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On the Road Again: Assessing the Use of Roadsides as Wildlife Corridors for Gopher Tortoises (*Gopherus Polyphemus*)

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Abstract.—**Small populations resulting from the impacts of habitat fragmentation are prone to increased risks of extinction because of a lack of population connectivity. Roads increase habitat fragmentation, but properly managed roadsides may be able to function as wildlife corridors. Here we use radiotelemetry to observe movement patterns of Gopher Tortoises (*Gopherus polyphemus*) along potential roadside corridors at the John F. Kennedy Space Center (KSC) in Florida, USA, to determine if tortoises use roadsides as movement pathways between larger habitat patches or as residential habitat. Additionally, we translocated tortoises to study the feasibility of roadsides to function as movement corridors. We found that roadsides are not used as a movement pathway but rather as an apparent long-term residential habitat. Only one tortoise was observed exiting the roadside corridor, and minimum convex polygon (MCP) home range sizes and distances traveled remain similar to those exhibited by tortoises in larger habitat patches. Following translocation, we observed a failure to return home, either by direct paths or by corridor use, for all but one tortoise. Instead, most tortoises remained along roadsides after only a brief period of exploration. Overall, we find that roadsides act as independent, residential habitat instead of as a movement corridor. Future studies should focus on understanding the actual suitability of roadsides, as they may function as ecological traps given their attractiveness but high risk of mortality. While we urge caution, current management should treat roadsides as residential locations for Gopher Tortoises and focus on reducing road mortality.**

Habitat fragmentation from human alteration is known to reduce biodiversity and disrupt key ecosystem functions (Saunders et al., 1991; Collinge, 1996; Fischer and Lindenmayer, 2007; Haddad et al., 2015). It impacts taxa by isolating populations; increasing inbreeding, genetic drift, and mortality; and altering behavior and population structure (Gilpin and Soulé, 1986; Keller and Largiadèr, 2003; Jaeger et al., 2005; 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 and Soulé, 1986; Beier and Noss, 1998).

Connectivity often can be achieved with wildlife corridors. Wildlife corridors were first conceptualized by Wilson and Willis (1975) as organism-centric paths to facilitate immigration. In contrast, 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 and Noss, 1998). Landscape corridors ("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 and Noss, 1998). Corridor effectiveness, however, is generally dependent on the focal species, so studies need to be taxon specific (Beier and Noss, 1998).

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Corridors may take the form of overpasses or tunnels to cross roads because they are large components of habitat fragmentation (Forman and Alexander, 1998; Forman et al., 2003). Roads are known to increase mortality and alter both behavior and population structure of populations adjacent to the roadways (Gibbs and Shriver, 2002; Mazerolle, 2004; Marsh et al., 2008; Clark et al., 2010). For example, roads act as artificial boundaries that shape the home ranges of even highly mobile and wide-ranging species such as Bobcat (*Lynx rufus*) and Coyote (*Canis latrans*; 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). Vermeulen (1994) and Haddad (2015) suggested that roadsides may actually be able to function as corridors to connect fragmented landscapes. Vermeulen (1994) studied this possibility with beetles; however, our goal was to test this possibility with a more-vagile keystone species.

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 because of 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. Gopher Tortoises are threatened in every state in which they are found and are a candidate species for federal listing (Berry and Aresco, 2014). 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 and Franz, 1982; Enge et al., 2006). Their burrows serve as refuge for over 360 species, many of which are also threatened, such as Eastern Indigo Snakes (*Drymarchon couperi*), Pine Snakes (*Pituophis melanoleucus*), and Gopher Frogs (*Rana capito*; Young and Goff, 1939; Jackson and Milstrey, 1989; Lips, 1991). On average, Gopher Tortoises move only short distances (<100 m) to forage and occupy home ranges <2 ha (Berish and Medica, 2014). In contrast, these animals are also highly mobile and capable of occupying home ranges up to 13 ha and of moving distances >3 km over the course of a season to find new areas to forage (Berish and Medica, 2014). These large movements are rare but have been suggested to be amplified by the presence of roads, as they may function as travel corridors during social encounters (McRae et al., 1981b; Douglass, 1990; Diemer, 1992; Smith et al., 1997). Insight into the use of roadsides by *G. polyphemus* may inform plans to properly manage and use roadsides as wildlife corridors and to 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 radiotelemetry 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 radiotelemetry 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).

