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RESEARCH ARTICLE

Navigating agricultural landscapes: responses of critically endangered giant tortoises to farmland vegetation and infrastructure

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Abstract
Context Interactions between wildlife and anthropogenic infrastructure, such as roads, fences, and dams, can influence wildlife movement, and potentially cause human-wildlife conflict. In the Galapagos archipelago, two species of critically endangered giant tortoise encounter infrastructure and human-modified vegetation in farms, which could influence movement choices.

Objectives We investigated factors influencing tortoise movement and habitat selection in the agricultural landscape of Santa Cruz Island, Galapagos.

Methods We examined the movement of 27 tortoises collected using GPS tracking between 2014 and 2020, in relation to the location of vegetation, ponds, fences, and roads.

Results We found that tortoises preferred pasture over native vegetation, but there was little difference among their preferences for native vegetation, crops, or invasive vegetation. Tortoises also travelled slower in pasture, and faster in invasive vegetation,

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compared to crops and native vegetation. Tortoises were more likely to be found closer to ponds than predicted by chance. Our results indicated that most fences were porous to tortoises, with limited impact on their movement. Tortoises were more likely to use areas near roads with low-traffic.

Conclusions Pastures, and ponds are important habitat for tortoises in farms and are likely to be used preferentially by tortoises. Overall, fences and roads did not strongly obstruct tortoise movements, however, this may lead to potential injury to tortoises on roads and property damage for farmers. To best identify priority areas for managing wildlife on farms, we recommend evaluating the combined effects of multiple anthropogenic landscape features on wildlife movements.

Keywords Fences · Galapagos · Human-wildlife conflict · Integrated step-selection functions · Resource selection · Roads

Introduction

Globally, land modification is increasing rapidly; only 20–34% of the Earth's terrestrial landscapes experience very low human impact (LeB et al. 2012; Riggio et al. 2020; Theobald et al. 2020). Land modification is usually associated with proliferation and expansion of infrastructure, such as roads and fences (Laurance et al. 2015). For instance, ~25 million kilometres of newly paved roads will likely be constructed worldwide by 2050 (Alamgir et al. 2017). As the human footprint expands outside urban areas, wildlife must navigate encounters with novel, man-made features, including transmission lines, railroads, bridges, fences, roads and dams (Coulon et al. 2008; Abrahms et al. 2016; Zeller et al. 2016; Prokopenko et al. 2017; Reinking et al. 2019; Eisaguirre et al. 2020). The ubiquity of man-made features in the landscape, allows us to asses the impact of specific infrastructure characteristics on animal movement such as type of road, or different fencing materials (Jakes et al. 2018). For example, various tortoise species in the Karoo region of South Africa encounter four main fence types (Lee et al. 2021). Trying to cross electric or fine mesh fences is more likely to result in mortality for these tortoises, whereas regular fences are more easily crossed, illustrating the importace of distinguishing the impacts of different types of infrastructure (Lee et al. 2021). Changes in land use, and expansion of different types of infrastructure, can strongly influence the movements of animals, especially migratory species (Wilcove and Wikelski 2008; Harris et al. 2009; Seidler et al. 2015; Shaw 2016).

Changes to animal movement patterns caused by human-modified land and infrastructure, such as roads and fences, can have cascading effects on the ecological dynamics of wildlife populations and their interactions with people (Cozzi et al. 2013; Beyer et al. 2016; Jakes et al. 2018). Natural areas converted to human-modified vegetation, such as farms, can attract wildlife, leading to property damage or crop consumption (Songhurst et al. 2016). For some species, avoidance of infrastructure can disrupt movement and reduce connectivity, causing population decline and loss of genetic diversity (Seidler et al. 2015; Cosgrove et al. 2018).

For example, road type has a strong impact on the abundance and demography of Mojave Desert Tortoises (*Gopherus agasszii)*, there are fewer and smaller tortoises within the vicinity of high-traffic roads compared to roads with medium- or low traffic, likely due to road mortality (Nafus et al. 2013). Likewise, the extinction risk of Blanding's turtles (*Emydoidea blandingii)* increased closer to roads (Beaudry et al. 2008). Individuals of other species, however, can be attracted to infrastructure for ease of travel; studies designed to examine the impacts of four-wheel drive trails on reptiles indicated that the density of most species increased with proximity to trails, possibly because trails facilitated movement, or thermoregulation (Munger and Ames 2001; Munger et al. 2003). Globally, however, wildlife interacting with transportation infrastructure is leading to increases in mortality risk for wildlife and property damage for people (Olsson and Widen 2008; St. Clair

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et al. 2019; Shilling et al. 2020). To adequately support wildlife movement in human-modified landscapes we need a detailed understanding of the influences of infrastructure and habitat change on wildlife.

Even isolated oceanic islands are not free of the global expansion of the human footprint (Russell and Kueffer, 2019). On Santa Cruz Island in the Galapagos Archipelago, for example, two critically endangered giant tortoise species (*Chelonoidis porteri* and *Chelonoidis donfaustoi)* regularly interact with human-modified vegetation and infrastructure. These tortoise species are morphologically and ecologically similar, and while both species use the agricultural area, their distributions do not overlap. *C. porteri* is found only in the west and *C. donfasutoi* in the east (Poulakakis et al. 2015). As both tourism and the local human population are predicted to continue to increase in the Galapagos (Epler 2007; Sampedro et al. 2018), interactions between tortoises and infrastructure are also likely to increase as human activities continue to expand (Yackulic et al. 2017; Pike et al. 2021). Many adult tortoises spend around half of each year (Blake et al. 2013; Pike et al. 2021) in the agricultural area in the highlands, where they regularly interact with roads, fences, ponds, and human-modified vegetation, such as pasture for livestock, various transitory and permanent crops, and areas of invasive vegetation (Laso et al. 2020; Pike et al. 2022). The aim of the Galapagos National Park Service is to increase the abundance and geographical range of these and other tortoise species, to their former levels. If successful, this will further increase the number of interactions between tortoises and anthropogenic landscape features (Blake et al. 2015b; Cayot et al. 2017). While tortoise population growth may be a desirable outcome for conservationists (MacFarland et al. 1974; Gibbs et al. 2014), increasing interactions between tortoises and farmers, including fence breakage, crop depredation, and tortoise-automobile interactions may lead to an increase in tortoise-human conflict, thereby undermining conservation efforts (Blake et al. 2015b; Benitez-Capistros et al. 2018, 2019). To support the recovering tortoise populations and minimise this conflict, policymakers and land managers must understand the influence of infrastructure and land use on tortoise movements.

We investigated the influence of infrastructural characteristics and human-modified vegetation cover on the movement dynamics of Santa Cruz tortoises, addressing the following questions and predictions:

(1) Are tortoises selective in their use of different vegetation types in farmland, specifically, vegetation dominated by invasive, native, crop, or pasture species? We predicted that tortoises would select crop and pasture vegetation and avoid invasive vegetation based on differences in forage quality (Pike et al. 2022).

(2) How do tortoises respond to ponds? We predicted tortoises would be strongly attracted to ponds because they provide opportunities for thermoregulation and drinking (Ellis-Soto 2021).

(3) What are the characteristics of fences, and do they limit tortoise movements? We predicted that tortoises would avoid complex fences with closely spaced posts, compared to fences with fewer posts, and a simpler structure.

