

2017

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David M. Delaney
University of Alabama, Birmingham

Fredric J. Janzen
Iowa State University, fjanzen@iastate.edu

Daniel A. Warner
University of Alabama, Birmingham

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Nesting stage and distance to refuge influence terrestrial nesting behavior of Painted Turtles (*Chrysemys picta*)

Abstract

Theory predicts prey should flee to safety when the fitness benefits of flight meet or exceed the costs. Empirical work has shown the importance of predation risk (e.g., predator behavior, distance to refuge) to prey flight behavior. However, less is known about the influence of flight costs. We monitored nesting Painted Turtles (*Chrysemys picta* (Schneider, 1783)) to examine their response to a human observer (potential predator) depending on the distance between a turtle and an observer, distance between a turtle and water (i.e., refuge), and nesting stage at the time of the encounter (i.e., searching for a nest site vs. constructing a nest). We found no evidence that the distance to an observer influenced flight decisions. However, turtles were less likely to flee as the distance to water increased, and turtles already constructing nests were more likely to continue nesting than those still searching for nest sites. Turtles that traveled farther from water and that were constructing nests may have continued nesting because they had invested considerable energy and were close to completing oviposition. Thus, the fitness benefits of being closer to successful oviposition may outweigh the costs of increased vulnerability to predators during this important and vulnerable period of reproduction.

Keywords

Risk assessment, flight initiation distance, fitness tradeoff, *Chrysemys picta*, painted turtle, escape, defense

Disciplines

Behavior and Ethology | Ecology and Evolutionary Biology | Terrestrial and Aquatic Ecology

Comments

This is a manuscript of an article published as Delaney, David M., Fredric J. Janzen, and Daniel A. Warner. "Nesting stage and distance to refuge influence terrestrial nesting behavior of Painted Turtles (*Chrysemys picta*)." *Canadian Journal of Zoology* 95, no. 11 (2017): 837-841. doi: [10.1139/cjz-2016-0206](https://doi.org/10.1139/cjz-2016-0206). Posted with permission.

**Nesting stage and distance to refuge influence terrestrial nesting
behavior in an aquatic turtle**

David M. Delaney, Fredric J. Janzen, and Daniel A. Warner

D.M. Delaney* (corresponding author) Department of Biology, University of Alabama at
Birmingham, Birmingham, Alabama, USA

dmdelane@iastate.edu

Phone: 217-343-7764

*current address: Department of Ecology, Evolution, and Organismal Biology, Iowa
State University, Ames, Iowa, USA

F.J. Janzen Department of Ecology, Evolution, and Organismal Biology, Iowa State
University, Ames, Iowa, USA

fjanzen@iastate.edu

D.A. Warner* Department of Biology, University of Alabama at Birmingham,
Birmingham, Alabama, USA

daw0036@auburn.edu

*current address: Department of Biological Sciences, Auburn University, Auburn,
Alabama, USA

Nesting stage and distance to refuge influence terrestrial nesting behavior in an aquatic turtle

David M. Delaney, Fredric J. Janzen, and Daniel A. Warner

Abstract: Theory predicts prey should flee to safety when the fitness benefits of flight meet or exceed the costs. Empirical work has shown the importance of predation risk (e.g., predator behavior, distance to refuge) to prey flight behavior. However, less is known about the influence of flight costs. We monitored nesting painted turtles (*Chrysemys picta* (Schneider, 1783)) to examine their response to a human observer (potential predator) depending on the distance between a turtle and an observer, distance between a turtle and water (i.e., refuge), and nesting stage at the time of the encounter (i.e., searching for a nest-site vs. constructing a nest). We found no evidence that the distance to an observer influenced flight decisions. However, turtles were less likely to flee as the distance to water increased, and turtles already constructing nests were more likely to continue nesting than those still searching for nest-sites. Turtles that traveled farther from water and that were constructing nests may have continued nesting because they had invested considerable energy and were close to completing oviposition. Thus, the fitness benefits of being closer to successful oviposition may outweigh the costs of increased vulnerability to predators during this important and vulnerable period of reproduction.

