

Terrestrial Salamanders Alter Antipredator Behavior Thresholds Following Tail Autotomy

MARGARET M. BLISS AND KRISTEN K. CECALA¹

Department of Biology, University of the South, Seawanee, TN 37383, USA

ABSTRACT: Prey animals avoid and survive encounters with predators through morphological and behavioral mechanisms, but these defenses can negatively affect fitness when individuals forgo foraging and reproductive opportunities. Although many studies have focused on the costs associated with antipredator behavior, few have evaluated how that behavior changes immediately following a nonlethal interaction with a predator. Understanding how differences in species ecology (i.e., autotomy and regeneration capabilities) influence antipredator behaviors prior to and following a predation attempt could provide insight into how animals cope with living among predators. In this study, we evaluated the antipredator and compensatory behaviors of Northern Zigzag Salamanders (*Plethodon dorsalis*) to determine how attempted predation affects behavioral responses to perceived predation risk. In a laboratory setting, we performed behavioral assays evaluating escape distance, exploratory movements, cover use, eating habits, and temperature preferences on individuals assigned to attacked (tail autotomy) and control treatments. We found differences in antipredator and compensatory responses between the two treatments, indicating that responses change relative to previous experiences with predators and present risk of predation. Our results indicate that attacked individuals had lower thresholds to elicit a behavioral response relative to control individuals and compensated for loss of resources and decreased locomotive ability by selecting warmer-temperature microhabitats. This study provides insight into how individuals cope with living amongst predators and emphasizes the need to explore behavioral changes following predation.

Key words: Caudata; Compensatory behavior; Defense; Postattack; Preattack; Regeneration

PREY INDIVIDUALS avoid lethal interactions with predators via behavioral modifications including activity and habitat selection (Ives and Dobson 1987; Lima and Dill 1990; Lima 1998; Roberts and Liebgold 2008), morphological traits (Harvell 1990; Anholt and Werner 1999; Tollrian and Harvell 1999), and chemical defenses (Pasteels et al. 1983; Trigo 2000). Prey have evolved these mechanisms to interrupt the predation sequence before and after detection and/or attack (Brodie et al. 1991; Bateman et al. 2014). Prey decrease probability of attack by using preattack defenses such as reducing activity or through specialized coloration (e.g., aposematic coloration or camouflage; Bateman et al. 2014). Prey decrease probability of mortality after attack or during a predator–prey encounter with postattack defenses including flight or morphological armor (Bateman et al. 2014). In the absence of mortality, preattack defenses can result in reduced foraging, and postattack defenses can involve energy expenditure and might incur substantial injury risk (Bateman et al. 2014). These antipredator mechanisms lead to a greater chance of survival, which should, in theory, result in greater reproductive success, but foregoing feeding and mating also affects prey fitness by lowering rates of growth and fecundity (Peckarsky et al. 1993; Lind and Cresswell 2005; Creel and Christianson 2008).

Prey must be able to balance energetic demands and fitness consequences with predator avoidance in order to survive. Although foraging and mating increase energy gains and overall fitness, prey can become conspicuous and vulnerable to predation (Sih 1992; Brown 1999; Brown et al. 2006). In other words, selection for the defense that maximizes survival rates relative to mortality rates results in the fittest individuals who are also able to detect potential predators accurately (Ducey and Brodie 1983; Brodie et al. 1991; Bateman et al. 2014). Past research (e.g., Brown et al.

2006) has established that the intensity of current antipredator behavior is an accumulation of immediate predation threat and previous exposure to or interactions with predators. Brown et al. (2006) identify how current and background predation risk influences the intensity of, and the threshold at which, an antipredator response is elicited in cichlid fish. Specifically, subjects experiencing frequent, high-risk alarm cues exhibit lower-intensity response relative to those individuals exposed to infrequent, low-risk cues. Prey might thus resolve the conflicting demands of fitness-enhancing activities by adjusting their threshold relative to the environmental context (Brown et al. 2006).

