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The interaction between giant tortoises and agriculture in the Galapagos Islands

"The love for all living creatures is the most noble attribute of man." - Charles Darwin

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Dedicated to my Mum,

an island girl,

a nature lover,

a free spirit

Acknowledgements

I acknowledge JCU is on the land of the Wulgurukaba and Bindal peoples and pay my respects to their Elders past, present and emerging and recognise Indigenous Australians are our nation's first conservationists and scientists.

I didn't realise I was taking on such a challenging feat of studentship until a friend of mine said as a complement "wow it is so incredible that not only are you doing a PhD but you are doing it overseas and, in another language" but, I took this as less of a complement and more of a 'what the hell have I done'. I would never have gotten this far if it weren't for the immense support and guidance that I have been so incredibly fortunate to receive from friends, family, peers, collaborators, and supervisors along the way.

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Publications Associated with this Thesis

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Chapter 3

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Chapter 4

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Statement of the Contribution of Others

My advisory panel Lin Schwarzkopf, Iain Gordon and Stephen Blake, provided fundamental advice, guidance and supervision on all aspects of the thesis. Lin, Iain and Steve are co-authors on the published articles that constitute chapters two, three and four and also chapter five that is being prepared for submission.

My external supervisor Steve initiated the Giant Tortoise Movement Ecology Programme (GTME) in 2009 and established the collaborative links with the Charles Darwin Foundation that have hosted GTME and provided research infrastructure support for the field work components of this project. The Galapagos Science Center also provided external research infrastructure and logistical support during field work and permit applications for this project.

Fruitful collaborations with other Galapagos Researchers resulted in two co-authored multidisciplinary publications that added value to two of my PhD chapters. Chapter three's publication included co-authors Dr. Fransisco Laso (University of North Carolina) and Dr. Gonzalo Rivas-Torres (Universidad San Francisco de Quito) with the use of their detailed agricultural vegetation maps. Co-authors Dr. Ainoa Nieto-Claudin (Charles Darwin Foundation), Anne Guezou (Galapagos Conservation Trust) and Dr. Sharon Deem (St. Louis Zoo Conservation Institute) provided their expert input into tortoise habitat preferences in chapter four's publication. Giant tortoise telemetry data in chapters two and three, and tortoise density data in chapter four was collected by field technicians Freddy Cabrera and Jose Haro (Charles Darwin Foundation). Field technician Freddy Cabrera contributed substantial data collection and is a co-author for publications arising from chapters two, three and four. Professor

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Thesis Abstract

One of the most pressing dilemmas of our time is determining how to satisfy the demands of a growing human population while still conserving biodiversity. The human population is expected to increase by another 4 billion people by the end of the century, and agricultural land modification to accommodate current human resource needs has already caused significant declines in wildlife populations. Agriculture often has an antagonistic relationship with biodiversity conservation; however, it may also offer opportunities to reconcile biodiversity loss and human enterprise. Outside of protected areas, agriculture can contribute to conservation by providing habitat for wildlife, either through land sparing, in which agricultural practices are intensified on existing land to increase production while avoiding clearing additional land, or land sharing, where low intensity agriculture is promoted, and farmland is shared with wildlife. Understanding the ecological functions of wildlife interactions with agricultural land is vital to inform the management of human–wildlife co-existence, and to promoting agricultural practices that support biodiversity.

On Santa Cruz Island in the Galapagos, where most highland habitat has been converted to agricultural land, critically endangered eastern (*Chelonoidis porteri)* and western (*Chelonoidis donfaustoi)* giant tortoises make a seasonal migration to the highlands, which they share with farmers. To support the conservation of giant Galapagos tortoises, we need a detailed understanding of the dynamics of their interaction with agriculture on Santa Cruz Island. The overarching aims of my thesis were to describe the interaction between agriculture and the ecology of giant tortoises in the humid highlands, and to identify opportunities for improved management.

I paired a long-term GPS tracking dataset on both species of giant tortoise on Santa Cruz Island, with spatial data on vegetation type, fences, land-use types, and roads. I also collected field data at landscape and local scales on fence structure, pond locations, and habitat structure, as well as tortoise density, carapace temperature, and behaviour in different land-use types. Using various analytical approaches, I described the spatiotemporal patterns of space use by giant tortoises on farms, (**Chapter 2**); determined the factors influencing tortoise movement and habitat use (**Chapter 3**); quantified habitat preferences in farms and described relationships with land-use type and vegetation structure (**Chapter 4**), and, finally, I determined the influence of land-use type and habitat characteristics on tortoise activity patterns (**Chapter 5**).

I found that tortoises used large areas of the agricultural zone and remained there for several months each year, often returning to the same areas in different years. When tortoises entered the agricultural area, they were attracted to ponds, pasture, and roads with low traffic levels. Tortoises preferred a mix of habitat structure that provided them with abundant forage, that did not obstruct their movement, and allowed opportunities for thermoregulation. Land-use type, infrastructure, and habitat structure all strongly influenced the distribution, abundance, and behaviour of tortoises in the agricultural area.

As both tortoise and human populations grow and develop in the future, there are multiple avenues to improve habitat for tortoises using farms. My findings provide evidence that can be used to support decisions balancing the needs of Galapagos tortoises in farmland with those of landholders for wildlife managers, and conservationists. To make farms more tortoise friendly, I recommend promoting short ground vegetation, reducing shrub cover, creating a heterogeneous mix of sun and

shade patches, and improving fencing that offers broadscale connectivity, while maintaining crop protection. Future research priorities include developing incentives to rehabilitate abandoned land, managing pond distribution, and investigating pathways to maximizing the benefits of agricultural land for tortoises and farmers.

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Chapter One: General Introduction

The global-scale changes to fundamental environmental processes caused by humans are now being recorded in the geological record as the Anthropocene (Lewis and Maslin 2015; Folke et al. 2021). Changes to Earth's biochemical and geological processes including nitrogen, water, and carbon cycles are occurring as a result of human influence, and include the impacts of agriculture (Steffen et al. 2011; Ruddiman 2013). Humans have been modifying natural areas for agricultural purposes since the dawn of the Neolithic period, over 11,000 years ago (Bocquet-Appel 2016). As they transitioned from foragers to farmers humans acquired the ability to store and redistribute resources in space and time, buffering them from natural stochastic processes (Whitehouse and Kirleis 2014; Bocquet-Appel 2016). The adoption of agriculture was a catalyst for the growth and success of human civilisations, as the stability afforded by agriculture enabled advances in technology, culture and standards of living (Whitehouse and Kirleis 2014; Vierra and Carvalho 2019).

The expansion of the human footprint has now reached over 75% of the Earth's land surface, and the extent, severity and pressure of this expansion has a strong relationship with the arability of land (Venter et al. 2016). Thus, while agriculture is recognised as one the keys to our success, it is also acknowledged as one of the major drivers of habitat loss for wildlife (Butler et al. 2007; Tilman et al. 2011, 2017; Said et al. 2016). Major concerns have been raised about the level of habitat loss and global biodiversity decline associated with our current agricultural practices, especially given that biodiversity loss also threatens the sustainability of our food, health, and cultural systems (Pereira et al. 2010; Landis 2017; Folke et al. 2021). There is a looming conflict between meeting the demands of a growing, more affluent human population, and biodiversity conservation (Gordon 2018).

Land sharing and land sparing explored

Worldwide, biodiversity is vanishing at an alarming rate, and while agriculture can create habitat loss for wildlife, under some circumstances, it may also provide habitat (Dirzo et al. 2014; Tilman et al. 2017). Ideally for conservation, no further demands would be placed on our natural systems, and habitat for wildlife could be restored, however, with the human population expected to increase by another 4 billion people by the end of the century (United Nations 2015), this outcome is not realistic. Maintaining intact natural areas is, undoubtedly, the preferred option for biodiversity conservation, however, when that is not feasible, what other options remain for providing wildlife habitat? In the search for solutions to the trade-off between biodiversity conservation and food production, two main strategies have emerged (Green et al. 2005; Kremen 2015; Loconto et al. 2020). The first is land sparing: the idea that if agriculture is intensified on existing farmland, additional natural areas can be spared (Green et al. 2005; Phalan et al. 2011). In this scenario, minimising further encroachment of the human footprint on remaining 'untouched' areas is paramount, as these areas tend to become increasingly rare and isolated (Venter et al. 2016; Riggio et al. 2020). For an example of land sparing, in Brazil, a major producer of agricultural commodities, it may be possible to increase productivity on existing pastural areas to meet growing demand for meat, crops and wood, liberating 36 million hectares of cultivated pasturelands (Strassburg et al. 2014). A recent review by Balmford (2021) has found >2500 empirical examples of species declining under farming and adds a lot of weight to the desirability of land sparing where most species would fare least badly. Overwhelmingly land sparing is the strategy that can produce the most resources such as food, fibre or fuel at least cost to biodiversity per unit area (Green et al. 2005; Phalan et al. 2011; Balmford 2021)

One of the risks of land sparing, however, is that it hinges on the assumption that intensifying agriculture on existing land does indeed free-up nearby intact natural areas for conservation (Balmford 2021). Achieving the benefits of land sparing therefore relies on governance strong enough to ensure that intensified agriculture does not incentivise people to continue to clear natural areas, given that land then becomes more profitable (Strassburg et al. 2014; Silveira dos Santos et al. 2020). In addition, pesticides and chemical fertilisers required to achieve greater productivity on existing land are also associated with negative environmental impacts (Matson and Vitousek 2006; Loconto et al. 2020). More generally, land sparing alone will not be enough to halt the biodiversity crisis, given the sheer scale of land already cleared and the relatively small proportion of remnant natural areas especially if they are situated in a 'biological desert' surrounded by human use areas (Kremen and Merenlender 2018; Crespin and Simonetti 2019). Finally, even if sufficient land could be liberated for conservation, restoring farmland to its natural state also includes a suite of challenges, and substantial effort (Hall et al. 2022).

The second strategy that has been proposed 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 habitat available to wildlife (Green et al. 2005; Phalan et al. 2011; Jiren et al. 2018). Agricultural land is typically located between urban environments and wilderness

(Gordon et al. 2016). Because urban environments are not very wildlife friendly, agriculture often forces wildlife into marginal areas or displaces them altogether (Gordon 2018). Land sharing can be especially beneficial on these marginal areas where farmland abates protected areas (Balmford 2021). This practice of lower impact wildlife friendly farming is probably most well represented in Europe where land modification has an extensive history and wildlife have adapted better to living in agricultural landscapes (Benayas and Bullock 2015).

For wildlife unable to meet their ecological needs from remaining natural areas, land sharing can be an important lifeline. Modifications that extend habitat available to wildlife 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). Land sharing can also provide additional benefits to land holders when farming practices also support ecosystem services such as pollination, pest reduction, and improvements in soil health and resilience (Benayas and Bullock 2015; Pywell et al. 2015). When land sharing is able to confer benefits both to farmers and to wildlife, it also aligns with the concept of 'Reconciliation Ecology', which looks at ways to redesign anthropogenic habitats so they have utility for people and for other species (Rosenzweig 2003a). Nevertheless, land sharing can be very difficult to implement (Crespin and Simonetti 2019). Many species decline with farming or their small geographical range or niche resources requirements make them incompatible with agricultural landscapes (Balmford 2021). Wildlife interacting with agriculture often leads to human-wildlife conflicts, for example if crop-depredation, property damage, or injury to people or wildlife is left unmanaged (Crespin and Simonetti 2019). Costs of wildlife friendly farming can also extend to large subsidies that are needed to support loses from lower production, resources needed to modify farms, or damage done by wildlife (Fischer et al. 2008; Pywell et al. 2012) Additionally, taking the route of low-impact farming may compromise productivity and thus still increase the need for land, if future resource demands cannot be met, especially in developing areas (Green et al. 2005; Crespin and Simonetti 2019).

The balance between meeting the needs of both wildlife, and farmers, is a delicate one. On an ideological level, these two strategies broadly represent two different approaches to conservation: either humans are kept apart from nature (land sparing), or humans are part of nature (land sharing) (Loconto et al. 2020). Both ideologies have their strengths and weaknesses, and the ecology of the wildlife in question, and the agricultural context will be important factors determining what approach is more effective for the situation at hand. Regardless, if we are to improve outcomes for biodiversity conservation, while fulfilling the resource needs of a growing human population, we need to invest in various strategies, and we need to reconcile various approaches to conservation, to ensure optimal outcomes for both humanity and biodiversity.

The Galapagos as a study system

At a global scale, management of trade-offs between agriculture and conservation is daunting, whereas at the landscape and smaller scales, there may be tractable systems in which human-wildlife dynamics can be optimised. Oceanic islands, where endemic communities are under recent threat from human colonisation, are microcosms that exemplify the processes also operating at global scales. The Galapagos Islands are one such system, in which the conflict between the wellbeing and economic needs of people, and biodiversity conservation, is evident. On some islands in the Galapagos, there is an emergent farmer-giant tortoise conflict occurring, requiring methods to better balance the needs of farmers and tortoises, both of whom use the humid highlands for resources (Caccone et al. 2017; Cayot et al. 2017a; Benitez-Capistros et al. 2018). The unique history of the Galapagos, and its present-day fame, have also together created a number of factors that make land-sharing a possible method to support both tortoise conservation and food production in the Galapagos.

Firstly, the archipelago was untouched until its discovery in 1535, and uninhabited until 1832 (Trueman et al. 2013). Because Galapagos is a chain of volcanic islands, it is geologically young (700 thousand to 4 million years old) so there is little topsoil accumulation, extensive bare volcanic rocky areas, and high aridity, such that the archipelago is challenging to inhabit (Heads and Grehan 2021). When people did settle in the Galapagos, they focussed on the few islands that had arable land, and sources of fresh water. Agriculture has, thus, only been established on a few islands with humid highland areas (Santa Cruz, San Cristobal, Isabela, and Floreana), as the highlands attract higher rainfall, and are more consistently productive than the arid lowlands (Wiggins and Porter 1971; Laso et al. 2020). Initially, the agricultural footprint in the humid highlands was relatively small, but then agricultural operations began gradually to expand as the population grew. Population growth rate increased from the 1970s onwards, with the advent of commercial fishing, and then the boom in tourism (Trueman et al. 2013).

When the Galapagos National Park Directorate (GNPD) was established in 1959, the vast majority of the archipelago was declared a protected area (97%) making it illegal to settle uninhabited areas, and human use areas that were already established typically became the limits of the national park (MacFarland et al. 1974). Prior to the establishment of the national park, large proportions of humid highland habitat had been cleared to support agriculture on four inhabited islands, and now, on some islands, not much of this habitat type remains (roughly 12% on Santa Cruz, 6% on San Cristobal, 79% on Southern Isabela, 62% on Floreana) (Watson et al. 2010; Trueman et al. 2013). The humid highlands are the most suitable zone for agriculture, however the risk that additional humid highland habitat will be cleared is low, as all agricultural areas are surrounded by national park, the borders of which are enforced by the GNPD (Valdivia et al. 2014).

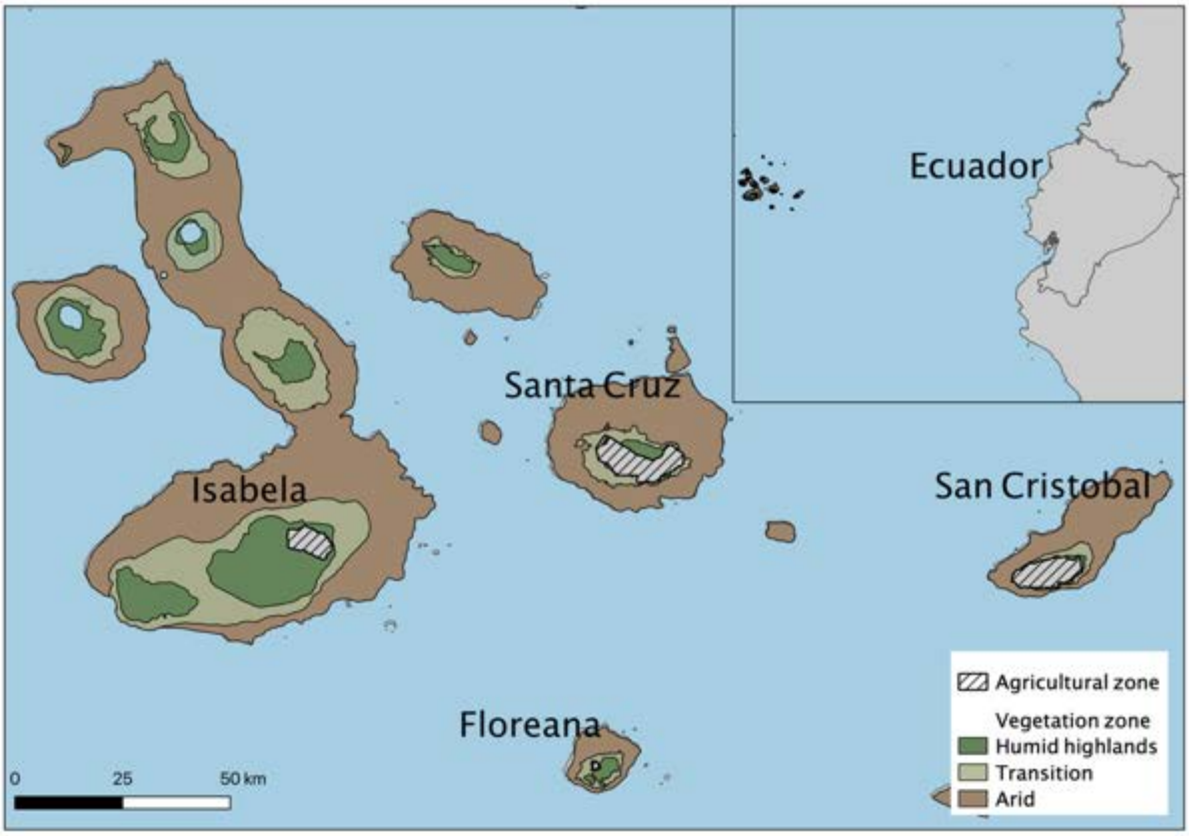

Figure 1.1. The Galapagos Archipelago, showing the four inhabited islands that have agriculture and various species of giant tortoises (tortoises now extinct on Floreana). Map inset shows the Galapagos Islands in relation to mainland Ecuador.

Secondly, the value and fragility of nature in the Galapagos has attracted the world's attention. In 1978, Galapagos was established as one of the first twelve World Heritage Sites established by the United Nations Educational, Scientific and Cultural Organisation (UNESCO), putting Galapagos on the map as an irreplaceable natural icon (Epler 2007). With the world's eyes on Galapagos, the government also introduced the 'Galapagos Special Law' in 1998, which established controls for immigration and ecosystem protection (Epler 2007; Valdivia et al. 2014). 'Ecotourism' is now the cornerstone of the economy in the Galapagos (Epler 2007), pre-pandemic in 2019, Galapagos received over 270,000 tourists and contributed $256 million USD to the Ecuadorian gross domestic product (Galapagos Governmental Council 2021). Of the approximately 32,000 local inhabitants, 51.4% have a tourism-related job (Galapagos Governmental Council 2021).

Tourism and extractive activities, however, can also be harmful if mismanaged or if regulations are poorly defined or enforced. In 2007, UNESCO placed the Galapagos Islands on a list of World Heritage Sites 'In Danger'; this alarming declaration sparked action from the governing bodies of the Galapagos to increase their measures of protection (Lu et al. 2013). Thus, if ecosystems become too degraded or species are lost, not only does this attract global attention, this also weakens the appeal of the Galapagos as an 'ecofriendly' tourism destination upon which the local economy depends (Lu et al. 2013; Galapagos Governmental Council 2021). Because of Galapagos' reputation as a world-renowned wildlife tourism destination, and part of Charles Darwin's legacy, sustainability and nature preservation are also tied to the economy (Lu et al. 2013). This scenario, in which the needs of wildlife benefit people economically, such that success depends on both being supported lends itself to exploring ways to pair conservation and human enterprise.

