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Trap Escape as a Driver of Capture Probability in Semiaquatic Snakes

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Abstract: Sampling biases resulting from capture methodology or animal behavioral responses can significantly skew our understanding of population size and structure. Behavioral responses to passive sampling with traps, such as trap-happy or trap-shy responses, can be accounted for in analyses using individual covariates but they require detailed understanding of the underlying behavioral mechanisms. We used a field experiment to investigate the impact of trap escape on capture rates and determine what traits influence trap escape rates between and within two species of semiaquatic snakes, *Liodytes pygaea* and *Nerodia fasciata*. We found that *L. pygaea* escaped significantly more often than did *N. fasciata*, smaller *L. pygaea* escaped at significantly higher rates than did larger conspecifics, and individual capture history significantly influenced escape rates in *N. fasciata*. Our findings highlight understudied sources of inter- and intraspecific capture heterogeneity in a common sampling technique, and we urge researchers to consider method-specific sampling biases when attempting to produce population parameter estimates for species that are difficult to detect.

Key words: Capture heterogeneity; Capture history; Mark–recapture; Sampling biases

Reptiles and amphibians can be abundant and vital components of ecosystems (Willson and Winne 2016). However, their cryptic behavior and seasonally variable activity patterns can complicate efforts to quantify their abundance. Raw or effort-corrected encounter rates, or counts (i.e., catch-per-unit-effort; CPUE), are often inappropriately interpreted as indices of abundance when the effects of low and/or variable individual detection probabilities are not accounted for (Willson et al. 2008). Understanding the heterogeneity that affects the detection process is also critical to accurately estimate basic demographic parameters, such as survival and abundance (Mazerolle et al. 2007; Willson et al. 2011; Rodda et al. 2015). In snakes, shifting environmental conditions, temporary emigration, sampling effort and method, observer bias, and individual life stage, sex, and reproductive state can all dramatically influence detection probability (Bonnet and Naulleau 1996; Gibbons et al. 1997; Prior et al. 2001; Ryan et al. 2002; Driscoll et al. 2012; Halstead et al. 2013; Boback et al. 2020). Consequently, it is imperative that we understand the multitude of sampling method biases relative to species, demographic groups, site characteristics, and sampling conditions before we can accurately measure metrics such as population demographics and dynamics that are vital for effective conservation action.

Capture bias that results in detection heterogeneity can be addressed using individual covariates or by subdividing demographic groups in analyses (e.g., Christy et al. 2010; Willson et al. 2011), but these adjustments require thorough understanding of the ecological or methodological drivers of heterogeneity. Furthermore, detection heterogeneity can result from individual behavioral responses. For example, an individual's capture history can influence its behavior such that its recapture probability differs from its initial capture probability through trap-happy or trap-shy responses (i.e., individuals showing increased or decreased capture probabilities, respectively, based on previous capture experiences; Nichols et al. 1984; Menkens and Anderson 1988). Such heterogeneity can severely affect the accuracy and precision of the resulting abundance estimates. For example, Willson et al. (2011) found that a trap-happy capture bias in Banded Watersnakes (*Nerodia fasciata*) resulted in abundance estimates one-third of those estimated when individual capture heterogeneity was explicitly modeled. Finally, snake mark–recapture studies have revealed significant unexplained latent heterogeneity in capture probability among individuals that cannot be explained by demographic drivers or individual capture history factors (Tyrrell et al. 2009).

Passive sampling methods such as traps can be highly effective for some snake species and can minimize detection probability heterogeneity related to observer bias and immediate environmental conditions (Keck 1994; Willson and Dorcas 2004; Willson and Gibbons 2010). Commercially available minnow traps have become a standard sampling tool for many aquatic herpetofauna, ranging from larval anurans to aquatic and semiaquatic snakes. However, traps are often physically selective and subject to factors affecting detection probability that may be unique when compared with other survey methods (King and Edgar 1977; Marsh 1984; Topping and Sunderland 1992; Rodda et al. 1999; Koivula et al. 2003). For example, trap escape (i.e., when individuals enter a trap but escape before they are documented) may be common in herpetofaunal research and likely influences detection probabilities (Rodda et al. 1992; Willson et al. 2005). Yet, outside studies of commercial fisheries (e.g., Stewart and Ferrell 2002; Arana et al. 2011), recapture probability heterogeneity associated with variable behavioral responses among individuals is poorly studied despite the strong influence it may exert on estimates of aquatic snake abundance (Willson et al. 2005).

