

## A COMPARISON OF THE FLIGHT INITIATION DISTANCES OF MALE AND FEMALE AMERICAN BULLFROGS (*LITHOBATES CATESBEIANUS*) AND GREEN FROGS (*LITHOBATES CLAMITANS*)

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**Abstract.**—Comparing the escape responses of two similar species can help to reveal the underlying causes of different antipredatory responses. In this study, we compared the flight initiation distances of American Bullfrogs (*Lithobates catesbeianus*) and Green Frogs (*Lithobates clamitans*). We predicted that larger individuals would allow a predator to approach more closely than smaller individuals because larger individuals can jump further than smaller individuals. Therefore, we expected the smaller species, *L. clamitans*, to have a greater mean flight initiation distance than *L. catesbeianus*, and we expected females (which were the smaller sex in the study) to have a greater flight initiation distance than males. We tested these predictions using a model snake that was pulled by an electronic toy car. This is a novel method that may yield more accurate flight initiation distances than using an approaching human as the predator. We found that *L. clamitans* had a significantly greater mean flight initiation distance (17.8 cm) than *L. catesbeianus* (13.4 cm). We did not, however, find a significant difference between the flight initiation distances of males and females within either species. We also did not find a significant correlation between frog size (snout-vent length and mass) and flight initiation distance for either sex of either species.

**Key Words.**—anti-predatory behavior; escape response; flight initiation distance; *Lithobates*

### INTRODUCTION

When an animal detects a predator, it must make a choice to either flee or hide, and neither choice is without risk (Broom and Ruxton 2005). Fleeing can reduce fitness unnecessarily by wasting energy and reducing the time which could be spent performing other activities, but choosing not to flee can lead to mortality if detected by the predator (Ydenburg and Dill 1986; Eason et al. 2006; Cooper and Frederick 2007). Therefore, the proposed optimal strategy for cryptic prey is to either flee as soon as a predator is detected or to remain in hiding and only flee if detected by the predator (Broom and Ruxton 2005).

Flight initiation distances are defined as the distance between the predator and the prey at the moment that the prey begins to flee, and many factors can affect them (Dill and Houtman 1989; Cooper 2006; Cooper et al. 2009). These factors include characteristics of the environment such as temperature and the proximity of a refuge (Rand 1964; Dill 1990; Cooper 2000); characteristics of the prey such as size, sex, genetics, and degree of crypsis (Heatwole 1968; Shine et al. 2000; Vanhooydonck et al. 2007); and characteristics of the predator's approach such as speed, direction, and starting distance (Cooper 1997a,b, 2003a; Cooper et al. 2003; see Stankowich and Blumstein 2005 for a meta-analysis of these factors).

Deciding when to flee is, therefore, a complex decision that uses knowledge of both the environment and predator to weigh the risk of being captured against the costs of fleeing and the benefits of continued foraging, reproduction, and defense of territories (Ydenburg and Dill 1986; Cooper and Frederick 2007).

Comparing the escape responses of two similar species may aid in the understanding of the roles that different factors play in deciding when to flee and when to hide because the similarities between the species can act as a form of control, allowing the differences in their flight initiation distances to be attributed to the few factors that differ between them (Hayes 1990; Bulova 1994; Vanhooydonck et al. 2007). To accomplish this, we compared the flight initiation distances of American Bullfrogs (*Lithobates catesbeianus*) and Green Frogs (*Lithobates clamitans*). Although there is a large size difference between the species, they are both superficially similar in appearance and frequently occupy the same habitats (Wells 1977; Clarkson and Devos 1986). Also, males of both species are territorial and will defend territories along banks, in emergent vegetation, and under trees and bushes (Emlen 1968; Wiewandt 1969; Ryan 1980; Clarkson and Devos 1986). Finally, these were the two dominant ranid species in the local wetlands (Pickerel Frogs [*Lithobates palustris*] were also present but in much lower numbers). Despite the similarities between *L. catesbeianus* and *L. clamitans*, no previous study has compared their escape responses. Several studies, however, have examined the responses of each species independently. Hayes (1990) and Cooper (2011) showed that both species tend to flee towards water and are more likely to dive if they are approached rapidly or actively pursued than if they are approached slowly and not actively pursued. Also, Tidwell and Hayes (2013) found that recently metamorphosed *L. catesbeianus* had significantly greater flight initiation distances than recently metamorphosed Oregon Spotted Frogs (*Rana pretiosa*). Finally, Heinen and Hammond (1997) compared recently metamorphosed

*L. clamitans* and Northern Leopard Frogs (*Lithobates pipiens*) and found that *L. pipiens* had a greater mean flight initiation distance.

