LITERATURE CITED

ANDREWS, R. M. 1982. Patterns of growth in reptiles. *In* C. Gans, and F. H. Pough (eds.), Biology of the Reptilia, Vol. 3, pp. 273–320. Academic Press, New York.

DOBSON, A. P., AND P. J. HUDSON. 1995. Microparasites: observed patterns in wild animal populations. *In* B. T. Grenfell and A. P. Dobson (eds.), Ecology of Infectious Diseases in Natural Populations, pp. 52–89. Cambridge Univ. Press, Cambridge.

DUNLAP, K. D., AND T. MATHIES. 1993. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. Copeia 1993:1045–1048.

———, AND J. J. SCHALL. 1995. Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. Physiol. Zool. 68: 608–621.

GULLAND, F. M. D. 1995. The impact of infectious disease on wild animal populations—a review. *In* B. T. Grenfell and A. P. Dobson (eds.), Ecology of Infectious Diseases in Natural Populations, pp. 20–51. Cambridge Univ. Press, Cambridge.

HUDSON, P. J., A. P. DOBSON, AND D. NEWBORN. 1998. Prevention of population cycles by parasite removal. Science 282:2256–2258.

REAGAN, D. P. 1996. Anoline lizards. *In* D. P. Reagan and R. B. Waide (eds.), The Food Web of a Tropical Rain Forest, pp. 321–345. Univ. Chicago Press, Chicago, Illinois.

———, AND R. B. WAIDE (eds.). 1996. The Food Web of a Tropical Rain Forest. Univ. Chicago Press, Chicago, Illinois.

ROUGHGARDEN, J. 1995. *Anolis* Lizards of the Caribbean: Ecology, Evolution and Plate Tectonics. Oxford Univ. Press, New York.

SCHALL, J. J. 1983. Lizard malaria: cost to vertebrate host's reproductive success. Parasitology 87:1–6.

———. 1990. Virulence of lizard malaria: the evolutionary ecology of an ancient parasite-host association. Parasitology 100:S35–S52.

———. 1992. Parasite-mediated competition in *Anolis* lizards. Oecologia 92:64–68.

———. 1996. Malarial parasites of lizards: diversity and ecology. Adv. Parasit. 37:255–333.

———, AND G. A. SARNI. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. Copeia 1987:84–93.

———, AND S. P. VOGT. 1993. Distribution of malaria in *Anolis* lizards of the Luquillo Forest, Puerto Rico: implications for host community ecology. Biotropica 25:229–235.

———, A. R. PEARSON, AND S. L. PERKINS. 2000a. Prevalence of malaria parasites (*Plasmodium floridense* and *Plasmodium azurophilum*) infecting a Puerto Rican lizard (*Anolis gundlachi*): a nine year study. J. Parasitol. 86:511–515.

———, H. R. PRENDEVILLE, AND K. A. HANLEY. 2000b. Prevalence of the tick, *Ixodes pacificus*, on western fence lizards, *Sceloporus occidentalis*: trends by gender, size, season, site, and mite infestation. J. Herpetol. 34:160–163.

STAATS, C. M., AND J. J. SCHALL. 1996. Malarial parasites (*Plasmodium*) of *Anolis* lizards: biogeography in the Lesser Antilles. Biotropica 28:388–393.

VAN SLYS, M. 1998. Growth and body condition of the saxicolous lizard *Tropicurus itambere* in southeastern Brazil. J. Herpetol. 32:359–365.

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Sexual Dimorphism in Malodorousness of Musk Secretions of Snakes

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Sexual dimorphism is a widespread phenomenon among animals (Darwin, 1871; Andersson, 1994). Differences between the sexes come in many forms, including both morphology (e.g., size, shape, coloration) and behavior (e.g., risk-taking or defensive behavior). Sexual differences in physiology also occur, with the best known examples being hormonal differences associated with reproduction. Sexual dimorphism also may take other forms, and here we report on sexual differences in the odor of musk secretions produced by two species of snakes.