(4) How do tortoises respond to different types of roads? We predicted that tortoises would be attracted to low-traffic roads, because roads facilitate movement, but would avoid roads with high traffic levels, because on these, frequently passing cars would cause disturbance.

Methods

Study site

Three main native vegetation types characterise Santa Cruz Island (Fig. 1A): arid lowlands, humid highlands, and a transition zone between these vegetation types (Wiggins and Porter 1971; Rivas-Torres et al. 2018). The humid highlands were first used for agriculture in the early 1900s, and now at least 88% of the humid highlands are modified to support agriculture (Watson et al., 2010; Trueman et al., 2013).

We collected location data from 27 GPS-tracked tortoises, of both species, in areas where they were using agricultural land between 2014 and 2020 (Blake et al., 2013). Tortoises were tracked using custom-built GPS transmitters (e-obs GMBH, Munich, Germany), that obtained hourly locations between 06:00 and 19:00 as tortoises are largely immobile at night (Bastille-Rousseau et al. 2016). Blake et al. (2013) provide a detailed description of tracking methods.

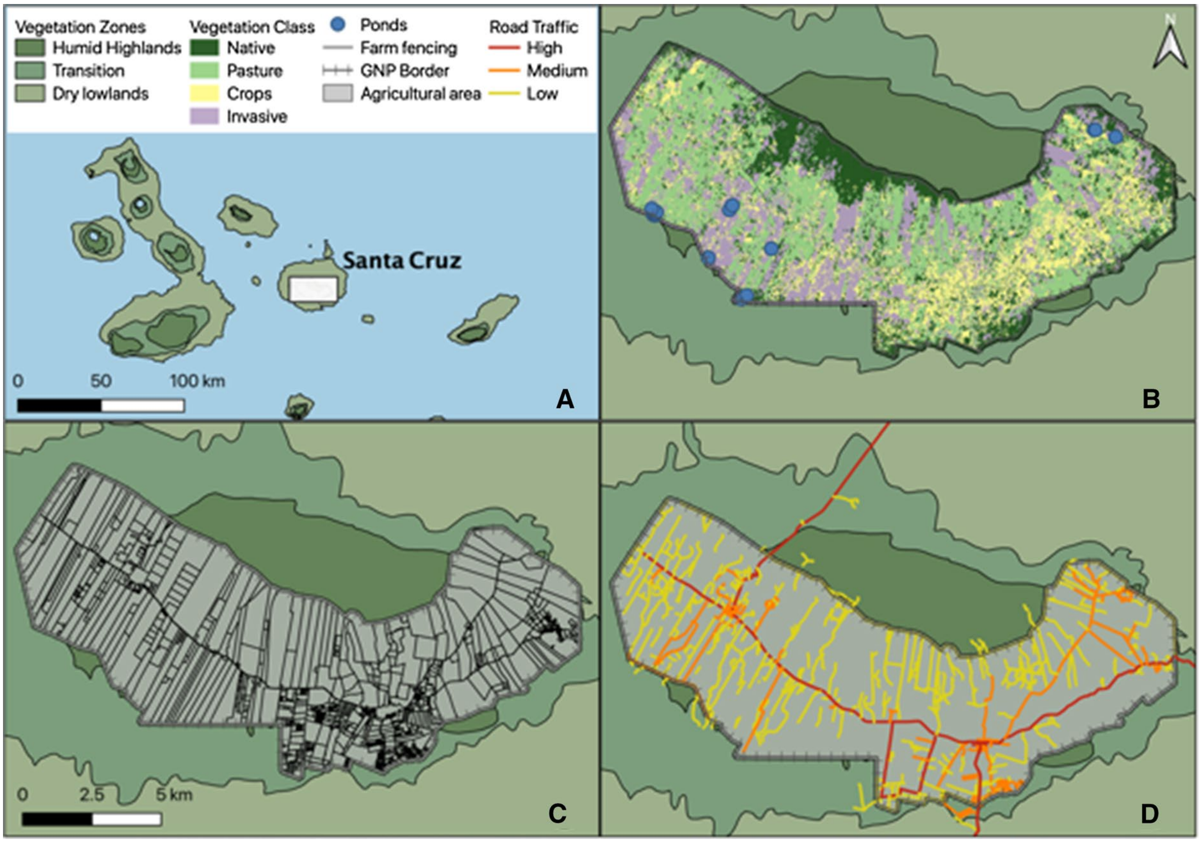

Fig. 1 Santa Cruz Island showing the covariates used to assess the effect of the agricultural landscape and roads on tortoise movement and habitat selection. **A** White rectangle indicates the location of the agricultural area shown in the other three maps; **B** Agricultural vegetation (green, yellow and purple areas) and ponds (blue dots); **C** Locations of farm fencing (black lines); **D** Three types of roads, based on levels of traffic (yellow: low-traffic roads, orange: medium-traffic roads, red: high-traffic roads)

Our sample of *Chelonoidis porteri*, from the western part of the island, included twelve males, seven females, and one juvenile. Our sample of *C. donfaustoi*, from the eastern part of the island, included four males and three females. The two species that are on Santa Cruz have recently been classified (2015) as two different species based on genetic differences, but are very similar in ecology, size, and physical appearance (Poulakakis et al. 2015). We tested for differences in responses to agricultural infrastructure and vegetation between species, and we found no evidence of such differences (Supplementary Information S1), thus we combined data for both species to obtain more statistical power to detect effects.

Determining habitat preference - integrated step-selection functions

Integrated step-selection functions use conditional logistic regression to determine the probability a habitat characteristic and or movement characteristic being ‘used’, as a function of what is ‘available’ in the landscape (Signer et al., 2019). ‘Available’ locations are simulated using parametric distributions of step lengths (the straight line distance between two consecutive GPS points), and turn angles (the turning angle between headings of two consecutive steps) that are parameterised using the observed step lengths and turn angles of the GPS tracked animals (Thurfjell et al. 2014; Michelot et al. 2019). Each ‘used’ (or observed GPS) location is allocated a set of 'available' or simulated locations, based on the distribution of step lengths and turn angles that could have been used. This set of used and available steps is called a 'strata' and can be considered the sampling unit of the models. Environmental covariates that are extracted at the end of a step can then be examined to determine if an animal is using that habitat characteristic more than is expected by chance, this is called 'selection'. If a habitat characteristic is used less than expected by chance, the behaviour is called 'avoidance' (Signer et al. 2019; Fieberg et al. 2021).

If an animal travels faster in the time period between locations, step lengths are longer, whereas if it travels slower, step lengths are shorter. To determine if habitat characteristics also influence animal movement, environmental covariates can be extracted at the beginning of a step and included in an interaction with step length to examine if animals are more likely to move faster or slower in specific habitats (Signer et al. 2019). Thus, when an interaction was included with tortoise step length for our models relating to questions on vegetation type, ponds, and road type, the environmental covariate in the interaction was extracted at the start of the step.

We used the 'amt' package to simulate 30 available steps for each 'used step' (i.e., each hourly GPS location) using an exponential distribution for step lengths and a Von Mises distribution for turn angles (Signer et al. 2019; Fieberg et al. 2021). The environmental covariates used in the models (vegetation class, fence type, land-use type, distance to roads, and distance to ponds, in meters) were rasterised in QGIS v.3.4. (QGIS Development Team, 2016) (Fig. 1B–D).