The primary goal of our study was to compare the antipredatory reactions of *L. catesbeianus* and *L. clamitans* in a controlled environment in order to further our understanding of amphibian flight initiation distances. Additionally, we wanted to compare the responses of males and females to see if there were any sexually mediated differences in flight initiation distances (Shine et al. 2000; King 2002a; Vanhooydonck et al. 2007). We also wanted to investigate the effect of body size on flight initiation distance (Martin and Lopez 1995). Because larger individuals can generally jump further than smaller individuals (Emerson 1978; Licht 1986; Rand and Rand 1966), we predicted that larger individuals would be able to escape a predator more easily than smaller individuals and, therefore, would allow the predator to approach more closely before fleeing. Because of this prediction, we expected the smaller species, *L. clamitans*, to have a greater mean flight initiation distance than *L. catesbeianus*, and we expected females (which were the smaller sex in the study) to have slightly greater flight initiation distances than males.

A final purpose of this study was to report a novel method for testing flight initiation distances. Studies on flight initiation distances have typically involved one or two researchers approaching an animal until it flees, but this method presents two obvious problems (Stankowich and Blumstein 2005). First, it has been well documented that the speed of an approaching predator can affect flight initiation distances, and it is difficult to standardize and precisely control a researcher's walking speed (Cooper 1997a, 2003a,b; Lord et al. 2001). Second, in many cases, humans are not a predator of the animal being studied, and some species are known to have different flight initiation distances for different predators (Walther 1969; Lord et al. 2001). As a result, studies which use humans as predator analogs may not accurately reflect the behavior

of the study organism when faced with a natural predator. Therefore, we used a model predator and battery operated car to present the study subjects with a more natural predator at a standardized approach speed.

## MATERIALS AND METHODS

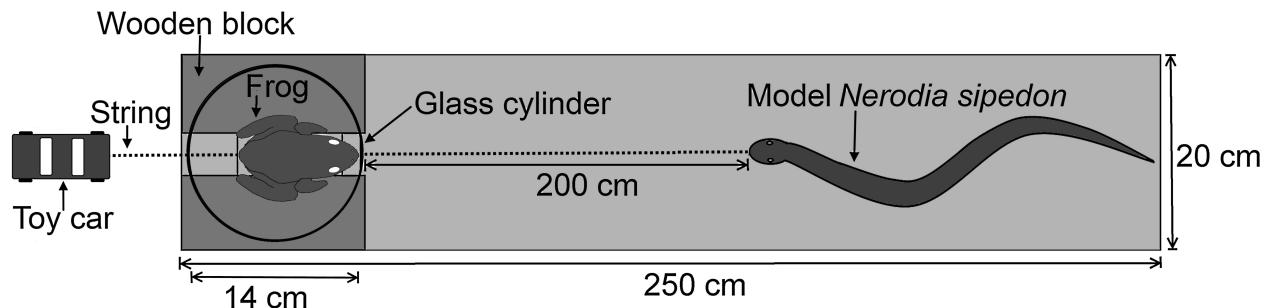
**Experimental design.**—We collected 58 *L. catesbeianus* (28 males, 30 females) and 51 *L. clamitans* (29 males, 22 females) in Abingdon, Maryland, at the Anita C. Leight Estuary Center (ACLEC; 39.45119°N, 76.26831°W), Bosely Conservancy (39.432530°N, 76.289581°W), and the section of Otter Point Creek that connects the two properties. We collected frogs at night in July and August 2011 (breeding was still ongoing), and we conducted all of the tests in the ACLEC laboratory between 0800–2000 the day after the frogs were collected. Although both species are predominately nocturnal, they are somewhat active during the day and respond to approaching predators during daytime (Wells 1977; DTM, pers. obs.). Also, animals should respond to visually detected predators (which is what we were testing) most readily during the day because it is easier to see an approaching predator in the daylight. Further, previous studies on the antipredatory responses of both species have been conducted during the day (Heinen and Hammond 1997; Cooper 2011). Prior to testing, we kept the frogs in aquaria (several frogs per aquaria) that contained several centimeters of water. The tanks were covered with towels to reduce stress and minimize contact with researchers. We tested each frog only once, and we released all of the frogs at their original locations within 24 h of capture.