Thirdly, enabling tortoises to use the humid highlands is important for tortoise conservation, because the humid highlands provide critical resources. During the dry season, food in the arid lowlands becomes limited, and large adults migrate to the humid highlands to forage, drink and rest, until the wet season returns, and a flush of new plant growth in the lowlands restores the suitability of the lowlands (Blake et al. 2013, 2021c; Bastille-Rousseau et al. 2017b; Yackulic et al. 2017). Tortoises that return to the lowlands during the wet season are rewarded with more nutritious vegetation from the new plant growth and by taking advantage of these vegetation dynamics tortoises are able to reach larger sizes (Blake et al. 2013; Yackulic et al. 2017). The humid highlands are unsuitable for nesting due to the high rainfall and lower temperature thus tortoises also return to lower elevations to lay their eggs, further perpetuating this cyclical journey, (Deem et al. 2023; see figure 1.2. for differences in highland and lowland habitats). This elevational movement was a regular occurrence for some species of tortoise, well before agriculture took place in this zone. Charles Darwin noted the well-worn paths transecting the islands from the tortoises' migration. In his journal, recording his 5-week experience in the Galapagos, he wrote: "when I landed at Chatham (San Cristobal) Island, I could not imagine what animal travelled so methodically along the well-chosen tracks" (Darwin 1839:463, about the paths tortoises made from the coast to the highlands). Nowadays, when tortoises migrate to the highlands, they must share some land with farmers. This dynamic exists to varying degrees on Santa Cruz, San Cristobal and Southern Isabela, where both tortoises and agriculture occur (tortoises are now extinct on Floreana, where both once occurred), but it is the most notable on the island of Santa Cruz (Conrad and Gibbs 2021).

Figure 1.2. On the left is a large female with a GPS tracking device attached to her carapace in a nesting area in the lowlands. On the right is a large male tortoise in a cattle farm in the humid highlands during the dry season.

Two species of giant tortoise are native to Santa Cruz, the Eastern Santa Cruz tortoise (*Chelonoidis donfaustoi*) and Western Santa Cruz tortoise (*Chelonoidis porteri*). These tortoise species are morphologically and ecologically similar, but genetically distinct, and both use the agricultural area, but have non-overlapping distributions (Poulakakis et al. 2015). The latest population estimates for these species were 3,400 for *C. porteri* and 400 individuals for *C. donfaustoi,* however, these numbers are dwarfed by the historical populations estimated at 35,000 and 13,500 respectively (Cayot et al. 2017a, b). Both species are Critically Endangered according to the IUCN Red List, fortunately however, due to concerted efforts from the GNPD scientists, and conservationists, their populations are slowly recovering from extensive exploitation, invasive species, and habitat changes (Gibbs et al. 2021). Supporting the long term population stability of giant tortoises is also important for the broader health of the islands' ecosystems, as tortoises are a keystone species (Hunter et al. 2021). Tortoises function as ecosystem engineers; through their dung they disperse seeds and move nutrients around the landscape, and as mega-herbivores their movements and feeding regimes also improve soil health, and maintain characteristic vegetation composition (Gibbs et al. 2010; Hunter et al. 2013; Ellis-Soto et al. 2017). Indeed, tortoises' influence on vegetation dynamics is so integral to their associated habitats, that on an island where the tortoises have gone extinct (Pinta) sterilised non-native tortoises have been introduced as a 'vegetation management tool' (Hunter et al. 2013).

Numbers of Eastern and Western giant tortoises on Santa Cruz are slowly increasing (Cayot et al. 2017a, b) and giant tortoises of both species continue to migrate to the highlands and find themselves in farms. At current low numbers, a mild but emerging conflict has been identified between tortoises and farmers (Benitez-Capistros et al. 2018). Tortoise-driven problems for farmers include: crop losses, fence breakage, livestock escape, road hazards, and pond destruction, while tortoises suffer from road strikes, disease transfer, habitat fragmentation, and, possibly, barriers to movement (Blake et al. 2015b; Benitez-Capistros et al. 2018; Nieto-Claudin et al. 2019).

The aim of the GNPD is to return tortoise populations to their historical numbers, while at the same time, tourism and the demands of agriculture are expected to increase (Sampedro et al. 2018). Given that most of the humid highlands are already being used for agriculture (88% on Santa Cruz) and clearing is discouraged by the National Park intensifying existing agricultural practices to spare more habitat for tortoises (a land-sparing approach) seems unlikely to eventuate. In addition, tortoises are already using farms, such that the present situation is already leaning more to a land-sharing strategy. Left unmanaged, however, if both giant tortoise populations and farming demands increase in the future, unguided land sharing is likely to exacerbate emerging conflict, and potentially undermine conservation efforts. The purpose of my research was, therefore, to investigate interactions between giant tortoises and agricultural land to describe the extent of tortoise use of farms, to provide evidence that could be used to manage both giant tortoise conservation and food production on Santa Cruz Island.

Thesis overview

Firstly, in Chapter 2, I quantified the spatial and temporal extent of tortoise interactions with farmland. I described patterns of space use in farms, over a nine-year period, of 45 GPS-tracked tortoises, to determine correlates with time spent in farms, number of farms visited by tortoises, and extent of philopatry. In Chapter 3, I investigated the response of tortoises to roads, fences, ponds, and human-modified vegetation using a tracking dataset of 27 tortoises, recorded over six years. This allowed me to determine features preferentially used by tortoises in the agricultural landscape, and the impact of infrastructure and vegetation on tortoise movement. In Chapter 4, I used tortoise density estimates from farms over two years, to investigate the relationship between tortoise density, land-use type, and vegetation structure. Finally, in Chapter 5, I recorded the behaviour of 242 tortoises on farms, and examined relationships among activity patterns, land-use type, and habitat characteristics. These findings contribute evidence on the distribution and behaviour of tortoises in farmland for landholders, wildlife managers, and conservationists in the Galapagos, to use for decision-making. As habitat for wildlife continues to decline, conservation options to allow tortoises to use the land, including land sharing, and land sparing, are becoming increasingly necessary, and this research provides knowledge allowing us to move towards human-wildlife co-existence in human-dominated land.

Chapter Two: Body size, sex and high philopatry influence the use of agricultural land by Galapagos giant tortoises

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Abstract

As agricultural areas expand, interactions between wild animals and farmland are increasing. Understanding the nature of such interactions is vital to inform the management of human–wildlife co-existence. We investigated patterns of space use of two Critically Endangered Galapagos tortoise species, *Chelonoidis porteri* and *Chelonoidis donfaustoi*, on privately owned and agricultural land (hereafter farms) on Santa Cruz Island, where a human–wildlife conflict is emerging. We used GPS data from 45 tortoises tracked for up to 9 years, and data on farm characteristics, to identify factors that influence tortoise movement and habitat use in the agricultural zone. Sixty-nine per cent of tagged tortoises used the agricultural zone, where they remained for a mean of 150 days before returning to the National Park. Large male tortoises were more likely to use farms for longer periods than female and smaller individuals. Tortoises were philopatric (mean overlap of farmland visits = 88.7 ± SE 2.9%), on average visiting four farms and occupying a mean seasonal range of 2.9 ± SE 0.3 ha. We discuss the characteristics of farm use by tortoises, and its implications for tortoise conservation and coexistence with people.

Introduction

Agricultural expansion is a major driver of land modification globally (Butler et al. 2007; Venter et al. 2016). As humans increase the geographical range of their activities, wild animals increasingly encounter human-modified areas (LaPoint et al. 2015; McClure et al. 2017). Agriculture typically expands into the most productive natural areas, which also provide important resources for wildlife, increasing the likelihood of negative human–wildlife interactions (Shackelford et al. 2015; Venter et al. 2016; Chopin et al. 2019). For example, migratory sandhill cranes *Antigone canadensis tabida* in North America congregate to overwinter in an area used increasingly for agriculture, which has led to crop use by the cranes and conflict with farmers (Boggie et al. 2018). In Africa, elephants *Loxodonta africana* move between foraging areas using paths that traverse land development and farms, leading to damage to crops and fences, and sometimes injury to people, livestock and elephants (Songhurst et al. 2016). Such overlap of space use by wildlife and people can result in human–wildlife conflicts (LaPoint et al. 2015; Panzacchi et al. 2016; Shaw 2016).

Understanding factors driving the interactions between wildlife and agriculture is necessary to appropriately manage any conflicts (Cozzi et al. 2019). Some species interact with farms only in certain seasons, or at specific locations (Tyrrell et al. 2017), requiring different management actions from species that interact with agricultural areas year-round or in less predictable ways. Thus, management strategies are likely to be more effective if they are based on knowledge of temporal and spatial patterns of wildlife–agriculture interactions (Tyrrell et al. 2017; Cozzi et al. 2019). For instance, to mitigate the impact of migratory sandhill cranes (McIvor and Conover 1994; Boggie et al. 2018), farmers harvest grain before the cranes arrive, and supplementary food is provided for cranes on public land to attract them away from farms (Boggie et al. 2018).

In Europe, information on the spatial extent of interactions between the wild boar *Sus scrofa* and farms allowed researchers to evaluate the risk of crop predation for different farms, and to recommend ways to reduce crop damage in targeted areas, thereby reducing human–wildlife conflict (Cozzi et al. 2019).

On the Galapagos Islands, there is potential for human–wildlife conflict between Critically Endangered giant tortoises and farm owners (Blake et al. 2015b; Benitez-Capistros et al. 2016, 2018). On Santa Cruz Island, eastern *Chelonoidis porteri* and western *Chelonoidis donfaustoi* giant tortoises migrate from the lowlands to the highlands during the cool, dry season, following seasonal shifts in high quality food resources (Blake et al. 2013; Yackulic et al. 2017). Farming on Santa Cruz Island began in the early 1900s, and c. 88% of highland areas in the most productive part of the island have been converted for agriculture (Watson et al. 2010; Trueman et al. 2013). As a result, tortoises have few natural areas available to them in the highlands, and use farmland extensively (Blake et al. 2015b, a; Benitez-Capistros et al. 2018), foraging on a variety of native and introduced plant species, and sometimes on crops (Blake et al. 2015a, b). Tortoises occasionally destroy crop plants and break fences, potentially allowing livestock to escape. In addition, they may transmit pathogenic bacteria to livestock (Blake et al. 2015a; Cayot et al. 2017a, b; Benitez-Capistros et al. 2018; Nieto-Claudin et al. 2019) Although negative interactions between tortoises and farmers are rare, some land owners construct barriers or displace and harass tortoises to discourage them from returning (Benitez-Capistros et al. 2018).

No comprehensive evaluation of the spatial and temporal use of farmland by giant tortoises has been carried out on the Galapagos Islands (Blake et al. 2015a), although this information is important for the description, quantification and potential mitigation of this emergent conflict (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) 2015; Guzmán and Poma 2015; Benitez-Capistros et al. 2018). Galapagos tortoises are keystone species that have suffered dramatic population declines caused by overexploitation, and their potential for recovery is hampered by invasive species and habitat loss (MacFarland et al. 1974; Blake et al. 2012; Gibbs et al. 2014). Balancing outcomes for famers and tortoises is, therefore, critical for the well-being of both people and wildlife.

The goals of our study were to: (1) quantitatively describe the spatiotemporal distribution of Galapagos tortoises in the agricultural zone of Santa Cruz Island, and (2) identify intrinsic and extrinsic factors that influence these patterns, to inform tortoise conservation and facilitate coexistence with people. We used existing data on the movement of tracked individuals of two species of giant tortoise: *C. porteri*, which occurs in the south-west of the island*,* and *C. donfaustoi*, which occurs in the east and south-east. The two species have only recently been recognised as genetically distinct (Poulakakis et al. 2015). They share many morphological and behavioural traits: both are partial seasonal migrants, and both use the agricultural zone (Bastille-Rousseau et al. 2016; Cayot et al. 2017a, b), but their ranges do not overlap. Therefore, to comprehensively investigate the use of agricultural land by tortoises, we included both species and the island's entire agricultural zone in our study. We addressed the following research questions and predictions: (1) Which factors influenced the duration of tortoise visits to the agricultural zone? As body size is correlated with the propensity to migrate into the highlands and the timing of migration, we predicted that larger individuals would remain in farmland for longer than smaller tortoises. (2) How did tortoises use space in the agricultural zone, and how many farms did they visit? Past analyses of migratory patterns suggested that some tortoises travelled long distances in the agricultural zone (Blake et al. 2012; Yackulic et al. 2017), thus we expected that individual tortoises would use several farms. (3) What was the extent of inter-annual philopatry within the agricultural zone? High levels of philopatry have been reported for other tortoise species (Bernstein et al. 2007; Lee et al. 2007), so we expected that these tortoises would revisit the same areas for multiple years.

Methods

Study area

The 986 km^2 Santa Cruz Island is an extinct volcano in the centre of the Galapagos Archipelago, 926 km off the coast of Ecuador. It rises to 860 m altitude and has three distinct vegetation zones (See Figure 2.1) that are influenced by local and annual weather patterns. There is a hot, wet season during January–May, and a cool, dry season during June–December (Trueman and D'Ozouville 2010). Arid lowlands are dominated by cacti and deciduous vegetation, and are most productive during the wet season (McMullen 1999; Rivas-Torres et al. 2018). Palo santo *Bursera graveolens* woodland occurs in the transition zone to the cooler, wetter climate of the humid highlands, which are more consistently productive throughout the year (McMullen 1999; Trueman et al. 2013). The natural vegetation of the humid highlands consists of *Scalesia* spp. forest at lower elevations, with ferns, sedges, grasses, and *Miconia* species dominating as humidity increases. However, most of this zone is now dominated by various introduced and invasive species (Jaramillo Díaz and Guèzou 2011; Blake et al. 2012; Laso et al. 2020). These vegetation zones have shaped tortoise migrations over the centuries (Yackulic et al. 2017). As the dry season approaches and the forage quality declines in the lowlands, the tortoises migrate to the highlands until the wet season returns. As agriculture expands in the highlands of Santa Cruz, tortoises increasingly encounter human-modified areas (Blake et al. 2013; Yackulic et al. 2017).

Land use on the island is in two broad categories: c. 12% is privately owned land (11.6% agricultural land and 0.4% urban area), and 88% is a national park managed by the Galapagos National Park Directorate (Figure 2.1). The private land includes most of the highland area, which is used predominately for agriculture, and the urban settlement of Puerto Ayora in the lowlands. In the agricultural zone, land is used mostly for livestock grazing (42%) and crops (43%). The remainder (15%) is used for private dwellings or tourism, or is abandoned land (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) 2015; Benitez-Capistros et al. 2018). As most of the land encountered by tortoises is, or has been, used for some form of agriculture, hereafter we refer to all private properties in the highland area as farms.

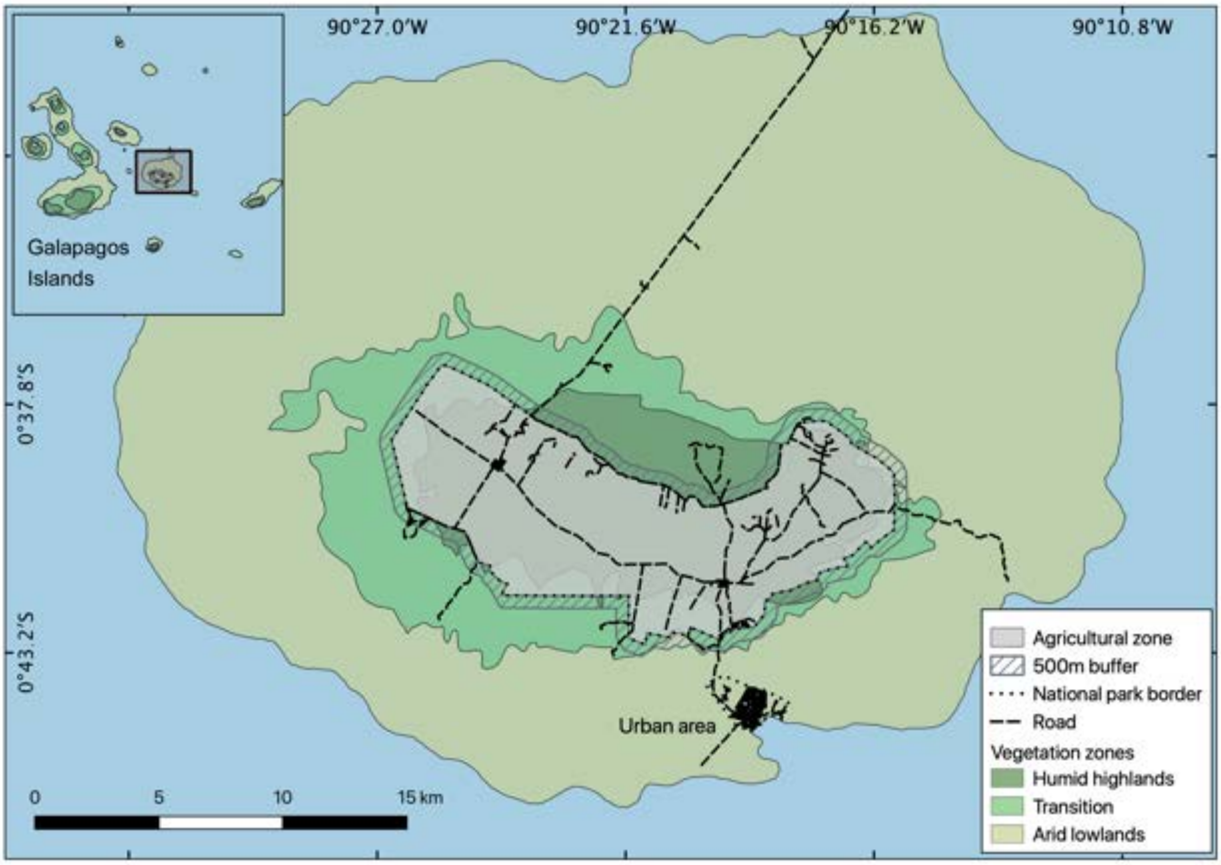

Figure 2.1. Santa Cruz Island, with the national park, a small urban area, and the agricultural zone that covers most of the humid highlands.

GPS tracking of tortoises

We collected data on tortoise movements during 2009–2018 on Santa Cruz Island. Twenty-seven tortoises of the western *C. porteri* (10 male, 17 female) and 18 individuals of the eastern *C. donfaustoi* (9 male, 9 female) species were fitted with GPS tracking devices (e-obs GmbH, Munich, Germany), following the animal handling procedures of the Galapagos National Park and the Max Planck Institute of Animal Behaviour (Blake et al. 2013). The majority of the GPS units were programmed to record locations hourly during 05:00–19.00 as tortoises are largely immobile at night, but some (15%) recorded locations at finer time scales or 12-hour intervals. Not all tortoises could be tracked in concurrent seasons because of tag failure; individual tortoises were tracked for a mean of 1,313 ± SE 139 days (range 102–2,936 days).

All tortoise location data used in this study are freely available online from Movebank (Wikelski et al. 2021). We combined the GPS locations of tortoises with spatial data on the extent of farms collected by the Galapagos Government Council in 2014 (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) 2015) .To assess how often tortoises migrated to the highlands, but did not access farms, we included tortoise movements within a 500 m buffer around the agricultural zone, which extended into the national park (Figure 2.1). To determine the duration of tortoise visits and their use of space in the agricultural zone, we used *QGIS 3.4* (QGIS Development Team 2018) to extract all locations of all tortoises that visited farms (31 tortoises during 2009–2018). Because tortoises were tracked continuously, but typically only used the highlands periodically, we created subsets of the GPS locations for each period that a tortoise used the agricultural zone. We defined a farmland visit as the time spent by a tortoise in the agricultural zone, from the first date of their presence within the 500 m buffer around the farms to the date they exited this area (113 unique farmland visits for 31 individual tortoises).

