

Design of Roadway Barriers to Reduce Desert Tortoise Mortality on Paved Road Infrastructure

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ABSTRACT. – We investigated methods for reducing highway-caused mortality of Mojave Desert Tortoises (*Gopherus agassizii*) using barriers at the Desert Tortoise Conservation Center, located near Las Vegas, Nevada. Experiments tested effectiveness of various barriers of different heights and made of different construction materials, sex-dependent behaviors including rate of escapes, appropriate height of a barrier, and adverse effects on other sympatric vertebrate species including potential entrapment. Informed by analyzing previous investigations, we tested captive adult desert tortoises (midline carapace length ≥ 180 mm) within enclosures made from 8 different common construction materials, quantified behavioral responses of individuals over several (4–14) days, and identified sex-dependent responses to these barriers. Both sexes pushed against see-through barriers more than solid barriers (58% males, 67% females) and males reversed direction of pacing more often than females (56%). Pen escapes related to pacing reversals and were generally by males. Direction reversals and escapes occurred mostly with wire mesh designs and low (20-cm) solid barriers. Frequency of body contact was not linearly correlated with larger mesh sizes. Solid barriers appear to offer the best deterrent but are more expensive. Animals that escaped in trials lasting several days were larger than average size and often escaped more than once. Tortoises escaped at weak points in barriers, such as gaps with the ground, pen corners, breaks in material, or by climbing over the barrier. In testing minimum effective barrier height for 3 types of barrier materials, none climbed over at 46 cm, 5 climbed over at 30 cm, and 19 others climbed over at lower heights. We observed native species interactions with our barrier enclosures ($n = 70$) and compared morphometric measurements of common desert reptiles vs. barrier dimensions. These data suggested that different barrier types preferentially affect specific sizes of animals although we observed no mortality. While solid barriers stop all reptiles, wire meshes entrap reptile species smaller than mesh size (such as *Callisaurus draconoides* and *Uta stansburiana*) and stop larger species (such as *Dipsosaurus dorsalis* and *Coluber flagellum*). Morphometric measures of juvenile tortoises indicated that they could pass through the 2 largest wire mesh sizes we tested.

KEY WORDS. – barriers; by-catch; entrapment; escape; *Gopherus agassizii*; highways; Mojave Desert Tortoise; mortality; roads; sex-dependent response

The use of barriers in conservation to protect wildlife populations against human intrusion and destruction of habitat has increased recently as human populations encroach farther upon open space (Jaeger and Fahrig 2004; Clevenger and Ford 2010; Woodroffe et al. 2014; Jakes et al. 2018). Barriers are particularly important where wildlife, such as amphibians and reptiles, are vulnerable to being killed while attempting to cross roads with vehicular traffic. Issues with barriers have included questions of construction and proof of effectiveness in

allowing natural movement without negative effects upon biological processes such as dispersal and migration (Lesbarreres and Fahrig 2012).

Mojave Desert Tortoise (*Gopherus agassizii*) populations located both north and west of the Colorado River are protected by the Endangered Species Act of 1973, as amended, as a Threatened species due to sharply declining populations (US Fish and Wildlife Service 2011; Allison and McLuckie 2018; Berry and Yee 2021). Declines are related to multiple factors: disease (upper respiratory tract

disease; Brown et al. 2004; Jacobson et al. 2014), effects of livestock grazing on food availability, energy and mineral developments, heavy raven predation on juvenile tortoises (Daly et al. 2019), increased interaction with human activity and construction, off-road vehicle recreational activities, and reduced habitat space (Berry 1986; Spotila et al. 1994; Boarman 2003; Daly et al. 2019) with low adult survival, habitat degradation and loss of habitat as major contributors. Efforts to improve the population status of this species have centered on disease prevention, habitat preservation, and increases in basic ecological knowledge. Habitat preservation efforts include the designation of Critical Habitat and reclaiming suitable habitat through fencing roadways and other human structures from the desert habitat.

Roads cause habitat fragmentation as well as direct mortality of tortoises. Roads have long been identified as a source of mortality for desert tortoise (Klauber 1932; Woodbury and Hardy 1948; Berry 1973, 1975; Berry and Nicholson 1984; Boarman et al. 1992, 1997) and more roads in the desert lead to more tortoise deaths due to collisions. Numerous studies (von Seckendorff Hoff and Marlow 2002; Wilson and Topham 2009; Nafus et al. 2013; Berry et al. 2014; Peadan et al. 2016, 2017) report fewer tortoise signs (scat, tracks, pellets, burrows, live and dead animals) near roads and increases in densities of signs with distance from the road. Forman and Alexander (1998) labeled this area as a road-effect zone. Characteristics of barriers along highways have received limited attention as to determining the best and most effective structures. Boarman et al. (1997) found that tortoises were effectively blocked by fencing along California State Highway 58 in the western Mojave Desert of California. Wilson and Topham (2009) recommended a mesh size of 1–2 inches with bottom edges buried, rounded corners at changes in fence direction, and ramps of large gravel for escape routes. Peadan et al. (2015) found a wider road-effect zone along interstate roads compared with county roads based on the difference in distribution of tortoise signs (burrows, pellets, scats, tracks, live animals, and carcasses). In many cases, wire mesh fencing has been placed along highways as a compromise between effectiveness, cost, and ease of maintenance but without strong scientific support (Lesbarreres and Fahrig 2012).

Fencing potentially increases effective habitat by restoring habitat viability along roadways and allowing natural replenishment of tortoise populations in these “dead zones.” The potential magnitude of this impact is enormous. Berry and Nicholson (1984) estimated 3325 km of road intrusion into areas that are critical habitat. Fusari (1982) estimated that 156,435 ha of habitat would be reclaimed if primary roads were fenced and 347,835 ha of habitat might be reclaimed if all roads were fenced. Therefore, recovery plans have included assessment of suitable barriers to prevent or reduce tortoise activity near

or on highways in order to reclaim habitat (Boarman and Kristan 2006; US Fish and Wildlife Service 2011).

Basic questions remain regarding barrier composition, material type, and barrier dimensions. Fusari (1982) observed significantly different behavioral responses by tortoises for 3 barrier types: solid, chicken wire, and hardware cloth. In Fusari’s study, the most fence-fighting behavior occurred with the chicken wire fence where visual and tactile cues conflicted because tortoises could see beyond the fence and put their head and limbs through the fence. Fence-fighting occurs when tortoises struggled against the fence, placed head or limb through the gap and tried to continue moving forward (leading to potential entrapment), or otherwise spent effort pushing against the barrier (Ruby et al. 1994). Research with captive tortoises comparing behavior with a variety of barriers ($n = 13$) also found differences between barriers in movement near and along the barrier and the degree of fence-fighting (Ruby et al. 1994). Tortoises behaved differently between solid and nonsolid barriers, with fewer interactions with solid barriers, and fence-fighting behaviors greatest with fences with large opening structures (chicken wire and chain-link fences). These are undesirable behaviors as the energy used by the tortoise is unproductive and the potential for thermal stress increases (Ruby et al. 1994; Peadan et al. 2017). Tests of other barrier attributes such as height included barriers all the same height (Fusari 1982) or heights varying with the material used (Ruby et al. 1994) but not tests of the same material at different heights. This question of height affects effectiveness (what minimum is needed to deter tortoises) and economics (cost reduced by using no more material than needed).

