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A STUDY OF THE DEFENSIVE BEHAVIORS OF FREE-RANGING DEKAY'S BROWNSNAKES, *STORERIA DEKAYI* (HOLBROOK, 1836)

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ABSTRACT: The defensive behaviors of free-ranging Dekay's Brownsnakes, *Storeria dekayi*, were studied at a site in Erie County, Pennsylvania, USA. Twenty-nine unique sequences of defensive behavior were documented. A total of 50 individual snakes (26 males and 24 females) provided 88 observations during the initial phase, of which 78% (n = 69) were of snakes that remained in place. Snakes were tapped with the investigator's hand to elicit defensive behaviors during the contact phase. Snakes were more than twice as likely to attempt to flee during the contact phase (46%) than during the initial phase (22%). During the contact phase, mean surface body temperatures were significantly higher in snakes attempting to flee (22.3 ± 1.3 °C) than those that remained in place (16.1 ± 2.2 °C). The most frequently observed response during the contact phase was dorso-ventral flattening of the head and body (n = 42). During capture, most snakes (94%) smeared their cloacal contents on themselves and the investigator's hand.

INTRODUCTION

Dekay's Brownsnake, *Storeria dekayi*, is a small natricine snake that is preyed upon by spiders, anurans, snakes (e.g., juvenile Milksnakes *Lampropeltis triangulum* [Gray 2014a]), birds, and numerous mammals, including raccoons, skunks, weasels, and opossums (Linzey and Clifford 1981; Ernst and Barbour 1989; Ernst and Ernst 2003). *Storeria dekayi* may have evolved a diverse repertoire of anti-predator behaviors, including passive (e.g., crypsis and concealment) and active (e.g., fleeing and open-mouth striking) defenses (Gray 2014c) in response to the pressures of predation by multiple predators. Like many ectotherms, locomotion and defensive responses in *S. dekayi* are influenced by environmental temperatures (Keogh and DeSerto 1994; Gerald and Claussen 2007); sex, microhabitat, and a snake's prior activity may also be important factors influencing defensive responses in snakes (Shine et al. 2000). Due to the complex interaction between these, and possibly other variables, the majority of studies regarding defensive behaviors in snakes are carried out in the laboratory (Durso and Mullin 2014).

Despite the abundance of *S. dekayi* in many areas of Pennsylvania and the Northeast, only a few anecdotal reports have been made on the defensive behaviors of free-ranging individuals (Bartlett 1987; Hayes 1987; Gerald and Graziano 2011). The goals of the current study were to 1) document the defensive behaviors of free-ranging *S. dekayi* during three phases: initial, contact (i. e., tapped with the hand), and capture; 2) determine if a significant difference existed between the surface body temperature of snakes that remained still and those that fled; and 3) compare the frequencies of defensive behaviors of *S. dekayi* in this study and those reported in the literature.

MATERIALS AND METHODS

Observations of defensive behaviors in free-ranging *S. dekayi* were made between 19 April and 6 August 2014 at a site in Erie County, Pennsylvania, USA. A description of the site was provided by Gray (2014a). Observations were made in the morning (37 visits between 0615-1200 hrs) and in the late afternoon (29 visits between 1626-1938 hrs), at times when *S. dekayi* are mostly inactive. *Storeria dekayi* (n = 50) were located by searching pre-existing debris (i.e., wooden paneling, shingles, linoleum, and carpeting) at the site. Defensive behavior observations were divided into three sequential phases. During the initial phase, debris items were quickly turned, and if a snake was present its surface body temperature (T_s) was immediately recorded with a hand-held non-contact infrared thermometer (Raytec MT-6) precise to 0.2ºC (accuracy of ±1% between 10-30ºC and ±1.5% outside this range). Snakes were observed for 10 seconds after their T_s were obtained. The initial phase was followed by the contact phase, which involved the snake being gently tapped near mid-body with the investigator's open hand, then observed for an additional 10 seconds. After the tap the open hand was held approximately 10 cm from the snake. The human hand has been demonstrated to be an effective stimulus for eliciting defensive responses in snakes (Keogh and DeSerto 1994). During the capture phase the snake was grabbed as near to mid-body as possible and observed in hand for a final 10 seconds. Any defensive behaviors or lack thereof were noted during each phase. Because

Table 1. The frequencies of defensive behaviors of Dekay's Brownsnake, *Storeria dekayi* for each phase are summarized below.

