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ORIGINAL RESEARCH

Habitat quality in farmland influences the activity patterns of giant Galapagos tortoises

Kyana N. Pike[1] · Stephen Blake[2,3,4] · Iain J. Gordon[5,6,7,8,9] · Lin Schwarzkopf[1]

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Abstract

Many Galapagos giant tortoises make seasonal migrations from arid lowlands in the wet season, to humid highlands in the dry season. However, for critically endangered Western Santa Cruz giant tortoises (*Chelonoidis porteri*), at least 88% of the habitat in the highlands is now used for agriculture. To understand the impact of agricultural land use on tortoise behavior, we conducted 242 30-minute observations of tortoises on farms. We (1) recorded the time tortoises spent eating, walking, and resting in three different land-use types, (2) measured their temperature, and (3) quantified their selection of fine-scale vegetation characteristics. We found that tortoises rest for significantly longer periods when they are in abandoned land, compared to livestock, grazing, and touristic land. Generally, tortoises rested for longer when they were cooler. Time spent eating was increased by the density and proportion of ground vegetation, while time spent walking was reduced by tall vegetation. These findings suggest that the distribution of land-use types and the fine-scale composition of thermoregulatory and grazing resources within farmland have important implications for the behavior of tortoises while in human-modified land. Wildlife managers and landowners wishing to support tortoises on farms should focus on rehabilitating abandoned land and encouraging a heterogenous mix of sun and shade, and short ground vegetation across land-use types.

Keywords Activity budgets · Agricultural land · Behavior · Dirichlet regression · *Chelonoidis porteri* · Migratory species · Thermal characteristics · Vegetation characteristics

Introduction

Worldwide, biodiversity is vanishing at an alarming rate. Agriculture can cause habitat loss for wildlife, but under some circumstances, it may also provide suitable habitat (Dirzo et al. 2014; Tilman et al. 2017). Ideally for conservation, no further demands would be placed

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Extended author information available on the last page of the article on our natural systems, and habitat for wildlife could be restored, however, with the human population expected to increase by 4 billion by the end of the century (United Nations 2015), this outcome is unlikely. Maintaining intact natural areas and reducing habitat loss for wildlife is the preferred option for biodiversity conservation (Green et al. 2005; Silveira dos Santos et al. 2020; Balmford 2021), however, when that is not feasible, maximizing the benefits of degraded lands for wildlife may be the best available choice for conservation (Kremen 2015; Johansson et al. 2016; Gordon 2018). One strategy to alleviate habitat loss for wildlife is land sharing (Phalan et al. 2011; Kremen 2015; Loconto et al. 2020). This approach encourages farmers to adopt practices that are wildlife friendly, thus increasing, or at least maintaining, habitat available to wildlife (Green et al. 2005; Phalan et al. 2011; Jiren et al. 2018).

For wildlife unable to meet their ecological needs from remaining natural areas, land sharing can be an important lifeline. Modifications that extend wildlife habitat can be small-scale, such as incorporating hedgerows or wildflowers into paddocks, to support greater diversities of pollinating birds and insects (Benayas and Bullock 2015). Shade-grown coffee, for example, in which coffee plants are grown under large native trees, is an instance of land-sharing, as farms are productive, while also providing habitat for many birds, reptiles, insects, and mammals (Borkhataria et al. 2012; Caudill et al. 2015). Not all farm types are optimal for providing habitat for wildlife, as some land-use types provide only low-quality habitat, or very few resources. For instance, in Spain, research by González del Portillo et al. (2021) showed that in cereal farmland, alfalfa farms provided better quality habitats for the endangered little bustard (*Tetrax tetrax*) during chick rearing than other farm types.

In higher quality habitats, wildlife can typically invest more time in activities that maximise energy acquisition, such as foraging, and minimise activities that expend energy, such as predator evasion or travel. Thus, measuring how well animals can balance their activity patterns in different habitats within human-modified land can be useful to determine the quality of these areas. For instance, measuring differences in the activities (such as resting, travelling, foraging, etc.) of Bale monkeys (*Chlorocebus djamdjamensis*), in fragmented and continuous forest was useful to differentiate the strategies they employed in the two habitat types as a function of their quality (Mekonnen et al. 2017). Measuring the balance of activities that either expend or acquire energy can provide insights that help clarify the implications of using human-modified land with varying habitat quality.