The general purpose of this study was to investigate additional strategies for reducing desert tortoise mortality along highways based on previous investigations (Fusari 1982; Boarman et al. 1997; Ruby et al. 1994). We sought to quantify behavioral reactions to a specific set of barriers, either solid or varying in mesh size, suitable in construction or retrofitting of highways in the Mojave Desert and elsewhere. Specifically, we 1) tested for variation in responses among barrier types including sex-dependent responses to these barriers and a relationship with mesh size of the barriers, 2) conducted a simple test of barrier height to identify minimum necessary height, and 3) assessed effects of barriers on other wildlife through monitored fence surveys and morphometric calculations. The ideal fencing material is one that encourages tortoises to leave the area of the barrier with minimum contact with the fence or barrier. However, tortoises are more likely to interact with the fence or pace along it (D.E.R., *pers. obs.*). We sought to evaluate whether alternatives besides solid materials or hardware cloth (Ruby et al. 1994) were available and effective. Other criteria such as cost, feasibility, and environmental impacts may determine the actual barrier type chosen in a habitat recovery plan.

Table 1. Construction type and heights tested of materials tested in barrier experiments with desert tortoises. NA = not applicable.

Material description	Gauge	Heights tested (cm)
5.1 × 5.1-cm wire mesh	16	46, 30, 20
1.3-cm hardware cloth	19	46, 30, 20
Galvanized steel	30	46, 30, 20
2.5 × 2.5-cm wire mesh	14	46
5.1 × 10.2-cm vertical wire mesh	14	46
1.9-cm diamond plastic mesh	NA	46
2.5 × 5.1-cm vertical wire mesh	16	46
Plycrete (concrete simulation: plywood and concrete)	NA	46

METHODS

The barriers tested in this study were chosen after evaluation of the previous studies by Fusari (1982) and Ruby et al. (1994), and then assessed for safety, environmental impact, durability, evaluations by other researchers, and cost effectiveness. Here we report on 3 experiments: behavioral responses of male and female adult tortoises in pens constructed of our selected materials, test of minimum barrier height required in both large test enclosures and a stacked-plank test, and effects on other desert vertebrate species.

We constructed research facilities at the Desert Tortoise Conservation Center (DTCC) near Las Vegas, Nevada, during March–April 1995. Field research was conducted in the spring (April–June) of 1995 using about 300 captive adult desert tortoises (≥ 180 -mm midline carapace length [MCL]) held at the DTCC. All our test animals had been maintained in large pens (about 4 ha) prior to testing in our barrier pens. We selected 8 types of barriers with different combinations of materials and barrier height ($n = 14$; Table 1) and constructed 2 pens of each material–height combination to increase sample size during testing. The 28 treatment pens, each 5 × 30 m in size, were arranged in a grid pattern with 10 m between adjacent pens. The rectangular shape maximized the continuous linear extent of the barrier material between corners. All construction was done by hand using methods to reduce habitat impacts. Pens simulated existing highway standards with heavy-duty T-posts every 5 m and a strand of nonbarbed wire at the top of the test material increased structural integrity. We buried the ground end of barrier materials 0–4 cm depending on topography. We left native vegetation intact in each pen, including common perennials like creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and rhatany (*Krameria parvifolia*). Artificial burrows (38 cm wide, 19 cm high, ~180 cm long) were built in each pen and were oriented randomly north or south along the long axis of the pen.

We also tested how the height of a barrier affected behavior for 3 types of barriers (Table 1). We constructed 3 pen types (5.1 × 5.1-cm wire mesh, 1.3-cm hardware cloth, 30-gauge galvanized steel sheet) at 3 different heights: 46, 36, and 20 cm. These 3 materials represent

different types of barriers based on previous testing (Fusari 1982; Ruby et al. 1994). Tortoises can see and get their limbs/head through 5 × 5-cm wire mesh; tortoises can see through but not put their limbs/head through 1.3-cm hardware cloth; and galvanized steel is an opaque barrier. Comparisons of behaviors in these pens tested how barrier height affected behavior and the different heights assessed the escape potential from any pen.

We used only adult tortoises with a 1:1 sex ratio throughout. Twenty tortoises (10 tortoises of each sex) were individually tested in each pen for 20 trials per pen type. We placed 1 tortoise in each pen and began observations the next day. A preliminary trial with several animals together in 1 pen indicated that social interactions would distract significantly from barrier testing because tortoises interacted with each other numerous times whenever placed in a new environment with other tortoises (D.E.R., *pers. obs.*). Trials ran 4–14 d, depending upon weather and the number of researchers making simultaneous observations (range = 1–5 researchers), with observations taking less time when 5 researchers were used. If several researchers conducted simultaneous observations, they were distributed evenly among pens. Pens were sampled in sequential order beginning with a randomly selected one. Before starting observations, we recorded shaded air temperatures at 1.5 m, 1 cm, and on the surface and noted weather conditions at 0800, 1200, and 1600 hrs Pacific Standard Time. Each pen was approached cautiously to avoid disturbing tortoises. If an animal was disturbed, the researcher waited until the animal resumed normal behavior before recording observations.

We observed each tortoise for 20 separate 6-min occasions for a total observation time of 2 hrs (defined as an observation set). We divided tortoise behaviors into 23 behavioral categories (Table 2) and documented frequency of these behaviors during our observations. During each 6-min period, we scored tortoise behaviors and barrier interactions at 15-sec intervals, timed by stopwatches, into one category on a standard data sheet. If a tortoise exhibited several behaviors, we scored the predominant behavior in an interval. The analysis unit was the average frequency of each behavioral category over the total time intervals per tortoise ($n = 20$) for each behavior.

Our analysis used the Kruskal-Wallis Test because the assumptions of analysis of variance were not met. First, Levene's test revealed that most data lacked homogeneous variances. Second, frequency distributions for most behavioral categories were Poisson distributed with numerous zero values and means were highly correlated with variances. Transformations could not normalize these data. Comparisons of behavioral patterns between solid vs. see-through barriers, barriers of different heights, male vs. female behavior for the same barrier type, and frequency of escape from enclosures by males or females were performed using the Mann-Whitney U-test, corrected for tied ranks (Sokal and Rohlf 2011). Probability levels less than 0.05 for each test were considered significant.