We conducted the tests in a cardboard trench (250 cm long, 20 cm wide, 25 cm tall) with a glass cylinder (14 cm diameter, 45 cm tall) placed at one end (Fig. 1). We used a rubber model of a Northern Water Snake (*Nerodia sipedon sipedon*; 70 cm total length, 5 cm diameter at widest point) to simulate a predator. *Nerodia sipedon sipedon*

is a common predator of both *L. catesbeianus* and *L. clamitans*, and it is frequently found at the collection sites (Brown and Weatherhead 2000; Himes 2003). Our model was large enough (gape index [ $\pi \times \text{jaw length} \times \text{jaw width}/4$ ] = 700 mm<sup>2</sup>) that all of the frogs should have perceived it as a threat (Shine 1991; King 2002b). In order to ensure that the frogs would respond to a model predator in the same way that they responded to an actual predator, we conducted several preliminary tests (not included in the data set) using a live snake, and the frogs' responses to the live snake were not observably different from their responses to the rubber snake. We released the frogs after the preliminary tests rather than using them again for the actual experiment.

At the start of each test, we placed the model snake in the trench (200 cm away from the glass cylinder) and attached it to a thin string that ran down the length of the trench, underneath the cylinder, out through a small hole in the back of the trench, and attached to a 3-volt, battery-operated toy car (Fig. 1). The car pulled the snake at a speed of 6.6 cm per second. To allow the string to pass underneath the cylinder, the cylinder was elevated 1 cm from the bottom of the trench using two wooden blocks. We lined the trench with plastic to reduce friction and allow the snake to be pulled more easily. The reduced friction also kept the cardboard from noticeably vibrating, which increased the probability that vision was the only sense that the frogs were using to evaluate the threat posed by the snake.

Once the model snake was positioned, we placed a frog in the glass cylinder and waited for it to assume a resting posture and remain there for at least 30 seconds. Preliminary observations showed that once a frog had remained still in the cylinder for at least 30 seconds, it would generally continue to sit still for several minutes. The frogs were, however, often active for several minutes before assuming a resting posture. For consistency, we made sure that the frogs were facing down the trench before starting the test. Sometimes the cylinder had to be



**FIGURE 1.** A diagram of the experimental set up (viewed from the top) at the start of a test. A battery-operated toy car was used to pull a model snake down the cardboard trench, towards the frog. The frog was in a glass cylinder that was elevated on two blocks, and the model snake was attached to the car by a string that ran under the cylinder and out of the back of the trench. As soon as the frog attempted to flee, the car (and thereby the snake) was stopped, and the distance between the snake and the frog was recorded. The image is not to scale.

rotated in order for the frogs to be facing the correct direction. This was done slowly to avoid disturbing the frogs, and they were allowed to re-acclimate after the cylinder had been rotated. We used marks on the bottom of the trench to record a frog's position at the start of the test. Once the frog was in place and was remaining stationary, we started the car, resulting in the snake being pulled down the trench, toward the frog. As soon as the frog made an escape response, we stopped the car, thereby stopping the model snake. To ensure consistency of human reaction time, the same researcher (DTM) always stopped the car. We only stopped the car for an escape response (turning or jumping), and did not stop it for other behaviors such as crouching. After stopping the car, we measured the flight initiation distance (i.e., the distance between the snout of the model snake and the frog's pre-response position) to the nearest 0.1 cm using a meter stick (Gregory 1979).

We sexed the frogs by looking at the size of the tympanic membrane as well as the color of the throat (Wells 1978; Howard 1981; Shepard 2002; Schulte-Hostedde and Schank 2009). We measured the snout-vent length (SVL) to the nearest 0.1 cm using vernier calipers, and we recorded the mass to 0.1 grams using an electronic scale (Willis et al. 1956; Bee and

Perrill 1996). We made all of the measurements after conducting the test in order to reduce stress and minimize contact with the subjects prior to the trials.