Snakes produce musk in cloacal glands at the base of their tails. Snake musk is assumed to have a defensive function because it is malodorous and is commonly secreted when a snake is captured or disturbed both within and outside the breeding season (Whiting, 1969; Greene, 1997). We had several reasons to think that the odor of musk might differ between males and females. First, Kissner et al. (1998a) found female-biased sexual dimorphism in cloacal gland size in plains garter snakes (*Thamnophis radix*) that did not appear to be a result of male gland size being constrained due to the hemipenes sharing space in the tail with the glands. They suggested that this difference may be a consequence of females relying more than males on musk secretions for defense from predators. Second, other studies of reptiles have shown that gravid female reptiles typically use defensive behaviors other than flight more than nongravid females or males, presumably because carrying eggs or embryos impairs movement (e.g., Bauwens and Thoen, 1981; Seigel et al., 1987; Schwarzkopf and Shine, 1992; Kissner et al., 1998b). Hence, females may rely on musk secretion in defense more than males, leading to differences in the quantity or the quality of the musk they produce. Third, Oldak (1976) found a difference in the composition of musk of male and female garter snakes (*Thamnophis elegans*), although he

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found no difference for *T. sirtalis*. Finally, our subjective impression from working with several species of snakes was that musk of females often seemed to smell worse than that of males.

If females do produce a more malodorous musk, this could simply be a consequence of females producing larger volumes of musk because they have larger glands. Alternatively, the same selection pressure that has favored larger cloacal glands in females also may have favored the production of more malodorous musk. As a first step to examining whether selection has favored the production of more malodorous musk in female snakes than in male snakes, we used human test subjects to assess whether musk from female snakes was more offensive in odor than musk from males. We assumed that if humans, with their relatively dull sense of smell, found a difference in odor between male and female musk, then predators with a more acute sense of smell should certainly detect the difference.

We used black rat snakes (*Elaphe obsoleta*) and eastern garter snakes (*T. sirtalis*) for this experiment simply because both species were subjects of our current research. We conducted a double-blind experiment. One experimenter prepared pairs of cotton swabs with musk secretions from one male and one female of the same species. We used 10 pairs of swabs with musk from black rat snakes and 10 pairs of swabs with musk from eastern garter snakes. The snakes in each pair were selected randomly from among a group of snakes recently captured in the wild and each individual was only used once. We conducted this experiment in early May before females should have ovulated, so that we could not assess whether females were reproductive. Musk was obtained by palpating the base of the tail. Care was taken to apply the same quantity of musk (estimated visually) to each pair of swabs in a given trial. The swabs were labeled "one" or "two", with numbers assigned randomly by sex. All swabs were prepared just prior to their presentation to the observers.

Once a pair of swabs was prepared they were given to a second experimenter who was unaware of which swab corresponded to which sex. Odor testing was done by 10 volunteer university students who were part of a snake ecology field course. These observers were unaware of the goal of our study and were told only that they were smelling musk secretions of snakes, with the goal of determining which swab in a pair was more offensive. We randomly divided the observers into two panels of five, with each panel used in alternate trials. For a given trial the pair of swabs was presented to each panel member individually (i.e., five observers per trial), with the sequence of panel members determined randomly for each trial. Each panel member was asked to identify (by pointing to it) which swab smelled more offensive and the experimenter recorded which swab was chosen. Because the swab numbers were concealed from the panel members, and the order of presentation of the two swabs to successive panel members was randomized, choices by panel members within a trial were independent. All trials were conducted out of doors and out of sight and hearing of other panel members. All trials were conducted over the course of several hours on one day.

After completion of the experiment, we scored which sex in a given trial had the more offensive musk. Because five observers smelled the swabs in each trial, the sex judged as having the most offensive musk was that chosen by three or more observers. We used the binomial test (Zar, 1984) to determine whether musk from females was chosen as smelling more offensive across all the trials more often than expected by chance. Significance of tests was assessed at alpha = 0.05.

For black rat snakes, the musk of females was chosen as more malodorous in nine of 10 trials. This result differed significantly from that expected by chance ($N = 10$, $P = 0.01$). For eastern garter snakes, the musk of females was chosen as more malodorous in 8 of 10 trials. Again, this result differed significantly from that expected by chance ($N = 10$, $P = 0.05$). Overall, the musk of females was chosen as more offensive in 85% of the trials. We also examined how consistent observers were in choosing the musk of females as more offensive (scored as identifying the female sample in the majority of the trials). Of 10 observers, nine were consistent in choosing female musk as more malodorous for both black rat snakes ($P = 0.01$) and eastern garter snakes ($P = 0.01$). The one exception in both cases was not the same observer.