Table 2. Behavioral categories of desert tortoises monitored during tests of experimental pens. The behavior that dominated each 15-sec interval was recorded.

Behavioral category	Description of behavior
Not moving not at barrier	Animal stationary in the pen
Not moving shade of barrier	Animal stationary but shaded by barrier
Not moving touching barrier	Animal stationary but touching barrier
Not moving adjacent to barrier	Animal stationary next to barrier
Walking	Animal is moving in the pen
Walking along barrier	Animal is moving along barrier
Walking along barrier contact	Animal is moving and contacts the barrier
Beak touch/beak push	Animal touches or pushes barrier with beak
Body touch	Animal touches barrier with body
Head/limb through barrier	Animal puts head or limb through barrier
Body push	Animal pushes against barrier with body
Climbing at corner	Animal tries to climb barrier at a corner
Climbing at shrub at barrier	Animal climbs barrier where shrub assists
Climbing at barrier elsewhere	Animal climbs barrier (not corner or shrub assist)
Reverse direction	Animal changes direction
Move away from barrier	Animal moves away from barrier
Move toward barrier	Animal moves toward barrier
Direction change in corner	Animal changes direction at a corner
Digging against barrier	Animal digs against barrier
Digging elsewhere	Animal digs elsewhere in pen
Feeding and drinking	Animal is eating or drinking
Animal escaped pen	Animal has escaped pen
Other behavior	Some behavior not otherwise listed

A second test for barrier height was done in a single pen using stacked planks. We constructed one 4.9×4.9 -m pen using 3.8×8.9 -cm wood firmly wedged between reinforcing bars driven into the ground. The height of the pen was adjustable from 9 to 36 cm in 9-cm increments when 1–4 wood boards were stacked. The enclosure included an artificial burrow. We tested 11 adults (6 females and 5 males) individually. A trial of a tortoise started with walls at maximum height (36 cm, 4 boards stacked on top of each other). Each day we lowered the height of the pen wall by 1 board (9 cm) until the tortoise escaped. Upon escape we recorded the wall height and placed a new animal for another trial in the pen. No behavioral observations were made in this test.

We documented the effects of our barrier materials on other animal species in 2 ways. First, we recorded all incidental observations of interactions between reptiles or small mammals and test barriers while conducting the primary enclosure experiments. Secondly, we compared selected standard morphological measures of appropriate species of lizards and snakes (considering only adult-sized animals) with fence measurements because these animals might be ensnared in mesh fences. This substituted for testing live specimens. We used these measurements to

identify which fence designs may be detrimental to the more common desert lizards and snakes found with desert tortoises in the Mojave Desert and that would encounter the same highway barriers. We compared this analysis with actual fence interactions recorded during the field season. We collected standard morphometric measurements from reptile specimens preserved in 70% ethanol at the Museum of Systematics and Ecology at the University of California, Santa Barbara. For each specimen, we measured snout–vent length, maximum head width, and maximum body width to the nearest millimeter. Maximum body width on snakes was taken wherever the maximum body width occurred, usually near midbody. Maximum body width on lizards was the linear distance between each knee joint when the femurs had been preserved perpendicular to the long axis of the body. We selected this measurement because our field observations suggested that animals usually became stuck when they could not get their hind limbs through the fence. We rated different fence materials using the following fence-encounter scenarios for probability of getting stuck: 1) N = not stuck, average adult lizard or snake cannot pass through fence beyond the head; 2) S = stuck possible, average adult lizard/snake can crawl through fence beyond the head region but not necessarily beyond the hind limb or midbody region respectively; 3) Y = yes pass, average lizard/snake can easily pass through without getting stuck in fence.

Using morphological measurements of juvenile tortoises, we similarly considered 3 scenarios whether juvenile tortoises could escape openings in some of the larger wire mesh fences with their plastron at 3 angles: parallel to the ground, at a 45° angle, and at a 90° angle regardless of whether tortoises could turn to these angles to try to escape. These projections were based on a system of regression equations that relate key morphological measurements to MCL (Berry and Woodman 1984).

RESULTS

Results of Kruskal-Wallis tests revealed that there were 8 behavioral categories for which particular fence designs elicited differential tortoise responses (Tables 3–9). The 8 categories were barrier-interaction categories and yielded more useful information than the remaining 7 nonsignificant categories that were not barrier interactions.

Our results suggested solid barriers may attract tortoises for thermoregulatory purposes. Tortoises frequently used barriers for shade and walked within a body length of the barrier (Table 3). They spent more time not moving in the shade of the barrier for solid barriers than see-through barriers (Table 4); this was the case for both sexes (Table 6). Although the category of not moving adjacent to barrier was statistically significant (Table 3), no clear patterns among barrier types were evident. However, females but not males spent more time not moving

Table 3. Frequency of occurrence of behaviors in barrier trials. Means are calculated averages for 20 6-min observation periods. Statistical tests for variation in the behavior of desert tortoises among all barrier types tested in enclosure experiment (Kruskal-Wallis tests: $n = 280$, $df = 13$). Only results < 0.1 are shown. NS is a result not statistically significant while significant (0.05) and highly significant (0.001) results are denoted by * and ***, respectively.

Behavioral category	Mean \pm SD	H (corrected for ties)	<i>p</i> -value
Not moving, not at barrier	13.3 \pm 4.61	19.49	0.10 NS
Not moving, shade of barrier	0.44 \pm 1.18	114.57	0.0001***
Not moving, adjacent to barrier	3.48 \pm 2.6	25.63	0.0191*
Walking along barrier	1.31 \pm 1.14	22.16	0.0429*
Walking along barrier contact	0.87 \pm 1.06	41.90	0.0001***
Head/limb through barrier	0.13 \pm 0.47	79.33	0.0001***
Body push	0.71 \pm 0.26	29.62	0.0053*
Climbing at barrier elsewhere	0.05 \pm 0.28	21.65	0.06 NS
Reverse direction	0.29 \pm 0.51	34.75	0.0009 NS
Feeding and drinking	1.10 \pm 1.26	21.12	0.07 NS
Animal escaped pen	0.19 \pm 0.99	39.99	0.0001***

adjacent to see-through barriers than solid barriers (Table 6).

Tortoises walked along certain barrier types more often than others (Table 3) with similar results for walking along or in contact with the fence. Male tortoises walked along the shorter 2 size-class barriers (20 and 30 cm) more than the highest barrier (46 cm) while females did not discriminate (Mann-Whitney U-test: males $U = 2864.5$, $p = 0.0538$; females $U = 2338.5$, $p = 0.703$). Similarly, males walked more often in contact with lower barriers while females did not (Mann-Whitney U-test: males $U = 2933.5$, $p = 0.0227$; females $U = 2281.5$, $p = 0.8993$). In addition, tortoises walked in contact with see-through barriers much more often than solid barriers (Mann-Whitney U-test: $p = 0.0001$) with both sexes exhibiting this tendency (Table 6).

