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THE PATHS LESS TRAVELED:
MOVEMENT OF GOPHER TORTOISES (*Gopherus polyphemus*)
ALONG ROADS AND RAILWAYS

by

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B.S. Wright State University, 2014

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
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Major Professor:
Christopher L. Parkinson

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ABSTRACT

Urbanization and an expanding human population have led to a large degree of habitat destruction and fragmentation. These, in turn, reduce biodiversity and wildlife population sizes on a global scale. Transportation infrastructure, such as roads and railways, are some of the largest contributors to habitat fragmentation. Roads are well-established to negatively impact wildlife, but some studies suggest a potential use in habitat connectivity by functioning as wildlife corridors to connect distant populations. Railways are similarly known to impact wildlife by increasing mortality rates as well as provide unique risks such as electrocution and entrapment when compared to roads. However, the influence of railways on the movement and behavior of most taxa remains understudied. Here, I used Gopher Tortoises (*Gopherus polyphemus*) at the John F. Kennedy Space Center as a model system to (1) determine whether roadsides are or could be used as a wildlife corridor to connect distant habitats and (2) evaluate the impacts of railways on tortoise movement and behavior while providing management implications for both roads and railways.

To examine the use of roadsides as wildlife corridors, I tracked the movement of individuals found along roadsides using radio-telemetry to determine if tortoises used the roadsides to move between inland and coastal habitat. In addition, I compared home range sizes of tortoises along roads to those of inland and coastal habitats to examine differences in spatial use patterns with regards to roads. I translocated tortoises from distant habitats into the roadside corridors to determine whether they would use the roadsides as a connective route to return to their original capture location. Overall, I determined that roadsides do not function as movement pathways, as even translocated tortoises remained along roads throughout the duration of the study. Instead, roads appear to function as long-term residential areas and potentially suitable

habitat. I suggest management of roadsides to reduce mortality and further studies to examine the potential of roadsides acting as ecological traps.

To study the impact of railways on tortoise movement and behavior I first used radio-telemetry to track the movement of tortoises found less than 100 m from railways. I simulated movement by using 1000 correlated random walks per tortoise to determine if the number of observed crossing events were significantly less than what would be expected by chance. Second, I measured behavior via continuous focal sampling for one hour to determine railway crossing ability and test for behavioral differences associated with the familiarity of the railways using a principal component analysis. Lastly, I tested if trenches dug underneath the rails could be used as a management strategy to alleviate the impact of railways on tortoises. I found that tortoises are unlikely to cross the railways and the number of observed crossing events were significantly less than what we would expect by chance. Additionally, familiarity with the railway did not have any influence on a tortoise's ability to cross nor their behavior. Trenches were frequently used to move from one side of the railway to the other and are, therefore, a valid management strategy to alleviate the impacts railways have on tortoise mortality, movement, and behavior.

Overall, I conclude that transportation infrastructure and the expanding human population have immense impacts on wildlife, especially on turtles and tortoises. I recommend further research continue to identify unique management strategies as well as alternative barriers that may play a large role in a species' decline.

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TABLE OF CONTENTS

LIST OF FIGURES	x
LIST OF TABLES.....	xiii
LIST OF ACRONYMS (or) ABBREVIATIONS	xiv
INTRODUCTION	1
Study Species	3
ON THE ROAD AGAIN: ASSESSING THE USE OF ROADSIDES AS WILDLIFE CORRIDORS.....	7
Methods	9
Current Roadside Corridor Use	10
Feasibility of Roadsides as Movement Corridors.....	12
Results	13
Current Roadside Corridor Use	13
Feasibility of Roadsides as Movement Corridors.....	14
Discussion.....	15
STOPPED DEAD IN THEIR TRACKS: THE IMPACT OF RAILWAYS ON TESTUDINE MOVEMENT AND BEHAVIOR	21
Methods	24
Radio-Telemetry.....	24
Behavior and Crossing Ability	26
Management Testing.....	28
Results	29
Radio-Telemetry.....	29
Behavior and Crossing Ability	29
Management Testing.....	30
Discussion.....	30
CONCLUSIONS	35
APPENDIX	38
REFERENCES.....	54

LIST OF FIGURES

Figure 1: KSC with the potential roadside corridors connecting coastal and inland habitat outlined in black. The two parts of this study were done along two different roads which are boxed and numbered. ① The study area for examination of current roadside corridor use using radio-telemetry to determine how Gopher Tortoises in this region spatially used the roadsides. ② The study area for translocation of tortoises along the roadside to determine if movement through the corridor back to their original home range was feasible..... 39

Figure 2: The potential roadside corridor used for study ① where current roadside corridor use was determined via radio-telemetry of tortoises captured along the roads. Eight example minimum convex polygon (MCP) home ranges are colored showing movement confined to areas along the corridor, but no movement directly through the corridor. Tortoise 5221 was the only tortoise observed moving from the corridor to coastal strand habitat over a distance of 500 m.. 40

Figure 3: The potential roadside corridor used for study ② where the feasibility of roadsides to function as movement corridors was assessed. Tortoises were translocated (dotted colored lines) from either inland or coastal habitat into the potential corridor. Daily radio-telemetry (solid colored lines) determined if tortoises would use corridors to return to their original home range as opposed to straight-line paths. 43

Figure 4: (a) Log-scaled minimum convex polygon (MCP) home ranges compared between habitat types (i.e. ruderal corridors, inland scrub, and coastal strand). Corridor tortoises occupied slightly smaller home ranges, but were insignificantly different due to the large variance seen in

their home ranges. Inland home ranges were obtained from Smith et. al (1997). (b) Log-scaled average distances traveled between tracking events (m) compared between habitat types (i.e. ruderal corridors, coastal strand), but excluding inland scrub for which the data was unavailable. Average distances were not significantly different between habitat types. 45

Figure 5: An example rose diagram (circular histogram) of a single inland tortoise’s (ID: 5250) direction of travel when the distance traveled was greater than 7 m. The Rayleigh test of directional uniformity displayed insignificance in the directional movement for both true and corridor homing. 46

Figure 6: (a) Gopher Tortoise (*Gopherus polyphemus*) found in the center of the railway trapped by the tall rails and facing dehydration. (b) An attempted, but failed escape over the rails by a tortoise during one of the behavioral observation trials. (c) Range map of Gopher Tortoises in the southeastern United States with highlighted federal protection status and study area at the John F. Kennedy Space Center (KSC). (d) The coastal strand study area at KSC with the railway outlined and two example observed tortoise trajectories achieved via radio-telemetry. 47

Figure 7: (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 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..... 49

Figure 8: (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 in the presence of a visual barrier..... 50

Figure 9: (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. 52

Figure 10: Principal component analysis (PCA) comparing tortoise behavior expressed over a one-hour observation period. Colors are based on railway familiarity with 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..... 53

LIST OF TABLES

Table 1: Tortoises tracked for routine movements along roadside corridors using radio-telemetry with home ranges and distances traveled. CL, Carapace Length; Tracking Events, the total number of times an individual was tracked; MCP, 100% minimum convex polygon home range in hectares; Mean Dist., average distance traveled between tracking events in meters. Inland data was taken from Smith et al. (1997).....	41
Table 2: Tortoises translocated along a roadside corridor at Kennedy Space Center and tracked via radio-telemetry with translocation distances, expected return bearings, and results of Rayleigh tests of directional movement significance by either true homing or corridor use. CL, Carapace Length; Tracking Events, the total number of times an individual was tracked; SLTD, straight-line translocation distance in meters; Exp. Return Bearing, expected direction of travel given true homing to their original capture location; True Homing, p-value indicating significance of travel in the direction of the expected return bearing; Corridor Use, p-value indicating significance of travel in the orientation of the corridor (inland: 270°; coastal: 90°) ..	44
Table 3: Radio-tracked tortoises with the observed and mean expected number of railway crossings based on Monte Carlo correlated random walk simulations. CL, Carapace Length.	48
Table 4: Ethogram of recorded <i>Gopherus polyphemus</i> behaviors.....	51

LIST OF ACRONYMS (or) ABBREVIATIONS

AICc.....	Sample-size corrected Akaike information criterion
ATS.....	Advanced Telemetry Systems
CL.....	Carapace length
CRW.....	Correlated random walk
Exp.....	Expected
FWC.....	Florida Fish and Wildlife Conservation Commission
GIS.....	Geographic Information Systems
GPS.....	Global Positioning System
KSC.....	John F. Kennedy Space Center
MCP.....	Minimum convex polygon
MINWR.....	Merritt Island National Wildlife Refuge
NPS.....	National Park Service
PCA.....	Principle component analysis
SLTD.....	Straight-line translocation distance
USFWS.....	United States Fish and Wildlife Service

INTRODUCTION

Habitat fragmentation is a global epidemic leading to a plethora of issues for the environment including: reduced biodiversity and biomass, alteration of nutrient cycles, and restriction of movement and gene flow (Saunders et al. 1991; Weathers et al. 2001; Fischer & Lindenmayer 2007; Haddad et al. 2015). The largest contributor of habitat fragmentation is increasing anthropogenic expansion (Saunders et al. 1991; McKinney 2006; Dirzo et al. 2014). Habitats are cleared for agriculture, urbanization, and transportation to sustain the continuous growth of the human population at the cost of healthy environmental processes and the conservation of ecosystems and species (Saunders et al. 1991; McKinney 2006; Dirzo et al. 2014; Haddad et al. 2015). The continued fragmentation of habitats has led to an immense need for research identifying unique management strategies for the continued conservation of ecosystems and species as well as areas requiring additional attention.

Transportation infrastructure, such as roads and railways, are the largest contributors to habitat fragmentation and have been of particular interest to ecologists due to their well-established impacts on wildlife mortality and overall declines (Forman & Alexander 1998; Forman 2000; Forman & Deblinger 2000; Forman et al. 2003). Roads are known to increase mortality of animals during crossing events and cause behavioral avoidance which inevitably leads to isolation and alteration of population connectivity (Madar 1984; Forman & Alexander 1998; Gibbs & Shriver 2002; Forman et al. 2003; Mazerolle 2004; Andrews & Gibbons 2005; Steen et al. 2006; Marsh et al. 2008; Shepard et al. 2008; Clark et al. 2010; Kociolek et al. 2011; Baxter-Gilbert et al. 2015). Despite this, some studies suggest that roads may be able to connect distantly isolated populations by functioning as wildlife corridors (Vermeulen 1994; Brown et al.

2003; Forman et al. 2003; Haddad 2015). Few studies have examined the feasibility of using or managing roadsides to connect fragmented populations, so more research is needed.

Parallel to the negative effects seen by roads on wildlife and ecosystems, other less-studied human-created barriers similarly impact species. Railways are known to increase mortality rates from wildlife-train collisions, but some animals are also vulnerable to entrapment or electrocution between rails (Forman et al. 2003; Dorsey 2011; Dorsey et al. 2015). Analogous to roads, the increased mortality and behavioral avoidance resulting from the presence of railways ultimately reduces population connectivity (Bartoszek & Greenwald 2009; Dorsey et al. 2015). However, few studies have been done to elaborate on the effects of railways on animal movement and most focus on a small subset of taxa (i.e. moose and bear; Dorsey 2011). Further studies are needed to determine the degree to which railways impact different taxa.

With both roads and railways, turtles are of particular interest for conservation and management. It is routinely shown that their sluggish terrestrial behavior leaves them exceptionally vulnerable to road mortality (Gibbs & Shriver 2002; Steen et al. 2006; Shepard et al. 2008). Management of turtles and tortoises around roads is mainly focused on providing tunnels (Sievert & Yorks 2015), but roadsides may actually be able to function as wildlife corridors to connect populations. For some species of tortoises, roadsides have been shown to be used for foraging and social encounters, elongate home ranges, and create potential travel corridors (McRae et al. 1981b, Smith et al. 1997, Berish and Medica 2014). Additionally, long-distance movements following translocations suggest a potential feasibility for movement between habitats along a roadside corridor (McCoy et al. 2013, Hinderle et al. 2015).

