

The role of innate and environmental influences in shaping antipredator behavior of mainland and insular gartersnakes (*Thamnophis sirtalis*)

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Abstract Vertebrates inhabiting islands are often characterized by fearlessness and tame behavior. While this relaxation of antipredator behavior has been documented in many species endemic to islands, fewer researchers have examined it in species that occur both in insular and mainland habitats. In addition, the mechanisms underlying this shift in behavior are still poorly known. For this work, antipredator behavior of island and mainland populations of the common gartersnake (*Thamnophis sirtalis*) was surveyed. Observed differences were explained in terms of innate tendencies and/or environmental influences using both neonates and adults in laboratory experiments designed to tease apart these two underlying mechanisms. While antipredator behavior of adults was positively correlated with the predation pressures associated with capture sites, neonate behavior did not fully reflect this pattern. However, some support for hard-wired antipredator behavior at birth was evident. Plasticity experiments also revealed that environmental factors appear to influence antipredator behavior. Thus, the data presented here suggest that predation pressures play a strong role in shaping the antipredator behavior of island animals and that the resulting behaviors are most likely the result of some combination of both nature and nurture.

Keywords Behavior · Innate · Island tameness · Nurture · Snake · *Thamnophis sirtalis*

Introduction

Vertebrates inhabiting islands are often characterized by fearlessness and tame behavior as a result of fewer predators than exist on comparable mainlands (Pimm 1987; Atkinson 1989; Case et al. 1992; Beauchamp 2004; Blumstein and Daniel 2005; Orrock 2010). This decrease in responsiveness to potential predators is believed to be due to some cost related to maintaining such behaviors (Magurran 1999; Blumstein 2006). However, not all island species with decreased predation pressures exhibit this relaxed nature (McLaughlin and Roughgarden 1989; Alcover and McMinn 1994), and the trend of fearlessness and tameness in island species has traditionally been based on studies of endemic island species (Stone et al. 1994) rather than species that occur both on the mainland and in insular habitats. As a result, much remains to be discovered regarding this unique phenomenon.

In this study, intraspecific variation in antipredator behavior of insular and mainland populations was examined, and the forces that may drive and maintain such variation were elucidated. To carry out this work, the common gartersnake, *Thamnophis sirtalis*, was selected, because it has been used as a model species for many behavioral studies (Seigel et al. 1987; Brodie and Garland 1993; Burghardt 1993; Seigel and Collins 1993; Rossman et al. 1996; Burghardt and Schwartz 1999; King et al. 2001; Badyaev et al. 2002; King 2002). The study was centered on the Beaver Archipelago in northeastern Lake Michigan (see map in Placyk and Burghardt 2011) and surrounding mainland, where *T. sirtalis* commonly occurs (Hatt et al. 1948; Placyk and Gillingham 2002). Antipredator behavior of several insular and mainland populations of *T. sirtalis* was examined using both neonate snakes naïve to environmental influences and wild-caught adult snakes in

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experiments designed to determine what behaviors may be present at birth, how environmental influences may shape behavior throughout life, and whether or not adult behavior results from some combination of the two. This was accomplished in three ways: (1) wild-caught adult antipredator behavior was examined, (2) neonates naïve to environmental influences were tested for antipredator behavior shortly after birth, and (3) neonates were used in an experiment to examine how environmental factors influence antipredator behavior over time.

