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Stopped Dead in Their Tracks: The Impact of Railways on Gopher Tortoise (*Gopherus polyphemus*) Movement and Behavior

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Habitat fragmentation is one of the leading causes of biodiversity decline and most commonly results from urbanization and construction of transportation infrastructure. Roads are known to negatively impact species, but railways can often cause similar effects. Certain taxa, such as turtles and tortoises, are more vulnerable to railways than others due to limitations in mobility. We studied the impact of rails on the movement and behavior of Gopher Tortoises (*Gopherus polyphemus*), a threatened, highly terrestrial species likely in frequent contact with railways. First, we used radio-telemetry to determine the frequency of railway crossings and compared this to correlated random walk (CRW) simulations to assess if tortoises were crossing the rails less frequently than is expected by unconstrained movement. Second, we placed tortoises into the railway and measured behavior for one hour to assess crossing ability. Lastly, we tested whether trenches dug underneath the rails could allow safe passage for tortoises. We found that railways impacted the movement of Gopher Tortoises. Gopher Tortoises crossed the railway less often than what would be expected by unhindered movement for five of our ten tortoises tracked. During behavioral trials, 0 of 24 tortoises placed within the railways were capable of escaping from the rails. Using game cameras, we detected tortoises using trenches dug underneath the rails and between the ties 68 times over the course of a single summer. For minimal financial cost, the trenches facilitated tortoise movement across the railway, maintained full rail functionality, and created an escape route for individuals that were trapped between the rails, and thus should be implemented as a mitigation strategy. Given the thousands of km of railways around the world, we recommend future studies focus on the new field of rail ecology.

HABITAT degradation and fragmentation are the largest causes of biodiversity decline due to reduction and isolation of habitat, restriction of animal movement, and exposure to an anthropogenically homogenized landscape (Saunders et al., 1991; Andrén, 1994; Collinge, 1996; McKinney, 2006; Haddad et al., 2015). Roads, in particular, are well documented to cause habitat fragmentation and negatively impact species (Forman and Alexander, 1998; Forman and Deblinger, 2000; Forman et al., 2003; Rytwinski and Fahrig, 2015). However, other barriers may have similar effects that remain understudied. Railways, for example, have been shown to impede movement and increase mortality in some species (mainly ungulates and bear), giving rise to the field of rail ecology (Dorsey, 2011; Dorsey et al., 2015; Heske, 2015; Popp and Boyle, 2017). Not only are wildlife at risk of collisions with trains, but railways also present unique risks such as electrocution and even entrapment in both active and inactive railways (Dorsey et al., 2015). Despite these unique, but clearly identified risks, little research has been done in the field of rail ecology for many taxa and, between the years of 1990 and 2014 across 14 different journals, only 17 rail ecology-focused articles have been published—15 times less than the number of road ecology-focused articles (Dorsey et al., 2015; Popp and Boyle, 2017).

Turtles and tortoises, in particular, appear to be heavily impacted by railways due to limited mobility and flexibility (Kornilev et al., 2006; Engeman et al., 2007; Iosif, 2012; Popp and Boyle, 2017). Kornilev et al. (2006) determined that Eastern Box Turtles (*Terrapene carolina*) were incapable of traversing the rails due to their small size. They noted that turtles could reach the top of the rail while standing erect on their hind limbs, but only one turtle successfully pulled itself over (Kornilev et al., 2006). Relatedly, Hermann's Tortoises (*Testudo hermanni)* were found to exhibit high mortality rates along railways (Iosif, 2012). Most recently, Heske (2015) noted that railways may be acting as a barrier to movement for small turtles. Turtles infrequently cross tall barriers; instead they patrol barriers in search of passage (Ruby et al., 1994; Peaden et al., 2017). Regardless of the influence of these barriers on turtles and tortoises, turtle-oriented railway management has been limited to a single study on Spotted Turtle (*Clemmys guttata*) crossings in Massachusetts (Pelletier et al., 2006). This study recorded only 16 crossing events over the course of two years, largely by the same few individuals (Pelletier et al., 2006). Overall, these studies suggest that railways may be an impediment to turtle movement, but no studies have explicitly examined railway crossing frequency, the impacts of railways on turtle movement and behavior, or thoroughly tested management actions that could reduce mortality.

Here we study the impact of railways on Gopher Tortoises (*Gopherus polyphemus*). This species is highly terrestrial and, given that there are over 18,200 km of railway throughout their range, they are likely to be in frequent contact with railways. Engeman et al. (2007) documented that *G.*

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polyphemus are frequently found between rails and face increased mortality due to becoming trapped, overheated, and dehydrated. *Gopherus polyphemus* are considered threatened in every state in which they are found and are a candidate species for federal listing in the USA. They are experiencing continued population decline from habitat loss and fragmentation, and finding ways to connect isolated populations may increase population sizes (Auffenberg and Franz, 1982; Enge et al., 2006). Gopher Tortoises function as ecosystem engineers throughout the Southeastern Coastal Plain in the USA by digging burrows that serve as refuges for themselves and over 360 documented commensal species, many of which are also protected (e.g., Eastern Indigo Snake [*Drymarchon couperi*], Pine Snake [*Pituophis melanoleucus*], and Gopher Frog [*Rana capito*]; Young and Goff, 1939; Jackson and Milstrey, 1989; Lips, 1991; Witz et al., 1991; Kent and Snell, 1994). Insight into the impacts of railways on *G. polyphemus* may assist conservation efforts in properly managing railways to conserve this flagship species, their commensals, as well as other turtle species.

