The effects of cues from kingsnakes on the reproductive effort of house mice

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Abstract It is not clear if rodents express inducible defenses in response to reptilian predators such as snakes. We tested the hypothesis that adult house mice Mus musculus decrease aspects of their reproductive effort upon 1 hour of exposure every 48 hours for a 25-day period to the fecal material and shed skins of a euryphagous ophidian predator, the kingsnake Lampropeltis getula, that had been fed mice. We found no significant differences in the total number of offspring born, the number of pups per litter, and the mean weight of pups in litters born to male and female mice that were exposed to predator cues and those mice that were not exposed to such cues. The lack of an inducible response may be associated with the low cost of an effective defense, or the lack of an effective defense against a generalist snake predator [Current Zoology 59 (1): 135–141, 2013].

Keywords Inducible defenses, Breeding suppression, Lampropeltis getula, Mus musculus, Predator-prey interactions

Animals have to deal with the threat of predation (Lima and Dill, 1990) and evolved a variety of anti-predator adaptations to reduce this threat (Harvell, 1990; Apfelbach et al., 2005; Hammill et al., 2008). These adaptations can be described by a continuum, at one end of which the defense is always expressed and is known as a constitutive or primary defense. At the other end of the continuum the defense is only expressed in the presence of a predator; this is known as an inducible or secondary defense. When an organism experiences spatially or temporally variable predation pressure, the effective anti-predator defense has a high cost, and the prey can accurately assess the risk of predation, inducible defenses will be favorable (Tollrian and Harvell, 1999; Moore et al., 2004; Apfelbach et al., 2005). However, if any of these requirements were to disappear, the defense would likely shift towards the other end of the continuum, and become fixed in the population. Inducible defenses can be exhibited as morphological changes, altered physiology and behavior, or shifts in the organism’s life history (Harvell, 1990; Tollrian and Harvell, 1999; Kavaliros and Choleris, 2001). Life history inducible defenses are of special interest, because of the trade-off between survival and reproduction (Frank, 1993; Riessen and Trevett-Smith, 2009; Aránguiz-Acuña et al., 2011).

Rodents have frequently been used as terrestrial models of inducible defenses because they are responsive to the chemical cues from mammalian predators. Unlike cues from other sensory modalities, chemical cues can linger in the environment, and only chemical cues can indicate the immediate or recent presence of a predator without the prey having to encounter them (Lima and Dill, 1990; Van Damme and Castilla, 1996; Vlautin et al., 2010). Thus, chemical cues can alert the potential prey in advance of any predation event, and allow for a greater degree of anti-predator responses. For example, many mammals exhibit varying behavior, space use, activity patterns and odours during reproductive periods (Cushing, 1985a, b). Multiple predators have learned to recognize these cues and exploit them while hunting (Ylönen et al., 1992; Zuk and Kolluru, 1998; Lima and Dill, 1990; Kats and Dill, 1998). In turn, many small mammals exhibit a temporary reduction in their reproductive behavior and physiology upon exposure to predator cues (Apfelbach et al., 2005), which should make the prey less susceptible to attacks from predators. An interesting aspect of the inducible defense research done with predator odour cues is the predator induced breeding suppression shown in field studies of bank voles Clethrionomys glareolus. The results of the studies suggested that the presence of least weasels Mustela nivalis suppressed reproduction in bank voles (Ylönen, 1989). Subsequent laboratory experiments (Ylönen, 1989; Ylönen and Ronkainen, 1994; Ronkainen and Ylönen, 1994; Koskela and Ylönen, 1995) indicated breeding suppression of bank voles by weasels and stoats, M. erminea too. Other researchers found that
Snakes are efficient rodent predators. Some snakes can exploit the scent marks produced by small mammals to signal their presence in an area. Madison (1978) reported that two species of snakes (Coluber constrictor and Elaphe obsoleta) exhibited non-random selection on adult meadow voles Microtus pennsylvanicus by selecting large males and lactating females with pups. Several other experiments deal with mammal defensive responses to reptilian predators, but they all examined behavior and analgesia rather than reproductive responses. For example, increases in sniffing, self-grooming, and escape behavior but not analgesic responses were observed in two strains of inbred mice in response to four-lined rat snake Elaphe quatuorlineata odor cues (Dell’Omo and Alleva, 1994). On the other hand, juvenile, but not adult meadow voles have an analgesic response to ophidian predators (Sakisda et al., 1993), and laboratory mice exhibited acute responses, such as decreased food intake and increased defecation rate in response to the olfactory cues of the rat snake (Weldon et al., 1987). Sex differences were found in the responses of spiny mice Acomys cahirinus to the olfactory cues from the fecal material, dry shed skin, and bedding of a sand boa Eryx jaculus. Specifically, males had a much lower pain threshold and exhibited a greater amount of exploratory behavior upon exposure to snake odors (Carere et al., 1999). This lack of information about the reproductive anti-predator responses of small mammals begs the question: do small mammals suppress aspects of their reproduction when they encounter the cues of snakes that consume them?

