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SMALL-SCALE GEOGRAPHIC VARIATION IN ANTIPREDATOR TACTICS OF GARTER SNAKES

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ABSTRACT: Garter snakes (*Thamnophis sirtalis parietalis*) in Manitoba court and mate at communal overwintering dens and then disperse to feeding ranges in summer. The restriction of mating activities to den areas may reduce gene flow between populations from adjacent dens, in turn allowing divergence in traits such as antipredator behavior. We quantified responses of adult male snakes to the approach of human observers at four dens, prior to dispersal in late spring. Larger snakes bit us more frequently than did smaller individuals, at all four dens. Although some of the dens were <20 km apart (and hence, individuals from each would likely encounter each other during summer), we found strong geographic differences in antipredator tactics (approach distance and propensity to bite). These differences may reflect genetic isolation of den populations, due in turn to den-based mating and philopatry. However, to rule out alternative explanations such as learned responses to different predation exposure, studies are needed on naïve snakes.

Key words: Canada; Metapopulation; Natricine; *Thamnophis sirtalis*

PREDATION is a major selective force on many kinds of organisms and has resulted in the evolution of complex morphological, ecological, and behavioral traits to reduce vulnerability (e.g., Lima and Dill, 1990; Vermeij, 1982). Thus, geographic variation in such selective forces within the range of a single wide-ranging species has the potential to generate local geographic variation in antipredator adaptations. Although intraspecific geographic variation in antipredator tactics has indeed been described (Farr, 1975; Foster and Endler, 1999), the evolution of intraspecific variation is constrained by gene flow. Thus, populations that frequently interbreed will tend to display similar gene frequencies over wide areas, even in the face of spatially heterogeneous selective forces (e.g., King,

1993; Storfer et al., 1999). Local divergence in antipredator tactics will evolve most easily in a species in which local populations constitute genetically separate entities.

Some of the best examples of the effects of gene flow on the geographic differentiation of antipredator behavior come from cases where interbreeding among populations constrains local adaptation. For example, the streamside salamander *Ambystoma barbouri* occupies heterogeneous habitats with conflicting selection pressures on antipredator tactics (Storfer and Sih, 1998). Some streams are ephemeral (so larvae should be active to feed and metamorphose before stream drying), whereas other streams are more permanent and contain pools with predatory fish (where larvae should remain inactive to avoid fish predation). The behavior of salamanders largely conforms to these predictions, but larvae from fish-exposed

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populations more isolated from fishless populations showed stronger antipredator responses than did larvae from less isolated populations (Storfer and Sih, 1998).

Thus, geographic variation in antipredator tactics at small spatial scales is most likely in taxa with restricted gene flow among local populations. In turn, the extent of gene flow will depend upon mating systems, and especially the degree to which individuals from consistent and discrete subpopulations remain in the vicinity of their overwintering dens during the mating season. North American garter snakes (*Thamnophis* spp.) provide an interesting model system in this regard. Especially in the colder, northern parts of their range, garter snakes overwinter in large communal dens and mate prior to dispersing to their summer ranges (Gregory 1974, 1977; Rossman et al., 1996). Thus, each den population will be reproductively isolated, to some degree, from neighboring populations (Gregory, 1977; Shine et al., 2001a). Perhaps reflecting this metapopulation structure, several authors have reported significant geographic variation in garter snake behavior (e.g., feeding preferences: Arnold 1981; Burghardt, 1970), including antipredator tactics. For example, Herzog and Schwartz (1990) compared antipredator behavior of neonatal *Thamnophis sirtalis* from Michigan with conspecifics from Wisconsin, which is 540 km away. Neonatal snakes from the two areas differed substantially in their tendency to strike at a threat stimulus, mirroring similar differences observed in adults from the same populations. Adult *Thamnophis elegans* also display geographic variation in antipredator tactics (unpublished study by K. de Quieroz 1992, cited in Burghardt and Schwartz, 1999). Such studies typically have compared animals from widely separated localities, but we have found a striking level of behavioral differences even between populations so close together that individuals from each would almost certainly encounter each other outside the breeding season.