Factors influencing the duration of tortoise visits to the agricultural zone

To determine the factors influencing the duration of farmland visits, we used linear mixed models, constructed with the *lme4 1.1.23* package (Bates et al. 2015) in *R 4.0.2* (R Core Team 2020). As tortoises visited farms on multiple occasions, all mixed models included individual tortoise identity as a random effect, to account for effects of repeat observations of the same individual (Grueber et al. 2011). We used the number of days per farmland visit (with a square root transformation to meet model assumptions) as the response variable and examined the effects of sex, size (curved carapace length), species and month of entry and exit as explanatory variables. Tortoises that arrived later in the cool, dry season might have visited farms for shorter periods than tortoises that arrived earlier in the dry season, because once the wet season begins, tortoises tend to migrate back to the lowlands. Therefore, to assess if there was a relationship between the time tortoises remained in the agricultural zone and the month they entered or exited, we included these in the model as fixed effects.

Space use by tortoises in the agricultural zone

To describe individual tortoise movement patterns in the agricultural zone, we first categorized movement strategies from continuous time movement models using the *ctmm 0.5.6* package in *R* (Calabrese et al. 2016). We selected this approach because it allows the user to incorporate telemetry error into model-fitting, which enables confidence intervals for model estimates. It also allows the user to select the appropriate movement model (e.g. Brownian motion, Ornstein–Uhlenbeck, independent identically distributed) for their data, to produce accurate and precise interpolations of an animals trajectory and space use, especially with respect to any biases resulting from spatial autocorrelations (Fleming et al. 2014, 2016). We used these models to estimate the occurrence distributions of tortoises, using time-series kriging to evaluate the number of farms visited, and how intensively individual tortoises used the farms. We excluded four tortoises with only one farmland visit as we could not examine philopatry. In addition, we excluded tortoises with farmland visits with too few locations to create a reliable estimate for their occurrence distribution, either because tortoises were in the highlands for too few days (n = 17 farmland visits), or were on a 12-hour tracking cycle (n = 4 tortoises and 10 farmland visits). The data filtering process produced a subset of 23 tortoises (*C. donfaustoi*: two females and six males; *C. porteri*: seven females and eight males) that made a total of 83 farmland visits. We checked tortoise locations for outliers attributed to equipment error (such as implausible locations) using the *outlie* function from the *ctmm* package in *R* (Calabrese et al. 2016). We then generated a variogram that incorporated telemetry error (GPS satellite dilution of precision) for each farmland visit for each tortoise, which we then used to seed the movement model fitting process using the *ctmm.fit* function with a perturbative hybrid restricted maximum likelihood (pHREML) optimiser to account for farmland visits with a small sample size. The *ctmm.fit* process estimated which movement model best characterized the animal's movement process and their movement parameters, based on their relocation data (Calabrese et al. 2016; Fleming and Calabrese 2017). We then used these underlying movement models to create an occurrence distribution estimate for 83 farmland visits for each of the 23 tortoises, to extract the 25, 50, 75, 95 and 99% utilization distribution contours.

All occurrence distribution estimates were exported as shapefiles using the *rgdal 1.4-4* package in *R* (Bivand et al. 2018). We performed an intersect analysis, in *QGIS*, to quantify the number of farms within each occurrence distribution polygon that contained the maximum likelihood 25, 50, 75, 95 and 99% utilization distribution contours. We also calculated the area enclosed by each contour in each farm to assess the proportion of farmland used by tortoises.

Inter-annual philopatry within the agricultural zone

We calculated the degree of spatial overlap among farmland visits for each individual tortoise using the overlap function in the *ctmm* package. The overlap function uses Bhattacharyya coefficients to compare the similarity between the tortoise's fitted continuous time movement models, with greater similarity indicating high fidelity to the same areas (Winner et al. 2018).

Model selection

For linear mixed models we used Akaike's information criterion (AIC) to assess model fit, prioritizing models with the smallest AIC value explaining the most variance (Burnham and Anderson 2002). To assess which model had the most explanatory power, we used model averaging, by establishing a top set of models that were within at least five AIC values of the top model. Using the AICmodavg package (Mazerolle

2015), only variables in the top set that had confidence intervals that did not include zero were considered reliable predictors (Symonds and Moussalli 2011).

Results

Of the 45 tortoises tracked, 31 (69%) migrated to the agricultural zone. We found females were less likely to visit the agricultural zone than males. Just over half (54%) of the tagged females migrated to the agricultural zone compared to 89% of tagged males. Only one tortoise (a *C. porteri* female) migrated from the lowlands into the 500 m buffer around the agricultural zone but did not enter farmland during the study period, however, she did so in other years. Thirteen of the 31 tracked tortoises remained in the agricultural zone for > 6 months (22% of all farmland visits), longer than the entire cool, dry season, and five tortoises remained for > 1 year (6% of all farmland visits). Female tortoises most often entered farmland in October (38% of 53 farmland visits by females) and usually left in February (35% of 53 visits), whereas males most often entered in August (25% of 60 farmland visits by males) and left in January (28% of 60 visits). Mean duration of farmland visits was 150 ± SE 11 days (range 2–765 days).

Factors influencing the duration of tortoise visits to the agricultural zone

Tortoise body size (curved carapace length) was the strongest predictor of the duration of farmland visits, followed by sex (Table 2.1, Figure 2.2). We found that larger male and female tortoises tended to spend longer in the agricultural zone, with the largest males staying for the longest periods of time. Males remained in the agricultural zone for a mean of 181 ± SE 6 days, compared to 116 ± SE 9 days for females. There was no significant effect of species, or the month of entry or exit, on the duration of farmland visits (Supplementary Table 2.1).

Table 2.1. Top variables identified by generalized linear mixed models for factors influencing the duration of tortoise visits to the agricultural zone. The analysis is based on 113 farmland visits by 31 tagged tortoises that were tracked in the agricultural zone during 2009–2018. For each model, the table shows the Akaike information criterion (AIC) value, the difference from the AIC score of the best model (ΔAIC), AIC weight from model averaging, the model estimate and standard error for the variables in the top set, and 95% confidence intervals.

Model	AIC	ΔAIC	AIC weight	Estimate ± SE	95% CI
Curved carapace length	654.86	0.00	0.82	0.071 ± 0.021	0.029, 0.116
Sex	658.11	3.25	0.16		
Female				10.194 ± 0.590	8.936, 11.428
Male				2.332 ± 0.810	0.641, 4.074
Null	662.75	7.88	0.02		

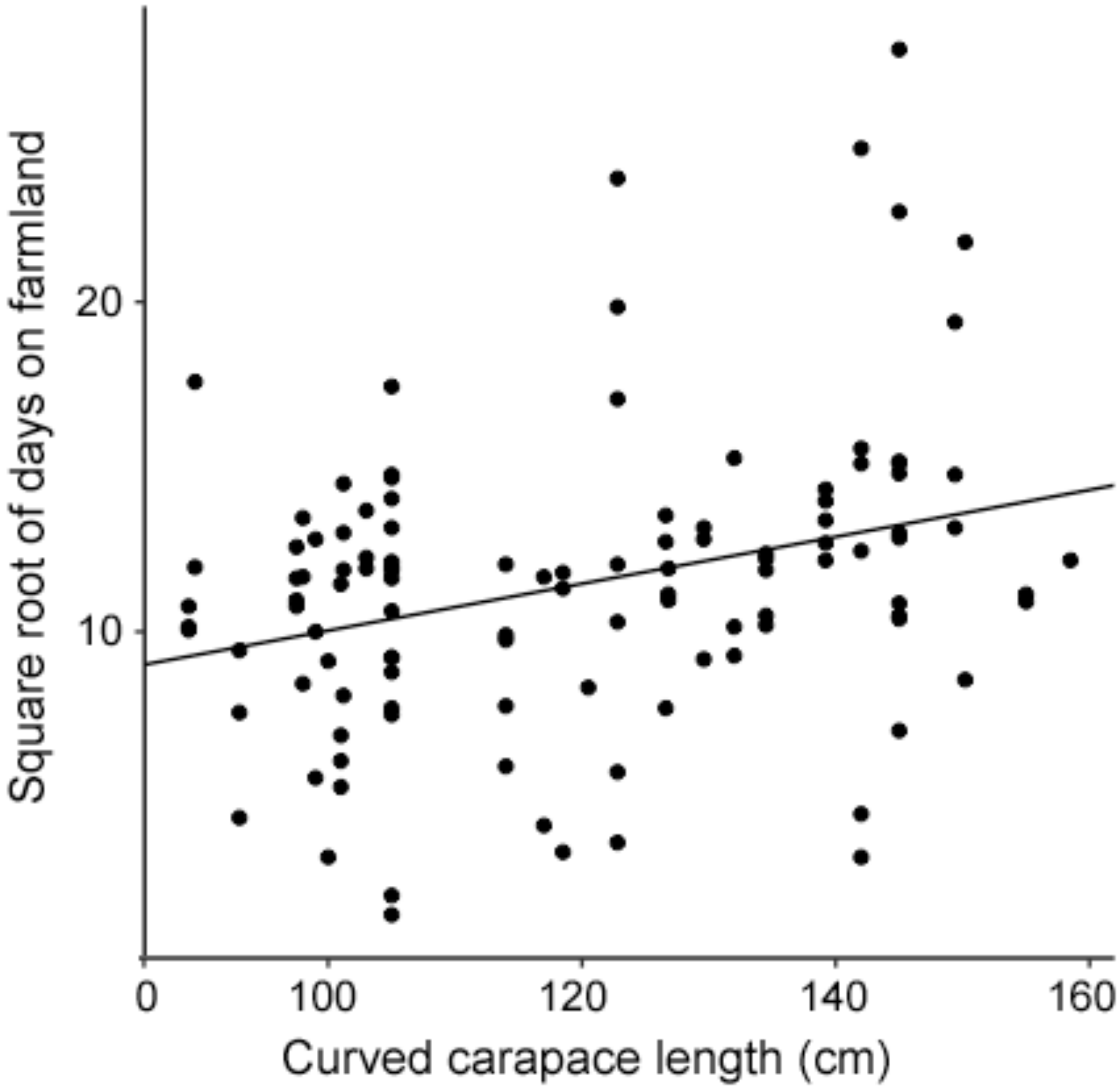

Figure 2.2. The relationship between the number of days spent on farms per farmland visit and the size (curved carapace length) of the individual tortoise. Data were taken from 113 farmland visits by 31 Galapagos giant tortoises (*Chelonoidis porteri* and *Chelonoidis donfaustoi*) tracked in the agricultural zone during 2009–2018. The trendline is from the best fit model from Table 2.1.

Space use by tortoises in the agricultural zone

Tortoise movements on farms were best described by the Ornstein–Uhlenbeck-F motion anisotropic model (fitted with telemetry error), indicating that movements were characterized by sporadic foraging periods within a range centred around a location (Fleming et al. 2014, 2016). The Ornstein–Uhlenbeck-F model showed that individuals walked a mean distance of 550 m per day (95% CI 520–579 m), and showed directional persistence for c. 1 hour (58 min, 95% CI 48.4–73.2 min). Tortoises varied in their intensity of use of different farms (Figure 2.3), using a mean of 4 ± SE 0.5 farms (range 1–24) within their 99% utilization distributions, but showed concentrated use of 2 ± SE 0.14 farms (range 1–7) within their 25% utilization distributions per farmland visit (Supplementary Table 2.2). During a farmland visit, tortoises used a mean of 2.9 ± SE 0.29 ha. This was on average < 10% of the total area of a farm, and < 1% of the farm was likely to be used intensely for activities such as foraging or resting (indicated by the 25% contour; Supplementary Table 2.2).

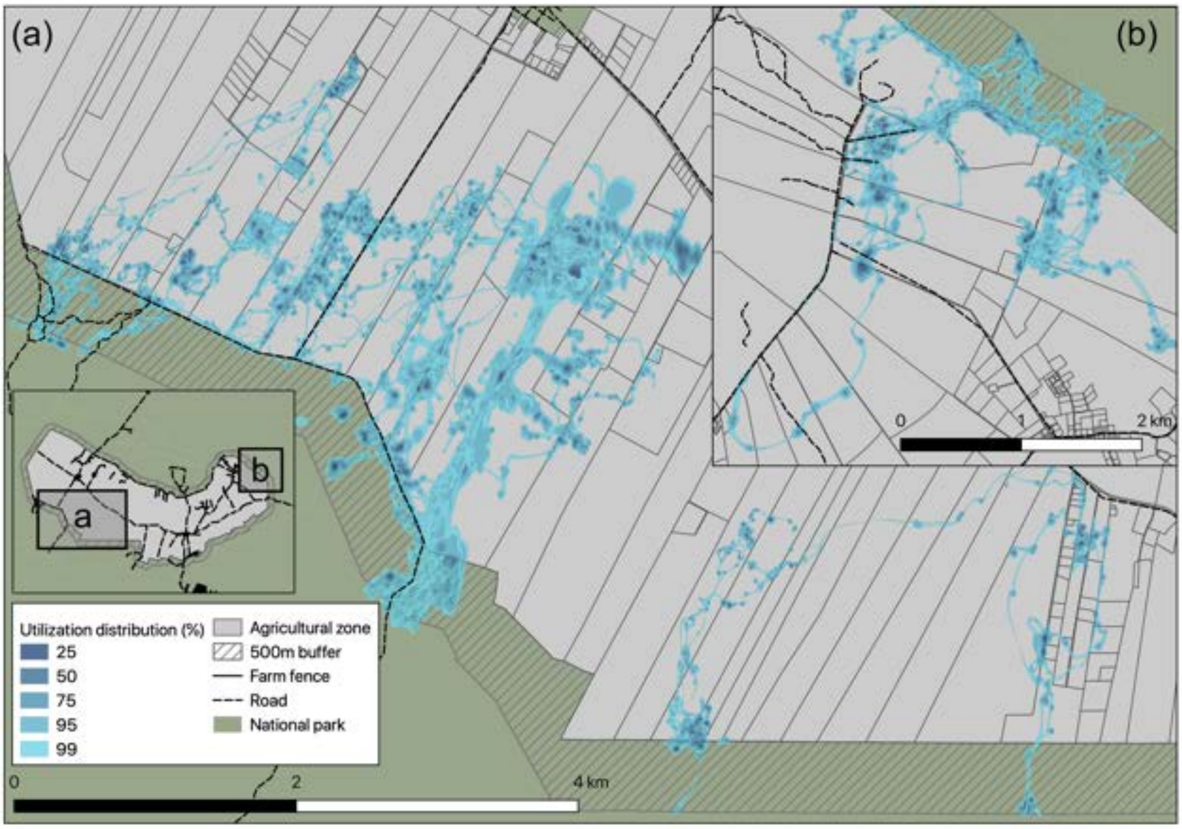

Figure 2.3. Use of farmland by tortoises in the agricultural area of Santa Cruz Island. Data were taken from 23 tortoises tracked during 2009–2018: (a) 14 individuals of *C. porteri* and (b) 9 individuals of *C. donfaustoi*. The shaded areas show the 25–99% maximum likelihood utilization distribution; darker shades indicate higher intensity of use.

Inter-annual philopatry within the agricultural zone

Individual tortoises showed a high degree of spatial overlap of their farmland visits among years (Supplementary Table 2.3). Overlap data were highly skewed (skewness = –2.24) towards > 80% overlap, indicating most tortoises had a strong affinity for the same areas across farmland visits (Figure 2.4). Tortoises showed consistently high philopatry over many years (i.e. overlap was high for farmland visits irrespective of the time interval between visits).

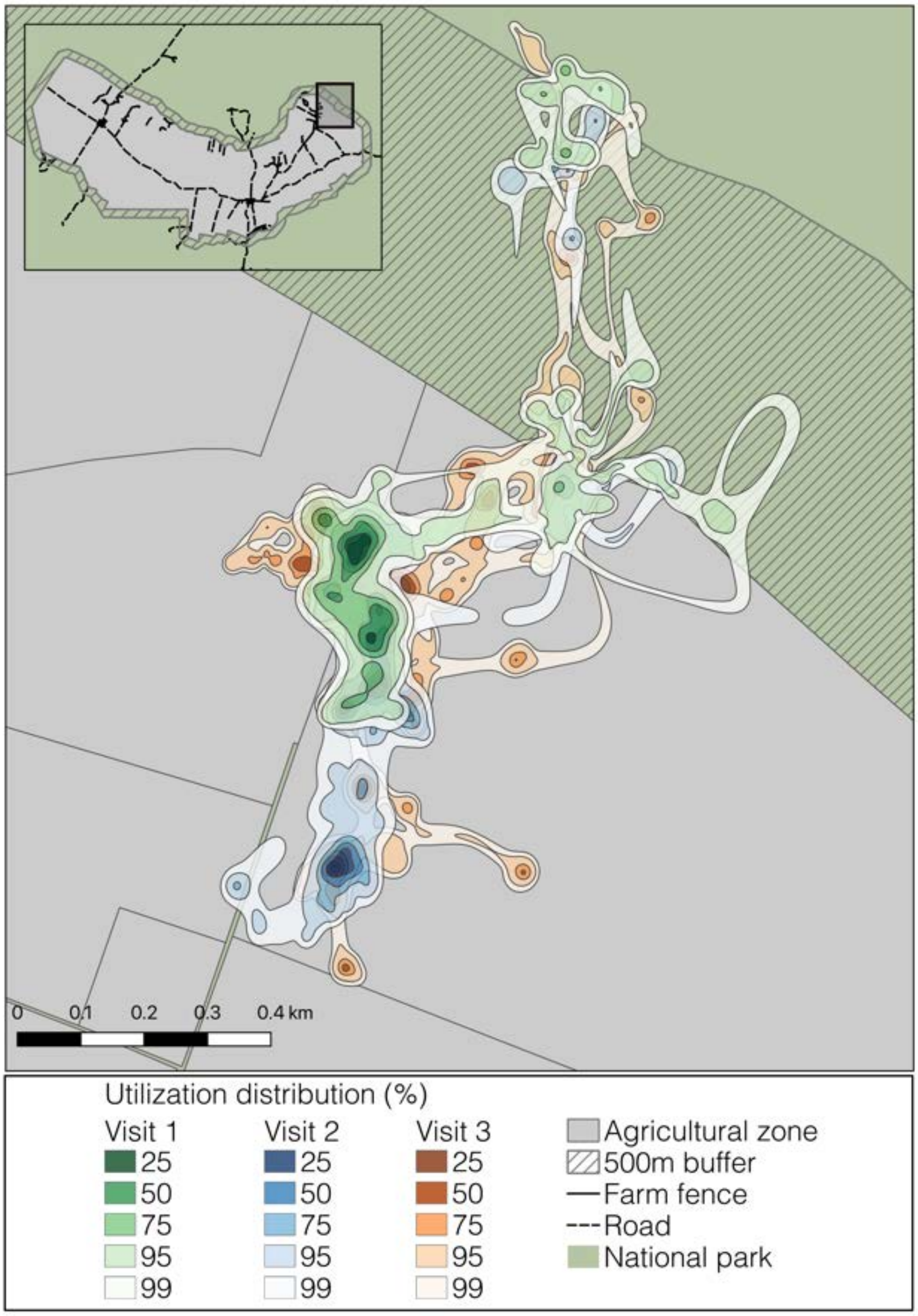

Figure 2.4. Occurrence distributions of one eastern Santa Cruz tortoise *C. donfaustoi* during three separate farmland visits in the agricultural zone. The shaded

areas show the 25–99% utilization distribution; darker shades indicate higher intensity of use. There is much spatial overlap of utilization between farmland visits, indicating high inter-annual philopatry within the agricultural zone.