Trap escape heterogeneity in aquatic snakes due to intraspecific factors (e.g., sex, size, and behavioral variation among individuals) and interspecific factors (e.g., size, morphology, habitat preferences, foraging and movement

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behavior) remains largely unexamined. In the only rigorous studies to explicitly examine aquatic snake escape rate from commercial minnow traps, Willson et al. (2005, 2008) found differences in escape rate among species and changes in escape rate among trap types and snake sizes. However, these studies lacked sufficient sample size to disentangle effects of species, body size, behavioral responses, and latent heterogeneity in capture probability among individuals. Individual behavioral response is often designated as either trap-happy or trap-shy but learned behavioral responses may also manifest as altered trap escape rates. Depressed or heightened escape rates may result in the same general capture patterns exhibited by truly trap-happy or trap-shy individuals through a different behavioral response.

To explore the role of trap escape in generating individual capture probability heterogeneity in aquatic snakes (Willson et al. 2005, 2011), we conducted a field experiment with two species of natricine snakes: Black Swamp Snakes (*Liodytes pygaea*) and Banded Watersnakes (*N. fasciata*). *Liodytes pygaea* is a small, cryptic, highly aquatic snake that feeds primarily upon larval amphibians and forages by probing underwater vegetation (Gibbons and Dorcas 2004; Durso et al. 2013), whereas *N. fasciata* is a larger, semiaquatic, generalist predator that forages both at the surface and underwater and is found in most aquatic habitats in the southeastern United States (Gibbons and Dorcas 2004). We released marked individuals into funnel traps and monitored their escape rates after 24 h. Many of the individuals used in this field experiment had extensive capture histories from previous research. In this experiment, we examined variation in escape rates between species, sexes, and based on the presence or absence of food items in animals' stomachs. We also examined the influence of body size and an individual's prior capture history on escape rates. Specifically, we tested the following hypotheses: (1) *L. pygaea* escapes at a higher rate than *N. fasciata* (Willson et al. 2005); (2) body size affects escape rate in both species, with smaller individuals escaping more frequently; (3) sex does not affect escape rate in either species (Willson et al. 2011); (4) the presence of food items in animals' stomachs lowers escape rate in both species because of decreased activity during digestion; and, (5) individuals with fewer previous captures escape at a higher rate than do individuals captured more frequently the previous year.

Materials and Methods

Study Site

We conducted our experiment 29 September–2 October 2005 at Ellenton Bay, a large fishless Carolina Bay wetland on the US Department of Energy's Savannah River Site, South Carolina, USA (for additional details on study site see Willson et al. 2011). We chose *N. fasciata* and *L. pygaea* as our study species because of longstanding interests in understanding their population dynamics and capture probabilities at Ellenton Bay and their robust populations and extensive capture histories in these populations (Willson et al. 2011). Both species can be effectively sampled using plastic minnow traps but are known to occasionally escape after capture (Willson et al. 2005; Durso et al. 2011).

Escape Trials

To evaluate escape rates of semiaquatic snakes, we experimentally released snakes into plastic minnow traps that were 43 cm long and 16 cm in diameter with 0.4-cm-wide mesh (Model 700, Gator Buckets; Willson et al. 2005; Winne et al. 2006a). Our study followed 5 mo of intensive capture–mark–recapture (CMR) sampling of this population wherein we set 465 minnow traps/night for 10 nights/mo during May–September 2005 (see Willson et al. 2011; Willson and Winne 2016 for sampling details). We brought snakes to the lab where we recorded demographic data, gave each snake a unique code by branding their ventral and lateral scales (Winne et al. 2006b), and returned them to their capture site. Immediately following the September 2005 sampling period, we trapped for four nights and modified our protocol to determine the escape capabilities of each snake. Immediately upon capture, we processed each snake in the field by determining its identification number (see Winne et al. 2006b), sex, snout–vent length (SVL), and visually determined whether they had a food bolus at the time of capture. We did not remeasure SVL for snakes that had been captured earlier in the month in order to reduce stress and handling time, and we gave all new snakes unique identification codes by very lightly branding the corner of one or two ventral scales. Once we processed an individual, we released it into an empty plastic minnow trap and placed the trap at its capture locality (in shallow water among emergent vegetation with approximately 3–5 cm of the trap remaining above water, the entrance funnel submerged, and a spacing of approximately 2 m between traps). Each trap had an associated flag labeled with the snake's identification number. After 24 h, we checked traps to determine which snakes had escaped. We used individual snakes only once in escape trials to avoid pseudoreplication. In total, we conducted escape trials with 100 individual *N. fasciata* and 96 individual *L. pygaea* over 4 d.