Key words: Risk assessment, flight initiation distance, fitness tradeoff, *Chrysemys picta*, painted turtle, escape, defense

Introduction

The ability of an animal to assess predation risk and behave accordingly has important fitness consequences (Ghalambor and Martin 2000, 2001; Persons et al. 2001). However, risk can vary depending upon environmental context (e.g., predator behavior, distance to refuge) and individual activity (e.g., foraging, sleeping). Dynamic investment in anti-predator behavior allows animals to respond to such extrinsic and intrinsic variation in risk. Individuals benefit by reducing predation risk, but they must balance costs such as loss of foraging or reproductive opportunities (Dill and Fraser 1984; Lima and Dill 1990; Heithaus and Dill 2002). For example, elk (*Cervus canadensis* (Erxleben, 1777)) prefer grassland habitat that increases foraging efficiency when wolves (*Canis lupus* (L., 1758)) are absent, but occupy wooded habitat to reduce predation risk when wolves are present (Creel et al. 2005). In addition, although bluegill (*Lepomis macrochirus* (Rafinesque, 1819)) foraging efficiency is highest in pelagic habitat, juveniles migrate to littoral vegetation to reduce predation risk by largemouth bass (*Micropterus salmoides* (Lacepède, 1802); Werner and Hall 1988). Thus, animals can assess environmental risks and benefits and should behave accordingly to maximize fitness tradeoffs.

During direct encounters with predators, prey must decide to remain in place or flee to safety. Theory predicts that animals are more likely to flee as the risk of predation increases, and that such flight decisions should maximize fitness (Ydenberg and Dill 1986; Cooper and Frederick 2007). This theory has been well tested by measuring flight initiation distance (FID), which is the minimum distance a prey animal allows a predator to approach before fleeing. This measure indicates how prey perceive risk. For example,

prey typically have longer FIDs when farther from refuge sites (Dill and Houtman 1989; McLean and Godin 1989; Dill 1990; Bonenfant and Kramer 1996; Stankowich and Blumstein 2005), presumably because risk is higher under such circumstances and increasing FID permits them to reach safety. Moreover, FID is influenced by other extrinsic factors, such as habitat (Martin and López 1995; Blumstein et al. 2004; Cooper and Wilson 2007; Camp et al. 2012), group size and composition (Dill and Ydenberg 1987; Ebensperger and Wallem 2002; Laursen et al. 2005; Ciuti et al. 2008), predator speed, size, and direction of attack (Kramer and Bonenfant 1997; Cooper 2006; Stankowich and Coss 2006; Cooper and Whiting 2007; Cooper and Stankowich 2010), as well as intrinsic factors, such as experience (Runyan and Blumstein 2004; Reimers et al. 2009), sex, body size and condition (Capizzi et al. 2007; Cooper 2007; Gotanda et al. 2009), and stress (Seltmann et al. 2012).

Most FID studies focus on factors likely to directly influence the ability of prey to flee effectively. Less work has focused on factors that influence the costs of flight, such as the loss of foraging or social opportunities. For example, after fleeing from predators, male great snipe (*Gallinago media* (Latham, 1787)) return to leks sooner when mating probability is high (Kalas et al. 1995), suggesting males tolerate higher predation risk when the cost of flight is high. Thus, the loss of opportunity can be great enough to influence how animals respond to risk and warrants further study. Furthermore, most FID studies are conducted while prey are foraging (Lima and Dill 1990). However, the specific activity an individual is engaged in could be an important factor in balancing flight tradeoffs, especially when different types of activities have different fitness

consequences. For example, reproduction occurs less often than foraging, but also has different influences on fitness. Accordingly, prey should tolerate higher risk for activities that have greater fitness benefits than for activities with little consequence to fitness (Ydenberg and Dill 1986; Cooper and Frederick 2007). For example, male broad-headed skinks (*Eumeces laticeps* (Schneider, 1801)) tolerate closer predator approaches when a female is present, presumably because of the cost of losing a mating opportunity (Cooper 1997a).

Aquatic turtles, such as the painted turtle (*Chrysemys picta* (Schneider, 1783)), are well suited for addressing these issues. Adult *C. picta* spend most of their time in water or basking on logs and rocks with direct access to water. If disturbed, *C. picta* flee into water (Polich and Barazowski 2016) and likely perceive water as safe habitat. However, mature females venture up to 600 m from water to construct a terrestrial nest (Ernst and Lovich 2009), which increases vulnerability to predators (Tucker et al. 1999; Tucker and Warner 2000). Nesting excursions for *C. picta* in Michigan have been reported to last 1.5–23 hours ($n = 6$, Rowe et al. 2005), and *C. picta* in Quebec spend 0.5–4.5 hours from initiation of digging until females leave the nest (Christens and Bider 1987). Evidence from another freshwater turtle, *Emydura macquarii* (Gray, 1830), suggests that predation risk increases with distance to water (Spencer 2002; but see Refsnider et al. 2015). Specifically, females nest close to water when fox (*Vulpes vulpes* (L., 1758)) predators are present, but nest farther from water to increase offspring fitness when foxes are absent. We monitored nesting *C. picta* to examine their response (continue to nest vs. flee) to a human observer (potential predator) depending on the