Tail autotomy, the deliberate severing of the tail aligned with a fracture plane in caudal vertebrae, is one last-chance antipredator mechanism used by salamanders (Wake and Dresner 1967; Beneski 1989). This defense increases prey survival by facilitating escape while the predator is distracted, and tail injury occurs in a manner to minimize fluid loss and tissue damage (Wake and Dresner 1967; Beneski 1989; Bely and Nyberg 2009). Additionally, because individuals utilizing tail autotomy are able to regenerate the lost structure, long-term costs associated with the tail's absence are negated (Bely and Nyberg 2009). Although tail autotomy results in immediate survival when alternative antipredator mechanisms fail, it compromises an individual's future survival and fitness (Marvin and Lewis 2013). Autotomized salamanders lose important fat energy reserves from the tail, and experience decreased locomotive ability and reproductive success (Mairona 1977; Scott and Fore 1995). Tail regeneration is also costly because it requires high caloric replacement and increases susceptibility to other physiological stressors (Marvin and Lewis 2013). Studies broadly focusing on antipredator costs have neglected to evaluate how prey behaviors change immediately postsurvival (i.e., after an unsuccessful predation attempt).

We studied the antipredator and compensatory behaviors in Northern Zigzag Salamanders (*Plethodon dorsalis*) to

¹ CORRESPONDENCE: e-mail, kkeccala@sewanee.edu

determine whether individuals act and perceive predation risk differently following a simulated predation attempt. Specifically, our study sought to evaluate exploratory movements, temperature preference, cover use, escape distance, and feeding rate in order to determine whether autotomized *P. dorsalis* individuals compensate and behave differently following an attack. Overall, we hypothesized that individuals will alter their behaviors in order to decrease vulnerability and risk effects associated with tail autotomy and predation. We predicted that attacked salamanders would increase antipredator behaviors by exploring less and using refuge more to avoid future detection by predators (Brodie et al. 1974). Reduced exploration might reflect compensation for the cost of regenerating the tail as an energetic trade-off between tail regeneration and overall activity levels. We also hypothesized that individuals will occupy warmer environments and increase feeding to compensate for energetic costs associated with tail loss and regeneration. Finally, we predicted that behavioral thresholds for escape movements would be lower for recently attacked individuals relative to control individuals.

MATERIALS AND METHODS

We evaluated the compensatory and antipredator behaviors of *P. dorsalis* because they are abundant in Tennessee, USA and experience tail autotomy (Bishop 1943). We had two different collection periods in March–April and October–November 2015, resulting in two separate combinations of treatments. We collected a total of 82 adult *P. dorsalis* individuals (snout–vent length [SVL] 34–47 mm; total length 48–85 mm) by flipping rocks and logs in a forested riparian area, and by looking in sandstone crevices at two sites located ~1.6 km apart in Sewanee, Franklin County, Tennessee that were visited during both collection periods. We did not collect any individuals having evidence of prior tail autotomy (e.g., coloration differences, blunt tail tips). During the first treatment period (March–April 2015; mean air temperatures of 8.6–13.3°C), we tested exploration, cover use, and feeding habits ($n = 20$ for each treatment). During the second treatment period (October–November 2015; mean air temperatures of 8.8–13.8°C), we evaluated escape distance and temperature preference ($n = 21$ for each treatment). Each of these time periods occur during the cooler season when *P. dorsalis* is surface active and likely to encounter predators (Petranka 1998). *Plethodon dorsalis* was housed at 10°C in Ziploc bags with moist paper towels prior to experimentation and were maintained for a maximum of 48 h before their behaviors were quantified. Before trials began, we measured body length (SVL and total length; ± 1 mm) and body mass (± 0.1 g), and then randomly assigned individuals to a predation or control treatment. Salamanders were tested in the order in which they were randomly assigned to a treatment ensuring interspersed observations of individuals from both treatments. The 42 salamanders assigned to the predation treatment experienced autotomy of 5–10% of the tail length by our applying pressure with forceps 2 mm from the tail tip, while the remaining 42 salamanders in the control group did not undergo tail loss. Experimental enclosures were 35 × 30 × 5-cm clear plastic boxes (marked with 28 5 × 5-cm squares on the bottom) in which subjects were tested individually.