To identify population-level habitat and movement-selection by tortoises on farms, while accounting for individual variation, we constructed our integrated step-selection functions following Muff et al. (2020). Population-level step-selection functions can be estimated using an Inhomogenous Poisson Process model with stratum-specific fixed intercepts, as it is the likelihood equivalent of a conditional logistic regression (i.e. SSF; Muff et al. 2020). We created a mixed effects model framework using the 'glmmTMB' package (Brooks et al. 2017) that included a random intercept for each individual, and allowed individuals to vary in their response to movement and habitat and characteristics, with a random slope for the main fixed effects in the models (see specific details for each model below). Because integrated step-selection functions are scale-dependent (Thurfjell et al. 2014; Bastille-Rousseau et al. 2018a), we customised each model to the spatial or temporal scale at which tortoises were likely to respond to the landscape features in question (see Table 1 for overview of covariates). As a result, models sometimes differed in the number of tortoises they included, as some tortoises may not have interacted with the specific landscape feature in the model at all, or too few times to allow the model to converge (see Supplementary Information S2 for sample size details). All models included step-length and the cosine of turn angle as terms, to account for general space-use behaviour (Forester et al. 2009; Signer et al. 2019).

How did tortoises respond to vegetation class in farmland?

We determined if tortoises selected or avoided different vegetation classes, and examined whether they moved slower or faster in each. Vegetation classes were determined using satellite imagery, automatically classified using a random forest algorithm, and validated with drone imagery, producing maps of vegetation at a 15-m resolution (Laso et al. 2020). We adapted these fine-scale vegetation data from Laso et al. (2020; see Supplementary Information S3 for details), to produce four main vegetation classes with which tortoises interacted (Fig. 1B). The four categories we used were: 'pasture' including grasses planted by farmers for livestock, and naturally occurring grasses on agricultural land. 'Invasive vegetation', which included various naturalised species, most commonly blackberry (*Rubus niveus*), guava (*Psidium guajava)*, and Cuban cedar (*Cedrela odorata*) that grow aggressively in large areas and negatively impact native biotia (Laso et al. 2020). 'Crops' included both permanent crops such as coffee and bananas, and transitory crops such as tomatoes, watermelon and corn. 'Native vegetation' was the remaining vegetation that occurs naturally on the islands, such as evergreen forest and shrublands, and humid tallgrass. To assess whether movement decisions were influenced by vegetation class we fitted a model including vegetation classes (i.e., native, invasive, pasture, or crop), and an interaction with tortoise step length (n = 24 tortoises, strata = 66,372). Because movement decisions are made over the

Table 1 Overview of covariates used in each of the models to assess either tortoise selection of habitat and/or movement characteristics while in the agricultural area of Santa Cruz Island

Model	Covariates	Description
1. Influence of vegetation on selection	Vegetation type +	Type of vegetation (either pasture, invasive, crop or native) tortoise was in at the end of the step (sampled at 5 h intervals)
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
2. Influence of vegetation on movement	Vegetation type : step length +	Type of vegetation (either pasture, invasive, crop or native) tortoise was in at the start of the step with an interaction with scaled step length
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
3. Influence on pond proximity on selection and movement	Distance to pond +	Log(distance to the nearest pond at the end of the step + 1)
	Distance to pond : step length +	Log(distance to the nearest pond at the start of the step + 1) and an interaction with scaled step length
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
4. Influence of type of fence crossing on selection	Fence type +	Whether the fence had a simple, or complex construction
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
5. Influence of proximity of low-traffic road on selection and movement	Distance to low-traffic road +	Log(distance to the nearest low-traffic road at the end of the step + 1)
	Distance to low-traffic road : step length +	Log(distance to the nearest low-traffic road at the start of the step + 1) and an interaction with scaled step length
	Step length	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
6. Influence of proximity of medium-traffic road on selection and movement	Distance to medium-traffic road +	Log(distance to the nearest medium-traffic road at the end of the step + 1)
	Distance to medium-traffic road : step length +	Log(distance to the nearest medium-traffic road at the start of the step + 1) and an interaction with scaled step length
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps
7. Influence of proximity of high-traffic road on selection and movement	Distance to high-traffic road +	log(distance to the nearest high-traffic road at the end of the step + 1)
	Distance to high-traffic road : step length +	Log(distance to the nearest high-traffic road at the start of the step + 1) and an interaction with scaled step length
	Step length +	Scaled distance between steps
	Turn angle	Cosine of the turn angle between steps

Only Model 1 had steps sampled at 5 h intervals, for all other models tortoise steps were sampled hourly

distance a tortoise can see, but vegetation classes occurred over areas greater than that, at a paddock scale, vegetation class selection was likely to occur over a longer time scale than individual movement selection by tortoises, as after walking one hour (the default sampling period) a tortoise would likely be in the same vegetation type. Therefore, to assess vegetation class selection patterns at a more appropriate scale, we re-sampled our used and available steps at 5-hour intervals between steps, and constructed another model with vegetation class (n = 21 tortoises, strata = 5738). As models with categorical variables designate one category as the reference factor, we chose the native vegetation category as the reference factor in the models, to determine how tortoises reponded to human-modified vegetation in comparison to native vegetation, for both the short- and long-time scale models.

How did tortoises respond to ponds in farmland?

Artificial and natural water bodies (hereafter referred to as 'ponds') are a common feature of the agricultural landscape on Santa Cruz, and are frequented by tortoises (Ellis-Soto 2021). Locations of ponds (n = 58) were collected in the field in 2019 (Fig. 1B; Ellis-Soto 2021). To investigate tortoise response to ponds in the agricultural area (both natural and man-made), we examined tortoise preference for proximity to ponds in the landscape, and their movement characteristics as their proximity to ponds changed. As the effect of the pond is expected to decrease, with distance from pond (Prokopenko et al. 2017), we incorporated this distance decay effect by adding 1 and taking the natural logarithm to the distance of the nearest pond to each tortoise step for our variable for tortoise distance to pond (hereafter called distance to pond). For each tortoise, we compared their used to available locations in relation to distance to the pond, and examined interactions between distance to pond and step length, expecting step length to decrease if they preferred to linger near ponds (n = 27 tortoises, strata = 73,711).

How do tortoises respond to simple vs. complex fences?

To first determine the structural attributes of fences in farmland, we conducted 205 "fence surveys" in 2019 in the east (82 surveys) and west (123 surveys) of the Santa Cruz highlands. At each fence survey, we selected a random 10-m section and recorded the fence's material, and the land-use associated with the fence as 'crop' (which included transitory or permanent crops or, rarely, housing) or 'non-crop' (which included paddocks for livestock, abandoned land, and land for tourism, forestry, or national park). For each fence, we recorded the distance between the ground and first wire, distance between posts, and height to the nearest mm, measured in three places along the 10-m survey (between 0 and 1 m, 4–5 m, and 9–10 m). To test for structural differences between 'crop' and 'non-crop' fences, we used univariate linear models with square root transformations in the 'stats' package in R V.4.0.2 (R Core Team, 2020).