distance between a female and observer, distance between a female and water, and nesting stage (searching for a nest-site vs. constructing a nest). We predicted females would flee when the observer was close because perceived predation risk should increase as the distance to a predator decreases. We also predicted females would be more likely to flee when farther from water because predation risk likely increases with distance from water (Spencer 2002). Lastly, we predicted females would be more likely to continue nesting when already in the process of nest construction than when searching for nest-sites because considerable energy had already been invested and females were likely closer to completing oviposition.

Materials and methods

We monitored 67 female painted turtles (*Chrysemys picta*) during the nesting season at two sites across two reproductive seasons. Field work took place from 7–19 June in 2014 and from 23–24 May and 15–30 June in 2015 at Round Lake State Park near Sagle, Idaho ($n = 41$) and from 20–24 June in 2014 and 25 May–14 June in 2015 at Smith and Bybee Wetlands in Portland, Oregon ($n = 26$). The main predators at both sites are likely humans (*Homo sapiens* (L., 1758)) and raccoons (*Procyon lotor* (L., 1758)), although Idaho turtles may also encounter American badger (*Taxidea taxus* (Schreber 1777)), black bear (*Ursus americanus* (Pallas, 1780)), bobcat (*Lynx rufus* (Schreber, 1777)), coyote (*Canis latrans* (Say, 1823)), mountain lion (*Puma concolor* (L., 1771)), and wolverine (*Gulo gulo* (L., 1758)). We located turtles via visual encounter surveys at known nesting areas. Surveyors slowly walked parallel to the water body and scanned for

nesting turtles. Although we did not record the angle of approach by observers (which could affect prey flight decisions; Cooper 1997a, 2003; Guay et al. 2013), most encounters were lateral to the turtle (rather than head on), and observers were not directly between or on the opposite side of the turtle and water. Most turtles were encountered by one observer, although neither observer identity nor number was recorded. Most nesting areas sloped slightly towards water with bare or sparsely vegetated soil and an open canopy. For example, during studies of nest behavior from 2013-2015 (unpubl. data) at these sites, turtles nested on slopes of $15 \pm 7^\circ$ SD ($n = 110$, Idaho) and $10 \pm 6^\circ$ SD ($n = 28$, Oregon) and with canopy openness of $46 \pm 6\%$ SD ($n = 62$, Idaho) and $76 \pm 3\%$ SD ($n = 10$, Oregon). Because of such homogeneity within sites, these factors probably had little effect on flight behavior in our study. *Chrysemys picta* rarely venture onto land, with the primary exception of nesting (Ernst and Lovich 2009). Thus, we considered all *C. picta* in the known nesting areas as females engaged in nesting. Furthermore, because of our frequent searches, turtles were initially encountered either searching for nest-sites or constructing nests, and likely had not progressed to laying eggs or returning to water after oviposition.

Although many studies use FID to examine risk assessment, we used an alternative method that allowed some females to continue nesting, which was required for our ongoing studies of nesting behavior. After locating a turtle, we marked the location of the human observer with a small stick or rock, visually marked the location of the animal, and recorded the nesting stage (i.e., searching for a nest-site vs. constructing a nest). All turtles either stopped moving (60/67) or immediately fled (7/67) during the initial

encounter, indicating they noticed the observer. Turtles that stopped moving remained in place with their neck extended while the observer was in sight, a behavior also reported for box turtles (*Terrapene ornata* (Agassiz, 1857); Legler 1960). Thus, we walked at least 10 m away to a location that reduced our visibility to the turtle, and that was not between or on the other side of a turtle and water, to observe its reaction (for similar methods, see Bateman et al. 2014). After the female finished nesting or fled, we recorded the response to the observer (i.e., continue nesting vs. flee). We then measured the shortest distance between the turtle and observer, and the distance between the turtle and water to the nearest 0.1 m. Our methodology differs from studies that measure FID because we did not approach turtles until they fled. Instead, we used turtle response (continue nesting vs. flee) as a binary dependent variable rather than FID (continuous).

