Copeia, 2005(1), pp. 196–200

Defensive Behavior of Free-Ranging Pygmy Rattlesnakes (*Sistrurus miliarius*)

Xavier Glaudas, Terence M. Farrell, and Peter G. May

Sistrurus miliarius **frequently bites humans in the southeastern United States. We used a large population of** ***S. miliarius*** **in central Florida to investigate the importance of several factors on the defensive behavior of this species. Upon detection of a snake, we tapped the snout of the snake with a gloved hand. We recorded whether the snake struck or fled. Our large sample size ($N = 336$) allowed us to make strong conclusions regarding the defensive behavior of this rattlesnake species. Overall, only 27 snakes (8%) bit the glove indicating that this species is rather nonaggressive. Initial posture was the only factor that influenced striking behavior; uncoiled snakes struck significantly more than coiled snakes. Fleeing behavior was affected by three variables: sex; whether the snake was about to shed; and initial posture. Females fled more often than males, as did snakes about to shed. Initial posture is the only factor that affected both response variables, and uncoiled individuals were more likely to flee than coiled snakes.**

Snakes have evolved some of the most elaborate and diverse antipredator mechanisms among reptiles (Greene, 1988). This diversity of antipredator behaviors, combined with the fact that venomous snakes are responsible for approximately 30,000–40,000 human deaths worldwide per year (Russell, 1983), has resulted in increased attention to defensive behaviors of snakes.

Increasing human pressure on the environment, through habitat destruction and fragmentation, and development of outdoor recreation have increased interactions between humans and certain species of animals (Aune, 1991; Lammers et al., 2000). Venomous snakes are among the few species of animals that pose a direct threat to humans. As a result, rattlesnakes have suffered from a reputation of being aggressive and vicious creatures (Klauber, 1972).

Factors that affect the defensive response of reptiles can be partitioned into intrinsic and extrinsic factors. Intrinsic factors to the organism, such as body temperature (Keogh and DeSerto, 1984; Layne and Ford, 1984; Goode and Duvall, 1989), size (Hailey and Davies, 1986; Whitaker and Shine, 1999), sex (Scudder and Burghardt, 1983), recent feeding (Herzog and Bailey, 1987), and experience (Glaudas, 2004) have all been found to affect snake defensive behavior. Extrinsic factors have received less attention. Gibbons and Dorcas (2002) revealed that threat severity was the major element in releasing a striking response in Cottonmouths (*Agkistrodon piscivorus*), and Shine et al. (2002) found that the location of the snakes influenced defensive behaviors.

Field experiments on the defensive behavior of venomous snakes are rare primarily because such studies are logistically difficult (Shine et al., 2002). However, areas with high population densities of venomous snakes provide an opportunity to examine defensive behavior pattern in free-ranging snakes. Our study organism, *Sistrurus miliarius*, occurs at very high density in central Florida. It has been described as fiery and irritable (Allen and Neill, 1950) and is responsible for many snakebites in Florida (Minton, 1987). We took advantage of a large population of *S. miliarius* to obtain adequate sample size and investigate the influence of several factors on the defensive behavior of this species. We determined whether the location of the snake, body size, sex, reproductive condition of mature females, initial posture; whether the snake had an obvious prey item in its gut; and whether the snake was about to shed influenced defensive behavior. The purpose of this study was to investigate whether this snake deserves its aggressive reputation and to determine the factors that influenced snake behavior with the goal of elucidating the adaptive significance of defensive behavior patterns in this small species of rattlesnake.

Materials and Methods

Study organism.—*Sistrurus miliarius* may be the smallest rattlesnake (typically 40–55 cm total body length; Ernst and Ernst, 2003). In the study population, snakes were active year-round with peaks of activity in March through April and September through November. Snakes in the study population feed mostly on lizards (*An-*

olis carolinensis, *Eumeces inexpectatus*, *Scincella lateralis*) and frogs (*Hyla* spp., *Rana utricularia*) and, in turn, are probably consumed by a variety of snakes (e.g., *Coluber constrictor*), carnivorous mammals (e.g., *Lynx rufus*, *Procyon lotor*), and birds of prey (e.g., *Buteo lineatus*, *Strix varia*; Farrell et al., 1995; May et al. 1996).

Study site.—The study site was an 8-ha semideciduous woodland located in Volusia County, Florida. Behavioral experiments were conducted in wet hammock and pine flatwoods habitats. The site was surrounded by a freshwater marsh adjacent to the Saint John's River. Sabal palm (*Sabal palmetto*), live oak (*Quercus virginianus*), and red bay (*Persea borbonia*) were the dominant vegetation (May et al., 1996).

Testing procedures.—We collected data two or three times a week from January 1993 to October 1995. Snakes were found visually by searching the study site on foot. Upon detection, one of us approached the rattlesnake, gently tapped it on the snout with a gloved hand and recorded whether the snake fled, rattled, or struck. A prior study found that a human hand elicits high levels of antipredator behavior (Herzog et al., 1989).