**Statistical analysis.**—We compared the mean flight initiation distances using a two factor ANOVA ( $\alpha = 0.05$ ) with species and sex as the factors (Zar 1996). The data did not violate the assumptions of ANOVA. We also calculated two sets of two-tailed Spearman rank correlation coefficients ( $\alpha = 0.05$ ) to test for associations between body size and flight initiation distance (Zar 1996). One set used SVL for body size, and the other used mass. Both sets tested males within each species, females within each species, and all individuals within each species. We used the Spearman rank test rather than a parametric test because the body size measurements were not normally distributed. We performed all tests in R 3.0.2 (R Development Core Team, Vienna, Austria).

## RESULTS

*Lithobates clamitans* had a greater mean flight initiation distance (17.8 cm) than *L. catesbeianus* (13.4 cm; Table 1). That is, *L. clamitans* did not allow the snake to approach as closely as did *L.*

**TABLE 1.** Mean flight initiation distance, snout-vent length (SVL), and body mass for each group of *Lithobates catesbeianus* and *Lithobates clamitans*.

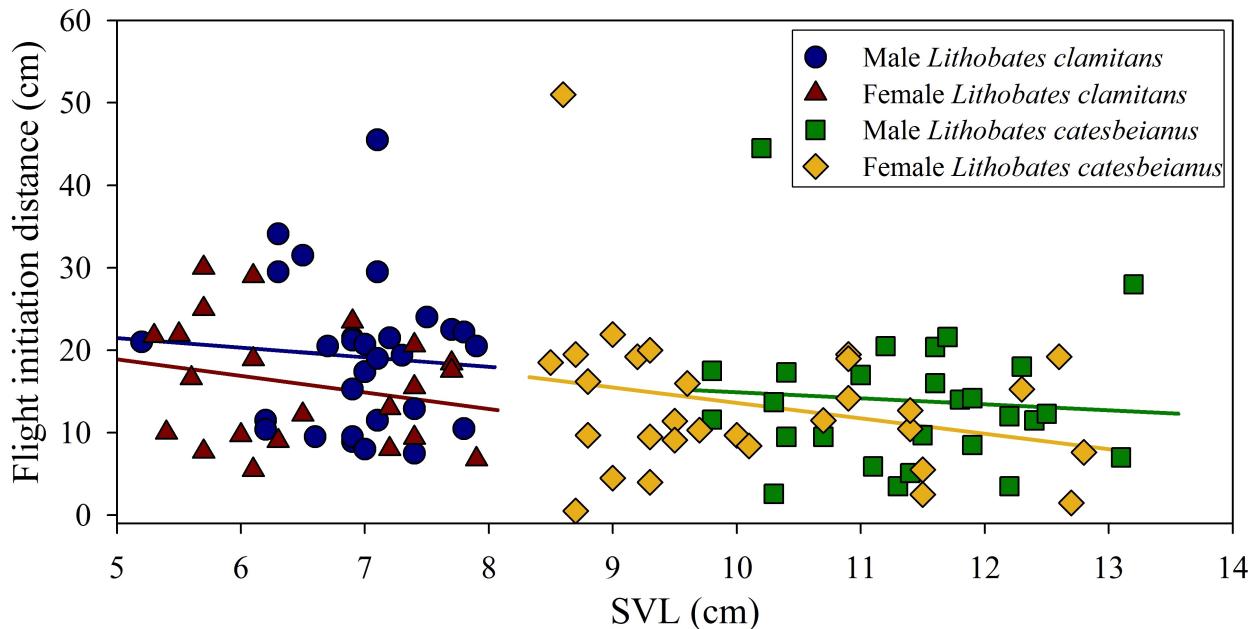
	No.	Mean distance (cm)	SD	Range	Mean SVL (cm)	SD	Range	Mean Mass (g)	SD
All <i>L. catesbeianus</i>	58	13.4	9.03	8.5–13.2	10.8	1.32	50.3–274.4	147.9	52.31
Male <i>L. catesbeianus</i>	28	13.5	8.81	9.8–13.2	11.4	0.94	105.0–274.4	169.6	38.23
Female <i>L. catesbeianus</i>	30	13.3	9.38	8.5–12.8	10.2	1.35	50.3–266.8	128.3	56.01
All <i>L. clamitans</i>	51	17.8	8.36	5.2–7.9	6.8	0.74	14.0–52.2	32.4	9.94
Male <i>L. clamitans</i>	29	19.2	8.92	5.2–7.9	7.0	0.58	14.0–52.2	33.8	7.98
Female <i>L. clamitans</i>	22	15.9	7.32	5.3–7.9	6.5	0.86	16.4–51.2	30.7	12.02

*catesbeianus*. The two-factor ANOVA showed that there was a significant main effect of species ( $F_{1,104} = 6.315$ ,  $P = 0.0135$ ), but there was not a significant main effect of sex ( $F_{1,104} = 1.231$ ,  $P = 0.2698$ ), or a significant interaction between species and sex ( $F_{1,104} = 0.639$ ,  $P = 0.4259$ ). The Spearman rank tests showed that there were no significant correlations between size and flight initiation distance for any of the groups ( $P > 0.16$  for all tests; Fig. 2).