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are a northern subspecies of the widely distributed common garter snake (*T. sirtalis*; Rossman et al., 1996). In the severely cold climate of central Manitoba's Interlake district, these small (<1 m) non-venomous snakes spend 8 mo each year

inactive in large communal hibernacula. They mate at the den immediately after emerging from the ground in spring, and then disperse up to 20 km to their summer ranges to feed (Gregory, 1974, 1977; Gregory and Stewart, 1975; Larsen, 1987; Lawson, 1989). Most snakes return to their home den to hibernate the following year. For example, >96% of Gregory's (1977) marked snakes returned in subsequent years to the den in which they were originally marked, despite the availability of alternative dens <1 km away. Juvenile garter snakes do not overwinter in communal dens in their first year of life (Gregory, 1977) and apparently find dens in later years by following substrate-deposited pheromonal trails left by adult snakes (Gregory 1974, 1977; Gregory and Stewart, 1975; Lawson, 1994; Mason, 1992). Presumably, most juveniles will encounter trails from individuals using the "parental" den, but some will follow trails to other dens. The philopatry of adults and high probability of recruitment of their juveniles to "parental" dens will allow genetic divergence among populations, even when snakes from different populations overlap in habitat use during summer (Gregory et al., 1987; Shine et al., 2001a). Den populations differ in the composition of sexual-attractiveness pheromones of females and in the courtship responses of males to those pheromones (LeMaster and Mason, 2002), confirming the existence of significant genetic divergence among den populations.

Predation is a major source of mortality and, hence, a potential selective pressure for garter snakes in Manitoba. Crows (*Corvus brachyrhynchos*) kill many snakes each year and, thus, impose strong selection on traits such as size, morphology, and antipredator tactics (Shine et al., 2001b). In keeping with this idea, the snakes display complex antipredator behaviors and possess bright red markings visible only during these displays (Passek and Gillingham, 1997; Shine et al., 2000). The numbers of snakes killed by crows differ enormously among dens; for example, three similar-sized dens within a 1-km radius in the Chatfield Community Pasture differ about tenfold in this respect, probably reflecting the local availability of trees that crows use for perching and nesting (R. Shine, personal observation).

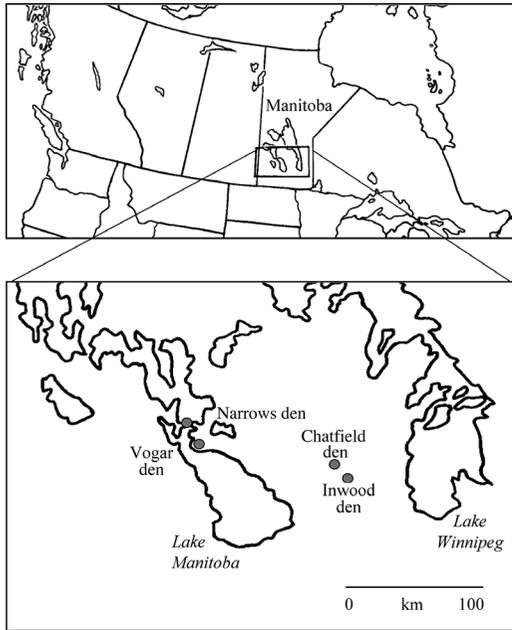


FIG. 1.—Location of four garter snake dens in Manitoba at which antipredator behaviors were scored for free-ranging snakes.

In the course of fieldwork on garter snakes in Manitoba, we were struck by apparent differences in antipredator behavior among snakes from different but nearby dens. To test the reality of that impression and to clarify the form and spatial scale of geographic variation in antipredator behavior, we conducted replicated trials at each of the dens to quantify snake responses.

MATERIALS AND METHODS

Study Area

We studied adult male garter snakes at four communal dens in southern Manitoba in May 2001. Each of these dens contained about 10,000 snakes. The southernmost den was 1.5 km N of the town of Inwood, 250 m E of Highway 17 in central southern Manitoba ($50^{\circ} 31' N$, $97^{\circ} 29' W$; “Inwood den”, see Fig. 1). The next den was 14 km north, in the Chatfield Community Pasture ($50^{\circ} 44' N$, $97^{\circ} 34' W$; “Chatfield den”). Another was 93 km northwest where we studied snakes near the town of Vogar ($50^{\circ} 45' N$, $98^{\circ} 30' W$; “Vogar den”). Lastly, 18 km northwest of the Vogar site, we found a den in a narrow isthmus of land separating the

northern and southern halves of Lake Manitoba ($51^{\circ} 10' N$, $98^{\circ} 50' W$; “Narrows den”, see Fig. 1). The Chatfield den was a natural limestone sinkhole, whereas the other three were beside limestone quarries.