The aims of this study were to (1) measure the frequency of railway crossings by *G. polyphemus* to determine if railways function as a barrier to movement, (2) to assess the physical ability of tortoises to cross railways and identify potential behavioral differences related to the local familiarity with railways, and (3) evaluate a management technique that could be used to alleviate the fragmenting effects of railways on populations. First, we hypothesized that railways would act as a barrier to movement. We used radio-telemetry to compare each individual's movements and number of crossing events to those predicted by randomized movement patterns. Second, we hypothesized that tortoises would not be able to cross the railways and that tortoises habituated to the railway would display more behaviors attempting to cross than those naïve to the railway. We used observational behavior trials to assess crossing ability and to determine if individuals found near the railways would be more likely to cross than those unfamiliar with such obstacles. Lastly, we tested if trenches dug between railway ties would effectively allow movement across the railway. To do this, we monitored trenches along the railway using game cameras to record crossing events.

MATERIALS AND METHODS

We conducted our study on and around an inactive railway in coastal strand habitat of the John F. Kennedy Space Center (KSC) in east-central Florida, USA. Despite being inactive, turtle entrapment and mortality is common along these rails, especially with *G. polyphemus* (M. R. Bolt, pers. obs.). The railway is enveloped by sand dunes at the northern end of the study area and crossed by a road to the south ends of the study site. These areas likely make crossing the railways much easier as they provide "bridges" over the railways, thereby increasing the chance of the present study not detecting a barrier effect when one actually exists (false negative; type II error) and placing a conservative bias on our results. All tortoises in this study were captured by hand, marked using standardized marginal scute hole-drilling procedures, and their carapace and plastron lengths were measured (Ernst, 1974). Sex was determined from external plastron shape, with males having a high degree of plastron concavity (McRae et al., 1981a). Only adults classified as greater than 23 cm carapace length for males or 24 cm for females were used in this study (Landers and McRae, 1982).

Radio-telemetry.—Between May 2015 and July 2016, Advanced Telemetry Systems R1930 transmitters (24 g; 40 pulses per minute) were used to track a total of ten adult tortoises (4 female: 6 male) found along the stretch of inactive railway. Transmitters were attached to the junction of anterior marginal and costal scutes by roughening both the shell and transmitter with sandpaper, cleaning the area with an alcohol swab, and placing the transmitter on the carapace of the tortoise. The transmitter was covered and adhered using West Marine Epoxy Putty Sticks (West Marine #3761483), and the antenna was wrapped around the marginal scutes of the carapace and adhered to the posterior marginal scutes using the epoxy.

Following transmitter attachment, tortoises were released at their original capture location and tracked by hand using a Telonics TR-4 receiver and RA-2AK H-antenna. Tracking occurred five days a week for approximately nine weeks to assess the frequency of railway-crossing events. Tracking was then reduced to once per week for the following year to capture potential long-term crossing events. Tortoises were tracked a total of 805 times, averaging 81 tracking events per individual. All individuals were tracked between 0600 and 1800 h. Once located, GPS coordinates were recorded using a handheld Garmin Oregon 450, and the side of the railway on which the tortoise occurred (i.e., east or west) was recorded. The observed number of crossing events was counted for each tortoise (Table 1).

For each tortoise, 1000 Monte Carlo correlated random walk (CRW) simulations were generated in the package 'adehabitatLT' in R to simulate movement (Calenge, 2006; Calenge et al., 2009; R Core Team, 2017). Simulations began at the initial capture location of each tortoise to ensure simulations fell within the tortoises' home range. The CRWs randomized the direction of movement between tracking events while maintaining the distance. Movement was confined to the coastal strand study area of KSC because no tortoise was ever recorded outside of this spatial extent. However, one tortoise (#5219) made such large movements between tracking events that simulations could not be contained to the same study area used for the other tortoises. For this tortoise, the study area was increased by 200 m to the east and west as this was the minimum area capable of containing the movements made by this tortoise. Doing this included habitats not used by tortoises (such as the ocean and marshes) but also induced a cautious bias on these simulated trials, as including areas farther away from the railways also decreased the likelihood of the tortoise crossing the railway during simulations.

The number of railway crossing events was counted for each simulation, and a distribution of predicted crossings was built for each individual. To determine if an individual avoided or was incapable of crossing the railways, we assessed if the observed number of railway crossings was significantly less (one-tailed) than the expected distribution built from the CRWs using a permutation test with the function 'as.randtest' in the package ade4 in R (Dray and Dufour, 2007; Shepard et al., 2008; R Core Team, 2017).

Behavior and crossing ability.—To test the ability of *G. polyphemus* to cross/escape from railways and for differences in behavior based on their familiarity with the railway, we measured behavior via continuous focal sampling for one hour on a total of 36 adult tortoises (19 female: 17 male). After capture, tortoises were grouped evenly into three categories: Habituated, Naïve, or Control. Habituated tortois-

Table 1. Radio-tracked tortoises with the observed and mean expected number of railway crossings based on Monte Carlo correlated random walk simulations. Tortoises that crossed the railway significantly less than expected by unconstrained movement have *P*-values less than 0.05. CL = carapace length.

