPS 320). Individual snakes were never relocated twice on a single day, and at least 15 hours

[1] Address correspondence to: Eric D. Roth, Department of Zoology, University of Oklahoma, 730 Van Vleet Oval, Norman, Oklahoma 73019, USA

TABLE 1. For each of the 15 radio-tracked *Agkistrodon piscivorus*, 95% MCP and 95% fixed kernel home-range estimations are displayed. The snake identification number (ID) corresponds to labeled home ranges in Figure 1. Population subunit (gravid female: GF, nongravid female: NGF, male: M), snout–vent length (SVL), year studied (year), number of days monitored (days), and total number of observations (Obs.) are also provided.

ID	Subunit	SVL (cm)	Year	Days	Obs.	MCP 95%	Kernel 95%
1	GF	64.0	2000	72	27	0.997	2.373
2	GF	58.0	2000	72	33	0.033	0.006
3	GF	55.5	2001	52	29	1.480	2.124
4	GF	55.5	2001	49	27	1.462	3.224
5	GF	54.0	2001	48	28	0.842	1.150
6	NGF	55.0	2000	59	22	0.405	0.912
7	NGF	60.0	2000	55	25	0.624	0.625
8	NGF	50.0	2001	48	28	0.369	0.760
9	NGF	53.0	2001	39	25	0.341	0.381
10	NGF	48.0	2001	40	26	0.119	0.409
11	M	53.0	2000	81	31	2.034	5.770
12	M	73.5	2001	27	20	3.337	14.18
13	M	61.5	2001	49	25	1.638	7.607
14	M	50.5	2001	49	30	0.999	1.274
15	M	56	2001	26	20	1.303	4.862

elapsed between each observation. Geographic coordinates were imported into ArcView 3.3 (Environmental Systems Research Institute, Inc., 1999), and home-range sizes were calculated with the Animal Movement Analysis Extension (Vers. 1.1, P.N. Hooge and B. Eichenlaub, Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, 1997) using 95% minimum convex polygons (MCPs; Mohr, 1947) and 95% fixed kernel methods (Worton, 1989) with least-squares cross-validation to determine smoothing parameters (Seaman and Powell, 1996).

Before comparing population subunits (i.e., males, nongravid females, and gravid females), the effects of body size were first examined. A simple regression was used to explore the relationship between body size or snout–vent length (SVL) and home-range size. Home ranges of population subunits were then compared using an ANCOVA with SVL as the covariate.

To address potential biases caused by variation in the duration of monitoring period and number of observations per individual, incremental area analyses (IAA) were used to graphically examine increases in home-range area over time and number of observations for each individual. Simple regressions were used to explore relationships between home-range area, number of observations, and monitoring duration. Finally, Kruskal-Wallis tests were used to compare average duration of monitoring periods and number of observations among population subunits.

RESULTS AND DISCUSSION

Fixed kernel methods often produced larger home-range estimates than MCPs. Inflated fixed kernel estimates may be related to the compact linear nature of the observed spatial use patterns, as fixed kernels often included additional terrestrial areas around the stream that most subjects never inhabited. Nonetheless, general conclusions and all statistical inferences remained constant regardless of which home-range estimator was used in the analyses. Thus, both home-range estimates are reported in Table 1, but further descriptive and inferential statistics are only reported for comparisons of MCPs.

Similar to observations from laboratory studies (Savitzky, 1992), *A. piscivorus* were generally located near the water/shore interface, exhibiting linear home ranges oriented around the stream (Fig. 1). These linear home ranges varied in size from 0.033–3.337 ha. To address home-range size variation, body size was first considered. As body size increased, home-range area increased ($r^2 = 0.429$, $F_{1,13} = 9.749$, $P < 0.01$). An ANCOVA, which compared the home ranges of population subunits with body size (SVL) as the covariate, showed no significant interaction ($F_{2,9} = 1.611$, $P = 0.252$). After the interaction term was removed from the model, the main effects of both body size ($F_{1,11} = 6.924$, $P < 0.05$) and population subunit groupings ($F_{2,11} = 5.584$, $P < 0.05$) were significant. Thus, after controlling for body size, significant differences in home-range size between population subunits remained. These results suggest that, although factors related to body size may influence spatial patterns, these factors alone do not account for differences observed in home-range area among population subunits.

Mean MCP home-range sizes (Fig. 2) were 1.86 ha ± 0.407 (mean ± SEM) for males, 0.963 ± 0.264 for gravid females, and 0.372 ± 0.081 for nongravid females. In contrast to prior studies on *A. piscivorus* (Tinkle, 1959; Wharton, 1969; Martin, 1982), males exhibited significantly larger home ranges than gravid (post hoc: Fisher's Protected Least Significant Difference [FPLSD]: $P < 0.05$) and nongravid ($P < 0.001$) females. Although larger home ranges in males of many snake species have been reported (e.g., Reinert and Zappalorti, 1988; Slip and Shine, 1988; Fitzgerald et al., 2002; Whitaker and Shine, 2003), causal mechanisms remain unclear. It has been suggested that similar spatial patterns in other taxa may be related to breeding system and reproductive strategies (e.g., Morreale et al., 1984; Reinert and Zappalorti, 1988; Ostfeld, 1990). Because territoriality has not yet been demonstrated in snakes, this hypothesis suggests that sex differences in spatial use will primarily occur as a result of male competition for
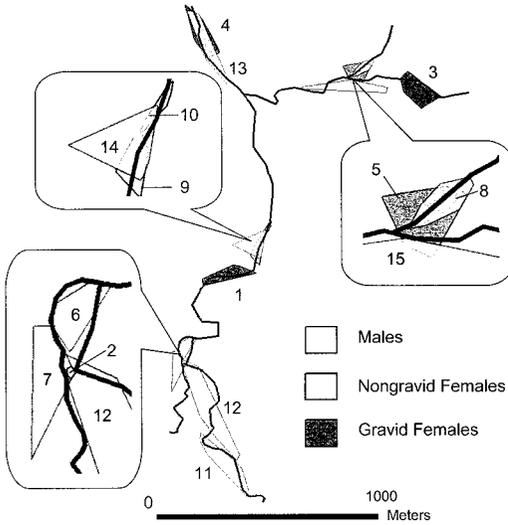
FIG. 1. Home-range (95% MCP) maps for radio-tagged *Agkistrodon piscivorus* categorized by population subunit. Identification numbers labeling each home range correspond with the individual identification numbers listed in Table 1. Inset boxes depict enlarged views of congested or overlapping areas.

