Movement Ecology

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Vegetation cover, topography, and low-traffic roads influence Sonoran desert tortoise (*Gopherus morafkai*) movement and habitat selection

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Abstract

Background Anthropogenic activities occurring throughout the Sonoran Desert are replacing and fragmenting habitat and reducing landscape connectivity for the Sonoran desert tortoise (*Gopherus morafkai*). Understanding how the structure of the landscape influences tortoise habitat use and movement can help develop strategies for mitigating the impacts of these landscape alterations, which are conservation actions needed to support the species' long-term persistence. However, how natural and anthropogenic features influence fine-scale habitat use and movement of Sonoran desert tortoises remains unclear.

Methods The goals of this study were to (1) understand how characteristics of the landscape shape tortoise habitat use and movement in order to (2) identify factors that may reduce habitat use or threaten landscape connectivity for the species by discouraging or restricting movement. We collected GPS telemetry data from 17 adult tortoises tracked for two summer monsoon seasons, when tortoises are most active, in a U.S. National Monument along the international border between Arizona, USA and Sonora, Mexico. We used Hidden Markov Models (HMMs) to assign GPS locations to an encamped or a moving state. We used the moving state data in integrated Step Selection Analyses (iSSA) to examine how range-resident Sonoran desert tortoises select habitat and respond to landscape features while moving.

Results Tortoises selected to move through areas of intermediate vegetation cover and terrain ruggedness and avoided areas far from desert washes and close to low-traffic roads. Tortoises increased their speed when approaching or crossing low-traffic roads but showed no detectable response to a highway.

Conclusion Bare earth or high vegetation cover, flat or extremely rugged terrain, areas far from desert washes, and low-traffic roads may discourage or restrict tortoise movement. Therefore, preventing the development of roads, activities that degrade washes, and activities that thin, remove, or greatly increase vegetation cover may encourage tortoise habitat use and movement within those habitats.

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Background

Resource selection studies enhance our understanding of how target species respond to features or processes occurring in the landscape [1–4]. These insights provide a foundation for conservation plans designed to identify important habitats, preserve landscape connectivity, and restore the ecological functions of degraded landscapes [1, 5]. Recent studies have demonstrated that we can further improve our understanding of how landscapes shape habitat use by incorporating animal movement behavior into these resource selection studies [1, 6].

Numerous studies have used GPS dataloggers to understand space use, habitat selection, and movement of North American tortoises (genus *Gopherus*; [7–11]). Preserving tortoise habitat and mitigating the negative impacts of anthropogenic disturbances on habitats have been identified as conservation priorities for *Gopherus* species like the gopher tortoise (*Gopherus polyphemus*) and the Mojave desert tortoise (*Gopherus agassizii*) [12, 13]. Studies examining tortoise movement and space use have demonstrated that both natural (e.g., terrain) and anthropogenic landscape features (e.g., fences and roads) can constrain or alter tortoise movement or habitat use [7–10]. For example, the use of GPS dataloggers has revealed that *G. agassizii* avoids areas of high slope, low vegetation coverage, and areas near roads, and that they alter their movement behavior when encountering anthropogenic features like fences and roads or disturbed areas [7–9]. These fine-scale insights into the influence of the landscape on tortoise habitat use and movement have provided valuable information applicable to developing or refining management actions intended to preserve or restore tortoise habitat such that it may facilitate landscape connectivity among tortoise habitats and populations. However, such studies have been limited to those tortoise species and populations protected under the Endangered Species Act (ESA), which excludes the Sonoran desert tortoise (*Gopherus morafkai*).

G. morafkai was denied listing under the ESA in 2022 based on findings suggesting their populations are not significantly declining throughout their range [14]. However, a recent IUCN Red List assessment found *G. morafkai's* populations and geographic range to be shrinking, warranting a "Vulnerable" status [15]. *G. morafkai* is threatened by climate change, wildfire, the invasion of non-native grasses, development, barriers to movement, and habitat loss and fragmentation [16–22]. Development and the spread of transportation infrastructure are increasing throughout the species' range [23, 24]. In Arizona, 70% of Sonoran desert tortoise habitat is within 1 km of development [20]. Furthermore, range-wide, urban development is projected to replace up to 10% of remaining tortoise habitat in the next 100 years [14]. Roads, which are proliferating throughout the species' range, fragment habitat and isolate tortoise populations and may cause direct mortality, increase risk of illegal collection, and reduce landscape connectivity among populations [16, 25–28]. Unpaved roads and off-road vehicle (OHV) use can degrade tortoise habitat (e.g., by removing vegetation cover), increase the risk of direct mortality or illegal collection, and may discourage tortoise movement [9, 28–30]. In addition to the individual effects a single road may have, the increasing density of these features has been linked to declines in tortoise populations [31]. Ultimately, anthropogenic activities that degrade or replace tortoise habitat may reduce landscape connectivity among tortoise populations by making them less permeable to movement, which may subsequently reduce demographic rescue, gene flow, and other processes that support the species' persistence [22, 32, 33]. For these reasons, protecting suitable tortoise habitat and preserving or restoring landscape connectivity have been identified as conservation priorities for *G. morafkai* [14, 15, 22].

Studies of *G. morafkai*'s space use, habitat use, and response to disturbance are relatively few compared to *Gopherus* species protected under the ESA (i.e., *G. polyphemus* and *G. agassizii*). Conservation plans for *G. morafkai* are thus partially dependent on knowledge of these protected species, particularly *G. agassizii* [16]. Although *G. agassizii* and *G. morafkai* are both desert tortoises and face similar threats [29], they differ in some aspects of their ecology, habitat use, and behavior [34]. For example, *G. agassizii* is most associated with flatter terrain whereas *G. morafkai* is most associated with steep and often rugged terrain [16, 35, 36]. It is plausible that behavioral differences may also extend to their response to disturbance or anthropogenic features, yet this remains unclear. Studies examining *G. morafkai*'s space use, habitat use, and response to disturbance may help understand which conservation actions developed for the well-studied *G. agassizii* may be applicable to *G. morafkai* or may help refine conservation strategies specific to the species.

Studies that have examined habitat use and space use of *G. morafkai* have found that topographic features like steep slopes and deeply incised desert washes are important habitat features [36–38], and that they make greater use of areas that are closer to washes and unpaved roads than what is available to them [28]. *G. morafkai* has been found to use microhabitat with more vegetation cover as both juveniles and adults [37, 38]. In contrast, another study examining habitat use at a larger spatial extent found vegetation to be less important than topographic and geomorphological features [36]. These studies have been limited to traditional survey methods (e.g., plot surveys and occupancy analysis) and radio-telemetry studies. While providing new and valuable information on the species' habitat use, these studies lack the finer temporal resolution of GPS telemetry, which has elucidated patterns in space use for other North American tortoises and so are likely capturing only a fraction of the species' daily activity and, possibly, habitat use. Furthermore, how landscape features, including anthropogenic features like roads, influence how and where *G. morafkai* moves remains unclear. The paucity of information on this subject specific to *G. morafkai* precludes the development of effective management strategies for the species.

