Herpetological Conservation and Biology 8(3):581−590.
Submitted: 15 April 2013; Accepted: 20 July 2013; Published: 31 December 2013.

Time in Captivity Affects Foraging Behavior of Ratsnakes: Implications for Translocation

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***Abstract.*—As wildlife populations decline or disappear, wildlife professionals are using management tools such as translocation to maintain viable populations, often with mixed results. Wild-to-wild translocations are often more successful than when captive animals are released, raising concerns that captivity may have deleterious effects on animals. Although the effects of captivity have been documented on a generational time-scale, effects within the lifetime of an individual have received much less attention. Here we examine how time in captivity affects foraging behavior of wild-caught Ratsnakes (*Elaphe obsoleta*). The longer Ratsnakes had been in captivity, the less successful and slower they were to react to prey in a simple laboratory discrimination task. Snakes that had been captive for a year or more performed no better than expected by chance. Captivity-induced degradation of ecologically important behaviors provides a potential mechanism underlying the poor performance of animals that are released into the wild following prolonged captivity. Our results also suggest that research using captive snakes may not always document behaviors representative of wild snakes.**

Key Words.—conservation; *Elaphe obsoleta*; prey detection; reintroduction; repatriation; snakes

Introduction

Wildlife professionals are increasingly turning to translocation as a management tool to maintain declining wildlife populations (Griffith et al. 1989). Translocation (the intentional release of captive-propagated and/or wild-caught animals into the wild for the purpose of establishing a new population, reestablishing an extirpated population, or augmenting a critically small population or managing nuisance animals; IUCN 2012), has been employed world-wide in hundreds of conservation programs with numerous taxa (e.g., Seddon et al. 2007). Many of these projects (33–52%) fail to establish successfully reproducing individuals and the true success rate is likely lower if failed projects disproportionately go unpublished (Scargle 2000). Comprehensive reviews of translocation projects have reported apparently greater success of reintroductions involving wild-to-wild translocations compared to the release of captive animals (Griffith et al. 1989; Wolf et al. 1996; Fischer and Lindenmayer 2000). Such reports have raised concerns that captivity may decrease the ability of individuals to survive in the wild following release (Kleiman et al. 1994; Snyder et al. 1996; Mathews et al. 2005).

Captive animal populations may show rapid changes (in three generations) in behavioral phenotypes (Connolly and Cree 2008; Guay and Iwaniuk 2008) and genotypes (Kraaijeveld-Smit et al. 2006) as a consequence of stunted learning and development, or selection favoring traits that are "adaptive" to captive conditions. These changes are often unexpected and potentially the detrimental consequences of captive rearing. Such changes can affect the success of translocation projects by promoting maladaptive behaviors related to foraging or predator avoidance. When released, many captive-born animals experience high rates of predation (Jule et al. 2008; Aaltonen et al. 2009) and starvation (Jule et al. 2008), or are reliant on anthropogenic food sources (Champagnon et al. 2012). Evidence indicates that the more generations a population of animals is maintained in captivity, the less likely individuals are to retain high levels of physical performance (Connolly and Cree 2008) or to react normally to predators (McPhee 2003; Kraaijeveld-Smit et al. 2006). While decreased physical performance and predator avoidance behavior of captive-born animals have been documented on a generational time scale (McDougall et al. 2006), effects on finer temporal scales for wild-born captives (within an individual's lifetime) have received much less attention.

The use of captive-born animals confounds our ability to separate and understand changes arising from selection as opposed to phenotypic changes arising during the course of captivity.

Wild-caught animals maintained in captivity for an extended time experience similar influences on their behavior as animals born in captivity. Indeed, long-term captive (but wild-born) animals in zoos and laboratories often display behaviors very different from those of free-ranging wild conspecifics (Fox 1968). Animals maintained in captivity are constrained from displaying natural and flexible behavior, which can lead to a reduced behavioral repertoire (Poole 1992) and altered behaviors (Fox 1968). In the only translocation study to directly investigate captivity effects on behavior of wild-caught individuals, Ben-David et al. (2002) showed that adult River Otters (*Lontra canadensis*) held in captivity for relatively short durations (nine months) suffered from increased predation and starvation upon release relative to wild conspecifics. A recent review found that behavior of captive animals becomes less repeatable over time (Bell et al. 2009). However, no study has yet investigated the effect of captivity duration on performance of wild-caught captive animals.

In many ways snakes appear to be ideal candidates for translocation because wild-caught individuals can be easily maintained and bred in captivity. Furthermore, evidence that some snake behaviors are "hard-wired" (Chiszar et al. 1993) suggests that captivity might have limited effects on snake behavior. Despite these characteristics, however, snake translocations have had mixed results (Nowak et al. 2002; Germano and Bishop 2008; Kingsbury and Attum 2009; Roe et al. 2010), with failure often due to abnormal behavior of released individuals. Future translocation and reintroduction efforts may therefore benefit from experimental assessment of how captivity affects snake behavior, and how those effects vary with time in captivity. In this study we compare the ability of wild-caught Ratsnakes (*Elaphe obsoleta*), held captive for varying lengths of time, to react to and locate prey. If captivity has a detrimental effect on behavior, snake performance should decline with increasing time in captivity.