Methods

Because sex, habitat, and body temperature of a garter snake can influence its antipredator response (Shine et al., 2000), we restricted attention to adult male snakes in open habitats <20 m from the den and worked only in the middle of the day (1000–1500 h) during fine, clear weather in spring (May 2001). For consistency, all tests were conducted by the same two people and within the same 10-d period. We selected a snake approximately 4 m away in an open area and walked directly towards it. We recorded the distance at which it fled from our approach. We then seized the snake by the midbody and held it for 10 s, recording whether or not the snake bit us during that period. We then took the animal’s cloacal temperature with an electronic thermometer, verified its sex, and recorded its snout–vent length (SVL). Previous work has shown that the responses of snakes to humans are similar to those elicited by stimuli that closely mimic natural predators (Burger, 1998; Shine et al., 2000).

RESULTS

We scored responses of 50 males at each of four dens. Body sizes and body temperatures, when tested, were similar among the four dens (Fig. 2a,b), but approach distances differed considerably (Fig. 2c). Snakes at the Inwood den typically tolerated our approach to within <1 m, but snakes at the Narrows den fled at about 1.8 m (one-factor ANOVA: $F_{3,196} = 8.37$, $P < 0.0001$; posthoc PLSD tests show that all comparisons have $P < 0.05$, except that Vogar did not differ from either Chatfield or Inwood). The proportion of snakes that bit us after capture also varied, from 44% at the Narrows to 14% at the Inwood den (Fig. 2d). At each den, the snakes that bit us were larger than those that did not bite (two-factor ANOVA with location and snake response as factors, SVL as dependent variable: location and interaction effects NS, “bite or not” effect: $F_{1,192} = 15.87$, $P < 0.0001$; see Fig. 3). Logistic