We recorded data on each of the following variables: location of the snake (on the ground vs above the ground on vegetation); snout–vent length (SVL); sex; reproductive condition of mature females; initial posture (coiled vs uncoiled); whether the snake had an obvious prey item in its gut; and whether the snake was about to shed (as indicated by cloudy eye). We later removed the rattling response variable from the analysis because very few snakes rattled (pers. obs.; Rowe at al., 2002). In our analysis, we used only data from a single encounter for each snake. Rattlesnakes that were large enough were PIT-tagged (typically around one year of age) to allow identifications of individuals. Because young-of-year snakes were too small to be PIT-tagged, we randomly selected 40 young-of-year snakes from available data so as to have representation of all size classes. Therefore, a single young may have been included twice in the analysis even though this was not likely to happen given the large size of the population.

After behavioral testing as above, we recorded PIT-tag number if any, size (SVL using a squeeze box), body temperature (using a thermocouple wire thermometer HH508 Digital thermometer Type K, Omega™), sex (using a cloacal probe), mass (using a spring scale), and reproductive condition and presence of prey (by palpating the ventral region). Even though small prey items may have been overlooked, we wanted to detect large prey items that were more likely to have an impact on locomotory abilities. Snakes were processed in the field immediately after the trial and released where they were found.

Statistical analysis.—We analyzed our data using multiple logistic regression analyses (MLR). Because we only had body temperature data for 128 rattlesnakes, we first ran a MLR including body temperature. However, this variable had no effect on striking ($\chi^2 = 0$, 1 df, $P < 0.94$) and fleeing ($\chi^2 = 2.75$, 1 df, $P < 0.1$). Thus, we decided to drop it from further analysis and used our larger dataset ($N = 336$). This enabled us to substantially increase our sample size and, thus, make stronger conclusions. In this analysis, all variables (except SVL, as well as body temperature in the earlier analysis, which were continuous variables) were nominal variables. All variables were entered simultaneously. We ran separate analyses for the two dependent variables (striking and fleeing). Because pregnancy results in the same physical constraints on a snake locomotion as a recent meal would (Shine et al., 2002), we combined both variables into one. We used the statistical package JMP for all statistical analyses (SAS Institute, Inc., Cary, NC).

Results

Most of the *S. miliarius* did not react to our approach and test. Of the 336 different snakes tested over the course of this study, 255 (75.9%) did not strike or flee when threatened. They usually remained in the position where found and did not visibly respond to our stimuli. Another 54 (16.1%) fled but did not strike, 13 (3.9%) struck and fled, and 14 (4.1%) struck but did not flee. Only 27 rattlesnakes (8%) struck after being provoked.

The MLR showed that the fleeing and striking responses were differently affected by the factors we considered. Striking was only affected by the initial posture of the snake: 17% of the uncoiled snakes struck at us compared to only 5% of the coiled rattlesnakes ($\chi^2 = 5.05$, 1 df, $P < 0.02$).

Fleeing was affected by three factors: sex; whether the snake was about to enter eccdysis; and initial posture. Sex was the most influential factor ($\chi^2 = 9.82$, 1 df, $P < 0.001$): 26% of females fled from our approach, whereas only 13% of males did so. Using the snakes for which we had body temperature data showed that there was no sex difference in body temperature (one-way ANOVA, $F_{1,126} = 0.34$, $P = 0.55$).

However, a one-way ANOVA with SVL as the dependent variable revealed that females were larger than males ($F_{1,134} = 4.78$, $P < 0.03$). Whether the snake was about to enter eccdysis (^{2} = 8.67, 1 df, $P < 0.003$) was also statistically significant. More snakes about to shed fled (28%) than snakes that were not about to enter eccdysis (18%). Finally, the initial posture was important in determining whether a snake would flee from us ($\chi^2 = 6.94$, 1 df, $P < 0.008$). Uncoiled snakes fled more often (35%) than coiled snakes (16%).

Discussion

Our results indicate that the species is not highly aggressive, as previously concluded for other species of venomous snakes (*Sistrurus catenatus*; Prior and Weatherhead, 1994; *Pseudonaja textilis*; Whitaker and Shine, 1999; *Agkistrodon piscivorus*; Gibbons and Dorcas, 2002; *Gloydius shedaoensis*; Shine et al., 2002). These findings suggest that venomous snakes are typically reluctant to strike in encounters with humans and support the suggestion that venom is primarily an offensive weapon used to subdue and predigest prey (Pough, 1979). Presumably, the costs of defensive striking generally outweigh the benefits for venomous snakes (Hayes et al., 2002).