Critically endangered Western Santa Cruz Galapagos tortoises (C*helonoidis porteri*), which occur on Santa Cruz Island in the centre of the Galapagos Archipelago, are partial migrants that regularly interact with agricultural land. During the wet season, the lowlands experience a surge in plant growth with high nutritional quality (Blake et al. 2013; Yackulic et al. 2017). During the dry season, however, larger tortoises are likely to experience an energetic deficit if they remain in the arid lowlands when food becomes limited, so most adults migrate upslope to the humid highlands, which are more consistently productive (Blake et al. 2013; Bastille-Rousseau et al. 2017b; Yackulic et al. 2017). This elevational migration evolved long before agriculture began on Santa Cruz in the early 20th century (Blake et al. 2013; Bastille-Rousseau et al. 2016). Today, the humid highlands of Santa Cruz Island are highly modified habitats, with at least 88% of the land area converted to agriculture (Watson et al. 2010). These seasonal vegetation dynamics are known to contribute heavily to the migratory cycle of adult tortoises, but questions remain about the impact of different farm types on tortoise behavior (Blake et al. 2013).

The impact of these land use changes on tortoise ecology is poorly known, but likely depends largely on the quality of habitats provided by these novel land-use types. Migratory western Santa Cruz tortoises spend the dry season in a matrix of different farm types (Watson et al. 2010; Pike et al. 2021, 2022b). Tortoises often remain on farms for long periods (five months on average) (Pike et al. 2021). Furthermore, giant tortoises are essential ecosystem engineers, as tortoises move through the landscape, they trample vegetation, their selective feeding creates gaps for recruitment, and their dung contains many seeds that are dispersed in nutrient rich material (Blake et al. 2012; Froyd et al. 2014; Bastille-Rousseau et al. 2017a; Ellis-Soto et al. 2017). Maintaining movement patterns and supporting the tortoise population has important implications for wider ecosystem health and stability (Gibbs et al. 2010; Hunter et al. 2013, 2021).

To better support management of the integrity of the migratory cycle of giant tortoises, we undertook a study of tortoise activity in the agricultural zone of Santa Cruz. Our aims were to quantify the activity patterns (eating, walking, and resting) of Western Santa Cruz giant tortoises during their time in the agricultural area, examining time spent, and to determine the relationships between land-use type, temperature, season, sex, size, and vegetation characteristics and the time spent by tortoises on various activities in farms. We addressed the following question:

What factors influence the time spent by tortoises eating, resting and walking whilst on farms? We anticipated that habitats with high grass and forb abundance would be associated with greater time spent feeding, that tortoises would rest more when it was cooler, and that tortoises would avoid walking in areas with dense vegetation.

Methods

Study site

The Galapagos archipelago is a chain of volcanic islands located approximately 1000 km from the coast of Ecuador. Native vegetation is characterized by three main zones, determined largely by aspect and elevation, the arid lowlands, the humid highlands, and a transition zone between the two (Wiggins and Porter 1971; McMullen 1999). The Galapagos Islands straddle the equator and have two main seasons, the hot, wet season during January–May, and a cool, dry season during June–December (Trueman and D'Ozouville 2010). The agricultural sector on Santa Cruz services the local population of approximately 18,000 inhabitants and supplements the large tourism sector. Over 200,000 tourists now visit Galapagos annually (Dirección del Parque Nacional Galápagos and Observatorio de Turismo de Galápagos. 2020), and this sector contributes substantially to the local and national economy. Tourism has also impacted the agricultural sector in two main ways. First, the rapid rise in tourism over the last three decades has led some agriculturalists to leave farming for more profitable jobs in tourism (Sampedro et al. 2018). This has resulted in ca. 22% of the agricultural area now being abandoned (Laso et al. 2020). Second, some landholders have repurposed a portion of their agricultural land for tourism, often involving giant tortoises as the key attraction (Benitez-Capistros et al. 2016).

Land-use types in the agricultural area are diverse: Livestock areas include native and introduced grasses for cattle and horses, crop areas include annual crops such as corn, tomatoes, and watermelon, and perennial crops such as coffee, pineapples, and banana. Abandoned land is typically colonised by invasive species including blackberry (*Rubus niveus*), Cuban cedar (*Cedrela odorata)* and guava (*Psidium guajava*). Finally, touristic land is often characterised by well-maintained lawns interspersed with a mix of native and introduced trees and shrubs (see Fig. 1 for the distribution of land-use types within our study area).