Materials and Methods

Study animals.—We compared the foraging ability of 11 long-term captive Ratsnakes (1–60 months in captivity) to that of 16 recently wild-caught Ratsnakes (< two weeks in captivity). The long-term captive Ratsnakes were part of the Savannah River Ecology Lab's (SREL) outreach program. These snakes were originally caught as adults from the local area (Aiken and Barnwell counties, South Carolina, USA), usually as a result of human-animal conflict (e.g., in chicken coops, residences, etc.). Long-term captive Ratsnakes had been maintained at the SREL animal care facility since capture. The 16 short-term captive Ratsnakes were collected opportunistically by hand from the same local area. We weighed each snake to the nearest gram and measured to the nearest centimeter (snout to vent length; SVL). We only used snakes with an SVL > 70 cm for foraging trials (see below); we excluded gravid females because they may not have been as food-motivated as non-gravid snakes. We calculated the body condition of each snake using the residuals of a regression of log transformed mass on log transformed SVL. Because all snakes were of similar size, this measurement of body condition avoids some of the potential biases of body condition calculations for snakes (Weatherhead and Brown 1996).

We housed all snakes individually in either 10- or 20-gallon glass aquaria or custom-built plastic and glass containers of similar size. Each had a substrate of aspen shavings, a water bowl, and a retreat shelter. We kept all animals on a 12:12 light:dark cycle at a constant temperature of 30° C. Long-term captive snakes had been fed thawed frozen mice weekly. Before being used in a trial, we fasted each snake for a minimum of seven days (range = 7–11: mean = 9.9 d) to ensure a strong appetitive response. Within their first two days of captivity, we offered each short-term captive snake a dead mouse (*Mus musculus*; purchased commercially frozen then thawed in warm water) weighing < 3% of their body mass. All snakes accepted the mouse, establishing the sight and smell of dead mice as desirable food items. After acceptance of the mouse, we then held snakes without food for a minimum of seven days (range = 7–14: mean = 8.3 d). We held short-term captive snakes for < 2 weeks prior to testing and we released them at their point of capture immediately after use.

Prey location trials.—Ratsnakes seasonally shift from diurnal to nocturnal activity (Sperry et al. 2013), suggesting that they may be capable of locating prey both visually (Mullin and Cooper 1998) and chemically (Saviola et al.

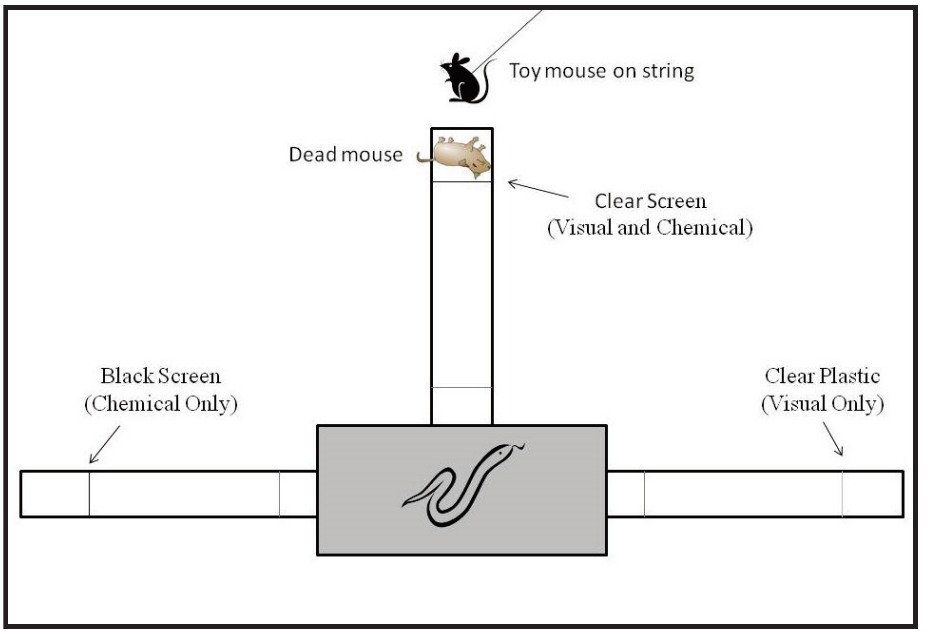

Figure 1. A schematic of the experimental apparatus to determine prey detection in Black Ratsnakes (*Elaphe obsoletus*).