We demonstrated that human observers found the musk produced by female garter snakes and female black rat snakes more malodorous than that produced by conspecific males. Because we were careful to use similar volumes of musk in our trials, we are confident that this difference was a consequence of differences in composition of male and female musk. Given that humans could distinguish this difference, it seems likely that many animals that prey on snakes should also recognize the difference. However, does a difference in malodorousness mean that a predator would be less likely to attack a female snake? Price and LaPointe (1981) presented mammalian predators of king snakes (*Lampropeltis getulus*) with food that was either treated or untreated with the snakes' musk. They found that some predators approached treated food more warily, refused to eat the treated food, or ate the treated food only after they had eaten the untreated food. These results suggest that the odor of musk has some deterrent effect, even if it is only to delay an attack. We now require experiments with real predators to determine whether they can distinguish between male and female musk and whether they behave differently as a consequence. Studies on the biochemical composition of musk secretions to determine whether the chemicals or concentrations of chemicals differ between the sexes are also needed.

If having more malodorous musk does confer some advantage in decreasing predation risk, why do males and females apparently not take equal advantage of this benefit? The answer may lie in sex differences in reliance on musk for protection. Kissner et al. (1998b) found that gravid female prairie rattlesnakes (*Crotalus viridis*) allowed closer approach by human observers than did males, similar to previous observations for lizards (Bauwens and Thoen, 1981; Schwarzkopf and Shine, 1992). If gravid females rely more on cryptic behavior to avoid predators, they would have to rely more on musk when crypsis fails. Sexual dimorphism in the size of cloacal glands (Kissner et al., 1998a) suggests that females invest more than males in the

amount of musk they produce, so dimorphism in odor may indicate that females also invest more in the quality of the musk they produce. Implicit in this hypothesis is that production of more malodorous musk involves non-trivial physiological costs.

Differences between the two species we studied suggest several possible insights into musk production. First, black rat snakes are oviparous and eastern garter snakes are viviparous. Because females of viviparous species are burdened with carrying a clutch of young for longer than oviparous females, one might expect that female garter snakes would rely more on musk for protection. However, the similarity of our results for the two species suggests that carrying a clutch for even a short time is sufficient to favor production of more malodorous musk. Second, female garter snakes generally reproduce every year, whereas female black rat snakes reproduce every other year on average (Blouin-Demers, unpubl. data). Thus, some of the female rat snakes we used were unlikely to have been reproductive. Nonetheless, sex differences were equally detectable in the two species, suggesting that female rat snakes produced more malodorous musk than males even when not reproductive. However, our panelists were only unanimous in declaring females more malodorous in some trials, while in other trials the difference was less clear cut. Furthermore, when interviewed after the experiment, panelists were unambiguous in declaring the musk of some individual snakes to have been much more unpleasant than that of others. Thus, individual snakes may vary their investment in musk according to their individual circumstances. Similarly, differences in predation risk among populations of the same species might produce different patterns of musk production, which might explain why we found a sex difference in musk odor in garter snakes, while Oldak (1976) found no sex differences in musk composition in this species. Increasing our understanding of the factors that affect variation in musk production in snakes might provide important insights into other aspects of snake ecology.

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Literature Cited

Andersson, M. B. 1994. Sexual Selection. Princeton Univ. Press, Princeton, New Jersey.

Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. 50:733–734.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. Appelton, New York.

Greene, H. 1997. Snakes: The Evolution of Mystery in Nature. Univ. California Press, Berkeley.

Kissner, K. J., M. R. Forbes, and D. M. Secoy. 1998a. Sexual dimorphism in size of cloacal glands of the garter snake, *Thamnophis radix haydeni*. J. Herpetol. 32:268–270.

———, D. M. Secoy, M. R. Forbes. 1998b. Rattling behavior of prairie rattlesnakes (*Crotalus viridis viridis*, Viperidae) in relation to sex, reproductive status, body size, and body temperature. Ethology 103:1042–1050.

Oldak, P. D. 1976. Comparison of the scent glands secretion lipids of twenty-five snakes: implications for biochemical systematics. Copeia 1976:320–326.

Price, A. H., and J. L. LaPointe. 1981. Structure-functional aspects of the scent gland in *Lampropeltis getulus splendida*. Copeia 1981:138–146.

Schwarzkopf, L., and R. Shine. 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. Behav. Ecol. Sociobiol. 31:17–25.

Seigel, R. A., M. M. Huggins, and N. B. Ford. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. Oecologia 73:481–485.

Whiting, A. M. 1969. Squamate cloacal glands: morphology, histology and histochemistry. Unpubl. Ph.D. Thesis, Pennsylvania State Univ., Station College.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, California.

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