Materials and methods

General methods

Gartersnakes were collected from field sites in both the lower (LP) ($n = 26$) and upper peninsula (UP) ($n = 30$) of Michigan and from the three largest islands of the Beaver Archipelago [i.e. Beaver Island (BI) ($n = 156$), High Island (HI) ($n = 54$), and Garden Island (GI) ($n = 54$)]. Given the size of Beaver Island and this work's focus on island phenomenon, it was possible to sample two Beaver Island sites nearly 1 km apart [i.e. Miller's Marsh (MM) ($n = 113$) and Sawmill (SM) ($n = 43$)] that vary in predator pressures (Placyk and Burghardt 2005). Following capture, snakes were placed, by site, into 61 × 32 × 33 cm aquaria to eliminate breeding and disease transmission between different populations. Aquaria were kept between 20 and 25°C on a 16:8-h light:dark cycle, to simulate northern Michigan summer conditions, with fresh water and shelter available at all times. Snakes were permitted to acclimate for 48 h after which behavioral testing was conducted. Since *T. sirtalis* is diurnal, all behavioral tests were conducted during photophase. Following behavioral testing, nonpregnant females and males were scale-clipped for future identification (Brown and Parker 1976), had tissue samples taken for genetic analyses (Placyk et al. 2007) and were released to their respective capture locations. It was also recorded if an animal was missing part of its tail or had other types of wounds or scars that may have been caused by a failed predatory attack, because such data may correspond with differences in antipredator behavior and because variation in this type of data has been documented in this system (Placyk and Burghardt 2005). Some pregnant females (determined via palpating for developing embryos) were held until parturition after which time they were released to their respective capture locations. Neonates were kept for additional testing (LP, $n = 154$; UP, $n = 21$; MM, $n = 79$; SM, $n = 16$; GI, $n = 50$; HI, $n = 16$) and were maintained in 15 × 30 × 9 cm cages with shelter, offered water ad libitum, and fed chopped worms (*Lumbricus* spp.) three times per week. Following neonate behavioral testing,

animals were released to the site of their mother's capture, maintained for other experiments, or transferred to other research facilities. Any adult snakes held more than 72 h and all neonates were submitted to a health screening before being released.

Antipredator behavior experiments

For standardized antipredator behavioral tests (modified by Mori et al. 1996 from Herzog and Burghardt 1986), test arenas consisted of 51 cm × 26.5 cm × 30.5 cm aquaria lined with a corrugated cardboard cage liner and sterilized with Alconox[®], a clinical, concentrated, anionic detergent powder. Trials began with snakes being left undisturbed for 30 s after which time the experimenter's finger was slowly brought within 2 cm of the snakes snout and held stationary for 60 s (nonmoving stimulus session). If the snake crawled away during the test, it was followed, with the extended finger in front of the snake. The snake was then given a 30-s undisturbed period followed by the researcher, again, extending the forefinger to within 1–2 cm of the snake's snout, but this time moving it back and forth at the rate of ca. 3–4 oscillations per second throughout the 60-s period (moving stimulus session). Finally, after another 30-s undisturbed period, the snake was gently tapped or had its body touched (head to tail) approximately once every second throughout the 60-s period (tapping stimulus session). Behavioral measures such as fleeing, anal gland discharge (musking), defecating, urinating, body flattening, striking, biting, head hiding, and tail wagging were recorded using counters for each time they occurred for each trial (Table 1). Adults were tested within 1–2 days after capture, and neonates were always tested 1–3 days after birth.

Significant differences in fleeing due to a site effect were evaluated using one-way ANOVAs followed by Tukey–Kramer multiple-comparison tests. Since all other observed behaviors occurred infrequently, Chi-squared tests of independence were used to determine if the frequency of the behavior was independent of the site. If a test indicated that site and the behavior were not independent of each other, the full Chi-squared model including all six sites was partitioned, and Fisher exact probability tests were used to determine pairwise differences with P values adjusted for multiple comparisons using Holm's method (Holm 1979; Aickin and Gensler 1996). Two-sample t tests and ANOVAs (for fleeing) and Chi-squared tests of independence (for all other behaviors) were also used to determine if differences exist in the behavior of adult snakes due to the presence of wounds from failed predatory attacks. For neonates, litter effects were controlled whenever possible by nesting litter within each site. A simple linear regression using litter means was used to determine if the number of times neonates fled from a

Table 1 Antipredator behaviors exhibited by common gartersnakes, *Thamnophis sirtalis*, during standardized antipredator testing [modified from Mori et al. (1996)]

Behavior	Description
Flee	The snake rapidly crawls away from the stimulus object. The snake may move around inside the arena or attempt to climb up the wall of the arena
Anal gland discharge (musking)	The snake expels products of the cloacal glands
Defecation	The snake expels feces from the cloaca
Urination	The snake expels uric acid from the cloaca
Strike	The snake, with either closed or open mouth, rapidly orients the head toward the stimulus object or straightens the anterior body to strike the stimulus. Actual contact with the stimulus object may or may not occur, but the snake does not hold on to the stimulus with its jaws
Bite	The snake strikes the stimulus and holds on to it with its jaws
Head hiding	The snake hides its head under part of its body
Tail wagging	The snake slowly or rapidly vibrates its tail
Flatten	The snake dorsoventrally flattens part of its body or its head

simulated predator was related to the number of times that dams fled from a simulated predator. This analysis could not be performed for any other behavior due to the infrequency of all other behaviors.