Materials and 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 (Fig. 1). Habitat along the roads consisted of short, ruderal (mowed) herbaceous cover that gradually transitioned to the road with no ditches or steep slopes. Adjacent to this, habitat transitioned into thick herbaceous cover, hardwood hammock, and ruderal woody cover that lacks groundcover and is largely considered unsuitable for tortoises because of the lack of food resources. We predicted that tortoises would use only 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). We used only adults classified as >23 cm straight-line carapace length for males or >24 cm for females (Landers and McRae, 1982). Sex was determined from external plastron shape, with males having a high degree of plastron concavity (McRae et al., 1981a). We attached R1930 transmitters (24 g; 40 ppm) (Advanced Telemetry Systems, Inc. [ATS], Isanti, Minnesota, USA) 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. Transmitters were adhered and covered using no. 3761483 Epoxy Putty Sticks

Table 1. Tortoises tracked for routine movements along roadside corridors using radiotelemetry at Kennedy Space Center, USA, 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 distance, average distance traveled between tracking events in meters. Inland data were taken from Smith et al. (1997).

ID no.	Sex	CL (cm)	Tracking events	MCP (ha)	Mean distance (m)
Roadside 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
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

(West Marine, Inc., Watsonville, California, USA). 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, we tracked tortoises by hand using a TR-4 receiver and RA-2AK H-antenna (Telonics, Inc., Mesa, Arizona, USA) between 0600 and 1800 h. Once located, we recorded tortoise locations with an Oregon 450 global positioning system (GPS; Garmin, Inc., Olathe, Kansas, USA). All analyses were run in R v3.3.1 (R Core Team, 2016).

Current Roadside Corridor Use.—We first sought to evaluate the current spatial use of roadsides and determine if these regions were 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 the Saturn Causeway (Fig. 1, 2A). It is ~5.5 km between coastal and inland habitats and varies in width from 25 to >200 m, but we predicted the corridor to be used in a much finer scale <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. We observed these tortoises 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