Behavioral observations

Between March to May 2019, we collected a total of 242 behavioral observations of tortoises, in the wet season ($n=114$), and again from November to December 2019 in the dry season ($n=128$). Tortoises are most active during the day, but show some seasonal differences in activity patterns (Blake et al. 2021). During the wet season, tortoise activity is unimodal, peaking in the morning to early afternoon, however in the dry season tortoises are inactive at midday, and show a second, smaller peak of activity, later in the afternoon (Rodhouse et al. 1975; Cayot 1987; Blake et al. 2021b). Thus, we recorded tortoise behavior for the first half of the day (between 06:30 to 12:30) when tortoises could be expected to be active in both seasons. Once a tortoise was located, the observer began a timed 30-minute focal observation (Altmann 1974) using binoculars from a distance of 5–15 m, during which the duration and type of all activities were recorded. During the focal observation, all behaviors of the focal individual, including eating, resting, walking, mating, and interactions with conspecifics or heterospecifics (see Supplementary Table 1 for full list of behaviors) were recorded. All observations were conducted by a single observer to minimize inter-observer

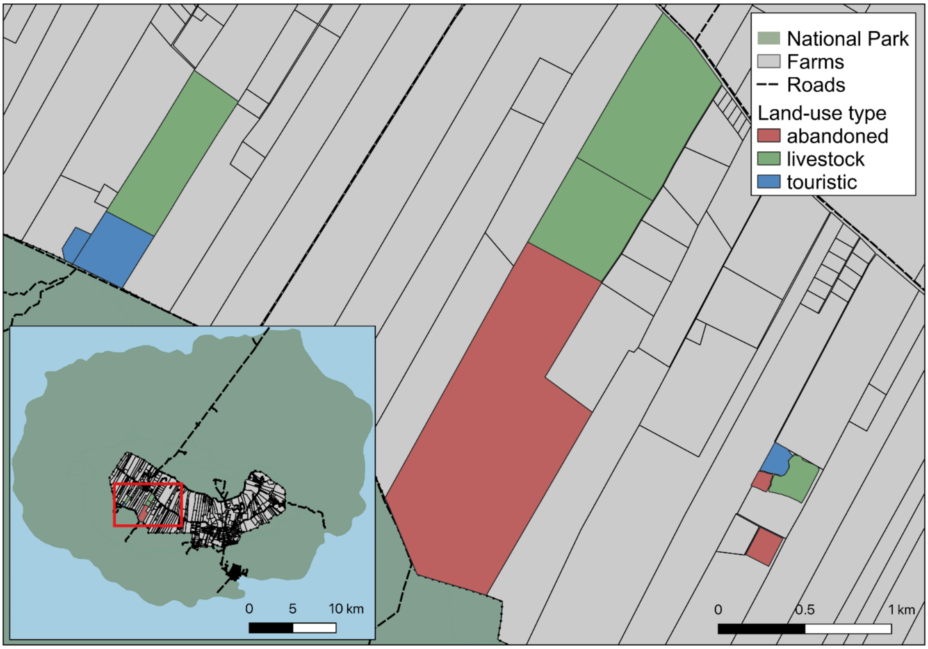

Fig. 1 The inset map to the left shows the location of the agricultural zone surrounded by national park on the island of Santa Cruz, the red rectangle within depicts the location of our study site. The larger map shows the distribution of representative land-use types within our study site.

bias. Data were collected on a Samsung TabA digital tablet using a pre-programed ethogram developed using BORIS software™ (Friard and Gamba 2016).

We also recorded fine-scale habitat characteristics in an area of 1 m^2 immediately in front of the focal tortoise. We estimated the percent cover of live vegetation, density of vegetation (very low, low density, high and very high; see Supplementary Fig. 1), and the mean height of ground vegetation (estimated to nearest 5 cm). After the observation, the tortoise's curved carapace length was measured with a flexible measuring tape, and their sex (male $n=109$, female $n=81$, undetermined/ juvenile $n=52$) was recorded. Each individual was marked with three small dots of nail polish either on the front right or left scute of their carapace, in a unique color combination. Unique identifications ensured that no tortoise was observed more than once on the same day, however some individuals were observed on more than one occasion during the study period ($n=26$).

All observations were made in accordance with strict animal handling procedures under the Galapagos National Park permit number PC-16-19 and animal ethics approval by James Cook University A2565. All 242 observations were conducted in the field, on free living giant tortoises at a distance that was judged not to have disturbed tortoise behavior (minimum 5 m). Before a focal observation began, a 5-minute acclimation period was taken to assess if the individual was disturbed by our presence, and if the tortoise was visibly disturbed (e.g., withdrawing their head) for more than 5 min, the observation was abandoned, and another tortoise was located ($n=1$ out of 243 observations). Processing time to mark individuals with nail polish and take curved carapace length and width measurements was minimised to limit temporary stress on the animal (2–5 min).