Fences that were structurally complex, with closely spaced posts (< 50 cm apart) and additional wire, had greater potential to impede tortoise movement than simple fences with few upright posts and less horizontal wire. Thus, when we encountered complex fences, (see Fig. 2) we also conducted 'gap surveys' to investigate the porosity of these fences to tortoises. We conducted a gap survey by walking the fence's length and recording any gaps > 50 cm and any signs of damage, such as broken wire or posts.

In the process of analysing and classifying fences, we found that 76% of fences around non-crop farms (defined above) were simple fences, and 86% of fences around crops were complex. Using the Ecuadorean Ministry of Agriculture's 2014 census, we extracted the locations of fences (Fig. 1C) and land-use types of farms (CGREG, 2015) and labelled any fence around crops 'complex' and around non-crop areas 'simple'. To evaluate fence crossings, we extracted all the instances when a tortoise step started in one land-use type (e.g. crops) but ended in a different land-use type (e.g.non-crop area), indicating a fence crossing. This allowed us to determine if tortoises selected or avoided crossing complex fences compared to simple fences (n = 25 tortoises, strata = 26,615). We expected that if complex fences were avoided by tortoises, they would be crossed much less than their availability would suggest.

How did tortoises respond to roads in farmland?

Roads in the Galapagos range from two-lane paved highways to seldom-used, single-lane dirt tracks. Road network data were obtained by combining local government data (CGREG) and open-source datasets (OpenStreetMaps). Tortoises may respond differently to different road types, so we separated roads into three categories: high, medium, or low traffic (Fig. 1D). Roads were classified based on a number

Fig. 2 Images of two typical fence types seen in the agricultural area of Galapagos. The left image shows an example of a complex fence, constructed with horizontal and vertical posts both < 50 cm apart; difficult for giant tortoises to cross. The right image shows a simple fence constructed with vertical and horizontal posts > 50 cm apart; easily crossed by tortoises. Gap transects, in which the number of gaps > 50 cm were quantified, were performed only on complex fences

of factors determined using satellite imagery, field surveys, and consulting with local residents (Laso 2021). Our classification is summarised as follows:

1. High-traffic roads included paved highways, primary, secondary, and urban roads that had relatively high vehicle traffic;
2. Medium-traffic roads included narrow gravel and service roads connected to main roads with higher vehicle traffic, and.
3. Low-traffic roads were tertiary and seasonal roads, constructed of gravel or dirt with relatively low traffic levels, or restricted vehicle access (see Supplementary Information S4 for examples of road types).

57% of the agricultural area had a road within 100 m: 6% of these were high-traffic roads, 12% medium-traffic roads, and 39% low-traffic roads. For each tortoise, we examined distance to the nearest road, and examined the interaction between distance to road, and tortoise step length. As above with ponds, to incorporate the decay of the road effect when tortoises were very far from roads we took the natural log + 1 to our distance to nearest road variables for all models (hereafter called distance to road, see Table 1). If tortoises preferred the road area, we expected their used steps to be closer to the road than their available steps. If tortoises travelled slower when closer to roads, we expected to see shorter step lengths (a positive interaction), alternatively if tortoises travel faster when closer to roads, we expected their step length would be longer when closer to roads (a negative interaction). To assess differences in tortoises response to road proximity based on road type, we constructure a separate model for each road type (n = 27 tortoises, strata = 73,711).

Results

How did tortoises respond to vegetation class in farmland?

We found that compared to native vegetation, tortoises were significantly more likely (mean odds ratio of 1.46) to be found in pasture (Fig. 3). Tortoises used crop and invasive vegetation about as much as native vegetation (Supplementary Information S5). We also detected differences in tortoise movement within vegetation classes. When tortoises were in pastures, they travelled significantly slower than when in native vegetation, whereas in invasive vegetation they travelled significantly faster. There was little difference between movement in crop and native vegetation (Supplementary Information S6) (Figs. 3, 4).

How did tortoises respond to ponds in farmland?

We found that tortoises responded strongly to pond proximity, and preferred locations closer to ponds, consequently avoiding distances further from ponds (mean odds ratio 0.62; Supplementary Information

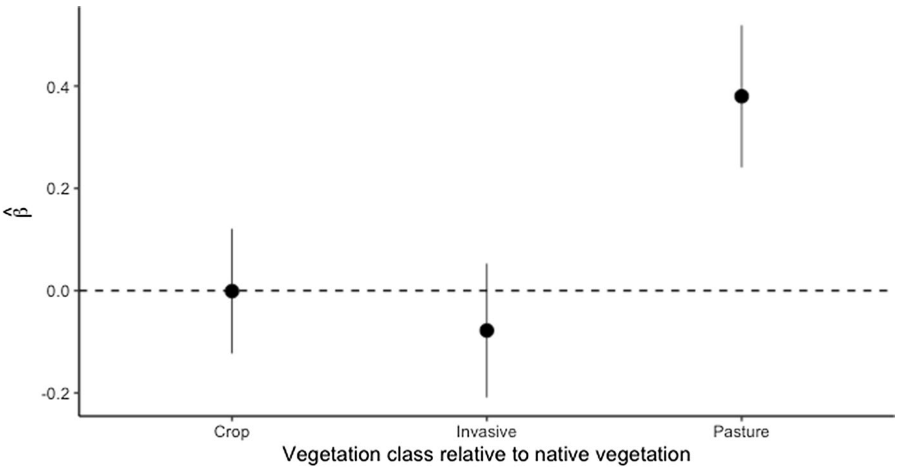

Fig. 3 Tortoise responses to human-modified vegetation compared to native vegetation use in the agricultural area of Santa Cruz, Galapagos. Tortoises preferred pastures, but there was little difference in their use of crop or invasive vegetation (measured at 5-hour timescales). Estimates above the zero (dashed) line indicate selection, and those below the line indicate avoidance. Error bars show the standard error of the mean

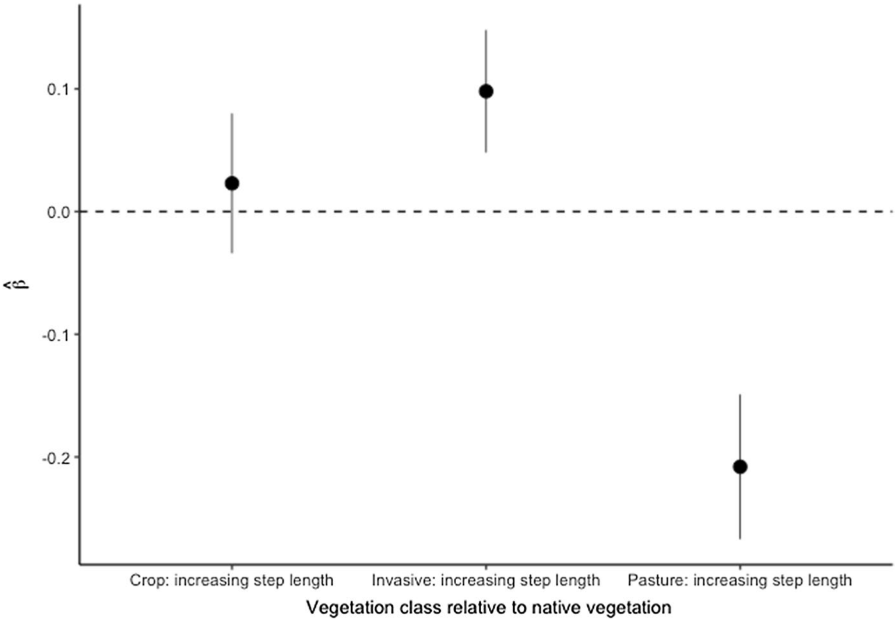

Fig. 4 Tortoise movement characteristics in human-modified vegetation, relative to native vegetation, in the agricultural area of Santa Cruz, Galapagos. Compared to native vegetation, tortoises moved slower in pasture, faster in invasive vegetation, and roughly the same speed when in crops. Estimates above the zero (dashed) line indicate selection, and those below the line indicate avoidance. Error bars show the standard error of the mean