In this study, we used GPS dataloggers to record fine-scale tortoise movements and combined Hidden Markov Models (HMMs) and integrated step-selection analyses (iSSA) to examine how *G. morafkai* selects habitat and responds to roads when moving. Generally, we expected *G. morafkai* to make selective decisions as they moved through the landscape. Hence, we expected that (1) tortoises would select to move through areas with landscape features associated with shelter (i.e., rugged terrain, vegetation cover, and incised washes); (2) tortoises would avoid flat terrain, bare earth, and areas near roads; and (3) tortoises would adjust their movement behavior when moving close to or crossing roads. Our findings provide insight into how landscape characteristics like rugged terrain, vegetation, or roads can alter space use and movement of range-resident tortoises. This information may be applied to the development of management plans focused on preserving or restoring habitat such that it maximizes use, increases permeability to movement, and minimizes the impacts of barriers on localized movement for *G. morafkai*.

Methods

Study species

Gopherus morafkai is a terrestrial, herbivorous tortoise found throughout most of the Sonoran Desert. It was described as a distinct species from *G. agassizii* in 2011 based on differences in genetics, habitat use, ecology, and behavior [39]. *G. morafkai* has an activity pattern that coincides with seasonal rains [40]. They may exhibit some activity in late winter or spring, but activity peaks following monsoon rains that arrive in late summer and give rise to food resources like annual plants [40]. During the winter and arid months of late spring and early summer, *G. morafkai* is largely inactive in shelters like boulder piles, caliche caves, packrat middens, and occasionally burrows of other animals, in which they may spend up to 90% of their lives [16]. *G. morafkai* is typically associated with rugged terrain, inhabiting rocky mountainsides, coalescing alluvial slopes (i.e., bajadas), and deeply incised ephemeral stream beds (i.e., washes) that provide resources like forage and shelter [16, 39, 41]. They are also known to occur lower on bajada slopes and, in lower densities, in valley floors, although tortoises in these habitats have been less thoroughly studied [41].

Study site

We studied tortoise movement and habitat selection between June and October 2021 and 2022 in Organ Pipe Cactus National Monument (OPCNM; Fig. 1). OPCNM is a 1,338 km^2 United Nations Educational, Scientific, and Cultural Organization (UNESCO) biosphere reserve managed by the National Park Service (NPS) in Pima County, Arizona (USA) along the United States-Mexico border. The study area experiences an annual average minimum temperature of 12.3 °C, an annual average maximum temperature of 29.9 °C, and annually receives 237.2 mm of precipitation [42]. OPCNM has a bimodal rainfall pattern of light rains occurring in winter and spring and heavy monsoon rains that typically occur from mid-June to late September and account for most of the annual precipitation. The landscape of the study area is characterized by two subdivisions of the Sonoran Desert biotic community: the Arizona Upland and Lower Colorado River Valley subdivisions [43]. The topography of OPCNM is comprised of rugged mountains, bajadas, and valleys with shallow or deeply incised washes. Elevation within the park ranges from approximately 297 m to 1,469 m above sea level. The study area is bounded to the north and west by US Fish and Wildlife Service and Bureau of Land Management land, to the east by the Tohono O'odham Nation, and to the south by the international border between Arizona, USA and Sonora, Mexico. Tall (~ 10 m) fencing, likely impermeable to tortoise movement [14], spans the entire southern boundary of the study area. Approximately 311 km of public roads, active and inactive service roads, and roads designed to facilitate access to remote areas of the park by United States Customs and Border Protection (USCBP) agents and law enforcement officers exist within the boundaries of the study area (hereafter referred to as low-traffic roads). The study area is also bisected by State Route 85, which is a high-traffic, high-speed highway that spans ~ 60 km from the international border of Arizona, USA and Sonora, Mexico north through the study area. OPCNM is one of the main protected areas for *G. morafkai* [15] and provides an opportunity to examine how tortoises select habitat in intact desert and areas where anthropogenic features occur, and how those features influence their movement.

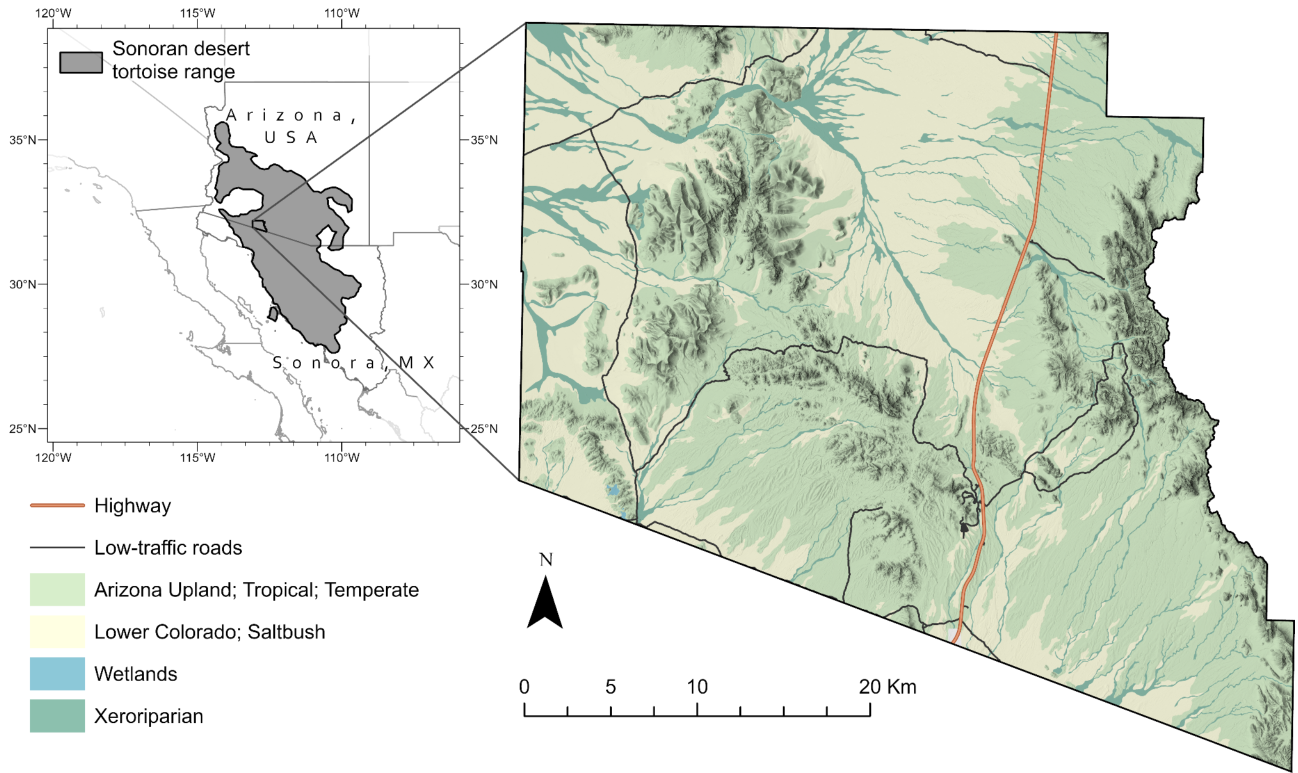

Fig. 1 Map of the study area, biotic communities, and roads within the study area. The study area is approximately central to the species' range. The predominant vegetation types are characterized by Arizona Upland and Lower Colorado subdivisions of the Sonoran Desert, and the terrain ranges from flat, intermountain valleys to rugged mountain peaks. Low-traffic roads in the study area are typically dirt, gravel, or partially paved, and a highway bisects the study area. Geospatial data for the Sonoran desert tortoise range boundary was downloaded from https://www.iucnredlist.org/species/97246109/97246177 and all other data used in the map were provided by the NPS

GPS telemetry data

Tortoises used in the study were found by actively searching potential habitat. Since we were interested in understanding how tortoises generally select for habitat or respond to roads, we attempted to balance the number of males and females in our study. We also included tortoises found lower on mountain slopes or in valleys where less is known about Sonoran desert tortoise habitat use [41, 44]. We did this by selecting approximately half of the study animals from areas greater than 1 km from the nearest 5-degree slope.