ID #	Sex	CL (cm)	# Tracking events	Observed crossings	Predicted crossings Mean	Predicted crossings Range	*P*
3116	Female	28.1	95	1	7.46	1–27	0.06
5233	Female	28.6	92	1	8.02	1–21	0.01**
5226	Female	24.6	51	0	4.38	0–20	0.13
5234	Female	30.5	92	0	8.72	0–29	0.01**
5224	Male	27.4	85	7	10.65	0–23	0.19
5219	Male	25.1	94	3	8.49	1–22	0.05*
5218	Male	25.7	50	1	8.49	0–20	<0.01**
5009	Male	31.5	66	0	2.94	0–24	0.39
5227	Male	29.1	92	0	5.41	0–22	0.12
5239	Male	27.7	88	0	10.86	0–29	<0.01**

es (7 female: 5 male) were those tortoises found between the rails or less than 100 m from the rails. The average distance from the rails for Habituated tortoises was 24 m (range: 0–78 m). These tortoises were assumed to be familiar with the railway and potentially have experience in crossing them. Naïve tortoises (6 female: 6 male) were those located greater than 100 m from the rails. This distance was chosen based on three criteria. First, Gopher Tortoises are known to rarely move more than 100 m from their home burrow as this range constitutes their secondary foraging distance (Ashton and Ashton, 2008). Secondly, with the telemetry data from the tortoises in this study ($n = 10$), we observed that no tortoise moved greater than 100 m perpendicular from the railway. Lastly, a concurrent study (Rautsaw et al., in press) found that tortoises from the nearby roadside habitat where Naïve tortoises were captured rarely migrate into the coastal strand habitat even at short distances. In reality, Naïve tortoises were captured at an average distance of 1,054 m from the rails (range: 126–3,168 m). This group of tortoises was assumed to be unfamiliar with railways and inexperienced in crossing them. An additional independent set of 12 tortoises was used as a control group. Control tortoises (6 female: 6 male) consisted of tortoises found within the distance ranges of both Habituated and Naïve groups with an average distance from the rails of 467 m (range: 4–3,036). However, unlike the previous groups, the behavior of these tortoises was not measured in railways but instead in a control scenario described below.

To control for biases and stress-induced behaviors associated with capture and processing, all tortoises were held indoors overnight and tested the following morning. Trials were standardized between 0700 h and 0900 h in May 2016 to avoid high temperatures and control for tortoise activity periods. Habituated and Naïve tortoises were moved to and tested in a 20 m stretch of the railway void of vegetation or other objects that could be used as leverage for crossing the rails (Fig. 1A). Vegetation along active railways is often controlled using herbicide spraying; therefore, choosing an inactive section of the railway devoid of vegetation represents the type of railways wildlife is more likely to encounter. Control tortoises were moved to and tested in a flat, grassy area of equal size. The control area was bordered with 2.5 cm x 2.5 cm wooden blocks laid on the ground to form a visual stimulus that may dissuade tortoises from crossing, but should not hinder physical movement (Fig. 1B). The goal of using the control group was to demonstrate that movement was clearly hindered by the presence of the railway. All tortoises were observed and behavior recorded for one hour (or until they crossed their respective barrier) at approximately ten meters, which did not alter the tortoise's behavior. Tortoises often walked towards the observers and did not retreat into their shells at this distance. Trials began after a five-minute acclimation period or when the tortoises began moving. During the allotted hour, behavior was recorded continuously using Neukadye Field Data mobile application on an Apple iPhone or iPad (Seigel, 2016). Recorded behaviors included: meandering, stationary, eating, hiding, digging, attempting to cross, flipped, and the amount of time remaining in a trial after a tortoise escaped their given plot (escaped time; Appendix 1). Additionally, the number of failed crossing attempts was recorded. After the trial, tortoises were returned to their original capture location. For each individual, the amount of time spent on each behavior was summed. The three groups (i.e., Habituated, Naïve, and Control) were compared using a principal component analysis (PCA) with 95% confidence ellipses in R.

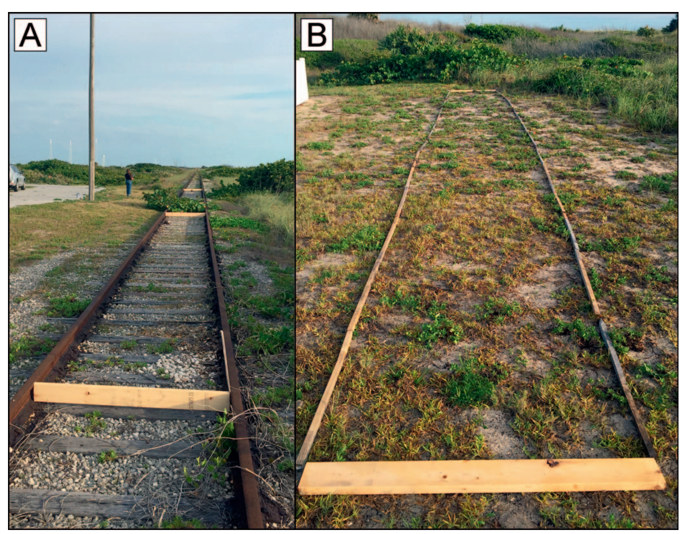

Fig. 1. (A) The 20 m railway plot in which Gopher Tortoises were tested for crossing ability and behavioral differences between Habituated ($n = 12$) and Naïve ($n = 12$) railway familiarity. (B) The control plot in which tortoises ($n = 12$) were tested for crossing ability and behavioral differences solely on the presence of a visual barrier.

Fig. 2. (A) The trench dug underneath the rails and between the railway ties. A game camera faces the entrance/exit on the west side of the railway to photograph Gopher Tortoises passing from one side to the other. (B) A series of pictures of a single Gopher Tortoise moving from the east side of the tracks to the west side.