Antipredator behavior plasticity experiments

A total of 188 neonates were evenly split and randomly assigned, in terms of sex, site, and litter, to one of three groups (LP, $n = 45$; UP, $n = 21$; MM, $n = 45$; SM, $n = 16$; GI, $n = 45$; HI, $n = 16$). Individuals from one group were handled only when their cage required cleaning, one group was gently handled (held in hand and prevented from falling) for 60 s at a time on a weekly basis, and one group was roughly handled (held in a shaking hand) for 60 s at a time on a weekly basis. After 42 days, all three groups were tested again using the standardized antipredator behavioral test. The 42-day treatment period began 10–12 days after birth.

Data collected following the 42-day treatment protocol were examined using one-way ANOVAs and Chi-square tests of independence to detect differences in behavior due to the treatment group (not handled, handled gently, handled roughly) to which the animal was assigned. Tukey–Kramer multiple-comparison tests and Fisher exact probability tests were then used to detect significant pairwise differences. Site and litter effects were detected using nested one-way ANOVAs and Chi-squared tests of independence.

Results

Antipredator behavior experiments

For adults, a significant site effect was detected for 8 of the 9 possible different responses that could have been exhibited ($P < 0.05$). In general, adults from mainland sites (LP and UP) and Beaver Island (BI) displayed a greater diversity of antipredatory responses (6–9 different types of responses) than adults from either Garden Island (GI) or High Island (HI) (2–5 different types of responses). Mainland Michigan, Beaver Island, Garden Island, and High Island were characterized by 16, 12, 4, and 2 potential predators, respectively (Placyk and Burghardt 2005). In addition, of the 9 different responses that were observed, adults from mainland sites and the two sites on BI (MM and SM) tended to display them each significantly more than adults from GI and HI (Table 2). As for specific site differences, LP, UP, and BI adults fled more frequently than HI and GI adults ($H_{5,328} = 188.84$, $P < 0.0001$; Fig. 1a). Adult snakes from both mainland Michigan sites bit the experimenter significantly more frequently than snakes from most of the islands (Table 2) and struck at the experimenter significantly more frequently than adults from MM and from GI and HI ($P < 0.05$; Table 2). Adult snakes from BI wagged their tails more frequently than snakes from GI or HI ($P < 0.05$; Table 2). Adults from the UP urinated more frequently than animals from HI ($P < 0.05$; Table 2). Adults from the two mainland sites defecated more frequently than animals from HI, and adults from the UP defecated more frequently than animals from GI ($P < 0.05$; Table 2). Adults from the UP discharged anal gland secretions (musked) more frequently than adult animals from most other sites, and MM adults musked more frequently than snakes from HI ($P < 0.05$; Table 2). Finally, LP adults flattened more frequently than MM adults ($P < 0.05$; Table 2). The presence of wounds from failed predatory attacks, however, did not result in significant differences for any of the observed antipredator responses ($P > 0.05$).

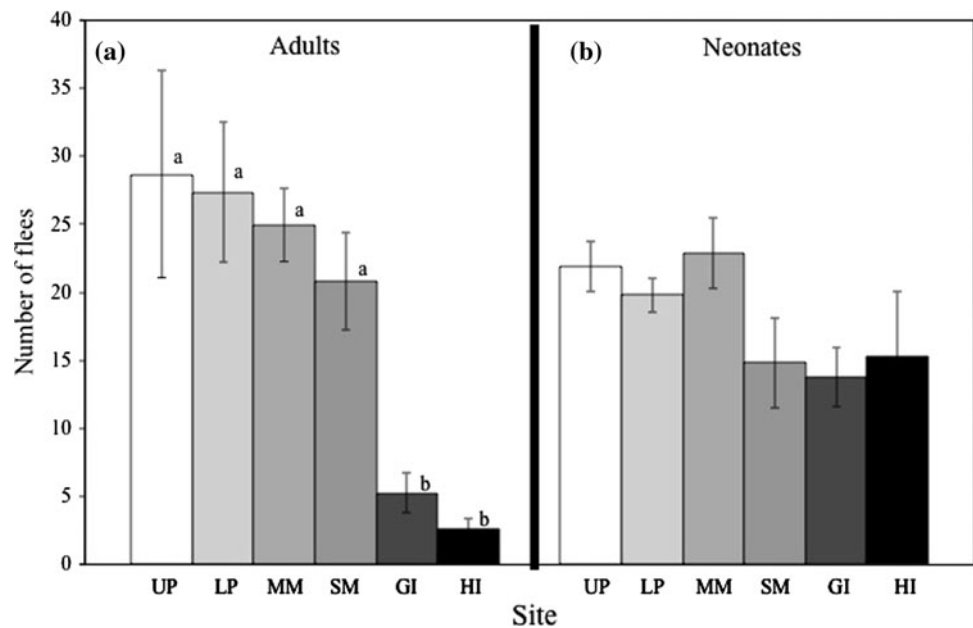
Unlike adults, neonates almost always exhibited all 9 antipredator behaviors regardless of where their mothers were collected. Neonates also appeared to be more reactive than adults, displaying many of these behaviors at greater frequencies (Table 3). However, significant differences due to a site effect were less pronounced than with the adults, with some of the behavioral differences that were found in neonates exhibiting different patterns in relation to site location. Although a simple linear regression indicated that there is a significant positive linear relationship between the number of times a dam fled from a simulated predator and the number of times her offspring fled from a simulated predator ($r^2 = 0.06$; $P < 0.001$), this relationship only