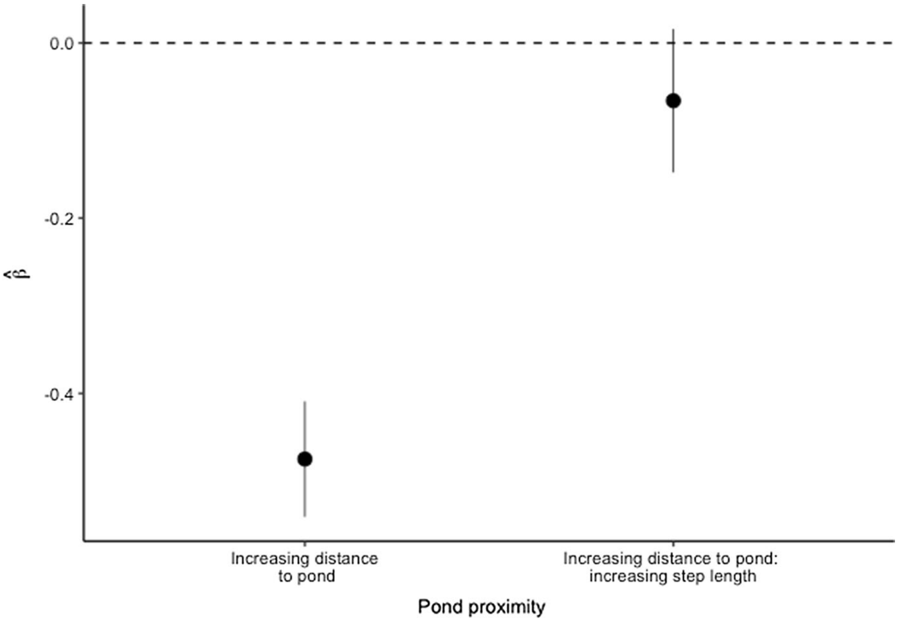

Fig. 5 Tortoise response to ponds in the agricultural area of Santa Cruz, Galapagos. Tortoises preferred to be closer to ponds. Estimates above the zero (dashed) line indicate selection, and those below the line indicate avoidance. Error bars show the standard error of the mean

S7). We found no influence of pond proximity on tortoise movement (Supplementary Information S7) (Fig. 5).

Fence structure

84% of the fences we investigated were constructed from barbed wire and live trunks of the *Porotillo* tree (*Erythrina fusca*), the remaining 16% were constructed either with wooden posts, stone or were chain-linked wire. Most of the fences we sampled (60%) met our definition of simple fences, 30% could be classified as complex, and 10% were intermediate. ‘Gap analysis’ of complex fences revealed that 21/28 complex fences (75%) had gaps (range = 1–10 gaps per gap survey), and, on average, a tortoise would encounter a gap it could cross every 86 m (± 12 m). While most gaps (69%) in fences appeared to be caused by damage to the structure (e.g., broken posts), some (31%) fences had built-in gaps. We found that fences constructed around crops had a barrier closer to the ground (mean distance = 25 cm ± SE 4 cm for crops vs 48 cm ± SE 1 cm for non-crop fences) ($t_{(203)} = 8.9$, $p = < 0.001$), and their vertical posts were closer together ($t_{(203)} = 3.2$, $p = < 0.001$), than fences around non-crop areas.

Did tortoises avoid crossing complex fences?

We found that fence crossings occurred often (we detected a total of 26,639 fence crossings), however, fences around non-crop areas were crossed more often (79% of crossing events) than fences around crops (21% of crossing events). We found tortoises were significantly less likely to cross complex fences (mean odds ratio of 0.91) than simple fences (Supplementary Information S8). We were expecting complex fences around crops to strongly restrict tortoise movement into crops, however, most tortoises in our sample crossed gaps in these fences at some point. Collectively there were 10,624 (16% of the used steps in the vegetation model) tortoise locations in crop vegetation.

How did tortoises respond to roads in farmland?

All the tortoises in our sample interacted with at least one type of road (low-, medium-, or high-traffic). Overall, we found that tortoises were more likely (mean odds ratio of 0.86), to be found closer to low-traffic roads than expected by chance (Table 2) whereas there was no significant impact of road proximity for medium and high-traffic roads (Supplementary Information S9–10). We did not detect a difference in tortoise movement in relation to their distance

Table 2 Model output for tortoise response to low-traffic roads in the agricultural area of Santa Cruz Island, Galapagos

Term	Estimate	SE	z	p-value
Distance to low-traffic road	− 0.149	0.062	− 2.400	0.016
Distance to low-traffic road : step length	− 0.049	0.036	− 1.350	0.179
Step length	0.040	0.004	9.730	> 0.001
Turn angle	− 0.249	0.005	− 46.760	> 0.001

Tortoises preferred to be closer to low-traffic roads. An interaction is denoted with " : "

to any of the road types (Table 2 and Supplementary Information S9–10).

Discussion

Tortoises used all vegetation types, and, compared to native vegetation, preferred pasture. The probability of finding tortoises in invasive or crop vegetation was approximately equal to native vegetation. We found tortoises moved most slowly in pasture, and faster in invasive vegetation relative to their movement in native vegetation. Tortoises were also more likely to be found closer to ponds and low-traffic roads. We found most fences were easy to cross, however tortoises preferred to cross fences with a simple rather than complex structure.

Movement speed can be informative for discerning behavioural state: moving slower may suggest foraging or resting, and moving faster may indicate travelling or searching. Here we found tortoises change their movement process in response to vegetation class. When tortoises were in pastures they tended to move slower, lingering in these areas, whereas when they were in invasive vegetation they moved quickly. To accurately add behavioural context, however, future studies could use accelerometers or behavioural-change-point analysis (Patterson et al. 2009).

Both species of Santa Cruz tortoises are generalist grazers that forage on a variety of ground plants, including cultivated grasses, such as sour grass (*Paspalum conjugatum)*, a species used extensively in livestock pasture (Blake et al. 2015a). Areas where the soil is tilled or shaded, for example corn crops, may have fewer ground plants, including the grasses and forbs eaten by tortoises. Areas with invasive species typically have high vegetation density, however, they have fewer of the vegetation characteristics preferred by tortoises, especially large grazing lawns, and are characterised by low tortoise density (Pike et al. 2022). It follows, then, that tortoises also travel faster while in invasive vegetation, and move slower in pasture. Food availability may, therefore, contribute to the differences we observed in resource selection and movement characteristics among vegetation classes.