The initial posture of the snake (uncoiled vs coiled) was the only variable that significantly affected the striking response of *S. miliarius*. The increased likelihood of detection and higher vulnerability to attack may cause selection for more active defensive responses in uncoiled snakes. To humans, crypsis in *S. miliarius* is less effective when a snake is stretched out and moving. The reputation for aggressive defense responses by *S. miliarius* may result from causal observers whom are more likely to find individuals of this small cryptic species when they are moving. *Sistrurus miliarius* is much more likely to respond defensively when it is encountered stretched out on open trail or road than when coiled in its typical foraging posture.

Three of the six independent variables we tested (i.e., sex, whether the snake was about to shed, and initial posture) had an influence on the snakes' fleeing response. The difference in defensive behavior among sexes suggests that females are behaviorally different to some extent. Differences in defensive behavior among sexes may be expected if males and females are morphologically or ecologically different, and has been reported for the sexually dimorphic Southern Watersnake (*Nerodia fasciata*; Scudder and Burghardt, 1983) and Common Gartersnake (*Thamnophis sirtalis*; Shine et al., 2000). Male and female *S. miliarius*, however, exhibit almost no sexual dimorphism (Bishop et al., 1996). Snakes that were about to shed also showed a higher propensity to flee. Perhaps, these snakes have impaired vision, which makes them more vulnerable to attack. In many species, snakes approaching eccdysis may remain closer to refuges and as a result may flee more often. Unfortunately, we have no data on the proximity of refuges that would allow us to test this idea. Whether the snake was moving when first discovered also influenced snake behavior. It has been suggested that moving snakes would flee in response to a predator because crypsis would be less efficient (Arnold and Bennett, 1984). Also, movement elicits prey attack in many predators (Shine and Sun, 2003). In our experiment, uncoiled snakes were generally moving when first discovered, thus providing this cue to potential predators. However, coiled snakes may benefit from remaining stationary by not providing a stimulus to attack to predators.

We did not detect any significant effect of other tested variables (i.e., location of the snake, reproductive condition/recent feeding, and SVL) on the overall defensive behavior of *S. miliarius*. Nevertheless, similar field studies made on other snake species have shown that pregnancy (Kissner et al., 1997), location of snake (Shine at al., 2002), and body size (Shine et al., 2003) can be clear determinants of defensive behavior in other species of snakes. This diversity of defensive behavior among species, either because of genetically driven behaviors or as a result of different ecological contexts (Shine et al., 2003) appears to be complex and may prevent the formulation of simple generalities.

Acknowledgments

We would like to thank J. W. Gibbons, L. A. Fedewa, R. N. Reed, M. E. Dorcas, and J. Van Dyke for providing useful comments on the manuscript and C. Bennington for statistical advice. This study was completed as a part of a master's thesis (XG) at the University of Georgia. Manuscript preparation was aided by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through the Financial Assistant Award DE-FC09–96SR18546 to the University of Georgia Research Foundation. Authorization to conduct this research was given by the U.S. Fish and Wildlife Special Use Permit 41550–3 (issued by

Lake Woodruff National Wildlife Refuge). No animal use protocol was required by Stetson University at the time the study was conducted.

Literature Cited

Allen, E. R., and W. T. Neill. 1950. The Pigmy Rattlesnake. Fla. Wildl. 5:10–11.

Arnold, S. J., and A. F. Bennett. 1984. Behavioural variation in natural populations. III. Antipredator displays in the Garter Snake *Thamnophis radix.* Anim. Behav. 32:1108–1118.

Aune, K. E. 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana, p. 86–94. *In:* Mountain lion–human interaction, symposium and workshop. C. E. Braun (ed.). Colorado Division of Wildlife, Denver.

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.

Ernst, C. H., and E. M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Institution Press, Washington, DC.

Farrell, T. M., P. G. May, and M. A. Pilgrim. 1995. Reproduction in the Dusky Pigmy Rattlesnake, *Sistrurus miliarius barbouri,* in central Florida. J. Herpetol. 29:21–27.

Gibbons, J. W., and M. E. Dorcas. 2002. Defensive behavior of Cottonmouths (*Agkistrodon piscivorus*) toward humans. Copeia 2002:195–198.

Glaudas, X. 2004. Do Cottonmouths (*Agkistrodon piscivorus*) habituate to human confrontations? Southeast. Nat. 3:129–138.

Goode, M. J., and D. Duvall. 1989. Body temperature and defensive behaviour of free-ranging Prairie Rattlesnakes, *Crotalus viridis viridis.* Anim. Behav. 38:360–362.

Greene, H. W. 1988. Antipredator mechanisms in reptiles, p. 1–152. *In:* Biology of the Reptilia. Vol. 16. C. Gans and R. B. Huey (eds.). Alan R. Liss, New York.

Hailey, A., and P. M. C. Davies. 1986. Effects of size, sex, temperature, and condition on activity metabolism and defence behaviour of the viperine snake, *Natrix maura.* J. Zool., Lond. (A) 208:541–558.