2012). Because the long-term captive snakes had become accustomed to diurnal feeding in which they were able to watch caretakers place food in their enclosures, we examined their ability to locate prey nocturnally when visual stimuli were absent or minimized, a necessary task for wild snakes. We presented all snakes with a discrimination task requiring them to use either chemical, visual, or coupled visual and chemical stimuli to locate prey in dark conditions. We performed all trials reported here in a room with a constant temperature of 30° C and constant light of 1 lux to approximate light conditions on a cloudy night. We placed snakes individually in a plastic holding container (33.8 cm L × 21.6 cm W × 11.9 cm H) with three clear tubes (10.2 cm diameter × 120 cm long) radiating out of it (one on each of three sides; Fig. 1). At the end of each tube was a compartment, one of which was baited with prey during each trial. We initially prevented snakes from entering any of the tubes by clear screen gates (aluminum window screen) placed between the holding container and the tube entrances. In each trial, we placed both a dead-thawed mouse and a life-like toy mouse on a string at the end of one tube either behind opaque screen made from six layers of charcoal fiberglass window screen (chemical stimulus only), a clear, solid plastic screen (visual stimulus only), or a clear barrier made from aluminum window screen (visual and chemical stimuli). Snakes were allowed access to all three tubes in each trial, but only one tube (randomly determined) contained prey in any given trial. Thus, in each trial there was one baited tube and two non-baited tubes. After allowing the snake 30 min to acclimate to the holding container (to cease escape behavior and to react to the prey), we removed the gates, which provided the snake access to all three tubes during the trial. We interpreted the snake entering one of the tubes as having reacted to the prey in that tube. After each trial we cleaned the tubes thoroughly with paper towels and an unscented commercial surface disinfectant and then subsequently rearranged in a randomly determined order.

We recorded the response of each snake as a multinomial variable with snakes entering the baited tube as having correctly "reacted to prey," snakes entering one of the unbaited tubes as "failed to react to prey," and snakes that remained in the holding container for the entire 30 minutes as "failed to respond." One of the authors (BAD) watching from behind a blind (and making the mouse on a string move in a life-like fashion) determined that a snake had "selected" a tube when its head was 25 cm from the holding container (marked by a piece of black tape around each tube). Under low light

conditions during trials, it was still (just) possible to detect the dark snakes in the clear plastic tubes. We also recorded the time from removal of the barriers to when the head of a snake was 25 cm from the container (defined as latency). We tested all 27 snakes three times, incorporating prey stimulus type, with the prey stimulus presented in a randomly selected order. The three tests for each snake occurred during the same day and we used "trial order" as a variable in our analyses to test for the ability of a snake to learn between trials. All trials took place between 1 June and 15 August 2011 or 1 May and 5 June 2012 from 0900 to 1400. Only one author (BAD) performed trials to eliminate inter-observer variability.

Data analysis.—We first compared the body condition of short and long-term captive snakes using a t-test. We then compared the number of short and long-term captive snakes that reacted to prey to that expected by chance (33%) using Chi-square analysis. Because we recorded the reaction to prey as a categorical response (choice of baited tube, choice of unbaited tube, or no choice), we used a generalized linear mixed model (GLMM) with multinomial logistic regression to compare the effect of captivity on reaction to prey. We used group (short vs. long-term captive), stimulus type (visual, chemical, or chemical and visual), body condition, time since last meal, and trial order as fixed factors, with snake ID as a random factor to account for individual variability and the repeated measures design. We compared latency to react to prey using a univariate generalized linear model (GLM) with the fixed factors of group, body condition, time since last meal, and trial order, with snake ID included as a random factor in all analyses. We explored the effect of time in captivity on the ability and latency to react to prey using linear regression analysis. In the linear regression analysis of captivity duration and reaction to prey success, we grouped trials in which snakes failed to react to prey with trials in which snakes failed to respond. In the analysis of captivity duration and latency, we terminated trials in which snakes failed to respond after 30 min. Thus, latency for these trials was determined to be 30 min.

Results

We tested 16 short-term captive and 11 long-term captive Ratsnakes for a total of 81 trials. Snakes failed to respond to prey in seven of 81 trials (8.6%; four for short-term captives and three for long-term captives). Short-term captive Ratsnakes moved into the baited prey tube at a rate greater than expected by chance (63% vs. 33%: $\chi^2 = 29.44$, df = 15, $P = 0.01$; Fig. 2); whereas, long-term captives did not (31% vs 33%: $\chi^2 = 22.31$, df = 15, $P = 0.99$). Snake group (short- vs. long-term captive) had a significant effect on the choice of a tube by an individual ($F_{2,79} = 3.56$, $P = 0.03$). Although long-term captive snakes tended to have a higher body condition, the difference was not significant ($t = 1.33$, $P = 0.10$). Stimulus type, body condition, time since last meal, and trial order did not have a significant ($P > 0.16$) effect on a snake's ability to detect and approach prey (Fig. 2). Although stimulus type did not have a significant effect on the reaction to prey by a snake ($P = 0.26$), long-term captive Ratsnakes reacted to prey at high rates (75%) when chemical and visual stimuli were coupled, whereas short-term captives reacted to prey at similar levels for all stimulus types. Snake group also had a significant effect on latency to react to prey ($F_{1,79} = 40.6$, $P = 0.02$), with short-term captive snakes approaching prey faster (mean ± SE: 400 ± 52 s) than long-term captive snakes (594 ± 111 s). Neither trial order, body condition, stimulus, nor time since last meal had a significant effect (all $P \geq 0.26$). Although not significant ($P = 0.23$), there was a trend for short-term captives to approach prey more quickly when chemical (260 ± 48 s) or chemical and visual (384 ± 49 s) stimuli were presented compared to visual stimulus only (556 ± 83 s; Fig. 3). No trend was detected for long-term captive snakes ($P = 0.72$). Using time in captivity as a continuous variable, we found a negative relationship between time in captivity and successful reaction to prey ($r^2 = 0.17$, $P = 0.03$; Fig. 4a) and a positive correlation between time in captivity and latency to react to prey ($r^2 = 0.47$, $P = 0.02$; Fig. 4b), indicating that the longer a snake had been in captivity, the less likely it was and the longer it took to approach prey.