Although the “head/limb through barrier” had highly significant results among barriers (Table 3), some barriers did not allow tortoises to put their head or limbs through a fence so further statistical comparisons with solid barriers were not appropriate. Among mesh fences, rates of interaction appear to diminish as mesh size decreases. Tortoises put their heads and/or limbs more through 46-cm 5.1 \times 10.2-cm mesh fence than 20-, 30-, and 46-cm 5.1 \times 5.1-cm mesh fences, and, to a much lesser extent, the 46-cm 2.5 \times 5.1-cm mesh fence. Tortoises pushed

with their bodies against see-through designs more than solid fences (Table 4). This pattern was significant in females (Table 6), but males showed a nonsignificant trend ($p = 0.059$). The correlation between frequency of “body push” and mesh size of fences was not linear, with the highest rate of interaction against 5.1 \times 5.1-cm mesh size (an intermediate size in the ranges tested).

“Beak touch/beak push” did not differ among all pen types (Table 3) with no sex-dependent response either (Table 6). However, there was a clear difference in comparisons between see-through and solid barriers, as tortoises interacted with see-through barriers more often than solid designs (Table 4), primarily as the result of the behavior of female tortoises (Table 6) since males did not discriminate between see-through and solid designs. Although “climbing at barrier elsewhere” was not statistically important among barrier types (Table 3), tortoises tended to climb galvanized steel barriers more often than see-through barriers (Mann-Whitney U-test: $p < 0.001$) and was observed in both sexes (Mann-Whitney U-test: males $p = 0.022$, females $p < 0.001$).

Males and females behaved similarly in their response between solid and see-through designs in 5 categories (Table 6), comparable to the overall response. Females but not males acted differently between solid and see-through designs in 3 categories (Table 6; not moving adjacent to

Table 4. Frequency of occurrence of behaviors in barrier trials contrasting solid and see-through types of barrier. Means are calculated averages for 20 6-min observation periods. Statistical tests for differences in behavior of desert tortoises (Mann-Whitney U-tests: $n = 280$). Both sexes are combined in the data. Only results < 0.1 are shown. NS is a result not statistically significant while significant (0.05) and highly significant (0.001) results are denoted by * and ***, respectively.

Behavioral category	Solid	See-through	U-value	<i>p</i> -value
Not moving, shade of barrier	1.42 \pm 1.84	0.05 \pm 0.24	12,239	0.0001***
Not moving, adjacent to barrier	2.91 \pm 2.30	3.47 \pm 2.69	9371.5	0.0239*
Walking along barrier contact	0.40 \pm 0.63	1.06 \pm 1.14	10,706	0.0001***
Beak touch/beak push	0.01 \pm 0.11	0.10 \pm 0.32	8700	0.0121*
Head/limb through barrier	0.00	0.18 \pm 0.55	9080	0.0001*
Body push	0.00	0.10 \pm 0.30	8800	0.0034*
Climbing at barrier elsewhere	0.15 \pm 0.48	0.01 \pm 0.10	8820	0.0001***
Reverse direction	0.11 \pm 0.32	0.37 \pm 0.55	9972	0.0002***
Animal escaped pen	0.08 \pm 0.67	0.24 \pm 1.09	8337	0.11 NS

Table 5. Frequency of occurrence of behaviors in barrier trials testing sex-dependent responses. Means are calculated averages for 20 6-min observation periods. Statistical tests for sexual differences in behavior of desert tortoises among all tested barrier types (Mann-Whitney U-tests, $n = 280$). All types of barriers are combined in the data. Only results < 0.1 are shown. NS is a result not statistically significant while significant (0.05) and highly significant (0.001) results are denoted by * and ***, respectively.

Behavioral category	Male (mean \pm SD)	Female (mean \pm SD)	U-value	<i>p</i> -value
Not moving touching barrier	1.65 \pm 1.98	1.21 \pm 1.99	11,282.5	0.0209*
Reverse direction	0.36 \pm 0.55	0.23 \pm 0.45	11,016.5	0.0197*
Feeding and drinking	1.02 \pm 1.30	1.18 \pm 1.22	10,969.5	0.0689 NS

barrier, beak touch/beak push, and body push) and the female response was responsible for the overall response being significant (Table 4). In another 3 categories, males and females acted with different frequencies but the frequencies for neither sex reached significance (Table 6).

Rates of reverses in direction varied highly significantly among fence designs (Table 3). Both sexes exhibited this pattern (Kruskal-Wallis test: males $H = 23.54$, $df = 13$, $p = 0.036$; females $H = 22.01$, $df = 13$, $p = 0.054$) but males reversed more often than females (Table 5). Both sexes reversed direction more often along see-through fences (Table 6), and along 20-cm galvanized steel (Mann-Whitney U: $p = 0.032$; females $p = 0.002$). Tortoises escaped from different barrier designs (Tables 7 through 9) in our tests, including all 3 heights of 1.3-cm hardware cloth, 20-cm-high galvanized steel fence, 20-cm-high 5.1 \times 5.1-cm mesh fence, and 46-cm-high 2.5 \times 5.1-cm vertical mesh fence. Five of these 6 types were see-through designs. Fifteen of 280 tortoises (5.4%; Table 7) escaped from test enclosures. Most escapees (13 of 15; 87%) were males ($\chi^2 = 6.667$, $df = 1$, $p < 0.05$). The 15 animals produced 66 escapes

out of 5656 (1.1%) observations during tests of enclosure pens. Of the 66 escapes, 24 were by climbing over barriers, 25 were by digging under barriers, and in 17 cases the method of escape was unknown (Table 7). Escapees were larger than the average of all tortoises ($n = 280$) used ($\chi^2 = 78.37$, $df = 14$, $p < 0.001$; Fig. 1). Male escapees ($n = 13$) were also larger than all male tortoises ($n = 140$) used in the experiment ($\chi^2 = 77.49$, $df = 12$, $p < 0.001$; Fig. 1). Because only 2 females escaped, no significant difference between the size of these escapees vs. all females ($n = 137$) in the experiment ($\chi^2 = 1.75$, $df = 1$, $p = 0.186$; Fig. 1) could be detected. The total sample size of males and female is 277 instead of 280 because 3 animals were not identified as to sex. Most escapees did so repeatedly (Table 8), averaging 4.4 escapes (range, 1–11). Repeated escapes were often through the same place in the barrier. The greatest number of individuals escaping and most frequent escapes occurred with 30-cm-high 1.3-cm-diameter hardware cloth (19 of 66, 29%; Table 7). Hardware cloth barriers (20, 30, and 46 cm) accounted for 10 of 15 (67%) escaped individuals and 34 of 66 (52%) escape occurrences. Escape by climbing over the barrier

Table 6. Frequency of occurrence of behaviors in barrier trials contrasting solid and see-through barriers with each sex calculated separately. Means are calculated averages for 20 6-min observation periods. Statistical test for variation in behavior of male and female desert tortoises between solid and see-through barrier types (Mann-Whitney U-tests, $n = 280$). Only results when one or both sexes were < 0.1 are shown. NS is a result not statistically significant while significant (0.05) and highly significant (0.001) results are denoted by * and ***, respectively.