Statistical Methods

We performed chi-squared analyses to determine whether there were interspecific differences in escape rates, intraspecific differences between sexes, and intraspecific differences between snakes that had or did not have food items. To account for natural body size differences between the species, we also performed a chi-squared analysis comparing escape rates of *L. pygaea* with a subset of 42 *N. fasciata* within the 200–465-mm SVL size range of the *L. pygaea* used in escape trials. We used logistic regression analyses to determine if there were significant effects of body size (SVL) and capture history (number of previous captures in 2005, see Willson et al. 2011; range of 1–18 captures for *L. pygaea* and 1–27 captures for *N. fasciata*) on escape probability within each species. We performed logistic regressions using the *glm* function in package *lme4* (Bates et al. 2015) and chi-squared tests using the chisq.test function in Program R (v4.1.2, R Core Team 2021), and used alpha values of 0.05 for all analyses.

Results

Escape rates differed significantly between species—61% of *L. pygaea* escaped within 24 h compared with 21% of *N.*

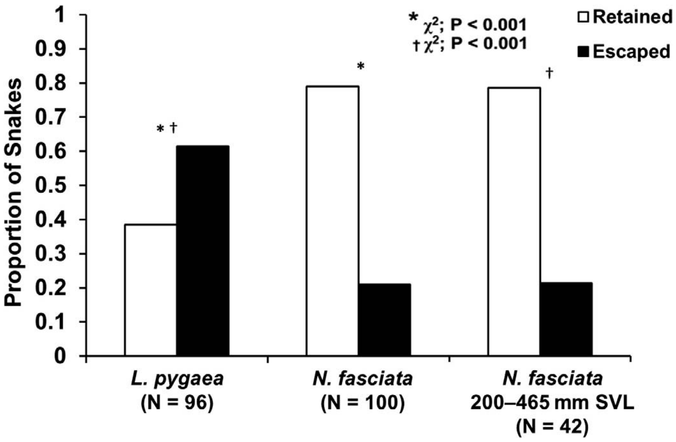

Fig. 1.—Escape rates of two species of semiaquatic snakes (*Liodytes pygaea* and *Nerodia fasciata*) experimentally released into aquatic funnel traps. A subset of 42 *N. fasciata* within the 200–465-mm SVL size range of the *L. pygaea* was compared with *L. pygaea* to account for natural size differences between the species. The significant difference between *L. pygaea* and the full sample of *N. fasciata* is noted with an asterisk (*) and the significant difference between *L. pygaea* and the subset of similarly sized *N. fasciata* is noted with a cross (†).

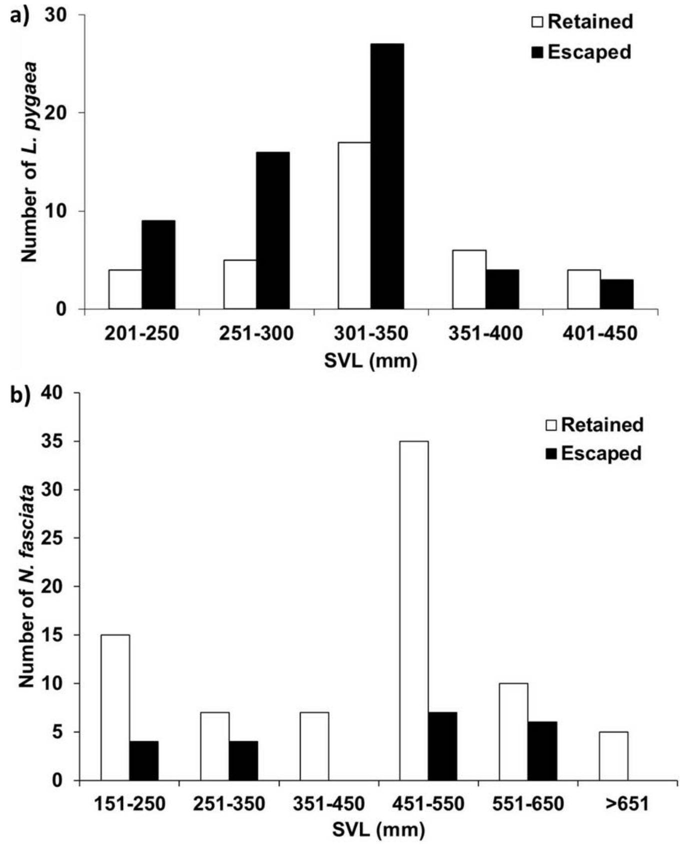

Fig. 2.—Escape frequency of *Liodytes pygaea* (a) and *Nerodia fasciata* (b), sorted by size (snout–vent length; SVL).