Thermal images

During each observation period, two thermal images were taken of the tortoise using a handheld Flir C2 Thermal camera (FLIR, Wilsonville USA). Images were taken from behind the tortoise, so that the tortoise's carapace and back legs took up roughly 1/4 of the frame, followed by another image in which the tortoise was roughly 1/8 of the frame, to sample a larger area of the ground. Flir thermal cameras take high-quality thermal images which provide a temperature ($\pm 2^{o}$ C) for each pixel, temperatures can then be extracted using the Flir software (FLIR 2017). The close-up image of the tortoise was used to extract the minimum, maximum, and mean temperature of the tortoise's carapace, and the skin of their hind legs. From the second image, the same method was applied to extract 15 individual temperatures of the ground immediately surrounding the tortoise, to determine the minimum, maximum and mean ground temperature. If an image could not be taken from behind the tortoise, i.e., because of obstructing vegetation, an image was taken from the front and skin temperature readings were recorded from the forelegs or head.

What factors influence tortoise activity on farms?

We focused on the ratio of time spent eating, walking, and resting, as these behaviors relate most directly to energy acquisition and energy expenditure. To determine the impact of intrinsic and extrinsic factors on tortoise behavior, we used Dirichlet regressions, which can use multiple categories of proportions as response variables in a regression model (Douma and Weedon 2019). Our response variables were the proportion of time tortoises spent walking, resting and eating, and our explanatory variables included: land-use type (livestock, touristic and abandoned land), carapace temperature (°C), mean ground temperature (°C), range of ground temperature (°C), sex (male, female, undetermined), curved carapace length (mm), season (wet, dry), and hour of the day. As vegetation characteristics were measured at a different time scale (i.e., at 5-min intervals) we created a separate analysis for vegetation alone (see below). Using the 'DirichletReg' package (Maier 2014) in R v.4.0.2 (R Core Team 2020), we created multiple models with different combinations of these variables and biologically relevant interactions (see Supplementary Table 2 for full set of models) and then compared values of Akaike's Information Criterion, corrected for small sample size (AIC_c), to that of a null model. Our model selection process was guided by changes in AICc relative to the null model, with lower AICc values considered to have more explanatory power (Richards 2005; Symonds and Moussalli 2011). However, we considered the second-best ranking model (a difference of 2.4 AICc values) to have more biologically relevant explanatory value (land-use type and carapace temperature vs. land-use type only) for capturing tortoise activity on farms and focussed on the second-best model instead. Observations during which a tortoise did not eat, walk or rest, or where the same individual was observed on more than one occasion (Dirichlet is not currently available for mixed effects regression models; (Douma and Weedon 2019) were excluded from the analysis, thus we had a total of 188 observations of tortoise behavior on farms for the combined activity analysis, although we could use most data when analysing activities individually for our mixed-effects models (below).

The influence of vegetation on tortoise activity on farms

Santa Cruz giant tortoises have diverse diets including grasses, forbs, and woody shrubs of native and introduced plant species (Blake et al. 2015, 2021b; Ellis-Soto et al. 2017). To assess the influence of vegetation on tortoise activity we sampled vegetation characteristics of a one-meter-diameter patch of vegetation directly in front of the tortoise. Every 5 min during the 30-minute focal observation we recorded ground vegetation characteristics including mean vegetation height (cm), vegetation density, and the percent of live vegetation. We then examined tortoise behavior in relation to vegetation characteristics as a binomial response for each behavioral category (walking, eating, resting) separately. We modelled each behavior separately, as Dirichlet regression (as above) is appropriate for data with multiple proportions but not binomial response variables, thus we used a different method of analysis for evaluating tortoise activity in relation to vegetation.

To assess the influence of vegetation characteristics on tortoise behavior, we used generalised linear mixed models (GLMMs) with a binomial distribution and logit link function using the 'lme4' package (Bates et al. 2015). Each model was constructed with tortoise ID as a random factor to account for repeat observations of the same individuals, both within (i.e., at 5 min intervals within a 30 min period) and between observations (for the individuals who were observed more than once). We constructed separate models for each behavior (eating, walking, and resting) and included vegetation height, density, and percent live vegetation as fixed effects. We created combinations of these fixed effects and used the reduction in AIC_c score relative to a null model to determine which combination of terms explained the most variation in the probability a tortoise was eating, walking, or resting (see Supplementary Tables 3–5 for full sets of models). We had a total sample size of 892 observations of tortoise behaviors in relation to differing vegetation characteristics from 168 tortoises. All continuous variables were centred, and multicollinearity and model assumptions were checked using the DHARMa package (Hartig 2020). All analysis was carried out in R v. 4.0.2 (R Core Team 2020).