Population Subunit

FIG. 2. Mean home-range size (95% MCP) and standard errors are depicted for each population subunit.

females during the breeding season. It is generally assumed that breeding among *A. piscivorus* occurs in the early spring, (Gloyd and Conant, 1990). This suggests that influences related to breeding activities were likely minimized for the duration of this study (May to August) and may not account for the differences in home-range size between sexes. These results combined with other studies that report larger home ranges for females (e.g., Madsen, 1984; Johnson, 2000) highlight a need to further explore alternative explanations, such as foraging strategies, predation pressures, and/ or social interactions that may be driving divergent spatial patterns between the sexes.

Reproductive state may also affect resource requirements and physiological needs, thus influencing spatial use (e.g., Shine, 1980; Reinert, 1993; Madsen and Shine, 2000). Although statistical differences were marginal (FPLSD: $P < 0.1$), gravid females tended to exhibit larger average home-range areas than nongravid females (Fig. 2.). This contradicts results from many studies that report significantly smaller home ranges for gravid females (e.g., Reinert and Zappalorti, 1988; Johnson, 2000; Whitaker and Shine, 2003). Future research exploring the effects of reproductive state on spatial use in *A. piscivorus* would be of interest.

Average home-range sizes, which ranged from 0.372 ha in nongravid females to1.86 ha in males, in this study were larger than those reported in previous studies on *A. piscivorus*. Wharton (1969) and Tinkle (1959) reported average home-range sizes of 0.14–0.17 ha. Martin (1982) reported average home-range values of 0.93 ha for females and 0.88 ha for males. When comparing *A. piscivorus* to other snake species of similar body size (e.g., *Agkistrodon contortrix*: 9.9-ha home range, Fitch 1960; *Crotalus cerastes*: 23.2 ha, Secor, 1994; *Heterodon platirhinos*: 50.2 ha, Plummer and Mills, 2000),
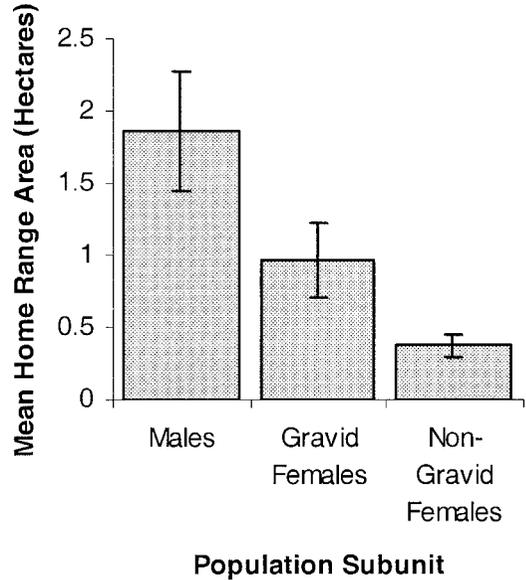
it is evident that average home ranges of *A. piscivorus* are relatively small. One direction of future research exploring the relatively small home ranges of *A. piscivorus* may focus on resource distribution. Inhabiting a relatively linear environment surrounding the stream allows movements to and from patchy resources, such as prey, retreat sites, and potential mates, to be directionally focused either upstream or downstream. Location of patchy resources within a simplified linear stream environment may be more efficient and reduce home-range size requirements compared to other species inhabiting a more complex two-dimensional area with resources scattered in many directions.

The timing and duration of this study may have also influenced home range estimates. Individuals were radio-tracked for 50.6 ± 3.4 (mean $\pm$ SE) days with 26.4 ± 0.97 (mean $\pm$ SE) observations per individual. Duration of monitoring periods varied between individuals ranging from 26–81 days, whereas observations per individual ranged from 20–33. Asymptotic curves from IAA suggest that observations were sufficient to produce reliable estimates of home-range size for the time period studied. Home-range size was not related to duration of monitoring period ($r^2 = 0.048$, $F_{1,13} = 0.656$, $P = 0.433$) or number of observations ($r^2 = 0.105$, $F_{1,13} = 1.525$, $P = 0.239$). Variation in duration of monitoring periods (Kruskal-Wallis, $H = 1.683$, $P = .431$) and number of observations (Kruskal-Wallis, $H = 3.296$, $P = 0 .192$) appeared to be randomized across population subunits. Thus, any bias resulting from random variation in length of tracking periods and number of observations appears minimal and does not account for significant differences in home-range size observed between population subunits. Nonetheless, monitoring periods were restricted to the summer months, thus limiting interpretations. Although anec-

dotal recapture observations (unpubl. data) are not suggestive of movements outside the summer home range in the early spring or late winter, it is plausible that larger home ranges may have been obtained if radio-telemetry studies had begun earlier in the year. This is especially true of males, if indeed breeding is occurring in the early spring, and males move more to increase mating opportunities.

This study has explored the spatial ecology of a snake population with consideration of factors that may influence spatial use. The spatial patterns of population subunits were compared by examining the effects of sex, reproductive state, and body size within an ecological context. Such comparisons enhance the general understanding of snake spatial ecology and provide the foundation for future comparative studies.