Tortoises were outfitted with very high frequency (VHF) radio-transmitters (RI-2B; Holohil Systems Inc.) and GPS dataloggers (i-gotU GT-600; Mobile Action Technology Inc.) affixed to the carapace using putty epoxy and positioned to minimize change in the animal's vertical profile. VHF and GPS equipment combined weighed less than 5% of the tortoises' body mass. All tortoises were adults with a midline carapace length greater than 190 mm and were handled following protocols from State of Arizona Scientific Activity License no. SP847069, National Park Service (NPS) Scientific Research and Collecting Permit no. ORPI-2022-SCI_0003, NPS Animal Care and Use Committee (IACUC) protocol no. 21036-04, and Texas Tech University IACUC protocol no. 21036-04. Tortoises were tracked to their location approximately monthly using VHF telemetry equipment to recover GPS dataloggers. The GPS dataloggers must be recovered for data to be manually downloaded. As purchased, they have a battery life of approximately 30 days when programmed to record a position every 30 min, 24 h per day. In 2021, we used custom-made 3D printed mounts that held the GPS logger following methods similar to Hromada et al. [8], which allowed dataloggers to be replaced monthly with fully charged dataloggers. In 2022, tortoises were outfitted with GPS dataloggers modified to maximize battery life and reduce recapture events, using methods following Paden et al. [45]. Tortoises tracked in 2022 were then typically captured once in June to deploy fully charged equipment and again in October to recover and download data. Upon downloading data from each GPS datalogger, inaccurate locations were identified and removed. We used several criteria to identify potentially erroneous locations: an elevational difference greater than 25 m between the elevation recorded by the GPS datalogger and a 30-meter digital elevation model (DEM), or locations that had both a high speed (600 m/hour or greater) and a high turning angle (>180° turn) between two consecutive locations, which reflect improbable tortoise movements.

After removing potentially erroneous positions, we recorded the minimum distance between the closest GPS position and the nearest road for each tortoise and the number of times each tortoise crossed any low-traffic road or the highway. To account for the accuracy of the GPS dataloggers, we only considered a tortoise to have crossed a road if it had moved a distance greater than 20 m (twice the approximate location error of the GPS dataloggers) from one side of the road and remained there for a minimum of one hour (twice the sampling interval), or two recorded GPS locations. The GPS dataloggers used in the study are reported to have an approximate location error of 10 m prior to screening for erroneous positions, and the location error should be minimally impacted by vegetation cover [46]. To confirm this, we performed four stationary GPS tests by placing GPS dataloggers in places tortoises may take refuge (e.g., under a bush or within a boulder pile), which we further describe in the Supplementary Materials.

Both the HMM and iSSA approaches we used to examine tortoise movement and selection assume temporal regularity (e.g., a regular sampling interval) in location data. Occasionally, scheduled data points (locations) were missing or delayed. This may have arisen from the tortoises' use of shelters (e.g., rock piles and caves), which can delay or preclude the collection of GPS locations [9, 45], or other instances where satellite signal is insufficient to record a location. To temporally regularize the data, we first split each study animal's movement trajectories into separate trajectories where gaps of 1.5 h (i.e., three locations) or greater existed. This was done to avoid imputing locations over long periods of time. Missing fixes resulting from tortoise shelter use, the removal of erroneous locations, and splitting trajectories at long gaps resulted in many short-duration tracks with occasional missing fixes. As we were interested in bouts of movement, we removed any trajectories under 6 h long, which represented sheltering tortoises. We then used a continuous-time correlated random walk model to impute missing locations into the movement trajectories where any gaps remained (i.e., one or two locations) and regularize the data to 30-minute sampling intervals. Imputation was performed using the 'crawlWrap' function in the *momentuHMM* package [47] in R version 4.3.0 [48]. This resulted in gapless, temporally regular movement trajectories that were 6 h or longer for use in our behavioral state assignments.

Behavioral state assignments

During their most active period, the summer monsoon season, *G. morafkai* is typically active in morning and evening, sheltering through potentially lethal mid-day heat and through the night [40]. Since our objective was to examine habitat selection and movement when tortoises are active (i.e., not sheltering), we isolated GPS locations reflecting movement from the overall GPS dataset. To accomplish this, we fit HMMs to assign GPS locations into different behavioral states. We predicted that a two-state model would differentiate between bouts of tortoise movement and when the animals are "encamped" (not moving or sedentary) which, as described in other studies using GPS dataloggers to study tortoise movement (e.g [10]), are readily apparent when visually inspecting GPS locations. We modeled transition probabilities as a function of time of day (hour) and air temperature, which we expected to influence whether a tortoise would be in the encamped state or moving. Air temperatures recorded at 5-minute intervals were downloaded from weather stations positioned throughout the study area (https://wrcc.dri.edu/organpipe/) and a rolling join was used to assign each GPS location the most recent air temperature from the closest station with available weather data. We then used the Viterbi algorithm to assign each GPS location to its most likely state [49]. Our behavioral state assignments were performed using R package *momentuHMM* [47]. After assigning behavioral states to the GPS locations, we visually inspected them in ArcGIS Pro 3.2.1 to ensure the behavioral state assignment captured the two states (i.e., "encamped" and "moving") we observed during our initial inspection of the GPS locations.

Predictors of selection and movement

We selected natural and anthropogenic features that we expected to influence tortoise habitat selection or movement as predictor variables in our selection and movement analysis. All predictor variables were rasters calculated at or resampled to 30-meter resolution, which we expected to be appropriate for the measurement error associated with our GPS dataloggers. For landscape characteristics (i.e., natural characteristics of the landscape), we included measurements of vegetation, terrain ruggedness, and distance from the nearest wash. To measure vegetation on the landscape, we calculated the mean modified soil-adjusted vegetation index (MSAVI2; [50]) for the 2021 and 2022 monsoon season independently. We chose this index because it is well-suited to quantifying vegetation greenness (i.e., cover of green vegetation) while compensating for the high reflectance of desert soils. Our calculations of mean MSAVI2 were derived from Sentinel II imagery using Google Earth Engine [51]. To quantify the ruggedness of terrain associated with tortoise habitat, we calculated the terrain ruggedness index (TRI) as described by Wilson et al. (2007; [52]) from a 30-meter USGS Digital Elevation Model using the 'terrain' function and an 8-cell neighborhood rule in the R package *terra* [53]. We used the 'Euclidean Distance' tool in ArcGIS Pro to calculate the distance from incised desert washes, which required us to build a custom model to map incised washes using a high-resolution (0.5 m) DEM provided from the NPS (described in Supplementary Materials). We compared our measures of terrain ruggedness, vegetation, and our wash layer with 60-centimeter aerial images from the National Agricultural Imagery Program (provided by the NPS) to ensure the variables were adequately capturing the landscape characteristics that we expected would influence tortoise habitat use and movement. This was necessary because our measure of terrain ruggedness (a first-generation ruggedness metric) can be correlated with slope, which can complicate its interpretation [54]. We used TRI because it has been widely used in resource selection studies and adequately captured the landscape features that we hypothesized to influence tortoise movement; we recommend Dilts et al. (2023; [54]) for alternative measures of terrain complexity or ruggedness. For anthropogenic features, we considered all roads other than the highway in the study area to be low-traffic roads. We expected all road types to influence tortoise movement but that the effect would differ based on road type (low-traffic or highway). We generated a raster reflecting the distance in meters from the nearest low-traffic road and from the highway using Open Street Maps (https://www.openstreetmap.org) and road data provided by the NPS, again using the 'Euclidean Distance' tool in ArcGIS Pro 3.2.1. We took the natural logarithm of the distance to washes and distance to roads variables as we expected the effect of these features on habitat section and movement would be close ranged. All predictor variables were scaled and centered.