Infrastructure, such as artificial water bodies, can also influence animal movement (Smit et al. 2007). On Santa Cruz, many farms had ponds for livestock and irrigation, which attracted large numbers of tortoises (Ellis-Soto 2021). Ponds may be used by tortoises for thermoregulation, because water can buffer short-term temperature fluctuations. In addition, ponds may be important for foraging in the dry season, when plant productivity can decline elsewhere (Blake et al. 2020b). Some previously ephemeral ponds are now maintained as permanent water sources, which may artificially elevate tortoise abundance or encourage tortoises to delay migration. In many ecosystems, large herbivores can overexploit local resources, or change their movement patterns in response to artificial water (Loarie et al. 2009). For example, artificial water bodies allow African savannah elephants (*Loxodonta africana*) to occupy areas they otherwise could not use, which can degrade surrounding vegetation (Loarie et al. 2009; Oliveira-Santos et al. 2016). Although a link between extended access to ponds and local resource exploitation has not been established, our previous research on these tortoises (Pike et al. 2021) showed that some individuals remain on farms longer than was optimal in the past (Yackulic et al. 2017), and increased pond availability may contribute.

Fences, constructed to delineate ownership, enclose livestock, and manage the spread of disease are often barriers to wildlife movement (Seidler et al. 2015; Gordon 2018; Jakes et al. 2018; Reinking et al. 2019). We expected fences would obstruct tortoise movement in the agricultural area, especially as this has been reported for other turtle and tortoise species (Peaden et al. 2017; Lee et al. 2021). Contrary to our expectations, fences in the agricultural area were not very effective barriers. Instead, most fences (60%) offered little resistance to tortoise movement, and included spaces large enough for adult tortoises to traverse them. While complex fences were present (30% of our sample), 75% had gaps at a mean interval of 86 m, rendering them fairly porous to tortoises. Thus, although complex fences may present a temporary obstruction, a tortoise is likely to either find a gap, or a simple fence, nearby, allowing passage. Therefore, tortoises were frequently recorded in crops surrounded by complex fences, and tortoises still regularly crossed between crops and other vegetation types, although less frequently than into vegetation types surrounded by simple fences.

Fences, as they are currently constructed, do not appear to be significant impediments to tortoise movements. This is important, because access to high-quality foraging grounds in the highlands provides energy critical for migrating tortoises (Blake et al. 2013; Yackulic et al. 2017; Bastille-Rousseau et al. 2018b). On the other hand, conflict with farmers can occur when fences around valuable crops are ineffective against tortoises, and farmers have reported economic losses from tortoise damage to crops and fences (Benitez-Capistros et al. 2018, 2019). The majority (69%) of the gaps in fences we encountered were caused by broken posts or wires, which can be expensive to repair (Benitez-Capistros et al. 2018) thus gaps often remain for sometime and make fences ‘leaky’. Giant tortoises can ‘bulldoze’ through poorly constructed fences, likely contributing to conflict with farmers. More durable fencing material around vulnerable crops would prevent access to tortoises and reduce income loss to farmers, although this would add to fence construction costs. However, maintaining connectivity between important tortoise habitats, such as pastures, ponds, and the Galapagos National Park will become more critical if fencing becomes more effective, because connectivity among habitat types is paramount for the effective conservation of these migratory tortoises.

Tortoises were more likely to be found close to low-traffic roads. An attraction to roads, and road-side habitats, has been documented for a number of large mammals such as Asian elephants (*Elephas maximus*) that use areas close to roads for foraging (Wadey et al. 2018; Eisaguirre et al. 2020), however this result is not typical for turtles (Boarman and Sazaki 2006; Beaudry et al. 2008; Shepard et al. 2008). Wildlife may be attracted to roads for multiple reasons, including ease of travel, foraging, thermoregulation, etc. (Rytwinski and Fahrig 2013; Bidder et al. 2015; Abrahms et al. 2016). Giant tortoises occur along these linear features, grazing on roadside vegetation and gathering on roads in heavy rain to drink from pools of water (KP and FC observations). Proximity to roads in the highlands may also confer thermoregulatory benefits in the agricultural area, which is generally much cooler and can be closer to the tortoise’s thermal minimum than the lowlands (Blake et al. 2020a). Indeed, carapace temperatures of Mojave Desert tortoises were higher closer to roads, although this may be negative for this species, which lives in high-temperature environments (Peaden et al. 2017). Although roads attractive to tortoises have relatively low traffic levels, travelling at lower speeds, there is still the risk of road-strikes, damaging vehicles, and injuring tortoises. Indeed, a tortoise sustained injuries from a vehicle collision on a medium-traffic road during fieldwork for this study (KP personal observation). Vehicle collisions are a well-known problem, affecting many other turtle species (Boarman and Sazaki 2006; Peaden et al. 2017). Vehicle strikes are currently infrequent for giant tortoises, and are high-profile events when they do occur (Cayot et al. 2017). But traffic is expected to increase, as tourism, and local demand for more roads to access the lowlands, also increase (Cayot et al. 2017; Sampedro et al. 2018). Road use by wildlife causes some of the best-known human-wildlife conflicts (van der Grift et al. 2013; Laurance et al. 2015) both globally and in Galapagos (Tanner and Perry 2007; García-Carrasco et al. 2020). Roads in the Galapagos also cause significant mortality to the island’s avifauna and lava lizards (Tanner and Perry 2007; García-Carrasco et al. 2020). To reduce wildlife mortality, for tortoises, Galapagos birds, and lava lizards, increased investment in road signage and speed limit enforcement are pre-requisites, and more creative solutions such as wildlife underpasses may be needed (Tanner and Perry 2007; García-Carrasco et al. 2020).

We found that the tortoises’ response to roads differed with road type in the agricultural area. Low-traffic roads were the most abundant, and tortoises tended to choose locations that were closer to these roads than expected by chance. On the other hand, we did not detect strong effects of medium and high-traffic roads, however they are also much less abundant making it difficult to capture instances when tortoises interact with these features. Futhermore, the differences in characteristics between high-traffic and medium- and low-traffic roads were stark. The 40-km-long, high-traffic road links the main township to the main port and the airport. This main road permits vehicles to travel at over 70 km/hr, and is in significantly better condition than the medium- and low-traffic roads, which are mostly dirt or gravel (Tanner and Perry 2007; García-Carrasco et al. 2020). It is unclear whether the roads and traffic levels are driving the patterns observed here or if it is another factor associated with road types and their levels of traffic that can explain this result. Regardless, the finding that tortoises tend to be found closer to some roads warrants continued attention to this area of research.

One limitation of our study was limited availability and resolution of the environmental co-variates we used. The spatial resolution of the land cover dataset is 15 m (Laso et al. 2020), but in reality, vegetation is rarely found in homogenous patches of that size, and this is a potential source of increased variability in our models. Also, we combined permanent crops (mostly coffee, bananas, and plantains) and transitory crops (mostly tomatoes, corn, watermelon, and cassava) as we did not have samples large enough to examine these two crop types separately (Laso et al. 2020). On Santa Cruz, transitory crops cover approximately 1% of agricultural land, and permanent crops 8% (Laso et al. 2020). Although combining crop types allowed for an overall insight into the selection of crops relative to other vegetation, this reduced our ability to discern differences in attractiveness among crop types for tortoises. Compared to most permanent crops on Galapagos, transitory crops are usually ground-cover plants, more susceptible to tortoise depredation and damage. If tortoises use transitory crop areas, it is likely to lead to income loss for farmers (Benitez-Capistros et al. 2018). However, without more samples of tortoise movement in different crop types, we are limited in our ability to recommend crop-specific management strategies for tortoises in these areas. We also note that the Galapagos Islands have different levels of human encroachment, and that our results for Santa Cruz Island represent the highest level of potential for human-wildlife conflict on the spectrum of conservation issues presently facing giant tortoises.