Behavior	Initial	Contact	Capture
Still	65	10	0
Fled	16	34	0
Head-hiding	1	6	0
Flattening	0	42	6
Defensive posture	0	22	3
Slight movement	0	2	4
Closed-mouth striking	0	5	1
Open-mouth striking	0	11	0
Gaping	0	1	0
Smearing cloacal contents	0	0	76

some individuals attempted to flee, not all phases were observed or were not observed in their entirety. For example, several snakes attempted to flee during the initial phase and were then captured, thereby skipping the contact phase. Other snakes attempted to flee immediately after being tapped, thus abridging the contact phase. Eleven of the 50 snakes in this study were observed on multiple occasions.

After the completion of the capture phase, each snake was sexed; its snout-vent length (SVL) and total length (TL) measured to the nearest mm by gently stretching along a ruler. Mass was obtained to the 0.1 gram with a spring scale. As in many natricine snakes, sex of mature *S. dekayi* was determined by examining the base of the tail. In males the hemipenes cause the sides of the base of the tail to bulge, whereas in females, the base of the tail is more tapered (Rossman et al. 1996). In neonates and young < 150 mm the hemipenes were manually everted in males by grasping the snake at mid-tail and rolling the thumb on the ventral surface towards the cloaca. Sex determination was further confirmed by examining relative tail length as per Hulse et al. (2001). Snakes were individually marked with a portable cautery unit (Winne et al. 2006) and released at the site of capture. The following list of potential defensive behaviors was generated by consulting the literature (summarized in Gray 2014c), and are classified as non-intimidating or intimidating.

Non-intimidating defensive behaviors:

Fleeing – The snake moves away from where it was initially observed; usually, but not necessarily, away from the investigator.

Head-hiding – The snake places its head beneath coils of the body and/or tail.

Remained in place – Is a collective term for all behaviors whereupon the snake did not make any attempt to flee. Unlike remaining still, the snake may display some movement (i.e., coiling, head-hiding, etc.).

Figure 1. A typical defensive sequence of Dekay's Brownsnake, *Storeria dekayi*. Once uncovered, the snake is initially still (upper left). During the contact phase the snake dorso-ventrally flattens its head and body, and assumes a defensive posture (upper right). While in a defensive posture the snake may gape its mouth while tongue-flicking (lower left). Finally, open-mouthed strikes may be employed at the end of the contact phase (lower right). Not illustrated is the smearing of the cloacal contents during the capture phase.

Smearing cloacal contents – The snake presses its vent against its body or the investigator's hand while releasing and smearing the contents of the cloaca and musk from the anal scent glands.

Still – The snake remains motionless and does not move from its original position.

Intimidating defensive behaviors:

Biting – The snake strikes with an open mouth and its teeth make contact with the investigator's hand.

Closed-mouth strike – From a defensive posture (defined below) the snake thrusts its head towards the investigator with a closed mouth, but does not make contact.

Defensive posture – The snake has its head off the substrate with the neck in an S-curve and aimed towards the investigator. The body is usually coiled but may be in a series of S-curves.

Dorso-ventral flattening – The snake spreads its ribs while simultaneously lowering its back, giving the snake a ribbon-like appearance.

Gaping – From a defensive posture the snake opens its mouth with the head towards the investigator, but not striking (i.e., there is no forward motion).

Open-mouth strike – From a defensive posture the snake thrusts its head towards the investigator with an open mouth but does not make contact.