Selection and movement analyses

To examine how tortoises select habitat and respond to roads while moving through the landscape, we used GPS locations assigned to the moving state, or movement trajectories, in integrated step-selection analyses (iSSA; [55]). In step-selection analyses, a "step" refers to a pair of sequential GPS locations. "Step length" refers to the distance in meters between paired points, and "turning angle" corresponds to the deviation in degrees between one step and the next. Step-selection analyses pair observed steps (e.g., derived from GPS data) with randomized available steps. This allows for a statistical comparison between what the animal selected on the landscape and what was available to it but not selected. We used the R package *amt* [56] to pair each observed step with 10 available steps. The step lengths of available steps were modeled from a gamma distribution and turn angles were modeled from a von Mises distribution, which we assumed would best represent the respective distribution of step lengths and turning angles [56]. We extracted values for each predictor variable at the start and end of each observed and available step. Values of predictor variables at the end of each step were used to test hypotheses about habitat selection. Values at the start of each step were used in interactions with predictor variables to test hypotheses about how that predictor variable influences movement parameters (e.g., step lengths and turning angles). We followed the approach of Muff et al. (2020; [57]) and used a Poisson formulation of a conditional logistic regression, included the unique ID of each step as a random intercept and fixed its variance to a large number, and we used individual-specific random coefficients for all predictor variables and interactions in our models. This allowed us to account for individual variation in selection and differences in habitat availability for each individual tortoise. All models were fit using R package *glmmTMB* [58].

We built a single model to quantify habitat selection of natural landscape characteristics by moving tortoises. We included quadratic terms for TRI and MSAVI2 as we expected selection responses may be non-linear for these variables. We built separate models, using a subset of tortoises, to isolate and test the effects of low-traffic roads and the highway on tortoise movement and habitat selection. Other tortoise species have been shown to adjust their movement and selection behavior near or when crossing dirt, unpaved, and low-traffic roads [7, 9]. We included movement data only from tortoises that came within 50 m of a low-traffic road at any point during the study ($N=7$) for our low-traffic roads model, expecting we would detect an effect within this range. There have been no studies explicitly addressing how highways influence movement and selection in this species; however, tortoise populations are less dense, and signs of their presence are often scarce within 1 km of roads [20, 26]. For the highway model, we included movement data only from tortoises that were found within 1 km of the highway ($N=6$). We included the logarithm of the step length and cosine of the turning angle in all models, which is recommended to account for the movement process underlying selection [55].

We then calculated the relative selection strength (RSS; [59]) for any significant effects of natural landscape characteristics or roads on selection. RSS is an estimate of how likely an animal is to select one location versus another based on the values of the predictor variable at those locations, while keeping the value of all other predictor variables constant. This allowed us to compare the relative probability of tortoises choosing locations across the range of values experienced by our sampled tortoises to the minimum value of that predictor variable. To calculate RSS for each significant predictor variable, we used the calculations described in Avgar et al. [59].

Results

GPS telemetry

We tracked a total of 17 adult tortoises (8 male, 9 female) over 2021 and 2022. This resulted in an average tracking period of 93 days per individual, ranging from 66 to 105 days each year between the months of June to October, during which tortoise activity peaks. The final dataset used in our behavioral assignment included 809 temporally regularized movement trajectories, comprising 54,513 locations from the 17 tortoises. The mean location error of the GPS data recovered from our stationary tests was under 10 m (Table S1). Tortoises crossed low-traffic paved roads a minimum of zero times and a maximum of 31 times during the study (Table S2). We observed only a single highway crossing during the study (Table S3). Although we recorded a single GPS location where a tortoise could conceivably have crossed a low-traffic road within the 30-minute sampling interval, we recorded no other evidence of road crossings nor locations that could have been confused with crossings (within the approximate location error of the GPS dataloggers and a road) for this individual.

Behavioral assignment

Using HMMs allowed us to assign GPS locations to one of two behavioral states: an encamped state and a moving state (Fig. 2). Step lengths were longer and turning angles were lower when tortoises were moving compared to when encamped. In the encamped state, step lengths were short and turning angles were high. (Fig. 2). Tortoises were more likely to be moving during the day (Fig. S1) and in cooler temperatures (Fig. S2).