Discussion

Compared to snakes that had been maintained in captivity for longer periods, short-term captive Ratsnakes located and reacted to prey at a higher rate in a discrimination task. Short-term captive

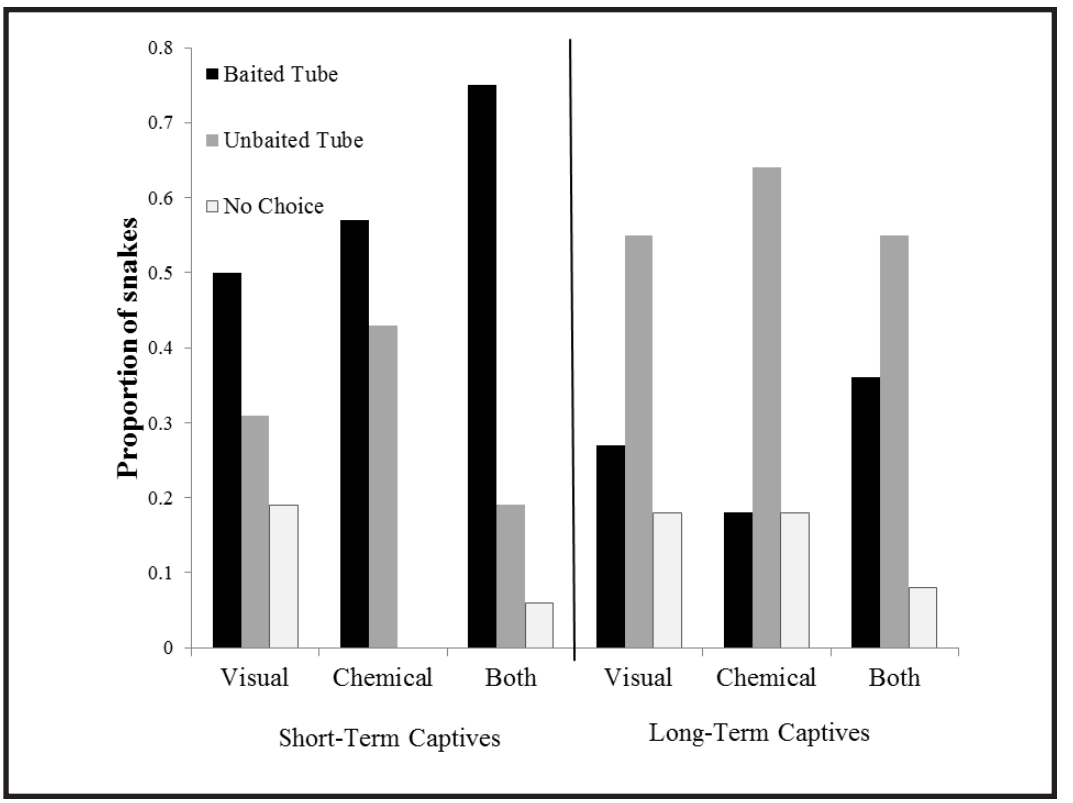

FIGURE 2. Proportion of short- and long-term captive Ratsnakes (*Elaphe obsoleta*) that entered the baited tube, an unbaited tube, or did not enter any tube in nocturnal foraging trials when the prey stimulus present was either visual, chemical, or both.