Discussion

Our main goal was to describe the spatial and temporal distribution of tortoise use of the agricultural zone of Santa Cruz Island, Galapagos, and to identify factors that influenced tortoise movement. We found that the agricultural zone was generally accessible to tortoises, as there was only one occasion when an individual migrated to the highlands but remained outside farmland, although the same individual entered farmland in other years. Tortoises intensively use small areas within multiple farms for prolonged periods during the cool, dry season for c. 5 months. Tortoises showed strong philopatry in space use within farms over multiple years. We found no evidence of species-specific differences in duration of stay on farms.

Factors influencing the duration of tortoise visits to the agricultural zone

Tortoise size and sex influenced the length of stay on farmland. Larger tortoises tended to spend the most time on farms, probably because they migrate into the highlands earlier than smaller individuals, to satisfy their higher absolute metabolic demands and food requirements (Yackulic et al. 2017; Bastille-Rousseau et al. 2018b). Although larger individuals generally spent more time in the agricultural zone, large males tended to spend more time than large females. Unlike males, females are constrained to delay their migrations to the highlands until they have nested (Blake et al. 2013). Farmers can expect that large individuals will be the first to arrive in the cool, dry season, and that smaller individuals will arrive later, but most tortoises leave farmlands at approximately the same time, regardless of sex or body size (Yackulic et al. 2017).

The extensive time tortoises spend in the agricultural zone indicates it is an important resource. Different land uses and crops could provoke conflict at different times of the year. For example, during the cool, dry season when forage quantity in the national park is low, tortoises congregate in the agricultural zone and compete with cattle for grass. There is some evidence that the presence of tortoises may increase the productivity of vegetation on Galapagos (Bastille-Rousseau et al. 2017a), and grazing herbivores often increase grass sward productivity if rainfall is high (Milchunas and Lauenroth 1993; Augustine et al. 2006). However, prolonged drought conditions during the dry season can reduce grass productivity, which can result in poor body condition and death of cattle (SB & FC, pers. obs.). Under such conditions, competition with the more resilient tortoises may have considerable impacts on cattle farmers.

Unlike cattle production, fruit and vegetable production on Galapagos increases during the hot, wet season, when tortoises use the agricultural zone less. We found, however, that a substantial percentage of farmland visits (22%) were for an extended period of time, and overlap of tortoises and fruits and vegetable crops could lead to increasing conflict. Currently, we do not have adequate data on where these crops are grown in relation to tortoise activity, which will be important for any future conflict mitigation. Such information could be used for zonal planning that minimizes spatiotemporal overlap between tortoises and crops.

Another potential problem associated with tortoises spending longer periods in the agricultural zone is the risk of exchange of pathogens, including bacteria that are resistant to antimicrobial treatments, between wild tortoises and livestock. In a sample of faeces of *C. porteri*, 100% contained microbes with resistance genes, making tortoises that use farmland a likely reservoir for resistant strains (Nieto-Claudin et al. 2019). Pathogen transmission between wildlife and livestock is a negative consequence of wildlife interactions with agriculture and could pose a risk to tortoises, livestock, and human health in the Galapagos islands (Gordon 2018; Nieto-Claudin et al. 2019).

Tortoises may remain longer on farms (beyond the months predicted based on a bioenergetics model by Yackulic et al., (2017). for several reasons. Firstly, food plants with high nutritional value, such as crops and introduced grasses and herbs used for cattle forage, are now a dominant component of tortoise diets in the agricultural zone (Blake et al. 2015a). These plants may fulfil the tortoises' energy requirements, reducing their need to migrate into the lowlands for the wet season. Secondly, many farmers maintain artificial ponds on their farms, typically for watering cattle (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) 2015), although ponds are also created specifically to attract tortoises for tourism. Tortoises are attracted to water bodies, and prior to conversion of land for agriculture, they would have mostly encountered ephemeral ponds in the highlands (Froyd et al. 2014). As with other wildlife species, the availability of multiple artificial freshwater ponds throughout the year might encourage tortoises to remain on farms longer than predicted from energy requirements alone. Thirdly, fences may restrict tortoise movement, as they do for other wildlife (Jakes et al. 2018). Tortoises may struggle to find their way off a fenced farm and thus remain on a farm for longer. However, during our study, we only saw one such example involving a tagged tortoise, and many farms remain relatively permeable for tortoises (the authors, unpublished data).

Space use by tortoises in the agricultural zone

Most tortoises used 1–4 farms, primarily during the cool, dry season, but one tortoise used 24 farms in a single visit. The proportion of each farm used by an individual tortoise is relatively small (< 8% of the area of an average farm; Supplementary Table 2.2), most of which is used with low intensity (e.g. for transit). Although at present tortoises generally use only a small proportion of farmland, tourism and the local population are expected to increase, and this could exacerbate negative interactions between farmers and tortoises (Sampedro et al. 2018). Local demand for beef and pork is also expected to increase, as Galapagos prohibits the import of these products (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG) 2015; Sampedro et al. 2018). Given that the agricultural zone cannot expand further, farmers will need to increase livestock densities on existing land to meet demand, and could be less tolerant of tortoises sharing forage with cattle, especially if forage quality continues to decline. We also found tortoise distribution on farmland was clustered, and the temporary sedentary ranges of individual tortoises overlapped extensively. This probably reflects variation in resource availability within farms (e.g. ponds, high-quality forage areas and shade), but fine-scale data on resource distribution are needed to quantify the influence of different resources on tortoise distribution. If the resources that tortoises use most frequently can be identified, land-use plans could be established at the level of individual farms, to enable physical separation of critical resources for tortoises from production areas.

Our estimates for the number of farms visited by tortoises are probably conservative. Our information on the location, extent and type of farm was based on the Galapagos Government Council's census conducted in 2014, and our data include tortoise movements beyond 2014, up to 2018. During this time, mean farm size has probably decreased, as land holders subdivide and sell land for residential development, or divide farms among family members. Land holders with smaller farms are more likely to report damage caused by tortoises, and to build barriers or harass and displace tortoises (Benitez-Capistros et al. 2018). In addition, because tortoises routinely use multiple farms, and this number is probably higher than our estimates, conservation strategies in the agricultural zone will require consultation and collaboration with a large, and increasing, number of landowners. Developing strategies on the management of mobile wildlife species, such as tortoises, on private land should involve all stakeholders.

Inter-annual philopatry within the agricultural zone

We found that, over 9 years, tortoises had a consistently high degree of spatial overlap among farmland visits, i.e. the same tortoises often re-used the same farms and the same areas on inter-annual visits, consistent with the observation that individuals tended to use the same migratory paths over years (Bastille-Rousseau et al. 2018b). Philopatry has been documented in a variety of tortoises and turtles (Bernstein et al. 2007; Lee et al. 2007). Consistently revisiting the same areas may indicate that tortoises use cognitive spatial maps to access important resources. For example, elephants and primates remember the location and distribution of important fine-scale resources, such as waterholes or fruiting trees, and use their cognitive spatial maps to guide long-distance movements to access these areas (Polansky et al. 2015; Hopkins 2016). Research with captive giant tortoises has demonstrated their long-term memory and cognitive abilities (Gutnick et al. 2020). Tortoises may use cognition and memory to find resources, and measures encouraging them to use areas where they do not damage fences or crops may be remembered and effective across multiple seasons.

Conclusion

We investigated the temporal and spatial patterns of farmland use by Galapagos tortoises, described the extent of the interaction, and identified the size of areas and the average number of landholders affected by wildlife movements. Our data suggest tortoises repeatedly use relatively small areas; this may facilitate land-use planning for tortoise conservation at the scale of individual farms. However, some tortoises moved across multiple farms, and the development of conservation strategies could involve large numbers of landowners. For Galapagos, a globally significant biodiversity hotspot, we recommend prioritizing further research to determine: (1) the socioeconomic and land-use trajectory of the agricultural zone across space and time, (2) the ecological requirements of giant tortoises that are met by farms, and the nature and scale of emergent negative interactions with people, and (3) strategies that can be used at different scales to enable sustainable coexistence of tortoises and people on inhabited islands. The situation we observed in Galapagos is an example of increasingly common wildlife–agriculture interactions. Our study demonstrates that knowledge of wildlife movement and space use on farms can be used to describe and quantify wildlife–farmland interactions, and how such data could contribute to improving strategies to manage human–wildlife interactions.

Chapter Three: Navigating agricultural landscapes: Responses of critically endangered giant tortoises to farmland vegetation and infrastructure

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Abstract

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

Introduction

Globally, land modification is increasing rapidly; only 20%-34% of the Earth's terrestrial landscapes experience very low human impact (Hooke 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 assess the impact of specific infrastructure characteristics on animal movement such as type of road, or different fencing materials (Jakes et al. 2018). For instance, 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 importance 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 4 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 et al. 2019; Shilling et al. 2020). To adequately support wildlife movement in human-modified landscapes we need 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 & 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. 2022b). 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. 2017a). 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:

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. 2022b).

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).

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.

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 (Figure 3.1A): 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).

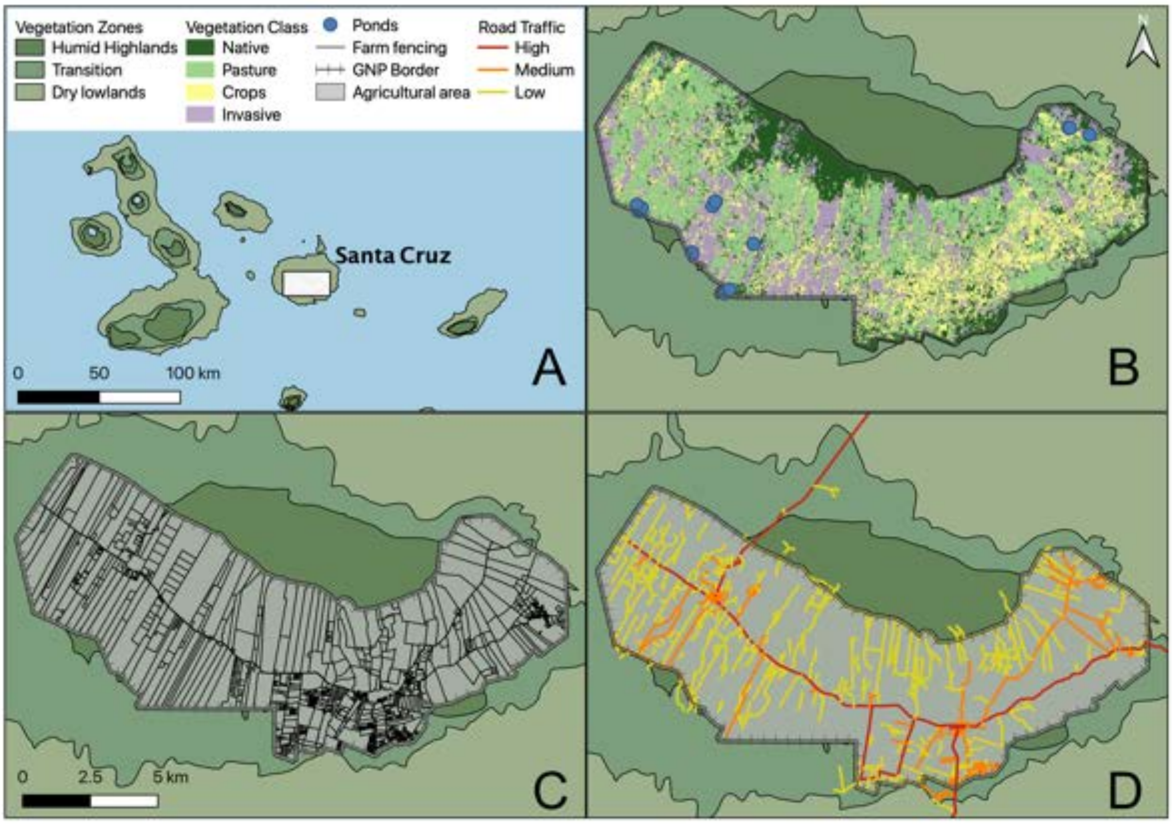

Figure 3.1. Santa Cruz Island showing the covariates used to assess the effect of the agricultural landscape and roads on tortoise movement and habitat selection. A. White rectangle indicates the location of the agricultural area shown in the other three maps; B. Agricultural vegetation (green, yellow 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).

We collected location data from 27 GPS-tracked tortoises, of both species, in areas where they were using agricultural land between 2014-2020 (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) provided a detailed description of tracking methods.

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 Table 3.1), 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) (Figure 3.1 B-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 3.1 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 Table 3.2 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).

Table 3.1. 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. Only Model 1 had steps sampled at 5 hour intervals, for all other models tortoise steps were sampled hourly.

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 hour 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

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 Table 3.3 for details), to produce four main vegetation classes with which tortoises interacted (Figure 3.1B). 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 speed (n= 24 tortoises, strata= 66,372). Because movement decisions are made over the 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= 5,738). 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 responded 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 (Figure 3.1B; 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 parks). 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 0m-1m, 4-5m, and 9-10m). 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.1.2.5033 (R Core Team, 2018).

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 Figure 3.2) 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.

Figure 3.2. 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 be crossed by tortoises. Gap transects, in which the number of gaps > 50 cm were quantified, were performed only on complex fences.

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 (Figure 3.1C) and land-use types of farms (Consejo de Gobierno del Régimen Especial de Galápagos (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 (Consejo de Gobierno del Régimen Especial de Galápagos (CGREG)

2015) 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 (Figure 3.1D). Roads were classified based on a number of factors determined using satellite imagery, field surveys, and consulting with local residents (Laso, 2021). Our classification is summarised as follows: high-traffic roads included paved highways, primary, secondary, and urban roads that had relatively high vehicle traffic; medium-traffic roads included narrow gravel and service roads connected to main roads with higher vehicle traffic, and low-traffic roads were tertiary and seasonal roads, constructed of gravel or dirt with relatively low traffic levels, or restricted vehicle access (see Supplementary Figure 3.1 for examples of road types).

Fifty-seven percent 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 3.1). 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 (Figure 3.3). Tortoises used crop and invasive vegetation about as much as native vegetation (Supplementary Table 3.4). 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 (Figure 3.4). There was little difference between movement in crop and native vegetation (Supplementary Table 3.5).

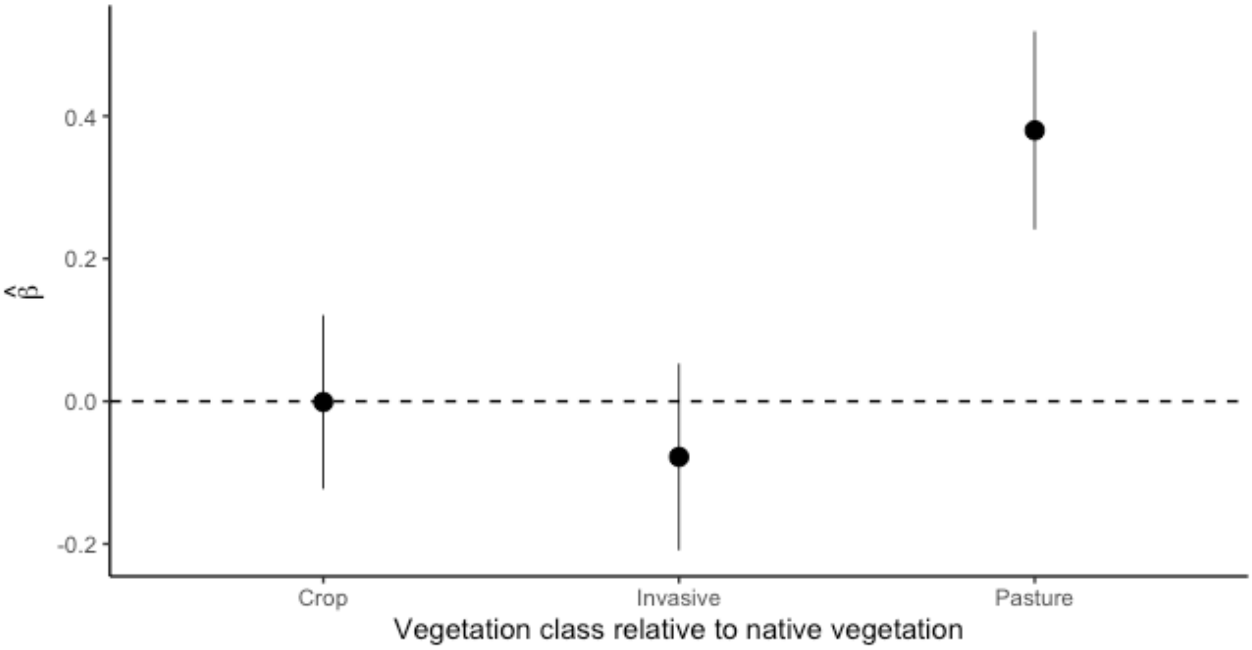

Figure 3.3. Tortoise responses to human-modified vegetation compared to native vegetation use in the agricultural area of Santa Cruz, Galapagos. Tortoises preferred pastures, but there was little difference in their use of crop or invasive vegetation

(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.

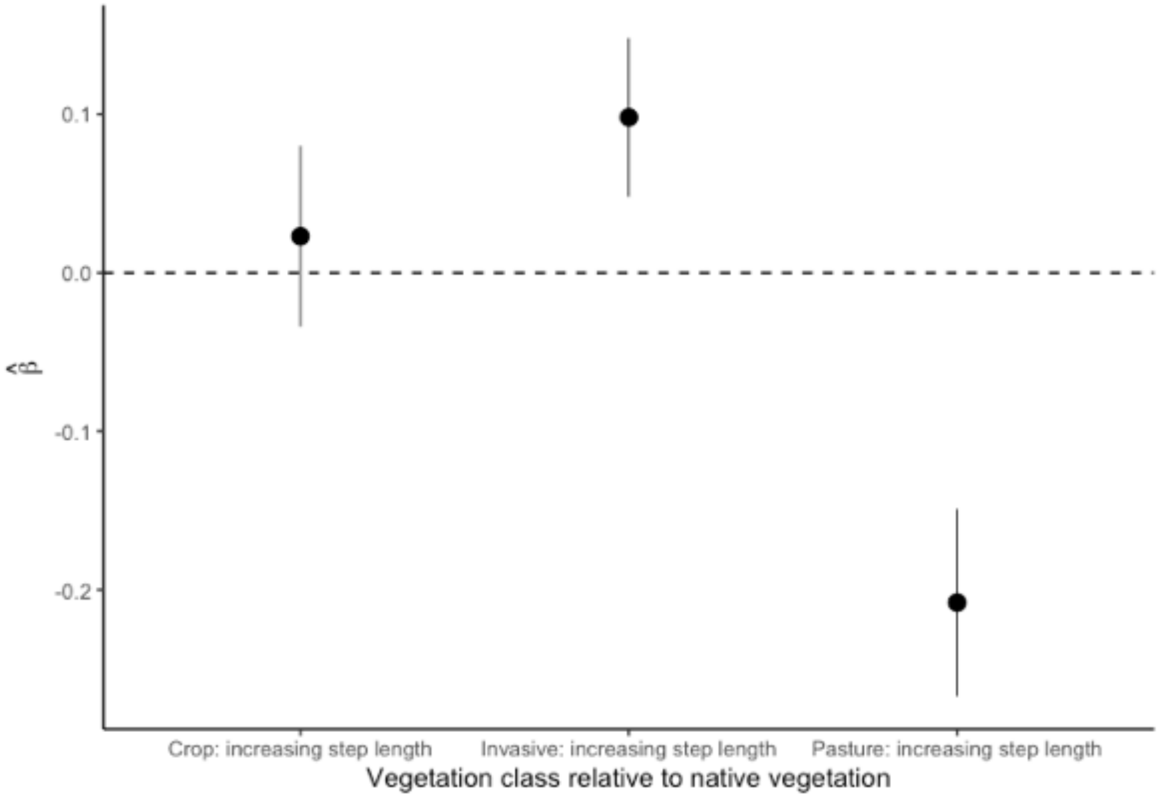

Figure 3.4. Tortoise movement characteristics in human-modified vegetation, relative to native vegetation, in the agricultural area of Santa Cruz, Galapagos. Compared to native vegetation, tortoises moved slower in pasture, faster in invasive vegetation, and roughly the same speed when in crops. Estimates above the zero (dashed) line indicate selection, and those below the line indicate avoidance. Error bars show the standard error of the mean.