Individuals from the first collection period (March–April 2015) experienced behavioral assays in the following order: exploratory movements, refuge use, and eating habits. In a room with indirect lighting (shaded windows) and immediately following tail autotomy (i.e., no acclimation period), we positioned control or attacked individuals alone in the center of an experimental enclosure. During a 20-min trial, we monitored exploration by tallying the percentage of squares in the enclosure entered by more than 50% of the salamander's body length. Enclosures for up to six subjects were placed on the ground, and we observed salamanders from a distance of 2 m and height of 1.25 m to minimize our effect on their behavior. Exploration trials began between 1400 and 1800 h at room temperature (18.3°C) and were immediately followed by the cover use and eating habit studies.

To test the hypotheses addressing cover use and eating habits, we housed individuals at 11.5°C and 96% relative humidity with a 10 : 14 h light : dark cycle in the test enclosures for 4 d with two damp paper towels as refuge and five crickets (3.2 mm) as potential prey. Individuals were checked daily in the morning (0900 to 1100 h), afternoon (1300 to 1600 h), and evening (1700 to 2000 h) to record cover use and number of crickets eaten for a total of 12 data points per individual.

Individuals ($n = 41$) captured during the second collection period (October–November 2015), experienced behavioral assays in the following order: escape distance after two simulated attacks followed immediately by a temperature preference assay. These behavioral assays were conducted using similar ambient parameters as the first set of behavioral assays at room temperature (i.e., indirect lighting, 1400 to 1900 h; 18.3°C), but each individual completed both sets of trials before the next individual was observed. To measure escape distance following predation, we individually acclimated all salamanders to the test enclosures for 5 min, then simulated a predator encounter by either autotomizing the tail or touching the tail (control treatment) with forceps. After initiating the treatment, we used a ruler to measure the Euclidean distance an individual moved from its starting position within the enclosure until it stopped moving for 5 s (Attempt 1). Five minutes later, we touched each individual's tail with forceps and measured the escape distance a second time (Attempt 2). All escape distance trials were conducted on a lab bench, and distance measurements did not result in salamanders changing position. We monitored temperature selection by placing an individual at the midpoint of a 1.75-m-long gutter lined with 5-mm damp plantation soil (ExoTerra), which was only altered by adding water to maintain soil saturation throughout the study. Although salamanders are known to use conspecific cues to locate themselves, interspersing observations of individuals from different treatments minimized bias that could be introduced by conspecific cue use that might encourage co-location or avoidance (e.g., Lutterschmidt et al. 1994; Gautier et al. 2006). One end of the gutter was placed on a hot plate set to the first or second heat setting and the other positioned in an ice bath to develop a thermal gradient from 2–27°C (Strickland et al. 2016). Although the gradient was not linear between these temperature extremes, a range was provided to allow for selection (see Appendix). We measured soil temperature

with the use of a thermometer (General Deluxe Digital Stem Thermometer) at each salamander's position within the enclosure every 20 min for six total observations over 2 h.

STATISTICAL ANALYSES

We finished behavioral assays with sample sizes of 20 and 21 subjects per treatment for the first and second experimental periods, respectively. We performed an a priori power analysis that indicated the power of our analyses would be 0.87 for a moderate effect size ($d = 0.5$). For repeated observations of position, we used frequency of refuge use data for each individual, or averaged temperature preference, to evaluate a single measure for these behavioral assays.

Because individuals were evaluated in two or three behavioral assays, we assessed our overall hypothesis that treatment (control or attacked) affected antipredator (escape distance, exploration, cover use) and compensatory (temperature preference, feeding rate) behaviors using repeated-measures multivariate analyses of covariance (MANCOVAs), with the individual as the repeated measure. Individuals were either assayed for exploratory movement, refuge use, and feeding rate or escape distances and temperature preference. Therefore, we conducted a repeated-measures MANCOVA for each set of treatments. Finally, we included size as a covariate that might allow large individuals to move further than small individuals. If individual identifier or size was a significant predictor in our MANCOVAs, we included the variables in post hoc univariate ANCOVAs to assess treatment effects on each behavioral response. For escape-distance trials, we performed a two-factor ANOVA evaluating if treatment and time interacted (predation Attempt 1 versus 2). To evaluate differences among groups, a Tukey post hoc analysis was performed for the escape distance trials. All statistical analyses were performed in R (R Development Core Team 2014) and, unless otherwise stated, values are reported as means \pm 1 SE.