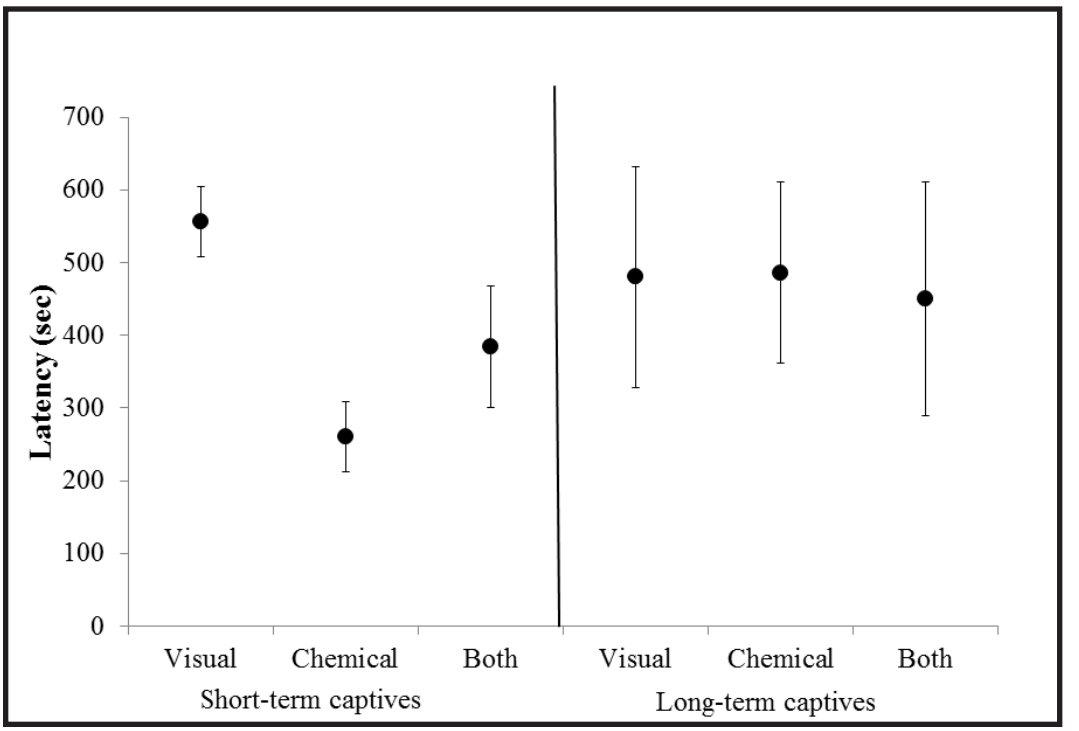

FIGURE 3. Latency to react to and approach prey of short- and long-term captive Ratsnakes (*Elaphe obsoleta*).