Mitigation testing.—Several management strategies exist to help wildlife cross road barriers including tunnels, bridges, and ladders (Dodd et al., 2004; Aresco, 2005; Woltz et al., 2008; Baxter-Gilbert et al., 2015; Sievert and Yorks, 2015). While the most effective solution is to remove the barrier completely, this is often not feasible. Here, we wanted to test a management strategy to encourage tortoise movement across railways and aid in the escape of trapped tortoises while maintaining full railway functionality. A bridge over the railway or tunnel under would be expensive to build, interfere with trains moving along the rails, and would not facilitate escape for entrapped tortoises. In contrast, trenches dug under the rails and between the railway ties are easy and cheap to construct and they maintain full railway functionality as the trenches were designed by the Massachusetts Bay Transportation Authorities (MBTA; Pelletier et al., 2006; Dorsey et al., 2015). Subsequent monitoring by MBTA revealed an infrequent use by a small number of Spotted Turtles (*Clemmys guttata;* Pelletier et al., 2006). However, trench effectiveness has not been empirically tested on a species known to be frequently impacted by railways.

To determine if this management strategy would encourage movement of tortoises, we dug two trenches separated by approximately 700 m along the railway at locations known to have high tortoise density and frequent mortality events between the rails based on previous studes and personal experience in the area (Martin et al., 2017; M. R. Bolt, pers. obs.). One Bushnell Natureview HD Max Game Camera (Bushnell 119439, Overland Park, KS) was placed on the west side of each trench facing the rails (Fig. 2). Photos were downloaded approximately once per week between 30 May 2016 and 30 August 2016 for a total of 184 trap days (92 per camera). Individual identity could often be discerned from size, shape, or markings on the animal. However, for individuals unable to be uniquely identified, photos had to be separated by at least 30 minutes to be considered unique events. Data was manipulated in R (R Core Team, 2017) using the package "camtrapR" (Niedballa et al., 2017). To establish actual trench use, for each photo we recorded whether the animal moved through the trench or only passed by the camera. Using these data, we determined the proportion of tortoises that were identified as using the trenches. Additionally, we determined the encounter rate of tortoises detected along the rails per day and the number of tortoises that used the trenches per day.

RESULTS

Radio-telemetry.—Tortoises were observed crossing the rails a total of 13 times, averaging 1.3 crossings per tortoise. However, most of the crossings (10 of 13 crossings) were restricted to two highly mobile males (#5224 and #5219; Table 1). Overall, expected crossings estimated from Monte Carlo simulations ranged from 0 to 29 crossings, depending on the tortoise, with an average of 7.54 expected crossings per tortoise. All tortoises had higher expected values than observed values, and observed values were significantly less than expected in five of ten tortoises, while several neared significance (Table 1). For example, the observed number of crossings for tortoise #5233 was significantly less than was expected (Fig. 3).

Behavior and crossing ability.—Of the 24 tortoises tested in the railway from both Habituated and Naïve groups, none successfully crossed the rails during the allotted hour. Multiple attempts were made to escape from the railway, with a median value of 12.5 failed crossing attempts per tortoise (range: 0–78 attempts). Two tortoises flipped over onto their carapaces through the duration of the trial; one

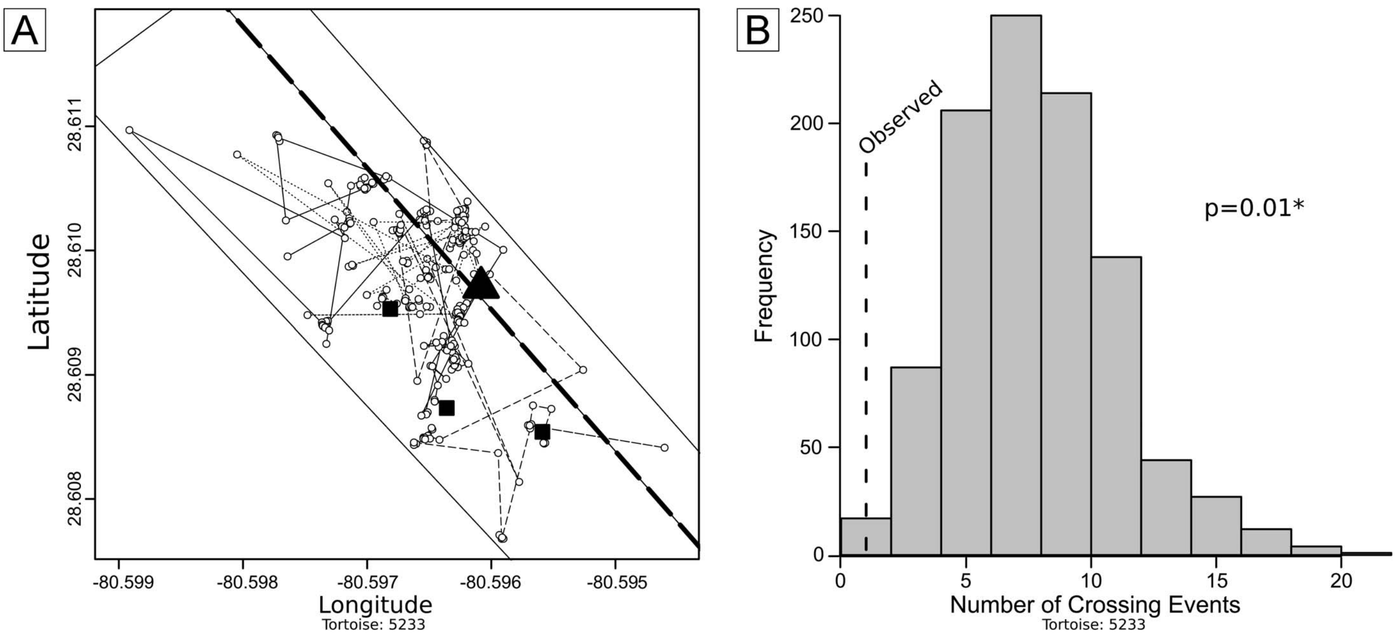

Fig. 3. (A) Three simulated correlated random walks (CRWs) by a single tortoise (ID: 5233) confined to the coastal strand habitat. Each simulation is a different patterned line with the start point designated by the triangle (▲) and the stop points designated by squares (■). Each simulation counted the number of times the tortoise crossed the railway (represented by the thick dotted line). (B) Histogram of the number of expected railway crosses based on 1000 simulated CRWs by a single tortoise (ID: 5233). The observed number of crosses is plotted with the dotted line and is significantly below the expected number of crosses.