Table 2 Frequency of antipredator behaviors (except fleeing) exhibited during standardized antipredator testing by adult common gartersnakes, *Thamnophis sirtalis*

Behavior	Site						χ^2	<i>P</i>
	LP	UP	MM	SM	GI	HI		
Bite	0.15 ^a	0.33 ^a	0 ^b	0.02 ^{ab}	0 ^b	0 ^b	44.60	<0.0001
Strike	0.23 ^a	0.33 ^a	0.01 ^b	0.09 ^{ab}	0 ^b	0 ^b	43.39	<0.0001
Tail wagging	0.12 ^{ab}	0 ^{ab}	0.12 ^a	0.14 ^a	0 ^b	0 ^{ab}	17.24	<0.001
Head hiding	0.12	0	0.11	0.09	0.01	0.02	9.25	0.10
Urination	0.04 ^{ab}	0.33 ^a	0.12 ^{ab}	0.14 ^{ab}	0.03 ^{ab}	0 ^b	15.01	0.01
Defecation	0.08 ^{ac}	0.33 ^a	0.07 ^a	0.12 ^a	0.01 ^{bc}	0 ^b	13.54	0.02
Musking	0.08 ^a	0.67 ^b	0.15 ^{bc}	0.05 ^{ac}	0.03 ^{ac}	0 ^{ac}	28.89	<0.0001
Flatten	0.08 ^a	0 ^{ab}	0 ^b	0 ^{ab}	0 ^{ab}	0 ^{ab}	21.76	<0.001
<i>n</i>	26	30	113	43	68	54		

Frequency is expressed as the number of individuals exhibiting the behavior divided by the total number of individuals per site. Snakes used for testing were collected from the lower (LP) and upper peninsula (UP) of Michigan, Miller's Marsh (MM) and Sawmill (SM) on Beaver Island, Garden Island (GI), and High Island (HI). *P* values calculated from Chi-squared tests of independence. Significant site differences for each behavior are indicated by different letters; values of *P* < 0.05 are shown in bold

Fig. 1 Mean number of times ($\pm 95\%$ CI) adult (a) and neonate (b) common gartersnakes, *Thamnophis sirtalis*, from the lower (LP) and upper peninsula (UP) of Michigan, Miller's Marsh (MM) and Sawmill (SM) on Beaver Island, Garden Island (GI) and High Island (HI) fled from a simulated predator during standardized antipredator testing. Different letters indicate significantly different means (*P* < 0.05) within each age class. Litter means, not individual means, are shown for neonates



explains 6% of the variation in the neonate fleeing data. An ANOVA indicated no significant site difference in the frequency of fleeing ($F_{5,294} = 1.24$, $P = 0.31$; Fig. 1b). Despite this lack of difference in fleeing, MM neonates musked significantly more frequently than LP neonates ($P < 0.05$; Table 3), and UP, HI, and SM neonates flattened their bodies more frequently than LP neonates ($P < 0.05$; Table 3). No significant differences in the frequency of strikes, tail wagging, urinating, head hiding, and biting were found between sites ($P > 0.05$). In addition, a litter effect was detected for neonate fleeing ($F_{35,336} = 5.53$, $P < 0.0001$), but this effect was controlled for by nesting litters within sites.