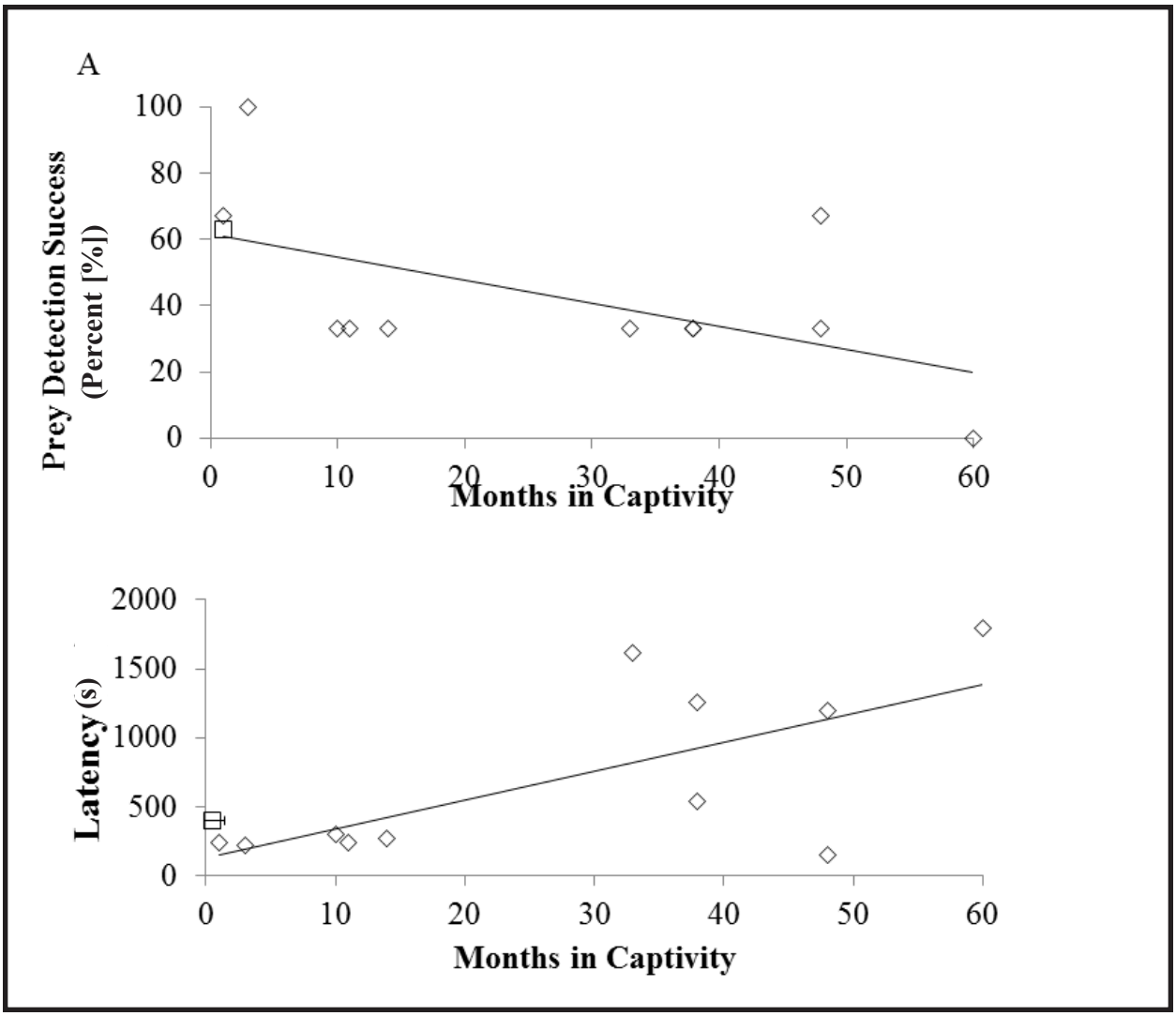

Figure 4. Effect of time in captivity on the ability of a Ratsnake (*Elaphe obsoleta*) A) to successfully react to prey and B) latency to react to prey. Diamonds are long-term captive Ratsnakes and squares are the means for the 16 short-term captive Ratsnakes.

snakes successfully reacted to prey 63% of the time, compared to 31% for long-term captive snakes, which performed no better than would be expected by chance. Short-term captive Ratsnakes also approached prey more quickly than their long-term captive counterparts (400 vs 594 s). When time in captivity was used as a continuous variable, we found that foraging performance declined with time in captivity. Our results indicate that Ratsnakes held in captivity for as little as 10 months were less successful and took longer to locate prey than snakes just brought into captivity. Two of the long-term captives had been brought into captivity only one and three months prior to being tested and located prey in 67 and 100% of trials, whereas three snakes held in captivity between 10 and 13 months located prey levels not different than by chance (33%). Because all snakes were captured as adults, the poor performance of long-term captives cannot be attributed to them never having developed normal foraging abilities in the wild. Whether snakes can re-learn these behaviors after release, how long it might take, and how their compromised foraging ability might affect survival after release, are unknown. However, our results do suggest that when translocated or reintroduced animals starve (e.g., Jule et al. 2008), a detrimental effect of time in captivity prior to translocation, independent of

developmental or selection effects of captivity, could be a contributing factor.

In the wild, Ratsnakes are often active nocturnally during the warmer months of the year (Weatherhead et al. 2012; Sperry et al. 2013). Presumably Ratsnakes must be able to shift their foraging strategy from a reliance on visual stimuli during diurnal foraging (Mullin and Cooper 1998) to chemical stimuli when foraging in the dark. Unsurprisingly, short-term captive Ratsnakes reacted to prey at greater than chance levels using visual, chemical, or combined stimuli. In fact, short-term captives most quickly approached prey when only chemical stimuli were present. In constrast, long-term captive Ratsnakes chose the baited tube in only 26% of trials, fewer than that expected by chance (33%). No trend was detected in the latency of long-term captive Ratsnakes to approach prey based on stimulus because they were slow to approach prey regardless of the available stimulus. Long-term captive snakes appear to have lost some capacity to shift between prey stimuli relative to short-term captive snakes.

The ability and speed with which snakes reacted to prey may be an artifact of their motivation to feed. We attempted to control for this by feeding each snake a dead mouse when captured (establishing their experience with the prey item) and then fasting each snake for a minimum of a week. We evaluated the body condition of each snake used in the trial, and although long-term captive snakes tended to be in better condition, the difference between the groups was not significant and condition did not have a significant effect on snake behavior in the trials.

The rapid degradation in foraging behavior we observed in Ratsnakes is clearly inconsistent with the notion that reptile behaviors are "hard-wired," although different behaviors may vary in their plasticity. For example, flight initiation distance of captive-bred and released iguanas in response to a predator threat did not differ from those of wild iguanas (Alberts et al. 2004). Additionally, Chiszar et al. (1993) found that foraging behaviors such as strike-induced chemosensory searching and tongue flicking response to blood by captive-born rattlesnakes and cobras were similar to those observed in wild conspecifics. The effect of captivity likely varies both among species and behaviors, but until evidence to the contrary is presented, the prudent assumption should be that traits that may affect survival in the wild should not be regarded as hard-wired.

Conservation practitioners involved in snake translocation or reintroduction projects should consider the potential effects of captivity on survival-related behaviors when designing animal handling and release protocols and when conducting post-release monitoring. For example, current head-starting projects for rare snakes such as the Eastern Indigo Snake (*Drymarchon couperi*) focus on the collection of eggs from wild-caught gravid females held in temporary captivity as the source of animals for reintroduction efforts (Godwin et al., unpubl. report). Because permanent removal of adults would likely negatively impact source populations and translocated adults might fail to settle at the release site (Kingsbury and Attum 2009), releasing captive-reared offspring has obvious benefits over release of wild-caught adults. Because our study indicates that temporary (one year or more) captivity might negatively affect animals, however, protocols that minimize animals' time in captivity may help increase post-release survivorship.