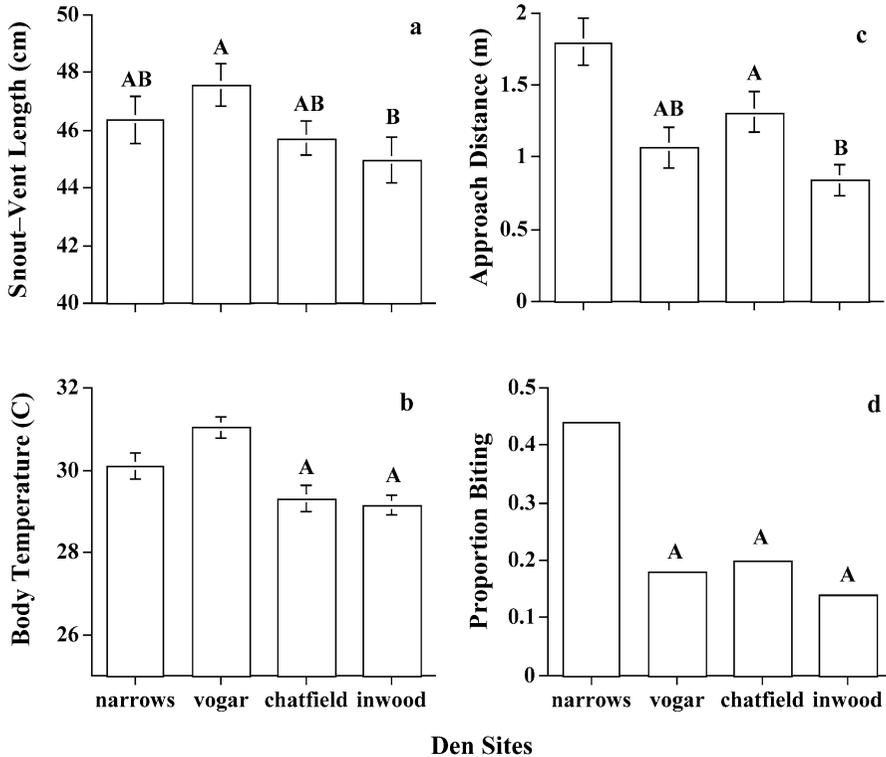


FIG. 2.—Comparisons among adult male garter snakes (*Thamnophis sirtalis parietalis*) from four communal dens in southern Manitoba. The snakes were similar in body sizes (A) and temperatures (B), but differed in approach distances when confronted by a human (c) and in the proportion of snakes that bit the investigator (d). Figures (a) to (c) show mean ± 1 SE. Sample size = 50 males per den; see text for statistical results. Letters above the histograms show subsets of data that do not differ from each other at $P < 0.05$.

regression confirmed that whether or not a snake bit us was affected by its location (log-likelihood ratio test: $\chi^2_3 = 15.38$, $P < 0.002$) and body size ($\chi^2_1 = 19.54$, $P < 0.0001$), but not by its body temperature ($\chi^2_1 = 0.39$, $P = 0.53$).

DISCUSSION

There are many examples of behavioral divergence among populations within widespread species (Foster and Endler, 1999), including antipredator behavior (Magurran, 1999), and our data on garter snakes provide yet another. The most interesting aspect of our results is their spatial scale, compared to the distances traveled by these snakes in the course of their annual cycle. These animals may travel >15 km from their dens to their summer ranges (Gregory and Stewart, 1975; Larsen, 1987), and there are no overt barriers to such movements because the entire region offers continuous habitat for garter snakes.

Nonetheless, antipredator behaviors differed considerably between snakes at dens <20 km apart (e.g., the Narrows versus Vogar). The Narrows snakes fled from us at about twice the distance as the Vogar snakes and were more than twice as likely to bite (Fig. 2).

Because we tested adult animals, we cannot determine whether there was any genetic basis to the observed behavioral differences. Plausibly, snakes at the four dens may be exposed to different predator species or densities, or may encounter those predators under different conditions. Any of these situations might modify the effectiveness of alternative antipredator responses and, hence, generate geographic divergence in antipredator tactics either through learning (if behaviors are flexible) or through natural selection (if behaviors are highly canalized). Previous studies provide clear evidence that garter snakes are capable of modifying their anti-

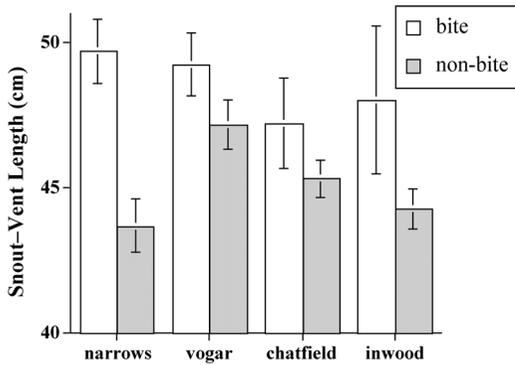


FIG. 3.—The body sizes (snout-vent lengths) of adult male garter snakes (*Thamnophis sirtalis parietalis*) from four communal dens in southern Manitoba that either bit or did not bite when captured. Figures show mean \pm 1 SE. Sample size = 50 males per den; see text for statistical results.

predator behavior in response to experiential stimuli (Herzog, 1990; Herzog et al., 1989). Nonetheless, an extensive literature also documents strong genetic influences on antipredator behavior in this genus (e.g., Brodie, 1989, 1993), hinting that the causal mechanisms may be genetic rather than experiential. In a previous intraspecific comparison of antipredator tactics in *Thamnophis sirtalis*, differences observed between adults of two populations were also evident in neonatal snakes (Herzog and Schwartz, 1990). The four populations that we studied also differ significantly in morphological traits known to exhibit high heritability (e.g., scale counts, location of coloration features), supporting the existence of genetic differentiation and, hence, the plausibility that genetic factors generate these behavioral differences among populations.

Nonetheless, these kinds of indirect data cannot resolve the issue of genetic versus experiential mechanisms for geographic divergence in antipredator tactics in adult snakes. For example, even if we assume a strong genetic basis for the behaviors coupled with genetic discontinuities among populations, phenotypic differences between the populations might still result from experiential factors. We would need studies on naïve (e.g., neonatal) snakes from the four den populations to rigorously distinguish between these alternatives, an approach widely used in previous studies (e.g., Burghardt and

Schwartz, 1999). Regardless of the mechanism generating this divergence in antipredator tactics among populations, however, the results are surprising: intuition would not predict that either selective forces or experiential factors would vary so dramatically across this small spatial scale.