Descriptive statistics include the mean ± 95% confidence interval, range, and sample size. I used Student's *t*-tests to compare means. An *F*-test was used to determine whether or not variances between samples were homogenous. If variances differed significantly, *t*-tests assuming unequal variances were used and are indicated with asterisks. Frequencies between phases were compared using the *G*-test and employing Williams' correction factor, which is used to reduce the possibility of committing a type 1 error (Fowler et al. 1998). For the comparison between the responses during the initial and contact phases, snakes were classified as either remaining still (i.e., all responses except fleeing) or fleeing, thus the number of behaviors in each phase equals the number of snakes involved. Conversely, in the general summary of defensive responses, each snake could display more than one behavior during any of the three phases. Therefore, the number of observed responses is equal to or greater than the number of individual snakes. Also, in the comparison between responses between the initial and contact phases I included data from seven snakes observed at the study site not included in the general summary of responses or the documented defensive sequences. For these seven snakes, only the initial phase or initial and contact phases were noted. Alpha for all tests was set at 0.05. With the exception of *G*-tests, which were calculated with pen and paper, all statistical analyses were done in Microsoft Excel 2010.

Figure 2. Dekay's Brownsnake, *Storeria dekayi* in a defensive posture and gaping.

Table 2. Summary of the frequencies of non-intimidating and intimidating defensive behaviors of Dekay's Brownsnake, *Storeria dekayi* during the contact and capture phases.

	Behaviors		
	Non-intimidating	Intimidating	Totals
Contact	52	81	133
Capture	80	10	90
Totals	132	91	223

RESULTS

Initial phase – Twenty-six male (mean SVL 185 ± 16 mm; mean mass 3.8 ± 0.7 g) and 24 female (mean SVL 228 ± 25 mm; mean mass 8.4 ± 2.5 g) *S. dekayi* provided 53 and 35 observations of defensive behavior, respectively. The initial phase had the lowest diversity of responses (n = 3), with remaining still being the most commonly observed behavior (n = 65; Table 1). Of the 88 observations made during the initial phase, 69 (78%) were of snakes that did not flee, whereas 19 (22%) were of those that did. Surface body temperatures (T_s) of male (mean 20.3 ± 1.7° C, range 3.8-28.8, n = 53) and female (mean 19.7 ± 1.8° C, range 7.4-30.6, n = 35) *S. dekayi* were not significantly different (t = 0.45, df = 86, P = 0.65). The T_s of snakes that did not flee (mean 19.4 ± 1.4° C, 3.8-30.6, n = 69) and those that attempted to flee (mean 22.3 ± 2.8° C, 4.8-28.8, n = 19) during the initial phase were marginally significant (t = -1.91, df = 86, P = 0.06).

Contact phase – The same male (n = 26) and female (n = 24) *S. dekayi* observed during the initial phase provided 40 and 30 observations of defensive behavior during the contact phase, respectively. The greatest diversity of responses (n = 9) occurred during the contact phase, with dorso-ventral flattening of the body being the most common behavior observed (n = 42; Table 1). Of the 70 observations made during the contact phase, 38 (54%) were of snakes that did not flee, whereas 32 (46%) were of those that did. The T_s of male (mean 19.1 ± 2.1° C, range 4.6-28.2 n = 40) and female (mean 18.7 ± 2.2° C, range 2.6-30.6, n = 30) *S. dekayi* were not significantly different (t =0.28, df = 68, P = 0.78). The mean T_s of snakes that remained in place (mean = 16.1 ± 2.2° C, 2.6-26.8, n = 38) was significantly lower (t* = -4.85, df = 58, P < 0.0001) than that of snakes that fled (mean 22.3 ± 1.3° C, 15.8-30.6, n = 32) during the contact phase.

The proportions of *S. dekayi* remaining in place and those that attempted to flee were significantly different between initial and the contact phases (G_{adj} = 10.29, df = 1, P < 0.01), with relatively more snakes fleeing during the contact phase (Table 1). The T_s of snakes that exhibited intimidating defensive behaviors (mean = 18.1 ± 1.9° C, 2.6-28.2, n = 44) and those that were non-intimidating (mean = 19.8 ± 2.8° C, 3.8-30.6, n = 27) during the contact phase were not significantly different (t = 1.11, df = 69, P = 0.27).

Capture phase – The 26 male and 24 female *S. dekayi* utilized in the initial and contact phases provided 53

Table 3. Defensive behaviors of Dekay's Brownsnake, *Storeria dekayi*, reported in select references (n = 27) and personally observed.

