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Road crossing structures for amphibians and reptiles: Informing design through behavioral analysis

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ABSTRACT

Road traffic causes significant amphibian and reptile mortality, which could be mitigated through the installation of road crossing structures that facilitate safe passage, but only if reptiles and amphibians are willing to use them. Through a series of behavioral choice experiments with frogs and turtles, we examined how aperture diameter, substrate type, length, and light permeability influenced individuals' preferences for specific attributes of crossing structures, and how individuals responded to various heights of barrier fences. Snapping turtles (*Chelydra serpentina*), green frogs (*Rana clamitans*), and leopard frogs (*Rana pipiens*) preferred larger diameter tunnels (>0.5 m) whereas painted turtles (*Chrysemys picta*) preferred tunnels of intermediate (0.5–0.6 m) diameter. Green frogs preferred soil- and gravel-lined tunnels to concrete- and PVC-lined tunnels. Painted turtles showed non-random choice of different lengths of tunnel, possibly indicating some avoidance of the longest tunnel (9.1 m); although no species preferred to exit via the longest tunnels (9.1 m), members of all four species used such tunnels. Green frogs preferred tunnels with the greatest light permeability. Fences 0.6 m in height were effective barriers to green frogs, leopard frogs, and snapping turtles, whereas 0.3 m fences excluded painted turtles. We conclude that tunnels > 0.5 m in diameter lined with soil or gravel and accompanied by 0.6–0.9 m high guide fencing would best facilitate road crossing for these and likely other frog and turtle species.

1. Introduction

Vehicles cause the deaths of millions of vertebrate animals on roads each day (Forman and Alexander, 1998). Roadways can also affect wildlife by obstructing movement patterns, and ultimately reducing and isolating populations (Spellerberg, 1998; Forman et al., 2003; Eigenbrod et al., 2008). Amphibians and reptiles may be particularly vulnerable to the effects of roads because they are slow-moving organisms that typically access multiple habitats seasonally to complete their life cycles (Hels and Buchwald, 2001; Steen et al., 2006; Roe and Georges, 2007). By increasing the permeability of roads through well-designed interventions, some detrimental impacts of roads could be alleviated (Yanes et al., 1995; Guyot and Clobert, 1997; Aresco, 2005). To this end, different types of crossing structures have been developed (Forman et al., 2003; Puky, 2003; Mata et al., 2008). The most successful structures for amphibians and reptiles appear to combine a system of guide fences and underpasses to funnel organisms beneath roadways (Dodd et al., 2004; Aresco, 2005). Despite

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the mitigation potential offered by road crossing structures, assessments completed to date suggest that nonfunctioning crossing structures are prevalent (Podloucky, 1989; Meinig, 1989). The failures of such structures appear to stem from inadequate considerations of placement, architectural design, and behavior of targeted organisms (Podloucky, 1989; Puky, 2003).

The costs of installing and maintaining road crossing structures are substantial (Mata et al., 2008), so more effort is warranted to determine the design attributes and placement strategies that maximize the return on the investment toward mitigation of road kill through deployment of such structures. In this study, we created a series of behavioral choice arenas to identify particular design attributes that might stimulate amphibians and reptiles to use road crossing structures. We built proto-typical crossing structures and evaluated preferences of individuals for crossing structure aperture, substrate, length, and light permeability. Concurrently, we evaluated the containment potential of various heights of guide fences. We examined individual behaviors of four species of amphibians and reptiles that are frequently killed on roadways in North America (Ashley and Robinson, 1996; Linck, 2000; Carr and Fahrig, 2001; Steen and Gibbs, 2004): green frogs (*Rana clamitans*), leopard frogs (*Rana pipiens*), painted turtles (*Chrysemys picta*), and snapping turtles (*Chelydra serpentina*). These species exhibit substantial terrestrial movement annually (e.g., Dole, 1968; Merrell, 1970; Quinn and Graves, 1998; Lamoureux and Madison, 1999), increasing their potential interaction with roadways (Paton and Crouch, 2002; Birchfield and Deters, 2005), which can impact their population sizes and structures (Fahrig et al., 1995; Carr and Fahrig, 2001; Steen and Gibbs, 2004; Steen et al., 2006). Although none of these species is considered threatened with extinction, the impacts of road mortality may be significant for specific populations (e.g., Steen and Gibbs, 2004; Rorabaugh, 2005).