was able to right itself after 732 s, but the other remained flipped until the trial's completion, 931 s later. In comparison, Control tortoises crossed their barrier in an average of only 137 s. Only one Control tortoise spent a large enough amount of time attempting to cross the barrier to warrant recording the behavior; the remainder of the tortoises easily crossed the barrier without pause and therefore their only behavior recorded was meandering. As the Control tortoises crossed the barrier in a very short amount of time, the remaining time was recorded as escaped time. This was also shown in the PCA as PC1 accounted for 88.6% of the behavioral variation and was largely made up of the differences in escaped time between the Control tortoises and the other two groups (Habituated and Naïve; Fig. 4). PC2 mainly consisted of variation in the amount of time spent meandering or stationary, but only accounted for 8.8% of the variation. Interestingly, no behavioral differences were observed between Habituated and Naïve tortoises as there was near complete overlap in their 95% confidence distributions (Fig. 4).

Mitigation testing.—Trenches connecting the east and west sides of the railway began to be used by *G. polyphemus* only four days following their installation (Fig. 2B). Over the course of 184 trap days (92 per camera), we detected tortoises moving along the rails on a total of 96 independent occasions with an encounter rate of 0.52 detections per day. For 68 (70.83%) of these detections, tortoises were identified using the trenches to move from one side of the rails to the other, 12 (12.50%) only passed by the camera, and the remaining 16 (16.67%) had insufficient data to confidently determine if they used the trench. There was an average of 0.36 detections per day of tortoises confidently identified as using the trench. While 16 capture events had photos too out of focus to identify individuals, we were able to identify at least 28 unique individuals moving along the railway from the remaining 80 capture events based on a combination of size, shell patterns, shell shape, and forelimb scalation.

DISCUSSION

Our results demonstrate that railways can act as a barrier for *G. polyphemus*. Our data confirm that tortoises found between rails are likely trapped and, as such, could become dehydrated and perish in the railway as none of our tortoises successfully escaped the railways during the behavioral trials. Additionally, from ten radio-tracked tortoises, we observed only 13 crossing events over the course of a year. Most of the observed crossings were isolated to two male individuals. This was expected as males are known to move larger distances (McRae et al., 1981b; Smith et al., 1997; Eubanks et al., 2003), but prior to an observed crossing, tortoises were often located near the north or south boundaries of our study area where crossing was likely easier due to the sand dunes and roads providing "bridges." It can be seen that the proximity to these areas increases directly before crossing (Supplemental Fig. 1; see Data Accessibility). Crossing events likely occurred at these bridge areas, but actual crossing location could not be ascertained. Successful crossings may have also occurred where there was sufficient vegetation to obtain the leverage needed to traverse the rails. However, active railways are likely to be well maintained and vegetation cleared for locomotives and increased visibility for larger animals to reduce mortality (Jaren et al., 1991; Dorsey et al., 2015).

Given the "bridge" locations at our study site and that the railway is poorly managed with patches of vegetation crossing the railway in some locations, there is an increased likelihood that our study may not detect a barrier effect when one does, in fact, exist. Despite having an increased likelihood of a false negative (type II error), railways were crossed significantly less than expected for five of ten tortoises, with all tortoises having lower observed values

