

Setting an evolutionary trap: could the hider strategy be maladaptive for white-tailed deer?

M. Colter Chitwood^{1,4} · Marcus A. Lashley² · Christopher E. Moorman³ · Christopher S. DePerno³

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Abstract An evolutionary trap occurs when an organism makes a formerly adaptive decision that now results in a maladaptive outcome. Such traps can be induced by anthropogenic environmental changes, with nonnative species introductions being a leading cause. The recent establishment of coyotes (*Canis latrans*) into the south-eastern USA has the potential to change white-tailed deer (*Odocoileus virginianus*) population dynamics through direct predation and behavioral adaptation. We used movement rate and bedsite characteristics of radiocollared neonates to evaluate their antipredator strategies in the context of novel predation risk in a structurally homogeneous, fire-maintained ecosystem. Neonate bedsites had greater plant cover values compared with random sites

($t = 30.136$; $p < 0.001$), indicating bedsite selection was consistent with the hider strategy used to avoid predation. We determined selection gradients of coyote predation on neonate movement rate and plant cover and diversity at bedsites during the first 10 days of life. Interestingly, neonates that moved less and bedded in denser cover were more likely to be depredated by coyotes, meaning that greater neonate movement rate and bedsites located in less dense cover were favored by natural selection. These results are counter to expected antipredator strategies in white-tailed deer and exemplify how an adaptive response could be maladaptive in novel contexts.

Keywords Coyote · Evolutionary trap · Hider strategy · Neonate · Predation · White-tailed deer

✉ M. Colter Chitwood
chitwoodmc@missouri.edu

Marcus A. Lashley
mal75@msstate.edu

Christopher E. Moorman
chris_moorman@ncsu.edu

Christopher S. DePerno
chris_deperno@ncsu.edu

- ¹ Fisheries and Wildlife Sciences Department, University of Missouri, 302 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA
- ² Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA
- ³ Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA
- ⁴ Present Address: Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

Introduction

An evolutionary trap occurs when an anthropogenic change in the environment causes an organism to make a decision that was formerly adaptive but now results in a maladaptive outcome (Schlaepfer et al. 2002). Decision-making rules (i.e., “Darwinian algorithms”; Cosmides and Tooby 1987) are expected to be adaptive because over evolutionary time they rely on cues correlated with reproductive success and survival (Williams and Nichols 1984). However, Darwinian algorithms are only as complex as necessary to enhance reproductive success and survival where species evolved; they are not so complex as to provide advantages in all introduced circumstances (Schlaepfer et al. 2002). Thus, when environments are altered, formerly reliable cues might not be associated with adaptive outcomes and organisms may be “trapped” by their evolutionary responses to the cues, which results in reduced reproductive success or survival (Schlaepfer et al. 2002).

Humans may now be the most important biotic selective force on Earth (Palumbi 2001), as they have altered nearly every environment at unprecedented rates and to unprecedented extents (Vitousek et al. 1997). In anthropogenically altered environments, evolutionary traps are important mechanistic explanations for declines of populations and species (Schlaepfer et al. 2002; Sherman and Runge 2002). Additionally, anthropogenic disturbances can benefit nonnative species (Byers 2002). The evolutionary trap concept is useful for understanding interactions between native and nonnative species because nonnatives can create novel ecological contexts to which the behaviors of native species may not be adaptive (Callaway and Aschehoug 2000; Shea and Chesson 2002).

The recent introduction and expansion of coyotes (*Canis latrans*) in the southeastern USA (Parker 1995) provides an opportunity to evaluate the potential for evolutionary traps to operate in a novel predator–prey system. In the region, white-tailed deer (*Odocoileus virginianus*) have been without a large canid predator [i.e., red wolf (*Canis rufus*)] since 1900 (Young and Goldman 1944), and coyotes are recent, nonnative additions to the landscape, having occupied the area primarily by anthropogenic means during the past 10–40 years (Hill et al. 1987; Gompper 2002). Other than accidental or purposeful releases of coyotes (see Hill et al. 1987), human alteration of the landscape or community structure (e.g., intensive logging, agricultural development) likely opened additional habitat to coyotes (Parker 1995). Before the arrival of coyotes, white-tailed deer persisted for decades with low predation risk (except for humans), but recent evidence indicates that direct predation of coyotes on neonates (Kilgo et al. 2012; Chitwood et al. 2015b) and adults (Chitwood et al. 2014) can be substantial and likely affects local deer population trajectory (Chitwood et al. 2015a).