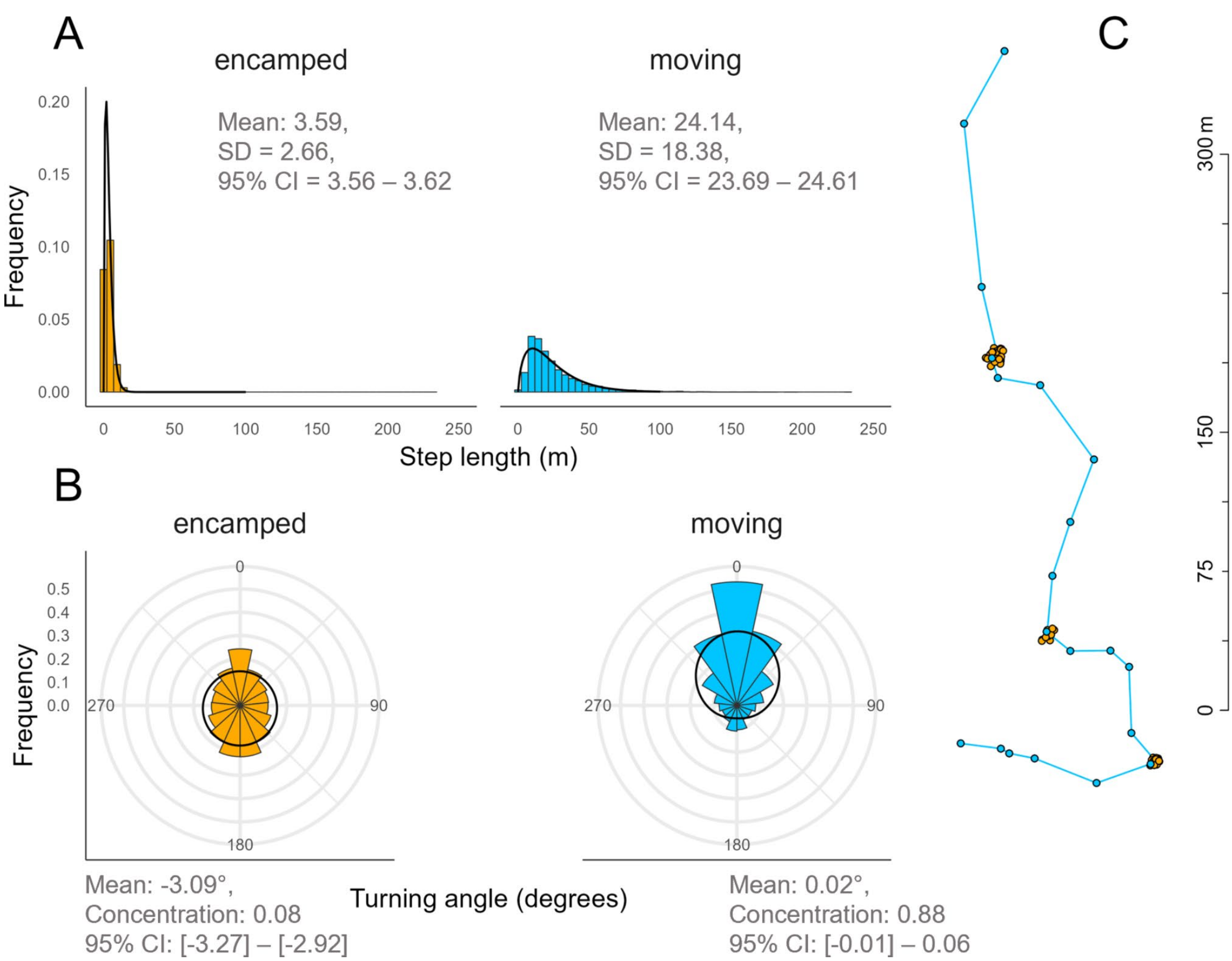

Fig. 2 Distribution of step lengths and turning angles for the encamped and moving states. Step length distributions (**A**) and turning angle distributions (**B**) for the encamped and moving states for the 17 tortoises tracked over the duration of the study. The encamped state is characterized by shorter step lengths and high turning angles, whereas the moving state is characterized by longer step lengths and lower turning angles. An example segment of a state-assigned movement trajectory from a single study animal is provided (**C**). This reflects GPS locations of a single tortoise collected over 40 h in their assigned behavioral states: clusters of orange points indicate when the tortoise is in the encamped state. Blue points and line segments indicate when the tortoise is in the moving state

Step selection models

After removing the encamped locations, we used the remaining 7,612 steps to examine tortoise habitat selection for natural landscape characteristics and roads, and to determine how roads influence tortoise movement. We found a significant effect of all natural landscape covariates (Fig. 3A) and low-traffic roads (Fig. 3B) on habitat selection. We also found a significant interaction between tortoise step length and distance from low-traffic roads indicating faster movements in proximity

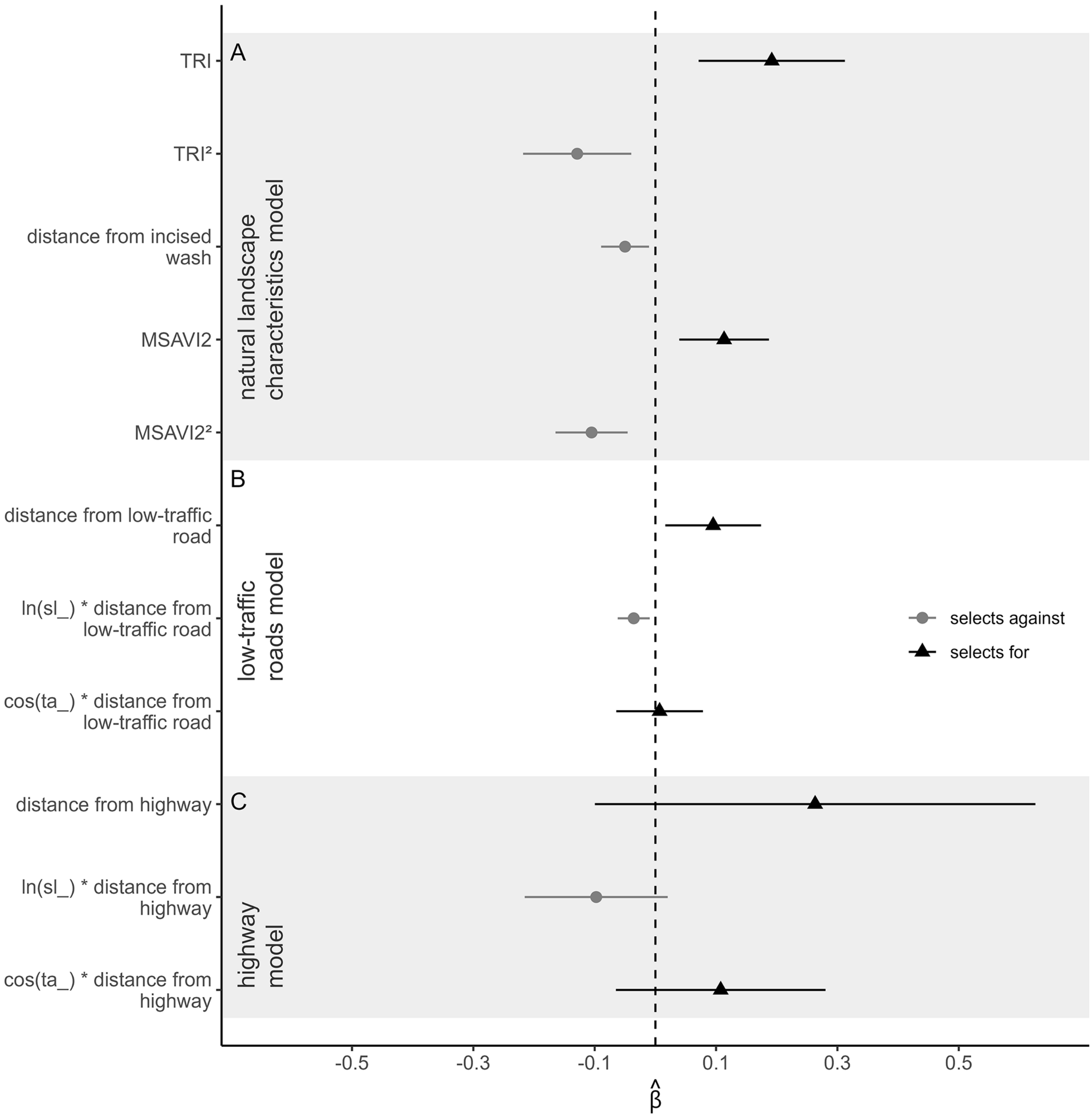

Fig. 3 Beta coefficients and 95% confidence intervals for all iSSA models. Beta coefficient estimates and 95% confidence intervals for selection (x-axis) of predictor variables (y-axis; natural landscape characteristics, low-traffic roads, and the highway) and interactions between movement parameters (the logarithm of step length and the cosine of turning angle) and predictor variables. Tortoises select intermediate values of terrain ruggedness (TRI) and vegetation index (MSAVI2) (**A**) and areas farther from low-traffic roads (**B**). They avoid extreme values of terrain ruggedness and vegetation index, and areas far from incised washes (**A**). Positive coefficients (black triangles) indicate selection and negative coefficients (grey circles) indicate avoidance. Coefficient estimates with 95% confidence intervals overlapping zero likely have little effect on selection. We performed one model for all natural landscape covariates (**A**) and separate models to isolate the effects of low-traffic roads (**B**) and the highway (**C**) on selection and movement

to those roads (Fig. 3B). We found no significant effect of low-traffic roads on turning angle nor any significant effect of the highway on selection or interactions with movement parameters (i.e., the log of step length and cosine of turning angle; Fig. 3C).