In some translocation projects, such as headstarting or repatriation, animals must be maintained in captivity for extended periods of time as individuals grow, permits are approved, or suitable habitat is acquired and restored. Environmental enrichment and soft release are management tools that can potentially offset the detrimental effects of captivity on post-release behavior. Enrichment entails increasing the complexity of captive housing to simulate natural conditions. Although enrichment falls short of providing the full range of natural stimuli and behavioral challenges encountered in the wild, it can provide increased sensory, motor, and cognitive demands (Poole 1992; Dinse 2004). Enrichment may enhance the ability of animals to perform ecologically relevant tasks such as refuge seeking, foraging, and reproducing (e.g., Almli and Burghardt 2006; Nicholson et al. 2007) and has been shown to improve survival of released individuals (Biggins et al. 1999). Soft release entails placing individuals in outdoor enclosures at the release site prior to being released, allowing animals to experience local environmental conditions and develop fidelity to a site (Kingsbury and Attum 2009). Soft release often allows animals to exhibit natural behaviors such as foraging and

refuge seeking and has proven effective for a number of successful translocation projects (e.g., Tuberville et al. 2005). Research is needed to determine how these tools can be used to enhance the ability of snakes to re-establish natural behaviors.

In addition to the implications for translocation programs, our results provide a note of caution for research on the behavior of captive snakes. For example, many studies examining snake foraging behavior use animals that have been in captivity for extensive periods of time (e.g., Saviola et al. 2012). When feasible, the behavior of captive and wild study subjects should be compared (Shivik 1998). Otherwise, caution should be used when inferring that the behavior of captive snakes reflects the behavior of those snakes in the wild.

Acknowledgments.—Funding for this project was provided by the Construction Engineering Research Laboratory of the Engineer Research Development Center (ERDC). We thank Tim Hayden for assistance in arranging funding. This work would not have been possible without the generosity and meticulous record-keeping of Sean Poppy and Angela Tucker in the SREL outreach program. Eric Nordberg, Mary Mack Gray, Brian Metts, Ashley Smith, Patrick Barnhart, Patrick Roberts, Caitlin Kupar, and Phil Vogrinc assisted in snake capture and husbandry. Partial support for manuscript preparation by TDT and use of animal facilities was made possible by Award Number DE-FC09-07SR22506 from Department of Energy to the University of Georgia Research Foundation. Animals were collected under South Carolina Department of Natural Resources permits # G-11-03 and 23-2012A. Animal procedures conformed to permits approved by the University of Illinois (IACUC #11054) and University of Georgia (AUP #A2011 04-007-Y2-A0).

Literature Cited

Aaltonen, K., A.A. Bryant, J.A. Hostetler, and M.K. Oli. 2009. Reintroducing endangered Vancouver Island Marmots: survival and cause-specific mortality rates of captive-born versus wild-born individuals. Biological Conservation 142:2181–2190.

Alberts, A.C., J.M. Lemm, T.D. Grant, and L.A. Jackintell. 2004. Testing the utility of headstarting as a conservation strategy for West Indian Iguanas. Pp. 210–219 *In* Iguanas: Biology and Conservation. Alberts, A.C, R.L. Carter, W.K Hayes, and E.P. Martins (Eds.). University of California Press, Berkley, California, USA.

Almli, L.M., and G.M. Burghardt. 2006. Environmental enrichment alters the behavioral profile of Ratsnakes (*Elaphe*). Journal of Applied Animal Welfare Science 9:85–102.

Bell, A.M., S.J. Hankison, and K.L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77:771–783.

Ben-David, M., G.M. Blundell, and J.E. Blake. 2002. Post-release survival of River Otters: effects of exposure to crude oil and captivity. Journal of Wildlife Management 66:1208–1223.

Biggins, D.E., A. Vargas, J.L. Godbey, and S.H. Anderson. 1999. Influence of prerelease experience in reintroduced Black-footed Ferrets (*Mustela nigripes*). Biological Conservation 89:121–129.

Champagnon, J., J. Elmberg, M. Guillemain, M. Gauthier-Clerc, and J.D. Lebreton. 2012. Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. Journal for Nature Conservation 20:231–241.

Chiszar, D., H.M. Smith, and C.W. Radcliffe. 1993. Zoo and laboratory experiments on the behavior of snakes: assessments of competence in captive-raised animals. American Zoologist 33:109–116.

Connolly, J.D., and A. Cree. 2008. Risks of a late start to captive management for conservation: phenotypic differences between wild and captive individuals of a viviparous endangered skink (*Oligosoma otagense*). Biological Conservation 141:1283–1292.

Dinse, H.R. 2004. Sound case for enrichment: Focus on environmental enrichment improves response strength, threshold, selectivity, and latency of auditory cortex neurons. Journal of Neurophysiology 92:36–37.