In conjunction with the evidence for potential movement along roadsides, their ability to move is often negatively correlated with herbaceous cover making open roadside corridors more

likely to be traveled than denser or impassable habitats (Auffenberg and Iverson 1979; McCoy et al. 2013). In regards to railways, their body structure makes traversing tall barriers difficult, as they do not have the strength and flexibility to pull themselves over the barrier (Ruby et al. 1994; Kornilev et al. 2006). This lack of mobility causes turtles to frequently become entrapped between rails (Kornilev et al. 2006; Iosif 2012; Gilson & Bateman 2015). Yet, little evidence has been provided demonstrating impacts of railways on turtle overall movement patterns or mortality and it is unknown whether behavioral acclimation plays a role in their ability to cross railways.

Here, I used Gopher Tortoises (*Gopherus polyphemus*) at the John F. Kennedy Space Center as a model system to (1) determine whether roadsides are or could be used as a wildlife corridor to connect distant habitats and (2) evaluate the impacts of railways on turtle movement and behavior while providing management implications for both roads and railways.

Study Species

Gopher Tortoise are the ideal organisms to accomplish these objectives because they occupy a variety of habitats, are capable of long-distance movements, and are frequently encountered in or around railways (Engeman et al. 2007). They are a medium sized Testudines (~23-28 cm long) found throughout the southeastern coastal plain of the United States (Breininger et al. 1994; Enge et al. 2006; Gopher Tortoise Management Plan 2012). While generally associated with frequently burned longleaf pine (*Pinus palustris*) habitats, Gopher Tortoises can be found in variety of other habitats including coastal sandy dunes and ruderal herbaceous communities (Breininger et al. 1994; Lau & Dodd 2015).

At KSC, male inland tortoises use and maintain an average of 16 burrows throughout a 1.9 ha home range, while female inland tortoises maintain an average of 9 burrows in a 0.6 ha

range (Smith et al. 1997). However, other studies have shown home ranges ranging from 0-13 ha, demonstrating the overall behavioral plasticity in home range sizes and movement patterns among individuals (Berish & Medica 2014). Average foraging movements of *G. polyphemus* are generally restricted to short distances (13-50 m) around a few burrows due to plentiful food resources, but secondary foraging distances are estimated at 100 m (Ashton & Ashton 2008). Longer movements (1-3 km) have been observed during seasonal food depletions and selection of different foraging areas (McRae et al. 1981b, Ashton and Ashton 2008, Berish and Medica 2014).

Movements of *G. polyphemus* most commonly occur during the day between the hours of 1300-1600 h, but bimodal activity in the mornings and evenings is also common during the hottest months (May-August) when activity is most frequent (Douglass and Layne 1978, Berish and Medica 2014). Juveniles, by comparison, exhibit shorter distance movements; daily movements average 8 m from their burrow, which is placed <15 m from the nest site (Pike 2006). Home ranges are smaller than adults with an increase through time as they age (Pike 2006). Juveniles maintain diurnal activity similar to adults, but activity occurs year round especially directly following hatching in August-November (Pike 2006).

Populations or colonies of Gopher Tortoises are defined as spatial aggregations of burrows and tortoises, but within these aggregates complex social cliques exist that influence movement and interactions (Guyer et al. 2014). Dispersal and movement of Gopher Tortoises occurs mainly by adult males visiting one to three females daily as well as searching for new mates in late summer/early fall when courtship occurs (Landers et al. 1980, McRae et al. 1981b, Diemer 1992, Berish & Medica 2014, Guyer et al. 2014). By comparison, female movement is maximal in the late spring when nesting occurs (Landers et al. 1980, McRae et al. 1981b, Diemer

1992, Berish & Medica 2014). Females are evenly distributed across multiple cliques, causing males to move large distances to court, mate with, and monitor multiple females (Johnson et al. 2009). This evidence suggests the exhibition of a scramble competition polygynous mating system, where males are competing by racing to reach each female first during their sexual receptivity period. Despite apparent scramble competition, intrasexual competition frequently occurs among males and females by exhibiting aversion behaviors in females and attempting to overturn one another via gular projections for males even after sharing burrows (Johnson et al. 2009, Guyer et al. 2014). These behaviors are indicative of female defense polygyny, but the even spatial distribution of females and movements of males most consistently support a scramble competition polygynous mating system (Johnson et al. 2009).

The distinct social cliques within Gopher Tortoise aggregates are male-centric, with few interactions occurring among cliques despite overlapping geography (Guyer et al. 2014). This is exemplified by tortoises passing nearby burrows to visit distant ones (Guyer et al. 2014). Cliques are likely formed by female aversion and male tendencies to monitor multiple females, but overall this evidence supports that tortoises are able to recognize, remember, and preferentially interact with individuals of their own clique (Guyer et al. 2014). Despite these well-established cliques, dispersal (movement away from social groups in which they were born with no apparent return tendency) occurs at all age and sex groups likely in search of non-kin partners (Guyer et al. 2014). Tortoises are more likely to move shorter distances in areas of high density because the benefits of remaining in a high resource area outweigh the risks of dispersal such as increased predation and inability to find new resources including mates (Guyer et al. 2012, 2014). Meanwhile, tortoises in areas of low density are more likely to move large distances because the

benefits of finding non-kin mates and other resources outweigh the risks of remaining in a low resource environment (Guyer et al. 2012, 2014).

Gopherus polyphemus are classified by the state of Florida as threatened due to habitat destruction and fragmentation by means of human urbanization and agriculture; the species suffered an 80% decline throughout their range (Auffenberg and Franz 1982). Other threats to tortoise populations include heavy predation, invasive species (both flora and fauna), and upper respiratory tract disease (Douglass and Winegarner 1977, Diemer 1986, Hicklin 1994, Seigel et al. 2003). *Gopherus polyphemus* are federally classified as threatened in the western portion of their range, but are only classified as a candidate species for listing under the Endangered Species Act throughout the remainder of their distribution. It is vital to collect information regarding habitat use and future complications they may face to address the long-term survival of this species as well as other commensal species.

The gopher-like burrows that they excavate, and for which they are named, function as refuges from inhospitable weather, predation, and disturbances such as wildfires not only for themselves, but also for over 300 invertebrate and 60 vertebrate commensal species (Hubbard 1893, Young and Goff 1939, Jackson and Milstrey 1989, Lips 1991). Many of these commensal species such as the Gopher Frog (*Lithobates capito*), Florida mouse (*Podomys floridanus*), burrowing owl (*Athena cunicularia*), and Eastern Indigo Snake (*Drymarchon couperi*) are state and federally protected (Eisenberg 1983, Jackson and Milstrey 1989, Lips 1991, Kent and Snell 1994). By providing conservation and management strategies for Gopher Tortoises, these other species are also positively impacted, making Gopher Tortoises an ideal system to study.

ON THE ROAD AGAIN: ASSESSING THE USE OF ROADSIDES AS WILDLIFE CORRIDORS

Habitat fragmentation from human alteration is known to reduce biodiversity and disrupt key ecosystem functions (Saunders et al. 1991; Collinge 1996; Fischer & Lindenmayer 2007; Haddad et al. 2015). It impacts taxa by isolating populations increasing the probability of inbreeding, genetic drift, increased mortality, and altered behavior and population structure (Gilpin & Soulé 1986; Gibbs & Shriver 2002; Keller & Largiadèr 2003; Jaeger et al. 2005; Marsh et al. 2008; Baxter-Gilbert et al. 2015). Habitat connectivity is important to offset the impacts of fragmentation as maintaining linkage between habitat patches can reduce the effects of small population sizes and lower risks of extinction (Gilpin & Soulé 1986; Beier & Noss 1998).

Connectivity can often be achieved through the use of wildlife corridors. Wildlife corridors were first conceptualized by Wilson and Willis (1975) as organism-centric paths to facilitate immigration. However, they can also be defined from an entirely landscape perspective as linear habitat, situated within a dissimilar matrix, that connects two or more larger patches of habitat (Beier & Noss 1998). These landscape corridors, hereby referred to simply as corridors, effectively provide connectivity for many species and are necessary as routes of retreat when dealing with areas prone to environmental change or with endemic species (Beier & Noss 1998). Corridor effectiveness, however, is generally dependent on the focal species and studies therefore need to be taxon specific (Beier & Noss 1998).

Corridors may take the form of overpasses or tunnels to cross roads since they are large constitutes of habitat fragmentation (Forman et al. 1998; Forman et al. 2003). Roads are known

to increase mortality and alter both behavior and population structure of populations adjacent to the roadways (Forman & Alexander 1998; Gibbs & Shriver 2002; Forman et al. 2003; Mazerolle 2004; Steen et al. 2006; Marsh et al. 2008; Clark et al. 2010; Kociolek et al. 2011; Baxter-Gilbert et al. 2015). Roads increase mortality and act as artificial boundaries that shape the home ranges of even highly mobile and wide-ranging species such as Bobcats and Coyote (Riley et al. 2003, 2006). Despite the clear negative impact of roads on many species, there may be understudied benefits associated with linking habitats (Vermeulen 1994; Haddad 2015). Roads are designed to function as corridors for human transportation, but, by their very nature, may also be able to function as corridors for other species as well (Haddad 2015). Vermeulen (1994) found that roadsides act as residential habitat for certain species of ground beetles in the Netherlands. Despite a lack of movement between larger habitat patches, they advised conservation planning to connect distant habitats via placement of smaller patches along the road for population establishment (Vermeulen 1994). It has thus been suggested that roadsides may actually be able to function as corridors to connect fragmented landscapes (Vermeulen 1994; Haddad 2015). Vermeulen (1994) studied this possibility with beetles; our goal is to utilize a terrestrial, highly vagile species under extensive conservation management applicable to an entire ecological community.

Here we use Gopher Tortoises (*Gopherus polyphemus*) as a focal species to determine if roadsides are, or could be, used as corridors to connect otherwise isolated habitat patches. Gopher Tortoises were selected due to their role as an ecosystem engineer throughout their range in the Southeastern Coastal Plain of the United States, as well as their high vagility and current conservation status. Their burrows serve as refuge for over 360 species, many of which are also threatened such as the Eastern Indigo Snake, Pine Snake, and Gopher Frogs (Hubbard 1893;

Young & Goff 1939; Jackson & Milstrey 1989; Lips 1991; Witz et al. 1991; Kent et al. 1997). Gopher Tortoises are highly mobile, occupying home ranges up to 13 ha and moving distances over three km over the course of a season to find new areas to forage (Berish & Medica 2014). They are considered threatened in every state in which they are found and are a candidate species for federal listing. They are under continued population decline from habitat loss and fragmentation and the connection of isolated populations may increase population sizes needed to maintain this species (Auffenberg & Franz 1982; Enge et al. 2006). Insight into the use of roadsides by *G. polyphemus* may inform plans to properly manage and use roadsides as wildlife corridors and further conserve both this flagship species and their commensal complements.

The aim of this study was to (1) evaluate the current spatial use of roadsides by *G. polyphemus* and (2) determine the feasibility of roadsides to be used as movement corridors between larger habitat patches. First, we used radio-telemetry to determine whether tortoises found along roadsides used this habitat to move between coastal and inland habitat and tested for differences in spatial use between habitats using home range estimation. Second, we combined the radio-telemetry with documented natural homing behaviors of *G. polyphemus* to assess whether roadsides would be used as corridors to return to natal home ranges (McRae et al. 1981b; Connor 1996; McCoy et al. 2013; Hinderle et al. 2015).

Methods

We conducted our study on roadsides linking coastal and inland habitat types at the John F. Kennedy Space Center (KSC) in east-central Florida, USA (Figure 1). Habitat along the roads consisted of short ruderal (mowed) herbaceous cover. Adjacent to this, habitat transitioned into thick herbaceous cover, hardwood hammock, and ruderal woody cover which lack ground-cover

and is largely considered unsuitable for tortoises due to the lack of food resources. We predicted that tortoises would only use the grassy roadsides and would rarely venture farther than the edges of the other habitat types. Beyond these habitats, lagoons and swales provide aquatic barriers to restrict further movement of tortoises as they rarely swim and are ill-adapted to do so.