How did tortoises respond to ponds in farmland?

We found that tortoises responded strongly to pond proximity, and preferred locations closer to ponds (Figure 3.5), consequently avoiding distances further from ponds (mean odds ratio 0.62; Supplementary Table 3.6). We found no influence of pond proximity on tortoise movement (Supplementary Table 3.6).

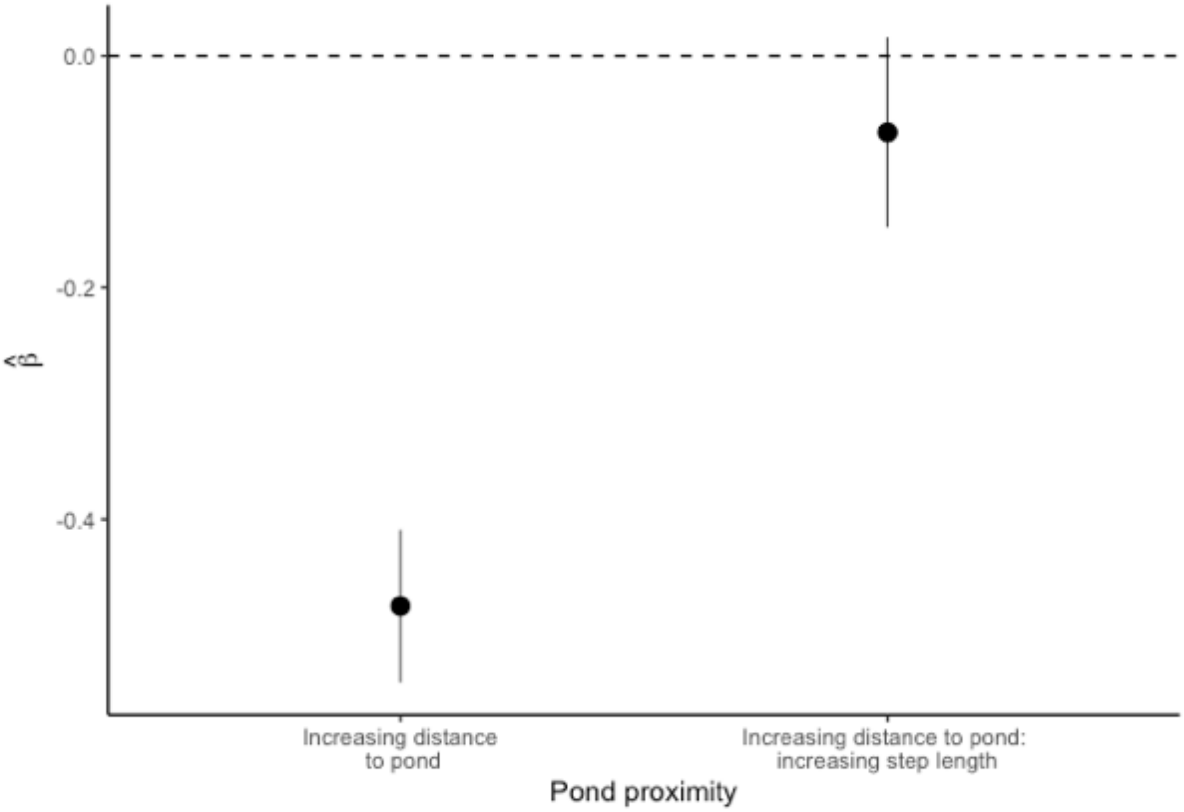

Figure 3.5. Tortoise response to ponds in the agricultural area of Santa Cruz, Galapagos. Tortoises preferred to be closer to ponds. Estimates above the zero (dashed) line indicate selection, and those below the line indicate avoidance. Error bars show the standard error of the mean.

Fence Structure

Eighty-four percent 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 Table 3.7). 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 3.2) whereas there was no significant impact of road proximity for medium and high-traffic roads (Supplementary Tables 3.8-9). We did not detect a difference in tortoise movement in relation to their distance to any of the road types (Table 3.2 and Supplementary Tables 3.8-3.9).

Table 3.2. Model output for tortoise response to low-traffic roads in the agricultural area of Santa Cruz Island, Galapagos. Tortoises preferred to be closer to low-traffic roads. An interaction is denoted with " :".

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

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. 2022b). 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. 2021b). 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 & 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. 2021a). 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. 2017a). But traffic is expected to increase, as tourism, and local demand for more roads to access the lowlands, also increase (Cayot et al. 2017a; 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. Furthermore, 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.

Chapter Four: Sharing land with giants: habitat preferences of Galapagos tortoises on farms

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Abstract

One of the most pressing dilemmas of our time is determining how to satisfy the demands of a growing human population while still conserving biodiversity. Worldwide, land modification to accommodate human resource needs has caused significant declines in wildlife populations. To help minimize biodiversity loss, we must support wildlife on human-dominated land, such as farms and urban areas, but our knowledge of how to do so is lacking. Agriculture is a major driver of land modification; but also has the potential to play a role in conserving biodiversity. To support critically endangered ecosystem engineers that use farms, such as giant Galapagos tortoises, we need to understand the characteristics encouraging or hindering them. To quantify tortoise habitat preferences, we assessed the relationship between tortoise density, habitat structure, and land-use type, by recording tortoise density on farms on Santa Cruz Island, Galapagos, over two years. Tortoise density was lowest in abandoned farmland and highest in tourist areas and was most strongly positively correlated with abundant ground cover, short vegetation, and few shrubs. The habitat features favoured by tortoises could potentially be manipulated to help support tortoise

conservation on farms. Measuring wildlife preferences in human-dominated areas is an important step towards balancing biodiversity conservation and human-enterprise.

Introduction

Among the most pressing issues of our time is the conflict between conserving biodiversity and meeting the water, energy, food, and space demands of a growing, and more affluent human population (Rosenzweig 2003a; Bullock et al. 2011; Hooke et al. 2012; Kremen 2015; Gordon et al. 2016). The human population is expected to increase by 4 billion by the end of the century (United Nations 2015), and the task of feeding this increasing population falls on our agricultural systems (Butler et al. 2007; Tilman et al. 2011). Agriculture is the leading cause of land modification, and therefore a key influence reducing biodiversity (Phalan et al. 2011; Neilly et al. 2016; Gordon et al. 2016). Many solutions have been proposed to reconcile biodiversity conservation and food production, and they typically involve land sparing (in which agriculture is intensified on existing land to avoid clearing more), or land sharing (in which agricultural land is made wildlife-friendly to share space with wildlife) (Phalan et al. 2011; Caudill et al. 2015; Gordon 2018). No single solution can resolve all of the complex problems facing biodiversity conservation and food production around the world, but sometimes one or the other of these two possibilities is a better option (Kremen 2015; Shackelford et al. 2015). For example, wildlife may require more space than land sparing alone can provide, and thus land sharing may be the preferred strategy to meet conservation objectives (e.g., for snow leopards *Panthera uncia* (Johansson et al. 2016). When land sharing is viable, the central issue is optimizing management practices to achieve both food production and conservation goals.

If sharing land with wildlife is to be a success, the habitat characteristics important for supporting wildlife must be identified. Typically, researchers assess the importance of environmental factors for wildlife by recording habitat variables that correlate positively with abundance of particular species in natural areas (Singh et al. 2009; VanDerWal et al. 2009); but some studies have quantified habitat preferences in human-modified areas such as farms (see Neilly & Schwarzkopf, 2018; Nordberg & Schwarzkopf, 2019). While knowledge of wildlife habitat preferences on agricultural land is limited, research does suggests that habitat heterogeneity, farm type, and land management influence wildlife use of farms (Benton et al. 2003; Hardman et al. 2016; Neilly et al. 2016). For example, in a grazing experiment, rufous bettongs (*Aepyprymnus rufescens*), a marsupial ecosystem engineer, preferred habitats with medium- to high complexity ground cover in areas moderately grazed by livestock, over low-complexity, heavily grazed areas (Neilly and Schwarzkopf 2018). Similarly, both coffee-plantation type (forest, shade or sun coffee) and specific habitat characteristics impact the abundance and species richness of small mammals found in coffee plantations in Costa Rica (Caudill et al. 2015). A greater understanding of the specifics of habitat preferences of wildlife using farmland is, therefore, useful for making informed decisions supporting land sharing for vulnerable wildlife.

On some islands in the Galapagos Archipelago, a hotspot for species endemism (Steinfartz 2011), agricultural land has replaced the majority of humid highland areas, which are important habitat for many endemic species, including threatened animals and plants (Watson et al. 2010). Since the Galapagos National Park was established in 1959, regulations have been implemented that discourage land clearing and protect the National Park, making further land clearing less of a threat, and land sharing more of a priority. Species richness and abundance of many species has declined in the humid highlands, including iconic Darwin's finches (Dvorak et al. 2012). Similarly, critically endangered endemic giant tortoises (generalist grazers *sensu* Blake et al., 2020) inhabit transformed and native highland habitats, often in large numbers, as this habitat type provides high energy grass forage (Blake et al. 2013; Yackulic et al. 2017; Bastille-Rousseau et al. 2018b; Pike et al. 2021). Giant tortoises have, however, been reduced to a fraction of their former numbers by past human exploitation (MacFarland et al. 1974). The remaining population is also facing health threats from various sources including invasive species (Carrion et al. 2011), pollution and exposure to antibiotics and chemicals (Nieto-Claudin et al. 2019, 2021). We do not understand the impact of agricultural land use on the ecology of the remaining tortoises (Blake et al. 2015b; Pike et al. 2021).

Galapagos tortoises are ecosystem engineers, making them important for seed dispersal, nutrient input and vegetation dynamics, and a high priority for conservation (Froyd et al. 2014; Gibbs et al. 2014; Bastille-Rousseau et al. 2017a). On high-elevation islands, Galapagos tortoises migrate from arid lowlands, where they breed, to the humid highlands, which are more consistently productive (Blake et al. 2013; Yackulic et al. 2017). Once tortoises are in the humid highland agricultural area, they remain for an average of 150 days, and interact with multiple landholders and farm types (Pike et al. 2021). In this study we were most interested in tortoise interactions with four land-use types: 1) livestock production (33% of farmland by area), 2) coffee production (6% of land area , 3) abandoned land (22% of farmland), and 4) land dedicated to tourism (hereafter referred to as 'touristic' land; % of land area unknown) (Laso et al. 2020). Touristic land includes agricultural land that has been repurposed to encourage wild tortoise use, as farmers generate revenue from tourists who wish to see tortoises in a semi-natural setting. Including touristic land was especially relevant, as it enabled us to evaluate the effectiveness of repurposing agricultural land to attract tortoises, and allowed us to compare tortoise use of land maintained for agricultural practices versus land maintained for tortoises. To facilitate and improve land sharing between tortoises and farmers, we sought to identify habitat features important for giant tortoises in the agricultural area.

Using a survey of tortoise density in four land-use types, and a survey of 12 habitat features, we estimated tortoise density by land-use type, and quantified how habitat influenced tortoise density across the agricultural landscape. We addressed two main questions relevant to land sharing options for conservation:

1. Does tortoise density differ among land-use types? We included livestock production, coffee production, abandoned land, and touristic land as land-use types. Based on the resources available in each land-use type, we predicted tortoise density would be highest on touristic land, which has more of the resources favoured by tortoises, followed by livestock production, coffee, and abandoned land.

2. *Which habitat structural features influence tortoise density most strongly?* We measured 12 variables related to the availability of food, shade, and ease of movement, to determine which had the strongest impacts on tortoise density. We predicted that tortoises would prefer habitat characteristics closely related to food availability.

Methods

Study Site

Santa Cruz Island is an extinct volcano in the centre of the Galapagos Archipelago, located approximately 1000 km from mainland Ecuador. There are three main vegetation zones in the Galapagos, the arid lowlands, the transition zone, and the humid highlands, the latter receives the most rainfall and is consistently productive (Wiggins and Porter 1971; McMullen 1999). Agricultural practices began in the humid highlands of Santa Cruz Island in the early 1900s and land clearing intensified mostly in the 1960s-70s, as more Ecuadorians moved from the mainland following government incentives to settle and cultivate the island (Trueman et al. 2013). The National Park was established in 1959 and the Galapagos special law, created in 1998, now restricts further settlement from the mainland and limits who can live on Galapagos (Lu et al. 2013). Over 88% of the humid highlands have been converted to support agriculture on Santa Cruz Island (Watson et al. 2010), however, now, with the establishment of the National Park borders and a limit on migration, farming has not expanded further.

The highlands supports three main livelihoods: cattle ranching, crop production, and tourism (Laso et al. 2020). The agricultural area has developed into a complex matrix of various land-use types, that includes pastoral areas for cattle and horses, annual crops (e.g., tomatoes, watermelons, corn), permanent crops (e.g., coffee, banana, pineapple), abandoned land, and tourism (Laso et al. 2020). Since the 1960s, the tourism industry has grown steadily and now brings over 200,000 visitors each year, making tourism the backbone of the local economy in the Galapagos (Epler 2007; Dirección del Parque Nacional Galápagos and Observatorio de Turismo de Galápagos. 2020). The rise in tourism has led some landholders to abandon productive land for more lucrative options in the tourism sector, predominantly in the township (Sampedro et al. 2018; Benitez-Capistros et al. 2019). A few other farmers have encouraged tourism in the highlands by re-purposing part of their farms, mostly for accommodation, or to attract tourists who pay to see giant tortoises roam their land in a semi-natural setting (Benitez-Capistros et al. 2016). Sections of abandoned land are now interspersed throughout the agricultural area and are mostly overgrown with invasive species that spill over into the neighbouring farms.

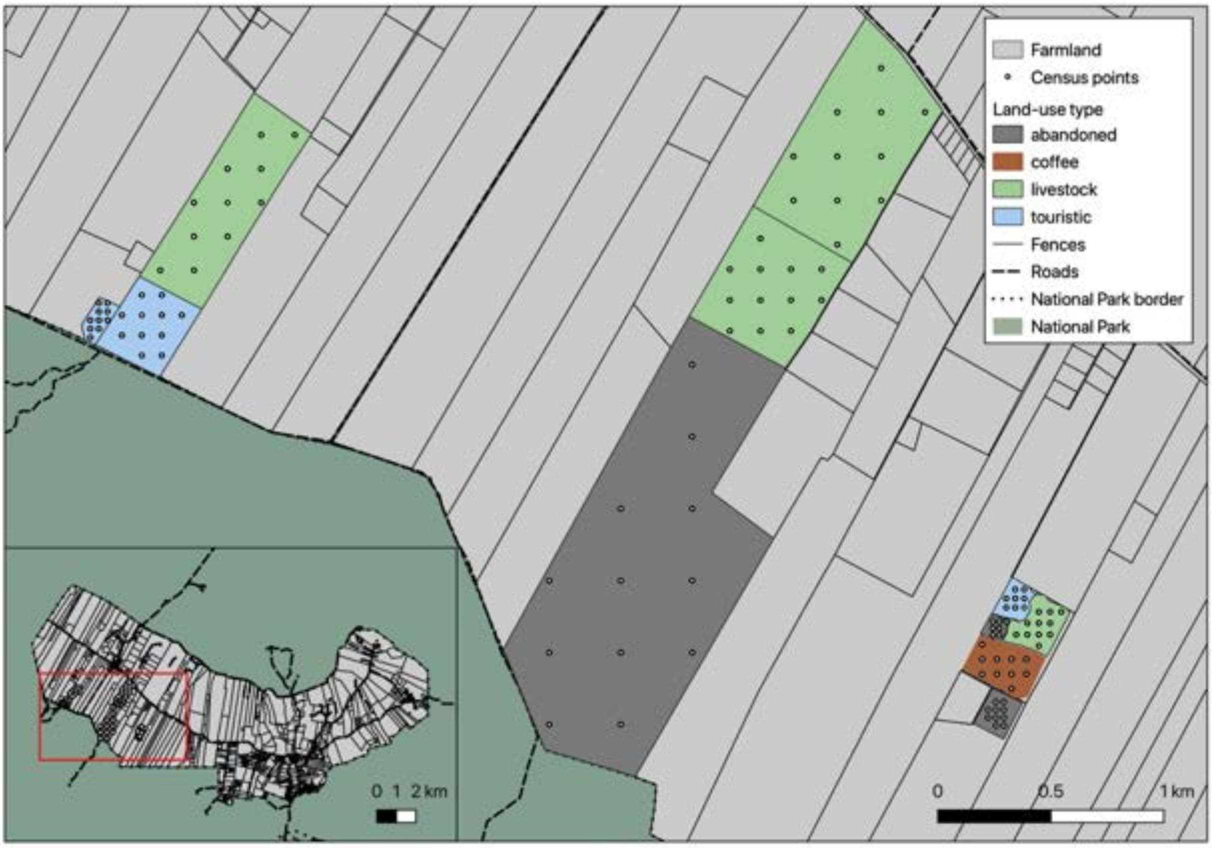

Figure 4.1. View of the western agricultural area in the highlands of Santa Cruz Island, Galapagos [red rectangle on inset of entire agricultural area] where a monthly giant tortoise survey took place. Small circles depict the location of the 108 survey points and their distribution in different land-use types on three different properties.

Measuring tortoise density

To describe patterns of tortoise density in agricultural areas, we performed a monthly survey on three properties in the south-western agricultural area of the highlands of Santa Cruz Island from October 2018 to December 2020. We were unable to conduct a survey in July 2019 and March, April, May and November 2020, so we conducted a total of 23 monthly surveys over the study period (15 surveys in the dry season and 8 surveys in the wet season). Each property had a mix of land-use types that included either coffee production, livestock production, tourism or abandoned land (Figure 4.1). Vegetation density, and tortoise detectability, varied by land-use type, so to enable distance sampling and estimates that accounted for differences in tortoise detectability among survey points, we designed their placement using 'Distance' software (Thomas et al. 2010). For each land-use type in each farm, we allocated 7-12 survey points with equidistant spacing, ranging between 25 – 300 m apart, depending on the size of the area, for a total of 108 survey points (Table 4.1). In the field, each survey point was located using a GPS and marked with flagging tape. We revisited each point on foot and recorded the presence of any tortoises within the radius around that point (i.e., a radius of 15m, 20m or 25m depending on size of the land-use area, Table 4.1) so density could be calculated for a known area. Surveys were conducted by field technicians towards the end of each month in the morning between the hours of 7am to 12pm and typically took three days to complete each census of 108 points across the three properties. Observers would scan each point for tortoises for a few minutes and when any tortoises (either males, females, or juveniles) were present within this radius, the distance from the centre of the point to the tortoise was measured with a digital rangefinder (Nikon Forestry Pro) to use to estimate tortoise detection probability. To account for differences in tortoise abundance that may arise from variation in detectability of tortoises, we used the ‘Distance’ package in R Studio v. 1.3.1073 (Miller et al. 2019; RStudio Team 2019) to calculate the probability of detecting a tortoise for each land-use type. Our detection functions were fit with either a half-normal or hazard rate distribution, depending on the land-use type and where possible the different plot sizes within each land-use type (see Supplementary Table 4.1, and Supplementary Figures 4.1 - 4.5 for details).