Dietary effects on inducible defenses have been well studied in aquatic vertebrates and insects. Chivers and Mirza (2001) reported that aquatic prey responded only to a predator that had been consuming conspecifics. Similar results were obtained in studies using involving terrestrial insects and their insect predators (Venzon et al., 2000). Examples of dietary effects in terrestrial vertebrates are scarce (Pillay et al., 2003), and sometimes the conclusions are contradictory. In studies involving garter snakes as predators, and salamanders and earthworms as prey, one researcher found that salamanders would only respond to the odors of snakes that had eaten conspecifics by avoiding the predator odor (Madison et al., 1999). In contrast, Murray and Jenkins (1999) found that salamanders would respond by avoiding the odors of both salamander-fed and earthworm-fed snake. It may be reasonable to infer that prey species could determine the diet of a potential predator, as several terrestrial vertebrates can determine what conspecifics have eaten by investigating their chemical signals (Galef and Wigmore, 1983; Walls et al., 1989; Vlautin et al., 2010).

In this paper, we determined whether the inducible defenses displayed by adult house mice Mus musculus can be triggered by their exposure to the cues of kingsnakes Lampropeltis getula that were fed a diet of house mice. We did so, by testing the hypothesis that adult house mice decrease aspects of their reproductive effort upon exposure to the shed skin and feces of a euryphagous (generalist) ophidian predator, the kingsnake. We predicted that mice develop inducible defenses, such as reduced reproductive effort, against predators that have consumed them. Specifically, house mice exposed to the cues of a kingsnake that was fed house mice would produce less litters, have fewer pups per litter, and 24 hours after parturition have pups that weighed less than those produced by house mice that were not exposed to cues from a kingsnake.

1 Materials and Methods
1.1 Animals
House mice were 2nd–4th generation males and females originally captured at the Meeman Field Station of The University of Memphis. The mice were kept on a 14:10 L: D cycle (lights on at 7 am, lights off at 9 pm, CST) and in a room in which the temperature was between 23–25 °C. The mice were housed with littermates until they were weaned at 4 weeks of age, and then housed with a same-sex littermate until they were 6 weeks old. The mice were separated from littermates and then housed singly for six weeks before being used in the study. Mice had continuous access to food (Purina Rodent Diet #5008, PMI Inc., St. Louis, MO, USA) and water. Mouse cages lined with wood chip bedding, and were cleaned once a week.

The predator species in this study was the kingsnake. These snakes are constrictors, and they will feed on a wide variety of organisms, including mice (Hubbs, 2009). Nine kingsnakes were used as the sources of predator cues in this experiment; these snakes were captured at the Meeman Field Station of The University
of Memphis 9–18 months prior to the start of the experiment. The kingsnakes were housed separately in opaque plastic boxes (30.5 × 30.5 × 61.0 cm) with a sliding, transparent plastic door, under a natural light cycle. Every snake had access to a hide box, a rough rock and continuous access to water. The kingsnakes were fed only mice, weekly, for the previous 5 months.