Fischer, J., and D.B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation 96:1–11.

Fox, M.W. 1968. Abnormal Behavior in Animals. W.B. Saunders, Philadelphia, Pennsylvania, USA.

Germano, J.M., and P.J. Bishop. 2008. Suitability of amphibians and reptiles for translocation. Conservation Biology 25:7–15.

Griffith, B., J.M. Scott, J.W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Guay, P.J., and A.N. Iwaniuk. 2008. Captive breeding reduces brain volume in waterfowl (Anseriformes). Condor 110:276–284.

IUCN. 2012. Guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. Gland, Switzerland and Cambridge: IUCN. http://www.issg.org/pdf/publications/translocation-Guidelines-2012.pdf.

Jule, K.R., L.A. Leaver, and S.E.G. Lea. 2008. The effects of captive experience on reintroduction survival in carnivores: a review and analysis. Biological Conservation 141:355–363.

Kingsbury, B.A., and O. Attum. 2009. Conservation strategies: captive rearing, translocation, and repatriation. Pp. 201–220 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). MacMillan Co., Aiken, South Carolina, USA.

Kleiman, D.G., M.R. Stanley Price, and B.B. Beck. 1994. Criteria for reintroductions. Pp. 287–303 *In* Creative Conservation: Interactive Management of Wild and Captive Animals. Olney, P.J.S., G.M. Mace, and A.T.C. Feisteners (Eds.). Chapman and Hall, New York, New York, USA.

Kraaijeveld-Smit, F.J.L., R.A. Griffiths, R.D. Moore, and T.J.C. Beebee. 2006. Captive breeding and the fitness of reintroduced species: a test of the responses to predators in a threatened amphibian. Journal of Applied Ecology 43:360–365.

Mathews, F., M. Orros, G. McLaren, M. Gelling, and R. Foster. 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. Biological Conservation 121:569–577.

McDougall, P.T., D. Reale, D. Sol, and S.M. Reader. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Animal Conservation 9:39–48.

McPhee, M.E. 2003. Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. Biological Conservation 115:71–77.

Mullin, S.J., and R.J. Cooper. 1998. The foraging ecology of the Gray Rat Snakes (*Elaphe obsoleta spiloides*) - visual stimuli facilitate location of arboreal prey. American Midland Naturalist 140:397–401.

Nicholson, T.E., K.A. Mayer, M.M. Staedler, and A.B. Johnson. 2007. Effects of rearing methods on survival of released free-ranging juvenile Southern Sea Otters. Biological Conservation 138:313–320.

Nowak, E.M.,T. Hare, and J. McNally. 2002. Management of "nuisance vipers": effects of translocation on Western Diamond-backed Rattlesnakes (*Crotalus atrox*). Pp. 535–560 *In* Biology of the Vipers. Shuett, G.W., M. Hoggren, M.E. Douglas, and H.W. Greene (Eds.). Eagle Mountain Press, Salt Lake City, Utah USA.

Poole, T.B. 1992. The nature and evolution of behavioural needs in mammals. Animal Welfare 1:203–220.

Roe, J.H., M.R. Frank, S.E. Gibson, O. Attum, and B.A. Kingsbury. 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. Journal of Applied Ecology 47:1253–1261.

Saviola, A.J., V.J. McKenzie, and D. Chiszar. 2012. Chemosensory responses to chemical and visual stimuli in five species of colubrid snakes. Acta Herpetologica 7:91–103.

Scargle, J.D. 2000. Publication bias: the file-drawer problem in scientific inference. Journal of Scientific Exploration 14:91–106.

Seddon, P.J., D.P. Armstrong, and R.F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Shivik, J.A. 1998. Brown Tree Snake response to visual and olfactory cues. Journal of Wildlife Management 62:105–111.

Snyder, N.F.R., S.R. Derrickson, S.R. Beissinger, J.W. Wiley, S.B. Smith, W.D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. Conservation Biology 10:338–348.

Sperry, J.H., M.P. Ward, and P.J. Weatherhead. 2013. Effects of temperature, moon phase and prey on nocturnal activity of Ratsnakes: an automated telemetry study. Journal of Herpetology 47:105–111.

Tuberville, T.D., E.E. Clark, K.A. Buhlmann, and J.W. Gibbons. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated Gopher Tortoises (*Gopherus polyphemus*). Animal Conservation 8:349–358.

Weatherhead, P.J., and G.P. Brown. 1996. Measurement versus estimation of condition in snakes. Canadian Journal of Zoology 74:1617–1621.

Weatherhead, P.J., J.H. Sperry, G.L.F. Carfagno, and G. Blouin-Demers. 2012. Latitudinal variation in thermal ecology of North American Ratsnakes and its implications for the effects of climate warming on snakes. Journal of Thermal Biology 37: 273–281.

Wolf, C.M., B. Griffith, C. Reed, and S.A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

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