Antipredator behavior plasticity experiments

Before the 42-day treatment period, neonates did not differ across treatment groups in the number of times they fled ($F_{2,137} = 0.29$, $P = 0.75$; Fig. 2) from a simulated predatory attack and in the frequency of strikes ($\chi^2 = 1.23$, $G^2 = 1.23$, $df = 2$, $P > 0.05$; Fig. 3) and bites ($\chi^2 = 1.14$, $G^2 = 1.15$, $df = 2$, $P > 0.05$). At the end of the 42-day treatment period, differences among the treatments were detected for fleeing ($F_{2,123} = 134.75$, $P < 0.001$; Fig. 2), striking ($F_{2,123} = 6.87$, $P = 0.001$; Fig. 3) and flattening ($\chi^2 = 6.94$, $G^2 = 7.17$, $df = 2$, $P < 0.05$). Specifically, animals that were roughly handled fled, struck, and

Table 3 Frequency of antipredator behaviors (except fleeing) exhibited during standardized antipredator testing by laboratory-born neonate common gartersnakes, *Thamnophis sirtalis*

Behavior	Site						χ^2	<i>P</i>
	LP	UP	MM	SM	GI	HI		
Bite	0.10	0.10	0.08	0.19	0.18	0.06	5.14	0.40
Strike	0.17	0.24	0.22	0.06	0.28	0.19	5.19	0.39
Tail wagging	0.54	0.57	0.51	0.56	0.58	0.75	3.50	0.62
Head hiding	0.15	0.10	0.11	0.13	0.08	0.06	2.62	0.76
Urination	0.34	0.33	0.34	0.31	0.26	0.44	2.06	0.84
Defecation	0.0	0.05	0.03	0.0	0.06	0.06	9.56	0.09
Musking	0.51 ^a	0.67 ^{ab}	0.72 ^b	0.69 ^{ab}	0.56 ^{ab}	0.75 ^{ab}	13.12	0.02
Flatten	0.0 ^a	0.10 ^b	0.05 ^{ab}	0.06 ^b	0.04 ^{ab}	0.13 ^b	13.43	0.02
No. of litters	12	2	11	4	8	4		
<i>n</i>	154	21	79	16	50	16		

Frequency is expressed as the number of individuals exhibiting the behavior divided by the total number of individuals per site. Neonates used for testing were born to mothers from the lower (LP) and upper peninsula (UP) of Michigan, Miller’s Marsh (MM) and Sawmill (SM) on Beaver Island, Garden Island (GI), and High Island (HI). *P* values calculated from Chi-squared tests of independence. Significant site differences for each behavior are indicated by different letters; values of *P* < 0.05 are shown in bold

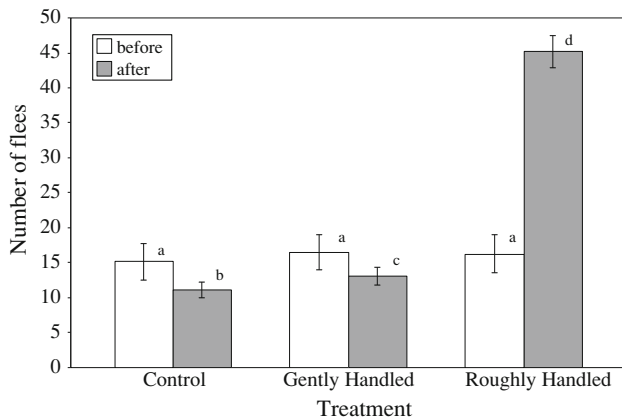


Fig. 2 Mean number of times ($\pm 95\%$ CI) neonate common garter snakes, *Thamnophis sirtalis*, fled from a simulated predator during standardized antipredator testing before and after treatments [not handled/control (*n* = 55), handled gently (*n* = 53), handled roughly (*n* = 51)] designed to examine plasticity of antipredator behavior. Different letters indicate significantly different means both within and across treatments (*P* < 0.05)

flattened their bodies (i.e. 42% compared to 20.4 and 22.6% for control and handled animals, respectively) more frequently than animals that were held or not handled (*P* < 0.05). No differences in biting, tail-wagging, musking, urinating, and defecating were detected (*P* > 0.05).