Hayes, W. K., S. S. Herbert, G. C. Rehling, and J. F. Gennaro. 2002. Factors that influence venom expenditure in viperids and other snake species during predatory and defensive contexts, p. 207–233. *In:* Biology of the vipers. G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.). Eagle Mountain Publ., Eagle Mountain, UT.

Herzog Jr., H. A., and B. D. Bailey. 1987. Development of antipredator responses in snakes. II. Effects of recent feeding on defensive behaviors of juvenile Garter Snakes (*Thamnophis sirtalis*). J. Comp. Psych. 100:233–242.

———, B. B. Bowers, and G. M. Burghardt. 1989. Stimulus control of antipredator behavior in newborn and juvenile garter snakes (*Thamnophis*). J. Comp. Psych. 103:233–242.

Keogh, J. S., and F. P. DeSerto. 1994. Temperature dependent defensive behavior in three species of North American colubrid snakes. J. Herpetol. 28: 258–261.

Kissner, K. B., M. R. Forbes, and D. M. Secoy. 1997. Rattling behavior of Prairie Rattlesnakes (*Crotalus viridis viridis,* Viperidae) in relation to sex, reproductive status, body size, and body temperature. Ethology 103:1042–1050.

Klauber, L. M. 1972. Rattlesnakes: their habits, life histories, and influence on mankind. Univ. of California Press, Los Angeles.

Lammers, M. O., M. Hapner, and D. Lanyard. 2000. Occurrence and behavior of Hawaiian Spinner Dolphins (*Stenella longirostris*) along leeward and south O'ahu: implications for conservation and management. Pac. Sci. 54:95–96.

Layne, J. R., and N. B. Ford. 1984. Flight distance of the Queen Snake, *Regina septemvittata.* J. Herpetol. 18:496–498.

May, P. G., T. M. Farrell, S. T. Heulett, M. A. Pilgrim, L. A. Bishop, D. J. Spence, A. M. Rabatsky, M. G. Campbell, A. D. Aycrigg, and W. E. Richardson II. 1996. Seasonal abundance and activity of a rattlesnake (*Sistrurus miliarius barbouri*) in central Florida. Copeia 1996:389–401.

Minton, S. A. 1987. Poisonous snakes and snakebite in the U.S.: a brief review. Northwest Sci. 61:130–137.

Pough, F. H. 1979. The effect of rattlesnake venom on digestion of prey. Toxicon 17:221–228.

Prior, K. A., and P. J. Weatherhead. 1994. Response of free-ranging eastern massasauga rattlesnakes to human disturbance. J. Herpetol. 28:255–257.

Rowe, M. P., T. M. Farrell, and P. G. May. 2002. Rattle loss in Pigmy Rattlesnakes (*Sistrurus miliarius*): causes, consequences, and implications for rattle function and evolution, p. 385–404. *In:* Biology of the vipers. G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.). Eagle Mountain Publ., Eagle Mountain, UT.

Russell, F. E. 1983. Snake venom poisoning. Scholium International, Inc., New York.

Scudder, R. M., and G. M. Burghardt. 1983. A comparative study of defensive behavior in three sympatric species of water snakes (*Nerodia*). Z. Tierpsychol. 63:17–26.

Shine, R., and L.-X. Sun. 2003. Attack strategy of an ambush predator: which attributes of the prey trigger a pit-viper's strike? Funct. Ecol. 17:340–348.

———, M. M. Olsson, M. P. Lemaster, I. T. Moore, and R. T. Mason. 2000. Effect of sex, body size, temperature, and location on the antipredator tactic of free-ranging gartersnakes (*Thamnophis sirtalis,* Colubridae). Behav. Ecol. 11:239–245.

———, ———, M. Fitzgerald, and M. Kearney. 2002. Antipredator responses of free-ranging pitvipers (*Gloydius shedaoensis,* Viperidae). Copeia 2002: 843–850.

———, X. Bonnet, and H. G. Cogger. 2003. Antipredator tactics of amphibious sea-snakes (Serpentes, Laticaudidae). Ethology 109:533–542.

Whitaker, P. B., and R. Shine. 1999. Responses of free-ranging brownsnakes (*Pseudonaja textilis*: Elapidae) to encounters with humans. Wildl. Res. 26: 689–704.

(XG) University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802; and (TMF, PGM) Department of biology, Stetson University, DeLand, Florida 32720. Present address: (XG) Department of Biological Sciences, University of Nevada, 4505 Maryland Parkway, Las Vegas, Nevada 89154-4009. E-mail: (XG) glaudasx@unlv.nevada.edu. Send reprint requests to XG. Submitted: 27 Oct. 2003. Accepted: 28 Oct. 2004. Section editor: T. W. Reeder.