2. Methods

We conducted experiments between 15 June–15 August, 2005 and 15 June–10 August, 2006 at the Three Rivers State Wildlife Management Area in Baldwinsville, New York, United States (43°N, 76°W) where we constructed a series of behavioral choice arenas to test animal responses to guide fences and crossing tunnels (Fig. 1). Crossing tunnel choice arenas were central, octagonal enclosures constructed of 3 mm thick, 1.2 m high, translucent corrugated plastic sheets, which allowed filtered light to penetrate the arenas while blocking all visual environmental cues. We constructed the arenas on level ground, and covered the top of each arena with a cotton drop cloth that blocked celestial cues, but allowed air and diffused light to penetrate the arena. Four different exit options radiated out from each arena as the only points of egress from the enclosures. Exit options were surrogate crossing structures formed from sections of corrugated black PVC (polyvinyl chloride) pipes, which are commonly used in road construction, and a readily available source material for crossing structures. To obscure views to the surroundings and establish an identical visual stimulus at each exit, we placed an opaque piece of plastic sheeting 0.6 m beyond the exit of each pipe.

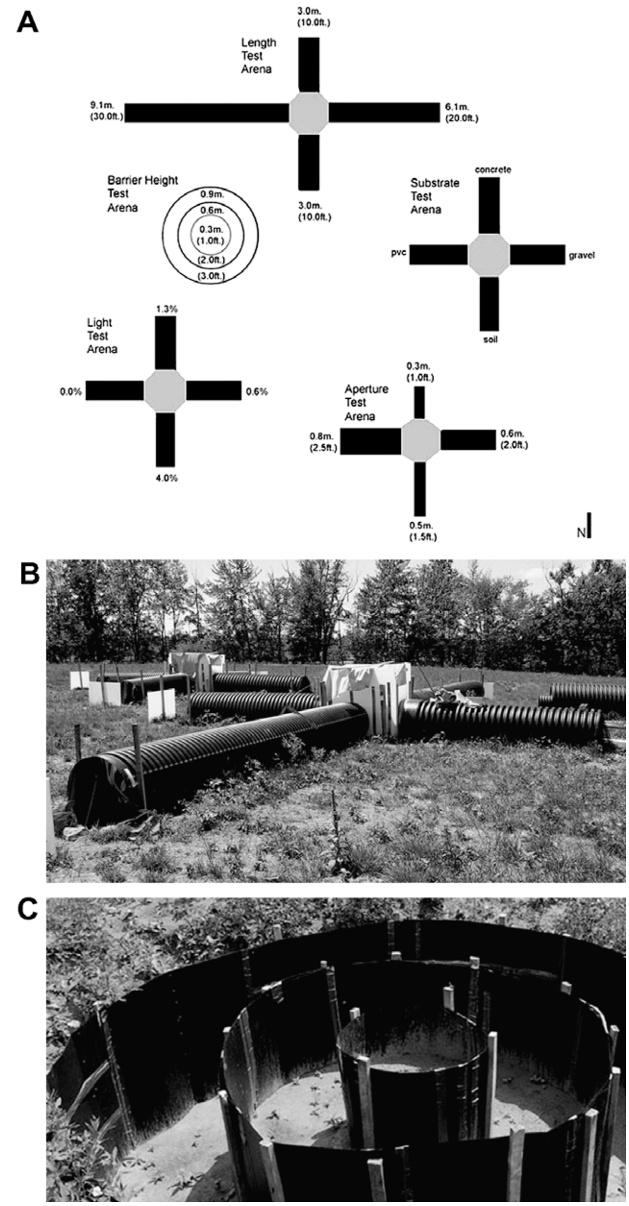

Fig. 1 – Behavioral choice arenas used in experimental evaluation of preference by frogs and turtles for variously designed road crossing structures, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006: design schematic (A) and actual deployments of choice arenas for crossing structures (B) and barrier heights (C).