Our evaluation of tortoise movement in relation to infrastructure and human-modified vegetation shows that these features can influence tortoise distribution and resource use in the agricultural area. Ponds, pasture and low-traffic roads may be used preferentially by tortoises for resources, and ease of travel, whereas invasive vegetation was quickly traversed by tortoises, potentially indicating that they were only moving through. Negative impacts resulting from these interactions with infrastructure and vegetation were more likely to affect landholders than tortoises, especially if tortoises cause damage to either infrastructure or valuable crops. Understanding and evaluating the influence of anthropogenic landscape features on wildlife movement and fine-scale resource use can be helpful in identifying the factors likely to cause, or exacerbate, negative interactions between humans and wildlife. To best identify priority areas for managing wildlife on farms in other systems, we recommend evaluating multiple anthropogenic landscape features and assessing the interplay between infrastructure and access to human-modified vegetation.

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Author contributions KP, LS, IG and SB conceived the ideas and designed methodology; FC collected the movement data and KP the fence structure data; FL categorized the road network data. FL and GRT produced the land cover data. KP analysed the data; KP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Movement and vegetation data are accessible through Movebank and Remote Sensing, the remaining data will be archived in Dryad.

Declarations

Competitng interests The authors have no relevant financial or non-financial interests to disclose

References

Abrahms B, Jordan NR, Golabek KA et al (2016) Lessons from integrating behaviour and resource selection: activity-specific responses of african wild dogs to roads. Anim Conserv 19:247–255

Alamgir M, Campbell MJ, Sloan S et al (2017) Economic, socio-political and environmental risks of road development in the tropics. Curr Biol 27:R1130–R1140

Bastille-Rousseau G, Murray DL, Schaefer JA et al (2018) Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling. Ecography (Cop) 41:437–443

Bastille-Rousseau G, Potts JR, Yackulic CB et al (2016) Flexible characterization of animal movement pattern using net squared displacement and a latent state model. Mov Ecol 4:15

Bastille-Rousseau G, Yackulic C, Gibbs J et al (2018) Migration triggers in a large herbivore: galapagos giant tortoises navigating resource gradients on volcanoes. Ecology 0:1–11

Beaudry F, deMaynadier PG, Hunter ML (2008) Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. Biol Conserv 141:2550–2563

Benitez-Capistros F, Camperio G, Hugé J et al (2018) Emergent conservation conflicts in the Galapagos islands: human-giant tortoise interactions in the rural area of Santa Cruz island. PLoS ONE 13:1–28

Benitez-Capistros F, Couenberg P, Nieto A et al (2019) Identifying shared strategies and solutions to the human-giant tortoise interactions in Santa Cruz, Galapagos: a nominal group technique application. Sustainability 11:1–25

Beyer HL, Gurarie E, Börger L et al (2016) “You shall not pass!”: quantifying barrier permeability and proximity avoidance by animals. J Anim Ecol 85:43–53

Bidder OR, Walker JS, Jones MW et al (2015) Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. Mov Ecol 3:1–17

Blake NJ, Parlin AF, Cumming I et al (2020) Thermoregulation. In: Gibbs JP, Cayot LJ, Tapia WA (eds) Galapagos giant tortoises. Elsevier Inc, Amsterdam, pp 175–205

Blake S, Guezou A, Deem S et al (2015) The dominance of Introduced Plant Species in the diets of migratory Galapagos Tortoises increases with elevation on a human-occupied island. Biotropica 47:246–258

Blake S, Tapia PI, Safi K, Ellis-Soto D (2020) Diet, behavior, and activity patterns. In: Gibbs JP, Cayot LJ, Tapia WA (eds) Galapagos giant tortoises. Elsevier Inc, Amsterdam, p 286

Blake S, Yackulic C, Wikelski M et al (2015b) Migration by Galapagos Giant Tortoises requires Landscape-Scale Conservation Efforts. 144–150

Blake S, Yackulic CB, Cabrera F et al (2013) Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. J Anim Ecol 82:310–321

Boarman WI, Sazaki M (2006) A highway’s road-effect zone for desert tortoises (*Gopherus agassizii*). J Arid Environ 65:94–101

Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Cayot LJ, Gibbs JP, Tapia WH, Caccone A (2017) *Chelonoidis porteri* The IUCN Red List of Threatened Species 2017: e.T9026A82777132

Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) (2015) Censo de Unidades de Producción Agropecuaria de Galápagos 2014 (UPA)– Cons. Gob. del Régimen Espec. Galápagos. Galapagos, Ecuador

Cosgrove AJ, McWhorter TJ, Maron M (2018) Consequences of impediments to animal movements at different scales: a conceptual framework and review. Divers Distrib 24:448–459

Coulon A, Morellet N, Goulard M et al (2008) Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. Landsc Ecol 23:603–614

Cozzi G, Broekhuis F, Mcnutt JW, Schmid B (2013) Comparison of the effects of artificial and natural barriers on large african carnivores: implications for interspecific relationships and connectivity. J Anim Ecol 82:707–715

Eisaguirre JM, Booms TL, Barger CP et al (2020) Novel step selection analyses on energy landscapes reveal how linear features alter migrations of soaring birds. J Anim Ecol. https://doi.org/10.1111/1365-2656.13335

Ellis-Soto D (2021) Giant tortoises connecting terrestrial and freshwater ecosystems. Galapagos giant tortoises. Academic Press, Cambridge, pp 308–309

Epler B (2007) Tourism, the economy. Population Growth, and Conservation in Galapagos

Fieberg J, Signer J, Smith B, Avgar T (2021) A ‘How to’ guide for interpreting parameters in habitat-selection analyses. J Anim Ecol. https://doi.org/10.1101/2020.11.12.379834

Forester JD, Im HK, Rathouz PJ (2009) Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565

García-Carrasco JM, Tapia W, Muñoz AR (2020) Roadkill of birds in galapagos islands: a growing need for solutions. Avian Conserv Ecol 15:1–8

Gibbs JP, Hunter EA, Shoemaker KT et al (2014) Demographic outcomes and ecosystem implications of giant tortoise reintroduction to Espanola Island. PLoS ONE, Galapagos. https://doi.org/10.1371/journal.pone.0110742

Gordon IJ (2018) Review: livestock production increasingly influences wildlife across the globe. Animal 2030:1–11

Harris G, Thirgood S, Hopcraft JGC et al (2009) Global decline in aggregated migrations of large terrestrial mammals. Endanger Species Res 7:55–76

Jakes AF, Jones PF, Paige LC et al (2018) A fence runs through it: a call for greater attention to the influence of fences on wildlife and ecosystems. Biol Conserv 227:310–318

Laso FJ (2021) Agriculture, Wildlife, and Conservation in the Galapagos Islands. University of North Carolina, Chapel Hill