All tortoises in this study were captured by hand, marked using standardized marginal scute hole-drilling procedures, and had their carapace and plastron lengths measured (Ernst 1974). Only adults classified as greater than 23 cm straight-line carapace length for males or 24 cm for females were used (Landers & McRae 1982). Sex was determined from external plastron shape, with males having a high degree of plastron concavity (McRae et al. 1981a). Advanced Telemetry Systems (ATS) R1930 transmitters (24 g; 40 ppm) 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, Watsonville, CA). The antenna was wrapped around the marginal scutes of the carapace and adhered to the posterior marginal scutes using the West Marine epoxy. Following release, tortoises were tracked by hand using a Telonics TR-4 receiver and RA-2AK H-antenna between 0600 and 1800 h. Once located, tortoise locations were recorded with a handheld GPS. All analyses were run in R v 3.3.1 (R Core Team 2016).

Current Roadside Corridor Use

We first sought to evaluate the current spatial use of roadsides and determine if these regions are acting as movement corridors or as resident habitat. We captured and re-released 22 tortoises (12 females; 10 males) at their original capture locations on the shoulders of the road joining coastal and inland habitats (Table 1). The corridor used in this study ran alongside a road entitled Saturn

Causeway (Figure 2). It is approximately 5.5 km between coastal and inland habitats and varies in width from 25 to over 200 m, but we predicted the corridor to be used in a much finer scale less than 100 m from the road. Tortoises were tracked on an approximate weekly basis between May 2015 and July 2016 for a total of 885 tracking events averaging 40 per individual. These tortoises were observed for movement out of the corridor and into coastal or inland habitat. To compare the movement patterns of tortoises found in the corridor to more typical habitats we also obtained data on coastal tortoises. Ten tortoises (4 females: 6 males) were captured in coastal strand habitat at KSC and tracked between May 2015 and July 2016 for a total of 812 events averaging 81 per individual. Lastly, data from inland tortoises, or tortoises captured from oak and palmetto scrub habitat at KSC, was acquired from Smith et al. (1997) for comparison of home ranges between roadside, coastal strand, and scrub habitat types.

GPS coordinates were entered into ArcMap 10.2.2 and 100% minimum convex polygon (MCP) home ranges were calculated for each tortoise in the package “adehabitatHR” (Table 1; Calenge 2006). Minimum convex polygons were chosen for home range approximation due to their simplicity and convenience of comparison to previous studies such as that of inland tortoises at KSC by Smith et al. (1997). MCPs are prone to overestimation of home range as they only use extreme outlier points to create the home range, but they perform well when little data is available and avoid many problems associated with other methods of home range estimation such as spatially autocorrelated data (Powell 2000). Corridor, coastal, and inland MCP home ranges were tested for significant differences using a linear regression. This model was then compared to a null regression and regression of home ranges by tortoise sex using sample-sized corrected AIC (AICc) to determine if other variables account for the variation seen in the home ranges more effectively than habitat.

Additionally, linear distance between data points was calculated in the package “adehabitatLT” (Calenge 2006; Calenge et al. 2009). The total distance traveled was calculated for each tortoise and divided by the number of tracking events to find the average distance traveled per tracking event (Table 1). This metric was likewise tested for significant differences between habitat and compared to that of a null model, sex, and carapace length. Inland tortoises were excluded for this part of the study, as linear trajectories were not calculated by Smith et al. (1997).

Feasibility of Roadsides as Movement Corridors

To determine the feasibility of roadsides to be used as movement corridors between larger habitat patches, we used a road farther north in Kennedy Space Center (Figures 1 & 3). This road was used instead because of the unpredictable movements the tortoises could make following translocation. Automotive-related mortality along this road was reduced as only KSC security officers and National Park Service employees drive this road. We first captured 6 tortoises (4 females: 2 males) from inland habitat and 7 tortoises (2 females: 5 males) from coastal habitat (Table 2; Figure 3). Following transmitter attachment, tortoises were translocated along the roadside corridor at randomly selected points between 2000 and 4000 meters away from their originating habitat (Figure 3). Actual straight-line translocation distance (SLTD) varied based on the capture location of each tortoise (Table 2). After translocation, tortoises were tracked daily over a single summer season based on the successful homing times of the closely-related *G. agassizii* (Hinderle et al. 2015). Overall, there was a total of 678 tracking events averaging approximately 52 per individual. Following this summer season, tortoises were recaptured and returned to their original location.

If tortoises are to use corridors as actual movement pathways, we would expect them to exhibit homing behaviors along the corridor as opposed to straight-line paths through unsuitable habitats. The compass bearing of translocation and of each recorded tracking event was determined using the package “geosphere” (Hijmans et al. 2016). The direction of translocation was inversed by 180° to determine the expected return bearing given true homing for each tortoise (Table 2). Tracking events with distances traveled less than 7 m were within GPS accuracy and led to biases in cardinal directions. Therefore, only data with distances greater than 7 m were used in analyses. Two Rayleigh tests of directional uniformity were done for each tortoise in the package “circular” (Lund & Agostinelli 2013). These tests were used to determine if tortoises moved in the expected homing direction or whether they followed the orientation of the corridors running directly east-west. The alternative hypothesis of the test was set to either the expected return bearing for each tortoise or direct east-west bearing for corridor. If tortoises exhibit true homing, we would expect their movements to be significantly directed towards that of a straight-line bearing. If tortoises use corridors to return home, we would expect their movements to be significantly directed in the same orientation of the corridor.

Results

Current Roadside Corridor Use

Only one of 22 tortoises along the potential roadside corridor was observed moving out of the corridor and into coastal habitat (ID: 5221; Figure 2). The remaining 21 tortoises stayed along the roadsides occupying typical home ranges when compared to previous studies’ and across habitat types (Berish & Medica 2014; Smith et al. 1997; Figure 2). Log-transformed 100% MCP home ranges of tortoises were compared between the corridor, coastal, and inland habitats using

a linear regression. No significant differences were found across habitat types ($R^2=0.07$, $p=0.08$; Figure 4a), but inland and coastal home ranges are marginally larger than corridor home ranges. Coastal and inland home ranges had median values of 0.85 (0.09-9.83) ha and 1.00 (0.27-5.29) ha, respectively. In comparison, corridor home ranges had a median value of only 0.42 ha with exceptionally large variation ranging from the smallest recorded value at 0.01 to one of the largest at 7.63 ha. There was no significant difference in home range sizes by sex ($R^2=0.04$, $p=0.17$), nor by the additive effect of sex and habitat ($R^2=0.14$, $p=0.28$). Comparison of these regression models to a null model demonstrate habitat to be the best predictor, but only by a $\Delta AICc$ of 0.8 from the null model.

Regressions were also performed on log-transformed average distance traveled between tracking events. These data were unavailable for inland tortoises, but there was no significant difference between corridor and coastal tortoises ($R^2=0.004$, $p=0.72$; Figure 4b). However, both sex and carapace length, respectively, had a significant effect on the average distances traveled ($R^2_{sex}=0.15$, $p_{sex}=0.03$; $R^2_{CL}=0.16$, $p_{CL}=0.02$). The model for carapace length as a predictor for the distances traveled had the lowest AICc and separated by 5.6 AICc from the habitat model, which fell below the null model.

Feasibility of Roadsides as Movement Corridors

From the 13 tortoises translocated, only one male individual from coastal habitat successfully returned home (ID: 5266). This tortoise returned home after only one day following a translocation of 2,058 m. This tortoise's expected and actual return direction was 90° ; in parallel with the orientation of the corridor. The roadside was likely used for this movement, but because movement occurred in a single day we cannot be certain of this tortoise's actual path home.

Therefore, these data were excluded from further analysis. The remaining 12 tortoises largely

remained along the road or nearby areas making long-distance movements in a single day followed by long resting periods (Figure 3). The roadsides acted as residential locations for tortoises to remain sedentary for weeks at a time. The tortoises largely positioned themselves underneath vegetative patches before, eventually, digging burrows along the roadsides.

The expected return bearing for true homing of inland tortoises ranged from 219.9°-266.4° with an expected return bearing for corridor use of 270° (Figure 5). The expected return bearing for true homing of coastal tortoises ranged from 63.5°-89.1° with the expected return bearing for corridor use of 90°. The Rayleigh test for directional uniformity found no significance in true homing in any of the tortoises (Table 2). In comparison, only one tortoise (ID: 5253) was found to make movements significantly oriented in the direction of the corridor (Table 2).

Discussion

Our results illustrate that Gopher Tortoises use roadways in much the same way they do other habitats. That is, not as corridors for movement but as habitats for longer-term residence. Neither home ranges nor distances traveled of tortoises found along the roadside corridor were significantly different than inland and coastal regions. With only one exception, tortoises located along the road generally remained in this area and made no attempts to move to either the coastal scrub or inland habitats located at the ends of the corridor. Only tortoise 5221 moved into the coastal scrub, moving over 500 m to do so (Figure 2).

Additionally, there was a lack of a homing response from translocated tortoises. Only tortoise 5266 successfully returned home in only one day following a translocation of over two km. Because of the rapid homing response, movement could not be detected along the corridor

and it is uncertain how the tortoise actually returned home. Of the remaining tortoises, none significantly oriented their movements in the direction of true homing and only tortoise 5253 was found to exhibit movements significantly oriented in the homeward direction of the corridor. The lack of a homing response via the Rayleigh tests may be due to all distances greater than 7 m being treated equal. Tortoise 5253 made a few short-distance movements along the corridor toward his original home, but subsequently dug a burrow and remained in this location for the remainder of the study period. Therefore, it is uncertain whether this tortoise was exhibiting true-homing or simply attempting to find an appropriate location to place a burrow. In this study, translocated tortoises made large movements during the first few days following their translocation, then dug burrows to take up residency along the roads and adjacent habitats. Their movements consisted of directly east-west movements parallel to the roadside, but these movements were not significantly oriented in the direction of their home. Tortoises may have taken up residency along roads as opposed to returning home due to the availability of open habitat and lack of traffic along this specific road. In addition, translocation distances might have been too great for the tortoises to identify landmarks used for navigation (McCoy et al. 2013).

Overall, these data indicate that while movement along the road is feasible and may occur on rare occasions, we conclude that it is unlikely as there is little evidence to support this concept. Instead, tortoises appear to use roadsides independently of larger habitat patches, treating them as areas for residency as opposed to a corridor for traveling between habitat patches. The roads used in this study at KSC experience very little traffic and can be considered a low-impact environment. In areas where traffic is higher, the noise pollution and increased mortality risk may result in tortoises exhibiting different behaviors than what we observed in this study. However, KSC roads were built in the 1960's to connect coastal and inland habitat. The

relatively recent construction of these roadsides (within the likely lifespan of many adult tortoises) suggest that tortoises either colonized the roadside areas naturally or may have been moved there during construction projects on the site (R. Bolt and R. Seigel, pers. comm.). Our data indicate that tortoises now use these roadsides for residency as opposed traveling between habitat types.

Roadsides may be attractive habitat to Gopher Tortoises to take up residency due to the openness of the habitat (Auffenberg & Franz 1982). Historically natural disturbances such as lightning-caused fires create open habitat that Gopher Tortoises prefer and use to maintain high population densities (S. Martin unpublished manuscript; Breininger et al. 1994). Natural fires are often suppressed by anthropogenic intervention, but other types of disturbances can act similarly to maintain open habitat such as prescribed fires and mowing. The regular maintenance of roadsides via mowing is generally considered habitat destruction or reduction of habitat quality, but this removal of shrub and overstory mimics some effects of natural fire by creating open, ruderal herbaceous habitat in which some species thrive. In many instances roads create a negative ecological impact on species (i.e. road-effect zone; Forman 2000; Forman & Deblinger 2000). For example, abundances of a *G. polyphemus* congener, the Desert Tortoise (*Gopherus agassizii*), were negatively impacted up to 800 m from the road due to high mortality rates and road avoidance (Boarman & Sazaki 2006). Interestingly, *G. polyphemus* appeared to use roadsides as residential locations, likely due to their creation of open-habitats (Breininger et al. 1994).

The open habitat found along roads likely attracts Gopher Tortoises, yet our tortoises were regularly observed moving into the marginal habitats of thick herbaceous cover, ruderal woody, and hammock habitats which are generally considered unsuitable for tortoises. These

habitats have little ground cover and food resources, yet tortoises and burrows were commonly found in these areas. Radio-telemetry shows that tortoises make large infrequent movements between unsuitable habitats and the more open roadsides. We hypothesize that tortoises use the roadside habitat for forage and socialization, but retreat to woody habitats for shelter. Future studies should focus on determining the foraging habits of tortoises moving between these habitats to elucidate why tortoises are making these large movements between habitat types. Additionally, future studies should include the edges of less suitable habitat when performing surveys or studying the habitat use of Gopher Tortoise since many of the tortoises observed along roadsides frequently retreated to burrows in these areas. Not including the edges of less suitable habitat may lead to underestimates in population density and misguide our understanding of Gopher Tortoise habitat use.