RESULTS

The MANCOVAs for exploratory movement, refuge use, and feeding rate revealed no effect of treatment ($Pillai_{3,37} = 0.14$, $P = 0.13$) or individual ($Pillai_{3,37} = 0.13$, $P = 0.15$), but that these dependent variables were affected by individual size ($Pillai_{3,37} = 0.22$, $P = 0.04$). Attacked salamanders moved into different squares 1.70 times more frequently than control salamanders during the 20-min trial period. We observed an interaction of treatment with size (Fig. 1A; $F_{1,38} = 6.64$, $P = 0.01$). Size was positively associated with exploration in the control treatment but negatively associated with exploration in the attacked treatment. Attacked salamanders did not use refuges more often more than control salamanders (Fig. 1B; $F_{1,38} = 0.11$, $P = 0.57$), but refuge use was higher in larger individuals ($F_{1,38} = 8.98$, $P = 0.005$). No difference in prey consumption was observed between the two treatments (Fig. 1C; $F_{1,37} = 0.39$, $P = 0.36$), or in association with size ($F_{1,38} = 1.24$, $P = 0.27$).

The MANCOVAs for temperature and escape distances from simulated attack revealed an effect of treatment ($Pillai_{3,37} = 0.35$, $P = 0.002$), but no significant effects of individual ($Pillai_{3,37} = 0.06$, $P = 0.55$) or size ($Pillai_{3,37} = 0.099$, $P = 0.30$). An ANOVA revealed that attacked