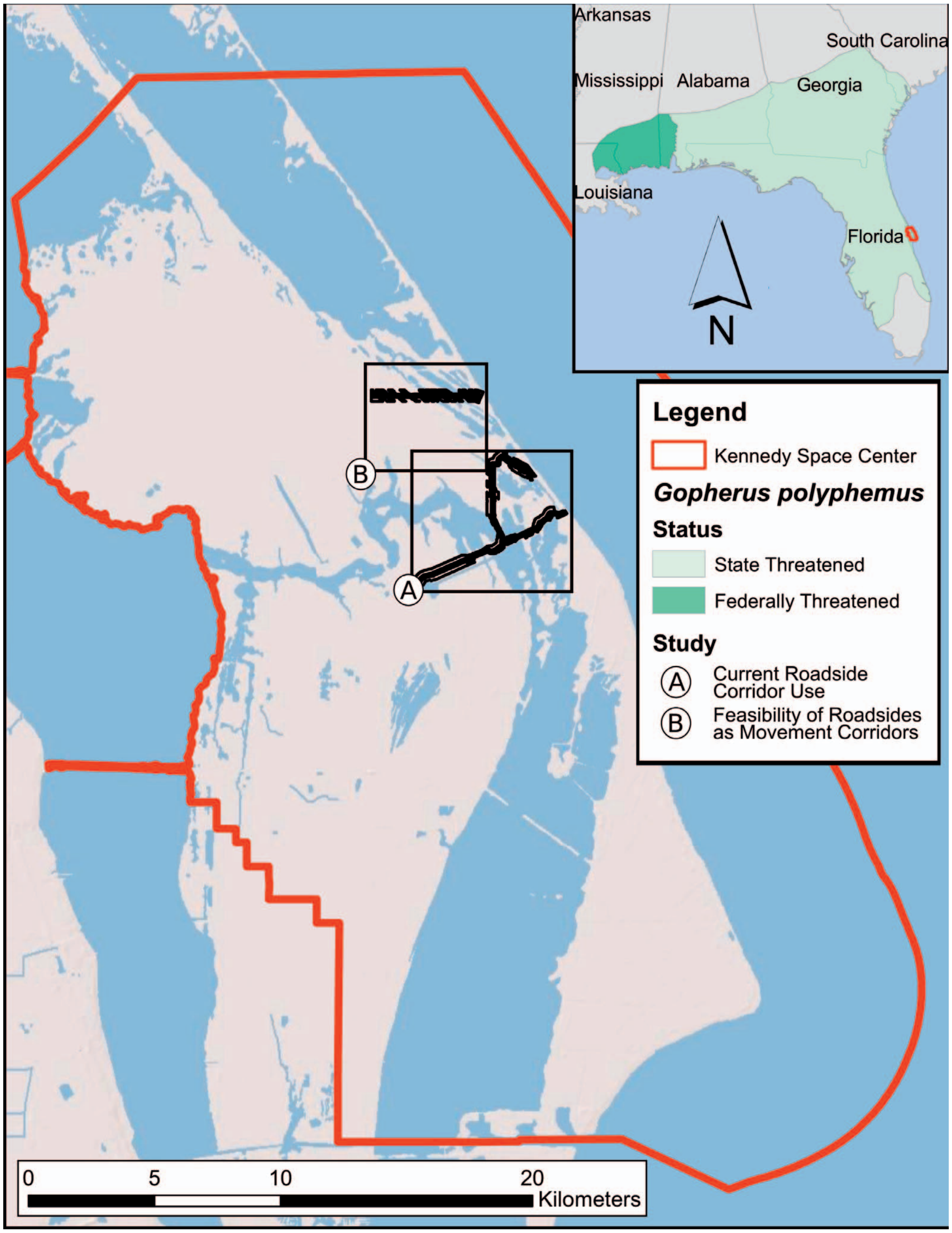

FIG. 1. Map of Gopher Tortoise range highlighting their conservation status in different parts of their range. Included is an outline of the study site at Kennedy Space Center, USA, with the potential roadside corridors connecting coastal and inland habitat outlined in black. We conducted both parts of this study along two different roads (boxed and labeled). Details of these two distinct sites appear in Figure 2. Box (A) is the study site for examining current roadside corridors use using radiotelemetry to determine how Gopher Tortoises in this region spatially used the roadsides. Box (B) is the study site for translocating tortoises along the roadside to determine if movement through the corridor back to their original home range was feasible.

typical habitats, we also obtained data on coastal tortoises. We captured 10 tortoises (4 females, 6 males) in coastal strand habitat at KSC and tracked them between May 2015 and July 2016 for a total of 812 events, averaging 81 per individual. Lastly, to compare home ranges between roadside, coastal strand, and scrub habitat types, we acquired data on inland tortoises, or tortoises captured from oak and palmetto scrub habitat at KSC, from Smith et al. (1997).

We calculated 100% minimum convex polygon (MCP) home ranges for each tortoise with the package 'adehabitatHR' (Table 1; Calenge, 2006). We chose MCPs to approximate home ranges because of their simplicity and convenience for comparing to previous studies, such as that of inland tortoises at KSC by Smith et al. (1997). The MCPs tend to overestimate of home ranges because they include extreme outlier points to create a home range; however, they perform well when little data are available and avoid many problems associated with other methods of home range estimation such as spatially autocorrelated data (Powell, 2000). We used linear regression to test for significant differences among corridor, coastal, and inland MCP home ranges. We then compared this model to a null regression and a regression of home ranges by tortoise sex by using sample-size corrected AIC (AICc; Burnham and Anderson, 2002) to determine if other variables accounted for