We used in shed snake skins and snake fecal material as stimuli in this experiment (Carere et al., 1999; Pillay et al., 2003; Starke and Ferkin, in press). Shed skins and fecal material were hand collected as they were generated from the snakes. Shed skins were kept in a refrigerator, whereas fecal material was kept in a freezer. Fecal material was thawed in the refrigerator the day before it was used in the experiment (Starke and Ferkin, in press). When thawed, the fecal material was quite pungent, and earlier studies recorded behavioral and analgesic effects on rodents exposed to frozen and thawed dry fecal material (Carere et al., 1999). Kingsnake cages were checked once per day for new fecal material and shed skins, and their cages were cleaned as needed. The experiments were approved by The University of Memphis IACUC protocols #0504 and #0506.

1.2 Experimental procedures

We used 48 mice (n = 24 males and n = 24 females) that were housed singly for at least three weeks as subjects in this study; these mice were 12 weeks of age at the start of the study. The mice were sexually mature but were virgins. These mice were weighed to the nearest 0.1 gram and then placed with an opposite-sex conspecific into a clear, breeding cage (30.5 × 35.5 × 22.8 cm). The paired mice were placed into two groups, a treatment group or a control group. The treatment group consisted of 12 pairs of male and female mice. Beginning on the day of pairing, mice in the treatment group received a 10.1 cm piece of shed kingsnake skin and one gram of the snake’s feces. The remaining 12 pairs of males and female received no cues from kingsnakes; these mice were considered to be controls. Starting on the day of pairing, the mice in the control group received a 10.1 cm piece of paper towel soaked in olive oil and one gram olive oil-soaked bedding. Previous studies have used rodents not receiving any snake cues as controls (Ylönen, 1989; Ylönen and Ronkainen, 1994; Fuelling and Halle, 2004; Starke and Ferkin, in press).

We followed the procedures detailed in Starke and Ferkin (in press) to present the stimulus cues to the pairs of mice in the treatment and control groups. For the treatment group, the fecal material mixed with wood shaving (in a Petri dish) and shed skin of the snakes were placed at opposite ends of each pair’s home cage. For the control group, the olive oil-soaked wood shavings (in a Petri dish) and the olive oil-soaked paper towels were placed at the opposite corners of each pair’s home cage. Mice in both the treatment and the control groups were exposed to these stimuli for one hour per day, between 08:00 and 10:00 h CST, every 48 hours, thereafter for 25 days. In all cases, the stimulus cues were removed from the cage of the mice after each one-hour exposure.

The experiment lasted 25 days. Thus, the mice in the control and treatment groups had a total of 13 one-hour exposures to the olive oil-soaked wood shavings and paper and snake cues, respectively. We did not record the amount of time that males and females in the treatment and control groups explored the snake cues and the olive-oil soaked paper and shaving. However, these cues were pungent to the human observers and likely detected by the mice when placed in their cages. Because the experiment lasted 25 days, which encompasses the 3-week gestation of house mice (Bronson, 1979), were able to record measures of pregnancy success of the females in the treatment and control groups by comparing the number of females in both groups that delivered litters. In addition, we were able to measure reproductive success of the females in the treatment and control groups by counting the number of pups born in each litter. These data were analyzed using an independent t-test. We also weighed and the pups in each litter 24 hours after parturition and determined if their body weight differed if they were sired by males and born to females that were or were not exposed to cues from kingsnakes. These data were analyzed using an independent t-test too. Lastly, we compared the body weight of the male and female mice in the treatment and control groups 1 hour before their initial exposure and 1 hour after their final exposure to their respective stimulus. We used a mixed ANOVA including a repeated measure factor (before and after experimental or control treatment), with sex and treatment as between-group variables, followed by Dunn’s multiple pairwise comparisons to detect differences between groups. In all tests, statistical significance was accepted P < 0.05.