There were no observable differences between the mechanism through which *L. catesbeianus* and *L. clamitans* responded to the model snake. In both species, crouching was often observed well before an escape response (50–100 cm from the snake). The escape response of both species was typically a single, strong jump. Preliminary testing showed that the frogs would generally continue jumping as long as the snake was moving and discontinue jumping as soon as it stopped. In a few of the actual trials (9 *L. catesbeianus* and 8 *L. clamitans*), the frog rapidly turned 180° rather than jumping. In preliminary testing where the snake was not stopped, this turn was usually followed by jumping.

## DISCUSSION

Our results show that *L. clamitans* has a significantly greater mean flight initiation distance than *L. catesbeianus*, suggesting that *L. catesbeianus* will allow a predator to approach more closely before fleeing. The reason for this difference is not clear. Both species are similar in appearance, habitat, and life history (Wells 1977; Ryan 1980; Clarkson and Devos 1986). The most obvious difference between them is that *L. catesbeianus* is much larger than *L. clamitans*, and previous research has confirmed that larger frogs can jump further than smaller frogs (Rand and Rand 1966; Emerson 1978; Licht 1986). Therefore, we predicted that *L. catesbeianus* would allow the model snake to approach more closely because their greater jump distance would allow them to escape more easily. However, while we



**FIGURE 2.** Flight initiation distance and snout-vent length (SVL) for each sex of each species. Spearman rank tests showed no significant correlation between flight initiation distance and SVL for any group.

correctly predicted the difference between the species, our rational for that prediction appears to be incorrect because there were no correlations between size and flight initiation distance within either species.

Another possible explanation for the difference between the species is that the relatively small size of *L. clamitans* causes them to be depredated by snakes more frequently than *L. catesbeianus* are, which should result in *L. clamitans* evolving an earlier response to an approaching snake. There are only two species of snake at the collection sites that are known to frequently eat frogs, the Eastern Garter Snake (*Thamnophis sirtalis sirtalis*) and *N. s. sipedon* (Hamilton 1951; Carpenter 1952). Both species are abundant at these sites and have been observed eating adult *L. clamitans*, but only *N. s. sipedon* is typically large enough to eat adult *L. catesbeianus* (DTM, pers. obs.). Therefore, we would expect adult *L. clamitans* to be eaten by snakes more frequently than *L. catesbeianus*, and, as a result, we would expect them to flee more readily when approached by a snake.

We also failed to find a significant difference

in the flight initiation distances of males and females, suggesting that both sexes will flee at the same distance from a predator. It should be noted that our results merely suggest a lack of inherent differences between the sexes. Escape responses in the wild can be affected by factors that we did not test, such as the proximity of potential mates, rival males, and refuge sites (Cooper 1999, 2003c).

There is no clear consensus on the effects of sex on flight initiation distance across taxa. Many studies have failed to find an effect of sex (McLean and Godin 1989; Burger and Gochfeld 1990; Cooper 2003d), but some studies have shown that males have greater flight initiation distances than females (Johnson 1970; Bulova 1994; Stone et al. 1994), while other studies have found the inverse (Walther 1969; Snell et al. 1988). The reasons for these discrepancies are not clear, but likely vary from one species to the next. For example, Johnson (1970) attributed the increased flight initiation distances of male Western Fence Lizards (*Sceloporus occidentalis*) to a low level of crypsis relative to juveniles and females, whereas Bulova (1994)

suggested that male Zebra-tailed Lizards (*Callisaurus draconoides*) had relatively high flight initiation distances because most of the females in the study were gravid. In contrast, Walther (1969) found that territorial male Thomson's Gazelles (*Gazella thomsoni*) had short flight initiation distances compared to either females or non-territorial males, and he attributed this result to a link between the gazelle's social behavior and anti-predator behavior (i.e., territorial males typically stood their ground in territory disputes, and this behavior carried over into their anti-predatory responses). It is unclear why there were no differences between the sexes in our trials. Our study subjects included territorial males and gravid females, both of which have reportedly been the basis for sexual differences in other studies, but they did not appear to impact our results.