Though direct predation is clearly of interest in ungulate population dynamics, our understanding of predator evasion behaviors of ungulate offspring is limited (Grovenburg et al. 2012). Much of the research is focused on how adult or fawn deer behave once they are attacked. For example, Lingle and Pellis (2002) documented how white-tailed deer and mule deer (*O. hemionus*) adults responded differently (i.e., facing the attack or fleeing it) when confronted by coyotes. Grovenburg et al. (2012) documented how escape cover contributed to white-tailed deer fawns' successful evasion of coyote and human chases. Additionally, maternal defense of fawns is a well-documented antipredator strategy (e.g., Lingle et al. 2005; Grovenburg et al. 2009). However, little research has addressed the behavioral decisions that reduce the chances of detection by the predator (i.e., the use of cover and crypsis) during the time when neonates rely on the hider strategy.

Predation pressure should elicit changes in deer behavior that reduce direct predation risk [e.g., increased vigilance (Lashley et al. 2014a; Cherry et al. 2015)]. Evolutionary history with red wolves has produced antipredator strategies that have persisted in deer populations prior to the arrival of coyotes. Neonatal deer are “hidiers” after birth, relying on crypsis and infrequent contact with their mothers to avoid detection by predators (DeYoung and Miller 2011). Moreover, experienced mothers appear more likely to lead fawns to dense cover in response to disturbances, distress calls, or predator odors (Smith 1991). We evaluated the behavior of neonatal white-tailed deer in the presence of a novel, nonnative predator, in a landscape dominated by anthropogenic fire. Because neonates rely on crypsis as the primary means of predator avoidance at young ages, predation risk from coyotes (assuming it is similar to evolutionary pressures exerted by red wolves) should exert pressure for neonates to move less and use cover (DeYoung and Miller 2011). Because of documented predation risk from coyotes at our study site, we hypothesized that neonates would be more likely to survive if they had lower movement rates and relied on greater plant cover and diversity at bedsites.

Study area

We conducted our study at Fort Bragg Military Installation (hereafter, Fort Bragg; 40,500 ha), which was owned by the US Department of Defense and located in the Sandhills physiographic region of central North Carolina, USA. Open longleaf pine (*Pinus palustris*) forests dominated the uplands, and they were managed with intensive growing-season prescribed fire on a 3-year fire-return interval. The understory of longleaf forests was primarily turkey oak (*Quercus laevis*) and wiregrass (*Aristida* spp.). Densely vegetated drainages that burned less frequently were interspersed throughout the landscape. An extensive, drivable firebreak network facilitated the implementation of the large-scale fire regime, while providing access for military vehicles (Lashley et al. 2014b). The fire regime resulted in structurally homogeneous uplands, which relegated dense cover to the long (and usually narrow) unburned drainages (~11% of land area at Fort Bragg; Lashley et al. 2014b).

Anecdotal observations and harvest data collected by on-site biologists indicated that deer density declined beginning in 1989, commensurate with the initiation and establishment of coyotes at Fort Bragg (Fort Bragg Wildlife Branch, unpublished data; Chitwood et al. 2015a). Throughout our study, deer population density was relatively low (~6 deer/km²), and deer hunting occurred from the first Saturday in September through 1 January

(Chitwood et al. 2015a). Coyotes were documented predators of adult female deer (Chitwood et al. 2014) and the leading cause of mortality for fawns (Chitwood et al. 2015b). Though bobcats (*Lynx rufus*) were a documented predator of neonates at Fort Bragg, 30 of 35 (86%) depredated fawns were linked to coyotes (Chitwood et al. 2015b). Population modeling based on vital rates (i.e., survival, fecundity) indicated the deer population was declining about 9% annually and that low fawn survival, driven largely by coyote predation, was the most important vital rate in explaining the decline (Chitwood et al. 2015a).