2 Results

One male mouse (a participant of the control group) died seven days into the experiment. Therefore, that pair was eliminated from the study. Twenty-three pairs of mice were included in the data analysis (12 pairs from the kingsnake treatment, experimental, group and 11
pairs from the control group). All data were analyzed using SigmaPlot Version 11.0.

2.1 Pregnancy success

The number of females that produced litters did not differ between the control and treatment groups (Binomial Critical Value test, both comparisons, \( P > 0.1 \)). Seven of 10 females in the snake-treatment group delivered litters, whereas 8 of 10 females in the control group delivered litters.

2.2 Reproductive success: Litter size

A total of 123 pups were born in this study; the pups were born one–four days after the mice in the treatment and control groups were given their final exposure to the snake cues or olive-oil soaked cues, respectively. Sixty-eight pups were born to control females and 55 pups were born to females exposed to snake cues. The litter size of control females ranged from 5-11 pups, with the average litter being 8.28 ± 0.79 pups. The litter size of females in the treatment group ranged from 6-10 pups, with the average litter being 7.8 ± 0.34 pups. There was no significant difference in the litter sizes of control and treatment females (\( t_{13} = 0.431, P = 0.674 \)).

2.3 Weight of pups in the litter

The weight of pups delivered by females exposed to snake cues ranged from 1.36 – 1.85 grams, with the average pup weight being 1.55 ± 0.07 grams. The weight of pups delivered by females in the control group ranged from 1.43 – 1.72 grams, with the average weight per pup being 1.57 ± 0.04 grams. There was no significant difference between the average weight of pups delivered by control and treatment females (\( t_{13} = 0.24, P = 0.814 \)).

2.4 Before and after weight of adult mice

The initial and final body weight of males and females in the snake cue and control groups differed (\( F_{3,42} = 5.89, P = 0.002 \)). There was a significant difference in body weights between initial and final body weights based upon sex (\( F_{1,42} = 21.511, P < 0.0001 \)), but not based upon treatment (\( F_{1,42} = 2.284, P = 0.138 \) or based upon the interaction of treatment and sex (\( F_{1,42} = 0.152, P = 0.698 \)). We did find a significant difference in the body weights of all females at the beginning and end of the experiment. Females gained weight during the study (Fig. 1); this effect may be due to gestation and lactation (Holm Sidák, \( P < 0.05 \)). Males, on the other hand, showed the opposite pattern (Holm Sidák, \( P < 0.05 \)). Males in both groups lost weight during the study (Fig. 2).

3 Discussion

We found no differences between the treatment and control groups in number of births, number of pups per litter, or mean weight of pups at birth, or mean weight of pups. These findings lend support to the hypothesis that captive mice do not alter reproductive effort in response to the shed skin and feces of an ophidian predator. Most of the earlier studies found their evidence of breeding suppression in decreases in the number of litters produced or juvenile recruitment (Ylönen, 1989; Ylönen and Ronkainen, 1994), and decreases in the proportions of reproductively active females (Fuelling and Halle, 2004). However, Ylönen and Ronkainen
(1994) reported that no differences existed between the litter sizes of the parent groups, despite having a reduction in the number of treatment pairs that produced litters. Heikkilä et al. (1993) also found a decrease in the average pup weight in predator odor-exposed red voles Clethrionomys rutilus without a litter size effect. In contrast, body weight responses of other prey organisms to mammalian predator odors have varied in past studies. For instance, Ylönen and Ronkainen (1994) reported that males and old female bank voles lost weight over the course of an experiment in which they were exposed to stoat cues, but other researchers reported no change in body weights for voles (Sundell et al., 2004) and rabbits exposed to fox odor (Monclús et al., 2005). Monclús et al. (2005) suggested that prey items under constant predation threat might be forced to feed, despite the risk.