fasciata ($\chi^2 = 33.19$, $P < 0.001$; Fig. 1). We also found that *L. pygaea* escaped at a significantly higher rate than did the subset of *N. fasciata* of comparable length ($\chi^2 = 18.73$, $P < 0.001$; Fig. 1). In *L. pygaea*, smaller individuals (shorter SVL) escaped more frequently than did larger individuals (logistic regression, $P = 0.02$; Fig. 2a), but escape probability was not related to body size in *N. fasciata* (logistic regression, $P = 0.70$; Fig. 2b). We found no effect of sex or food status on escape rate for either *N. fasciata* ($\chi^2 = 1.18$, $P = 0.28$; $\chi^2 = 1.42$, $P = 0.23$) or *L. pygaea* ($\chi^2 = 1.39$, $P = 0.24$; $\chi^2 = 0.35$, $P = 0.55$). We found that there was no effect of capture history on escape rate in *L. pygaea* (logistic regression, $P = 0.47$; Fig. 3a), but *N. fasciata* individuals with fewer prior captures escaped at a higher rate (logistic regression, $P = 0.01$; Fig. 3b).

Discussion

Of the 196 individual snakes in our study, 41% escaped during the 24-h trial period, which strongly indicates that unadjusted capture rates (counts or catch-per-unit effort) are underestimates of true abundance and the number of snakes entering traps. Our results support our hypothesis regarding interspecific variation in escape rates: *L. pygaea* escaped at a significantly higher rate than did *N. fasciata*, likely as a result of their smaller head and body size and more aquatic behavior. Escape rate was negatively related to body size in *L. pygaea*, supporting our hypothesis linking smaller size to higher escape rates, but this was not the case for *N. fasciata*. Neither sex nor food status significantly affected escape rate in either species, suggesting that neither factor altered activity levels in captured snakes. Although individual capture history did not affect *L. pygaea* escape rate, our hypothesis that individuals with more extensive capture histories would escape less frequently was supported in *N. fasciata*.

Our finding of significant interspecific variation in escape rate reinforces those of Willson et al. (2005), and our larger

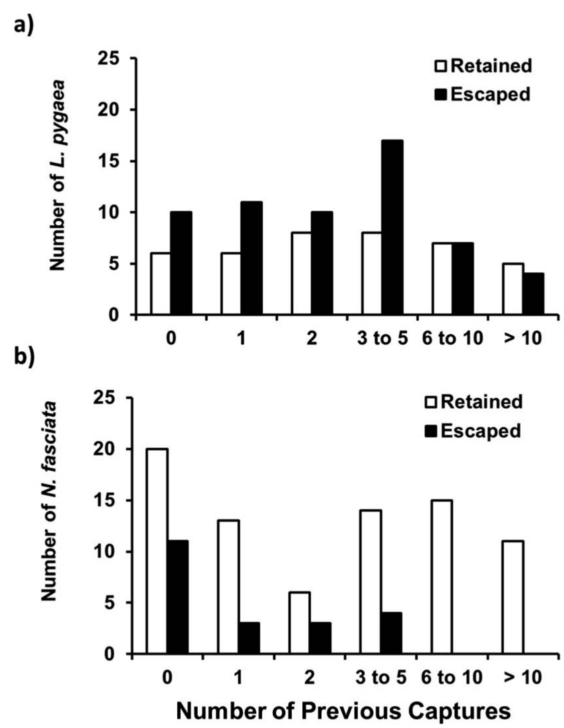

Fig. 3.—Escape frequency of *Liodytes pygaea* (a) and *Nerodia fasciata* (b) sorted by number of previous captures.

sample sizes allowed us to explicitly address the mechanisms driving differences in escape rate between species. *Liodytes pygaea* escaped at a considerably higher rate than did *N. fasciata*, even in comparison to *N. fasciata* of similar body size. While the smaller proportional head sizes of *L. pygaea* may facilitate escape through the trap funnel for larger *L. pygaea, N. fasciata* of comparable body lengths had heads small enough to easily fit through trap funnels. Thus, we suggest that elevated trap escape rates in *L. pygaea* are driven primarily by behavioral mechanisms related to foraging. *Liodytes pygaea* is thought to forage by probing underwater vegetation and burrows while *N. fasciata* is more likely to forage at the surface (CTW and JDW, personal observations). Trap funnels were submerged, so it seems plausible that *L. pygaea* would encounter funnels more frequently while foraging underwater, whereas *N. fasciata* foraging at the surface would be less likely to locate the funnel and escape.