Materials and methods

During January–May, 2011–2012, we captured adult females using tranquilizer guns. We immobilized deer with Telazol (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN, USA), xylazine hydrochloride (2.5 mg/kg; Congaree Veterinary Pharmacy, Cayce, SC, USA), and ketamine hydrochloride (5 mg/kg; Midwest Veterinary Supply, Burnsville, MN, USA) in 2-cc transmitter darts. We GPS-collared (Wildcell, Lotek Wireless Inc., Newmarket, Ontario, Canada; fix rate = 2.5 h) all females captured in 2011, but in 2012, some females received GPS-collars, while the rest received VHF only (Model 2510B, Advanced Telemetry Systems, Isanti, MN, USA). We deployed vaginal implant transmitters (VIT; Model M3930, Advanced Telemetry Systems) to facilitate capture of neonates. The VITs contained a temperature-sensitive switch to detect expulsion from the vaginal canal and a precise-event timer to log the time (in 30-min intervals) passed since parturition. Implant procedures followed Bowman and Jacobson (1998) and Carstensen et al. (2003), except that we did not trim protruding antennas (Kilgo et al. 2012). At 80-min postinjection, we antagonized the xylazine hydrochloride with tolazoline hydrochloride (10 mg/kg; Midwest Veterinary Supply, Burnsville, MN, USA) and monitored the deer until recovery. Deer capture and handling was approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (10-143-O).

We monitored VIT signals intensively (\leq every 8 h) during the fawning season (see Chitwood et al. 2015b for details) and allowed \geq 2 h after the parturition time derived from the VIT timer before initiating a search. The time delay provided time for grooming and initial bonding between female and neonate(s). Also, during peak fawning each year, we used volunteers and undergraduate students (10–40 individuals) to conduct two organized fawn searches (\sim 2–3 h); volunteers walked side-by-side along transects through all cover types, and searches occurred in

areas where we had worked to capture adult females, which reduced chances that opportunistic captures were biased by cover type or proximity to roads (Chitwood et al. 2015b). When we located neonates, we used latex gloves to deploy expandable breakaway radiocollars (Diefenbach et al. 2003; Model M4210, Advanced Telemetry Systems) equipped with a motion-sensitive mortality switch on a 4-h delay. We estimated age of opportunistically captured neonates using new hoof growth (Sams et al. 1996) and behavior.

We monitored neonates intensively for the first 10 days of life to increase the chances of recovering fawn remains and evidence of predators (coyote or bobcat) when mortalities occurred (see Chitwood et al. 2015b for details). We assigned final cause of mortality based on field evidence and predator DNA, if necessary (Chitwood et al. 2015b). To obtain bedsite locations, we relocated neonates via homing once every 24-h period for the first 10 days of life, at all times of day or night. Opportunistic fawns were relocated for the first 10 days of life based on their estimated age at capture (not for 10 days past capture). We checked the location of the radiocollared adult female and did not approach if she was in close proximity to the neonate. We approached neonates quietly to minimize disturbance but close enough for a visual relocation [with ambient light or with the aid of forward-looking infrared (FLIR)]. Once we located the bedded neonate, we took a GPS point, noted the actual bedsite's bearing and distance from the GPS point, and took detailed field notes defining the location of the bedsite. This approach allowed us to minimize disturbance to the neonate, while maximizing our success for returning to the exact bedsite for subsequent data collection (approximately 1 month later).

Because neonates are highly susceptible to predation early in life, particularly in the first week (e.g., Kilgo et al. 2012; Chitwood et al. 2015b), we determined movement rate and vegetative cover at bedsites for the first 10 days of life. We used movement rate between known bedsites as a surrogate for overall movement rate and acknowledge that our approach does not account for additional bedsites used between subsequent homing attempts. We used ArcMap 10 (ESRI, Redlands, CA, USA) to calculate movement distances (in meters) for each neonate for the first 10 days of life using its sequential points. We calculated movement rate for each neonate by dividing the cumulative distance moved by the number of days it lived [i.e., m/day (for up to 10 days of age)]. We measured vegetative structure at known neonate bedsites using a modified vegetation profile board (Nudds 1977). Approximately 1 month after the bedsite was used by the fawn, we returned to the location and estimated percent cover from 0 to 1 m in 2 50-cm height categories. We assigned visual obstruction values of 0, 1, 2, 3, 4, or 5 in each height category, and the values

represented vegetative coverage of 0, 1–20, 21–40, 41–60, 61–80, or 81–100%, respectively. We placed the board at plot center (i.e., in the bedsite) and viewed it at a height of 1 m (to standardize the view of the observer), from 10 m away, along bearings of 0°, 120°, and 240°. We averaged estimates from the 2 height categories to provide 1 number for percent cover along each bearing. Additionally, to assess plant diversity along each bearing, we recorded the number of plant species contributing to the coverage of the board in the 2 height categories. We determined final Nudds board scores and final plant diversity scores by taking the average of the 3 profile bearings at each bedsite and then averaging across all bedsites for that neonate.