Behavioral category	Sex	Solid (mean \pm SD)	See-through (mean \pm SD)	U-value	<i>p</i> -value
Not moving, not at barrier	M	14.14 \pm 5.31	12.72 \pm 4.48	2186	0.09 NS
	F	13.59 \pm 4.64	13.54 \pm 4.49	2055	0.96 NS
Not moving, shade of barrier	M	0.97 \pm 1.36	0.08 \pm 0.30	2581	0.0001***
	F	1.80 \pm 2.11	0.02 \pm 0.15	3320	0.0001***
Not moving, adjacent to barrier	M	3.06 \pm 2.41	3.70 \pm 2.71	2084	0.23 NS
	F	2.75 \pm 2.23	3.76 \pm 2.68	2508.5	0.0315*
Walking	M	0.74 \pm 0.74	0.79 \pm 0.76	1884	0.80 NS
	F	0.98 \pm 0.82	0.72 \pm 0.67	2383.5	0.08 NS
Walking along barrier contact	M	0.43 \pm 0.65	1.04 \pm 1.06	2441	0.0019*
	F	0.36 \pm 0.61	1.08 \pm 1.24	2749	0.0004***
Beak touch/beak push	M	0.03 \pm 0.17	0.12 \pm 0.36	1995.5	0.13 NS
	F	0.00	0.09 \pm 0.28	2222	0.0458*
Head/limb through barrier	M	0.00	0.19 \pm 0.64	2065	0.0296*
	F	0.00	0.17 \pm 0.43	2354	0.0068*
Body push	M	0.00	0.10 \pm 0.29	2012.5	0.059 NS
	F	0.00	0.10 \pm 0.03	2244	0.0334*
Climbing at barrier elsewhere	M	0.09 \pm 0.28	0.02 \pm 0.14	1960	0.0667*
	F	0.20 \pm 0.59	0.00	2325	0.0003***
Reverse direction	M	0.17 \pm 0.38	0.43 \pm 0.59	2237.5	0.0189*
	F	0.07 \pm 0.25	0.30 \pm 0.5	2481	0.0046*
Other behavior	M	0.23 \pm 0.77	0.10 \pm 0.72	1977	0.09 NS
	F	0.11 \pm 0.39	0.16 \pm 0.78	2055.5	0.92 NS

Table 7. Type of barrier, number of escaped desert tortoises, number of escape occurrences observed, and method of escaping if known. Over = tortoise climbed over fence; Under = tortoise dug under fence; Unk = method of escape unknown or could not be determined.

Material	Height (cm)	No. of animals escaping	No. of escape occurrences	Method		
				Over	Under	Unk
5.1 × 5.1-cm mesh	20	1	3	0	0	3
1.3-cm hardware cloth	20	2	11	6	0	5
Galvanized steel	20	2	17	13	0	4
1.3-cm hardware cloth	30	7	19	5	10	4
1.3-cm hardware cloth	46	1	4	0	4	0
2.5 × 5.1-cm mesh	46	2	12	0	11	1
Total occurrences		15	66	24	25	17
% of total				36	38	26

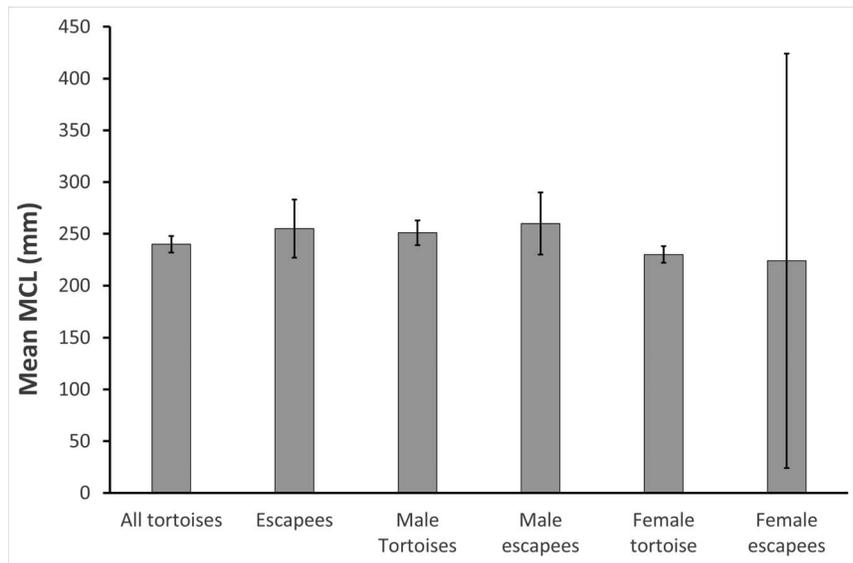


Figure 1. Tortoises escaped fencing by either climbing over or under the fencing in tests of 3 different barrier materials (5.1 × 5.1-cm wire mesh, 1.3-cm hardware cloth, and galvanized steel) at 3 heights (46, 30, and 20 cm). Mean midline carapace length and 95% confidence limits are shown for all animals used, and the males and females used compared to escapees for each category.

Table 8. Number of repeated escapes by tortoises that escaped enclosures (*n* = 15).

	No. of total escapes							
	1	2	3	4	5	6	8	11
No. of animals	2	2	2	2	3	2	1	1

Table 9. Stacked-plank pen test for minimum height of barrier to prevent escapes. Numbers of escapes by desert tortoises (*n* = 11) reported for 4 barrier heights. The height of the pen was reduced from the maximum 36 × 9-cm each day during the test.

Pen height (cm)	No. of males	No. of females	Total
36	1	0	1
27	4	5	9
18	4	5	9
9		1	1
Total	5	6	11
Mean MCL (mm)	277	252	

(*n* = 24) occurred with 20-cm hardware cloth (*n* = 6), 30-cm hardware cloth (*n* = 5), and 20-cm galvanized steel (*n* = 13) (Table 7). No identifiable escapes occurred by climbing over 46-cm-high material. Escapes by digging under (*n* = 25) occurred with hardware cloth and 2.5 × 5.1-cm wire mesh (Table 7). Escapes by unknown methods (*n* = 17) occurred in 5 different types of enclosures (Table 7) and at all 3 material heights. Time in pens affected the probability of escape since trials lasted 4–14 d. First escapes occurred between 1 and 12 d. We found a positive correlation (*r* = 0.915) between the number of days in a test enclosure and the percentage of individuals who escaped (Fig. 2). By the 12th day, the probability of escape increased by about a factor of 7 compared with the second to fourth day.