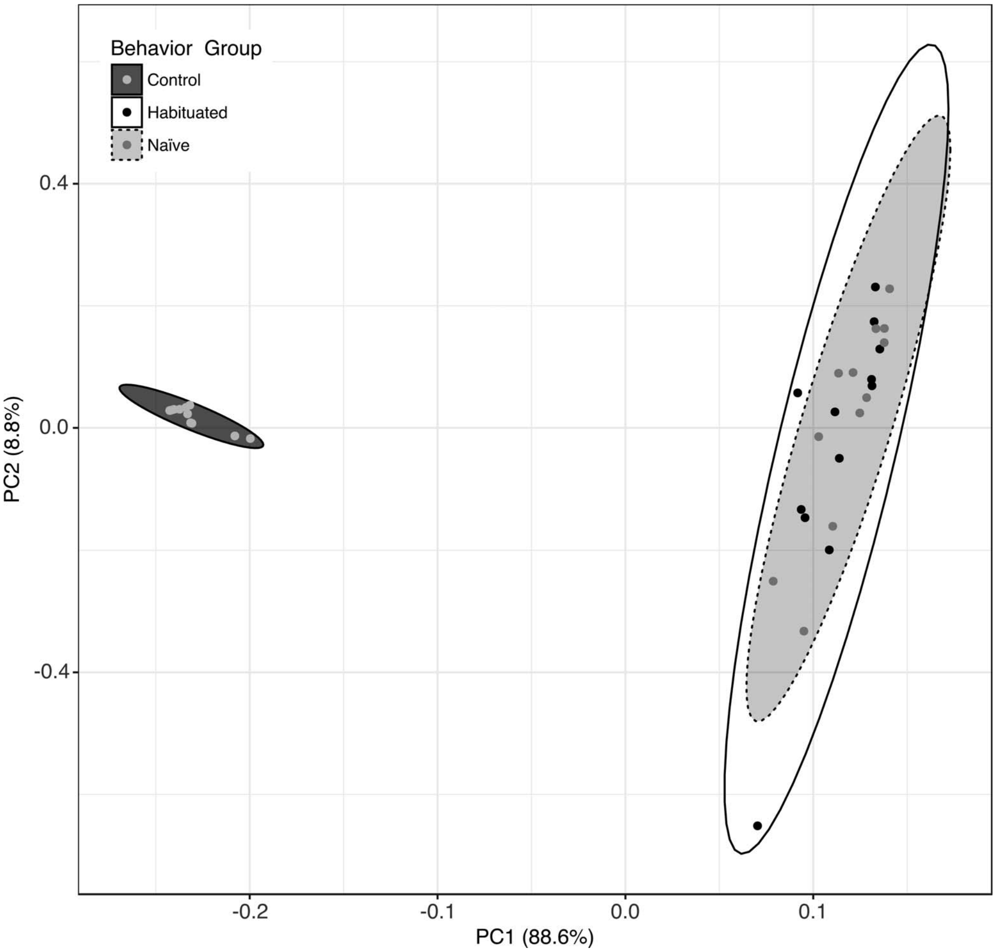

Fig. 4. Principal component analysis (PCA) with 95% confidence ellipses comparing tortoise behavior expressed over a one-hour observation period. Confidence ellipse fills are based on railway familiarity in addition to the control group. Control tortoises fall well outside the multivariate space of tortoises placed in the railway, demonstrating the inability of tortoises to cross railways.

than what was expected by the CRWs, demonstrating a clear hindrance of movement. While the seaward side of the railway at KSC has less habitat and lower tortoise density than the inland side (Martin et al., 2017), it is abundant in food and inland tortoises are often observed attempting to reach the seaward side. Gopher Tortoises are very active and frequently move among burrows (McRae et al.,1981b; Smith et al., 1997; Eubanks et al., 2003); therefore, we believe our simulations accurately depict tortoise movement in the absence of a barrier.

Over the one-hour trial periods, only Control tortoises were able to cross their barriers. This is expected as the visual barrier presented to Control tortoises was much shorter (2.5 cm) than the railway rail (15 cm). Additionally, no behavioral differences were observed among the 24 tortoises of varying railway familiarity, suggesting that familiarity does not impact a tortoise's behavior; tortoises will exhibit the same behavior to try to escape from the railway regardless of prior experience. While tortoises were able to stand erect on their hind limbs, with their forelimbs on or over the rails, they were unable to obtain leverage or pull themselves over to escape. On average, each tortoise placed within the rails failed to pull itself over the rails approximately 12.5 times. Our plots used for behavioral trials for Habituated and Naïve tortoises (Fig. 1A) were blocked at 20 m length by 5 cm x 15 cm framing lumber (i.e., a box was formed with the rails and the lumber) to prevent further movement within the rails. These secondary barriers gave tortoises two perpendicular walls they could use as leverage to climb out. Almost all attempted crossing events occurred at these locations, yet none of the 24 Habituated or Naïve tortoises were able to escape the railways. Despite the large size of Gopher Tortoises when compared to Box Turtles, our results corroborate those found by Kornilev et al. (2006) that railway crossing and escape are unlikely occurrences.

Despite the recent removal of the railway north of our study site, tortoise carcasses are still regularly found between the rails (M. R. Bolt and R. Rautsaw, pers. obs.), demonstrating a clear impact. When presented with a barrier, *Gopherus* have been shown to patrol the barrier in search of a passageway through or around the barrier (Ruby et al., 1994; Peaden et al., 2017). Gopher Tortoises in our study paced around the perimeter of the plot in search of an escape route, supporting the findings of Ruby et al. (1994). Well-maintained railways extend for hundreds of kilometers through the state and likewise may act to completely fragment populations of turtles. While other factors are likely larger contributors to habitat fragmentation, railways will disrupt the natural dispersal patterns and migration dynamics as well as social behaviors between opposite sides of the railway. These consequences may be amplified the longer that populations are separated. Given the results from our radio-telemetry and behavioral trials, we predict that nearly all tortoises in the vicinity of railways are susceptible to becoming entrapped or experiencing reduced movement and dispersal. Since there are no behavioral means for tortoises to adjust to railways, management is needed to alleviate the impacts railways are having on tortoises.

Trenches not only provide means of population connectivity across railways, but also an escape route for entrapped tortoises. The trenches we dug underneath the rails and between the railway ties were heavily used by *G. polyphemus*, with a tortoise recorded using a trench once every 2.7 days. One tortoise was captured on camera falling from the center of the rails into a trench, enabling it to escape. Photos show this tortoise was foaming at the mouth and likely suffering from dehydration as the temperature recorded by the camera at the time was 48°C. Unfortunately, no other turtle species were encountered using the trenches, but *T. carolina* are frequently encountered along and trapped within the railway and would likely be encountered given a longer survey period (M. R. Bolt and R. Rautsaw, pers. obs.). Implementation of railway tie trenches may reduce the negative effects associated with fragmentation, population isolation, and small population sizes to increase population viability of this state-threatened species and its commensal counterparts. Additionally, other species of turtle were frequently observed deceased in the railways including Eastern Box Turtles (*T. carolina*), Chicken Turtles (*Deirochelys reticularia*), and Florida Softshells (*Apalone ferox*; M. R. Bolt and R. Rautsaw, pers. obs.). In combination with previous studies and reports which have found increased mortality and an inability to cross railways, our results and personal observations of other turtle species carcasses in the railways suggest this issue transcends *Gopherus* (Kornilev et al., 2006; Iosif, 2012). Lastly, for managers, the trenches are easily put in place by digging out the sediment or rocks between two railway ties to allow enough room beneath the rail for a tortoise to walk normally through. This can be estimated using the average height of tortoise burrows in the area. The trenches take only an hour to dig using a shovel, but many could be put in place in a much shorter amount of time with more efficient construction equipment.