Table 4.1. An overview of the distribution of survey points by land-use type, and the total area sampled, for each land-use type of giant tortoise sampling on Santa Cruz Island, Galapagos.

Land-use type	**Number of survey points**	**Combined maximum sample area of survey points (m^2)**
Abandoned	28	33615
Coffee	10	19635
Livestock	43	76655
Touristic	27	35500

We examined differences in tortoise selection of habitat structure and land-use type during the dry season. As tortoises are seasonal migrants, they reach their highest density in the agricultural area during the dry season, because resources are limited in the more arid lowlands (Blake et al. 2013; Yackulic et al. 2017). Although some tortoises remain in the agricultural area during the wet season, after a surge in lowlands plant growth (Pike et al. 2021), their numbers are much lower. Because of small sample sizes, low numbers make it difficult to make precise estimates of abundance in relation to habitat and land-use type in the wet season. Broadly, however, patterns of tortoise abundance appeared similar in the dry and wet seasons, thus, we chose to focus on the dry season (Supplementary Figure 4.6).

Measuring habitat structure

Plant communities in the agricultural area typically vary by land-use type, creating a structurally diverse vegetation community (Guézou et al. 2010; Laso et al. 2020). Livestock areas often include a mix of cultivated and naturally germinated grasses and herbs, interspersed with fruit trees, often *Cirtus spp.* or guava *Psidium guajava* (Laso et al., 2020). Abandoned land typically includes invasive and naturalised species of grasses, herbs, shrubs, and trees (e.g., *P. guajava*, *Rubus niveus*, *Cedrela odorata*, *Zygsigum jambos*) that grow aggressively in a mixed forest. Coffee plantations mostly grow *Coffea arabica* or *C. canefora* (robusta) varieties as shade crops with other trees, e.g. *Cirtus spp.* or cedar *C. odorata (*Laso et al., 2020), and touristic land has well-manicured grazing lawns of grass and herbs with patches of shrubs and native and introduced trees for shade. Santa Cruz tortoises are diet generalists (Blake et al. 2021b), and the structure of these plant communities is likely to impact food availability, thermal resources and tortoise movement more broadly, and influencing the number of tortoises likely to use an area. To better understand the relationship between habitat structure and tortoise density, we collected data on habitat structural composition in the agricultural area. At each survey point, 12 vegetation structural characteristics were estimated in 10-m radius circular plots. Within each circular plot, the presence or absence of a pond, the percent cover of ground vegetation, mean height of ground cover, number of shrubs, mean shrub height, percent coverage of shrubs, number of trees in three height categories (1-4, 4-8 and >8 m), percent projected canopy cover, number of trees bearing fruit, and an estimate of the extent of fruit fall (1 to 10 fruits = low extent, 11 to 20 fruits = medium extent, and > 20 fruits = high extent).

Analysis

To quantify differences in tortoise density among land-use types, we used a negative binomial, zero-inflated regression model for count data *via* maximum likelihood from the 'countreg' package (Zeileis and Kleiber 2020). Given that tortoise detectability varied among land use types and, thus, survey points, we standardised our results by using both survey point area, and detectability, as offsets in our models. We modelled total tortoise abundance for the dry season for each survey point as the response variable, and land-use type as the explanatory variable (n = 108 survey points). As our models are based on total tortoise abundance for the dry season per *survey point*, we have also included post-hoc estimates of mean dry season density per hectare throughout the results so that these estimates are also more easily compared to other studies.

To determine the relationship between tortoise density and habitat structure, we took a two-step approach. First, we used boosted regression trees (BRT) as a variable selection method to measure the relative influence of each of the 12 habitat variables, to determine which variables were appropriate candidates for further modelling. Using BRT from the 'dismo ' package (Hijmans et al. 2020), we identified variables that consistently showed greater influence on tortoise density than expected by chance, and used only those variables in our next step, which assessed the direction and strength of their relationship with tortoise density. Our BRTs included a tree complexity of five, to allow for up to five interactions, a bagging fraction of 0.5 (i.e., 50% of the training data were discarded to avoid overfitting), and a learning rate of 0.0025 (smaller relative learning rates are preferred, to shrink the contribution of each tree as it is added sequentially to the model). We used these parameters for the BRT as this combination of learning rate and tree complexity provided enough trees (close to 1000) without overfitting (Elith et al. 2008).

We then constructed models with combinations of the habitat variables identified in our BRTs as having the most influence on tortoise density and assessed which model had the greatest power in predicting variation in tortoise density, using Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Burnham and Anderson, 2002). All models followed the same structure as modelled previously for land-use type: a negative binomial zero-inflated regression, with standardised area and detection probability as an offset. We checked for collinearity among model terms using the 'car' package (Fox and Weisberg 2019) and inspected model residuals for model fit. We then selected the most parsimonious model with the best improvement in AIC_c value, compared to our null model.

Results

How did tortoise density differ among land-use types?

Tortoise density was strongly related to land-use type. Over the sampling period, abandoned land had the lowest total tortoise density per point of 1.8 tortoises (scaled up to a mean of 3.9 tortoises per hectare per survey, 95% CI 2.1 to 7.0) compared to all other land-use types (Figure 4.2). Compared to abandoned land, tortoise density was 1.6 times greater in coffee (scaled up to a mean of 6.0 tortoises per hectare per survey, 95% CI 2.5 to 14.2), 1.3 greater in livestock (scaled up to a mean of 5.0 tortoises per hectare per survey, 95% CI 2.6 to 9.8), and 2.8 times greater in touristic land (scaled up to a mean of 10.8 tortoises per hectare per survey, 95% CI 5.4 to 21.7; Figure 4.2, panel A); however, only the differences between abandoned land and touristic land were statistically significant (Supplementary Table 4.2). The zero-inflation component of our model identified livestock as having a significantly higher probability of being zero-inflated than the other land-use types (Supplementary Table 4.2). This model also outperformed our null model by 27 AIC_c values.

Which habitat structure variables influenced tortoise density?

The BRTs identified six habitat structure variables as having a more relative influence on variation in tortoise density than expected by chance: percent ground and height of cover, number and height of shrubs, percent canopy cover, and number of trees between 1-4m (Supplementary Table 4.3). Modelling using these characteristics revealed that tortoise density was highest when there was more low ground cover, and fewer shrubs, and the best model outperformed the null model by 34 AIC_c values (Figure 4.2, see Supplementary Table 4.4 for a full set of candidate models). Our model predicted total density of tortoises was 2.3 ± 0.13 SE tortoises per survey point (scaled up to a mean of 4.9 tortoises per hectare per survey, 95% CI 3.8 to 6.3), and tortoise density increased by 0.8% with a unit increase in percent ground cover, decreased by 1.3% with a unit increase in the height of ground cover, and decreased by 1.3% with a unit increase in shrubs (Table 4.2). None of these habitat structure variables impacted the probability of zero-inflation, according to the zero-inflation component (Supplementary Table 4.5).

Table 4.2. Output from the best-ranking, most parsimonious model determining which habitat structure variables had a strong impact on giant tortoise density in the agricultural area of Santa Cruz Island, Galapagos. Model estimates have been back transformed and show the multiplicative impact of each habitat variable on total tortoise density per survey point in the agricultural area.

Term	Estimate	SE	z-value	P value	Low CI	High CI
Count model						
(Intercept)	2.322	0.128	6.566	0.000	1.806	2.986
Ground cover	1.008	0.006	1.275	0.202	0.996	1.021
Number of shrubs	0.987	0.006	-2.259	0.024	0.976	0.998
Height of ground cover	0.987	0.006	-2.303	0.021	0.975	0.998

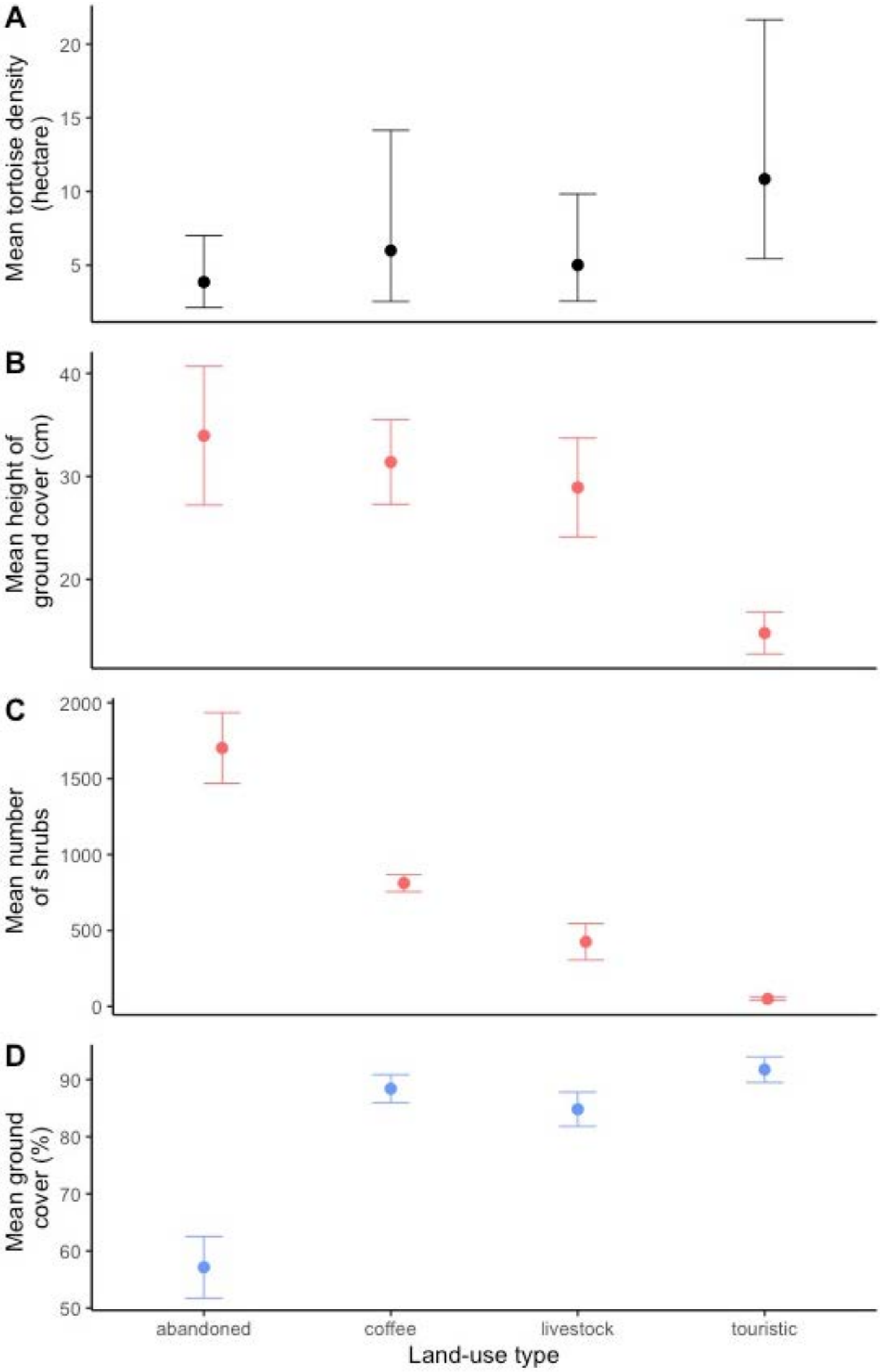
A
Mean tortoise density (hectare)
20
15
10
5
B
Mean height of ground cover (cm)
40
30
20
C
Mean number of shrubs
2000
1500
1000
500
0
D
Mean ground cover (%)
90
80
70
60
50
abandoned
coffee
livestock
touristic
Land-use type

Figure 4.2. A. Estimated mean dry season density per hectare (with 95% confidence intervals) for each land-use type, based on estimates from our model with land-use type and tortoise density (Supplementary Table 4.2). The following three panels (B,C,D) show, for each land-use type, the raw mean value scaled up to a hectare (± standard errors from raw data) of the habitat structure variables identified in our habitat structure model as most important. Tortoises preferred less of the features shown in red (panels B & C) and more of the features shown in blue (D). Note that land-use types characterised by each preferred habitat variable also had higher tortoise density, and those characterised by more non-preferred variables had fewer tortoises.

Discussion

We found strong evidence that land-use type and habitat structure impact giant tortoise density in agricultural landscapes on Santa Cruz Island, Galapagos. Abandoned land had consistently low tortoise density, and the worst combination of habitat features: less and taller ground cover, and more shrubs (Figure 4.2). In contrast, touristic farms had the highest tortoise density and the best combination of features to encourage tortoises: higher coverage of shorter vegetation, and fewer shrubs (Figure 4.2). Our results showed that tortoise density increased with the percent cover of ground vegetation: tortoises are generalist grazers (Rodhouse et al. 1975; Blake et al. 2021b) so a higher percentage coverage of ground vegetation is probably indicative of greater food availability. We also found tortoises occurred at higher densities in areas where ground vegetation was shorter, which is typical of many large, herbivorous grazers (Drescher et al. 2006; Hebblewhite et al. 2008; Raynor et al. 2016). The preference for short vegetation may occur because, as ground vegetation matures, the amount of indigestible fibre increases, while protein content declines, thus nutritional value is lower relative to younger, faster growing vegetation, termed the 'forage maturation hypothesis' (Fryxell 1991; Bergman et al. 2001). Large herbivores typically, preferentially feed on younger, more nutritious forage (Drescher et al. 2006; Hebblewhite et al. 2008).

Tortoises also preferred areas with low shrub density. Tortoises may avoid shrubs for two principal reasons. Firstly, due to competition for light and nutrients, shrub density is negatively correlated with ground vegetation cover, reducing the availability of ground vegetation (Eldridge et al. 2011), and secondly, as with taller vegetation of any type, a dense understory with many shrubs can impede tortoise movement (Gibbs et al. 2014). Abandoned land is typically characterised by many invasive blackberry shrubs (*Rubus niveus*) which grow in thick, spiny masses. In such areas, tortoises were consistently absent. However, in areas with only a few shrubs, which were native (e.g. *Chiococca alba*), and have a less dense growth form, tortoises occurred at times (KP personal observation), likely seeking shade and cover from high wind and rain (Rodhouse et al. 1975).

While land-use type clearly had a strong overarching impact on tortoise density in the agricultural area, our results suggest that habitat structure could potentially be altered to modify tortoise distribution and abundance. The Galapagos highlands are already completely modified habitats and are not pristine, therefore changes to vegetation structure to better manage tortoises in these areas is not ethically questionable. Altering habitat features to encourage wildlife in agricultural areas has been used previously, for example, reducing tree density to encourage deer for game hunting, or planting wildflowers and native grains on farmland to increase wild pollinator diversity (Gallo and Pejchar 2016; Hardman et al. 2016). Furthermore, giant tortoises are ecosystem engineers, with the capacity to modify their own environments (Gibbs et al. 2010, 2014; Ellis-Soto et al. 2017; Hunter et al. 2021). For example, the very high density of giant tortoises (*Geochelone gigantea*) on Aldraba, which are ecologically similar to Galapagos tortoises, is linked to the promotion and maintenance of 'tortoise turf', which are areas of low cropped grasses and sedges with little woody vegetation, preferred by tortoises (Hnatiuk et al. 1976a). Similarly, Galapagos tortoises using livestock areas may also contribute to the maintenance of pastural areas by promoting grazing lawns (Hunter et al. 2021). It is possible, therefore, that tortoises are currently influencing habitat structure in a way that is potentially beneficial to farmers, and assisting the process by modifying vegetation structure in areas where tortoises have lower density (such as abandoned land) could promote this feedback loop. We recognise however, that the ecological services of tortoises may not always align with the needs of farmers, such as in maintaining an area for crops.

Not all land-use types are equally compatible with land sharing between resource production and wildlife conservation. Here, we found repurposed farmland designed to support tortoises for tourism is highly compatible with tortoise conservation, and is used the most by tortoises. Historical density of tortoises across the Galapagos is estimated at 2.5 tortoises per hectare of suitable habitat (Gibbs and Goldspiel 2021), however, touristic land appears to attract roughly 11 tortoises per hectare in the dry season, and is clearly favoured by tortoises. Landowners derive significant income from tourism and facilitate tortoise use of their land, however there are currently only a few farms on Santa Cruz that have this type of operation. There may be potential for more landholders to diversify their income by repurposing sections of their farms for tourism, and, indeed, social research has shown this is desirable for many landholders in

Galapagos (Benitez-Capistros et al. 2018, 2019). However, questions remain over the economic cost-to-benefit ratio of transforming productive land for tourism, how income from tortoise viewing compares to traditional farming, and how to provide the infrastructure and expertise required to make this transformation (Benitez-Capistros et al. 2018, 2019). Market saturation and local competition may also influence the viability of the tortoise viewing option for landholders, reducing its usefulness as a tortoise management option. Additionally, the impact of these areas on stress and wellbeing of tortoises is unknown and requires further research. Regardless, the success of touristic farms demonstrate that farmland can be altered to successfully support giant tortoises at higher densities, although it may be at the expense of food production in some areas, leading to more of a land-sparing and less of a land-sharing outcome.

Coffee had the second highest density of tortoises of the four land-use types, so, contrary to our predictions, the coffee plantation was regularly used by tortoises. The coffee plantation was characterised by some of the habitat features preferred by tortoises, such as a high percentage ground cover of vegetation. There were many shrubs in the coffee plantation, which normally deters tortoises, but these were mostly coffee shrubs planted in wide rows, that do not impede tortoise movement (KP personal observation), or reduce percent ground cover, unlike invasive shrubs (Figure 4.2). There appears, therefore, to be important grazing resources for tortoises in coffee plantations, and this land-use type could have potential for land sharing. The compatibility of tortoises and coffee plantations has not yet been well researched, to our knowledge, and would benefit from further investigation, especially determining the costs and benefits to tortoises and coffee producers of tortoise use of these crops.

Livestock areas had the third highest tortoise density in our study, and supported twice the density of tortoises in the dry season than historical estimates (5 tortoises per hectare vs 2.5 tortoises). Livestock areas are designed to suit grazers, so this land-use type is generally suitable for grazing tortoises. Indeed, there is evidence to suggest giant tortoise herbivory may even improve productivity of herbaceous vegetation, especially relative to grazing by introduced herbivores, such as goats (Bastille-Rousseau et al. 2017a). Socioeconomic research has shown that cattle farmers are more tolerant of tortoises than are crop farmers, and perceive tortoises as less of a threat to their enterprises. Together, these factors make livestock production more compatible than cropping for land sharing with tortoises (Benitez-Capistros et al. 2018). At the tortoises' current low population level (Cayot et al. 2017a), significant competition between tortoises and cattle for resources has not been a major concern, however, if circumstances change and tortoise density on farms increases, as is possible given their population is slowly increasing (Tapia A. et al., 2021), or resource availability decreases (e.g., *via* climate change), this relationship may become less salubrious for farmers. In the semi-arid grasslands of the African Sahel, high cattle density is associated with low density of the African spurred tortoise (*Centrochelys sulcata*), another large grazing tortoise (Petrozzi et al. 2018). It is unclear, however if the negative association between cattle and tortoise density is a result of direct competition, habitat loss or poaching and hunting of tortoises (Petrozzi et al. 2018), regardless, the density of tortoises and cattle in Galapagos should be closely monitored to mitigate potential issues. Additionally, sharing land with livestock may cause other issues for tortoises, for example, exposure to potentially harmful agricultural chemicals, or development of antibiotic resistance (Nieto-Claudin et al. 2019, 2021). At present, the humid highlands remain a critical habitat for tortoises during the dry season, and future management by private landholders, and the Galapagos National Park, will need to consider land sharing with tortoises.