Turtles experience high mortality on roads especially in high traffic areas (Gibbs & Shriver 2002; Steen et al. 2006). They may also be more vulnerable to predation and poaching as they are more conspicuous in this habitat. Juvenile Gopher Tortoises experience exceptionally low survival rates from predation, especially at KSC (Pike & Seigel 2006). This potential for being more easily detected alongside roads may further decrease survival rates causing bias for adults in the population's age-structure while adult survival is reduced due to vehicle impacts. Therefore, the high visibility and vehicular impacts may highly reduce survival and reproductive success. While Gopher Tortoises may utilize this habitat commonly at KSC, in combination with the unmanaged and less-resourceful habitats that generally border roadsides, the attractive open roadsides may instead function as ecological traps for Gopher Tortoises. However, survival and reproductive rates are currently unknown along roads and future studies should focus on these dynamics to further understand how roads and roadsides are impacting population dynamics.

Vermeulen (1994) found that roadsides were rarely used for movement between habitat patches, but were residential habitat for two of three beetle species he studied. Based on his observed dispersal distances, he likewise hypothesized the use of roadsides as breeding grounds to connect populations genetically (Vermeulen 1994). He recommended that roadsides be managed via the creation of larger habitat areas at maximum dispersal distances (Vermeulen 1994). We found similar results and conclude that roads are used as apparent long-term residential habitat as opposed to movement corridors. Based on these findings, we recommend comparable management strategies. Primarily, management should be made to reduce road mortality through the use of mitigation strategies such as tunnels under roads and walls to prevent movement onto the roads (Ruby et al. 1994; Dodd et al. 2004; Woltz et al. 2008). Secondly, we recommend that roadside habitat be enhanced by widening and naturalizing small areas along the road with native scrub vegetation. This will provide miniature habitat patches that provide increased food resources, allow populations to establish, and link distant locations. If roadsides function as ecological traps, their naturalization may provide more resources to counter these effects and produce higher survival and reproductive rates. Nonetheless, these mini-habitat patches will need to be regularly burned to maintain open habitats needed by Gopher Tortoises. We recommend the placement of these mini-habitat patches at a maximum distance of 500 meters.

These recommendations will not only enhance connectivity of Gopher Tortoise populations, but also of the commensal species which use their burrows. However, we urge caution due to the potential that these regions act as ecological traps, especially on medium to high traffic roads where mortality for tortoises is highest. Along these roads, the risk of mortality may be too high for the implementation of such management without copious mitigation

strategies to reduce mortality. Nonetheless, additional studies are needed to understand how roadsides can be managed to function as wildlife corridors for other species.

STOPPED DEAD IN THEIR TRACKS: THE IMPACT OF RAILWAYS ON TESTUDINE MOVEMENT AND BEHAVIOR

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, Andr en 1994, Collinge 1996, McKinney 2006, Haddad et al. 2015). Roads, in particular, are well documented to cause habitat fragmentation (Forman and Alexander 1998, Forman and Deblinger 2000, Forman et al. 2003). Roads increase mortality from wildlife-vehicle collisions and negatively alter both the behavior and genetic structure of multiple taxa (turtles, amphibians, small mammals, snakes, birds, insects) (Gibbs and Shriver 2002, Mazerolle 2004, Rico et al. 2007, Clark et al. 2010, Kociolek et al. 2011, Baxter-Gilbert et al. 2015). However, other barriers may have similar effects but remain understudied in comparison (Forman and Alexander 1998, Forman and Deblinger 2000, Dorsey et al. 2015). Railways, for example, may similarly impede movement and increase mortality not only from impacts with trains, but also from electrocution and entrapment between the rails (Dorsey et al. 2015). Entrapment can even occur on rails that have been inactive for several years, yet little research has been done in the field of rail ecology (Dorsey et al. 2015).

The few studies that exist examining rail ecology clearly demonstrate an increase in mortality, habitat fragmentation, and restriction of movement associated with railways (van der Grift 1999, Dorsey 2011, Dorsey et al. 2015). Railways have likewise been shown to alter the behavior of species, even at large distances, as well as their genetic population structure (Ito et al. 2005, Bartoszek and Greenwald 2009, Dorsey et al. 2015). Most of the information available is isolated to a small set of species, mainly ungulates and bears (Dorsey 2011). It is speculated

that railways impact species at a lesser level than roads, but certain taxa may actually be more vulnerable to railways due to risks of entrapment or electrocution (Dorsey et al. 2015). Further investigation is needed into the full impacts of railways on wildlife.

Turtles and tortoises (Testudines), 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). 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 were able to 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). Because of this same inability to cross rail lines in Hermann's Tortoises (*Testudo hermanni*), high mortality rates were observed along railways (Iosif 2012). Individual turtles are infrequently able to cross such obstacles, but often instead only patrol the barrier in an attempt to find means of crossing (Ruby et al. 1994). Additionally, the effectiveness of Testudine-based railway management is 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 Testudines may be able to cross railways by modifying their behavior and movement along the barrier, yet no study has been done to explicitly examine railway crossing frequency, the impacts of railways on Testudine movement and behavior, or management actions that could reduce mortality.

Here we use Gopher Tortoises (*Gopherus polyphemus*) as a model system. *Gopherus polyphemus* was selected due to its large body size as compared to other North American Testudines, which was predicted to facilitate movement over the rails. Additionally, *G. polyphemus* are highly terrestrial, making them likely to encounter railways throughout their

range. Engeman et al. (2007) documented that *G. polyphemus* are often found between rails and face increased mortality from becoming trapped, overheated, and dehydrated (Figures 6a & 6b). *Gopherus polyphemus* are considered threatened in every state in which they are found and is a candidate species for federal listing (Figure 6c). They are experiencing continued population decline from habitat loss and fragmentation and finding ways to connect isolated populations may increase population sizes and genetic diversity (Auffenberg and Franz 1982, Enge et al. 2006). Gopher Tortoises function as ecosystem engineers throughout the Southeastern Coastal Plain by digging burrows that serve as refuges for themselves and over 360 other documented species (Young and Goff 1939, Jackson and Milstrey 1989, Lips 1991, Witz et al. 1991, Kent et al. 1997). Some of the species that use their burrows are legally protected such as: Eastern Indigo Snake (*Drymarchon couperi*), Pine Snake (*Pituophis melanoleucus*), and Gopher Frog (*Lithobates capito*). Insight into the impacts of railways on *G. polyphemus* may assist conservation efforts in properly managing railways to conserve this flagship species, their commensals complements, and other Testudine species.

The aim of this study was 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 effects railways have in bisecting populations. First, we used radio-telemetry to determine whether railways act as a barrier to movement by comparing each individual's movements and number of crossing events to those predicted by randomized movement patterns. Second, we used observational behavior trials to assess crossing ability and to determine if individuals found near the railways are more likely to cross than those unfamiliar with such

obstacles. Lastly, we tested a management strategy to connect areas bisected by the railway using game cameras to record tortoises along the modified railway.

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 (Figure 6d). Despite being inactive, the railway is a site of frequent Testudine entrapment and mortality, especially of *G. polyphemus* (M.R. Bolt personal communication, Figure 6a). 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. 1981). Only adults classified as greater than 23 cm carapace length for males or 24 cm for females were used (Landers and McRae 1982).

Radio-Telemetry

Between May 2015 and July 2016, Advanced Telemetry Systems R1930 transmitters (24 g; 40 ppm) were used to track a total of 10 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, Watsonville, CA). The antenna was wrapped around the marginal scutes of the carapace and adhered to the posterior marginal scutes using the West Marine 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 possibility of frequent railway-crossing events. Tracking was then reduced to once per week 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, along with which side of the railway the tortoises occurred (e.g. east or west). GPS coordinates were entered in ArcMap 10.2.2 and the observed number of crossing events was counted for each tortoise (Table 3).

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). Beginning at the initial capture location of each tortoise, 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 (Figure 7a). 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. To account for this, the study area was increased by 200 meters to the east and west. Doing this included habitats not used by tortoises, such as the ocean and marshes, and therefore reduced biological relevance. However, including areas farther away from the railways also decreased the likelihood of the tortoise crossing the railway during simulations and was therefore a good test of the true impact of the railway on movement.

The number of railway crossing events was counted for each simulation and a distribution of predicted crossings was built for each individual (Figure 7b). 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 (Figure 7b; Calenge 2006, Shepard et al. 2008, Calenge et al. 2009). Lastly, we used a generalized linear model with Gaussian distribution to test for differences in expected crossing based on sex and size (carapace length) to determine if other factors played a role in a tortoise's ability to cross.

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 tortoises (7 female: 5 male) were found either in the tracks or within 100 meters of the tracks. This distance was used based on a combination of the maximum movement made by a radio-tagged tortoise perpendicular to the tracks and documented secondary foraging distances (Ashton and Ashton 2008). These tortoises are presumably familiar with the railway and may have experience in crossing them. Naïve tortoises (6 female: 6 male) were those located any distance greater than 100 meters from the railroads and were presumably 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 both habituated and naïve familiarities, but unlike the previous groups, the behavior of these tortoises was not measured in railways but 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 (Figure 8a). Vegetation along active railways is often controlled using herbicide spraying, and so choosing an inactive section devoid of vegetation represents the type of railroads wildlife is more likely to encounter. Control tortoises were moved to and tested in a control area of equal size in a flat, grassy area. 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 (Figure 8b). All tortoises were observed and behavior recorded for one hour (or until they crossed their respective barrier) at a distance between five and ten meters. Based on preliminary tests, tortoise behavior was unaltered at this distance and allowed for accurate recording of behaviors. 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 escaped time (Table 4). 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) in R. It was predicted that Control tortoises would have no difficulty in crossing the visual barrier and would fall out separately from the other two groups. Habituated tortoises were predicted to exhibit more behaviors associated with crossing the tracks such as meandering,

attempting cross, or even successful crossings when compared to Naïve tortoises, which were predicted to be more stationary due to unfamiliarity with the setting.

Management Testing

Several management strategies exist to help wildlife cross road barriers including tunnels, bridges, and ladders (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 or through the railway would be expensive to build and interfere with locomotive movement. A full tunnel under the rails would likewise be difficult to build and would not aid in the escape of tortoises already trapped between the rails. Instead, a trench under the rails and between the ties is a feasible option; it is easily dug, will maintain full railway functionality, and has been effective for Spotted Turtles (*Clemmys guttata*) in Massachusetts (Pelletier et al. 2006, Dorsey et al. 2015; Figure 9a).

To determine if this management strategy would encourage movement of Testudines, we dug two trenches along the railway at locations known to have high tortoise density and frequent mortality events between the rails. One Bushnell Natureview HD Max Game Cameras (Bushnell 119439, Overland Park, KS) was placed on the west side of each trench facing the rails (Figure 9a). 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 in order to be considered unique events. For each photo, we recorded whether the animal moved through the tunnel or only passed by the camera to establish actual trench use. Using these data, we determined the

proportion of detected tortoises that used the trenches overall and for each camera. Additionally, we determined the encounter rate of tortoises detected along the tracks per day and the number of tortoises that used the trenches per day.

Results

Radio-Telemetry

Tortoises were observed crossing the tracks 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, small males (#5224 & #5219; Table 3). Overall, expected crossings estimated from Monte Carlo simulations ranged from 0 to 29 crossings, depending on the tortoise, with an average of 7.54 crossings per tortoise. All tortoises had higher expected values than what was observed, and observed values were significantly less than expected in 5 of 10 tortoises, while several neared significance (Table 3). There was no difference in expected crossing ability based on tortoise gender ($F=0.14$, $p=0.71$) or size ($F=0.47$, $p=0.51$).