In the stacked-plank height experiment, most animals (9 of 11, 89%) escaped at the 18-cm height (Table 9) with a nearly even distribution of males to females (4:5) after being in the pen 2 d. Only 1 tortoise (280-cm MCL male, roughly average size for our sample) escaped at the

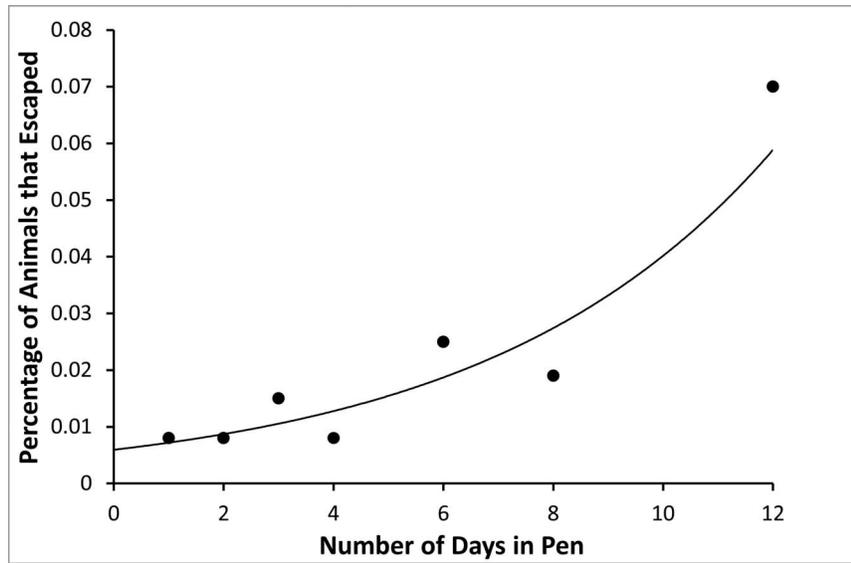


Figure 2. Time spent in pens correlation to escape frequency. Trials lasted from 4 to 15 d. An exponential curve fit ($r = 0.915$) was found between the number of days spent in a test enclosure and the percentage of animals that escaped.

maximum height of 36 cm. A 233-mm MCL female did not escape until the barrier height was lowered to 9 cm.

We accumulated 70 observations of encounters between 8 vertebrate species and the experimental barriers (Table 10). We observed 3 small mammals (*Ammospermophilus leucurus*, *Xerospermophilus tereticaudus*, and *Sylvilagus auduboni*), 4 lizards (*Aspidoscelis tigris*, *Gambelia wislizenii*, *Phrynosoma platyrhinos*, and *Uta stansburiana*), and 1 snake (*Coluber flagellum*). We observed no mortality in those encounters. Eighty-one percent of observations (51 of 70) were of lizards and snakes and were characterized by ease of passage (Table 10). We observed antelope ground squirrels (*A. leucurus*) interacting with various barriers ($n = 13$, Table 11) without problems by jumping or climbing over any barrier with 1 observation of an antelope ground squirrel running through a barrier (46-cm 5.1×10.2 -cm mesh fence). We had single observations of a round-tailed ground squirrel (*X. tereticaudus*) with the 46-cm 5.1×5.1 -cm mesh and an Audubon’s cottontail (*S. auduboni*) with the 46-cm 5.1×10.2 -cm mesh barriers.

Based on morphometric measurement comparisons of lizards and snakes with barrier gaps, the substantial range

in size of our comparison species meant there were no clear-cut lizard- or snake-“friendly” designs (Table 12). The maximum size of juvenile tortoises that could escape a fence based on morphometric measures varied with the angle of the plastron (parallel, 45° or 90°) to the ground (Table 13).

DISCUSSION

Our experiments were designed to further identify effective attributes of barriers. The enclosure experiments sought to determine more precisely which fence designs in terms of their material and height effectively retain tortoises and to identify attributes useful for designing effective yet cost-effective highway barriers. We confirmed that tortoises act differently with solid vs. see-through barriers but there is additional variation among barriers of different mesh sizes and with sex-dependent differences to some barrier types. Barrier height affects tortoise behavior and the chance of escape changes between low (20-cm) or medium (30-cm) height barriers vs. high (46-cm) barriers.

Both sexes spent more time next to the solid barriers than next to the see-through designs (whether tortoises

Table 10. Types of encounters observed for lizards and snakes with various see-through fence materials. Numbers refer to the frequency of encounters. Ease of passage through barrier was coded as N = could not pass through fence; E = passed through fence easily; and D = passed through fence with difficulty. $n = 51$.

Species	1.3-cm hardware cloth	1.9-cm diamond plastic mesh	2.5×2.5 -cm wire mesh	2.5×5.1 -cm mesh	5.1×5.1 -cm mesh	5.1×10.2 -cm vertical wire mesh
<i>Aspidoscelis tigris</i>	2E/6D	2E/5D	6E	1E	7E	6E
<i>Gambelia wislizenii</i>	2N	1N	1D	1E	—	—
<i>Phrynosoma platyrhinos</i>	—	—	—	—	2E	2E
<i>Uta stansburiana</i>	—	—	—	—	4E	—
<i>Coluber flagellum</i>	1N	—	—	—	2E	—
Total	11	8	7	2	15	8

Table 11. Frequency and type of encounters with various barrier design by adult antelope ground squirrels (*Ammospermophilus leucurus*).

Barrier type	Jumped/ climbed over fence	Passed through fence
20-cm 1.3-cm hardware cloth	2	—
20-cm 5.1 × 5.1-cm mesh	1	—
31-cm 1.3-cm hardware cloth	1	—
31-cm galvanized steel	1	—
46-cm 1.3-cm hardware cloth	2	—
46-cm 2.5 × 2.5-cm mesh	3	—
46-cm 2.5 × 5.1-cm vertical mesh	1	—
46-cm 5.1 × 5.1-cm mesh	—	1
46-cm 5.1 × 10.2-cm mesh	1	—
Total	12	1

were moving or not). Solid barriers may actually attract tortoises for thermoregulatory purposes. Our observations from the springtime trials indicated that tortoises used sun-warmed faces in the early morning on cold but sunny spring days and were found flush (on the leeward side) of solid barriers on sunny but cold windy days. On hot days (this study; summertime, Ruby et al. 1994) tortoises avoided the sun by either taking refuge in a burrow, under a shrub, or lying in the shadow of the pycrete barriers. Peadar et al. (2017) found tortoises were warmer and moved more near structures, suggesting an increased energy expenditure and risk of thermal stress near barriers. We observed that both sexes climbed against solid barriers much more often than see-through designs. Tortoises could escape by climbing over low (20-cm) galvanized steel pens, which demonstrates that adequate height is important for effective solid barriers. Both sexes walked in contact with see-through barriers more often than solid barriers and females did this behavior more than males, although this was unrelated to the actual mesh size. Thus, see-through designs may elicit more interactive responses from tortoises, particularly females, which is an undesirable trait for fences.