Defensive Behavior	Sources
Crypsis or concealment	X
Death-feigning	2, 14, 16, 18, 22
Flattening	1, 3, 4, 7, 8, 10, 12, 13, 16, 17, 19, 20, 22, 23, 25, X
Fleeing	7, 13, 16, X
Gaping	X
Head-hiding	2, 16, 22, X
Inflate or puffing up	3, X
Inoffensive	5, 7, 9, 10, 11, 12, 13, 15, 17, 19, 21, 23, 24, 25,26, 27, X
Lip-curling or flaring	12, X
Musking /smearing feces	2, 3, 6, 7, 8, 10, 11, 13, 16, 17, 18, 19, 20, 22, 23, 25, X
Remain still	13, X
Strike posture	3, 10, 12, 13, 18, X
Striking	1, 3, 12, 18, 22, X
Twisting or thrashing	3, 11, 17, X

Sources: 1. Ashton and Ashton 1981; 2. Ballinger et al. 2010; 3. Bartlett 1987; 4. Bartlett 2001; 5. Bishop 1927; 6. Collins et al. 2010; 7. Conant 1938; 8. Conant and Collins 1998; 9. Fowler 1907; 10. Harding 1997; 11. Holman 2012; 12. Hulse et al 2001; 13. Krulikoski 2004; 14. Liner 1977; Logier 1958; 16. Mason and Hill 2008; 17. McCauley 1945; 18. Miller 2013; 19. Oldfield and Moriarty 1994; 20. Palmer and Braswell 1995; 21. Pope 1964; 22. Rowell 2012; 23. Schmidt and Davis 1941; 24. Trauth et al. 2004; 25. Vogt 1981; 26. Froom 1972; 27. Mount 1975; X. Pers. obs.

and 35 observations during the capture phase, respectively. With five behaviors, the capture phase had the second most diverse display of responses (Table 1), of which smearing cloacal contents was the most commonly observed (n = 76) behavior. The proportion of non-intimidating and intimidating defensive behaviors was significantly different between the contact and capture phases (G_{adj} = 61.93, *df* = 1, *P* < 0.01), with *S. dekayi* employing intimidating defensive behaviors relatively less often during capture (Table 2). The T_s of *S. dekayi* that displayed intimidating defensive behaviors during the capture phase averaged 18.8 ± 5.8° C (7.4-26.2, n = 8), compared to an average of 20.5 ± 1.2° C (4.6-30.6, n = 76) for observations of snakes that were non-intimidating (*t* = 1.99, *df* = 82, *P* = 0.41).

Unique sequences of defensive behaviors – Twenty-nine defensive sequences were documented (Appendix 1), with the most commonly observed (n = 14) consisting of snakes initially attempting to flee, thereby skipping the contact phase, and then smearing cloacal contents during the capture phase. The second most common defensive sequence (n = 11) consisted of snakes remaining still during the initial phase, attempting to flee during the contact phase, then smearing cloacal contents during capture. Of 11 snakes that were observed two or more times, six displayed a different sequence during each encounter, whereas the other five individuals repeated one or more sequences from 1-5 times (Appendix 2). For example, an adult female observed on six occasions always remained still during the initial phase. When tapped during the contact phase, she usually flattened her body dorso-ventrally while assuming a defensive posture, followed by striking (n = 4; Figure 1). On one occasion these behaviors were accompanied by gaping (Figure 2), while during another occasion head-hiding preceded the defensive posture and striking. Two other variations included one instance when during the contact phase she only flattened; during the other she attempted to flee during the contact phase. During capture she always smeared the contents of her cloaca.

Figure 3. A Milksnake, *Lampropeltis triangulum* regurgitating a Dekay's Brownsnake, *Storeria dekayi*. Note the smeared feces on the dorsal surface of the *S. dekayi* (arrow).

DISCUSSION

General summary of responses – The results of this study corroborate previous reports of defensive behaviors of *S. dekayi*. For example, in a review of 27 sources (Gray 2014c), the three most commonly reported defensive behaviors were inoffensive/remain still, smearing cloacal contents (i.e., feces), and dorso-ventrally flattening (Table 3). Death-feigning has been reported to occur in *S. dekayi* (Liner 1977; Gerald 2008), but was not observed in the present study. Lip-curling, in which the supralabial scales are curled upward, exposing the teeth, has also been previously reported for *S. dekayi* (Hulse et al. 2001), and was observed on a few occasions during the present study. However, since lip-curling almost always accompanied other behaviors (e.g., dorso-ventrally flattening, gaping, striking) it was not included as a separate category. None of the *S. dekayi* in the present study were observed biting, however, they are capable of doing so (pers. obs.). Smearing of the cloacal contents is apparently used, unsuccessfully, as a defense against Milksnakes. On three occasions juvenile *L. triangulum* regurgitated *S. dekayi* that had feces smeared on them (Figure 3). However, it is possible that feces may have been released after ingestion.