We analyzed data with SAS software (version 9.4; SAS Institute 1997). To test our three hypotheses, we used logistic regression with female response to the observer (continue nesting vs. flee) as a binomial dependent variable and distance to observer, distance to water, nesting stage, year, site, and all 2- and 3-way interactions as independent variables. Non-significant terms were sequentially removed, starting with higher-order interactions, to construct the final model. Year, site, and all interactions were not significant (all $P \geq 0.1114$) and were removed from the final model. Furthermore, we calculated phi (ϕ), the effect size, for independent variables by dividing the χ^2 statistic by n and taking the square root of that value (Rosenthal 1991). Effect sizes allowed us to compare the relative influence of each independent term on flight behavior.

Results

Distance to the observer did not influence whether females continued to nest or fled (Fig. 1A; $\chi^2 = 1.3108$, $P = 0.2523$, $\phi = 0.14$). However, females closer to water fled more often than females farther from water (Fig. 1B; $\chi^2 = 6.5161$, $P = 0.0113$, $\phi = 0.31$). Turtles that continued nesting ($n = 48$) averaged 4.6 m (± 0.6 SE) from the observer and 17.1 m (± 1.9 SE) from water, in contrast to turtles that fled ($n = 19$), which averaged 6.6 m (± 1.1 SE) from the observer and 3.9 m (± 0.8 SE) from water. In addition, females searching for nest-sites ($n = 27$) were more likely to flee to water than females already constructing nests ($n = 40$; Fig. 2; $\chi^2 = 11.2339$, $P = 0.0008$, $\phi = 0.41$).

Discussion

The relationship between predation risk and flight behavior is well documented, yet less is known about the influence of flight costs. In addition, most risk assessment studies focus on foraging animals, whereas less is known about flight behavior during reproduction. To address these issues, we monitored nesting painted turtles (*Chrysemys picta*) to examine their response to an observer depending upon the distance to an observer, distance to water, and nesting stage. We found no evidence that distance to an observer influenced turtle flight decisions. However, turtles were less likely to flee as the distance to water increased and when constructing nests compared to when searching for nest-sites. A possible explanation for variation in flight behavior is that the fitness benefits of completing oviposition once already started (i.e., far from water and when constructing nests) may outweigh the costs of being far from the refuge of water.

An important assumption of FID studies is that predation risk increases as predator distance decreases (Ydenberg and Dill 1986). However, we found no effect of distance to an observer. In contrast, other freshwater turtles, *Mauremys leprosa* (Schweigger, 1812) and *Trachemys scripta* (Schoepff, 1792), emerge from their shells sooner when human observers are farther away, indicating lower perceived risk as observer distance increases (Martín et al. 2005; Polo-Cavia et al. 2008). We recorded distance to the observer as the shortest distance during a turtle-observer encounter, but most turtles (90%) froze at that time and made their flight decision when the observer was out of sight. Thus, the distance the observer previously approached may not be as important for risk assessment as simply knowing that an observer is in the area. Moreover, prior distance to the observer is likely a poor metric for predation risk in this context and system. In addition, any effect of distance to the observer ($\phi = 0.14$) may be overshadowed by the effects of distance to water ($\phi = 0.31$) and nesting stage ($\phi = 0.41$) in *C. picta* during terrestrial excursions.

Flight initiation distance increases with distance to refuge for many vertebrates (Dill and Houtman 1989; McLean and Godin 1989; Bonenfant and Kramer 1996; Cooper 1997b; Guay et al. 2013), but we observed the opposite pattern for *C. picta* (i.e., turtles farther from water were less likely to flee). Turtles have very different morphologies (e.g., bony shell) from previously tested taxa, but fishes with armored morphologies respond less severely to predators than more vulnerable fishes (McLean and Godin 1989). Thus, the armored body plan of turtles may contribute to their contrasting response. However, it is more likely that energetic investment in arduous terrestrial

locomotion, and presumably being closer to oviposition, increased turtle tolerance of observers. Moreover, most terrestrial predators are considerably faster than turtles, and thus fleeing when far from water may have little to no benefit. Similarly, lizards tolerate higher predation risk when the benefits of foraging (Cooper et al. 2003; Cooper and Pérez-Mellado 2004) and mating (Cooper 1997a; Cooper 2009) are higher. In line with this interpretation, turtles constructing nests were more likely to continue nesting than those searching for nest-sites. Thus, the fitness benefits of being closer to oviposition may outweigh the costs of being farther from refuge. Future work that records investment into reproduction on a continuous scale (e.g., time spent nesting) rather than a binary variable (searching for vs. constructing a nest) will give insight into this interpretation.