For both barrier and crossing structure tests, all test subjects (*C. serpentina*, $n = 62$; *C. picta*, $n = 74$; *R. clamitans*, $n = 135$; *R. pipiens*, $n = 187$) were gathered from wetlands, ponds and fields within a 10 km radius of the experimental site and promptly returned to their places of origin after trials (usually within 2 h). Test subjects were first placed within an acclimation chamber inside the central octagonal chamber to acclimate for 5 min. The acclimation chamber was constructed of a PVC ring 0.4 m high with a diameter of 0.6 m, and covered by a white cotton cloth. The observer then pulled a string attached to the acclimation chamber from an anchor point 1.5 m outside the arena to lift the ring and release the animal, thereby preventing direct visual contact between the test subject and the observer.

Experimental trials for individual test subjects extended for 15 min. At the terminus of each pipe, we installed a pitfall trap to collect released animals as they exited from their tunnel of choice. If an animal had not exited the arena after 15 min, a choice of no decision (a "balk") was recorded and the animal was transferred to another arena. To reduce the influence of repeated exposure to stimuli, and because experimental returns tend to diminish through repeated testing of subjects (Martin and Bateson, 1986), we tested individuals no more than once in each experiment. Turtles were tested individually whereas frogs were tested individually or in groups of 2–17 individuals.

- *Experiment 1: Aperture diameter* – We used 4, 3.0-m-long pipes of diameters 0.3 m, 0.5 m, 0.6 m, and 0.8 m, lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 2: Substrate type* – We used four identical sections of 0.6 m diameter and 3.0-m-long pipe lined with concrete, soil, gravel, or bare PVC.
- *Experiment 3: Pipe length* – We used four, 0.6 m in diameter pipe sections two of which were 3.0 m, one 6.1 m, and one 9.1 m in length. All pipes were lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 4: Light permeability* – We used four sections of 0.6 m diameter, 3.0-m-long pipe with overhead punctures of 0%, 0.65%, 1.3%, or 4.0% of the pipe's surface area, rendered by drilling 0.5 cm holes in the upper surface of pipes. Pipes were lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 5: Barrier heights* – To test effective heights of barrier fences, we used opaque, corrugated plastic fences to construct three nested, circular enclosures with substrates of packed soil (Figs. 1 and 2) of heights 0.3 m, 0.6 m, and 0.9 m. Experimental subjects were placed in the center of each arena and allotted 15 min to attempt to scale the bounding fence. To motivate these desiccation-avoiding animals to leave the enclosures, we covered the ground of each arena with a dry sand substrate.

We tested the null hypothesis that choice of exit pipe was independent of design attribute by contrasting the observed frequency of choice against a null expectation of an equal number of individuals choosing each type of egress. All choice data were evaluated with the *G* statistic for the log-likelihood ratio goodness of fit test with Williams' correction for continuity (Sokal and Rohlf, 1995); we interpreted tests with probabilities < 0.05.

It is well known that many species of amphibians and reptiles can use a variety of environmental cues to home toward particular locations (Russell et al., 2005), and that studies have examined the homing abilities of the particular species used in this study (e.g., Martof, 1953; Dole, 1968; DeRosa and Taylor, 1978; Quinn and Graves, 1998; Lamoureux and Madison, 1999). The design of our experimental apparatus allowed for the masking of some of the environmental cues, but not all. To address concerns that the compass orientation of the pipes might influence individual choices due to the homing instincts of the subjects, we analyzed the propensity of individuals to choose the same orientation in subsequent trials. To do so, we compiled choice sequences for individuals that were placed consecutively in each arena and we compared their propensity to choose an egress of the (1) same orientation as its previous choice and (2) same orientation as its initial choice. We calculated 95% confidence intervals about the estimate of the average propensity (% of choices) of individuals to track their earlier choices and determined if the confidence intervals included the null expectation of 25% chance of selecting the same orientation as the earlier choice (given four possible alternatives in each arena).