Results

We observed tortoises conducting a range of behaviors including: eating, drinking, walking, resting, wallowing, copulating, aggression, defence, and vigilance. The dominant tortoise behavior was resting (51% of focal duration), followed by eating (24% of focal duration) and walking (10% of focal duration). Less commonly, tortoises were also observed mating (2% of observations), in antagonistic interactions with conspecifics (6% of observations), and approached by tourists, vehicles or livestock (23% of observations).

What factors influenced tortoise activity on farms?

Land-use type and temperature had a strong impact on the ratio of time tortoises spent eating, walking, and resting. Tortoises spent the most time eating in touristic areas, and the least time eating in abandoned land. Tortoises in abandoned land rested for significantly longer than did tortoises in livestock or touristic areas (Fig. 2). There was also evidence for a weak trend for tortoises to rest more when they were cooler, as on average a tortoises resting time would decrease by 4% with each increase in carapace temperature, however,

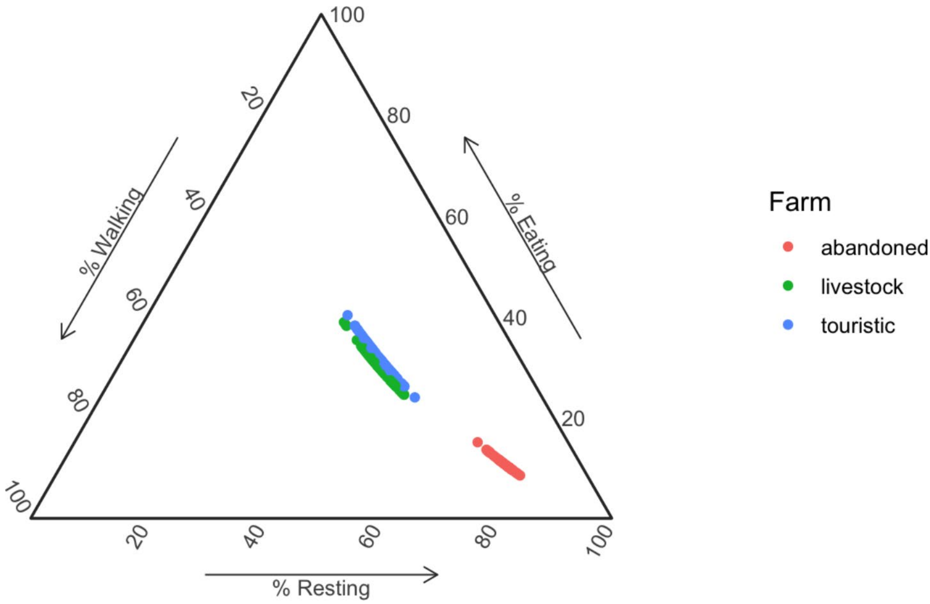

Fig. 2 Tortoises on farms in Santa Cruz Island, Galapagos spend higher proportions of time resting when in abandoned land. Figure depicts the predicted values from the Dirichlet regression's model from Table 1, $n = 188$)

this difference was not statistically significant ($p = 0.08$, Table 1). The proportion of time tortoises spent walking was not influenced by either land-use type, or temperature (Table 1).

The characteristics of vegetation in farms also impacted tortoise activity. The probability of a tortoise eating was influenced by both vegetation height and an interaction between the proportion of vegetation cover and vegetation density. This model outperformed the null model by 59.2 AIC_c values (Supplementary Table 3). The probability of a tortoise eating was positively correlated with vegetation cover, however the strength of this effect depended on vegetation density (Table 2). We found that increasing vegetation cover in the very low-density category increased eating probability by 7.9%, compared to 5.1% for low density and 4.1% for very dense, with no significant difference between the probability of eating and vegetation cover in the dense category.

The probability of a tortoise walking was most strongly predicted by vegetation height and vegetation density, and our best model outperformed the null model by 13.4 AIC_c values (Supplementary Table 4). Tortoises were less likely to walk as vegetation height and density increased. Lastly, the finding that vegetation density weakly decreased the probability of tortoises resting was best explained by vegetation density, such that tortoises were less likely to rest when vegetation was very dense. Density, however, was not a very strong predictor of resting behavior, as it only just outperformed the null model (improvement in AIC_c = 3.5;Supplementary Table 5), suggesting vegetation density did not have a strong influence on resting behavior, compared to other sources of variability we did not measure.