An incorrect decision in these circumstances can be lethal. Adult *C. picta* have been depredated during nesting events (Ernst 1974; Wilbur 1975; Rowe et al. 2005), and this lethal phenomenon has been recorded in other aquatic turtles during terrestrial nesting forays (Ernst 1976; Seigel 1980; Tucker et al. 1999; Spencer 2002). The turtle's bony shell, while likely to protect against many adversities, therefore is not a perfect antipredator solution. Consequently, the "life-dinner principle" should apply, with the expectation that turtles should prefer to expend energy by fleeing rather than excessively risking a permanent loss of fitness (Dawkins and Krebs 1979). Thus, our finding of reduced likelihood to flee as distance to water increased suggests the fitness benefits of oviposition must be greater than the risk of depredation under these circumstances.

Important aspects of our study methods and system differ from previous work on risk assessment behavior. We did not approach animals until they fled, as is done in FID

studies. Instead, we recorded a binary dependent variable as whether turtles fled or continued nesting after encountering an observer. Recording FID results in each test subject fleeing, hindering further observation. However, our methodology allowed additional observations (e.g., clutch size) to be recorded for another study on nesting behavior for turtles that did not flee. If other studies result in some animals fleeing, the use of a similar methodology to ours can yield insight into risk assessment in that system without the loss of focal data. In addition, turtles and other taxa with multiple antipredator strategies have the option to flee from a predator or use an alternative strategy, such as retraction into the shell. In our study, very few turtles retracted into their shell. Flight was always an option because we did not touch or restrain turtles. Nevertheless, having an alternative option to flight likely influenced flight decisions. For example, turtles far from water may rely on retraction into the shell as the main antipredation mechanism because the chance of escape by flight decreases with distance to refuge. Future work is needed to parse out the roles of escape likelihood, alternative antipredation strategies, and reproductive investment on aquatic turtle flight behavior.

Risk of predation is an important determinant of prey flight response. Yet, how costs associated with flight, such as the loss of opportunity, influence prey decisions during predator-prey encounters is understudied. Our objectives were to examine the response of nesting *Chrysemys picta* depending upon the distance to an observer, distance to water, and nesting stage. We show that distance to an observer did not influence turtle flight decisions. However, turtles were less likely to flee as distance to the water increased and when constructing nests compared to when searching for nest-sites. These

findings suggest *C. picta* tolerate higher predation risk when investment into reproduction is high, and provide rare evidence that the costs of flight are important in balancing flight decisions. In addition, our findings suggest the likelihood of escape may influence decisions to flee, particularly for animals that have additional anti-predator strategies such as morphological defense. Future work that examines flight decisions by taxa with multiple antipredator strategies (e.g., porcupine, skunk) and control for the complexity in these systems will shed light on the context dependence of risk assessment behavior.

Acknowledgements

We thank C. Brumbaugh-Smith, C. Cates, T. Mitchell, E. Pazaski, S. Tiatragul, L. Tinsley, F. Wideman, and D. Williams for field assistance. Comments from the Janzen lab, L. Beck, M. Delaney, and L.A. Stuckemeyer improved this paper. This work was supported by the National Science Foundation (IOS-1257857 to F.J.J and D.A.W.). This research was approved by the University of Alabama at Birmingham Institutional Animal Care and Use Committee (140410079).

References

- Bateman, P.W., Fleming, P.A., Jones, B.C., and Rothermel, B.B. 2014. Defensive responses of gopher tortoises (*Gopherus polyphemus*) are influenced by risk assessment and level of habituation to humans. *Behaviour*, **151**: 1267–1280. doi:10.1163/1568539X-00003184.
- Blumstein, D.T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C., and Daniel, J.C. 2004. Locomotor ability and wariness in yellow-bellied marmots. *Ethology*, **110**: 615–634. doi:10.1111/j.1439-0310.2004.01000.x.
- Bonenfant, M., and Kramer, D.L. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behav. Ecol.* **7**: 299–303. doi:10.1093/beheco/7.3.299.
- Camp, M.J., Rachlow, J.L., Woods, B.A., Johnson, T.R., and Shipley, L.A. 2012. When to run and when to hide: the influence of concealment, visibility, and proximity to refugia on perceptions of risk. *Ethology*, **118**: 1010–1017. doi:10.1111/eth.12000.
- Capizzi, D., Luiselli, L., and Vignoli, L. 2007. Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. *Amphibia-Reptilia*, **28**: 403–407. doi:10.1163/156853807781374827.
- Christen, E., and Bider, J.R. 1987. Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in Southwestern Quebec. *Herpetologica*, **43**: 55–65.