LITERATURE CITED

BURKETT, R. D. 1966. Natural history of Cottonmouth Moccasin *Agkistrodon piscivorus* (Reptilia). Univ. of Kansas Publications Museum of Natural History 17:435–491.

CLARK, D. R. J. 1974. The Western Ribbon Snake (*Thamnophis proximus*): ecology of a Texas population. Herpetologica 30:373–379.

DENT, L., AND W. I. LUTTERSCHMIDT. 2001. The ichthyofauna of Harmon and Wynne Creeks sampled within the center for biological field studies, Walker County, Texas. Texas Journal of Science 53:139–146.

FITCH, H. S. 1960. Autecology of the copperhead. Univ. of Kansas Publications Museum of Natural History 13:85–288.

FITZGERALD, M., R. SHINE, AND F. LEMCKERT. 2002. Spatial ecology of arboreal snakes (*Hoplocephalus stephensii*, Elapidae) in an Australian forest. Austral Ecology 27:537–545.

FORD, N. B. 2002. Ecology of the Western Cottonmouth (*Agkistrodon piscivorus leucostoma*) in northeastern Texas. *In* G. W. Shuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.), Biology of the Vipers, pp. 167–177. Eagle Mountain Publishing, Eagle Mountain, UT.

GLOYD, H. K., AND R. CONANT. 1990. Snakes of the *Agkistrodon complex:* a monographic review. Society for the Study of Amphibians and Reptiles. Contributions to Herpetology 6:1–614.

HARESTAD, A. S., AND F. L. BUNNELL. 1979. Home range and body weight—a reevaluation. Ecology 60:389–402.

JOHNSON, G. 2000. Spatial ecology of the Eastern Massauga (*Sistrurus c. catenatus*) in a New York peatland. Journal of Herpetology 34:186–192.

KELT, D. A., AND D. H. V. VUREN. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80:337–340.

MACARTNEY, J. M., P. T. GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. Journal of Herpetology 22:61–73.

MACE, G. M., AND P. H. HARVEY. 1983. Energetic constraints on home-range size. American Naturalist 121:120–132.

MADSEN, T. 1984. Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. Copeia 1984:707–713.

MADSEN, T., AND R. SHINE. 2000. Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. Austral Ecology 25:670–675.

MARTIN, D. L. 1982. Home Range, Movements, and Activity Patterns of the Cottonmouth, *Agkistrodon piscivorus*, in Southern Louisiana. Unpubl. master's thesis, Univ. of Southwestern Louisiana, Lafayette.

MCNAB, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97:133–140.

MOHR, C. O. 1947. Table of equivalent populations of North American Small Mammals. American Midland Naturalist 37:223–249.

MORREALE, S. J., J. W. GIBBONS, AND J. D. CONGDON. 1984. Significance of activity and movement in the Yellow-Bellied Slider Turtle. Canadian Journal of Zoology 62:1038–1042.

OSTFELD, R. S. 1990. The ecology of territoriality in small mammals. Trends in Ecology and Evolution 5:411–415.

PERRY, G., AND T. J. GARLAND. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. Ecology 83:1870–1885.

PLUMMER, M. V., AND N. E. MILLS. 2000. Spatial ecology and survivorship of resident and translocated Hognose Snakes (*Heterodon platirhinos*). Journal of Herpetology 34:565–575.

REINERT, H. K. 1993. Habitat selection in snakes. *In* R. A. Seigel and J. T. Collins (eds.), Snakes: Ecology and Behavior, pp. 201–240. McGraw-Hill, Inc, New York.

REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705.

REINERT, H. K., AND R. T. ZAPPALORTI. 1988. Timber Rattlesnakes (*Crotalus horridus*) of the Pine Barrons: their movement patterns and habitat preference. Copeia 1988:964–978.

SAVITZKY, B. C. A. 1992. Laboratory studies on piscivory in an opportunistic pitviper, the Cottonmouth, *Agkistrodon piscivorus*. *In* J. A. Campbell and E. D. Brodie Jr. (eds), Biology of the Pitvipers, pp. 347–368. Selva Press, Tyler, TX.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

SECOR, S. M. 1994. Ecological significance of movements and activity range for the Sidewinder, *Crotalus cerastes*. Copeia 1994:631–645.

SHINE, R. 1980. "Costs" of reproduction in reptiles. Oecologia 46:92–100.

———. 1987. Intraspecific variation in thermoregulation, movements and habitat use by Australian Blacksnakes, *Pseudechis porphyriacus* (Elapidae). Journal of Herpetology 21:165–177.

SLIP, D. J., AND R. SHINE. 1988. Habitat use, movements and activity patterns of free-ranging Diamond Pythons, *Morelia spilota spilota* (Serpentes: Boidae): a radiotelemetric study. Australian Wildlife Research 15:515–531.

TIEBOUT, H. M. I., AND J. R. CARY. 1987. Dynamic spatial ecology of the water snake, *Nerodia sipedon*. Copeia 1987:1–18.

TINKLE, D. W. 1959. Observations of reptiles and amphibians in a Louisiana swamp. American Midland Naturalist 62:189–205.

WEBB, J. K., AND R. SHINE. 1997. A field study of spatial ecology and movements of a threatened snake species, *Holocephalus bungaroides*. Biological Conservation 82:203–217.

WHARTON, C. H. 1969. The Cottonmouth Moccasin on Sea Horse Key, Florida. Bulletin of the Florida State Museum. Biological Sciences 14:228–272.