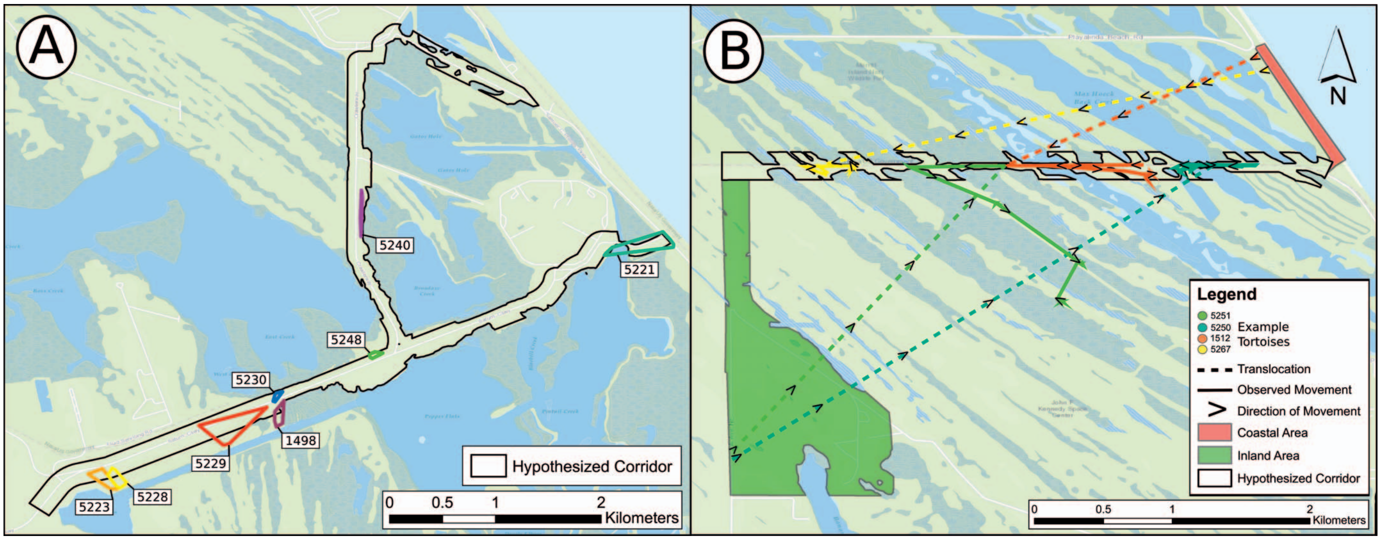

FIG. 2. Details of the two distinct sites within Kennedy Space Center, USA, used for the different parts of this study where (A) and (B) correlate to the study sites outlined in Figure 1. (A) Map of the study site where current roadside corridor use was determined via radiotelemetry of tortoises captured 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 individual observed moving from the corridor to coastal strand habitat over a distance of 500 m. (B) Map of the study site where we assessed the feasibility of roadsides to function as movement corridors. We translocated tortoises (dotted colored lines) from either inland or coastal habitat into the potential corridor. Daily radiotelemetry (solid colored lines) determined if tortoises used corridors rather than straight-line paths to return to their original home range.

the variation seen in the home ranges more effectively than did habitat.

Additionally, we used the package 'adehabitatLT' (Calenge, 2006; Calenge et al., 2009) to calculate the linear distance between data points. We calculated the total distance traveled for each tortoise and divided it 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 habitats and compared to that of a null model, sex, and carapace length. We excluded inland tortoises 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 KSC (Figs. 1, 2B). We used this road instead because of the unpredictable movements that tortoises could make following translocation. Only KSC security officers and National Park Service employees drive this road, so it had reduced automotive-related mortality. We first captured six tortoises (four females, two males) from inland habitat and seven tortoises (two females, five males) from coastal habitat (Fig. 2; Table 2). After attaching the transmitters, we translocated tortoises along the roadside corridor at randomly selected points between 2,000 and 4,000 m away from their originating

TABLE 2. Tortoises translocated along a roadside corridor at Kennedy Space Center, USA, and tracked via radiotelemetry 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 in centimeters (cm); tracking events, the total number of times an individual was tracked; SLTD, straight-line translocation distance in meters; expected 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°). * indicates significance ($P < 0.05$).