The positive coefficient for TRI indicates that tortoises selected rugged terrain, while the negative coefficient for the quadratic term (TRI^2) indicates that selection for terrain ruggedness was non-linear. Tortoises were more likely to select areas of higher terrain ruggedness compared to areas of lower terrain ruggedness (e.g., desert flats) until values exceeded approximately 31 where selection reversed (Figs. 3A and 4A). For example, fewer than 7% of tortoise steps (i.e., GPS locations) ended in TRI values above 31, despite ~3,000 steps being available to them within that range. Similarly, selection for the vegetation index (MSAVI2) was non-linear. Tortoises strongly selected to move through vegetated areas compared to bare earth (MSAVI2 values near 0). For example, fewer than 8% of tortoise steps ended in MSAVI2 values under 0.15, while ~23% of all steps available to them fell within that range of values. Selection strength began to decrease as vegetation index values approached the maximum values available to the tortoises (Figs. 3A and 4B). A description of what TRI and MSAVI2 values correspond to on the landscape can be found in the Supplementary Materials (Fig. S3 and Fig. S4, respectively) and are described in the Discussion. We found that tortoises were less likely to move through areas further from incised washes then closer to incised washes (Fig. 3A), though the effect was weaker than other predictor variables (Fig. 3A) and became less pronounced as tortoises moved through areas greater than 50 m from the nearest wash (Fig. 4C). These results suggest that rugged terrain, vegetation, and incised washes encourage tortoise movement (Fig. 3A), but that very rugged terrain and higher vegetation cover may discourage or limit tortoise movement (Fig. 4A and B).

Tortoises also avoided moving close to low-traffic roads (Figs. 3B and 4D) and increased their step length (i.e., speed) when moving near low-traffic roads, evidenced by a significant negative coefficient for the interaction between the log of the step length and distance to the nearest low-traffic road (Fig. 3B). These findings suggest

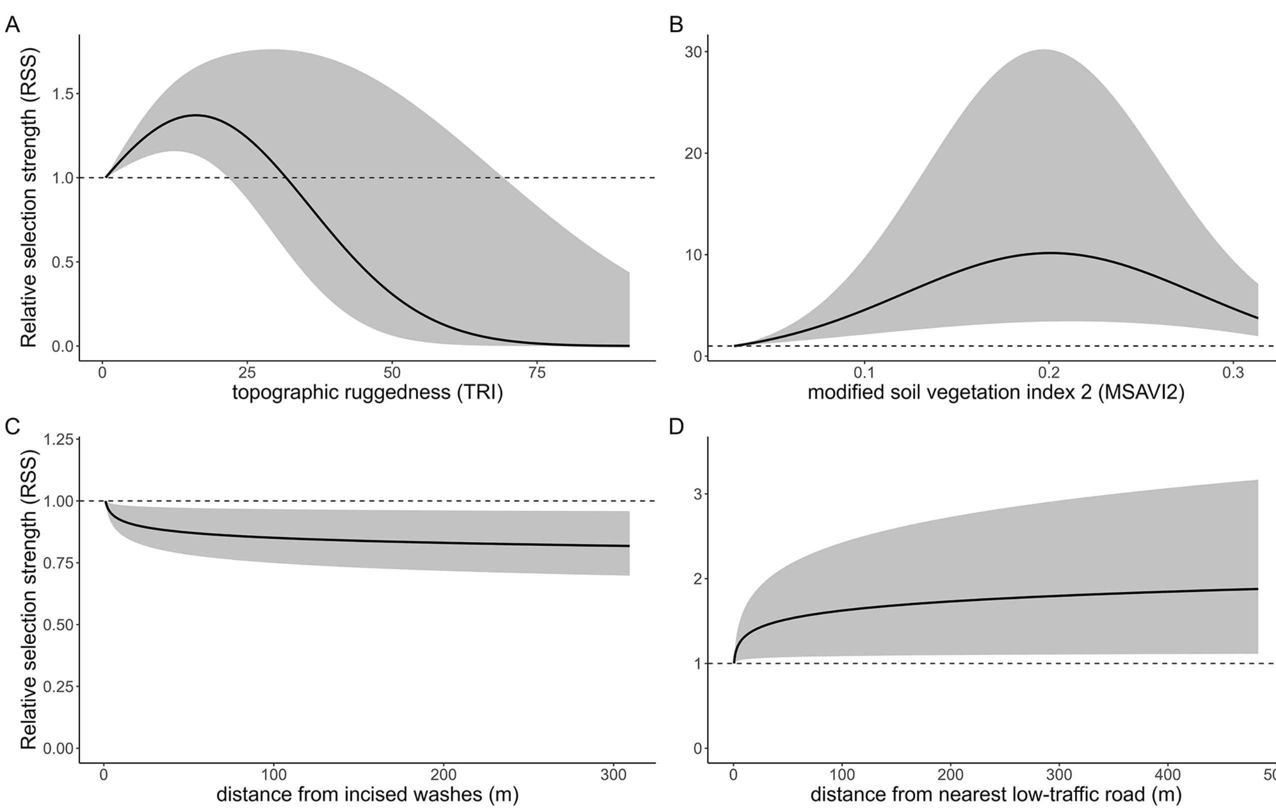

Fig. 4 Tortoises selected areas closer to incised washes and of intermediate terrain ruggedness and vegetation index. Relative selection strength (RSS) and 95% confidence intervals for landscape covariates and roads included in the selection models for which significant relationships were found (Fig. 3). The RSS calculated in this study reflects the likelihood of moving into a location with a value of the landscape covariate exceeding that of the minimum value of the covariate. RSS values greater than 1, indicated by the dashed line, indicate selection. RSS values less than 1 indicate avoidance. An RSS value of 5 for a certain value of a covariate indicates that a tortoise is 5 times more likely to select a location with that value compared to a location with the minimum value of that covariate

that areas near low-traffic roads may be lower-quality movement habitat. Tortoises appear more likely to move faster when near or crossing low-traffic roads. Although demonstrating a similar trend, the lack of a significant effect of the highway on habitat selection or movement (Fig. 3C) suggests that tortoise interactions with the highway were too few to detect a significant effect or selection for areas far from the highway (e.g., home range selection) may have already occurred prior to our study.

Discussion

We demonstrated that vegetation, moderately rugged terrain, and areas with incised desert washes may encourage tortoise movement, whereas bare earth, high vegetation cover, flat and extremely rugged terrain, areas far from incised washes, and low-traffic roads may restrict or discourage movement typical of range-resident tortoises. Desert tortoises are referred to as "corridor-dwellers", meaning a corridor that supports connectivity among habitats or populations must be sufficiently wide to allow for multiple tortoises' home ranges to overlap and have sufficient resources to support those individuals [60, 61]. Our results highlight important habitat features and characteristics that may promote or discourage range-resident movement behaviors of adult tortoises, like foraging and mate-seeking. Additionally, our results are reflective of tortoises from steep slopes and tortoises from lower bajadas and valleys where comparatively little is known about tortoise habitat use. So, although our results are most directly applicable to managing intra-patch connectivity, our study provides insights that may be applicable to managing the matrix surrounding high-quality tortoise habitats, thus increasing the permeability of the matrix between tortoise habitats or populations.

We found that tortoises strongly select areas with vegetation coverage compared to areas with little to no vegetation. Vegetation is an important food and shelter resource for desert tortoises [17, 62], and our results corroborate studies that have found vegetation cover to be an important predictor of their habitat use at different spatial scales [36–38]. One such study, which examined *G. morafkai*'s microhabitat selection, suggested that management actions should maintain or possibly increase vegetation cover in the landscape [37]. Although our results partially support this prescription, we found that tortoises are less likely to select areas of higher vegetation cover compared to areas of intermediate vegetation cover available to them. Areas of higher vegetation index values in the study area (>0.3 MSAVI2; Fig. S4) are typically characteristic of shaded reaches of large washes, forested areas, or roadside thickets that are denser than the surrounding landscape. Weaker selection of these areas may suggest that tortoises avoid moving through such dense vegetation when traversing their home range, possibly because dense vegetation is more resistant to movement.