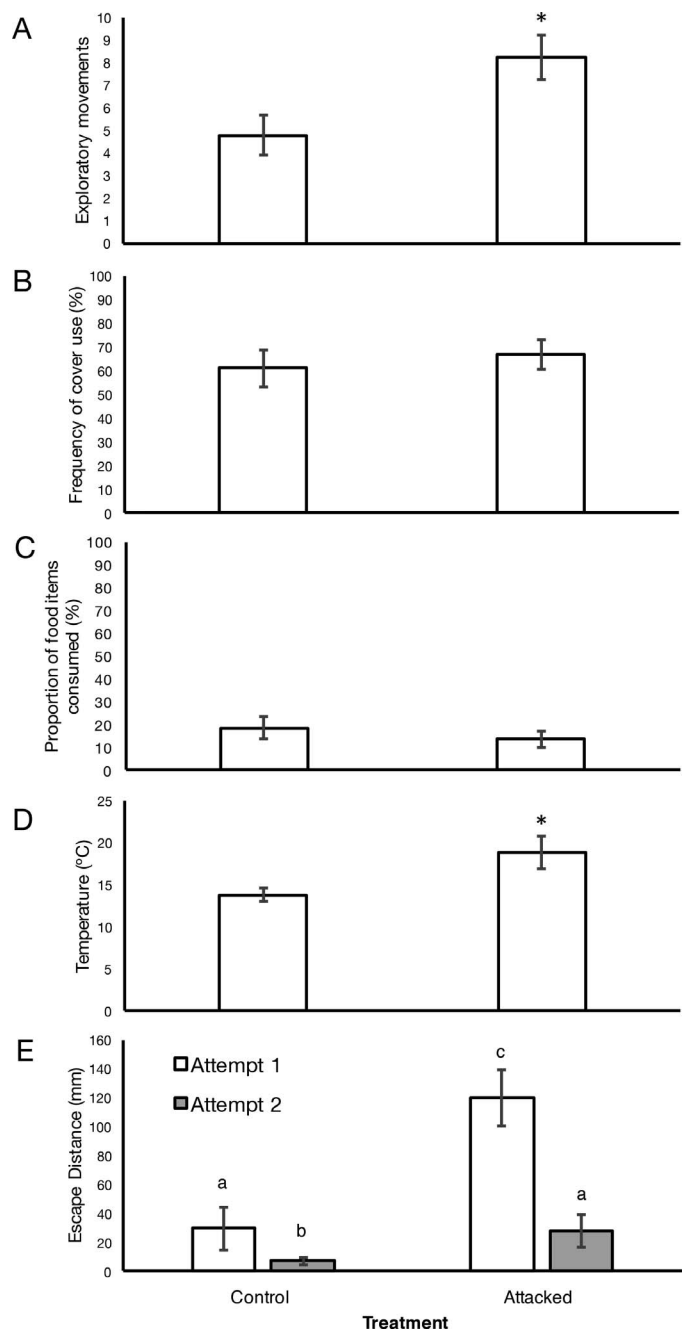


FIG. 1.—Compensatory and antipredator behaviors of *Plethodon dorsalis* assigned to attacked and control treatments in terms of exploration (A), cover use (B), prey item consumption (C), temperature preference (D), and escape distance after two predation attempts (E). Asterisks and letters indicate statistically significant differences as indicated by Tukey post hoc tests. Values are shown as means \pm 1 SE.

salamanders selected warmer microhabitats ($18.9 \pm 2.0^{\circ}\text{C}$), whereas control salamanders selected cooler microhabitats ($13.8 \pm 0.8^{\circ}\text{C}$; Fig. 1D; $F_{1,42} = 50.0$, $P = 0.03$). There was a significant interaction between treatment and time in the escape distance trials (Fig. 1E; $F_{2,46} = 4.72$, $P = 0.01$). Although both groups experienced a diminished response to the second predation attempt, the difference was greatest in attacked individuals with attacked salamanders fleeing 4.0 times further than control individuals immediately after tail

autotomy (Attempt 1) and 3.9 times further than control individuals after the second predation attempt (Fig. 1E).

DISCUSSION

Experiments involving unsuccessful predation resulting in injury have documented that animals alter their behavior following attempted predation. In this study, we simulated a predation attack and quantified subsequent behaviors of *P. dorsalis* and found that autotomized individuals alter their antipredator and compensatory behaviors following tail autotomy. We found that attacked individuals altered exploratory movements, escape distance, and temperature preference, but not refuge use or feeding rate. Our results demonstrate that salamanders compensated for tail loss by preferring warmer microenvironments that might accelerate the physiological processes of tail regeneration or healing, but not by increasing feeding rates. Attacked *P. dorsalis* exhibited greater antipredator responses immediately following treatment by fleeing further than control subjects from a second touch stimulus. Contrary to our refuge and exploration hypotheses, autotomized salamanders did not use cover more frequently and explored a novel enclosure more than control individuals, although we did observe an interaction with size. Larger, and presumably older, salamanders explored enclosures at higher rates than smaller individuals in the control treatment, but explored at lower rates than smaller individuals in the attacked treatment. These results indicate that adults might have prior experience with attacks and that immobilization following attack might be a learned antipredator strategy (Ferrari et al. 2008).

Our results support the hypothesis that attacked salamanders would flee following induced tail autotomy, most likely to avoid subsequent attacks (Heithaus et al. 2009), but we found that attacked salamanders explored more in a novel setting following simulated attack, which contradicted our hypothesis that they would remain immobile in a novel environment. Because we did not provide refuge within the novel enclosure, attacked salamanders could have increased movement behavior in an attempt to find cover (Martin and Lopez 2001). Although attacked individuals with shorter tails could have a maneuverability advantage, individuals with autotomized tails tend to experience decreased locomotion, making this non-adaptive explanation unlikely (Mairona 1977). Furthermore, semiaquatic plethodontids retained maximal swimming performance with 70% of their tail length, but terrestrial movement speed was unimpeded after autotomy (Marvin 2010, 2013). Additionally, autotomized salamanders in this study preferred warmer microhabitats during temperature preference trials, potentially a compensatory response to tail autotomy to increase physiological rates associated with tail regeneration. Warm temperatures raise metabolism and energy requirements (Feder 1983), increase the rate of physiological processes such as tail regrowth (Marvin and Lewis 2013), enhance escape performance (Marvin 2013), and alter outcomes of competitive interactions (Wise and Jaeger 1998; Liles et al. in press), any of which could lead to greater survival in environments with high predation risk and competition.