To confirm that neonates were selecting bedsites consistent with our understanding of the behavior of the species (i.e., using dense cover), we compared used bedsites with random, unused sites for all fawns captured. We chose unused sites by taking a random bearing and distance (>20 and <100 m) from the known bedsite. We used a *t* test to compare cover values between the used and unused bedsites. To account for dependence of bedsites for each fawn, we used the average bedsite value for each fawn (and did the same for the unused sites); this resulted in each fawn only having 1 bedsite value (and each fawn having 1 corresponding unused bedsite value).

Viability selection is selection that acts to increase an individual's probability of survival, given the behaviors of interest. To test for viability selection on neonate behaviors based on coyote depredation, we calculated selection gradients (Lande and Arnold 1983) for survival to 10 days of age. Selection gradient analysis employs multiple regression to evaluate the relationship between relative fitness (w) and standardized trait values ($z'_{1...n}$) for multiple traits (Lande and Arnold 1983). The basic model is

$$w_{ij} = \beta_0 + \beta_1 z'_{i1} + \beta_2 z'_{i2} + \dots + \beta_n z'_{in}$$

where fitness variance (i) in each environment (j) is partitioned into effects of each of n traits (DeWitt and Langerhans 2003). Multiple regression provides n partial regression coefficients (i.e., selection gradients, $\beta_{1...n}$), which describe selection acting directly on the traits of interest ($z_{1...n}$; DeWitt and Langerhans 2003). The response variable, relative fitness, is defined with respect to the mean fitness of the population (i.e., fitness value \div mean fitness value); our analysis used survival to 10 days of age (i.e., 0 = died, 1 = survived) as the measure of fitness. For the selection gradient analysis, we included neonates for which we had movement and bedsite data and whose fates were either “survived” or “depredated by coyote” in the first 10 days of life. We used standardized trait values of neonate movement rate, bedsite cover, and bedsite plant diversity as variables in the selection gradient analysis. We

conducted all statistical analyses in JMP Pro 10 (SAS Institute Inc., Cary, NC, USA).

Results

We radiocollared 59 neonates via VITs (23 in 2011 and 36 in 2012). Additionally, we added 6 neonates (4 in 2011 and 2 in 2012) to our sample via opportunistic encounters; all 6 opportunistic captures were less than 5 days old. Coyote predation was the leading cause of mortality at Fort Bragg, accounting for 30 neonate deaths for the entire study period (full length of monitoring was 16 weeks; see Chitwood et al. 2015b for complete details about survival estimation for 10 days and 16 weeks). We documented 325 bedsites used by 60 fawns during the study (some fawns had to be excluded because we lost access to bedsites due to prescribed fire or military activity); mean bedsite Nudds board cover values for each fawn ($\bar{x} = 3.93$, SE = 0.13, $n = 60$) were greater ($t = 30.136$, $p < 0.001$) than those from random, unused sites ($\bar{x} = 3.13$, SE = 0.14, $n = 60$), indicating neonates selected bedsites with greater cover.

We performed the 10-day selection gradient analysis on a subset of neonates because we removed nonpredatory sources of mortality and fawns with missing data from consideration. Of the 30 total coyote depredations reported by Chitwood et al. (2015b), 10 occurred in the first 10 days of life. However, for 4 of those neonates, we were unable to obtain a movement rate because they were killed within 2 days of birth or we lost access to bedsites (due to prescribed fire or military activity); thus, they were excluded from the selection gradient analysis. Thus, the full sample of 65 neonates reported by Chitwood et al. (2015b) was reduced to 35. Selection gradient analysis of 35 neonates (6 depredated by coyotes in the first 10 days of life + 29 that survived past day 10) revealed that greater neonate movement [i.e., $\bar{x} = 268.8$ m/day (SE = 26.0, $n = 29$) versus $\bar{x} = 138.2$ m/day (SE = 22.5, $n = 6$)] was favored by natural selection (i.e., coyote predation was biased toward neonates that moved less; Table 1; Fig. 1).