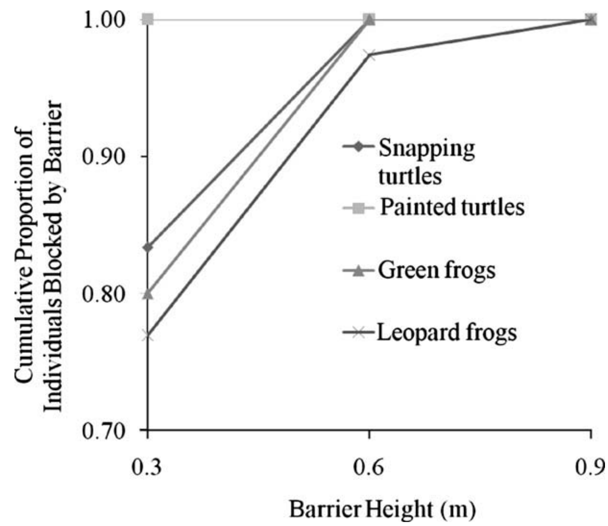

Fig. 2 – Barrier height efficacy for blocking passage by snapping turtles, painted turtles, green frogs and leopard frogs, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006. Values represent the cumulative proportion of individuals released at the center of the barrier experimental set-up (see Fig. 1) blocked by barriers of successively greater heights.

3. Results

When placed in the arenas, most individuals being tested attempted to leave via one of the choices of egress (i.e., they did not "balk"): snapping turtles balked most frequently (56%), followed by green frogs (32%), leopard frogs (23%), and painted turtles (16%) (difference in balking propensity among species: G_{adj} 28.4, df 3, $P < 0.001$).

Among test subjects that did not balk, in *Experiment 1: Aperture diameter* choice of pipe was non-random for snapping turtles and painted turtles, and highly suggestive for leopard frogs (Table 1); individuals of both turtle species showed a tendency to use pipes of the mid-size diameters more frequently than pipes with the largest and smallest diameters. For *Experiment 2: Substrate type* we detected non-random choice only for green frogs (Table 1); individuals used soil- and gravel-lined pipes more often than the concrete- and PVC-lined pipes. For *Experiment 3: Pipe length* both leopard frogs and painted turtles showed some degree of avoidance of the longest pipes, although only the data for painted turtles were non-random. For *Experiment 4: Light permeability* both

Table 1 – The crossing structure choices made by frogs and turtles as related to aperture diameter, substrate type, pipe length, and light permeability, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006

Species	n(%)				G(adj.)	P
Aperture Diameter (m)	0.3	0.5	0.6	0.8		
Green frog	8(16)	13(27)	12(24)	16(33)	2.732	0.435
Leopard frog	16(25)	18(28)	24(12)	30(35)	7.729	0.052
Snapping turtle	2(6)	14(44)	10(31)	6(19)	10.852	0.013
Painted turtle	6(17)	14(39)	14(39)	2(6)	13.547	0.004
Substrate type	Concrete	Gravel	Soil	PVC		
Green frog	6(13)	17(38)	18(40)	4(9)	14.866	0.002
Leopard frog	18(29)	20(32)	12(19)	12(19)	3.250	0.355
Snapping turtle	6(19)	9(29)	8(26)	8(26)	0.620	0.892
Painted turtle	15(37)	10(24)	8(20)	8(20)	2.939	0.401
Pipe length (m)	3	3	6.1	9.1		
Green frog	12(26)	9(19)	11(23)	15(32)	1.553	0.670
Leopard frog	12(22)	13(24)	22(40)	8(15)	7.180	0.067
Snapping turtle	11(37)	6(20)	8(27)	5(17)	2.652	0.449
Painted turtle	12(30)	4(10)	18(45)	6(15)	11.829	0.008
Light permeability (%)	0	0.6	1.3	4		
Green frog	9(17)	14(26)	9(17)	22(41)	7.789	0.051
Leopard frog	12(24)	12(24)	7(14)	20(39)	6.989	0.072
Snapping turtle	9(31)	4(14)	7(24)	9(31)	2.464	0.482
Painted turtle	12(26)	11(23)	7(15)	17(36)	4.285	0.232