Differences within treatment groups between the two testing days were also detected. Specifically, animals in the control group ($t_1 = 2.96$, *P* < 0.01; Fig. 2) and in the group that was gently handled ($t_1 = 2.64$, *P* = 0.01; Fig. 2) fled less frequently at the end of their treatments, whereas animals from the roughly handled group fled more frequently at the end of their treatment ($t_1 = -18.07$,

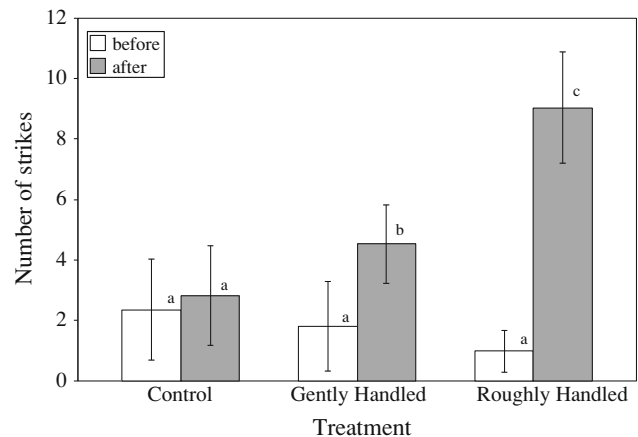


Fig. 3 Mean number of times ($\pm 95\%$ CI) neonate common garter snakes, *Thamnophis sirtalis*, struck at a simulated predator during standardized antipredator testing before and after treatments [not handled/control (*n* = 55), handled gently (*n* = 53), handled roughly (*n* = 51)] designed to examine plasticity of antipredator behavior. Different letters indicate significantly different means both within and across treatments (*P* < 0.05)

P < 0.0001; Fig. 2). All three treatment groups bit more frequently at the end of the treatment period than at the beginning (*P* < 0.05). The two groups that were handled struck more frequently at the end (52.8 and 90.2% for the gently handled and roughly handled groups, respectively) of their treatments than before (20.8 and 21.6% for the gently handled and roughly handled groups, respectively) the treatments were initiated (*P* < 0.05), whereas the control group did not vary in the frequency of strikes they exhibited between the two testing periods (41.8% at the end of the treatment period vs. 29.1% prior to the treatment period; *P* > 0.05).

No site effect was detected for fleeing ($F_{4,123} = 1.28$, $P = 0.30$) and striking ($F_{4,123} = 0.35$, $P = 0.84$). When controlling for a litter effect by nesting litters in each site, both fleeing ($F_{14,123} = 1.91$, $P = 0.03$) and striking ($F_{14,123} = 1.79$, $P = 0.05$) exhibited significant litter effects.

Discussion

Antipredator behavior experiments

Adult snakes from both mainland sites and both BI sites tended to exhibit antipredator behaviors more frequently than snakes from GI or HI. These data suggest that the pattern displayed by adults in this regard corresponds with the richness of predators at each site. Snakes at both mainland sites occur with more predators (16) than any of the island snakes, and snakes from BI occur with more predators (12) than snakes on either GI (4) or HI (2) (Placyk and Burghardt 2005). While the types of predators also vary from site to site, this may have less of an influence on the variation in behavior that was documented, as every site includes aquatic and terrestrial predators, sit-and-wait and active foragers, and predators that rely on visual stimuli to find their prey as well as those that rely on chemical stimuli (Placyk and Burghardt 2005, 2011). However, the role of different types of predators on antipredator behavior was not specifically examined here, and future research on this topic may be warranted in this system. Regardless of the selection pressures driving the variation that was documented here, the differences that were seen may be due to either an innate component (either present at birth or resulting from a hard-wired ontogenetic shift in behavior), environmental influences that have occurred over the lifetime of individuals from each population, or a combination of the two. To understand the possible influence of innate components present at birth on antipredator behavior in these populations, I tested neonate snakes under the same conditions as adults. Since neonates were naïve to the occurrence of predatory attacks, they had no experience by which to shape their response to a simulated attack.

In adults, site differences were detected. On the other hand, although neonates born to dams from the two mainland sites and MM fled more than neonates from HI or GI, indicating possible evolutionary adaptive changes that correspond with predator pressures, these differences were not significant. However, a simple linear regression did indicate that the more a dam fled the more her offspring fled, indicating some genetic/parental connection between neonate and adult fleeing behavior. Few other similarities, however, were found between neonate responses and adult

responses. In fact, UP and island neonates were, in general, more defensive than LP neonates. There are several possible explanations as to why adult behavior patterns and neonate behavior patterns vary.