Abandoned land supported the fewest tortoises and is also unproductive for farmers. Currently, abandoned land makes up 22% of the agricultural area of Santa Cruz, and is a problem for both agriculturalists and the National Park, because it acts like a reservoir for highly invasive species which are difficult to manage once they spill over to farms and protected areas (Khatun 2018; Laso et al. 2020). This issue can then become compounded when invasive species established in the National Park and can also re-enter agricultural land. More generally, abandoned agricultural land needs to be managed to provide suitable habitat for wildlife (Benayas and Bullock 2015; Zakkak et al. 2015). In Europe, abandoned agricultural land is characterised by fewer bird species compared to traditional rural landscapes, and is, therefore, recognised as a significant environmental threat (Zakkak et al. 2015). Clearing invasive plants from abandoned land is typically very expensive, so such areas remain unmanaged (Khatun 2018; Laso et al. 2020). If incentives, policies, and awareness campaigns were introduced in the Galapagos to rehabilitate abandoned land to make it productive of livestock or crops, our results suggest that these areas could potentially both support more tortoises, and confer more financial benefits to landholders, in addition to reducing reservoirs of invasive species.

We have identified some of the key factors that influence tortoise density in the agricultural area of Santa Cruz Island, although there are some caveats to our conclusions. We included a variety of habitat variables that we considered most relevant to tortoises, but we omitted a few that are also likely to be important. For example, tortoises use wallows, and thus ponds are important to tortoise distribution and resource use (Ellis-Soto 2021). Our method was too coarse to detect an impact of ponds on tortoise density, as ponds mostly fell outside our survey points. We were also limited in our ability to survey all farm types, as for instance, we had no samples in annual crops (corn, tomatoes), and only one in a permanent crop: coffee, and in only a single farm. Thus, our results may not be representative of coffee farms more generally, nor all crops. Furthermore, proximity to roads, as well as traffic levels, and types of fences, may also be important to consider in future evaluations of habitat suitability (Beaudry et al. 2008; Blake et al. 2015b; Peaden et al. 2017). Lastly, we prioritised an examination of the preferences of tortoises, a critically endangered keystone species, however, we acknowledge their preferences may not be a good measure of habitat suitability for other native species using farmland. Ideally, management should consider land sharing improvements based on preferences of other species (e.g., see Geladi et al., 2021 for birds in Galapagos), in conjunction with our findings for tortoises.

Conclusions

Understanding the drivers of wildlife distributions in agricultural lands allows us to make informed decisions on modifications to promote land sharing with vulnerable wildlife. For critically endangered Galapagos giant tortoises, we have identified several preferred habitat features, and determined how they relate to land-use type. This information may be utilised by landholders, agriculture policy makers, and the Galapagos National Park Directorate when designing strategies to make agricultural areas more tortoise-friendly, without necessarily compromising land productivity. Specifically, reducing dense shrub cover and promoting cover of shorter ground vegetation, especially in abandoned land, would likely support tortoises in farmland areas. We have highlighted here that on agricultural land, evidence-based management is still required to support tortoises, and that there is potential to benefit both food production and tortoise conservation through this process. Overall, our results have demonstrated the importance of measuring wildlife preferences within human-dominated areas as a first step towards balancing the needs of biodiversity conservation and human-enterprise.

Chapter Five: Activity patterns in transformed landscapes: Land use, temperature, and vegetation impacts habitat quality of farmland for migratory giant Galapagos tortoises

Abstract

Many giant Galapagos tortoises make seasonal migrations from arid lowlands in the wet season, to humid highlands in the dry season. However, at least 88% of the habitat for critically endangered Western Santa Cruz giant tortoises (*Chelonoidis porteri*) in the humid highlands, is now used for agriculture. To understand the impact of agricultural land use on tortoise activity patterns, we conducted 242 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 and touristic land. Generally, tortoises rested for longer when they were cooler. Time eating was increased by the density and proportion of vegetation, while 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 behaviour of tortoises in their dry season range. Wildlife managers 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.

Introduction

Globally, long distance migrations and migratory species are under unprecedented threat from anthropogenic change (Wilcove and Wikelski 2008; Harris et al. 2009; Shaw 2016). Compared to residents, migrants acquire the resources for growth, survival, or reproduction from multiple locations (Shaw 2016; Bastille-Rousseau et al. 2017b). Often, one or more of the habitats traversed by migratory animals have been modified by humans, exposing them to multiple threats that can jeopardize migration, and lead to negative consequences for their activity and survival (Wilcove and Wikelski 2008; Harris et al. 2009). Land modification can fragment habitat, which decreases connectivity within migratory networks. In Tanzania, the migration of Serengeti wildebeest is vulnerable to road development projects that threaten to fragment habitat and create a migration barrier that could cause the population to decline by roughly 30% (Holdo et al. 2011). Additionally, degraded habitats may increase the time migrants need to obtain sufficient energy reserves to enable successful migration, or cause them to forfeit migration (Domer et al., 2021; Xu et al., 2021). When migratory species use human-modified land within their migratory network, evaluating the impact of these areas is important to determine ways to support the integrity of migrations.

Migratory species juggle complex energy budgets to ensure the success of their journey (Hebblewhite et al. 2008), and using human-modified habitats can have both positive and negative impacts on migrants. In China, the western population of white-naped cranes (*Atigone vipio*), relies on wetlands as important stopovers to re-fuel along their migratory route to their wintering grounds in the Yangtze River Basin. However, landcover change and loss of wetlands to development has caused the cranes to shift their migration to a less stable route, and is likely to continue the decline of the population (Jia et al. 2021). Some species, however, can also benefit from human-modified areas, if they provide more food or other benefits compared to natural areas. For example, isotope signatures have revealed that greater snow geese (*Chen caerulescens*) feeding on corn crops in Canada have more fat deposits, and reach migration condition sooner than geese feeding in non-agricultural areas (Gauthier et al. 2005). Similarly, migratory Dunlin (*Calidris alpina*) prefer to spend the night in rice fields during their winter range in California, as these agricultural areas provide better thermal conditions, less wind and less predators than nearby wetlands (Barbaree et al. 2015). The quality of the anthropogenic habitats used by migratory species in their migratory networks can determine how well these habitats support migrants, both during their journey and at their destinations (Johnson et al. 2006; Yackulic et al. 2017).

Migration can be very energetically expensive, and for their journey to be worthwhile, migrants need to maximise the benefits at their destination to offset the costs of migration (Bastille-Rousseau et al. 2017b; Yackulic et al. 2017). In higher quality habitats, migrants 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, including within human-modified land, can be useful to determine the quality of these areas for migratory species. 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 elucidate their energy use strategies between the two habitat types and the quality of these habitats (Mekonnen et al. 2017). Although Bale monkeys are not migratory, the same process of measuring the balance of activities that expend or acquire energy can provide similar insights for migratory species during their range residency, and ultimately help understand the implications of using human-modified land with varying habitat quality.

Critically endangered Western Santa Cruz Galapagos tortoises, that occur on Santa Cruz Island, are a partially migratory species that regularly interacts with human-modified land. During the wet season, the lowlands offer a surge in plant growth with high nutrition, as well as good nesting habitat (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). The humid highlands of Santa Cruz Island, however, are also now highly modified habitats, as at least 88% of this area has been converted to agricultural land (Watson et al. 2010). Migratory western Santa Cruz tortoises, therefore, spend the dry season in a matrix of different farm types (Watson et al. 2010; Pike et al. 2021, 2022b). Migratory tortoises remain in farms for long periods (five months on average), and some skip migration and remain in the humid highlands (Pike et al. 2021). These seasonal vegetation dynamics contribute heavily to the migratory cycle of adult tortoises, and questions remain about the impact of different farm types on tortoise behaviour. Furthermore, giant tortoises are essential ecosystem engineers, as tortoises move through the landscape they trample vegetation and 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). Thus, maintaining their movement patterns has important implications for wider ecosystem health and stability (Gibbs et al. 2010; Hunter et al. 2013, 2021).

To better support the integrity of the migratory cycle of giant tortoises, we need to understand the impact of agricultural land on tortoise activity during their time in human-modified habitats. Our aims here were to first quantify the activity patterns of western Santa Cruz giant tortoises during their time in the agricultural area, examining time spent eating, walking, and resting, and second, to determine the intrinsic and extrinsic factors that correlated with the time spent engaging in these behaviours. We observed tortoise behaviour while in the agricultural area, and evaluated 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 sought to address the following research question:

What factors influence the time spent by tortoises eating, resting and walking whilst on farms ? We anticipated that tortoises would eat more in areas with characteristics indicating higher food availability, that resting behaviour would be influenced most strongly by temperature, 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 (McMullen 1999). On Santa Cruz island, the majority of the humid highlands have been cleared for agriculture, and now less than 12% of native humid highland habitat remains (Watson et al. 2010). The agricultural sector on Santa Cruz services the local population of approximately 18,000 inhabitants and supplements the large tourism sector. Pre-pandemic, more than 270 000 tourists were visiting 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, and has also impacted the agricultural sector in two main ways. First, the rise in tourism has led some agriculturalists to leave farming for more profitable jobs in tourism (Sampedro et al. 2018), resulting 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, and encompass many different vegetation communities. 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, 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.

Behavioural observations

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). Between March to May 2019 we collected a total 242 behavioural 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. 2021b). During the wet season, tortoise activity is unimodal including 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 behaviour 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 would begin a timed activity focal observation (Altmann 1974) from 5-15m away, using binoculars, during which the duration and type of all activities were recorded. Before a focal observation began, there was a five-minute acclimation period 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 five minutes, the observation was abandoned, and another tortoise was located. During the focal observation, all behaviours of the focal individual, including eating, resting, walking, mating, and interactions with conspecifics or heterospecifics (see Supplementary Table 5.1 for full list of behaviours) were recorded for 30 minutes, using a pre-programed ethogram developed using BORIS software^{TM} on a Samsung TabA digital tablet (Friard and Gamba 2016). Behaviours lasting for a period of time were called 'state' behaviours (e.g., walking) and their start and end time were recorded, whereas 'point' behaviours were instantaneous (e.g., grunt) and only an occurrence time was recorded.

We also recorded fine-scale habitat characteristics at five-minute intervals, starting at minute 0 throughout the 30-minute observation period. Fine-scale habitat characteristics were estimated for the 1 m^2 immediately in front of the tortoise, and included the percent cover of live vegetation, density of vegetation (as very low density, low density, high density and very high density; see Supplementary Figure 5.1), and the mean height of ground vegetation (to nearest 5 cm). After the observation, the tortoise's curved carapace length was measured with a flexible measuring tape, and their sex (male, female, or undetermined) 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 colour 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 sampling regimes (n= 26 tortoises).

Thermal images

During each observation, two thermal images were taken of the tortoise using a handheld Flir2 Thermal camera. 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 (± 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 chose to focus on the balance between time spent eating, walking, and resting, as these behaviours likely relate most directly to energy acquisition and energy expenditure, from our repertoire of behaviours. To determine the impact of intrinsic and extrinsic factors on the activities of giant tortoises in the agricultural area, 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 5.2 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. We considered the most biologically relevant model with the lowest AIC_c score to be the model with the most explanatory power for tortoise activity on farms (Richards 2005; Symonds and Moussalli 2011). 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 behaviour on farms for the combined activity analysis, although we could use most data when analysing activities individually (below).

The influence of vegetation on tortoise activity on farms

Diet studies of Santa Cruz giant tortoises have demonstrated that tortoises eat a wide range of vegetation including grasses, forbs, and woody shrubs of native and introduced plant species in the highlands (Blake et al. 2015a, 2021b; Ellis-Soto et al. 2017). Given giant tortoises are generalist herbivores, and there is an a abundance of plant species eaten by tortoises in the highlands, we chose to focus on vegetation characteristics that are likely to influence their behaviour. To adequately determine the influence of vegetation on tortoise activity (for example, do they switch from walking to eating when they encounter a suitable foraging patch?) it was necessary to frequently sample vegetation characteristics very close to the tortoise. We recorded ground vegetation characteristics at regular five-minute intervals during the 30-minute focal observation (to give six measurements of vegetation per observation). At each five-minute interval we estimated the characteristics of a one-meter-diameter patch of vegetation directly in front of the tortoise, recording mean height of the vegetation (cm), density of the vegetation, and the percent live vegetation within the quadrat. We then examined tortoise behaviour in relation to vegetation characteristics as a binomial response for each behavioural category (walking, eating, resting) separately. We modelled each behaviour 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 determine the influence of vegetation characteristics on tortoise behaviour, we used generalised linear mixed models with a binomial distribution and logit link function from 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-minute intervals within a 30-minute period) and between observations (for the individuals who were observed more than once). We constructed separate models for each behaviour (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 5.3-5.5 for full sets of models). We had a total of 892 records of vegetation characteristics recorded for behaviours of 168 individuals, as not all observations also recorded vegetation characteristics. 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

While in the agricultural area we observed tortoises conducting a range of behaviours including: eating, drinking, walking, resting, copulating, fighting, pursuing conspecifics, defending themselves, being vigilant, and wallowing. The dominant tortoise behaviour 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?

We found that land-use type and temperature had the strongest impact on the balance 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 (Figure 5.1). Tortoises also tended to rest more when they were cooler, as tortoises with higher carapace temperatures rested 4% less than did tortoises with cooler carapaces, however, this difference was not statistically significant (p=0.08, Table 5.1). The proportion of time tortoises spent walking was not statistically influenced by either land-use type, or temperature (Table 5.1).

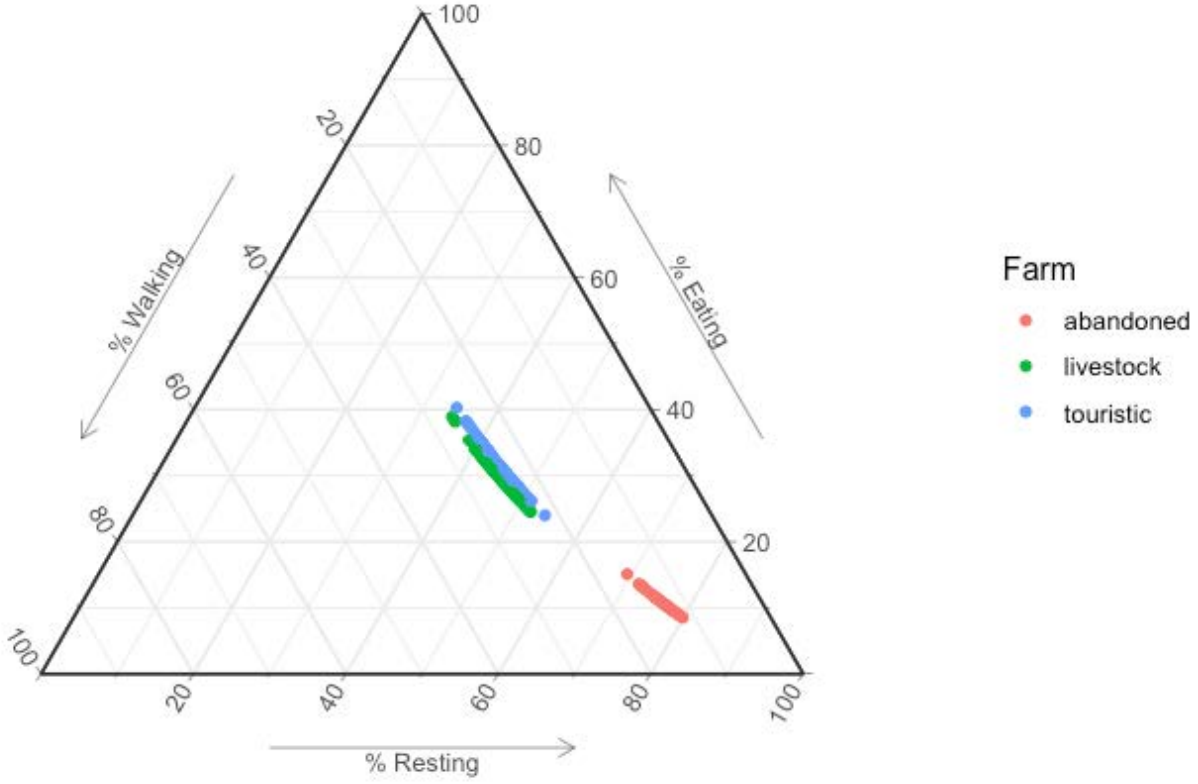

Figure 5.1. Tortoises on farms in Santa Cruz Island, Galapagos spend higher proportions of time resting when in abandoned land. Figure depicts the predicted values from the Dirichlet regression's top model from Table 5.1, n= 188).

Table 5.1. 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. The top model shows time eating was impacted by land-use type, with abandoned land as 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.

Beta-Coefficients for proportion of time eating

Term	Estimate	SE	z value	p value	Low CI	High CI
(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
Mean carapace temperature	0.010	0.019	0.526	0.599	-0.027	0.046

Beta-Coefficients for proportion of time walking

Term	Estimate	SE	z value	p value	Low CI	High CI
(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
Mean carapace temperature	-0.008	0.019	0.422	0.673	-0.046	0.03

Beta-Coefficients for proportion of time resting

Term	Estimate	SE	z value	p value	Low CI	High CI
(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
Mean carapace temperature	-0.037	0.021	1.728	0.084	-0.079	0.005

We found that 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 5.3). In three of the four vegetation density categories, an increase in vegetation cover also increased the probability of a tortoise eating, however the strength of this effect depended on the category of vegetation density (Table 5.2). 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 density, and our best model outperformed the null model by 13.4 AIC_c values (Supplementary Table 5.4) . We found that tortoises were less likely to walk in taller, and denser vegetation. We found that as vegetation height increased, tortoises were less likely to walk (decrease in the probability of walking by 8% with each 1 cm increase in vegetation height). Lastly, we found the probability of a tortoise 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 behaviour, as it only just outperformed the null model (improvement in $AIC_c = 3.5$ (Supplementary Table 5.5), suggesting vegetation density did not have a strong influence on resting behaviour, compared to other sources of variability we did not measure.

Table 5.2. 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 behaviour 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

The ways in which giant tortoises spend their time once they enter farmland in the humid highlands is shaped by several key factors. Here we found that both land-use type, and vegetation characteristics best explained tortoise eating behaviour. In touristic land, tortoises ate for significantly longer periods than did tortoises in abandoned land. Tortoises were also more likely to eat in areas with a high proportion of vegetation cover, and high vegetation density. Most of the ground vegetation in the highlands is eaten by tortoises, however, we still observed some selection of vegetation based on their characteristics. This suggests these large generalist herbivores are considering the costs and benefits of where they forage within the agricultural landscape, by selecting areas in which they obtain more calories per mouthful (Pyke 1984; Bergman et al. 2001). Tortoise eating behaviour, similar to other large herbivores, is consistent with the forage maturation hypothesis, which suggests that grazers will preference forage with higher ratios of digestible content to fibre (Fryxell 1991; Hebblewhite et al. 2008). Given giant tortoises have much lower metabolic demands than mammalian herbivores, the result that tortoises are selective about forage location might seem surprising. However, for giant tortoises on Aldabra (*Aldabrachelys gigantea*), an ecological analogue to Galapagos tortoises, research on their energy assimilation efficiency shows that Aldabran tortoises can assimilate only 34.5% of the energy from their forage (Hamilton and Coe 1981). Thus, despite having lower metabolic demands relative to their mammalian counterparts, it is still likely to be beneficial for tortoises to be selective, foraging in higher quality habitats (i.e., easily digestible dense green pasture) as it is harder for them to assimilate the energy from vegetation (Franz et al. 2011).