Shown are the numbers (percentages) of individuals using a particular pipe to exit the arenas, where n = number of non-balking individuals. All tests have 3 df.

frog species showed non-random movement through the pipes, although the results for neither turtle species were significant (Table 1); for both frog species, the pipe with the most permeable surface area received the greatest usage.

Across all trials, no species indicated a preference for a particular compass direction. Confidence intervals (95%) about the observed percentage of individuals both repeating the compass direction taken in their first trial and repeating the direction of each previous trial included the null expectation of 25%. More specifically, the tendency to orient in the same compass orientation as initial choice was as follows (average % of choices made by individuals followed by 95% lower and upper confidence levels and n individuals): green frog 21.6% (7.3, 35.8 [17]), leopard frog 29.0% (13.0, 44.9 [23]), snapping turtle 30.6% (21.6, 39.5 [51]) and painted turtle 31.1% (20.1, 42.1 [37]). Similarly, the tendency to orient in the same compass orientation as previous choice was as follows: green frog 17.6% (3.0, 32.3 [17]), leopard frog 28.3% (12.6, 44.0 [23]), snapping turtle 30.6% (21.5, 39.7 [51]), and painted turtle 28.4% (17.7, 39.1 [37]).

Evaluation of effectiveness of various barrier heights, *Experiment 5* (Fig. 2), indicated that painted turtles could not cross barriers of heights 0.3 m, but most other species could. This stated, 0.6 m high barriers excluded most individuals and 0.9 m virtually all: of 93 organisms tested, only a single leopard frog traversed the 0.9-m-high barrier.

4. Discussion

Our analysis indicates that although turtles and frogs will traverse crossing structures of widely varying features, certain attributes of these structures do influence the patterns of usage. Tunnel aperture diameter was evidently important; three of the four species tested indicated avoidance of the 0.3 m diameter tunnels. Although other studies have suggested that some amphibians and reptiles will use larger culverts (e.g., Yanes et al., 1995; Aresco, 2005), we are unaware of studies that indicate usage or avoidance of such narrow tunnels. In addition to simply excluding access by larger turtles, the narrow sides and low roofs of these tunnels may make it impossible for anurans to use their characteristic saltatory locomotion while traversing the tunnels.

In trials testing for the acceptability of particular substrates within the tunnels, only green frogs showed significantly non-random choice. The skin of amphibians is more prone to desiccation than that of many other vertebrate animals and dehydration rates of green frogs is correlated with substrate type (Mazerolle and Desrochers, 2005). Green frogs were the more aquatic frog of the two species that we tested (Martof, 1953; Merrell, 1970), and perhaps desiccation risk influenced their preference against concrete and PVC. Similarly, a previous study found that agile frogs (*Rana dalmatina*) and water frogs (*Rana esculenta*) were more likely than common toads (*Bufo bufo*) to choose a tunnel lined with soil over a substrate of bare concrete (Lesbarreres et al., 2004).

In relation to tunnel length, it is important to note that although no species evidently preferred it, all of the species used the 9.1 m pipe as a means of egress. From a designer's perspective, this result is encouraging because road crossing structures typically need to be this long or longer to traverse the full length of roadways, which are often > 18.3 m wide (a distance we were unable to evaluate due to material limitations). The slight avoidance of our longest tunnels by painted turtles, and possibly leopard frogs, may indicate that these species might avoid even longer lengths of pipe. Future tests of length and choice could offer insights into the maximum length of pipes these species are able to navigate.