Body size had a significant effect on escape rate for *L. pygaea*, mirroring the findings of previous research that suggests aquatic minnow trapping often produces size-biased samples (Willson et al. 2008; Halstead et al. 2013). The mechanism driving size-related capture bias appears to vary both by species and life-stage because escape rates of juveniles and neonates of some species can be extremely high given their ability to escape through trap mesh. Large-headed species like *N. fasciata* quickly grow too large to escape through the trap mesh, while slim-headed species like *L. pygaea* maintain high escape rates as subadults by escaping through the mesh (Willson et al. 2008). However, as discussed above, *L. pygaea* likely maintains a high escape rate even at larger sizes through its highly aquatic behavior. It is widely acknowledged that subadult snakes are often undersampled relative to adults, hampering efforts to fully understand population characteristics (Pike et al. 2008; Bauwens and Claus 2018). Although ontogenetic behavioral factors such as prey choice and microhabitat use undoubtedly decrease rates of trap encounter or entry (Lardner et al. 2009, 2014), our results suggest that trap escape may play a significant role in further depressing juvenile detection probabilities for some species. Sampling adjustments that reduce trap escape should allow more accurate representation of this poorly understood demographic group.

We did not find an effect of sex on escape rate, but we did not test gravid females in escape trials because the trials took place after the parturition seasons for both species, so differences in activity levels or behavior directly related to reproductive activity that may affect escape rates were not examined in this study. However, sex-related differences may be prominent at other times of year. Male activity can increase dramatically during mate searching, possibly increasing the likelihood of escape, and gravid females of some natricine species exhibit reduced activity and increased body girth that could lead to lower escape rates (Brown and Weatherhead 1999; Isaac and Gregory 2004). These seasonal shifts in activity present interesting hurdles that should be addressed in future research. The presence of a food item in an individual's gut also had no significant effect on escape rate, suggesting that it did not significantly alter activity levels after snakes were captured. However, prey items that entered traps were typically small (mostly paedomorphic salamanders and tadpoles) and, given that the prey were able to enter traps themselves, it is unlikely that a snake in a trap would consume a meal large enough to prevent its escape through a funnel.

The significant effect of capture history on *N. fasciata* escape rate may be driven by a learned behavioral response, innate behavioral differences among individuals, or interplay between the two. However, individuals were only tested once, so we are unable to separate these possibilities. Individuals that, by chance, are frequently captured and fail to escape may be more likely to become trap-happy, exhibiting a positive behavioral response that results in previously captured snakes being more likely to be recaptured. Having previously experienced capture with no notable negative effects and possibly having found easy prey within a trap, these trap-happy individuals may expend less effort attempting to escape upon capture, or even remain within traps voluntarily. Indeed, previous CMR analyses on these populations show that *N. fasciata* exhibited strongly trap-happy responses, with recapture probability as much as five times greater than initial capture probability in some seasons (Willson et al. 2011). The results of our research at least partially explain that response showing variation in escape probability among individuals. It also seems likely that there exist innate behavioral differences between individuals wherein snakes with higher activity levels or increased underwater foraging effort are more likely to encounter the funnel after capture and escape from the trap. Capture history did not significantly affect escape frequency of *L. pygaea*, but there was a trend toward decreasing escape frequency with more previous captures that may have proved consequential with a larger and more balanced sample. Further research that repeatedly tests individuals over time or directly manipulates individual trap history before examining the resulting capture and escape rates of individuals are needed to address the importance of learned vs. innate behavioral response behaviors to detection probabilities in this system.

We identified several sources of inter- and intraspecific variation in escape rates when using one of the most common sampling techniques in aquatic snake research. The variation in escape rate resulting from differences in individual size and behavioral response could lead to sampling biases that significantly affect estimation of abundance and vital rates. Once understood, this heterogeneity can be addressed through parameterization of CMR models and perhaps minimized through future refinement of trap design and sampling schemes. The results of our study also highlight the need for continued research to remedy the issues that we have identified and to explore the latent variation we were not able to explain. All sampling methods present inherent biases and unique challenges (Fitch 1961). However, commercial minnow traps remain the most efficient method for sampling many aquatic snake species, and simple modifications can be made that both increase capture rate and decrease escape rate (Halstead et al. 2013). Trap designs from both aquatic and terrestrial snake research have incorporated one-way flaps that prevent escape, increased funnel sizes to facilitate capture of larger individuals, and added leads that guide snakes to the funnel entrance (Vice et al. 2005; Willson et al. 2008; Halstead et al. 2013). Additional adjustments could be made to reduce escape by elongating funnel entrances, adding flap variations that reduce escape without discouraging initial entrance, and decreasing mesh size to reduce escape of juveniles (Willson et al. 2008). Combining innovative trap designs with a more complete understanding of trapping biases will greatly improve our ability to accurately measure and understand snake population and community dynamics.

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