WHITAKER, P. B., AND R. SHINE. 2003. A radiotelemetric study of movements and shelter-site selection by free-ranging brownsnakes (*Pseudonaja textilis*, Elapidae). Herpetological Monographs 17:130–144.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Cues Used by Raccoons to Find Turtle Nests: Effects of Flags, Human Scent, and Diamond-Backed Terrapin Sign

RUSSELL L. BURKE,[1,2] CHRISTINE M. SCHNEIDER,[3] AND MICHAEL T. DOLINGER[4]

[1]*Department of Biology, Hofstra University, Hempstead, New York 11549, USA; E-mail: biorlb@hofstra.edu*
[3]*2631 Central Avenue, Baldwin, New York 11510, USA*
[4]*2162 Jackson Place, Bellmore, New York 11710, USA*

ABSTRACT.—We simulated nests constructed in an area heavily used by ovipositing Diamond-backed Terrapins (*Malaclemys terrapin*) and foraging raccoons (*Procyon lotor*), to investigate the cues used by raccoons to locate terrapin nests. Marking nests with flags did not increase predation rates, and human scent decreased predation rates. Raccoons seemed to locate nests based on soil disturbance, ocean-water scent, or a combination of these cues.

Throughout their range, raccoons (*Procyon lotor*) are often important predators of turtle nests (Mitchell and Klemens, 2000). Cues they use to locate nests are largely unknown but probably involve both sight and olfaction, as raccoons have good eyesight and an excellent sense of smell (Zeveloff, 2002). In addition to the natural cues that may be left behind by nesting turtles, researchers studying turtle reproductive ecology often mark the location of nests after observing oviposition, leaving potentially informative markers and human scent. Inexpensive marking techniques vary but include numbered stakes (e.g., Congdon et al., 1983) and vinyl flags (e.g., Feinberg and Burke, 2003; also F. Janzen and A. Georges, pers. comm.). Predators may learn to associate such marking techniques with the nearby presence of nests, and, thus, these markers may influence predation rates.

We investigated the importance of natural and artificial cues using artificial nests placed on the island of Ruler's Bar Hassock (RBH) in Jamaica Bay Wildlife Refuge (JBWR), New York. Approximately 2000 nests of *Malaclemys terrapin* are laid each year on RBH, and raccoons depredate 93% of these nests (Feinberg and Burke, 2003). There are no other significant nest predators. Most of this predation occurs at night, but visibility at night at this site is often good (RLB, pers. obs.). Raccoons on RBH have had ample opportunity to learn about flags because orange vinyl flags, placed close to nests, have been used for five years to mark terrapin nests, and some individual raccoons have lived on the island for at least three years (K. M. Broadwater and R. L Burke, unpubl. data). Our experiments were similar to those of Tuberville and Burke (1994) except that we used artificial nests; we worked in an area where raccoons potentially had extensive experience with flags; we avoided the use of equipment that might influence raccoon behavior; and we investigated cues other than just flags.

MATERIALS AND METHODS

Artificial nests were placed in three different areas of dunes and mixed grasslands, each of which was in-

[2] Corresponding Author.

tensively used by nesting terrapins and nest-predating raccoons. Trials took place between 14 July and 5 August 2003, and between 5 and 30 July 2004, within the normal nesting season for this area. In 2003, 16 artificial nests were constructed for each treatment; in 2004, 40 nests were constructed for each treatment. Artificial nests were monitored for signs of digging by raccoons daily for four days after construction, because nearly all raccoon predation on terrapin nests occurs in the first four day after oviposition (Feinberg and Burke, 2003). Artificial nests were considered "depredated" if there were signs of raccoon digging anywhere between the flags at the nest site.

We constructed nine types of artificial nests with different combinations of features to explore which cues raccoons use to locate nests. Only eight treatments were constructed each year—Treatment 3 was used only in 2004, and Treatment 4 was only used in 2003.

Treatment 1 was a "control" treatment, in that we tried to simulate most closely a real terrapin nest flagged as nests have been on this site since 1998 (Feinberg and Burke, 2003). As was typically done during that time, flags were placed approximately 25 cm to each side of the nest. Nest holes were hand dug to a depth of approximately 10 cm, as is typical for terrapin nests of this area. Surgical gloves were worn to mask human scent, except where noted below. We filled the excavated hole with terrapin-scented sand, which we made by placing an adult female terrapin in a box with beach sand for at least 30 min (Marchand et al., 2002). The filled excavation was smoothed over to reduce visual cues, as terrapin nests in this area are nearly always visually inconspicuous.

Treatments 2 and 3, designed to test whether the flags themselves could serve as visual cues, were identical to Treatment 1, except that flags were placed farther from the nest for 2 (60 cm to each side) and for 3 (100 cm to each side). We assumed these flags would be too far apart to serve as good cues of nest location.

Treatment 4 was designed to determine whether raccoons had learned to associate orange flags specifically with nests but would ignore flags of other colors. This treatment was identical to Treatment 1, except green flags were used instead of orange.

Treatment 5 was designed to determine whether moisture itself was a cue to the presence of a nest. This treatment was identical to Treatment 1 except plain sand was used to fill the excavated hole.

Treatment 6 was designed to determine whether flags alone could serve as sufficient stimulus to cause exploratory digging. For this treatment, flags were placed as in Treatment 1, but no digging or other manipulations were used.

Treatment 7 was designed to determine whether human scent influenced predation rates. This treatment was identical to Treatment 1, except gloves were not worn, and human saliva was mixed with plain sand to fill the hole.

The last two treatments were designed to elucidate the importance of different scents as cues. These treatments were, therefore, identical to Treatment 6, except that for Treatment 8 approximately 50 mL of ocean water was poured over the "nest site" and for Treatment 9 approximately 50 mL of fresh water was poured over the "nest site."