- Ciuti, S., Pipia, A., Ghiandai, F., Grignolio, S., and Apollonio, M. 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). *Behav. Processes*, **77**: 408–412. doi:10.1016/j.beproc.2007.09.001.
- Cooper, W.E. 1997a. Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. *Herpetologica*, **53**: 464–474.
- Cooper, W.E. 1997b. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* **75**: 943–947. doi:10.1139/z97-113.
- Cooper, W.E. 2003. Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology*, **109**: 617–626. doi:10.1046/j.1439-0310.2003.00912.x
- Cooper, W.E. 2006. Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology*, **112**: 858–864. doi:10.1111/j.1439-0310.2006.01240.x.
- Cooper, W.E. 2007. Compensatory changes in escape and refuge use following autotomy in the lizard *Sceloporus virgatus*. *Can. J. Zool.* **85**: 99–107. doi:10.1139/Z06-200.
- Cooper, W.E. 2009. Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behav. Ecol. Sociobiol.* **63**: 1765–1771. doi:10.1007/s00265-009-0799-1.
- Cooper, W.E., and Frederick, W.G. 2007. Optimal flight initiation distance. *J. Theor. Biol.* **244**: 59–67. doi:10.1016/j.jtbi.2006.07.011.
- Cooper, W.E., and Pérez-Mellado, V. 2004. Tradeoffs between escape behavior and

- foraging opportunity by the balearic lizard (*Podarcis lilfordi*). *Herpetologica*, **60**: 321–324. doi:10.1655/04-20.
- Cooper, W.E., and Stankowich, T. 2010. Prey or predator? Body size of an approaching animal affects decisions to attack or escape. *Behav. Ecol.* **21**: 1278–1284. doi:10.1093/beheco/arq142.
- Cooper, W.E., and Whiting, M.J. 2007. Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology*, **113**: 661–672. doi:10.1111/j.1439-0310.2007.01363.x.
- Cooper, W.E., and Wilson, D. 2007. Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard *Sceloporus virgatus*. *Behaviour*, **144**: 1235–1254. doi:10.1163/156853907781890940.
- Cooper, W.E., Pérez-Mellado, V., Baird, T., Baird, T.A., Caldwell, J.P., and Vitt, L.J. 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behav. Ecol.* **14**: 288–293. doi:10.1093/beheco/14.2.288.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K., and Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**: 3387–3397. doi:10.1890/05-0032.
- Dawkins, R., and Krebs, J.R. 1979. Arms races between and within species. *Proc. R. Soc. B.* **205**: 489–511. doi:10.1098/rspb.1979.0081.
- Dill, L.M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish,

- Melanochromis chipokae*. Environ. Biol. Fishes, **27**: 147–152.
- Dill, L.M., and Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. **16**: 65–71. doi:10.1007/BF00293105.
- Dill, L.M., and Houtman, R. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel. Can. J. Zool. **67**: 233–235. doi:10.1139/z89-033.
- Dill, L.M., and Ydenberg, R.C. 1987. The group-size - flight distance relationship in water striders (*Gerris remigis*). Can. J. Zool. **65**: 223–226. doi:10.1139/z87-036.
- Ebensperger, L.A., and Wallem, P.K. 2002. Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. Oikos, **98**: 491–497. doi:10.1034/j.1600-0706.2002.980313.x.
- Ernst, C.H. 1974. Effects of hurricane Agnes on a painted turtle population. J. Herpetol. **8**: 237–240.
- Ernst, C.H. 1976. Ecology of the spotted turtle, *Clemmys guttata* (Reptilia, Testudines, Testudinidae), in southeastern Pennsylvania. J. Herpetol. **10**: 25–33. doi:10.2307/1562924.
- Ernst, C.H., and Lovich, J.E. 2009. Turtles of the United States and Canada. 2nd ed. The Johns Hopkins University Press, Baltimore, M.D.
- Ghalambor, C., and Martin, T. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Anim. Behav. **60**: 263–267. doi:10.1006/anbe.2000.1472.
- Ghalambor, C.K., and Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-