ID no.	Sex	CL (cm)	Tracking events	SLTD (m)	Expected return bearing	*P*-value: True homing	*P*-value: 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

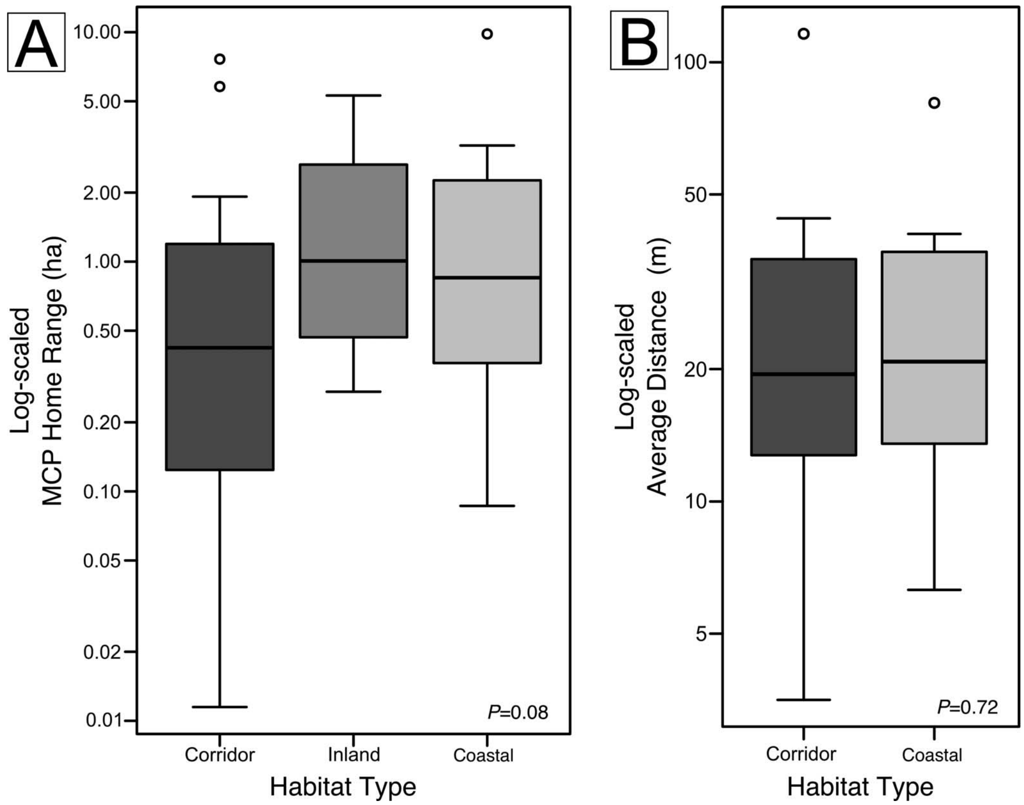

FIG. 3. (A) Log-scaled minimum convex polygon (MCP) home ranges compared between habitat types (i.e., ruderal corridors, inland scrub, and coastal strand). Corridor tortoises occupied slightly smaller home ranges but were not significantly different because of the large variance seen in their home ranges. 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 were unavailable. Average distances were not significantly different between habitat types.

habitat (Fig. 2B). Actual straight-line translocation distance (SLTD) varied based on the capture location of each tortoise (Table 2). After translocating the tortoises, we tracked them daily over the summer of 2016, based on the successful homing times of the closely related Desert Tortoise (*Gopherus agassizii*) (Hinderle et al., 2015). Overall, there was a total of 678 tracking events averaging ~52 per individual. Following this summer season, we recaptured and returned tortoises to their original locations.