Railways are a common occurrence across the globe. Within the range of *G. polyphemus* alone, there are approximately 18,200 km of railways that could be potentially impacting this species, and there are over 50 turtle species throughout the United States, which may lead to a much larger impact at a taxonomic scale as turtles are one of the most at risk clades to disturbance-induced impacts (Congdon et al., 1993). Furthermore, railways are less common in the United States than in other parts of the world such as Europe and Asia, where thousands of kilometers of railways are likely impacting turtle populations. More research on rail ecology is needed in these regions in particular to determine to what degree railways are impacting wildlife. Further studies are needed to identify which species are under the highest risk of becoming entrapped in railways and whether they would benefit from the implementation of trenches between railway ties. Additionally, indirect effects such as avoidance behavior to active railways remain untested. Lastly, as high speed railways become increasingly common, they are likely to impact wildlife differently than freight rails (Dulac, 2013). The field of rail ecology needs to expand to elucidate the impacts of both freight and high-speed railways on not only turtles, but a plethora of other wildlife as well (Dorsey et al., 2015; Popp and Boyle, 2017).

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DATA ACCESSIBILITY

Telemetry, behavior, and game camera data are available in Mendeley Data (DOI: 10.17632/x29nms6yr6.1) along with the R script used to trim and analyze the data. Supplemental Figure 1 is available at http://www.copeiajournal.org/ce-17-635.

LITERATURE CITED

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Aresco, M. J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549–560.

Ashton R. E., and P. S. Ashton. 2008. Natural history and management of the Gopher Tortoise *Gopherus polyphemus* (Daudin). Krieger, Malabar, Florida.

Auffenberg, W., and R. Franz. 1982. The status and distribution of the Gopher Tortoise (*Gopherus polyphemus*), p. 95–126. *In*: North American Tortoises: Conservation and Ecology. R. B. Bury (ed.). United States Fish and Wildlife Service, Washington, D.C.

Baxter-Gilbert, J. H., J. L. Riley, D. Lesbarrères, and J. D. Litzgus. 2015. Mitigating reptile road mortality: fence failures compromise ecopassage effectiveness. PLOS ONE 10:e0120537.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calenge, C., S. Dray, and M. Royer-Carenzi. 2009. The concept of animals' trajectories from a data analysis perspective. Ecological Informatics 4:34–41.

Collinge, S. K. 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. Landscape and Urban Planning 36:59–77.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Dodd, C. K., Jr., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

Dorsey, B., M. Olsson, and L. J. Rew. 2015. Ecological Effects of Railways on Wildlife, p. 219–227. *In*: Handbook of Road Ecology. R. van der Ree, D. J. Smith, and C. Grilo (eds.). John Wiley & Sons, Ltd, Chichester, UK.

Dorsey, B. P. 2011. Factors affecting bear and ungulate mortalities along the Canadian Pacific Railroad through Banff and Yoho National Parks. Unpubl. master's thesis, Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana.

Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Dulac, J. 2013. Global land transport requirements: estimating road and railway infrastructure capacity and costs to 2050. International Energy Agency, Paris.

Enge, K. M., J. E. Berish, R. Bolt, A. Dziergowski, and H. R. Mushinsky. 2006. Biological Status Report: Gopher Tortoise (*Gopherus polyphemus*). Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Engeman, R. M., H. T. Smith, and G. S. Kaufmann. 2007. *Gopherus polyphemus* (Gopher Tortoise) Mortality. Herpetological Review 38:331–332.

Ernst, C. H. 1974. A new coding system for hardshelled turtles. Transactions of the Kentucky Academy of Science 35:27–28.

Eubanks, J. O., W. K. Michner, and C. Guyer. 2003. Patterns of movement and burrow use in a population of Gopher Tortoise (*Gopherus polyphemus*). Herpetologica 59:311–321.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology 14:36–46.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. L. France, C. R. Goldman, K. Heanue, J. Jones, F. Swanson, T. Turrentine, and T. C. Winter. 2003. Road Ecology: Science and Solutions. Island Press, Washington, D.C.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–9.

Heske, E. J. 2015. Blood on the tracks: track mortality and scavenging rate in urban nature preserves. Urban Naturalist 4:1–13.

Iosif, R. 2012. Railroad-associated mortality hot spots for a population of Romanian Hermann's Tortoise (*Testudo hermanni boettgeri*): a gravity model for railroad-segment analysis. Procedia Environmental Sciences 14:123–131.

Jackson, D. R., and E. G. Milstrey. 1989. The fauna of Gopher Tortoise burrows, p. 86–98. *In*: Proceedings of the Gopher Tortoise Relocation Symposium. J. E. Diemer, D. R. Jackson, J. L. Landers, J. N. Layne, and D. A. Woods (eds.). Nongame Wildlife Program Technical Report No. 5. Florida Game and Fresh Water Fish Commission, Gainesville, Florida.

Jaren, V., R. Andersen, M. Ulleberg, P. H. Pedersen, and B. Wiseth. 1991. Moose-train collisions: the effects of vegetation removal with a cost-benefit analysis. Alces 27: 93–99.