- taking in birds. *Science*, **292**: 494–497. doi:10.1126/science.1059379.
- Gotanda, K.M., Turgeon, K., and Kramer, D.L. 2009. Body size and reserve protection affect flight initiation distance in parrotfishes. *Behav. Ecol. Sociobiol.* **63**: 1563–1572. doi:10.1007/s00265-009-0750-5.
- Greene, H.W. 1988. Antipredator mechanisms in reptiles. *In* *Biology of the Reptilia*, Volume 16. *Edited by* C. Gans, and R.B. Huey. Branta Books, Ann Arbor, M.I. pp. 11–113.
- Guay, P.J., Lorenz, R.D.A., Robinson, R.W., Symonds, M.R.E., and Weston, M.A. 2013. Distance from water, sex and approach direction influence flight distances among habituated black swans. *Ethology*, **119**: 552–558. doi:10.1111/eth.12094.
- Heithaus, M.R., and Dill, L.M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**: 480–491. doi:10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2.
- Kalas, J.A., Fiske, P., and Saether, S.A. 1995. The effect of mating probability on risk taking: an experimental study in lekking great snipe. *Am. Nat.* **146**: 59–71. doi:10.1086/285787
- Kramer, D.L., and Bonenfant, M. 1997. Direction of predator approach and the decision to flee to a refuge. *Anim. Behav.* **54**: 289–295. doi:10.1006/anbe.1996.0360.
- Laursen, K., Kahlert, J., and Frikke, J. 2005. Factors affecting escape distances of staging waterbirds. *Wildlife Biol.* **11**: 13–19. doi:10.2981/0909-6396(2005)11[13:FAEDOS]2.0.CO;2.
- Legler, J.M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata*

- Agassiz. Univ. Kansas Publ., Mus. Nat. Hist. **11**: 527–669.
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640. doi:10.1139/z90-092.
- Martín, J., and López, P. 1995. Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. *Can. J. Zool.* **73**: 129–132. doi:10.1139/z95-014.
- Martín, J., Marcos, I., and López, P. 2005. When to come out from your own shell: risk-sensitive hiding decisions in terrapins. *Behav. Ecol. Sociobiol.* **57**: 405–411. doi:10.1007/s00265-004-0887-1.
- McLean, E.B., and Godin, J.J. 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos*, **55**: 281–290.
- Persons, M.H., Walker, S.E., Rypstra, A.L., and Marshall, S.D. 2001. Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae). *Anim. Behav.* **61**: 43–51. doi:10.1006/anbe.2000.1594.
- Polich, R.L., and Barazowski, M. 2016. Flight initiation distance in a freshwater turtle, *Chrysemys picta*. *Chelonian Conserv. Biol.* **15**: 214–218. doi:10.2744/CCB-1164.1
- Polo-Cavia, N., López, P., and Martín, J. 2008. Interspecific differences in responses to predation risk may confer competitive advantages to invasive freshwater turtle species. *Ethology*, **114**: 115–123. doi:10.1111/j.1439-0310.2007.01441.x.
- Refsnider, J.M., Reedy, A.M., Warner, D.A., and Janzen, F.J. 2015. Do trade-offs between predation pressures on females versus nests drive nest-site choice in

- painted turtles? Biol. J. Linn. Soc. **116**: 847–855.
- Reimers, E., Loe, L.E., Eftestøl, S., Colman, J.E., and Dahle, B. 2009. Effects of hunting on response behaviors of wild reindeer. J. Wildl. Manage. **73**: 844–851. doi:10.2193/2008-133.
- Rosenthal, R. 1991. Meta-analytic procedures for social research. 2nd ed. Sage Publications, Inc. Newbury Park, C.A.
- Rowe, J.W., Coval, K.A., and Dugan, M.R. 2005. Nest placement, nest-site fidelity and nesting movements in midland painted turtles (*Chrysemys picta marginata*) on Beaver Island, Michigan. Am. Midl. Nat. **154**: 383–397. doi:10.1674/0003-0031(2005)154[0383:NPNFAN]2.0.CO;2.
- Runyan, A.M., and Blumstein, D.T. 2004. Do individual differences influence flight initiation distance? J. Wildl. Manage. **68**: 1124–1129. doi:10.2193/0022-541X(2004)068[1124:DIDIFI]2.0.CO;2.
- SAS Institute. 1997. SAS/STAT user's guide. Statistical Analysis Systems Institute, Cary, N.C.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution, **42**: 849–861. doi:10.2307/2408904.
- Seigel, R.A. 1980. Predation by raccoons on diamondback terrapins, *Malaclemys terrapin tequesta*. J. Herpetol. **14**: 87–89.
- Seltmann, M.W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., and Hollmén, T. 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. Anim. Behav. **84**: 889–896.