Six of the documented defensive behaviors: dorso-ventrally flattening, defensive posture, closed-mouth and open-mouth striking, gaping, and smearing of the cloacal contents, appear to require a tactile stimulus (i.e., contact) to elicit. However, Gerald and Graziano (2011) observed a *S. dekayi* that smeared cloacal contents over its body without previously being handled. Head-hiding

may also require contact; six of the seven observations of this behavior occurred only after contact was made. Hayes (1987) noted that three *S. dekayi* exhibited head-hiding behavior after being poked and prodded with his finger. Open-mouth striking and gaping were only observed during the contact phase; while smearing of the cloacal contents was only observed during the capture phase. There were no responses that were exclusive to the initial phase.

Initial phase – The low number of defensive responses elicited during the initial phase was not entirely unexpected. Like many snakes, *S. dekayi* are solitary and seclude themselves in shelters or within vegetation to avoid interactions with predators. In the present study, all *S. dekayi* were found beneath debris. It is possible that many of the snakes found had sought the seclusion of the cover objects to rest and may have been sleeping when discovered. The timing of sampling can influence the antipredator behaviors observed (Llewelyn et al. 2010). For instance, a diurnal snake encountered near its overnight retreat early in the morning will likely be cold, thereby substantially influencing its choice of anti-predator tactics (Llewelyn et al. 2010). *Storeria dekayi* are reportedly nocturnal during much of the active season, except in early spring and late fall (Ernst and Barbour 1989). All observations in the present study were made during daylight between 0615 and 1938 hrs. If *S. dekayi* sleep or rest during this time, this would partially explain the lack of a response (i.e., remaining still) for snakes during the initial phase. The number of snakes that fled during the initial phase may have been inflated due to contact with the cover object. For example, if a snake was wedged between the substrate and the cover object, lifting that cover object may have resulted in a tactile stimulus that elicited fleeing behavior.

It was also expected that most snakes during the initial phase would not attempt to flee. Many predators such as birds, some snakes (e. g., *Coluber constrictor*) and some mammals (e. g., cats) are attracted by movement (Edmunds 1974). Remaining still to avoid detection may help protect *S. dekayi* from these visually-oriented predators. It may also be the only option for snakes at low temperatures. Crawling speed of *S. dekayi*, as well as that of other snakes, increases with temperature (Peterson et al. 1993; Keogh and DeSerto 1994; Gerald and Claussen 2007). Thus, a *S. dekayi* with a high body temperature, and the resulting increased crawling speed, would give potential predators a smaller window of opportunity to capture them. Conversely, at lower temperatures, the ability of a snake to flee may be ineffective as a means of escape (Schieffelin and de Queiroz 1991) and require other defensive strategies. In a study of *T. sirtalis* in Manitoba, Shine et al. (2000) observed that snakes with body temperatures ≥ 12° C tended to flee, whereas colder individuals remained cryptic or flattened and/or gaped and struck. They also reported the threshold for flight in *T. sirtalis* was 8-12° C. Incidentally, Shine et al. (2000) also noted that male *T. sirtalis* tended to flee at lower temperatures than females. The threshold for flight in *S. dekayi* has not been determined, but is likely similar to that of *T. sirtalis*. The lowest T_s recorded for a *S. dekayi* that fled during the contact phase in the present study was 15.8° C. During the initial phase *S.dekayi* fled at T_s as low as 2.6° C.

Compared to the number of observations of snakes that remained still (n=69), the sample size for snakes that fled (n =19) during the initial phase was relatively small. Furthermore, the data for snakes that fled during the initial phase contained an outlier value of 4.8° C; the next lowest value was 11.4° C. A follow-up study utilizing a larger sample may detect a more significant difference in T_s between groups. Therefore, during the initial phase of an encounter with a predator, even at normal activity temperatures, it may be advantageous for a snake to remain still rather than flee.