Tortoises inserted their head and limbs through any fence that allowed them to do so. Because we tested a range of mesh openings, we found the frequency of this behavior was only loosely correlated with mesh size. Head or limb insertion should not be desirable as fence-fighting behavior increased in frequency or tortoises could be entangled in the barrier, as observed by Fusari (1982) and Ruby et al. (1994) with chicken wire. Another negative attribute of larger mesh designs is that hatchling and juvenile tortoises can pass through and enter the highway right-of-way zone. The loose correlation between fence-fighting and large gap mesh fences suggests that effective barriers should be either solid when possible or have small meshes.

The most important finding about barrier height of our enclosures was no escapes at high (46-cm) heights and fewer but not zero escapes at medium (30-cm) heights. The frequency of climb-over escapes (36%) and escapes under the barrier (38%) was similar, with an additional 26% by unknown method. Where the method of escape was unknown, it was not obvious to observers that escape under the barrier occurred so we suspect that at least some unknown escapes could be climbs over the barrier. Tortoises usually climbed over low (20-cm) barriers but escaped from higher pens by exploiting weak areas of fence construction or digging under the fences. Tortoises may dig against the fence and this was not the result of constructing a natural burrow. We correlated the frequency of reversing behavior with the probability of escaping by either sex in see-through and 20-cm galvanized steel barrier enclosures. Male tortoises tended to walk along with or without touching the low (20-cm) and medium (30-cm) barriers more often than the high (46-cm) barriers. Males were more predisposed to explore the 2 lower heights of barrier regardless of construction material. Higher structures, such as the 46-cm barriers, discouraged pacing behavior. The majority of climb-over escapes occurred with hardware cloth, possibly because tortoises can claw the small mesh size. Climb-over escapes were

Table 12. Comparisons between morphometric measurements for lizards and snakes and fence materials tested in this experiment. The data are coded for potential for entrapment or passage as follows: N = average adult not able to penetrate barrier beyond head; S = average adult could get stuck in fence; Y = average adult able to pass completely through the fence.

Species	1.3-cm hardware cloth	1.9-cm diamond plastic mesh	2.5 × 2.5-cm wire mesh	2.5 × 5.1-cm vertical mesh	5.1 × 5.1-cm mesh	5.1 × 10.2-cm vertical wire mesh
Lizards						
<i>Callisaurus draconoides</i>	S	S	S	S	Y	Y
<i>Aspidoscelis tigris</i>	S	S	S	S	Y	Y
<i>Dipsosaurus dorsalis</i>	N	S	S	S	S	S
<i>Gambelia wislizenii</i>	N	S	S	S	S	S
<i>Phrynosoma platyrhinos</i>	N	N	S	S	S	S
<i>Sceloporus magister</i>	N	S	S	S	S	S
<i>Uta stansburiana</i>	S	S	S	S	Y	Y
Snakes						
<i>Crotalus cerastes</i>	N	S	S	S	Y	Y
<i>Crotalus scutulatus</i>	N	N	S	S	Y	Y
<i>Coluber flagellum</i>	N	S	S	S	Y	Y
<i>Pituophis melanoleucus</i>	N	S	S	S	Y	Y

Table 13. Maximum sizes of juvenile desert tortoises (mm MCL) that could escape through mesh fences based on morphometric measurements.

Mesh size (cm)	Plastron parallel to ground	Plastron at 45° angle to ground	Plastron at 90° angle to ground
2.5 × 2.5	—	—	—
2.5 × 5.1	—	—	48
5.1 × 5.1	66	92	66
5.1 × 10.2	66	92	109

most common with 20-cm-high material but a few occurred with 30-cm material. Since no escapes were recorded at 46 cm, we suggest that this height is tortoise-proof. This assumes that longer exposures would not result in escapes because wild tortoises would not be expected to persist along a barrier for several days in a row. Some escapes (probably dig-under escapes) were a result of tortoises exploiting minor weaknesses in barriers. This might include small areas where the bottom of the barrier was at or slightly above ground level or places where fence sections (abutting panels of material or in corners) were not tied together sufficiently. Tortoises repeatedly pushed against these spots until they were able to create or widen a gap enough to pass through the barrier. Since many of our tortoises escaped repeatedly, individuals vary in their ability to recognize and exploit weaknesses in barriers. We conclude that tortoises are persistent searchers and must be treated as experts at finding and exploiting barrier weaknesses. Burying fence bottoms is important because tortoises may exploit even a small gap between the bottom of a fence and the underlying soil. Reses et al. (2015) observed similar behavior by diamond-backed terrapins (*Malaclemys terrapin*). A depth of 15 cm in the ground seems sufficient to anchor a fence and prevent gap formation. An alternative to burying fence is folding flexible fence materials at the bottom toward the habitat side of the barrier and backfilling with soil. Barriers should be constructed outside of a “clear zone” defined by federal highway standards for traffic safety, which is 9 m from the roadway edge for relatively flat, high-speed roadways.

Our observation that male tortoises were more likely to escape than females (13 of 15 escapees were males) was not surprising based on other studies of tortoise behavior (Berry 1986; Ruby and Niblick 1994). Males tortoises reach larger body sizes than females and behave more aggressively than females. There may be a tendency for larger animals to escape although our sample of females was too small for analysis. Longer exposure times increased escape potential as our measured escape probability increased by a factor of 7 over 12 d. Careful construction measures and regular maintenance schedules are necessary to reduce the likelihood of escape through the barriers we used. It also represents a requirement for barriers in wetlands (Reses et al. 2015) or along highways crossing water ways (Aresco 2003; Heaven et al. 2019).

Our construction crew built the test enclosures more carefully than an average construction crew because they were aware of its intended use as a research tool. This has implications for design and construction of barriers along roadways, including 1) burying fences with no gaps at the bottom of barriers, 2) tight construction specifications so that no gaps occur in the barrier, 3) regular inspection of barriers during construction by an individual experienced with desert tortoise behavior to look for potential weaknesses, and 4) postconstruction, continued periodic inspections for locations that could be exploited by tortoises.

Our tests of necessary height identified a height needed to prevent climb-over escapes. Only 1 tortoise escaped at a height of 36 cm in the stacked-plank test and a few climb-over escapes in the barrier type × height tests occurred at 30 cm but none at 46 cm. This suggests that a minimum barrier height between 36 and 46 cm would be completely effective at precluding climb over escapes. In the stacked-plank experiment, planks placed one upon one another resulted in small ledges of a few millimeters wide between the planks because they did not fit perfectly and could allow tortoises to climb more effectively. This may have produced results that are material-specific but general agreement between the 2 types of tests suggests that if a material-specific effect is occurring, its magnitude is relatively small.