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, and a range of 0 to 78 attempts. Two tortoises flipped over onto their carapaces through the duration of the trial; one 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, with a range of 17 to 469 s. Only one tortoise spent a large enough amount of time attempting to cross the barrier to warrant recording the behavior; the remainder of the tortoises

crossed the barrier with such ease as it was only recorded as meandering. The remainder of the time for Control tortoises consisted of escaped time. The PCA shows a pattern of clear separation of railway-tested and Control tortoises, supporting the hypothesis that railways function as a barrier to movement and that tortoises are unlikely to cross (Figure 10). Interestingly, however, no behavioral differences were observed between Habituated and Naïve tortoises (Figure 10). This suggests that tortoises behave similarly regardless of familiarity with the railways in their attempts to escape.

Management Testing

Trenches connecting the east and west sides of the railway began to be used by *G. polyphemus* only four days following their installation (Figure 9b). Over the course of 184 trap days (92 per camera), 90 tortoises were detected moving along the tracks with an encounter rate of 0.49 tortoises per day. Fifty-five (61%) of these tortoises were identified using the trenches to move from one side of the tracks to the other, 17 (19%) only passed by the camera, and the remaining 18 (20%) had insufficient data to confidently determine if they used the trench. An average of 0.30 tortoises were encountered using the trenches per day to move from one side of the tracks to the other.

Discussion

Our results clearly show that railways act as a barrier to movement for *G. polyphemus* and substantiate the observations of tortoises that are often encountered trapped, dehydrated, or deceased in the railway. From 10 radio-tracked tortoises, we observed only 13 crossing events over the course of a year. Railways were crossed significantly less than expected for 5 of 10 tortoises, with all tortoises having lower observed values than what was expected by the CRWs.

This demonstrates a clear hindrance of movement, with neither gender nor size of adults found to influence a tortoise's ability to cross.

While the seaward side of the railway at KSC has less habitat and lower tortoise density than the inland side (S. Martin, unpublished manuscript), it still has abundant food and inland tortoises are often observed attempting to reach the seaward side. Gopher Tortoises are very active and frequently move among burrows; as such, we believe our simulations accurately depict tortoise movement in the absence of a barrier. Most of the observed crossings were isolated to two male individuals. Males are known to move larger distances to court, mate, and monitor multiple females across their home range to defend them against rival males (Johnson et al. 2009, Guyer et al. 2014). Prior to an observed crossing, tortoises were generally located near the north or south boundaries of our study area. At these edges the railway either ended and was enveloped by sand dunes or was crossed by the nearest road. These areas simplified crossing by providing “bridges” over the tall rails. Crossing events likely occurred at these 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).

Over the one hour trial periods, only control tortoises were able to cross. No behavioral differences were observed among the 24 remaining tortoises of varying railway familiarity. This shows that familiarity does not impact behavior and tortoises will exhibit the same behavior to attempt to escape the railway. 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. Additionally, our plots (Figure 8) were blocked at 20 m length by 5 cm x 15 cm

framing lumber, giving tortoises two perpendicular walls they could use as leverage to climb out. Most attempted crossing events occurred at these locations, yet no tortoise was 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.

The recent removal of the railway north of our study site allows for connectivity of our KSC tortoise population, but tortoise carcasses are still regularly found between the rails, demonstrating a clear impact. When presented with a barrier, *Gopherus* has been shown to patrol the barrier endlessly in search of a passageway through or around the barrier (Ruby et al. 1994). This determination to cross likely leads to increased mortality from rail entrapment and complete bisection of populations. 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 bisect populations of Testudines. This bisection of populations will disrupt the natural dispersal patterns and migration dynamics as well social behaviors between opposite sides of the railway. These consequences may be amplified the longer that they are separated. We conclude that nearly all tortoises in the vicinity of railways are susceptible to becoming entrapped or experiencing reduced movement potential, and that there is no behavioral means of tortoises adjusting to railways other than to avoid them entirely. Therefore, management to alleviate the impacts of railways is needed.

Tunnels underneath roads have been shown to dramatically reduce mortality of turtles (Dodd et al. 2004), but in order to aid in turtles that become trapped in railway tracks, a different method must be used. To accommodate this need, we tested a management strategy that could be

used to not only allow the movement of Gopher Tortoises from one side of the railway to the other, but also allow trapped tortoises an escape route. The trenches we dug underneath the rails and between the railway's ties were heavily used by *G. polyphemus*, with a tortoise recorded using a trench once every 3.3 days. One tortoise was observed falling from the center of the tracks 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 Testudine species were encountered using the trenches, but *T. carolina* are frequently encountered along and trapped within the railway and, given a longer survey period, would likely have been observed.

Implementation of railway tie trenches may permit greater movement between habitats and reduce mortality due to rail entrapment. These, in turn, will 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 Testudines were frequently observed deceased in the railways including Eastern Box Turtles (*Terrapene carolina*), Chicken Turtles (*Deirochelys reticularia*), and Florida Softshells (*Apalone ferox*). 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 Testudine species carcasses in the railways suggest this issue transcends *Gopherus* (Kornilev et al. 2006, Iosif 2012).

Here we clearly demonstrate the negative impacts of railways on Gopher Tortoises, which likely extend beyond our study species to other species of turtles and tortoises. In light of this, we also validate a management strategy to alleviate their effects. Railways are common in the United States; within the range of *G. polyphemus* alone, there are approximately 18,200 km

of railways that could be potentially impacting this species. However, over 50 Testudine species range throughout the United States, leading to a much larger impact. Furthermore, railways are less common in the United States than in other parts of the world such as Europe and Asia. In these regions of the world, thousands of km of railways are likely impacting Testudine 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 could benefit from the implementation of trenches between railway ties. Additionally, high speed railways are becoming increasingly common as a method to reduce CO₂ emissions throughout the world. As high-speed railways are likely to impact wildlife differently than freight rails, the field of rail ecology needs to expand to elucidate the impacts of these railways on wildlife (Dorsey et al. 2015).

CONCLUSIONS

Transportation infrastructure, such as roads and railways, are large contributors to habitat fragmentation and are known to have substantial impacts on wildlife and the environment (Forman & Alexander 1998; Forman 2000; Forman & Deblinger 2000; Forman et al. 2003).

Through my research, I have demonstrated that Gopher Tortoises are a great model for understanding population connectivity when impacted by these different types of transportation infrastructure. I have shown that, despite a clear potential for movement by tortoises along roads, roadsides instead act as long-term residential areas and as potentially suitable habitat. Tortoises found along roads tended to maintain home ranges comparable to those habitats with which they are more usually associated. Additionally, translocated tortoises remained along roads instead of traversing back to their original capture location demonstrating the potential suitability of this habitat for establishment and colonization.

Railways provide unique risks when compared to roads and I have clearly shown their impact on the movement and behavior of Gopher Tortoises. Tortoises tended to cross railways less likely than expected by chance and no tortoises were able to escape from the railway following placement between the rails for one-hour. Additionally, familiarity with the railway did not enhance a tortoise's ability to escape nor alter their behavior demonstrating the unique risk of entrapment that is not exhibited on roads.

For both roads and railways, I suggest management to reduce their impacts on Gopher Tortoises. For roads, I first suggest management to reduce road mortality by utilizing walls, barriers, and tunnels for enhanced connectivity across roads and prevention of movement onto roads. In addition, I suggest the creation of miniature habitat patches along roads where wildlife

can retreat have sufficient resources for population maintenance given the potential habitat suitability of roadsides. With regards to railways, I tested the implementation of trenches dug between railway ties as a management strategy using game cameras. I found this technique extremely effective at enhancing movement across railways as well as enabling tortoises to escape from the railways when they become entrapped. Given the frequent use, I suggest their placement along railways especially at high density areas.

While my research focused on Gopher Tortoises, it is significant for many other species as well as the fields of ecology and conservation biology. Primarily, Gopher Tortoises function as ecosystem engineers throughout their range in the Southeastern United States. Enhancing the conservation efforts and management decisions for Gopher Tortoises not only impacts this iconic species, but also over 360 commensal species which use their burrows. Yet, this research is also relevant to other species found along roads and railways. Here I have demonstrated potential benefits of roads that is largely ignored in the literature as roads may function as suitable habitat for some species. By reducing mortality and using roads as wildlife corridors or as suitable habitat, we may be able to enhance connectivity and reduce the impacts of habitat fragmentation. In addition, railways are understudied for many taxa. Here I have demonstrated that railways may impact some taxa more heavily than previously thought due to unique risks such as entrapment.

In addition, this research is relevant to the broader fields of ecology and conservation biology. For example, roadsides may act as an ideal system in which to study ecological trap theory. While the open habitat that roads provide appear suitable for Gopher Tortoises, the high mortality seen on roads for turtles and tortoises may create an ecological trap. Further research is needed to examine survival and reproductive rates of Gopher Tortoises along roads to determine

their potential benefits and impacts on population dynamics. I also frequently observed tortoises moving into dense hammock habitat with little ground cover from the road. I hypothesize that tortoises use the roadside habitat for food, but retreat to the more woody habitats for shelter. Future studies should focus on determining the foraging habits of tortoises moving between these habitats to elucidate why tortoises are making these large movements between habitat types. Lastly, I demonstrated a clear impact of railways further underlining the importance of the field of rail ecology. I suggest future studies examine other vulnerable taxa to understand how much this lesser studied transportation infrastructure impacts our environment.

APPENDIX: FIGURES & TABLES

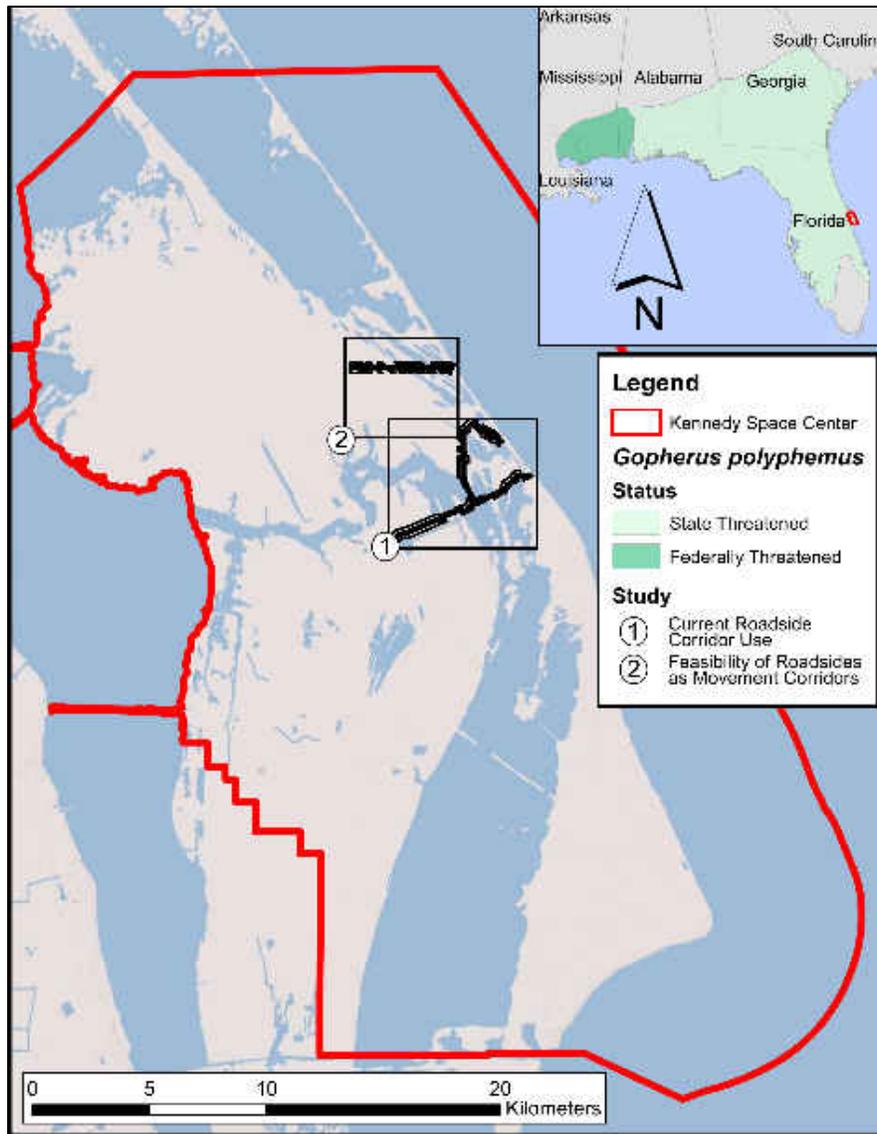


Figure 1: KSC with the potential roadside corridors connecting coastal and inland habitat outlined in black. The two parts of this study were done along two different roads which are boxed and numbered. ① The study area for examination of current roadside corridor use using radio-telemetry to determine how Gopher Tortoises in this region spatially used the roadsides. ② The study area for translocation of tortoises along the roadside to determine if movement through the corridor back to their original home range was feasible.