Understanding the mechanisms underlying this nonlinear relationship may be of growing importance as processes that can change the structure or availability of vegetation, like wildfire, the invasion of non-native grasses, OHV use, and development, continue to occur in the region. Management practices that support native vegetation (e.g., preventing OHV use) may help ensure the conservation of habitat that provides forage, shelter, and that facilitates or encourages tortoise habitat use and movement. Based on our finding that selection weakens as vegetation cover increases, we hypothesize that dense stands of vegetation, including those created by non-native grasses, could conceivably discourage movement and form a physical barrier (i.e., physically costly to move through) or a perceptual barrier (i.e., perceived risk), as has been shown for other vertebrates [63]. We recommend that future studies seek to understand tortoise habitat use and movement in areas where disturbances or non-native grasses have changed the native vegetation.

As anticipated, tortoises were more likely to select areas of intermediate terrain ruggedness and areas close to incised washes than areas that had extreme values of terrain ruggedness (i.e., flat or extremely rugged terrain) or areas farther away from incised washes. Rocky mountain slopes and deeply incised washes are associated with tortoise shelter [36, 37, 40]. Compared to flat terrain, selection strength was higher for values of TRI that correspond to bajada slopes, rocky mountainsides, and areas with a high density of smaller washes or adjacent to deeply incised washes (Fig. S3). The similarities between previous studies and this study indicate that rugged terrain and incised washes are important to desert tortoises at multiple scales of selection [36, 37, 41, 44]. However, our findings highlight a threshold (>~31 TRI) at which tortoises select areas of intermediate terrain ruggedness compared to more rugged slopes when moving. In the study area, TRI values above this threshold are characteristic of very steep slopes above bajadas and mountainsides tortoises inhabit (Fig. S3). We expect that, despite being associated with rugged terrain, very steep and rugged terrain is costly for *G. morafkai* to traverse. Tortoises in the study area can be found kilometers from the nearest slope in areas where complex terrain is surrounded by otherwise flat terrain (e.g., valleys), especially where deeply incised washes provide tortoises shelter (e.g., caliche caves). However, selection strength for incised washes was relatively weak compared to other predictor variables. We expect this is the result of a combination of the conservative definition of availability used in our study and because most of the tortoises tracked in the study inhabit areas with a high density of incised washes: the difference in the distance from the nearest incised wash for each observed tortoise location and its paired available points were relatively little. Approximately 85% of tortoise locations (i.e., GPS locations) were within 100 m of an incised wash, which reinforces our findings that incised washes are important landscape features for *G. morafkai* as has been found in other studies (e.g. [41, 44]).

Compared to vegetation, topographical or geomorphological features like rugged slopes and incised washes are not typically regarded as manageable aspects of the landscape. However, areas where these features occur may be important targets for management actions focused on preserving tortoise habitat and facilitating range-resident movement behaviors. For example, tortoises may be more likely to attempt crossing sections of roads that intersect incised washes, so areas where roads intersect important habitat features like incised washes may be priority areas for the installation of "tortoise-friendly" road crossing structures (e.g., road culverts) or road-side fencing that may reduce tortoise mortality and facilitate tortoise movements within their home ranges and habitats. Washes in the study area and surrounding region may serve as corridors for human foot-traffic [64] and vehicular traffic from border patrol agents, both of which may reduce tortoise habitat quality. Management efforts (e.g., trash removal or vegetation restoration) targeting washes that receive intensive foot traffic or vehicle traffic may benefit tortoises that use those washes or the surrounding areas.

We found that tortoises were more likely to select areas farther from low-traffic roads than close to them, and that they increased their speed (i.e., made longer steps) when moving near or crossing low-traffic roads. Previous studies that used GPS telemetry to examine fine-scale movement and habitat selection of *G. agassizii* have found similar results to ours: tortoises typically avoided moving near unpaved roads and low-traffic roads and increased their movement speed when near them [7, 8, 30]. These studies posited that an increase in speed near low-traffic roads may indicate avoidance behavior; tortoises may be increasing their speed near roads because they offer less refuge from sun exposure, predation, and other risks [8, 9]. Peaden et al. [7] found that tortoises moved faster and had higher carapace temperatures when near a road than when farther from it, suggesting roads may cause tortoises to increase the energy they spend to access resources and may experience a greater risk of thermal stress [7]. Roads in our study area may have a similar effect on *G. morafkai* and may increase the distance tortoises need to move to access resources. In contrast to our findings, Grandmaison et al. [37] found *G. morafkai* selected microhabitat closer to gravel roads than areas available to them, which could be explained by lower traffic volumes, structural similarities to desert washes, and greater availability of forage on the roadside that may attract desert tortoises [37, 65]. This contrasting pattern may be reflective of site- or context-specific differences between the roads in each of the studies (e.g., differences in traffic volume). For example, a study using GPS telemetry found tortoises alter their movement behavior in different ways near dirt roads that experience different levels of local anthropogenic disturbance [9]. Alternatively, the contrast between the findings of Grandmaison et al. [37] and our findings may be reflective of the contrast in temporal resolutions used: the use of VHF telemetry in their study may not have captured the range of activity that is possible with the use of GPS telemetry.

While 6 tortoises tracked in our study crossed low-traffic roads, the number of road crossings in our study were ultimately rare. With the exception of a single individual that regularly crossed a paved section of a low-traffic road (31 times over two years), the remaining 5 individuals that crossed low-traffic roads did so only one to 5 times over two years (Table S2). The scarcity of road crossings in our study reinforces our findings that suggest that tortoises are likely reluctant to move near or across roads. These roads and adjacent habitats may serve as a perceptual barrier to movement; tortoises may perceive these roads as a potential risk of exposure or predation and may thus be reluctant to approach or cross them. The proliferation of roads (i.e., spreading in extent and increasing in density) has the potential to cause negative individual- and population-level consequences for tortoises, as has been found in other studies [26, 31, 66]. These roads continue to be created through illegal OHV use and border patrol activities by the USCBP in the study area and surrounding region. Consequently, we recommend the closure of unused or unnecessary roads, which is indicated as a suggested management action in the recovery plan for the closely related *G. agassizii* [13] and the Candidate Conservation Agreement (CCA) for *G. morafkai* [22]. We also recommend the restoration of habitats degraded by road development or OHV use as a potential strategy to increase landscape connectivity for *G. morafkai* and support the persistence of their populations.

In contrast to our expectation, we found no significant effect of the high-traffic highway on tortoise movement behavior or habitat selection. This lack of avoidance was unexpected given that high-traffic paved roads have been shown to have a variety of negative impacts on tortoises and tortoise populations [26, 27] and that, during our study, the highway bisecting the study area received approximately 10 to 570 times as many vehicles per year than low-traffic roads in the park [67]. Although several tortoises in our study frequently moved or sheltered within meters of the highway, we only observed a single crossing event during the study (Table S3). Similarly, Hromada et al. [9] found that only four of 28 tracked tortoises found within a kilometer of a highway crossed it and attributed the scarcity of crossing events to potential avoidance behavior, or possibly because tortoises established home ranges near but not including the highway [9]. Previous studies have demonstrated that *G. morafkai* displays high fidelity to their home ranges (e.g., [68]). Tortoises tracked in our study were all adults, and it is likely that they may have established home ranges in areas adjacent to the highway and, since establishing their home range, have become indifferent to it or are willing to take advantage of resources (e.g., incised washes or vegetation) adjacent to the highway. However, our finding that tortoises selected habitat farther from low-traffic roads may indicate that avoidance could be more severe for roads with higher traffic volumes, resulting in too few interactions between tortoises and the highway to detect a significant effect.