We examined a 2×8 contingency table for significant heterogeneity among the treatments from each year, using a goodness of fit test. On the basis of these results, we analyzed 12 comparisons (Treatment 1 vs. all other treatments, and Treatment 6 vs. 5, 8 and 9) post hoc with 2×2 contingency tables, using the two-tailed "unplanned tests of the homogeneity of replicates tested for goodness of fit" procedure (Sokal and Rohlf, 1981). This test uses critical values of the X^2-test based on Šidák's multiplicative inequality (Rohlf and Sokal, 1995) and compensates for both the post hoc nature of these tests and the fact that multiple tests are done simultaneously.

RESULTS

We regularly observed Raccoon footprints throughout the area during these experiments, and saw no sign of other nest predators. Overall, 48% (215/448) of the nests were "depredated." Of these, 71% were depredated in the first night, 10% in the second night, 13% in the third night, and 6% in the fourth night.

Only Treatment 6 (in 2004), the artificial nests that had been constructed with flags but without digging, and Treatment 7 (both years), the nests deliberately constructed so as to have high levels of human scent, had no predation at all (Fig. 1). Our control treatment, meant to simulate real terrapin nests, had the highest predation rate (88% and 95%, Fig. 1). There was significant heterogeneity among the treatments in 2003 ($G_H = 85.22$, df = 7, $P<0.001$) and in 2004 ($G_H = 243.7$, df = 7, $P < 0.001$). Only two comparisons of the 2003 data showed significant differences between treatments at the $P \leq 0.05$ level: Treatment 1 vs. 6 ($G_H = 24.70$) and 7 ($G_H = 31.80$). Only five comparisons of the 2004 data showed significant differences between treatments at the $P \leq 0.05$ level: Treatment 1 vs. 5 ($G_H = 28.95$), 6 ($G_H = 85.61$), 7 ($G_H = 85.61$), 9 ($G_H = 60.4$) and Treatment 6 vs. 8 ($G_H = 36.18$). All df = 9. For the 2004 data, Treatment 5 vs. 6 ($G_H = 21.40$) was close to the $G_H = 23.526$ for $P \leq 0.05$ level.

DISCUSSION

Raccoons responded to some of our artificial nests in a manner much as they did to real Diamond-Backed Terrapin nests. Raccoons at this site depredate about 93% of terrapin nests, and most of this predation occurs in the first night after oviposition (Feinberg and Burke, 2003). Raccoons preyed upon our control nests at rates as high as their predation on real nests, and most artificial nests were depredated in the first night, as were real terrapin nests.

Our initial question was whether orange flags, placed close (25 cm away) to recently oviposited terrapin nests, increased the likelihood that they would be depredated. Because depredation rates for treatments 2 and 3, where flags were considered too distant from nests to indicate nest location, were similar to (and not significantly different) those of our main control, Treatment 1, we conclude that close flags did not increase the likelihood of depredation. Thus our results agree with those of Tuberville and Burke (1994) that experimenters using flags to mark nests may have no impact on predation rates.

The observation that predation rates were significantly lower for treatments with close flags but lacking either digging (6) or terrapin scent (5) suggests it is not
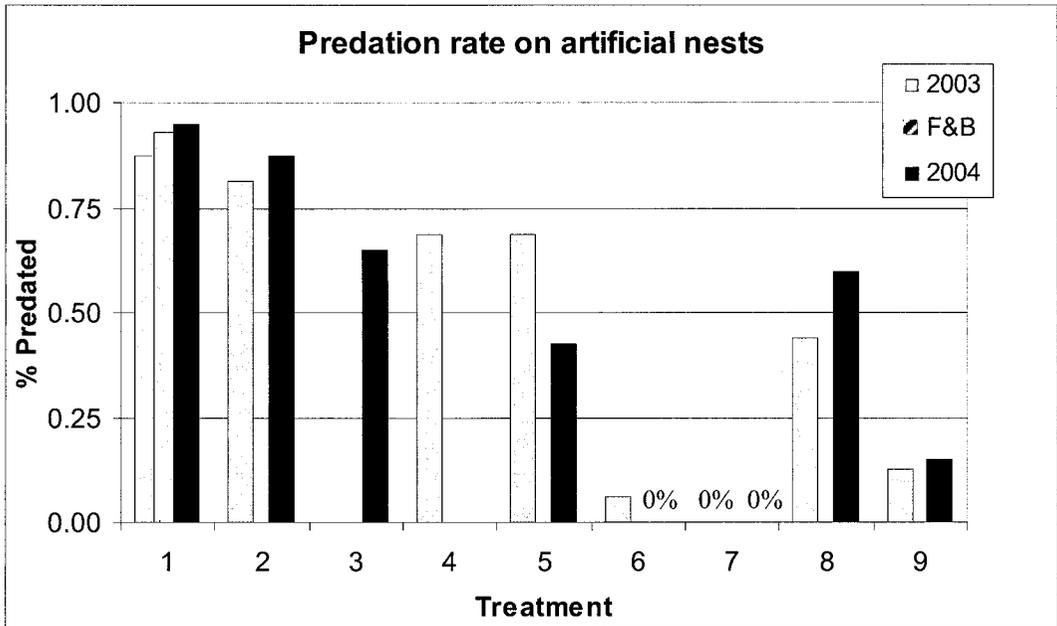
Fig 1. Comparison of depredation rates on real terrapin nests (F & B = Feinberg and Burke, 2003) with artificial nests constructed in 2003 and 2004. See text for description of treatments.

the flags themselves that indicate nest locations to raccoons but digging and/or the scent of terrapins instead. These results differ from those found by Mroziak et al. (2000) who found that sea turtle nests covered by antipredator cages were depredated by raccoons at higher rates than noncaged nests. They also found that most depredation on caged nests occurred in the latter half of incubation (Mroziak et al. 2000), but even if compared immediately after oviposition, caged nests were depredated at higher rates than noncaged nests (K. Rusenko, pers. comm.). Raccoons at their site were so highly trained to the use of cages as cues that any cages left on the beach, with or without nests, were excavated (K. Rusenko, pers. comm.). We have not detected a similar phenomenon at flagged terrapin nests at JBWR.