The similarity in use of cover by *P. dorsalis* assigned to the two treatments could be attributed to the high relative humidity values within their housing enclosures. In natural habitats, plethodontid salamanders prefer cool, moist environments that allow them to maintain high rates of oxygen uptake through the skin, making them less likely to retreat to refugia (Spotila 1972; Feder 1983). We also did not detect a difference in feeding rates between individuals in the two treatments. Marvin and Lewis (2013) report that increased feeding positively affects tail regeneration in salamanders. Whereas salamanders lost 60% of their tail in the Marvin and Lewis (2013) experiment, we autotomized 5–10% of the tails of our subjects, which could indicate that compensatory feeding responses might be conditional upon the quantity of fat loss. Plethodontids have a relatively low metabolic rate that allows them to fast for long periods of time (Feder 1983). The 4-d period during which we studied prey consumption in *P. dorsalis* might have been too brief to evaluate this compensatory behavior properly. Finally, these trials occurred early in the active period of *P. dorsalis* when they might allocate more energy toward reproduction rather than compensating for tail autotomy (Petranka 1998). Further studies with longer feeding trials, and those that measure individual change in mass, are needed to evaluate changes in feeding rates properly.

Our study supports the idea that antipredator and compensatory behaviors change relative to previous experiences with predators and present risk of predation. The results from our movement and escape distance experiments indicate that attacked salamanders reacted to a predation attempt according to the threat-sensitive predator hypothesis, which posits that prey evaluate local predation risk and respond according to the degree of the immediate threat (Helfman 1989; Helfman and Winkelman 1997; Brown et al. 2006). Attacked salamanders responded to a simulated predator attack by fleeing further than control salamanders, indicating that attacked salamanders had a lower threshold posttreatment (the minimum amount of predation risk to elicit behavioral responses; Brown et al. 2001; Mirza and Chivers 2003; Brown et al. 2006). Individuals that did not experience attempted predation had a higher behavioral response threshold consistent with the risk-allocation hypothesis, which maintains that prey should not respond to alarm cues when there is no immediate threat in an environment (Lima and Bednekoff 1999; Brown et al. 2006). We found consistent differences in the thresholds required to elicit behavioral responses to perceived risk in *P. dorsalis*. These results are consistent with studies in which lizards with autotomized tails had higher perceived risk (Downes and Shine 2001; Cooper 2003), but we observed a rapid decline in this threshold over 5 min between Attempt 1 and Attempt 2. Salamanders with intact tails could have higher behavioral thresholds (i.e., only respond to high levels of risk) because they did not experience a recent attack or because they still have tail autotomy as a last line of defense should predation risk suddenly increase. Further studies should investigate if behavioral thresholds in salamander species vary based on their locomotory reliance on the tail (e.g., Bennett et al. 1989).

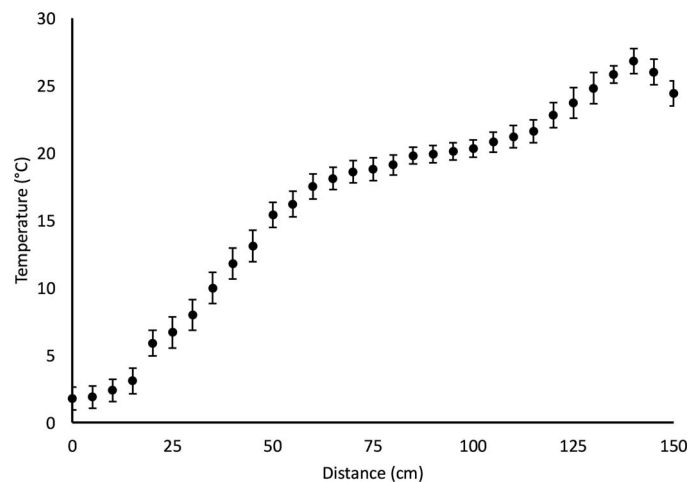
The present study identifies how last-chance antipredator mechanisms change behavioral thresholds based on assessment of risk. Because few studies exist on animal behavior immediately postsurvival, we recommend that future studies evaluate antipredator and compensatory behavioral differences between animals capable and incapable of autotomy and regeneration. Moreover, our study demonstrates that survivors of a predation attempt act differently than conspecifics not experiencing an attack, but further research must evaluate how long these behavioral differences persist. Beginning to understand how differences in species ecology (i.e., autotomy and regeneration capabilities) influences antipredator behaviors prior to and following a predation attempt could provide insights into how animals cope with living among predators.