Perhaps the most important observation of other species’ interaction with the test barriers was absence of mortalities in 70 encounters. A total of 1960 m of barrier length was exposed 24 hrs/d for nearly 3 mo. Our incidental observations probably underestimate the number of encounters by resident vertebrates (both diurnal and nocturnal) with the barriers and we cannot rule out scavenging between observations. We had only 1 case of entrapment, a rate much lower than previous research (Ruby et al. 1994), which may have resulted from the different combination of barriers that we tested in this study. Both our field observations and our morphometric measurements indicate different types of barriers have significantly different effects on specific species. There were no obviously “lizard-friendly” designs because of the varying sizes of animals. The 1.9-cm diamond plastic mesh, 2.5 × 2.5-cm mesh, and 2.5 × 5.1-cm vertical mesh seemed most potentially hazardous for most lizard species. The fences with the largest gaps (5.1 × 5.1-cm and 5.1 × 10.2-cm vertical mesh) were potentially hazardous because they could trap larger lizard species but allow smaller or more slender species to enter the highway right-of-way. The 1.3-cm hardware cloth could be hazardous to smaller or more slender species such as *Callisaurus*, *Aspidoscelis*, and *Uta*, but relatively harmless to larger lizard species such as *Dipsosaurus*, *Gambelia*, and *Sceloporus* (Table 12). Similar but more clear-cut trends occurred with snakes (Table 12). The 1.9-cm diamond plastic mesh, 2.5 × 2.5-cm mesh, and 2.5 × 5.1-cm vertical mesh seemed to be the most hazardous for most

snake species. Fences with the largest gaps (5.1×5.1 -cm and 5.1×10.2 -cm vertical mesh) would not trap snakes and would permit them to pass and enter the highway right-of-way. Smallest mesh sizes seemed the most “friendly”, as all 4 snake species were retained by this material. Solid barriers like galvanized steel and plycrete prevent all reptiles from passing through and protect them from being run over. With larger wire mesh fences (5.1×5.1 or 5.1×10.2 cm), some larger reptile species could be caught but smaller species could pass through. Indeed, one of us (W.B.J., *pers. obs.*) rescued an adult *Coluber flagellum* that had become stuck in a hardware cloth fence elsewhere in the Mojave Desert. While the barrier does not induce mortality directly, large-mesh fences allow these species to pass through the barrier and be killed by vehicles. The smaller mesh sizes (1.3-cm hardware cloth, 1.9-cm plastic diamond, 2.5×2.5 cm, and 2.5×5.1 cm) could trap smaller reptile species but would not allow larger reptile species from passing through, thereby protecting part of the indigenous reptile population. No small mammal seemed impeded by our barriers. The tested barrier heights and materials would not directly harm squirrels but would not stop them from entering highway right-of-way zones either. Larger mammals such as coyote and kit fox would pass over the barrier.

Some larger wire mesh fences would not stop juvenile tortoises (MCL < 180 mm) based on morphometric measurements as they could escape through the openings (Table 13). The largest juvenile tortoises might be able to escape from 5.1×10.2 -cm mesh if they turn at a 90° angle, perpendicular to the ground. If they could not turn to 90° , then the 5.1×10.2 -cm and 5.1×5.1 -cm mesh have an identical maximum escape size. The largest individual that could escape from a 2.5×5.2 -cm mesh fence is 48 mm, roughly the size of a hatchling tortoise. No tortoise of any size can pass through the 2.5×2.5 -cm mesh fence. We have no data on the frequency of juvenile tortoises approaching a barrier but a general relationship exists between tortoise size and mobility. The likelihood of smaller animals, which move less, encountering a barrier is lower than that of a larger animal. Juvenile animals have less effect on the evolutionary stability of the population than larger animals (Heppell et al. 1996; Heppell 1998) because adult survival, particularly of females, is most important for maintaining population size.

Fencing along roads may restore useful habitat (Fowle 1996; Berry et al. 2020) and reduce mortality across roadways where nesting migration or local movement puts animals at risk (Reses et al. 2015). The trade-off for barriers is that roads also segregate and subdivide local populations and reduce or prevent genetic exchange that would otherwise occur in the evolution of the species. Roads without fencing may still divide populations that are reluctant to cross even small roads and result in extirpation given enough time (Peadan et al. 2017). More information is needed on usage of corridors or passages under roads and methods to direct animals to these structures

(Lesbarreres and Fahrig 2012). Culvert use has been documented in the desert tortoise (Fusari 1982; Boarman 1995) as well as other species of turtles (Aresco 2005; Markle et al. 2017; Heaven et al. 2019; Read and Thompson 2021; Waltham et al. 2022). However, use of culverts by desert tortoises can cause mortality (Lovich et al. 2011). To determine the long-term effectiveness of fences and culverts for retaining or directing tortoises and other species of turtle, researchers must consider the specific requirements of the species for spatial usage, movement, nesting migration, and other biological needs. If fencing is not effective, poorly maintained, or only partial in coverage, animals may choose to utilize gaps or holes in exclusion structures rather than the ecopassages available (Baxter-Gilbert et al. 2015) or travel to where fencing ends (Markle et al. 2017). Long-term observation and maintenance of fencing structures are necessary to determine the effectiveness of the barriers with time (Berry et al. 2014).

ACKNOWLEDGMENTS

Funding support was provided by the Clark County (Nevada) Short-term Habitat Conservation Plan (HCP) and administered by Clark County, primarily by C. Robinson. The study was conducted at the DTCC, a facility managed by the Bureau of Land Management (BLM). The Las Vegas District Office of BLM, particularly S. Slone and M. Berkowitz, allowed use of the facility. Michelle Berkowitz also provided tortoises for the experiment. C. La Bar, R. Williams, R. Watkins, and D. Syzdek with Southern Nevada Environmental, Inc., provided Clark County-managed tortoises for our experiments.

The members of the Clark County HCP Planning and Implementation Committee provided many ideas, suggestions, and critical review of this project. We received informal critical review of the project from H. Avery, K. Berry, W. Boarman, and J. Lovich. P. Medica and T. Duck provided specific ideas for barrier materials.

Our dedicated research crew included M. Beach, K. Folk, A. Klatzker, and T. Street and our innovative construction team: P. Frank (leader), E. Green, R. Woodard, and P. Woodman. The project was approved by the Institutional Animal Care and Use Committee of Drexel University.

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Received: 2 December 2021

Revised and Accepted: 2 February 2023

Published Online: 31 May 2023

Handling Editor: Jeffrey E. Lovich