If tortoises 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. We determined the compass bearing of each translocation and recorded tracking event using the package 'geosphere' (Hijmans, 2017). 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 traveled distances <7 m were within GPS accuracy and led to biases in cardinal directions. Therefore, we used only data with distances >7 m in our analyses. We performed two Rayleigh tests of directional uniformity for each tortoise in the package 'circular' (Agostinelli and Lund, 2013). We used these tests 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 toward 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 as the corridor.

RESULTS

Current Roadside Corridor Use.—We observed only 1 (ID: 5221) of 22 tortoises along the potential roadside corridor moving out of the corridor and into coastal habitat (Fig. 2A). The remaining 21 tortoises stayed along the roadsides occupying typical home ranges when compared to previous studies and across habitat types (Smith et al., 1997; Berish and Medica, 2014; Fig. 3). We used a linear regression to compare log-transformed 100% MCP home ranges of tortoises among the corridor, coastal, and inland habitats. No significant differences were found across habitat types ($R^2 = 0.11$, $P = 0.08$, $n = 46$; Fig. 3A), but inland and coastal home ranges were 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 of 0.01 to one of the largest of 7.63 ha. There was no significant difference in home range sizes by sex ($R^2 = 0.04$, $P = 0.18$, $n = 46$) nor by the additive effect of sex and habitat ($R^2 = 0.13$, $P = 0.12$, $n = 46$). Comparison of these regression models to a null model demonstrated habitat to be the best predictor, but by a ΔAICc of only 0.8 from the null model.

We also performed regressions on log-transformed average distance traveled between tracking events. These data were

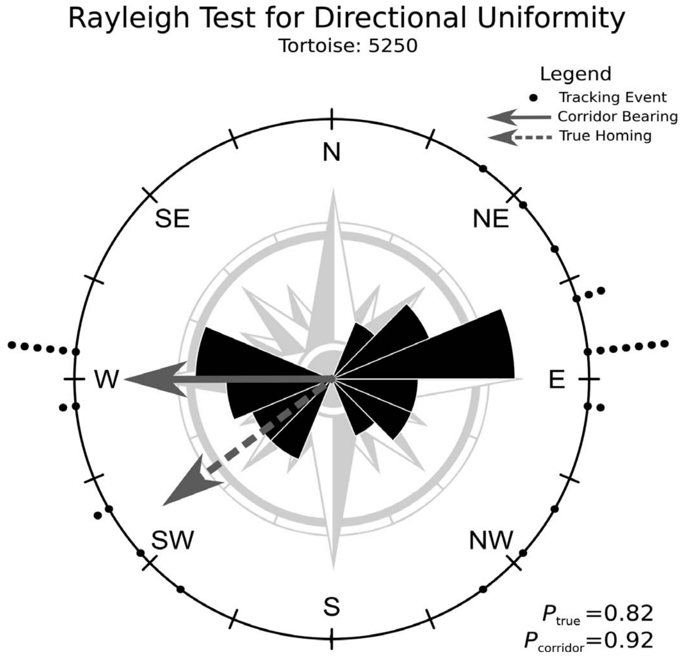

FIG. 4. An example rose diagram (circular histogram) of a single inland tortoise's (ID: 5250) direction of travel when the distance traveled was >7 m. The Rayleigh test of directional uniformity displayed insignificance in the directional movement for both true and corridor homing.

unavailable for inland tortoises, but there was no significant difference between corridor and coastal tortoises ($R^2 = 0.004$, $P = 0.72$, $n = 32$; Fig. 3B); however, both sex and carapace length (CL), respectively, had a significant effect on the average distances traveled ($R^2_{sex} = 0.15$, $P_{sex} = 0.03$, $n_{sex} = 32$; $R^2_{CL} = 0.16$, $P_{CL} = 0.02$, $n_{CL} = 32$). The model for CL as a predictor for the distances traveled had the lowest AICc and was separated by 5.6 AICc units from the habitat model that fell below the null model.