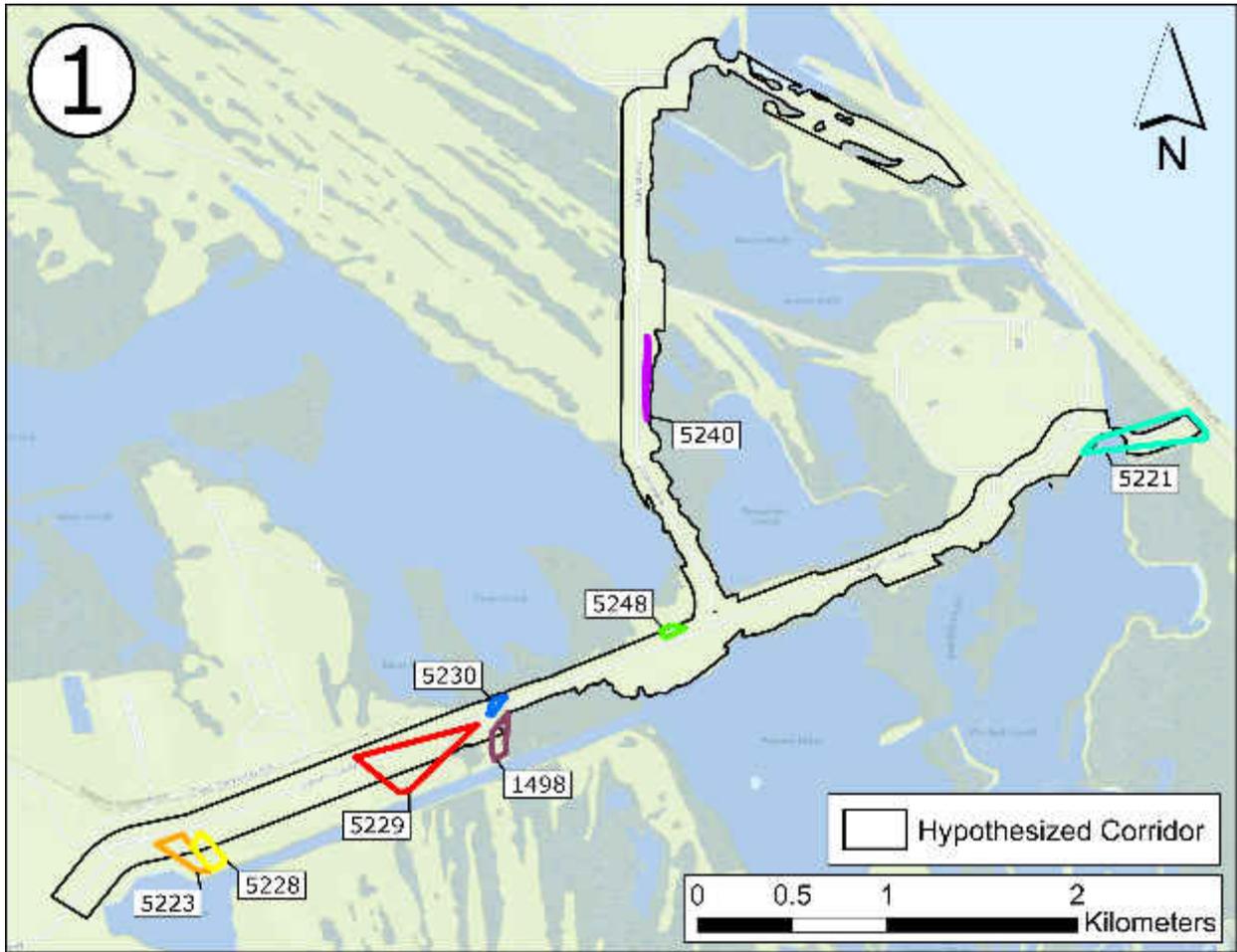


Figure 2: The potential roadside corridor used for study ① where current roadside corridor use was determined via radio-telemetry of tortoises captured along the roads. Eight example minimum convex polygon (MCP) home ranges are colored showing movement confined to areas along the corridor, but no movement directly through the corridor. Tortoise 5221 was the only tortoise observed moving from the corridor to coastal strand habitat over a distance of 500 m.

Table 1: Tortoises tracked for routine movements along roadside corridors using radio-telemetry with home ranges and distances traveled. CL, Carapace Length; Tracking Events, the total number of times an individual was tracked; MCP, 100% minimum convex polygon home range in hectares; Mean Dist., average distance traveled between tracking events in meters. Inland data was taken from Smith et al. (1997).

ID #	Sex	CL (cm)	Tracking Events	MCP (ha)	Mean Dist. (m)
Corridor Tortoises					
5229	Female	31.5	59	7.63	42.4
5223	Female	30.8	57	1.92	18.5
5220	Female	30.0	58	1.27	22.5
1498	Female	29.0	36	1.19	23.5
5225	Female	30.3	28	0.91	37.6
2237	Female	28.0	25	0.79	16.1
5248	Female	31.8	51	0.37	68.3
5236	Female	29.7	25	0.18	13.8
5242	Female	27.1	39	0.09	8.7
5241	Female	32.3	11	0.02	5.8
5247	Female	31.8	51	0.02	3.5
5260	Female	29.2	12	0.02	243.3
5221	Male	25.6	44	5.79	35.6
5228	Male	24.6	58	1.52	40.7
5246	Male	29.2	51	0.85	52.2
5237	Male	24.7	57	0.80	24.9
5235	Male	25.5	56	0.47	15.5
5230	Male	29.6	32	0.31	45.8
5240	Male	26.7	10	0.30	116.1
5238	Male	27.5	58	0.16	10.1

5222	Male	29.5	56	0.12	32.8
ID #	Sex	CL (cm)	Tracking Events	MCP (ha)	Mean Dist. (m)
5272	Male	26.7	11	0.01	12.8
Coastal Tortoises					
5233	Female	28.6	93	2.26	22.9
3116	Female	28.1	96	0.91	27.7
5234	Female	30.5	93	0.79	21.1
5226	Female	24.6	51	0.12	11.0
5219	Male	25.1	95	9.83	85.5
5224	Male	27.4	86	3.21	39.6
5218	Male	25.7	50	1.08	40.6
5227	Male	29.1	93	0.37	13.5
5237	Male	27.7	89	0.36	25.4
5009	Male	31.5	66	0.09	6.3

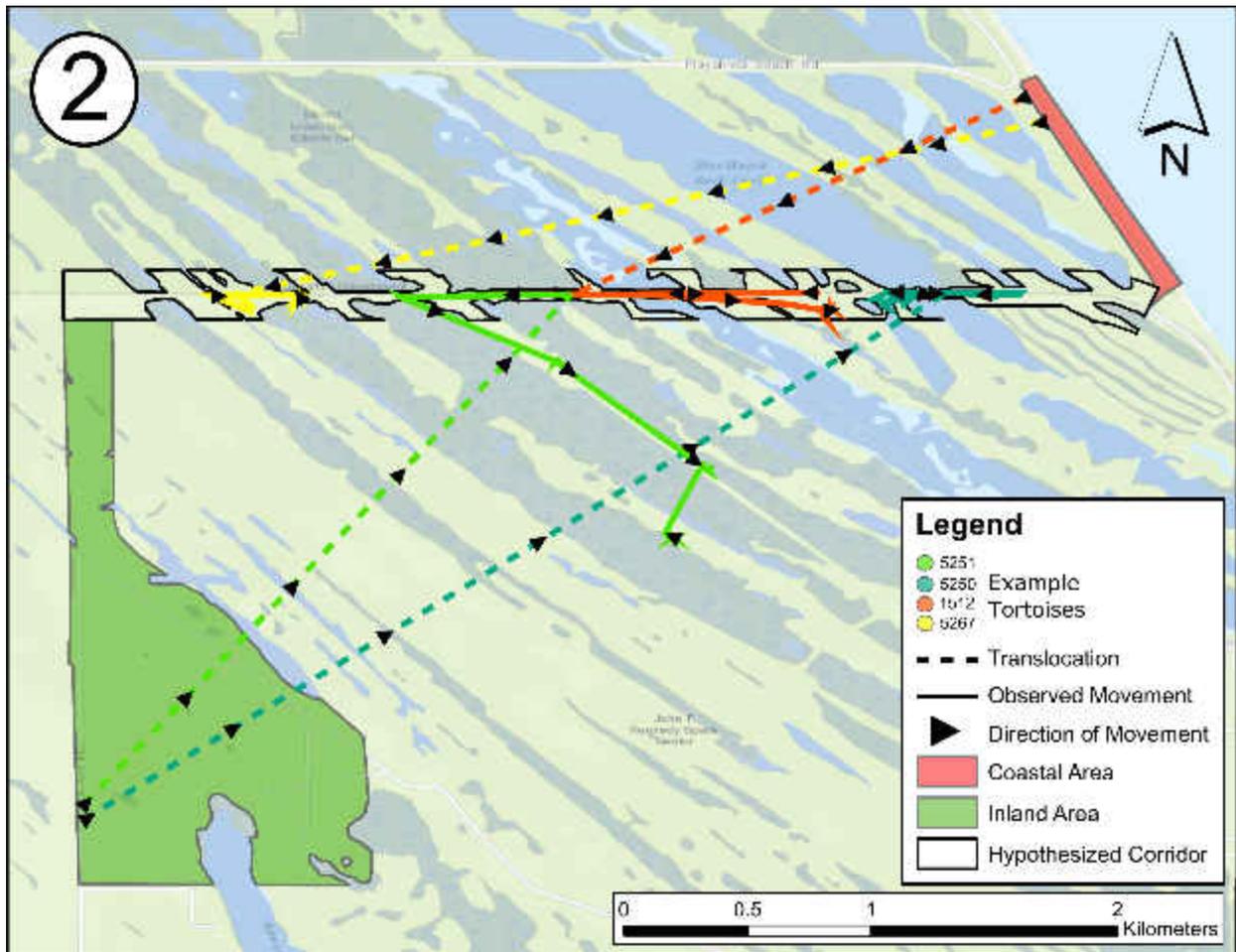


Figure 3: The potential roadside corridor used for study ② where the feasibility of roadsides to function as movement corridors was assessed. Tortoises were translocated (dotted colored lines) from either inland or coastal habitat into the potential corridor. Daily radio-telemetry (solid colored lines) determined if tortoises would use corridors to return to their original home range as opposed to straight-line paths.

Table 2: Tortoises translocated along a roadside corridor at Kennedy Space Center and tracked via radio-telemetry with translocation distances, expected return bearings, and results of Rayleigh tests of directional movement significance by either true homing or corridor use. CL, Carapace Length; Tracking Events, the total number of times an individual was tracked; SLTD, straight-line translocation distance in meters; Exp. Return Bearing, expected direction of travel given true homing to their original capture location; True Homing, p-value indicating significance of travel in the direction of the expected return bearing; Corridor Use, p-value indicating significance of travel in the orientation of the corridor (inland: 270°; coastal: 90°).