Table 1 Results from the Dirichlet regression on the influence of land-use type and carapace temperature on tortoise activity patterns on farms in Santa Cruz Island, Galapagos. There were differences in the time spent eating among land use types (abandoned land was the reference category). Time spent walking was similar among land-use types and temperatures. Time resting was impacted most strongly by land-use type, and also slightly by carapace temperature (here as MCT for mean carapace temperature)

Term	Estimate	SE	z value	p value	Low CI	High CI
Beta-Coefficients for proportion of time eating						
(Intercept)	-1.378	0.151	9.101	<2e-16	-1.675	-1.081
Touristic	0.408	0.206	1.981	0.048	0.004	0.811
Livestock	0.272	0.196	1.389	0.165	-0.112	0.655
MCT	0.010	0.019	0.526	0.599	-0.027	0.046
Beta-Coefficients for proportion of time walking						
(Intercept)	-1.216	0.153	7.945	0.000	-1.516	-0.916
Touristic	-0.027	0.204	0.135	0.893	-0.427	0.372
Livestock	-0.062	0.196	0.315	0.753	-0.446	0.322
MCT	-0.008	0.019	0.422	0.673	-0.046	0.03
Beta-Coefficients for proportion of time resting						
(Intercept)	0.490	0.196	2.502	0.012	0.106	0.874
Touristic	-1.122	0.243	4.611	0.000	-1.599	-0.645
Livestock	-1.179	0.236	4.987	0.000	-1.642	-0.716
MCT	-0.037	0.021	1.728	0.084	-0.079	0.005

Table 2 The influence of vegetation characteristics on tortoise activity patterns on farms on Santa Cruz Island, Galapagos. The table shows the results for each of the three separate response variables (yes/no eating, walking and resting). The probability of eating was best explained by the interaction between the density of vegetation and the percent of live vegetation in a patch, whereas vegetation height and density were more important influences on the probability of walking. Resting behavior was not strongly influenced by vegetation characteristics

Term	Estimate	SE	*p*-value	Low CI	High CI
Eating					
(Intercept)	0.048	0.027	0.000	0.016	0.143
vegetation height	1.020	0.013	0.131	0.994	1.046
% vegetation: very low density	1.079	0.021	0.000	1.039	1.120
% vegetation: low density	1.057	0.026	0.023	1.008	1.108
% vegetation: dense	0.991	0.019	0.633	0.955	1.028
% vegetation: very dense	1.041	0.015	0.006	1.011	1.072
Walking					
(Intercept)	0.013	0.011	0.000	0.003	0.069
vegetation height	0.914	0.034	0.016	0.850	0.984
low density	2.731	1.792	0.126	0.755	9.881
dense	0.323	0.243	0.132	0.074	1.407
very dense	0.430	0.312	0.244	0.104	1.779
Resting					
(Intercept)	2.491	0.981	0.020	1.151	5.390
low density	0.583	0.250	0.207	0.252	1.349
dense	1.063	0.483	0.893	0.436	2.592
very dense	0.388	0.182	0.043	0.155	0.972

Discussion

Influences on time spent eating

Galapagos tortoise behavior in the agricultural zone of Santa Cruz Island is shaped by two factors: land-use type, and vegetation characteristics. In touristic land, tortoises ate for significantly longer periods than they did in abandoned land. Tortoises were also more likely to eat in areas with a high proportion of vegetation cover, and high vegetation density. Most species of ground vegetation in the highlands are eaten by tortoises (Blake et al. 2015), however, we still observed some selection of vegetation based on its height, coverage, and density. This suggests that food selection by these large generalist herbivores is influenced by costs and benefits of where they forage within the agricultural landscape, and they select areas in which they optimize foraging efficiency (Pyke 1984; Bergman et al. 2001). Tortoise feeding behavior, similar to other large herbivores, is consistent with the forage maturation hypothesis, which suggests that grazers will prefer forage with higher ratios of digestible content to fibre (Fryxell 1991; Hebblewhite et al. 2008). Such dietary selectivity might seem surprising given the low metabolic demands of ectothermic giant tortoises. However, research on energy assimilation efficiency of giant tortoises on Aldabra (*Aldabrachelys gigantea*), an ecological analogue to Galapagos tortoises, indicates that they can assimilate only 34.5% of the energy available in their forage (Hamilton and Coe 1981). Thus, despite having lower metabolic demands relative to their mammalian counterparts, tortoise energy budgets will be maximized by selecting immature, high quality forage over more abundant, but lower quality older forage (Franz et al. 2011).