Despite the potential for road avoidance, tortoises do attempt to cross high-traffic roads that present a higher risk of mortality than low-traffic roads. Tortoise highway-crossings and road mortalities are occasionally observed in the study area (pers. obs. 2022). Numerous studies have demonstrated population declines related to road mortality and reduced tortoise densities or reduced tortoise abundance up to four kilometers from highways [26, 66, 69]. Tortoise fencing (i.e., fencing designed to reduce tortoise mortalities) is commonplace along highways throughout the protected *G. agassizii*'s habitat and has been found to effectively reduce tortoise road mortalities [66]. Although recommended as a conservation action [22], tortoise fencing is not widely used throughout the range of *G. morafkai*. Previously existing structures like drainage culverts (designed to allow runoff to pass under the road) may facilitate safe passage for tortoises attempting to cross barriers like highways, which has been documented, when tortoise fencing is present (e.g., [10]). In the study area, the highway (SR-85) and the border wall are likely the most significant anthropogenic barriers to tortoise movement and landscape connectivity. Drainage culverts along SR-85 and flood gates and small openings designed for wildlife along the border wall may allow tortoises to cross these barriers. We recommend future research evaluating the efficacy of previously existing structures (e.g., drainage culverts or wildlife passages developed for other species), or structures designed to facilitate the movement of other wildlife as crossing structures for tortoises. Furthermore, identifying cost-effective strategies for increasing the permeability of barriers to tortoise movement may help facilitate gene flow, demographic rescue, and other processes and should be a priority area for future research.

In this study, we demonstrated how natural and anthropogenic landscape characteristics can influence tortoise movement and habitat selection. However, the applicability of our study to populations throughout the species' range and to landscape connectivity among those populations may be limited by the number and age of individuals tracked, the limited distribution of these individuals in respect to the species' range, and the duration of the study. Tortoises could display different patterns in habitat selection and movement at different ages or when making non-resident movements, like dispersal events or temporary exploratory movements or sallies. For example, a study examining space use of *G. morafkai* found that immature tortoises are more likely to disperse or make temporary exploratory movements outside of their home range than adults [70]. Previous studies have also demonstrated that *G. morafkai* is capable of long-distance, interpopulation movements (at least in the absence of impermeable barriers to movement), which may be important for processes like gene flow and demographic rescue among populations that manifest through landscape-scale connectivity [21]. It is plausible that tortoises may select habitat differently during exploratory movements or dispersal events compared the normal (i.e., day-to-day) range-resident movement behavior of tortoises in our study. Therefore, our results are best interpreted as trends in habitat selection and movement relevant to adult, range-resident tortoises. We recommend future studies attempt to capture a greater variety in age classes, which may be limited by the technology available (i.e., size and weight relative to an immature tortoise), and attempt to capture different movement behaviors, which may be more likely with a longer study. Such studies may reveal differences in habitat selection and movement response to landscape characteristics than demonstrated by our results.

Although the responses of our study animals to natural and anthropogenic landscape characteristics generally followed similar trends in habitat selection (Fig. S5), tortoises living in different habitat contexts (e.g., more developed or degraded areas) or experiencing different environmental conditions (e.g., drought) may show different responses to landscape characteristics. For example, one study animal inhabiting particularly rugged terrain displayed the opposite response in selection of rugged terrain. While this opposite response was likely due to the available terrain (i.e., most steps used by the tortoise were less rugged than the surrounding terrain), it demonstrates that individual tortoises may display different selection responses and that studies examining tortoises in different habitat types or landscape contexts may yield different results. Our study took place during two monsoon seasons with above-average rainfall [42]. The relationship between *G. morafkai* space use and drought remains unclear [70], despite the documented negative impacts of short- and long-term drought on desert tortoises [14, 71, 72], but it is possible that tortoises were moving more frequently and farther during our study than they may have in a drier year. We recommend that future studies examine fine-scale habitat selection for *G. morafkai* during drier years, which may reveal a lesser or greater reliance on certain landscape characteristics that may help tortoises to persist during drought.

While iSSA allowed us to relax certain assumptions that have been shown to produce bias in resource selection studies [55, 57], our approach used a conservative definition of availability. Studies examining resource selection for *G. morafkai* at any scale are still few. We recommend that future studies examine resource selection for *G. morafkai* at different spatial and temporal scales throughout the species' range and seek to discern patterns between use of space and resources incorporating different movement behaviors and age classes, and in light of drought, and natural and anthropogenic disturbances.

Conclusions

In this study, we elucidated patterns in habitat use and response to roads for adult, range-resident Sonoran desert tortoises as they move through the landscape. We highlighted how characteristics of tortoise habitat transition from facilitating or encouraging tortoise movement to restricting or discouraging it. We demonstrated that low-traffic roads may degrade or reduce tortoise movement habitat, and that management actions focused on maintaining vegetation at natural densities (e.g., preventing off-road vehicle use, wildfire, or the invasion of nonnative grasses), preserving moderately rugged areas and areas with incised desert washes, and restoring unused roads may encourage habitat use and facilitate localized movements. Applying such management actions to degraded areas between tortoise habitats may enhance landscape connectivity for *G. morafkai*. Maintaining landscape connectivity through connected habitats is critical for this long-lived species, especially as roads and other barriers continue to proliferate throughout the Sonoran Desert [15]. Our work helps refine the collective understanding of this species' habitat use and movement behavior and which provides valuable information for management strategies and conservation plans focused on supporting *G. morafkai*'s long-term persistence.

Abbreviations

GPS	Global positioning system
HMM	Hidden Markov model
iSSA	Integrated step selection analysis
ESA	Endangered Species Act
OHV	Off-Highway Vehicle
OPCNM	Organ Pipe Cactus National Monument
UNESCO	United Nations Education Scientific, and Cultural Organization
NPS	National Park Service
USCBP	United States Customs and Border Protection
VHF	Very-High Frequency
IACUC	Institutional Animal Care and Use Committee
DEM	Digital Elevation Model
MSAVI2	Modified Soil Vegetation Index II
TRI	Terrain Ruggedness Index
RSS	Relative Selection Strength
CCA	Candidate Conservation Agreement

Supplementary Information

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Supplementary Material 1

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Author contributions

SWS developed the methods, performed all analyses, and drafted the manuscript. NEM and KGK wrote the proposals that funded the work, financially supported the research, provided valuable feedback on the manuscript, and edited the manuscript. All authors read and approved the final manuscript.

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Data availability

GPS tracking data used in the study are not publicly available due to the sensitivity of tortoise locations and other resources within the study area and are restricted by data use agreements with the NPS.

Declarations

Ethics approval and consent to participate

All tortoises were handled in accordance with State of Arizona Scientific Activity License no. SP847069, National Park Service (NPS) Scientific Research and Collecting Permit no. ORPI-2022-SCI_0003, NPS Institutional Animal Care and Use Committee (IACUC) protocol no. 21036-04 and Texas Tech University IACUC protocol no. 21036-04.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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