ID #	Sex	CL (cm)	Tracking Events	SLTD (m)	Exp. Return Bearing	<i>p</i>	
						True Homing	Corridor Use
Inland Tortoises: Happy Creek							
5249	Female	29.0	71	3090.7	237.3°	0.88	0.97
5250	Female	28.5	60	3733.5	235.0°	0.82	0.92
5251	Female	28.9	75	2714.6	219.9°	0.38	0.56
5252	Female	27.4	59	3411.9	232.0°	0.12	0.15
5265	Male	24.0	64	3194.5	241.7°	0.51	0.48
5283	Male	27.8	55	3198.2	266.4°	0.94	0.94
Coastal Tortoises: Canaveral National Seashore							
1510	Female	30.3	7	2925.5	89.1°	0.10	0.10
5261	Female	29.2	11	2861.7	76.4°	0.89	0.90
1512	Male	33.3	53	1801.4	63.5°	0.11	0.10
5253	Male	28.2	61	2042.2	75.3°	0.06	0.05*
5266	Male	30.3	2	2058.3	89.9°	NA	NA
5267	Male	28.0	60	2975.8	76.4°	0.44	0.33
5281	Male	26.7	55	2185.8	76.2°	0.70	0.71

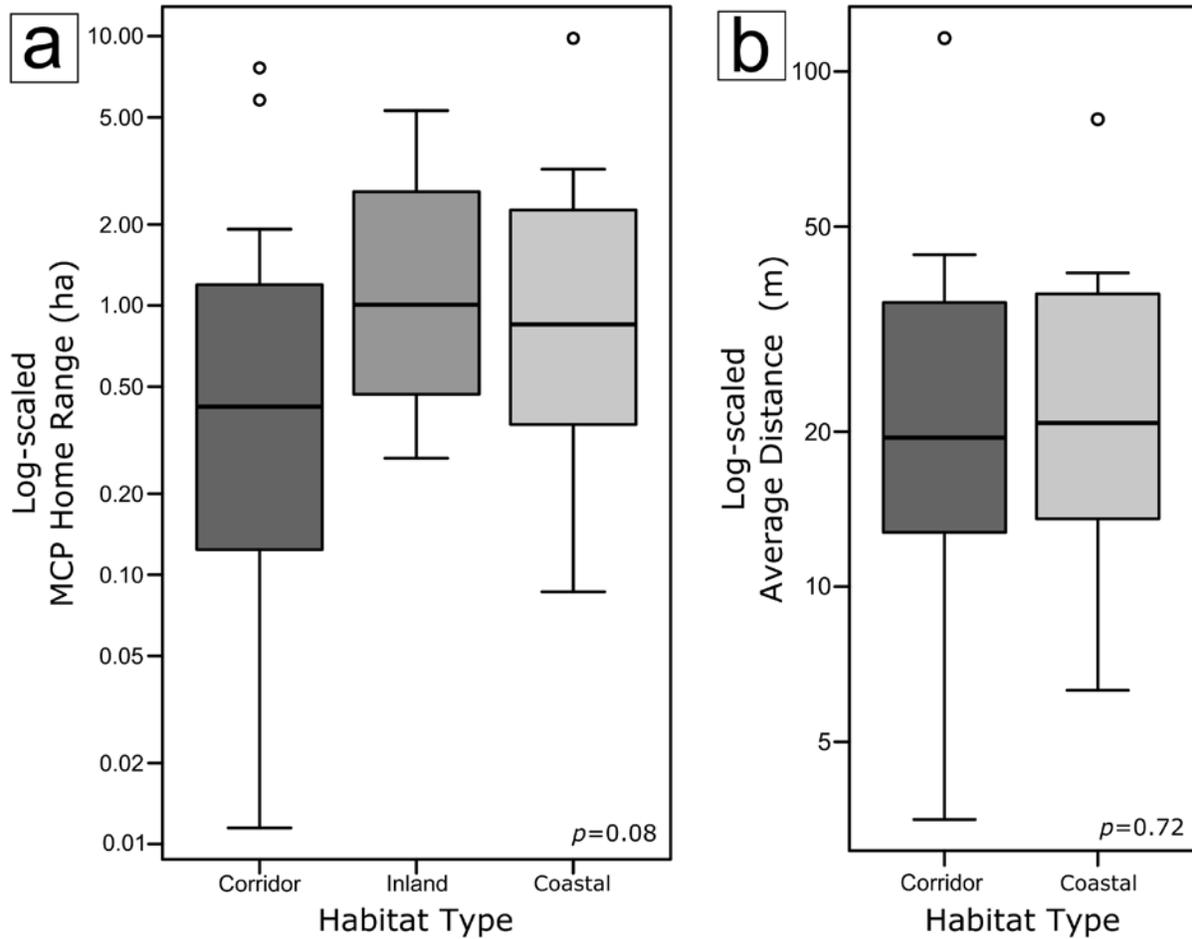


Figure 4: (a) Log-scaled minimum convex polygon (MCP) home ranges compared between habitat types (i.e. ruderal corridors, inland scrub, and coastal strand). Corridor tortoises occupied slightly smaller home ranges, but were insignificantly different due to the large variance seen in their home ranges. Inland home ranges were obtained from Smith et. al (1997). (b) Log-scaled average distances traveled between tracking events (m) compared between habitat types (i.e. ruderal corridors, coastal strand), but excluding inland scrub for which the data was unavailable. Average distances were not significantly different between habitat types.

Rayleigh Test for Directional Uniformity

Tortoise: 5250

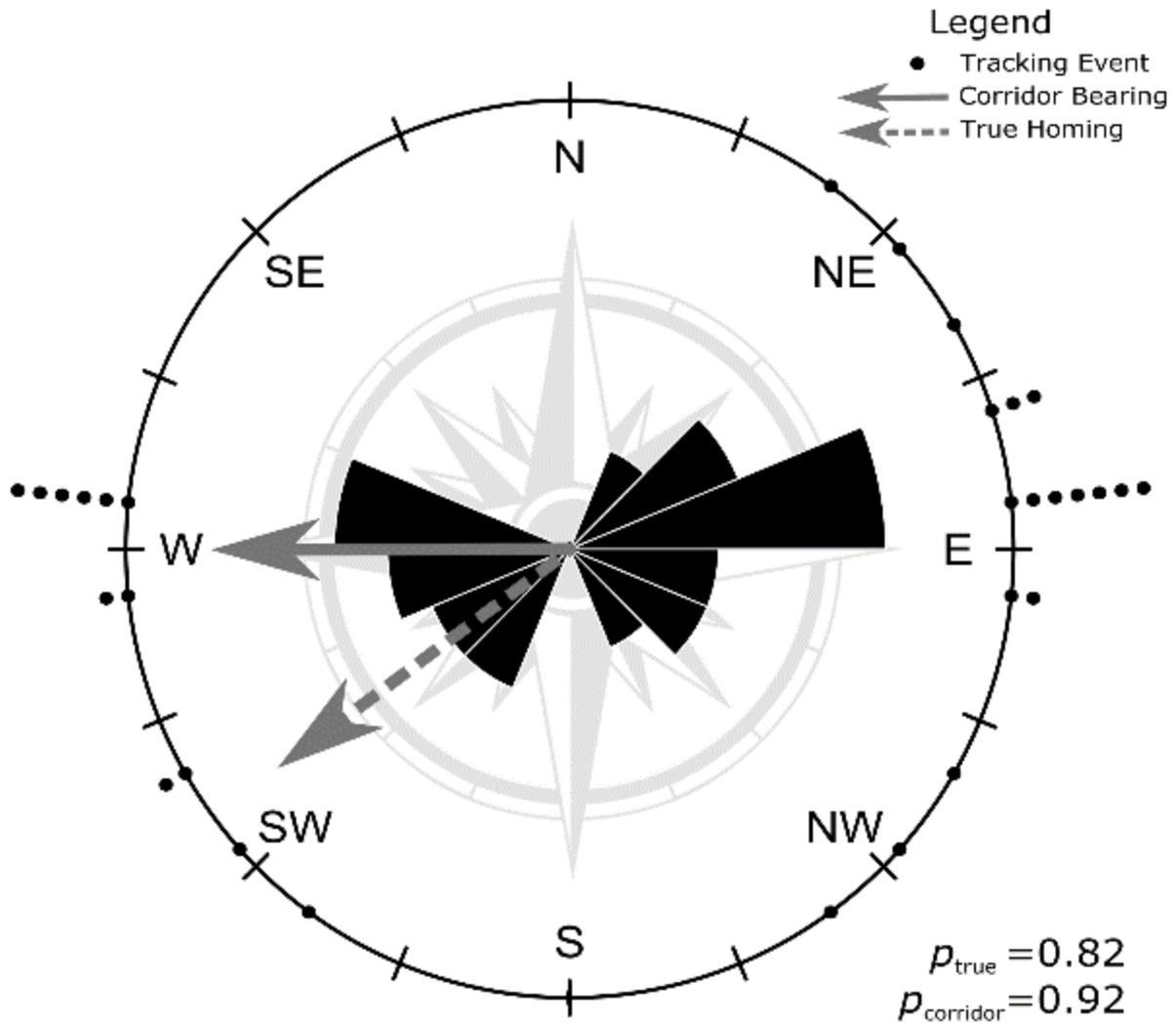


Figure 5: An example rose diagram (circular histogram) of a single inland tortoise's (ID: 5250) direction of travel when the distance traveled was greater than 7 m. The Rayleigh test of directional uniformity displayed insignificance in the directional movement for both true and corridor homing.

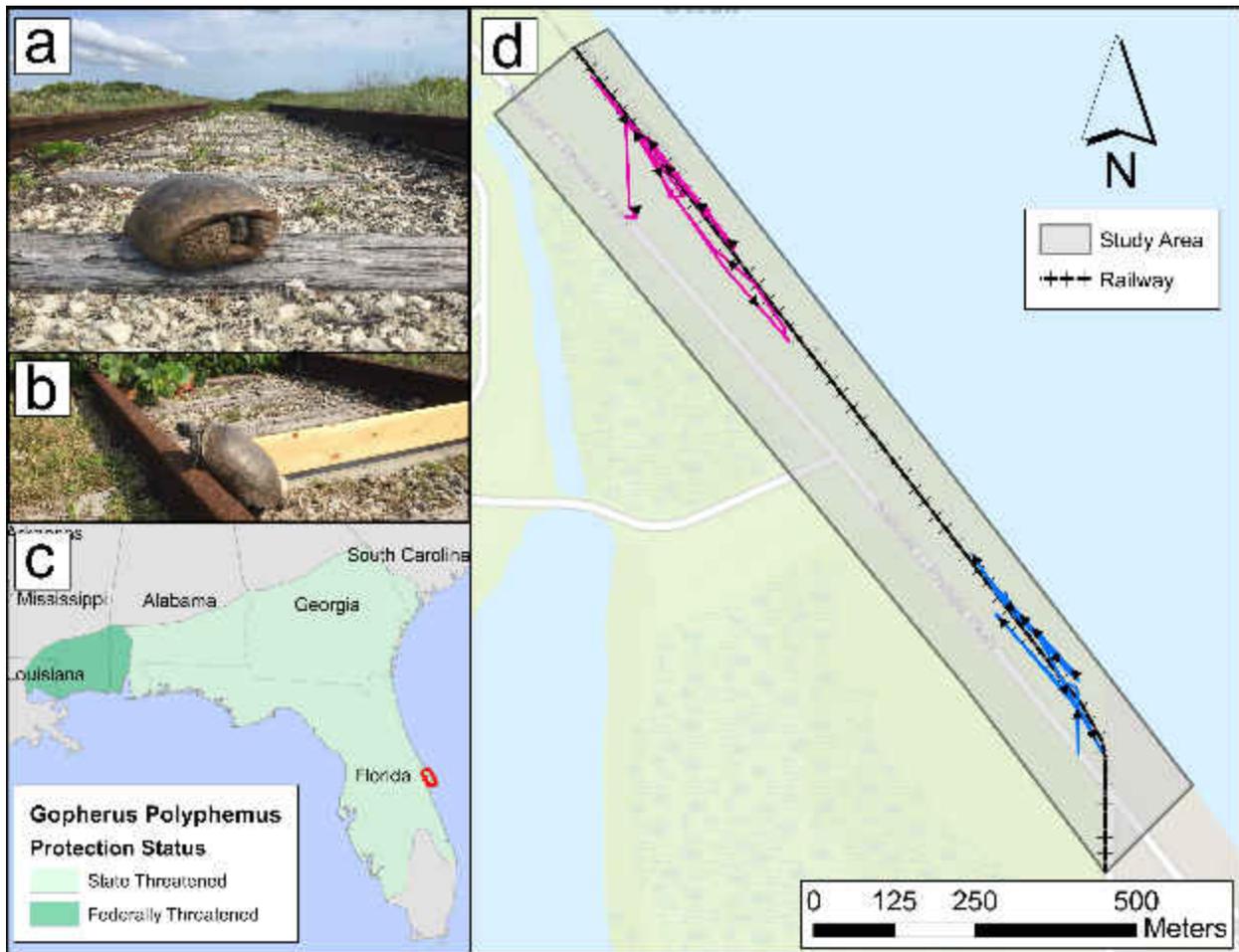


Figure 6: (a) Gopher Tortoise (*Gopherus polyphemus*) found in the center of the railway trapped by the tall rails and facing dehydration. (b) An attempted, but failed escape over the rails by a tortoise during one of the behavioral observation trials. (c) Range map of Gopher Tortoises in the southeastern United States with highlighted federal protection status and study area at the John F. Kennedy Space Center (KSC). (d) The coastal strand study area at KSC with the railway outlined and two example observed tortoise trajectories achieved via radio-telemetry.