Contact phase – During the contact phase snakes that fled were significantly warmer than those that did not. This may indicate that once a snake reaches a temperature threshold, it is more advantageous to flee than to remain still after contact with a predator. While a greater proportion of snakes attempted to flee during the contact phase than during the initial phase, it was surprising that the majority of individuals would attempt other defensive measures, such as dorso-ventrally flattening. Dorso-ventrally flattening the head and body is assumed to make a snake appear larger and more formidable than it actually is, and when done suddenly may startle a potential predator, giving the snake a moment to escape (Edmunds 1974; Parker and Grandison 1977). It is possible that this behavior is effective against diurnal visually-oriented predators, such as birds, or nocturnal predators with acute night vision. The lower profile may also make the snake harder to grasp. Dorso-ventral flattening of the body ranked as the fourth most commonly observed defensive behavior in the current study; while in a literature review of 27 sources it ranked third (Gray 2014c). Several studies have suggested that lower temperatures elicit more aggressive responses in *Thamnophis* (Fitch 1965; Heckrotte 1967; Arnold and Bennett 1984). However, results from studies by Schieffelin and de Queiroz (1991), and Keogh and DeSerto (1994) support the converse trend. The results of the present study were inconclusive in determining whether or not snakes were more intimidating at lower or higher temperatures.

Capture phase – Tactile cues are readily shown to be important in the rapid change in behavior of many snakes once touched or picked up (Ford and Burghardt 1993). In the present study *S. dekayi* displayed non-intimidating behaviors (e. g., remaining still, fleeing, head-hiding) during the initial phase, followed by considerable intimidating behavior (e. g., flattening, defensive posturing, and striking) during the contact phase. However, once restrained during the capture phase, snakes reverted to employing non-intimidating behaviors, especially smearing of their cloacal contents. Smearing of the cloacal contents on themselves or potential predators appears to be one of the more commonly reported defensive behaviors of *S. dekayi*, and may make the snake unpalatable either by a nasty taste or foul smell. The difference in intimidating defensive responses between the contact and capture phases of *S. dekayi* are somewhat expected. The primary effect of striking in small snakes may be to startle or bluff a potential predator (Greene 1988). This may explain why *S. dekayi* readily strikes during the contact phase, but hardly at all during capture. Based on its universal application by numerous snake lineages (Greene 1997; Ernst and Ernst 2003) smearing of feces must have some positive survival value.

Unique sequences of defensive behaviors – Compared to a sympatric population of the Common Gartersnake, *Thamnophis sirtalis*, *S. dekayi* has a more diverse repertoire; *T. sirtalis* exhibited 27 unique sequences of defensive behaviors, whereas *S. dekayi* had 29 (Gray 2014c). The main difference in the unique sequences of defensive behaviors of *S. dekayi* and *T. sirtalis* is that the latter species more often includes biting as a response. The

more diverse repertoire of *S. dekayi* may be due in part to its relatively smaller size. One would expect smaller snakes to have a greater number of potential predators than larger ones. *Storeria dekayi* are more abundant than *T. sirtalis* at the Erie County site, and predators may encounter the former more frequently than the latter. Juvenile *L. triangulum* at the Erie County site are known to consume *S. dekayi*, but not *T. sirtalis* (Gray 2014a). However, elsewhere *T. sirtalis* is preyed upon by *L. triangulum* (Hulse et al. 2001; Ernst and Ernst 2003). During much of the active season, especially during summer, *S. dekayi* are nocturnal and remain inactive under cover objects during the day. Possibly, *L. triangulum* are hunting *S. dekayi* that are inactive under cover objects. A topic of particular interest for future study would be to determine whether or not *S. dekayi* respond in a stereotypic fashion towards specific predators, such as ophiophagous snakes. For example, rattlesnakes (*Crotalus sp.*) respond to Kingsnakes (*Lampropeltis getula*) with a posture known as body bridging (Klauber 1927; Carpenter and Gillingham 1975). Weldon (1982) noted that *Storeria* and *Thamnophis* exhibited escape reactions (i.e., rapid and vigorous crawling) when placed into a cage with an Eastern Kingsnake (*L. getula*).