Table 1 Selection gradient (β') of coyote depredation on neonatal white-tailed deer survival ($n = 35$) using 3 field-based behavioral decisions (movement rate, vegetative cover at bedsites, and plant diversity at bedsites) that could relate to fawn survival at Fort Bragg Military Installation, NC, USA, 2011–2012

Behavior	β'	SE	p^a
Movement rate	0.17	0.07	<0.01
Bedsite cover	−0.15	0.08	0.03
Bedsite plant diversity	0.07	0.08	0.18

^a $\alpha = 0.05$

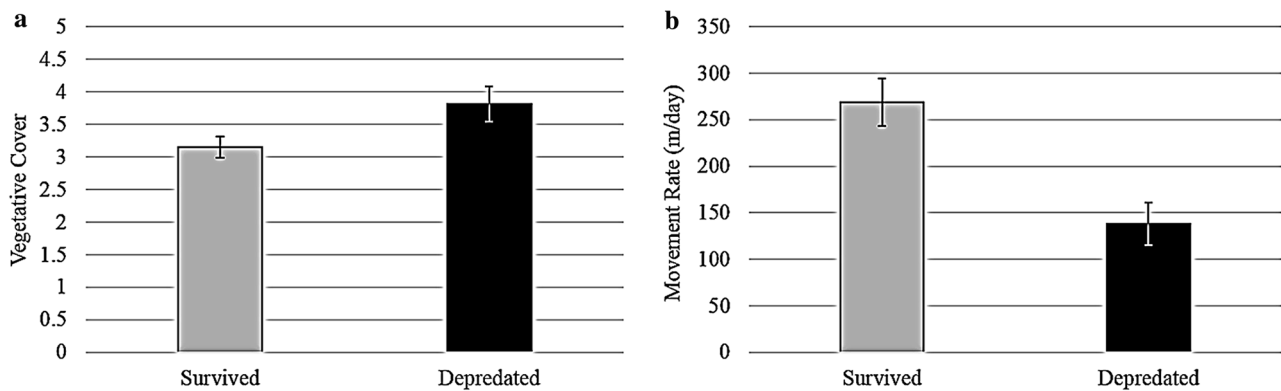


Fig. 1 Mean bedsite vegetative cover values (**a**; 0 = no visual obstruction, 5 = 81–100% visual obstruction) and movement rate (**b**; m/day) for white-tailed deer fawns that survived to 10 days of age

Additionally, neonate use of bedsites with lower Nudds board cover values [i.e., $\bar{x} = 3.15$ (SE = 0.16, $n = 29$) versus $\bar{x} = 3.81$ (SE = 0.27, $n = 6$)] was favored by natural selection (i.e., coyote predation was biased toward neonates selecting denser cover; Table 1; Fig. 1). Behaviors associated with neonate selection of bedsite plant diversity did not show evidence of selection by coyote predation (Table 1).

Discussion

Our results for movement and bedsite cover were counter to our hypothesized antipredator strategies for neonatal deer and might exemplify how an adaptive response can become maladaptive in novel contexts. Intuitively, neonates should minimize movement because they evolved to rely on cryptic coloration (Lent 1974) and lack of scent (Johnson 1951; Mech 1984; Linnell et al. 2004) to avoid detection by predators, particularly at young ages. Strong selection for antipredator traits likely explains the fact that, when alarmed, neonate white-tailed deer and red deer (*Cervus elaphus*) exhibit bradycardia and reduced respiration (Espmark and Langvatn 1979, 1985; Jacobsen 1979); white-tailed deer less than 45 days old exhibit bradycardia in response to recorded wolf howls (Moen et al. 1978). Additionally, neonate pronghorn (*Antilocapra americana*) tended to be depredated most at 11–20 days of age (see Byers and Byers 1983 for discussion), which represented a “window of vulnerability” when they could not outrun predators but displayed increased activity. Similarly, Litvaitis and Shaw (1980) suggested risk was greatest after the first couple weeks of life when white-tailed deer fawns began moving more. Given that a hiding strategy is advantageous for young ungulates, abandoning the strategy at a young age is counterintuitive. We should expect that neonates would move less under high predation risk, but our data indicated that moving more

($n = 29$) and those that were depredated by coyotes in the first 10 days of life ($n = 6$), Fort Bragg Military Installation, NC, USA, 2011–2012. Error bars indicate standard error (SE)

conferred greater survival, while moving less predisposed neonates to depredation.