We further considered the possible impact of other cues that might indicate the locations of terrapin nests to raccoons, such as human scent, increased soil moisture, subsurface soil disturbance, flag color, "Diamond-Backed Terrapin-scent," and "ocean water scent." We found that flag color had no apparent influence on predation rates. A dramatic result we detected was associated with Treatment 7, in which human scent was deliberately augmented. This treatment had significantly lower predation rates than our main control (Treatment 1). This indicates that raccoons are not attracted to real terrapin nests by human scent as we expected, and they may actually be repelled.

Results from Treatment 5 indicate that nest excavation, even when carefully refilled and, in the absence of other cues, can serve to raise predation rates to levels similar to the control (1). We conclude that soil disturbance, perhaps detected visually, is an important cue indicating nest location to raccoons. Researchers

who avoid disturbing the soil surface around nests may avoid influencing predation rates.

The sand surrounding freshly laid terrapin nests is typically damp (RLB, pers. obs.), and this is presumably caused by voiding of the turtle's bladder prior to egg laying, as has been observed in other turtles (RLB, pers. obs.; Patterson, 1971). Patterson (1971) found that this liquid facilitated digging and delayed predation. In contrast, we found that artificial "nests" made with ocean water (8) had much greater levels of predation (44–60%) than did similar nests made with fresh water (9, 13–15%). These differences were large but not statistically significant. However, when coupled with the observations that those nests made with fresh water alone (9) were predated significantly less than the control, and that ocean water poured on the ground (8) resulted in significantly higher "depredation" rates that flags alone, these results suggest that raccoons distinguished between the scent of fresh water and the scent of ocean water. Thus, the presence of ocean water may serve as an important olfactory cue to predators, and this should be investigated further. For example, this result might be different for raccoons that routinely depredate nests of freshwater turtles, rather than those of terrapins.

Our results should reassure researchers studying reptile nests and predation rates that markers, even as conspicuous as flags, may not influence predation rates. Further, our results suggest that both surface soil excavation and turtle scent, together or separately, can be important cues for predators. Researchers that do not alter either of these factors may have little or no influence on nest predation rates.

Burke and J. Feinberg made helpful editorial suggestions.

LITERATURE CITED

CONGDON, J. D., D. W. TINKLE, G. L. BREITENBACH, AND R. C. VAN LOBEN SELS. 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingi*. Herpetologica 39:417–429.

FEINBERG, J. A., AND R. L. BURKE. 2003. Nesting ecology and predation of Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. Journal of Herpetology 37: 517–526.

MARCHAND, M. N., J. A. LIVAITIS, T. J. MAIER, AND R. M. DEGRAAF. 2002. Use of artificial nests to investigate predation of freshwater turtle nests. Wildlife Society Bulletin 30:1092–1098.

MITCHELL, J. C. AND M. W. KLEMENS. 2000. Primary and secondary effects of habitat alteration. *In* M. W. Klemens (ed.), Turtle Conservation, pp. 5–32. Smithsonian Institution Press, Washington, DC.

MROZIAK, M. L., M. SALMON, AND K. RUSENKO. 2000. Do wire cages protect sea turtles from foot traffic and mammalian predators? Chelonian Conservation Biology 3:693–698.

PATTERSON, R. 1971. The role of urination in egg predator defense in the desert tortoise (*Gopherus agassizii*). Herpetologica 27:197–199.

ROHLF, F. J., AND R. R. SOKAL. 1995. Statistical Tables. 3rd ed. W. H. Freeman and Co., New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co., New York.

TUBERVILLE, T. D., AND V. J. BURKE. 1994. Do flag markers attract turtle nest predators? Journal of Herpetology 28:514–516.

ZEVELOFF, S. I. 2002. Raccoons: A Natural History. Smithsonian Institution Press, Washington, DC.

Sex Differences in Body Size and Ectoparasite Load in the Ball Python, *Python regius*

FABIEN AUBRET,[1,2,3] XAVIER BONNET,[1,4] MATHEWS HARRIS,[4] AND STÉPHANIE MAUMELAT[1]

[1]Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France
[3]Université de Poitiers, Poitiers, France
[4]IUCN, 28 Rue Mauverney, 1196 Gland, Switzerland

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

[2] Corresponding Author. Present address: Zoology Department, University of Western Australia, 6009 Crawley, Perth, Western Australia, Australia; E-mail: aubretf@cyllene.uwa.edu.au

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℃; $N = 415$ 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 ± 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; § gravid females not included.