The lack of a reproductive inducible defense for mice in response to a snake differs with earlier the research done with rodents and mammalian predators and was somewhat surprising. We offer several possible explanations for our findings. It should be noted that not all of the following conjectures are mutually exclusive. First, house mice may be unable to interpret the chemical cues of the kingsnakes as a threat. However, this seems unlikely in light of the observed acute anti-predatory responses that other rodents have shown to chemical cues from reptiles and other snakes (Weldon et al., 1987; Dell’Omo and Alleva, 1994; Carere et al., 1999). In addition, some snakes may attempt to conceal their fecal matter from potential prey items (Pillay et al., 2003). It is possible, that house mice do not view a kingsnake as a great a threat of predations compared to mammalian predators, such as mustelids, which cause rodents to alter their behavior (Ylönen, 1989; Jędrzejewski et al., 1993, Ylönen and Ronkainen, 1994; Koskela and Ylönen, 1995; Fuelling and Halle, 2004). Second, kingsnakes do not have a temperature regulation demand added to their resting metabolic rate, and thus do not need to consume as much food per body weight as endotherms (Pough, 1980). Some snakes can go months without eating (Hubbs, 2009), and thus the mouse may have given birth and weaned her litter before the snake began hunting again and the need to express an inducible defense against them make not be needed. However, most snakes will not wait until they have absolutely exhausted their metabolic stores before they begin hunting again, and many of the snakes in this study would kill and consume prey items as frequently as they were offered (Hubbs, 2009; personal observations).

Third, snakes also become inactive when they are about to slough their skin (Hubbs, 2009); perhaps, mice are aware of the snake’s potential for inactivity. Next, it is possible that kingsnakes, being food generalists that do not exclusively consume house mice (Hubbs, 1999), do not induce a reduction of reproductive effort in house mice. In our study, however, mice were exposed to snakes that only consumed house mice. This suggests that house mice did not learn that kingsnakes were predators and do not display inducible defenses related to reproductive capacity against them. Last, the lack of an antipredator response related to reproductive capacity may be due to the fact that the mice were exposure to kingsnake cues for only 1 hour every 48 hours for a 25-day period. Perhaps, house mice require a longer exposure to the cues of a kingsnake to have a reduction in reproductive capacity. Although this is possible, it is unlikely that free-living mice dams would not move their nests away from predators with whom they have prolonged or continuous exposure (Dickman, 1992). Nevertheless, it seems highly disadvantageous for a prey item to assume that there is no threat. Models and empirical data suggest that it is almost always better for prey to overestimate the risk of predation that to underestimate it (Bouskila and Blumstein, 1992; Dickman, 1992).

We also cannot rule out the possibility that since we used 4th generation of laboratory-raised house mice their inducible defenses were somehow lost due to captivity or their lack of exposure to predators. This seems unlikely, however. Bramley et al. (2000) found that wild rats from a New Zealand island devoid of mammalian predators, avoided five of six mammalian predator odors. In addition, Fuelling and Halle (2004) used field sites with historically low rates of predation, and attributed their findings to the fact that mustelids are common predators of the species. Moreover, it is difficult to imagine that selection against inducible defenses would appear so quickly in house mice that originated from a free-living population. However, it is not inconceivable that inducible defenses may be turned on and off (Rissien and Trevett-Smith, 2009).

A more parsimonious explanation for our findings, however, may be that house mice maintain reproductive status despite high predation risk because there are opportunistic breeders that require an extremely high rate of reproduction (Bronson, 1979). House mice can breed as long as a sufficient amount of food is available to maintain reproduction (Bronson, 1979). From an evolutionary perspective, it is likely that adult house mice
may not possess an inducible defense against snake predators because the costs of long term responses are too high when compared to the benefits (i.e., Frank, 1993, Hammill et al., 2008).

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