Snakes vary widely in their responses to predators, both among individuals within populations and geographically within species (Greene 1988). Herzog and Burghardt (1986) demonstrated significant differences among three species of *Thamnophis* in the defensive behaviors directed towards a threatening stimulus (i. e., a human finger), with *T. melanogaster* being the most reactive. Durso and Mullin (2014) demonstrated that both intrinsic (sex, size) and extrinsic (temperature) factors influenced the death-feigning behavior of Plains Hog-nosed Snakes (*Heterodon nasicus*), and it is likely that a combination of these factors influence the defensive behaviors of *S. dekayi* also. Snakes may also react differently to human interaction than they would when encountering one of their natural predators (Greene 1997). A biting shrew or cat would be expected to produce a different response than being tapped or grabbed by a human hand. Furthermore, laboratory studies have demonstrated that snakes may habituate to repeated testing, in some cases becoming increasingly passive after being handled over several days (Herzog et al. 1989; Glaudas 2004). It is unlikely that free-ranging snakes would become more passive following successive attacks by potential predators. All these examples, and likely many more that could be cited, demonstrate the complex interactions that make interpreting defensive behavior data obtained from snakes in the wild difficult.

The data regarding defensive behaviors of free-ranging *S. dekayi* presented herein establish a baseline for future studies. While the present study documented the defensive responses of exposed snakes, it would be of particular interest to determine whether or not *S. dekayi* respond differently to predators in confined spaces, such as under cover objects, than they would in the open. When a snake is wedged in between a cover object and the substrate, certain defensive responses might not be possible (e.g., striking, fleeing). Also more study is needed to better understand the relationship between T_s and defensive responses of free-ranging *S. dekayi*. *Storeria dekayi* are able to flatten their bodies dorsoventrally while swaying at T_s as low as -0.6 °C (Gray 2014b). Determining the T_s threshold needed for each defensive response to be employed would improve our understanding of such a relationship.

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APPENDIX 1

The following is a summary of the 29 defensive sequences observed in Dekay's Brownsnakes, *Storeria dekayi*, (n = 50) from Erie, Pennsylvania, USA. Defensive behaviors are defined in the text.

Initial Phase	Contact Phase	Capture Phase	Frequency
Still	Flattened Defensive posture Open-mouth strikes	Smeared cloacal contents	6
Still	Flattened Closed-mouth strikes	Smeared cloacal contents	1
Still	Fled	Smeared cloacal contents	11
Fled	N/A Closed-mouth strikes	Flattened	1
Still	Flattened Fled	Smeared cloacal contents	9
Still	Flattened Head-hiding Defensive posture Closed-mouth striking	Smeared cloacal contents	2
Still	Flattened	Remained flattened Smeared cloacal contents	3
Still	Still	Slight movement	2
Still	Flattened Defensive posture Open-mouth strikes Fled	Smeared cloacal contents	3
Still	Head-hiding Flattened Defensive posture	Smeared cloacal contents	1
Still	Still Flattened	Slight movement	2
Still	Still Flattened Fled	Remained flattened Defensive posture Smeared cloacal contents	1
Still	Flattened Head-hiding	Smeared cloacal contents	1
Still	Flattened Defensive posture Closed-mouth strikes Open-mouth strikes	Defensive posture Smeared cloacal contents	1
Still	Flattened Defensive posture Head-hiding Fled	Smeared cloacal contents	1
Still	Still	Smeared cloacal contents	2
Still	Slight movement	Smeared cloacal contents	2
Still	Defensive posture Closed-mouth striking	smeared cloacal contents	1
Still	Still Fled	Smeared cloacal contents	3
Fled	N/A	Smeared cloacal contents	14
Still	Flattened Defensive posture Fled	Smeared cloacal contents	3
Still	Head-hiding Flattened Fled	Smeared cloacal contents	1
Still	Flattened	Smeared cloacal contents	4
Still	Flattened Defensive posture Gaping Open-mouth strikes	Flattened Smeared cloacal contents	1
Still	Flattened Defensive posture Fled	Flattened Defensive posture Smeared cloacal contents	1
Still Head-hiding	Fled	Smeared cloacal contents	1
Still	Flattened Defensive posture	Smeared cloacal contents	1
Still	Defensive posture	Smeared cloacal contents	1
Still Fled	N/A	Smeared cloacal contents	1

APPENDIX 2

Below is a summary of the defensive sequences of individual Dekay's Brownsnakes, *Storeria dekayi*, that were tested twice or more.