|	Females	Males	N	F	P
Neonates					
Snout–vent length (cm)	38.3 ± 2.7	38.3 ± 3.04	603	0.001	0.97
Tail length (cm)*	3.4 ± 0.5	3.4 ± 0.4	603	0.23	0.62
Body mass (g)	59.5 ± 9.7	58.4 ± 10.6	603	1.67	0.20
Body condition*	59.5 ± 8.2	58.3 ± 8.2	603	3.0	0.08
Jaw length (mm)*	27.6 ± 1.2	27.5 ± 1.3	487	2.5	0.11
Head width (mm)**	9.9 ± 0.5	9.8 ± 0.5	489	1.02	0.32
Skull length (mm)**	26.5 ± 1.2	26.4 ± 1.3	63	0.79	0.37
Eye diameter (mm)**	3.7 ± 0.2	3.8 ± 0.5	422	1.0	0.32
Growth in SVL (cm)*	5.7 ± 1.7	5.1 ± 1.5	106	4.0	0.048
Gain in BM (g)***	2.6 ± 2.8	1.7 ± 3.4	106	1.76	0.19
Juveniles					
Snout–vent length (cm)	72.0 ± 18.0	73.4 ± 18.4	69	0.10	0.75
Tail length (cm)*	5.7 ± 1.7	5.7 ± 1.6	68	0.09	0.76
Body mass (g)	380.4 ± 285.6	394.4 ± 276.6	67	0.04	0.84
Body condition (g)*	389.7 ± 285.6	385.59 ± 276.6	64	0.05	0.81
Jaw length (mm)*	32.8 ± 4.5	33.1 ± 5.4	43	0.54	0.47
Number of ticks*	8.1 ± 13.9	4.3 ± 8.1	55	1.98	0.16
Adults					
Snout–vent length (cm)	116.2 ± 10.3	111.3 ± 10.3	576	24.73	<0.0001
Tail length (cm)*	8.7 ± 1.1	8.6 ± 1.1	288	0.54	0.46
Body mass (g)§	1275.7 ± 359.0	1181.5 ± 333.2	327	5.93	<0.015
Body condition (g)*§	1229.4 ± 359.0	1227.8 ± 333.2	324	0.01	0.95
Jaw length (mm)*	44.3 ± 3.4	43.6 ± 3.1	286	6.68	0.01
Ventral scales	204.8 ± 3.3	201.4 ± 5.1	193	13.8	<0.001
Number of ticks*	6.7 ± 7.1	10.4 ± 10.6	267	11.3	< 0.001
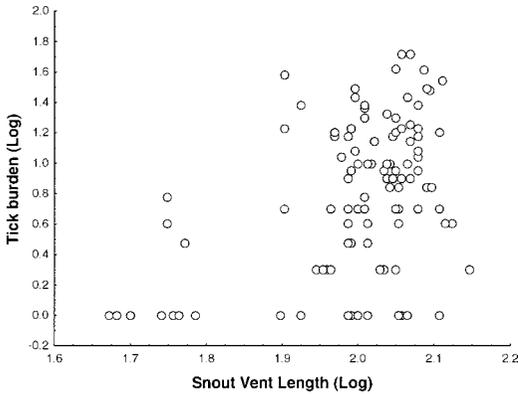
FIG. 1. Relationship between the amount of ticks and SVL in male ball pythons.

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 Kruskall 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; Reimchem, 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.

LITERATURE CITED

ANDREWS, R. M. 1982. Patterns of growth in reptiles. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia. Vol. 13, pp. 273–320. Academic Press, New York.

AUBRET, F., X. BONNET, R. SHINE, AND S. MAUMELAT. 2003. Clutch size manipulation, hatching success and offspring phenotype in the Ball Python (*Python regius*). Biological Journal of the Linnean Society 78:263–272.

BISHOP, L. A., T. M. FARRELL, AND P. G. MAY. 1996. Sexual dimorphism in a Florida population of the rattlesnake *Sistrurus miliarius*. Herpetologica 52:360–364.

BONNET, X. 1996. Gestion des réserves corporelles et stratégie de reproduction chez *Vipera aspis*. Unpubl. master's thesis, Université de Lyon I, Lyon, France.

BONNET, X., R. SHINE, G. NAULLEAU, AND M. VACHER-VALLAS. 1998. Sexual dimorphism in snakes: different roles favour different body plans. Proceedings of the Royal Society of London B Biological Sciences 265:1–5.

BONNET, X., G. NAULLEAU, AND R. SHINE. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

BONNET, X., F. LAGARDE, B. T. HENEN, J. CORBIN, K. A. NAGY, G. NAULLEAU, K. BALHOUL, O. CHASTEL, A. LEGRAND, AND R. CAMBAG. 2001. Sexual dimorphism in steppe tortoises: influence of the environment and sexual selection on body shape and mobility. Biological Journal of the Linnean Society 72:357–372.

BULL, C. M., AND D. BURZACOTT. 1993. The impact of tick load on the fitness of their lizard hosts. Oecologia 96:415–419.

BUNDY, D. A. P. 1988. Gender-dependent patterns of infection and disease. Parasitology Today 4:186–189.

BURRIDGE, M. J. 2001. Ticks (Acari : Ixodidae) spread by the international trade in reptiles and their potential roles in dissemination of diseases. Bulletin of Entomological Research 91:3–23.

CAMILLERI, C., AND R. SHINE. 1990. Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. Copeia 1990:649–658.

CAMPBELL, B. G. 1972. Sexual Selection and the Descent of Man. Aldine, Chicago.

DARWIN, C. R. 1871. The Descent of Man, and Selection in Relation to Sex. Murray, London.

FITCH, H. S. 1981. Sexual size differences in reptiles. Univ. of Kansas Museum of Natural History Miscellaneous Publications 70:1–72.

FOLSTAD, I., AND A. J. KARTER. 1992. Parasites, bright males, and the immunocompetence handicap. American Naturalist 139:603–622.

FOLSTAD, I., A. C. NILSSEN, O. HALVORSEN, AND J. ANDERSEN. 1989. Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? Oikos 55:87–92.

FORSMAN, A., AND R. SHINE. 1997. Rejection of nonadaptive hypotheses for intraspecific variation in trophic morphology in gape-limited predators. Biological Journal of the Linnean Society 62:209–223.

GRANT, P. R. 1975. The classic case of character displacement. Evolutionary Biology 8:237–337.

———. 1985. Selection on bill characters in a population of Darwin's finches in *Geospiza conirostris* on Isla Genovesa, Galapagos. Evolution 39:523–532.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.

HOUSTON, D., AND R. SHINE. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. Journal of Animal Ecology 62:737–748.