- doi:10.1016/j.anbehav.2012.07.012.
- Spencer, R.J. 2002. Experimentally testing nest site selection: fitness trade-offs and predation risk in turtles. *Ecology*, **83**: 2136–2144. doi:10.1890/0012-9658(2002)083[2136:ETNSSF]2.0.CO;2.
- Stankowich, T., and Blumstein, D.T. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. B.* **272**: 2627–2634. doi:10.1098/rspb.2005.3251.
- Stankowich, T., and Coss, R.G. 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav. Ecol.* **17**: 246–254. doi:10.1093/beheco/arj020.
- Tucker, J., and Warner, D.A. 2000. Mud accumulation in nesting aquatic turtles (*Emydidae*) in Illinois. *Chelonian Conserv. Biol.* **3**: 753–755.
- Tucker, J.K., Filoramo, N.I., and Janzen, F.J. 1999. Size-biased mortality due to predation in a nesting freshwater turtle, *Trachemys scripta*. *Am. Midl. Nat.* **141**: 198–203. doi:10.1674/0003-0031(1999)141[0198:SBMDTP]2.0.CO;2.
- Werner, E.E., and Hall, D.J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology*, **69**: 1352–1366.
- Wilbur, H.M. 1975. The evolutionary and mathematical demography of the turtle *Chrysemys picta*. *Ecology*, **56**: 64–77. doi:10.2307/1935300.
- Ydenberg, R.C., and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Study Behav.* **16**: 229–249. doi:10.1016/S0065-3454(08)60192-8.

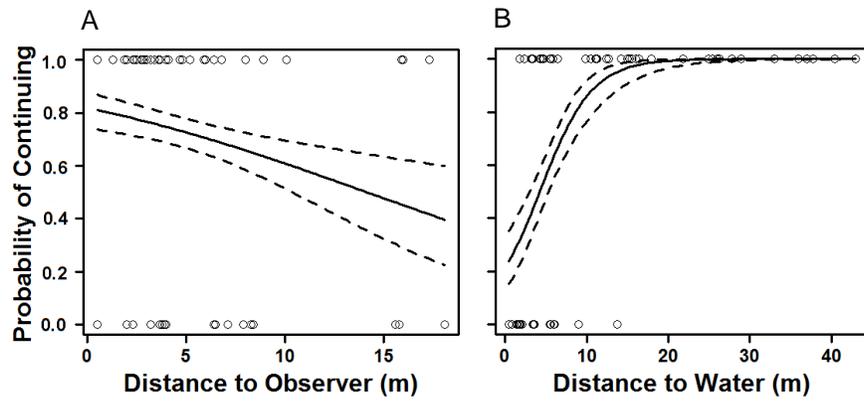


Figure 1 Probability of continuing to nest depending upon the distance between a nesting painted turtle (*Chrysemys picta*) and (A) an observer ($\chi^2 = 1.3108$, $P = 0.2523$) and (B) water ($\chi^2 = 6.5161$, $P = 0.0113$) after encounters with an observer. Probability of continuing to nest was estimated using cubic splines (Schluter 1988). Dashed lines represent standard errors calculated with Bayesian methods. Open circles along the top and bottom axes represent individual turtle encounters.

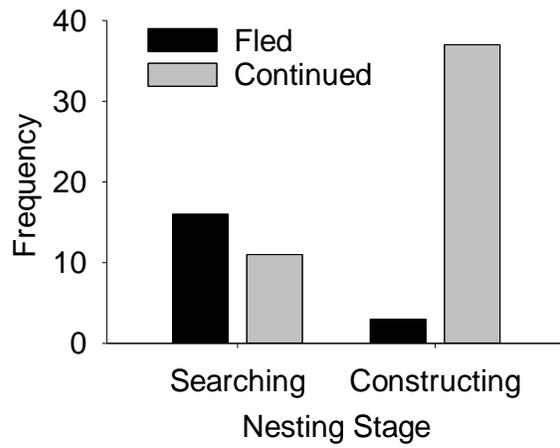


Figure 2 Effect of nesting stage (i.e., searching for a nest-site vs. constructing a nest) of painted turtles (*Chrysemys picta*) on decisions to continue nesting or flee to water after encounters with an observer ($\chi^2 = 11.2339$, $P = 0.0008$).