Table 3: Radio-tracked tortoises with the observed and mean expected number of railway crossings based on Monte Carlo correlated random walk simulations. CL, Carapace Length.

ID #	Sex	CL	# Tracking	Observed	<u>Predicted Crossings</u>		
		(cm)	Events	Crossings	Mean	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**

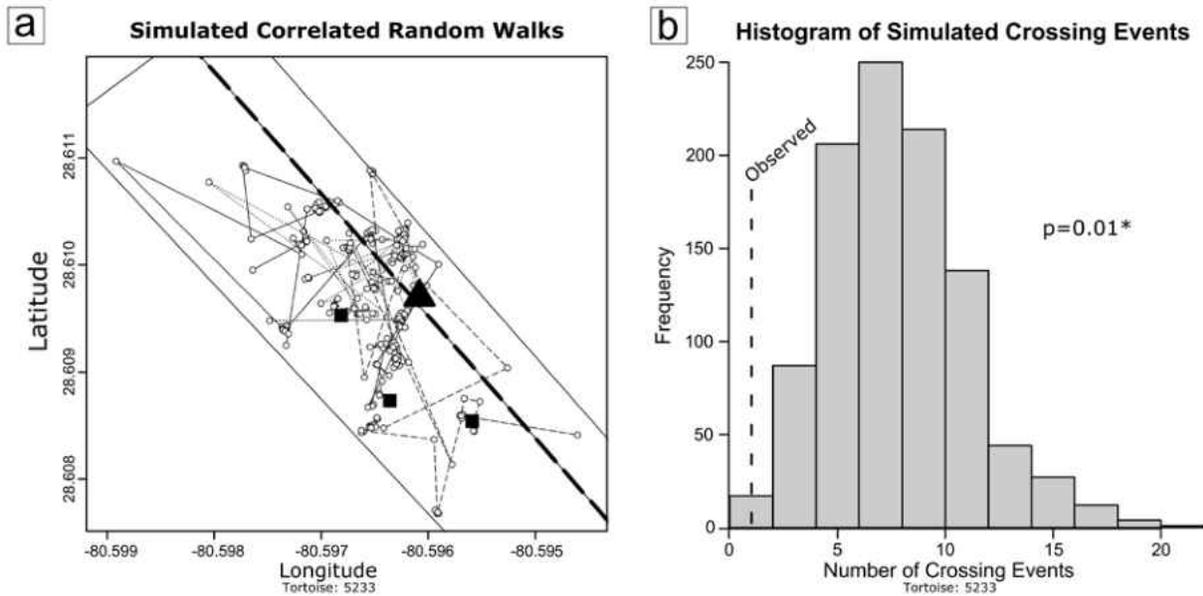


Figure 7: (a) Three simulated correlated random walks (CRWs) by a single tortoise (ID: 5233) confined to the coastal strand habitat. Each simulation is a different patterned line with the start point designated by the triangle (▲) and the stop points designated by squares (■). Each simulation counted the number of times the tortoise crossed the railway represented by the thick dotted line. (b) Histogram of the number of 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.

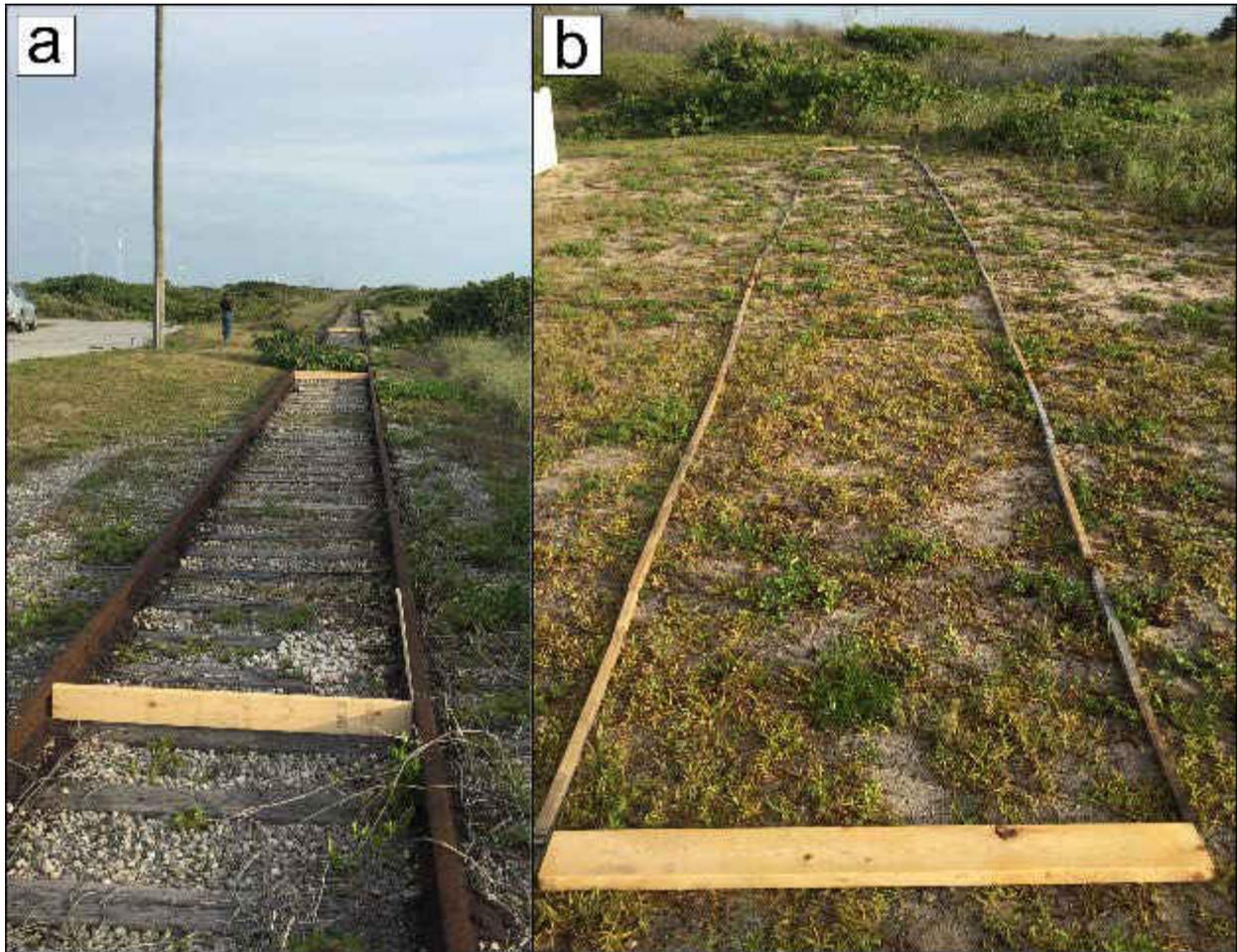


Figure 8: (a) The 20 m railway plot in which Gopher Tortoises were tested for crossing ability and behavioral differences between Habituated (n=12) and Naïve (n=12) railway familiarity. (b) The control plot in which tortoises (n=12) were tested for crossing ability and behavioral differences solely in the presence of a visual barrier.

Table 4: Ethogram of recorded *Gopherus polyphemus* behaviors.

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	Overtured on carapace and attempts to right itself by circular forearm movements
Escaped	State	Time spent escaped from the barrier in question
Cross Success	Event	A successful crossing over one of the two rails and subsequent all to the opposite side of the rail
Cross Fail	Event	A failed crossing over one of the two rails and subsequent fall to the center of the railway.



Figure 9: (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.

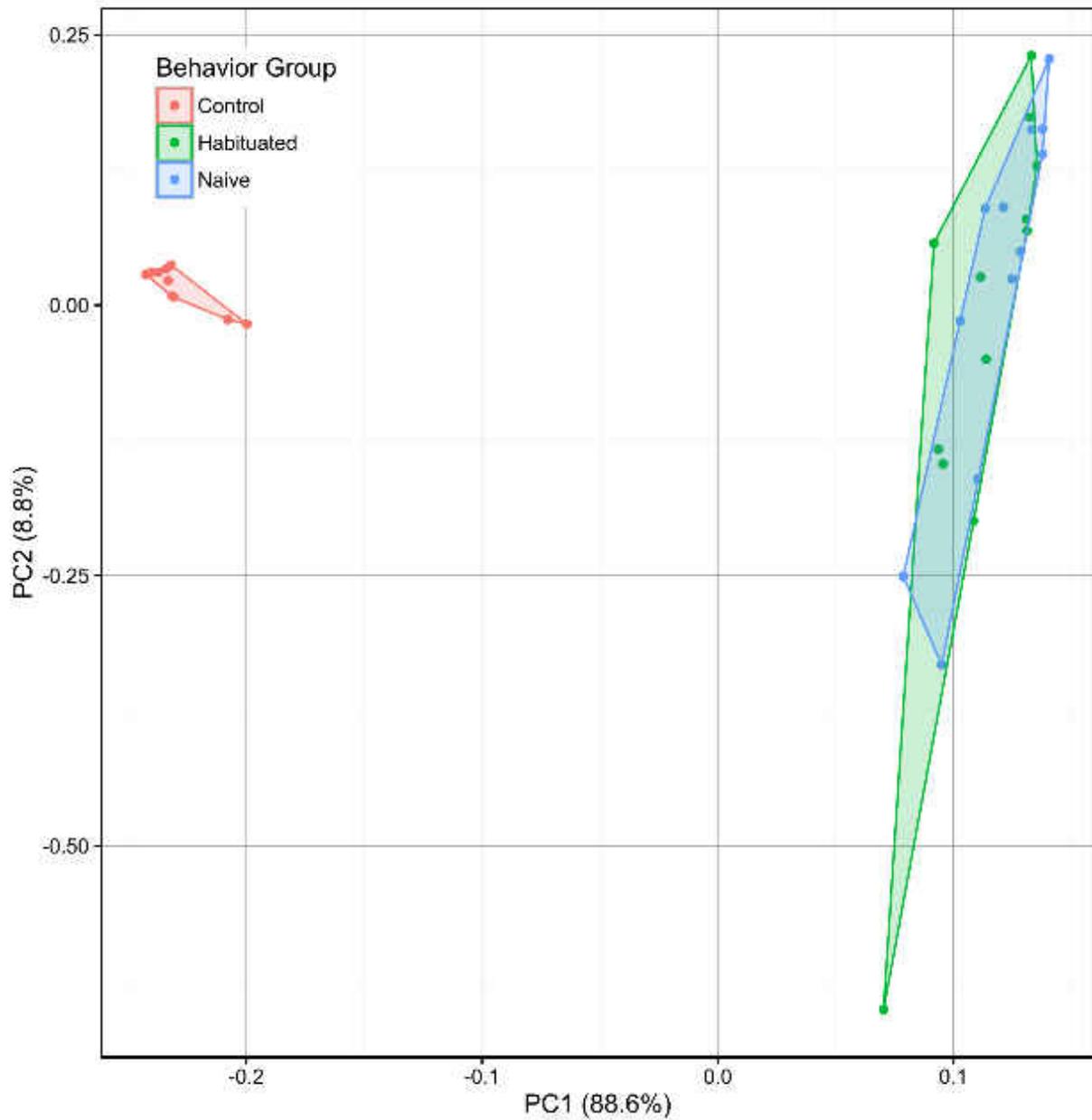


Figure 10: Principal component analysis (PCA) comparing tortoise behavior expressed over a one-hour observation period. Colors are based on railway familiarity with the control group. Control tortoises fall well outside the multivariate space of tortoises placed in the railway demonstrating the inability of tortoises to cross railways.

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