Within the limited literature on road crossing structures, the importance of light availability is unresolved. For example, Jackson and Tyning (1989) observed that when spotted salamanders (*Ambystoma maculatum*) move through tunnels with greater light penetration their speed is increased. In our study, leopard frogs and green frogs preferred the pipe with the greatest density of openings on the upper surface. The reasons for these preferences remain unclear, and warrant further investigation. Whatever the case, light availability may be among the least tenable attribute of road crossing structures because such structures are generally buried under roadways and largely impermeable to light. This said, light reflected from external sources (e.g., moonlight) and or emanating from internal sources (solar-powered bulbs) could be used to illuminate to varying degree the interior of such structures.

Our results indicate that barriers between 0.6 m and 0.9 m in height could prevent most individuals of the species we examined from accessing road surfaces as well as effectively guide them into crossing structures. Some caution in interpreting these results may be warranted because test subjects may have become fatigued crossing each successive barrier of successively greater height, rendering choices not independent of one another. However, observations in the field indicated that animals repeatedly bounded to (frogs) or reached to (turtles) predictable heights limited more by the saltatory ability imposed by morphology than physiological state. Effective heights could likely be increased by employing "lips" at the tops of barriers and, for climbing species, constructing barriers of materials with slick surfaces to prevent toe holds. Barriers of relatively modest height thus appear to provide an effective and economical means of both excluding frogs and turtles from roads, and guiding them toward road crossing structures.

Although we attempted to isolate behavioral responses to specific attributes of road crossing structures in a rigorous experimental design, our study nevertheless had limitations. First, many individuals, particularly of snapping turtles, simply did not make choices. It is unclear whether similar balking rates would be exhibited if study subjects had encountered crossing structures while in a truly migratory behavioral state (Guyot and Clobert, 1997; Birchfield and Deters, 2005; Aresco, 2005). Trial subjects were in various motivational states when tested, having been removed from their habitats when likely engaged in a variety of behaviors not necessarily associated with migration. Because the life cycles of snapping turtles, painted turtles, green frogs, and leopard frogs involve varying degrees of seasonal mobility (Obbard and Brooks, 1980; Carr and Fahrig, 2001; Steen and Gibbs, 2004), an organism tested during a period of migration could exhibit different preferences than an organism tested outside of a period of seasonal movement. The impact of seasonal movement and migratory patterns, and their potential influence on patterns of choice should be considered further and are the focus of ongoing studies (J.P. Gibbs, unpublished data). Balking rates are relative because due to the constraints of the weather, time, and trials of other individuals it was not possible to leave study subjects in the arenas without a time limitation. We suspect that balking rates would diminish, and patterns of selectivity become more resolved, if animals were provided with more extended trial periods within which to make a choice.

A further, potential limitation was that we deployed frogs in batches during some trials but do not know the extent to which one individual's choice was independent of another. Given the rapidity of most frogs' departures we saw no obvious indication of a "follow the leader" effect; nevertheless, the extent to which both amphibians and reptiles use pheromonal and visual cues to mediate their behaviors should be explored and could easily be done in an experiment such as this employing substrates imbued or not with skin secretions (pheromone cues) or supporting physical models (visual cues). Although many studies have indicated that amphibians use a variety of cues during migration, no studies to our knowledge have documented frogs using other migrating frogs as guides (Russell et al., 2005).

Despite its limitations, our study represents an experimental approach to resolving preference for attributes of road crossing structures by amphibians and reptiles. Our results provide general guidelines that can contribute to the design of more behaviorally palatable crossing structures. More specifically, we conclude that effective crossing structures can be constructed out of round PVC pipe, that these structures should be at least 0.5 m in diameter, that they should be lined with soil or gravel, and that they should be installed in tandem with a 0.6 m–0.9 m high guide fence.

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