Acknowledgments.—We thank S. Drukker, B. Sadler, N. Hua, M.C. Murphy, B. McKenzie, A. Emerson, and G. Frupp for help with specimen collection, and K. McGhee and M. Schrader for comments that improved earlier drafts of this manuscript. All research was carried out in accordance with an approved protocol from the University of the South Animal Care and Use Committee (Cecala-7-2015), and a Tennessee Scientific Collection Permit (#3970).

LITERATURE CITED

- Anholt, B.R., and E.E. Werner. 1999. Density-dependent consequences of induced behavior. Pp. 218–230 in *The Ecology and Evolution of Inducible Defenses* (R. Tollrian and C.D. Harvell, eds.). Princeton University Press, USA.
- Bateman A.W., M. Vos, and B.R. Anholt. 2014. When to defend: Antipredator defenses and the predation sequence. *American Naturalist* 183:847–859.
- Bely, A.E., and K.G. Nyberg. 2009. Evolution of animal regeneration: Re-emergence of a field. *Trends in Ecology and Evolution* 25:161–170.
- Beneski, J.T., Jr. 1989. Adaptive significance of tail autotomy in the salamander, *Ensatina*. *Journal of Herpetology* 23:322–324.
- Bennett, A.F., T. Garland, and P.L. Else. 1989. Individual correlation of morphology, muscle mechanics, and locomotion in a salamander. *American Journal of Physiology, Regulatory, Integrative and Comparative Physiology* 256:R1200–R1208.
- Bishop, S.C. 1943. *Handbook of Salamanders: The Salamanders of the United States, of Canada, and of Lower California*. Comstock Publishing Company, USA.
- Brodie, E.D., Jr., J.A. Johnson, C.K. Dodd, and C.K. Dodd, Jr. 1974. Immobility as a defensive behavior in salamanders. *Herpetologica* 30:79–85.
- Brodie, E.D., Jr., D.R. Formanowicz, Jr., and E.D. Brodie, III. 1991. Predator avoidance and antipredator mechanisms: Distinct pathways to survival. *Ethology Ecology and Evolution* 3:73–77.
- Brown, G.E., J.C. Adrian, Jr., T. Patton, and D.P. Chivers. 2001. Fathead minnows learn to recognize predator odour when exposed to concentrations of artificial alarm pheromone below their behavioral-response threshold. *Canadian Journal of Zoology* 79:2239–2245.
- Brown, G.E., A.C. Rive, M.C.O. Ferrari, and D.P. Chivers. 2006. The dynamic nature of antipredator behavior: Prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behavioral Ecology and Sociobiology* 61:9–16.
- Brown, J.S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research* 1:49–71.
- Cooper, W.E., Jr. 2003. Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). *Behavioral Ecology and Sociobiology* 54:179–187.
- Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23:194–201.
- Downes, S.J., and R. Shine. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82:1293–1303.
- Ducey, P.K., and E.D. Brodie, Jr. 1983. Salamanders respond selectively to contacts with snakes: Survival advantage of alternate strategies. *Copeia* 1983:1036–1041.
- Feder, M.E. 1983. Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica* 39:291–310.
- Ferrari, M.C.O., F. Messier, and D.P. Chivers. 2008. Larval amphibians learn to match anti-predator response intensity to temporal patterns of risk. *Behavioral Ecology* 19:980–983.
- Gautier, P., K. Olgun, N. Uzum, and C. Miaud. 2006. Gregarious behaviour in a salamander: Attraction to conspecific chemical cues in burrow choice. *Behavioral Ecology and Sociobiology* 59:836–841.
- Harvell, C.D. 1990. The ecology and evolution of inducible defenses. *Quarterly Review of Biology* 65:323–340.
- Heithaus, M.R., A.J. Wirsing, D. Burkholder, J. Thomson, and L.M. Dill. 2009. Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78:556–562.
- Helfman, G.S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology* 24:47–58.
- Helfman, G.S., and D.L. Winkelman. 1997. Threat sensitivity in bicolor damselfish: Effects of sociality and body size. *Ethology* 103:369–383.
- Ives, A.R., and A.P. Dobson. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. *American Naturalist* 130:431–447.
- Liles, L.A., K.K. Cecala, J.R. Ennen, and J.M. Davenport. In press. Elevated temperatures alter competitive outcomes and body condition in southern Appalachian salamanders. *Animal Conservation*. DOI: <http://dx.doi.org/10.1111/acv.12342>.
- Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- Lima, S.L., and P.L. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Lima, S.L., and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* 16:945–956.
- Lutterschmidt, W.I., G.A. Marvin, and V.H. Hutchinson. 1994. Alarm response by a plethodontid salamander (*Desmognathus ochrophaeus*) conspecific and heterospecific “Schreckstoff.” *Journal of Chemical Ecology* 20:2751–2759.
- Mairona, V.C. 1977. Tail autotomy, functional conflicts and their resolution by a salamander. *Nature* 265:533–535.
- Martin, J., and P. Lopez. 2001. Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. *Behavioral Ecology* 12:386–389.
- Marvin, G.A. 2010. Effect of caudal autotomy on aquatic and terrestrial locomotor performance in two desmognathine salamander species. *Copeia* 2010:468–474.
- Marvin, G.A. 2013. Critical tail autotomy for reduction of maximal swimming performance in a plethodontid salamander (*Desmognathus quadramaculatus*). *Journal of Herpetology* 247:174–178.
- Marvin, G.A., and M. Lewis. 2013. Effect of temperature, photoperiod, and feeding on the rate of tail regeneration in a semiaquatic plethodontid salamander. *Journal of Thermal Biology* 38:548–552.
- Mirza, R.S., and D.P. Chivers. 2003. Response of juvenile rainbow trout to varying concentrations of chemical alarm cue: Response thresholds and survival during encounters with predators. *Canadian Journal of Zoology* 81:88–95.
- Pasteels, J.M., J.C. Grégoire, and M. Rowel-Rahier. 1983. The chemical ecology of defense in arthropods. *Annual Review of Entomology* 28:263–289.
- Peckarsky, B.L., C.A. Cowan, M.A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74:1836–1846.
- Petranka, J.W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, USA.
- R Development Core Team. 2014. R: A Language and Environment for Statistical Computing, Version 3.1.3. Available at <http://www.R-project.org/>. R Foundation for Statistical Computing, Austria.
- Roberts, A.M., and E.B. Liebgold. 2008. The effects of perceived mortality risk on habitat selection in a terrestrial salamander. *Behavioral Ecology* 19:621–626.
- Scott, D.E., and M.R. Fore. 1995. The effect of food limitation on lipid levels, growth, and reproduction in the marbled salamander, *Ambystoma opacum*. *Herpetologica* 51:462–471.

- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist* 139:1052–1069.
- Spotila, J.R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:95–125.
- Strickland, J.C., A.P. Pinheiro, K.K. Cecala, and M.E. Dorcas. 2016. Relationship between behavioral thermoregulation and physiological function in larval stream salamanders. *Journal of Herpetology* 50:239–244.
- Tollrian, R., and C.D. Harvell. 1999. The evolution of inducible defenses: Current ideas. Pp. 306–321 in *The Ecology and Evolution of Inducible Defenses* (R. Tollrian and C.D. Harvell, eds.). Princeton University Press, USA.
- Trigo, J.A. 2000. The chemistry of antipredator defenses by secondary compounds in Neotropical Lepidoptera: Facts, perspectives and caveats. *Journal of the Brazilian Chemical Society* 6:551–561.
- Wake, D.B., and I.G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. *Journal of Morphology* 122:265–303.
- Wise, S.E., and R.G. Jaeger. 1998. The influence of tail autotomy on agonistic behaviour in a terrestrial salamander. *Animal Behaviour* 55:1707–1716.



APPENDIX—The thermal profile in the temperature selection enclosure yielded a range of temperatures available for selection by salamanders (*Plethodon dorsalis*). Temperatures were measured every 5 cm and quantified four times over 2 h. Error bars indicate ± 1 SE.

Accepted on 6 February 2017
Associate Editor: Chris Gienger