As partial seasonal migrants, the tortoises' main motivator for migrating to the highlands during the dry season may be to exploit the lower quality (relative to the lowland's wet season growth) but higher quantity highland vegetation, as larger tortoises incur an energy deficit if they fail to migrate (Blake et al. 2013; Bastille-Rousseau et al. 2017b; Yackulic et al. 2017). As Yackulic et al's (2017) bioenergetic models shows, sensitivity to variation in forage availability increases with body size. On Aldabra, the giant tortoises that exploit coastal habitat during the rainy season can access more food, and also have higher reproductive outputs, compared to resident tortoises that remain inland (Swingland and Coe 1978). On Galapagos, tortoises that migrate to the highlands and use touristic farms are likely obtaining more energy per unit time, especially when compared to conspecifics in abandoned land.

We also found that the probability of eating increases when tortoises encounter a patch with higher percent cover of vegetation in areas with otherwise low vegetation density within the quadrat. This result is likely caused by instances when a tortoise is travelling along a road or path (where the density of vegetation is low on average) and is likely to switch to eating when it finds a vegetation patch with a relatively higher proportion of vegetation. There are many paths and dirt roads that cut through the agriculture area, where fringing vegetation is cut periodically for maintenance (author personal observation) and is easy to access for tortoises. This agrees with our previous work that demonstrated tortoises were attracted to roads with low levels of traffic (Pike et al. 2022a), and that tortoises can often be found travelling along roads and eating roadside vegetation (author and peer observations). Similar results have been found for other large herbivores that move large distances. Asian elephants (*Elephas maximus*) for example, have been recorded showing preference for vegetation along roads (Yamamoto-Ebina et al. 2016; Wadey et al. 2018).

Influences on time spent resting

The variables best explaining variation in resting behavior for tortoises in the agricultural area were land-use type and carapace temperature, while vegetation characteristics had very little impact. We found that tortoises in abandoned land rested for significantly more time than did tortoises in livestock, and touristic areas. The potential reasons for resting more while in abandoned land are unclear. Possibly, individuals in abandoned land cannot find suitable forage, and rest to conserve energy. Alternatively, it is possible they rest to assimilate food acquired elsewhere. Further examination of the reasons for increased resting in abandoned land by Galapagos tortoises is required to determine the causes of this behavior.

There was also some evidence that carapace temperature influenced resting behavior because tortoises rested more at lower carapace temperatures. Although the humid highlands are considerably cooler than the lowlands (Trueman and D'Ozouville 2010), temperatures in this area generally span a range within which large tortoises can comfortably operate (Blake et al. 2021). One exception to this, however, is when tortoises are close to vegetation, or in dense shade, because, as the humid highlands are already much cooler, tortoises are more likely to experience temperatures below their thermal minimum in these circumstances (Blake et al. 2021a). Abandoned land, which is overgrown with invasive vegetation, is usually heavily shaded, and offers limited access to sunny areas. In cooler temperatures tortoises also need more time to digest their food, and lower temperatures could potentially encourage them to rest more to aid digestion (Sadeghayobi et al. 2011). On the other hand, livestock areas represent the opposite to abandoned land in their thermal and vegetative conditions. Livestock areas are characterized by large grazing lawns exposed to the sun, with a few shade trees scattered in the landscape that tortoises can often be found under in hotter parts of the day (author personal observation). However, if tortoises need shade from the sun and livestock areas have no trees, adjacent abandoned land may then be of use. Touristic land provides the most heterogenous mix of sun and shade, characterized by large open grazing lawns with more trees and native shrubs than grazing land. This may help explain why temperature was only showing a weak signal in our results, as within the humid highlands, the resources available for thermoregulation and the thermal conditions within land-use types were more limited in abandoned land, compared to livestock and touristic areas. While this result was not statistically significant ($p = 0.08$), it is possible that the availability of sun and shade among land-use types is still of biological importance for these ectothermic giant tortoises, especially while in abandoned land. This also suggests tortoises may need to select habitat components that not only offer ample foraging opportunities but also meet more complex thermoregulatory requirements.

Influences on time spent walking

We found that vegetation characteristics had a moderate impact on tortoise walking behavior while on farms. Tortoises were less likely to walk in areas with tall vegetation and were more likely to walk in areas with little to no vegetation. This agrees with our previous research on broad-scale patterns of farm use by tortoises that revealed that tortoises generally avoided areas with tall vegetation (Pike et al. 2022b), as well as other work that demonstrated dense vegetation can obstruct tortoise movement (Hunter et al. 2013). Of the three behaviors we examined, walking is the most energetically expensive, and having to walk through tall and thick vegetation requires more energy than walking on short, cropped lawns or paths and roads with little vegetation.