Kent, D. M., and E. Snell. 1994. Observations of vertebrates associated with Gopher Tortoise burrows in Orange County, Florida. Florida Field Naturalist 22:8–10.

Kornilev, Y. V., S. J. Price, and M. E. Dorcas. 2006. Between a rock and a hard place: responses of eastern box turtles (*Terrapene carolina*) when trapped between railroad tracks. Herpetological Review 37:145–148.

Landers, J. L., and W. A. McRae. 1982. Growth and maturity of the Gopher Tortoise (*Gopherus polyphemus*) in southwestern Georgia, USA. Bulletin of the Florida State Museum of Biological Sciences 27:81–110.

Lips, K. R. 1991. Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in southcentral Florida. Journal of Herpetology 25:477–481.

Martin, S. A., R. M. Rautsaw, R. Bolt, C. L. Parkinson, and R. A. Seigel. 2017. Adapting coastal management to climate change: mitigating our shrinking shorelines. The Journal of Wildlife Management 81:982–989.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

McRae, W. A., J. L. Landers, and G. D. Cleveland. 1981a. Sexual dimorphism in the Gopher Tortoise (*Gopherus polyphemus*). Herpetologica 37:46–52.

McRae, W. A., J. L. Landers, and J. A. Garner. 1981b. Movement patterns and home range of the Gopher Tortoise. American Midland Naturalist 106:165–179.

Niedballa, J., A. Courtiol, and R. Sollmann. 2017. camtrapR: camera trap data management and preparation of occupancy and spatial capture-recapture analyses. R package version 0.99.9. https://CRAN.R-project.org/package=camtrapR

Peaden, J. M., A. J. Nowakowski, T. D. Tuberville, K. A. Buhlman, and B. D. Todd. 2017. Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biological Conservation 214:13–22.

Pelletier, S. K., L. Carlson, D. Nein, and R. D. Roy. 2006. Railroad crossing structures for spotted turtles: Massachusetts Bay Transportation Authority—Greenbush rail line wildlife crossing demonstration project, p. 414–425. *In*: Proceedings of the 2005 International Conference on Ecology and Transportation. C. L. Irwin, P. Garrett, and K. P. McDermott (eds.). Raleigh, North Carolina.

Popp, J. N., and S. P. Boyle. 2017. Railway ecology: underrepresented in ecology? Basic and Applied Ecology 19:84–93.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rautsaw, R. M., S. A. Martin, K. Lanctot, B. A. Vincent, M. R. Bolt, R. A. Seigel, and C. L. Parkinson. In press. On the road again: assessing the use of roadsides as wildlife corridors for Gopher Tortoises (*Gopherus polyphemus*). Journal of Herpetology.

Ruby, D. E., J. R. Spotila, S. K. Martin, and S. J. Kemp. 1994. Behavioral responses to barriers by Desert Tortoises: implications for wildlife management. Herpetological Monographs 8:144–160.

Rytwinski, T., and L. Fahrig. 2015. The impacts of roads and traffic on terrestrial animal populations, p. 237–246. *In*: Handbook of Road Ecology. R. van der Ree, D. J. Smith, and C. Grilo (eds.). John Wiley & Sons, Ltd, Chichester, UK.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation—a review. Conservation Biology 5:18–32.

Seigel, R. A. 2016. Data collection and storage, p. 32–42. *In*: Reptile Ecology and Conservation: A Handbook of Techniques. C. K. Dodd, Jr. (ed.). Oxford University Press, New York.

Shepard, D. B., A. R. Kuhns, M. J. Dreslik, and C. A. Phillips. 2008. Roads as barriers to animal movement in fragmented landscapes. Animal Conservation 11:288–296.

Sievert, P. R., and D. T. Yorks. 2015. Tunnel and fencing options for reducing road mortalities of freshwater turtles. University of Massachusetts Transportation Center Final

Report 12.02. Massachusetts Department of Transportation, Boston, Massachusetts.

Smith, R. B., D. R. Breininger, and V. L. Larson. 1997. Home range characteristics of radiotagged Gopher Tortoises on Kennedy Space Center, Florida. Chelonian Conservation Biology 2:358–362.

Witz, B. W., D. S. Wilson, and M. D. Palmer. 1991. Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. American Midland Naturalist 126:152–158.

Woltz, H. W., J. P. Gibbs, and P. K. Ducey. 2008. Road crossing structures for amphibians and reptiles: informing design through behavioral analysis. Biological Conservation 141:2745–2750.

Young, F. N., and C. C. Goff. 1939. An annotated list of the arthropods found in the burrows of the Florida Gopher Tortoise, *Gopherus polyphemus*. The Florida Entomologist 22:53–62.

Appendix 1. Ethogram of recorded behaviors of *Gopherus polyphemus* in response to placement within the railway or control plots. Behavior is recorded to determine if tortoises habituated to the railway exhibit different behaviors than those naïve to the railway due to familiarity with the location.

Behavior	Type	Definition
Meandering	State	Active walking
Stationary	State	Motionless
Eating	State	Feeding on vegetative material
Hiding	State	Fully tucked into shell
Digging	State	Digging
Attempting cross	State	An attempt to cross a rail with at least one forelimb on rail head
Flipped	State	Overturned on carapace and attempts to right itself by circular forearm movements
Escaped	State	Time spent escaped from the barrier in question within a one-hour trial
Cross success	Event	A successful crossing over one of the two rails
Cross fail	Event	A failed crossing over one of the two rails and subsequent fall to the center of the railway