Feasibility of Roadsides as Movement Corridors.—Of the 13 translocated tortoises, only one male (ID: 5266) from coastal habitat successfully returned home. 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 (Fig. 2B). 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° to 266.4°, with an expected return bearing for corridor use of 270° (Fig. 4). The expected return bearing for true homing of coastal tortoises ranged from 63.5° to 89.1°, with the expected return bearing for corridor use of 90°. The Rayleigh test for directional uniformity found no significance for any tortoise's movement in the direct direction of their capture location (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 by 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 >500 m to do so (Fig. 2A).

Additionally, there was a lack of a homing response from translocated tortoises. Only one adult male tortoise (ID: 5266) successfully returned home in only 1 d following a translocation of >2 km. Because of the rapid homing response, we could not detect movement along the corridor and we are uncertain how the tortoise actually returned home. Of the remaining tortoises, none significantly oriented their movements in the direction of true homing and only one other male tortoise (ID: 5253) exhibited movements significantly oriented in the homeward direction of the corridor. The lack of a homing response via the Rayleigh tests may be because of all distances >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, we are uncertain whether this tortoise exhibited homing or simply attempted 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 and 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 because of 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 although movement along the road is feasible and may occur on rare occasions, we conclude it unlikely as little evidence exists 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 travel corridor between habitat patches. The roads at KSC used in this study 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. KSC roads were built in the 1960s to connect coastal and inland habitat. The relatively recent construction of these roadsides (within the lifespan of many adult tortoises) suggests that tortoises either colonized the roadside areas naturally or may have been moved there during construction projects on the site (RB and RS, pers. obs.). Our data indicate that tortoises now use these roadsides for residency as opposed to traveling between habitat types.

Roadsides may be attractive habitat to Gopher Tortoises for residency because of the openness of the habitat (Auffenberg and Franz, 1982). Historically, natural disturbances such as lightning-caused fires create open habitat that Gopher Tortoises prefer and use to maintain high population densities (Breininger et al., 1994; Martin et al., 2017). Natural fires often are suppressed by anthropogenic intervention, but other types of disturbances (e.g., prescribed fires and mowing) can act similarly to maintain open habitat. 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 and Deblinger, 2000). For example, abundances of a *G. polyphemus* congener, Desert Tortoises (*G. agassizii*), were negatively impacted up to 4,000 m from the road because of high mortality rates and road avoidance (Hoff and Marlow, 2002; Boarman and Sazaki, 2006). Interestingly, *G. polyphemus* appeared to use roadsides as residential locations, likely because of the open habitats created (Breininger et al., 1994).

The open habitat found along roads likely attracts Gopher Tortoises; yet, we regularly observed our tortoises moving into the marginal habitats of thick herbaceous cover, ruderal woody, and hammock habitats generally considered unsuitable for tortoises. These habitats have little groundcover and food resources, yet tortoises and burrows were commonly found in these areas. Radiotelemetry 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 Tortoises because 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 and Shriver, 2002; Steen et al., 2006). Turtles 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 and 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 because of vehicle impacts. Therefore, the high visibility and vehicular impacts may highly reduce survival and reproductive success. Although Gopher Tortoises may commonly utilize this habitat 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. Survival and reproductive rates are currently unknown along roads, however, 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 by creating 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 reduce road mortality through the use of mitigation strategies such as tunnels under roads and walls or ditches to prevent movement onto the roads (Ruby et al., 1994; Dodd et al., 2004; Woltz et al., 2008). Secondly, we recommend enhancing roadside habitat 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 spacing these mini-habitat patches at a maximum distance of 500 m.

These recommendations will enhance connectivity not only for Gopher Tortoise populations but also for the commensal species that use their burrows. We urge caution, however, because of the potential for these regions to 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.

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