Genetic divergence between adjacent populations of these highly vagile organisms will be facilitated by the fact that mating occurs at the overwinter den. Communal use of dens will not generate genetic separation among populations if mating occurs during the dispersed phase, as in rattlesnakes (Greene, 1997), but can do so if mating occurs during the aggregated phase, as in garter snakes (Gregory and Stewart, 1975). In keeping with this scenario, local populations of garter snakes are known to display significant among-population variation in several genetically determined aspects of behavior (e.g., Arnold, 1981; Brodie, 1989; Burghardt and Schwartz, 1999) as well as morphology (Rossman et al., 1996), and mate recognition systems (i.e., sex pheromone composition and male courtship responses: LeMaster and Mason, 2002). Previous studies, however, have relied upon comparisons between populations separated by relatively long distances and, presumably, little opportunity for gene flow (e.g., 540 km, Burghardt and Schwartz, 1999; Herzog and Schwartz, 1990; 240 km, LeMaster and Mason, 2002; 120 km, Brodie, 1993). Our study shows striking divergence even when the dens are so close to each other that animals from each would encounter each other every year in the course of their summer foraging activities.

The processes responsible for this geographic variation remain unclear. The differences might reflect behavioral flexibility, or local adaptations, for example, the intensity of predation among sites may vary geographically. Equally likely, however, genetically-based differences might accumulate through non-selective processes such as drift or hybrid introgression. The population that was most distinctive behaviorally in our study (the Narrows) is also the most distinctive morphologically, perhaps due to introgression with another species (the plains garter snake, *Thamnophis radix*) that is widespread west of Lake Manitoba. Multivariate analyses of morphological traits (especially scale counts and color pattern) used to discriminate *T. sirtalis*

from *T. radix* (Rossman et al., 1996) revealed homogeneity among the Vogar, Chatfield, and Inwood den populations, but a significant shift towards *radix*-like morphology, including definite hybrids, in animals from the Narrows den (R. Shine, unpublished data). Thus, introgression of genes from *radix*, a more "nervous" species than *sirtalis* (Herzog et al., 1992), may explain the unusual antipredator tactics of the Narrows snakes. Nonetheless, the behavioral differences among dens were quantitative rather than qualitative. For example, the trend for active retaliation (i.e., biting) only by larger snakes was seen in all four populations (Fig. 3), plausibly reflecting the futility of this behavior for smaller animals.

In summary, red-sided garter snakes at four nearby dens (in some cases, <20 km apart) displayed substantial differences in their responses to our approach. Snakes at some dens fled at greater distances and were more likely to bite us than were snakes at other dens. This system thus provides an unusually clear example of geographic variation in behavior at a small spatial scale.

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A NEW TREEFROG (HYLIDAE: *HYLA*) FROM SOUTHERN ECUADOR AND A DESCRIPTION OF ITS ANTIPREDATOR BEHAVIOR

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ABSTRACT: We describe a new species of *Hyla* from southern Ecuador that is diagnosed by the absence of an omosternum; the presence of an enlarged, curved, and pointed prepollex in males; features of coloration; and an associated suite of presumed anti-predator behaviors. Upon capture, frogs exuded a white, sticky fluid; continued perturbation elicited a defensive posture in which white patches on the posterior sides of the limbs and the vent were displayed. The phylogenetic relationships of *H. tapichalaca* with respect to the *H. armata*, *H. larinopygion*, and *H. pulchella* groups are discussed.

Key words: Antipredator behavior; Anura; Ecuador; *Hyla armata* group; *Hyla larinopygion* group; *Hyla pulchella* group; *Hyla tapichalaca*; New species

ECUADOR is among the most biologically diverse countries and hosts the richest (per unit of area) amphibian fauna in the world,

including 425 formally described species (Coloma and Quiguango-Ubillús, 2000–2002). In addition, Duellman's (1999) model of the rate of discovery and descriptions of new species in South America predicts that this

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