Laso FJ, Benítez FL, Rivas-Torres G et al (2020) Land cover classification of complex agroecosystems in the non-protected highlands of the Galapagos Islands. Remote Sens. https://doi.org/10.3390/RS12010065

Laurance WF, Peletier-Jellema A, Geenen B et al (2015) Reducing the global environmental impacts of rapid infrastructure expansion. Curr Biol 25:R259–R262

LeB Hooke R, Martin-Duque JF, Pedraza J (2012) Land transformation by humans: a review. Geol Soc Am. https://doi.org/10.1130/GSAT151A.1.Figure

Lee ATK, Macray MB, Ryan PG, Alexander GJ (2021) Tortoise mortality along fence lines in the Karoo region of South Africa. J Nat Conserv 59:125945

Loarie SR, Aarde RJV, Pimm SL (2009) Fences and artificial water affect african savannah elephant movement patterns. Biol Conserv 142:3086–3098

MacFarland CG, Villa J, Toro B (1974) The Galapagos giant tortoises (*Geochelone elephantopus)* Part II: conservation methods. Biol Conserv 6:198–212

Michelot T, Blackwell PG, Matthiopoulos J (2019) Linking resource selection and step selection models for habitat preferences in animals. Ecology 100:1–22

Muff S, Signer J, Fieberg J (2020) Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using bayesian or frequentist computation. J Anim Ecol 89:80–92

Munger JC, Barnett BR, Novak SJ and Ames AA (2003) Impacts of off-highway motorized vehicles on the reptile and vegetation of the Owyhee Front. Idaho Bur L Manag Tech Bull No.03–3:27

Munger JC, Ames AA (2001) Impacts of off-highway motorized vehicles on sensitive reptile species in Owyhee county, Idaho. Idaho Bur L Manag Tech Bull No. 01–6:32

Nafus MG, Tuberville TD, Buhlmann KA, Todd BD (2013) Relative abundance and demographic structure of Agassiz's desert tortoise (*Gopherus agassizii*) along roads of varying size and traffic volume. Biol Conserv 162:100–106

Oliveira-Santos LGR, Forester JD, Piovezan U et al (2016) Incorporating animal spatial memory in step selection functions. J Anim Ecol 85:516–524

Olsson MPO, Widen P (2008) Effects of highway fencing and wildlife crossings on moose Alces alces movements and space use in southwestern Sweden. Wildlife Biol 14:111–117

Patterson TA, Basson M, Bravington MV, Gunn JS (2009) Classifying movement behaviour in relation to environmental conditions using hidden Markov models. J Anim Ecol 78:1113–1123

Peaden JM, Nowakowski AJ, Tuberville TD et al (2017) Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biol Conserv 214:13–22

Pike K, Blake S, Cabrera F et al (2021) Body size, sex and high philopatry influence the use of agricultural land by Galapagos giant tortoises. Oryx. https://doi.org/10.1017/S0030605320001167

Pike KN, Blake S, Gordon IJ et al (2022) Sharing land with giants: habitat preferences of Galapagos tortoises on farms. Glob Ecol Conserv. https://doi.org/10.1016/j.gecco.2022.e02171

Poulakakis N, Edwards DL, Chiari Y et al (2015) Description of a New Galapagos giant tortoise species (Chelonoidis; Testudines: Testudinidae) from Cerro Fatal on Santa Cruz Island. PLoS ONE. https://doi.org/10.1371/journal.pone.0138779

Prokopenko CM, Boyce MS, Avgar T (2017) Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J Appl Ecol 54:470–479

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reinking AK, Smith KT, Mong TW et al (2019) Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter. Ecosphere. https://doi.org/10.1002/ecs2.2722

Riggio J, Baillie JEM, Brumby S et al (2020) Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. Glob Chang Biol 26:4344–4356

Rivas-Torres GF, Benítez FL, Rueda D et al (2018) A methodology for mapping native and invasive vegetation coverage in archipelagos: an example from the Galápagos Islands. Prog Phys Geogr 42:83–111

Russell JC, Kueffer C (2019) Island Biodiversity in the Anthropocene–Annu Rev Environ Resour 44:31–60

Rytwinski T, Fahrig L (2013) Why are some animal populations unaffected or positively affected by roads? Oecologia 173:1143–1156

Sampedro C, Pizzitutti F, Quiroga D et al (2018) Food supply system dynamics in the Galapagos Islands: Agriculture, livestock and imports. Renew Agric Food Syst. doi: https://doi.org/10.1017/S1742170518000534

Seidler RG, Long RA, Berger J et al (2015) Identifying impediments to long-distance mammal migrations. Conserv Biol 29:99–109

Shaw AK (2016) Drivers of animal migration and implications in changing environments. Evol Ecol 30:991–1007

Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA (2008) Roads as barriers to animal movement in fragmented landscapes. Anim Conserv 11:288–296

Shilling F, Collinson W, Bil M et al (2020) Designing wildlife-vehicle conflict observation systems to inform ecology and transportation studies. Biol Conserv 251:108797

Signer J, Fieberg J, Avgar T (2019) Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol 9:880–890

Smit IPJ, Grant CC, Devereux BJ (2007) Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large african savanna park. Biol Conserv 136:85–99

Songhurst A, McCulloch G, Coulson T (2016) Finding pathways to human-elephant coexistence: a risky business. Oryx 50:713–720

St. Clair CC, Backs J, Friesen A, et al (2019) Animal learning may contribute to both problems and solutions for wildlife-train collisions. Philos Trans R Soc B Biol Sci. https://doi.org/10.1098/rstb.2018.0050

Tanner D, Perry J (2007) Road effects on abundance and fitness of Galápagos lava lizards (*Microlophus albemarlensis*). J Environ Manage 85:270–278

Theobald DM, Kennedy C, Chen B et al (2020) Earth transformed: detailed mapping of global human modification from 1990 to 2017. Earth Syst Sci Data 12:1953–1972

Thurfjell H, Ciuti S, Boyce MS (2014) Applications of step-selection functions in ecology and conservation. Mov Ecol 2:1–12

Trueman, M., Hobbs, R.J., & Van Niel, K. (2013). Interdisciplinary historical vegetation mapping for ecological restoration in Galapagos– Landsc. Ecol. 28: 519–532. https://doi.org/10.1007/s10980-013-9854-4

van der Grift EA, van der Ree R, Fahrig L et al (2013) Evaluating the effectiveness of road mitigation measures. Biodivers Conserv 22:425–448

Wadey J, Beyer HL, Saaban S et al (2018) Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. Biol Conserv 218:91–98

Watson J, Trueman M, Tufet M, Henderson S, Atkinson R (2010) Mapping terrestrial anthropogenic degradation on the inhabited islands of the Galapagos Archipelago. Oryx 44:79

Wiggins IL, Porter DM (1971) Flora of the Galapagos Islands. Stanford University Press, Stanford

Wilcove DS, Wikelski M (2008) Going, going, gone: is animal migration disappearing? PLoS Biol 6:1361–1364

Yackulic CB, Blake S, Bastille-Rousseau G (2017) Benefits of the destinations, not costs of the journeys, shape partial migration patterns. J Anim Ecol 86:972–982

Zeller KA, McGarigal K, Cushman SA et al (2016) Using step and path selection functions for estimating resistance to movement: pumas as a case study. Landsc Ecol 31:1319–1335