JI, X., AND P.-Y. SUN. 2000. Embryonic use of energy and post-hatching yolk in the gray rat snake, *Ptyas korros* (Colubridae). Herpetological Journal 10:13–17.

JI, X., P.-Y. SUN, S.-Y. FU, AND H.-S. ZHANG. 1997. Utilization of energy and nutrients in incubating eggs and post-hatching yolk in a colubrid snake, *Elaphe carinata*. Herpetological Journal 7:7–12.

KEIRANS, J. E. 1972. Redescription of *Amblyomma fulvum* Neumann 1899 (Acarina: Ixodidae), a parasite of the giant anaconda in northern South America. Journal of Medical Entomology 9:138–139.

KING, M. B., AND D. DUVALL. 1990. Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. Animal Behaviour 39:924–935.

KING, R. B. 1989. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? Biological Journal of the Linnean Society 38:133–154.

KING, R. B., AND J. TURMO. 1997. The effects of ecdysis on feeding frequency and behavior of the Common Garter Snake (*Thamnophis sirtalis*). Journal of Herpetology 31:310–312.

KING, R. B., T. D. BITTNER, A. QUERAL-REGIL, AND J. H. CLINE. 1999. Sexual dimorphism in neonate and adult snakes. Journal of Zoology, London 247:19–28.

O'BRIEN, R. G., AND M. K. KAISER. 1985. MANOVA method for analysing repeated measures designs: an extensive primer. Psychological Bulletin 97:316–333.

PACKARD, G. C., AND M. J. PACKARD. 1988. The physiological ecology of reptilian eggs and embryos. *In* C. Gans and R. Huey (eds.), Biology of the Reptilia. Vol. 16, pp. 524–605. Alan R. Liss, New York.

PERRY, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polyepis* (Iguania): evidence from intraspecific variation in foraging behaviour and diet. Canadian Journal of Zoology 74:1238–1245.

PLUMMER, M. V., AND N. E. MILLS. 1996. Observations on trailing and mating behaviors in Hognose Snakes (*Heterodon platirhinos*). Journal of Herpetology 30:80–82.

POULIN, R. 1996. Sexual inequalities in helminth infections: a cost of being male? American Naturalist 147:287–295.

REIMCHEN, T. E. 1980. Spine deficiency and polymorphism in a population in a population of *Gasterosteus aculeatus*: an adaptation to predators? Canadian Journal of Zoology 68:1232–1244.

REIMCHEN, T. E., AND P. NOSIL. 2001. Ecological causes of sex-biased parasitism in threespine stickleback. Biological Journal of the Linnean Society 73:51–63.

SCHNEIDER, C. C., B. ROTH, AND H. D. LEHMANN. 1971. Untersuchungen zum Parasit-Wirt-Verhaltnis der Zecke *Amblyomma testudinis* (Conil 1877). Zeitschrift fur Tropenmedizin und Parasitology 22:2–17.

SEIGEL, R. A., AND N. B. FORD. 1987. Reproductive ecology. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 210–252. MacMillan, New York.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

SHINE, R. 1977. Habitats, diet and sympatry in snakes: a study from Australia. Canadian Journal of Zoology 55:1118–1128.

———. 1978. Sexual size dimorphism and male combat in snakes. Oecologia 33:269–277.

———. 1986. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. Oecologia 69:260–267.

———. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64:419–461.

———. 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. American Naturalist 138:103–122.

———. 1993. Sexual dimorphism in snakes. *In* R. A. Seigel and J. T. Collins (eds.), Snakes: Ecology and Behavior, pp. 49–86. McGraw-Hill, New York.

———. 1994. Sexual size dimorphism in snakes revisited. Copeia 1994:326–346.

SHINE, R., AND D. CREWS. 1988. Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. Evolution 42:622–630.

SHINE, R., AND P. HARLOW. 1996 Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. Ecology 77:1808–1817.

SHINE R., T. MADSEN, M. ELPHICK, AND P. S. HARLOW. 1997. The influence of nest temperatures and maternal brooding on hatchling phenotypes in water pythons. Ecology 78:1713–1721.

SHINE R., P. S. HARLOW, J. S. KEOGH, AND BOEADI. 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. Functional Ecology 1998:248–258.

SLATKIN, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.

SLIP, D. J., AND R. SHINE. 1988. The reproductive biology and mating system of Diamond Pythons, *Morelia spilota* (Serpentes: Boidae). Herpetologica 44:396–404.

STAMPS, J. A. 1993. Sexual size dimorphism in species with asymptotic growth after maturity. Biological Journal of the Linnean Society 50:123–145.

TERENIUS, O., H. A. MEJLON, AND T. G. T. JAENSON. 2000. New and earlier records of ticks (Acari : Ixodidae, Argasidae) from Guinea-Bissau. Journal of Medical Entomology 37:973–976.

TINSLEY, R. C. 1989. The effects of host sex on transmission success. Parasitology Today 5:190–195.

TRIVERS, R. L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–269.

VORIS, H. K., AND H. H. VORIS. 1983. Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioral, and ecological relationships. American Zoologist 23:411–426.

WADE, G. N. 1976. Sex hormones, regulatory behavior, and body weight. Advances in the Study of Behavior 6:201–279.

WEATHERHEAD, P. J., F. E. BARRY, G. P. BROWN, AND M. R. FORBES. 1995. Sex ratios, mating behavior and sexual size dimorphism of the Northern Water Snake, *Nerodia sipedon*. Behavioral Ecology and Sociobiology 36:301–311.

WIKELSKI, M. 1999. Influences of parasites and thermoregulation on grouping tendencies in marine iguanas. Behavioral Ecology 10:22–29.

ZUK, M. 1990. Reproductive strategies and disease susceptibility: an evolutionary viewpoint. Parasitology Today 6:231–233.