Management implications

The composition of different land-use types in the agricultural area has important implications for the habitat quality and conservation capacity of agricultural land for critically endangered giant tortoises. The three land-use types we examined differed in their effect on tortoise behavior, and consequently are likely to impact the energetic strategies of migratory individuals in their highland range. Our previous research showed that tortoise density is lowest in abandoned land (Pike et al. 2022b) and that tortoises tend to move more rapidly through this land-use type than others (Pike et al. 2022a). Here we found that individuals using abandoned land ate less and rested more. Taken together, this suggests abandoned land is probably used less by giant tortoises as there is less to eat, movement is more difficult, and the thermal environment is characterized by dense cool shade in the already cooler humid highlands. In contrast, touristic land, although not abundant in the landscape, is favored by tortoises. Tortoises can move freely in and out of touristic land as fences are permeable (author unpublished data), and tortoises spend the most time eating and the least time resting in touristic land than other land-use types. While touristic land appears to be higher quality habitat for tortoises in the dry season, the impact of tourists on tortoise wellbeing or health, are still unknown and in need of investigation. Livestock areas also support tortoises, that eat more and rest less than tortoises in abandoned land, but our previous research (Pike et al. 2022b) showed tortoise density in livestock areas is relatively low. The capacity of livestock areas to support giant tortoises could be increased, possibly by maintaining preferred vegetation height such as through rotational stocking and potentially increasing the thermal heterogeneity of habitat available to tortoises by adding trees for shade. We recognize however, that land sharing with tortoises is a complex topic and ideally, the viability of potential modifications would also be discussed with farmers, and research into the benefits for other farmers or livestock also conducted.

Limitations

While we have uncovered some of the dynamics of tortoise patterns of behavior in farmland, this comes with some caveats that limit the generality of these results. Firstly, we worked in only a subset of land-use types found in the agricultural area. Further examination of tortoise abundance and behavior in other land-use types, especially coffee and transitory crops, are needed to establish a more complete understanding. Secondly, our temporal window for observing tortoise behavior was biased towards the first half of the day as tortoises are active during the morning in both seasons (Rodhouse et al. 1975; Blake et al. 2021b). Thus, while we have described activity patterns for tortoises for the first half of the day, there may be additional processes occurring in the afternoon that cause those patterns to shift. Lastly, we recognise that our assumptions about the links between energy budgets and patterns or behavior (e.g., eating more equates to more energy assimilation) need further verification. It is reasonable to assume that tortoises that spend more time eating and less time resting, and walking, are more likely to benefit from an energy surplus that can be translated to growth or improved body condition.

Conclusions

Previous studies have shown that the agricultural area remains an important area of giant tortoises and that the characteristics of farmland influences their movement, density, foraging and health (Blake et al. 2015; Nieto-Claudin et al. 2021; Pike et al. 2021, 2022a, b). Through this study we now have a more detailed understanding of what tortoises are doing once they enter farmland. We have shown that land-use type, and properties of vegetation which influence thermal characteristics, are important determinants of Galapagos tortoise patterns of behavior in the agricultural zone of Santa Cruz Island. The differences in the behavioral patterns of giant tortoises using different farm types, indicate that tortoises are likely choosing activity patterns that reduce energetic or opportunity costs to them by resting more when habitat quality is poor, walking more in easier-to-manoeuvre terrain, and foraging more when vegetation characteristics are favourable. Our improved understanding of the tortoises' behavior in the agricultural area, now opens the way to further investigate how differences in habitat quality in farms may impact other stages of the migratory cycle. Future research should investigate how time spent in the highly modified humid highlands could impact the decisions to migrate and duration of time in this habitat, body condition, and ultimately fitness.

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Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Kyana N. Pike[1] · **Stephen Blake**[2,3,4] · **Iain J. Gordon**[5,6,7,8,9] · **Lin Schwarzkopf**[1]

✉ Kyana N. Pike
kyana.pike@my.jcu.edu.au

[1] College of Science and Engineering, James Cook University, I James Cook Drive, Townsville 4814, Australia

[2] Department of Biology, Saint Louis University, Saint Louis, USA

[3] Max Planck Institute for Animal Behaviour, Radolfzell, Germany

[4] Wildcare Institute, Saint Louis Zoo, Saint Louis, USA

[5] Central Queensland University, Townsville, Australia

[6] James Hutton Institute, Craigiebuckler, Aberdeen, Scotland, UK

[7] Fenner School of Environment and Society, The Australian National University, Canberra, Australia

[8] CSIRO, Townsville, Australia

[9] Protected Places Initiative, National Environmental Science Program, RRRC, Cairns, Australia