Snake ID	Date	Initial Response	Contact Response	Capture Response
Sd 100 F	11-May-14	still	fled	smeared cloacal contents
	30-May-14	still	flattened defensive posture closed- and open-mouth strikes	defensive posture smeared cloacal contents
	31-May-14	still	flattened head-hiding defensive posture open-mouth strikes	smeared cloacal contents
	4-Jun-14	still	flattened defensive posture open-mouth strikes	smeared cloacal contents
	13-Jun-14	still	flattened	smeared cloacal contents
	14-Jun-14	still	flattened defensive posture gaping open-mouth strikes	flattened smeared cloacal contents
Sd 124 M	29-May-14	still	flattened head-hiding	smeared cloacal contents
	31-May-14	still	defensive posture closed-mouth strikes	struggled
	4-Jun-14	still	flattened fled	smeared cloacal contents
	16-Jul-14	still	slight movement	smeared cloacal contents
Sd 225 M	27-Apr-14	still	slight movement	n/a
	31-May-14	still	flattened fled	smeared cloacal contents
Sd 247 F	11-May-14	still	flattened closed-mouth strikes	smeared cloacal contents
	23-May-14	still	fled	smeared cloacal contents
Sd 248 M	13-May-14	still	flattened fled	smeared cloacal contents
	29-May-14	still	flattened	flattened smeared cloacal contents
Sd 255 M	24-May-14	still	still flattened	slight movement
	29-May-14	still	slight movement fled	smeared cloacal contents
	31-May-14	still	slight movement fled	smeared cloacal contents
	13-Jun-14	fled	n/a	struggled
	28-Jun-14	fled	n/a	struggled
Sd 259 F	30-May-14	still	flattened defensive posture head-hiding fled	smeared cloacal contents
	7-Jun-14	still	flattened closed-mouth strikes fled	smeared cloacal contents defensive posture
	13-Jun-14	still	head-hiding flattened fled	smeared cloacal contents
	19-Jun-14	still	flattened defensive posture fled	smeared cloacal contents
	16-Jul-14	still	still	smeared cloacal contents
Sd 265 M	7-Jun-14	still	fled	smeared cloacal contents
	14-Jun-14	still	flattened slight movement open-mouth strikes	smeared cloacal contents defensive posture smeared cloacal contents

APPENDIX 2 - CONTINUED

Snake ID	Date	Initial Response	Contact Response	Capture Response
Sd 268 M	19-Jun-14	fled	n/a	
	25-Jun-14	still	flattened fled	smeared cloacal contents
	12-Jul-14	still	fled	defensive posture smeared cloacal contents
	16-Jul-14	still	flattened fled	smeared cloacal contents
	25-Jul-14	fled	n/a	smeared cloacal contents
	29-Jul-14	still	defensive posture	smeared cloacal contents
	6-Aug-14	fled	n/a	smeared cloacal contents
	9-Aug-14	fled	n/a	smeared cloacal contents
	18-Aug-14	fled	n/a	smeared cloacal contents
Sd 273 M	6-Jul-14	fled	n/a	smeared cloacal contents
	25-Jul-14	still	flattened defensive posture fled	smeared cloacal contents
	29-Jul-14	fled	n/a	smeared cloacal contents
	6-Aug-14	still fled	n/a	smeared cloacal contents
Sd 9001 M	13-Jun-14	still	flattened fled	struggled
	19-Jun-14	still fled	n/a	smeared cloacal contents
	25-Jun-14	still	flattened slight movement fled	smeared cloacal contents
	28-Jun-14	still	flattened	struggled
	25-Jul-14	still	flattened	smeared cloacal contents
	29-Jul-14	still	flattened defensive posture	smeared cloacal contents
	6-Aug-14	still	flattened	smeared cloacal contents