To begin with, predation pressures that influence neonates may differ from those that influence adults. Generally, smaller animals tend to have more predators than larger animals, and this may explain why, in general, neonates responded to a simulated predator more than adults. However, this does not explain the significant site differences that were detected for the neonates. One explanation is that these site differences may be due to the underlying genetics of these populations (Mori et al. 1996; Mori and Burghardt 2000). Burghardt and Schwartz (1999) found neonates born to mothers from Wisconsin were more reactive than neonates born to LP mothers. Since UP animals are derived from Wisconsin populations (Placyk et al. 2007), the difference seen between UP and LP populations may be the result of the underlying genetics of these populations. The data presented here also indicate that neonates from MM, SM, and HI are more reactive than the LP neonates in some regards (musking, body flattening) despite more predators existing at the LP site. Using mtDNA sequence data, Placyk et al. (2007) found that most individuals sampled (80.9%) from the Beaver Archipelago are derived from UP populations rather than LP populations. Since many of the behaviors exhibited by adult animals correspond with predator richness, but not with neonate behaviors, the antipredator plasticity experiment was useful in determining the role of environmental influences on adult behavior.

Antipredator plasticity experiments

At the end of the treatment period, snakes in the group that experienced simulated predatory attacks on a regular basis fled more and struck more than animals from the other two treatment groups. In addition, snakes from all three treatment groups bit more, snakes that were gently handled struck more, and snakes from both the control group and the group that were gently handled fled less at the end of the treatment period. These results indicate two things. First, environmental influences on snakes appear to affect the antipredator behavior exhibited by adult snakes, which may be one reason why differences between antipredator responses displayed by adults and neonates were noted. Second, maturational/ontogenetic shifts in behavior (Herzog et al. 1992), as, perhaps, evidenced by the increase in biting across all treatment groups, may also account for differences in adult and neonate behavior. A similar study conducted with neonate gartersnakes from mainland Wisconsin (Herzog 1990) indicated that early experience with simulated predatory attacks and the resulting increase in

antipredator behavior were long-lasting, further supporting my data and assertions that the antipredator behavior of the adults may have resulted from phenotypic plasticity.

General discussion

While this study indicates that some island populations were less reactive or more “tame” than mainland populations, these differences were only seen in adults from two of the four islands. However, despite these mixed results, the traditional view that island populations or species become less fearful on islands based on the idea that there are generally fewer predators in island systems is supported here, as both of the islands in which relaxation of antipredator behavior (Coss 1999) was documented were characterized by fewer potential predators than the islands that did not differ from the mainland populations. However, despite the support the present and previous works (Blazquez et al. 1997; Bonnet et al. 2005; Aubret et al. 2010) provide for the hypothesis that island animals are less reactive than mainland animals, caution should still be taken before applying the island tameness hypothesis broadly, as a variety of factors (both intrinsic and extrinsic) need to be taken into account when examining such geographic variation in behavior. The work presented here also suggests that there may be both innate and environmental forces at work in shaping the behavior exhibited by insular populations.

While Bonnet et al. (2005) and Aubret et al. (2010) indicated that the insular tiger snake (*Notechis scutatus occidentalis*, Elapidae) populations are more placid than mainland populations as the result of phenotypic plasticity, few others have examined the mechanisms behind the changes they see between mainland and insular populations. The data collected for this study suggest that the behavioral differences that were detected are likely the result of both environmental and innate influences, rather than only environmental influences, but the study system used for this study is thousands of years old (Hough 1958), whereas insular tiger snake populations are only a few hundreds of years old. Aubret et al. (2007) suggested that adaptively plastic behavioral responses may influence the rate or route of evolutionary transitions between habitats possibly indicating that these initial differences in behavioral responses resulting from plasticity may be the precursor to evolutionary change. It is possible that insular tiger snake populations are in earlier stages of divergence than the Beaver Archipelago gartersnake populations. Clearly, island tameness appears to be driven by decreases in predation pressure. However, the development and maintenance of behaviors resulting from this relaxation appear to be a complex combination of innate and environmental influences and warrants additional, detailed experimentation on the topic.

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