It is also interesting that there was no correlation between body size and flight initiation distance. The literature contains mixed results concerning the effects of body size on flight initiation distance. For birds, several multi-species studies have shown that larger species tend to have greater flight initiation distances than smaller species (Cooke 1980; Holmes et al. 1993; Blumstein 2006). In reptiles and fish, however, the results are mixed. Studies on Bicolor Damselfish (*Pomacentrus partitus*), Queen Snakes (*Regina septemvittata*), Striped Plateau Lizards (*Sceloporus virgatus*), and Chuckwallas (*Sauromalus obesus* and *S. varius*) all failed to find an effect of body size (Shallenger 1970; Layne and Ford 1984; Smith 1996; Helfman and Winkelman 1997), but studies on Brook Trout (*Salvelinus fontinalis*), Iberian Rock Lizards (*Lacerta monticola*), Black Iguanas (*Ctenosaura similis*), Marine Iguanas (*Amblyrhynchus cristatus*), and four species of Parrot Fish (*Scarus* spp. and *Sparksoma viride*) found that longer individuals within each species had greater flight initiation distances (Shallenger 1970; Grant and Noakes 1987; Burger and Gochfeld 1990; Martin and Lopez 2003; Gotanda et al. 2009). In contrast, research on Brook Sticklebacks (*Culaea inconstans*) found

that longer individuals had shorter flight initiation distances. There is little data available on the effects of size on the flight initiation distances of amphibian species. Nevertheless, research on Iberian Green Frogs (*Pelophylax perezi*) has shown that smaller individuals allow predators to approach more closely than larger individuals do (Martin et al. 2005). Despite this variation among studies, a meta-analysis showed that for most species, larger individuals tend to have greater flight initiation distances (Stankowich and Blumstein 2005). Our results differ from those of Stankowich and Blumstein (2005) and Martin et al. (2005) in that we did not find a relationship between size and flight initiation distance within species. The reason for this result is unclear, but we should acknowledge the possibility that our size range was not large enough to detect such relationships (Layne and Ford 1984). Martin et al. (2005), for example, compared juveniles with adults, whereas we looked for relationships only among adult frogs.

A final point of interest is the fact that our flight initiation distances were much shorter than the values that have typically been reported in other studies. For example, Tidwell and Hayes (2013) reported that recently metamorphosed *L. catesbeianus* never had flight initiation distances of less than 1,700 cm, and their mean flight initiation distance was 6,100 cm. Similarly, Cooper (2011) found that adult *L. catesbeianus* fled at a mean distance of 1,460 cm when approached along the shoreline and 1,520 cm when approached perpendicular to the shoreline. These flight initiation distances are markedly different from our results of 13.4 cm for *L. catesbeianus* and 17.8 cm for *L. clamitans*. Our results are, however, similar to those of Heinen and Hammond (1997) who found that recently metamorphosed *L. catesbeianus* and Northern Leopard Frogs (*Lithobates pipiens*) typically fled when the predator was within 20 cm. This difference may be explained by a difference in the type of predator used. Tidwell and Hayes (2013) and Cooper (2011) both used a human to simulate a predator,

whereas we used a rubber snake, and Heinen and Hammond (1997) used a live snake. It should be noted, that the starting distance of our trials was only 200 cm so the lengthy distances reported by Tidwell and Hayes (2013) and Cooper (2011) were not possible in our study. Nevertheless, our test subjects allowed the snake to traverse almost that entire distance before attempting to flee, and several lines of evidence suggest that humans do not elicit the same anti-predatory response as a more natural predator (such as a snake). First, several studies have shown that predator size and type can affect flight initiation distance (Walther 1969; Dill 1974; Hurley and Hartline 1974; Helfman and Winkelman 1997; Lord et al. 2001). Second, in many natural situations, a frog would be able to see and respond to an approaching human at a much greater distance than a natural predator such as a snake. Therefore, we recommend that future studies make use of a model predator to better represent natural responses. The exact method that we used requires animals to be in an artificial environment, but it would be easy to modify this method for use in the field (e.g., attach a long rod to the front of a battery powered car so that it pushes a model predator).

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