Our study site is a fairly open, homogeneous landscape where frequent anthropogenic prescribed fire has the effect of isolating the densest cover along fairly linear, low-lying drainages. With little structural heterogeneity on the landscape (see Lashley et al. 2014b, 2015), coyotes hunting for neonates in cover are relegated to those same drainages. As hidiers, young neonates should benefit from bedsites with the most cover, and studies have documented white-tailed deer neonates selecting well-vegetated bedsites (e.g., Butler et al. 2009, this study). However, if coyotes are able to thoroughly hunt the limited cover available, high predation rates on fawns should be expected. Additionally, coyotes may have other reasons to hunt densely vegetated drainages because small mammals, which are an important component of coyote diet at Fort Bragg (Swingen et al. 2015), appear to be more available in this cover type. Sasmal et al. (2017) showed that *Peromyscus* spp. abundance was greater in drainages than in the frequently burned upland pine forests. Thus, the hiding strategy evolutionarily adapted for neonatal white-tailed deer might fail them at our study site, providing evidence for an evolutionary trap.

Though our results provide empirical evidence for an evolutionary trap, we must consider limitations in the interpretation. First, our sample size is small and relies on less-than-perfect understanding of movement in the first 10 days of life (due to our efforts to reduce potential biases on neonatal behavior). Similarly, we must acknowledge that we did not measure movements of the mother (e.g., how long between nursing bouts, how far to move with the fawn at each visit), which could bias our assessment of fawn movement. Second, other variables could affect neonatal survival (e.g., body condition, health status) and were unmeasured (e.g., Crespi 1990), and multicollinearity may exist among any of the measured or unmeasured traits

(e.g., Schluter and Smith 1986). For example, we did not assess body condition or health status, so we were unable to account for how such metrics could relate to movement rate and, therefore, survival. Third, we cannot assume causality (e.g., Wade and Kalisz 1990), and we must acknowledge the potential for our monitoring efforts to have biased the behaviors of the neonates, their mothers, and hunting coyotes. Though we used a FLIR unit to aid in locating the neonate at a distance (so that it would not have reason to flush), our presence in the area or our departure could have initiated a flight response in some neonates, which would force those fawns to choose new bedsites and potentially bias their risk of predation. Acknowledgment of these limitations is important because research on selection is often observational (rather than experimental), making causal inferences problematic (Janzen and Stern 1998).

Another important consideration is that adult female behavior may be a crucial component in understanding the predator–prey dynamic, particularly with respect to neonates. Though we did not evaluate fine-scale movements or behaviors of adult females, they may serve as cues for coyotes (or other predators) to search cover for hiding neonates. Similarly, it is possible that coyotes cue on parturition behavior, which contributes to direct mortality of the female or her resulting neonates. On the same study site, Chitwood et al. (2014) documented 4 adult females depredated by coyotes, 3 of which occurred during the fawning season, and they speculated that pregnant females may have been vulnerable targets for coyotes. Predation pressure from coyotes on adult females could be just as important as pressures exerted on neonates and may affect our interpretation of neonatal behavioral traits. For example, behavioral cues from the female may override any benefit to reduced neonate movement by prompting coyotes to search in areas where females spend the most time or leave the most scent.

At Fort Bragg, the relative novelty of coyotes as predators of deer and the intense prescribed fire regime represent the types of anthropogenically induced changes that can create evolutionary traps for otherwise well-adapted organisms. The premise of evolutionary traps hinges on past selective pressures shaping behaviors that were previously adaptive (Robertson et al. 2013). In our case, we suggest white-tailed deer neonates fell victim to an evolutionary trap, as evidenced by selection against the previously adaptive hider strategy. Other research has documented similar effects of nonnative predators transforming formerly adaptive behaviors into maladaptive ones (e.g., Igual et al. 2007), so evolutionary traps might be a useful framework for predicting and managing the potential impact(s) of nonnative species introductions (Schlaepfer et al. 2005). Future research should continue to explore the evolutionary trap concept in long-lived

vertebrates, which undoubtedly have complicated behavioral traits that affect survival and are difficult to isolate and measure in field studies.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement This article does not contain any studies with human participants performed by any of the authors. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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