As seasonal migrants, the tortoises' main motivator for migrating to the highlands during the dry season may be to allow them to exploit the lower quality (relative to the lowland's wet season growth) but higher quantity highland vegetation, as 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 show, once tortoises reach a certain size (~80kg) they have higher absolute metabolic demands and are more sensitive to variation in food density. In Aldabra, the giant tortoises that exploit coastal habitat during the rainy season can access more food, and also have higher reproductive outputs, compared to those inland (Swingland and Coe 1978). In the 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.

Interestingly, 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 apparently counterintuitive result is likely caused by instances when a tortoise is travelling along a road or path and is likely to switch to eating when it finds a vegetation patch with a relatively high proportion of vegetation of a desirable height, although the density of vegetation is low on an absolute scale. There are many paths and dirt roads that intersect the agriculture area, where fringing vegetation is cut periodically for maintenance (KP 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 (KP and peer observations). Similar results have been found for other large herbivores that move large distances. Asian elephants (*Elephas maximus*) for example, have also 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 behaviour 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 longer than did tortoises in livestock, and touristic areas. The reasons for resting more while in abandoned land are not well understood. Possibly, individuals in abandoned land cannot find much forage, and rest to conserve energy. Alternatively, it is possible they rest there for other reasons, for example to assimilate food acquired elsewhere. If they are indeed less able to access food resources there, individuals that use abandoned land may have to make up for the reduction in time spent eating, by remaining longer in the highlands, for example some individuals remained for more than a year (Pike et al. 2021). These 'carry-over effects' of habitat quality are well documented for other migratory species, such that individuals unable to assimilate sufficient resources before migration may delay migrating, or have poorer body condition (Norris and Taylor 2006; McKinnon et al. 2015; Bastille-Rousseau et al. 2018b). Further examination of the reasons for increased resting in abandoned land by Galapagos tortoises is required to determine the causes of this behaviour.

There was also some evidence that carapace temperature influenced resting behaviour because tortoises rested more at lower carapace temperatures. The humid highlands are considerably cooler than the lowlands throughout the year (Trueman and D'Ozouville 2010; Blake et al. 2013; Bastille-Rousseau and Wittemyer 2019). Most of the time, however, temperatures in the humid highlands span a range within which large tortoises can comfortably operate, without having to spend too much time behaviourally thermoregulating (Blake et al. 2021a). Because temperatures are cooler overall in the highlands, research has shown that individuals close to vegetation, or in dense shade, are more likely to experience temperatures below their thermal minimum (Blake et al. 2021a). Indeed, this scenario parallels results for giant tortoises on Aldabra that also face a tradeoff between time spent feeding and resting, when temperatures approach their thermal limits (Swingland and Frazier 1980). On Aldabra the inverse occurs, tortoises migrate to the warm coastal plains to exploit the seasonal vegetation, but on hotter days must stop foraging and seek out shade trees under which to rest under or risk death from overheating when temperatures approach their thermal maximum (Swingland and Frazier 1980).

While there are fewer temperature fluctuations in the highlands of Galapagos, the ability to thermoregulate remains an important consideration for tortoises (Blake et al. 2021a). Among land-use types, the resources available for thermoregulation were very different. Abandoned land, which is overgrown with invasive vegetation, is usually heavily shaded, and offers limited access to sunny areas, whereas 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. 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. Additionally, cooler temperatures also increase the time tortoises need to digest their food, and lower temperatures could potentially encourage them to rest more to aid digestion (Sadeghayobi et al. 2011). This also suggests tortoises may need to select for habitat components that not only offer ample foraging opportunities but also meet more complex thermoregulatory requirements. 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.

Influences on time spent walking

We found that vegetation characteristics had a moderate impact on tortoise walking behaviour while on farms. Our results showed that 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 behaviours we examined here, walking is likely to be the most energetically expensive. It is likely having to walk through tall and thick vegetation requires more energy than walking on short, cropped lawns or paths and roads with little vegetation. These results, combined, support the idea that tortoises are making movement decisions that minimise movement in more challenging terrain.

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 activity patterns, and consequently are likely to impact the energetic strategies of migratory individuals in their highland range. Our previous research showed that abandoned land supported the fewest tortoises and other land-use types were preferred over abandoned land (Pike et al. 2022b). Here we found that individuals using abandoned land were also eating less and resting 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 less suitable. In contrast, touristic land, although not abundant, is favoured by tortoises. Tortoises can move freely in and out of touristic land as fences are permeable (KP unpublished data), and those individuals utilizing this land-use type are also spending the most time eating and the least time resting of any land-use type. While this land-use type appears to be higher quality habitat for tortoises in the dry season, the impact of approaches from tourists on tortoise wellbeing or health, however, are still unknown and in need of investigation (manuscript in preparation). Livestock areas also have potential to support tortoises, allowing for more eating and less resting as compared to abandoned land, but our previous research (Pike et al. 2022b) showed tortoise density in livestock areas is relatively low. With slight modifications, the capacity of livestock areas to support giant tortoises could be increased, possibly by maintaining preferred grass heights and potentially increasing the thermal heterogeneity of habitat available to tortoises by adding some shade trees. Ideally, the viability of potential modifications would also be discussed with farmers, and research into the benefits for other livestock also conducted.

Limitations

While we have uncovered some of the dynamics of tortoise activity patterns in farmland, this comes with some caveats that limit the generality of these results. Firstly, while we have demonstrated there are important differences in tortoise behaviours among these land-use types, we recognise these are a subsample of the land-use types available in the agricultural area, and we encourage further examination of tortoise behaviour in relation to other land-use types, especially coffee and transitory crops, for a more complete picture. Secondly, our temporal window for observing tortoise behaviour only included the morning, as tortoises are active during the morning in both seasons (Rodhouse et al. 1975; Blake et al. 2021b). Other studies, however, have used high frequency accelerometers to broadly capture activity patterns of this species, and have found that, in the dry season, tortoises show a small secondary peak of activity in the afternoon (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 activity patterns (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

We have shown that land-use type, thermal characteristics, and properties of vegetation are important determinants of Galapagos tortoise activity patterns in the agricultural area. The differences in the activities of giant tortoises using different farm types during their migratory circuit, indicates that tortoises are likely choosing activity patterns that reduce energetic or opportunity costs to them by resting more when thermal conditions or habitat quality is poor, walking in easier-to-manoeuvre terrain, and foraging more when vegetation characteristics are favourable. Understanding some of the patterns in tortoise activity 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 timing of tortoise migration, body condition and ultimately fitness.

Chapter Six: General Discussion

Synthesis and future directions

One of the most important ways that agriculture reduces the area of natural land available to native species is through clearing of natural vegetation, either to make room for crops, or to encourage grassland for grazing species (Hooke et al. 2012). Around the world, approximately 5 billion hectares of natural ecosystems (roughly 38% of the global land surface) have been converted to cropland and pasture for grazing livestock (Food and Agriculture Organization of the United Nations 2020). After land conversion to agriculture takes place, often over thousands of years, it is difficult to imagine how these areas would look today in their unaltered state. In some cases, we are not even aware of the composition of original natural ecosystems, prior to agricultural conversion. Recent clearing, however, often leaves remnant vegetation, and these areas provide refuge for native species. In addition, native species can sometimes use or even benefit from agricultural land, either partially or completely fulfilling niche requirements (McIvor and Conover 1994; Gauthier et al. 2005; Goswami et al. 2014). The use of agricultural land by native species ranges from a conservation problem, in which native species do not obtain all they need, and are negatively affected, to a human-wildlife interaction problem, in which native species use agricultural areas, and cause damage or are a nuisance or danger to humans (Goswami et al. 2014; Shackelford et al. 2015; Kross et al. 2018; de la Torre et al. 2021). Thus, the conversion of native vegetation to agricultural land creates complex outcomes for both humans and native species.

On islands, because of limited space and often extensive habitat conversion, native species can be particularly strongly impacted by agriculture. For example, in the

Galapagos, the Santa Cruz highlands would once have been thickly vegetated with forests of giant daisy trees (*Scalesia pedunculata*), and Galapagos guava (*Psidium galapageium*), surrounded by native and endemic shrubs, herbs, ferns, epiphytes and mosses (McMullen 1999). Nowadays, the island's highlands are dominated by productive pastural lands characterised by native and introduced grasses and herbs that feed herds of cattle and horses (Laso et al. 2020). In addition, these fertile areas support crops of coffee, pineapples, bananas, corn, and many staples for the local community and large tourism sector (Laso et al. 2020). Given the giant tortoises' extraordinarily long lifespan (possibly up to 200 years: Gibbs & Goldspiel, 2021), there should be some individuals alive today that witnessed these changes taking place during their migration to the highlands for important resources.

The primary objective of my thesis was to improve our understanding of the ecology of tortoises using farms in the highlands, to provide information that could be used to balance tortoise habitat use with agricultural practice, to facilitate tortoise population recovery alongside sustainable management of farmer livelihoods. This research is the most comprehensive study to date, investigating how these land use changes influence giant tortoise habitat use, movement, behaviour, abundance, and temporal and spatial patterns of farm use in the highly modified humid highlands. Here, I synthesise the most salient and novel insights generated from this research, and their implications for the management of tortoises. I end with a discussion of priorities for future research, and lessons for wildlife conservation in agricultural areas more broadly.

Contributions to understanding tortoise farmland interactions

Before my study, research on tortoises in farms on the Galapagos Islands focussed on the social dimensions of the interaction between giant tortoises and farmers. Work done by Benitez-Capistros et al. (2018, 2019), demonstrated that a conflict was emerging between these groups, as the attitudes and perspectives of farmers towards tortoises using farmland had negative aspects, and highlighted that this interaction needed management. Information on the ecology of tortoises using farms, however, was lacking. At the conclusion of my research, we now have a much more detailed understanding of the impact of farmland use on critically endangered giant tortoises. Initially, there was a concern that some tortoises may be migrating to the highlands, but that they would encounter major barriers disrupting their migration (Blake et al. 2015b). In **Chapter 2**, I found that, broadly speaking, Eastern and Western tortoises on Santa Cruz have access to large areas of the humid highlands, and come and go, but tend to stay for prolonged periods in the dry season. **Chapter 3** demonstrated that once tortoises are within the humid highlands, low- and medium-traffic roads and most fences remain porous, and relatively short barriers to movement occur at a localised scale (< 100 m), especially when they encounter complex fences, particularly around crop farms. While in the agricultural area, tortoises are likely to interact with multiple land holders (**Chapter 2**) and distribute their time in multiple land-use types. The distribution of resources and structure of the habitat encountered by tortoises influence not just to their relative abundance (**Chapter 4**), but also their behaviour (**Chapter 5**).

Throughout my research, a strong link emerged between land-use type and tortoise relative density and behaviour, likely because habitat structure and resources are nested within land-use type. **Chapter 4** demonstrated that tortoises use farms with livestock, coffee, abandoned land, as well as touristic land. The movement data, from

Chapter 3, showed they also sometimes use remnant natural areas, or areas dedicated to other annual and permanent crops. Tortoise density in livestock farms was lower than in other areas, however, the extensive area of livestock farms means the total abundance of tortoises was greatest in this land-use type. Livestock farming is also the primary agricultural land-use type, and the largest land use by area in the highlands of Santa Cruz (Laso et al. 2020) making the availability of this habitat important for the wider tortoise population. When tortoises are in livestock areas, they tend to move slowly (**Chapter 3**) spend much of their time feeding on short vegetation (**Chapter 5**), consistent with the forage maturation hypothesis for optimisation of forage selection (Hebblewhite et al. 2008). However, when it comes to tortoise density, the much less common but high-quality habitat in touristic land attracts the highest density of tortoises. Tortoises in touristic farms have free access to ponds, an attractive resource (**Chapter 3**), and other habitat features are maintained to suit tortoises' preferences. For example, grass and herbs are mown regularly, promoting new growth. On touristic land, there are also fewer shrubs, and grounds are maintained to allow easy movement by walking tourists. The solitary animals, however, display more antagonist interactions with each other, and in response to approach from humans when in touristic land compared to other land-use types (unpublished data from **Chapter 5**).

Results from **Chapter 4** showed that coffee plantations appear to have important resources for tortoises, when access is possible (**Chapter 3** showed crops are the land use most likely to have 'complex fences' that have tightly spaced fence posts). Although my sample size was small (n = 1 coffee farm), my observation that tortoises use coffee farms agrees with results from **Chapter 3,** that showed many tortoise locations were recorded in crops over the six year tracking period, and coffee is the dominant crop (Laso et al. 2020). Thus, tortoises are occasionally using coffee farms.

One of the more surprising results from my work was that abandoned agricultural land appears to be the least favourable to tortoises. The tortoise movement data (**Chapter 3**) showed that overall tortoises tend to travel relatively further in abandoned land, rather than travel shorter distances as seen in pastural areas. This probably reflects tortoises attempting to limit their total time in abandoned land, the least favourable land-use type for tortoises (**Chapter 2**). In abandoned land they encounter heavily shaded areas, with a dense underbrush of invasive blackberry shrubs, that make it difficult to move and limit access to feeding on ground vegetation (**Chapter 4**). While in abandoned land, ectothermic tortoises experience cooler temperatures and spend more of their time resting overall than in touristic or livestock areas (**Chapter 5**).

Management implications and future research

The insights generated from my research are highly relevant to the management of tortoises in the agricultural area in Santa Cruz and potentially elsewhere on the Galapagos Islands. Since the work of Benitez Capistros et al. (2018), I am not aware of any significant management interventions to change the trajectory of the tortoise famer relationship away from a mild but emerging conflict. The majority of tortoises can move through the humid highlands and feed and rest relatively unimpeded, and most farmers are tolerant of tortoises and negative interactions with them, such as crop depredation, and tortoise harassment is limited (Benitez-Capistros et al. 2018). Additionally, both tortoises and farmers can potentially derive some benefits from their relationship. Tortoises clearly need to utilise farmland for access to abundant forage, ponds, and resting areas, but farmers can also potentially obtain economic and possibly ecological benefits from tortoise visits, as well. The few landholders who repurpose some of their land for touristic activities are engaging in a land-sparing approach. Although this form of land sparing does not increase food production, it is still a model from which farmers can benefit financially through ecotourism.

Another potential avenue where tortoises and farmers could benefit, from a land-sharing perspective, would be to invest further research into tortoise-friendly coffee growing schemes that improves the quality of tortoise habitat on coffee farms in exchange for a higher market value for the coffee product. My preliminary research indicates coffee farms have some of the vegetation characteristics that tortoises prefer and had a tortoise density that was higher than livestock areas, however, access to these areas is likely to be restricted because of complex fencing. This suggests that coffee farms, could potentially provide more habitat for tortoises and warrants further research into this interaction. Currently, however, there is still little known about the impact of encouraging tortoises to use coffee farms both for tortoises and farmers. To investigate the feasibility of developing a tortoise-friendly coffee scheme, future research could focus on collecting baseline data of tortoise density, activity patterns, and access to coffee farms more broadly. Data on the capacity of tortoises to damage coffee plants at different growth stages, and any other potential challenges to farmers would also need to be investigated. Following this, would be experimental trials to determine guidelines for best practice of creating improved habitat for tortoises alongside profitable coffee growing. If accreditation and guidelines were developed to make coffee farms more tortoise friendly, as long as it was not too expensive to engage in the scheme (Dietz et al., 2020), farmers following these regulations could potentially increase their revenue from coffee sold with a tortoise-friendly accreditation (similar to Rainforest Alliance or Roundtable on Sustainable Palm Oil products).

Less obvious benefits for farmers that engage in land sharing could also be derived from some of the ecosystem services for which tortoises, as ecosystem engineers, are known (Gibbs et al. 2010). Cattle farmers, for example, may also benefit from nutrient cycling and improvements in habitat quality provided by tortoises (Society et al. 1983; Blake et al. 2012; Bastille-Rousseau et al. 2017a). I found that giant tortoises prefer short, cropped ground cover, and areas with at least some trees, and pond access, and these habitat characteristics are also likely to benefit cattle, another large herbivore. However, it is still common to see some livestock areas overgrown with very tall and thick fields of elephant grass (*Pennisetum purpureum*), with little to no shade trees. Although I did not study the habitat preferences of cattle, I noticed that the overgrown areas tended to be avoided not just by tortoises but also by cattle. I would expect that if incentives were developed to improve this habitat for tortoises (e.g., cutting grass or planting grass species that do not grow so high, maintaining a low density of trees etc.), cattle would also find this habitat more favourable. Furthermore, there may be ecosystem services giant tortoises can provide to farms in terms of their ability to improve soil quality or vegetation regeneration that would be useful to explore as possible incentives that encourage land sharing. Giant tortoises on Aldabra for example, are known for their ability to promote the growth of 'tortoise turf' through their seasonal grazing activity (Hnatiuk et al. 1976b; Calow et al. 1983). Determining if improving habitat for tortoises on livestock farms also benefits livestock, both by investigating what ecosystem services giant tortoises may provide to farms, and whether livestock habitat preferences overlap with tortoise preferences, would be the next step to encouraging successful land-sharing relationships.

The ecological similarities between tortoises and cattle, however, also raise the question of competition for resources between the taxa. With tortoises at low density, compared to historical population estimates, this has not been a major concern. However, if tortoise density, cattle density, or vegetation productivity changes to a level that makes this relationship untenable, land sharing will not be sustainable. There are likely to be optimal densities of tortoises and cattle that vary with climate and future research could focus on pasture consumption rates of giant tortoises especially between seasons to understand this relationship better.

Another direct management action that could improve outcomes for both farmers and tortoises includes changes to fence construction. Results from my research suggest overall connectivity is broadly maintained across the agricultural landscape, although other migratory barriers may still remain outside of the agricultural area such as from invasive vegetation (Blake et al. 2015b). I have demonstrated, from tortoise movement data, that tortoises cross numerous fences, but crossing fences is not without cost to farmers, if fences are broken, and may injure tortoises. While measuring tortoises, I noticed the majority had scratched carapaces, most likely from crossing barbed wire fences. Although these were superficial injuries, tortoises have a thin dermal layer with nerves and blood vessels connecting their scutes (Doneley et al. 2018). I would recommend investigating any links between scratches from fences and the spread of tortoises pathogens, especially the shell fungus (Sutton et al. 2013) that is common on giant tortoises in farms (KP unpublished data and peer observations). Another change in fence construction by farmers which may benefit tortoises is encouraging farmers to use non-barbed wire for the horizontal wire strand closest to the ground, as this may help prevent scratched carapaces. Future research could include trials with smooth wire in a subset of farms to determine how effective this replacement would be at maintaining the integrity of the fence and identifying any potential problems such as allowing calves to escape. Ideally, these trials would include discussions with farmers on the feasibility and costs of replacing barbed wire with smooth wire before large scale recommendations were made.

Social science research also revealed that one predominant complaint of farmers was the cost of repairing damaged fences (estimated at $ USD 13/m) and any subsequent crop damage ($USD 2.8/m^2) by tortoises (Benitez-Capistros et al. 2018). My research on fence gaps (**Chapter 3**), substantiates the claim that fence damage is common, although it does not confirm that tortoises are always responsible. Regardless, this highlights the need for research into improved and effective fence construction around crops vulnerable to damage from tortoises in particular, to minimise economic losses and maintain positive attitudes towards land sharing in compatible land-use types. Ideally, guidelines on maintaining broader connectivity for tortoises, to allow them to move freely through non-crop farms without damaging fences, should be developed.

I also recommend further research on the interaction between tortoises and non-coffee food crops (e.g., tomatoes, yuca, pineapples etc.), as I was limited in my ability to include this land-use type, however, it is likely to be important in promoting positive tortoise-farmer relations. Improved connectivity could also be complemented by promoting planting and harvesting of crops during the times of the year when tortoise density is lowest (informed by **Chapters 2** and **4**) in farms where possible, to create temporal partitioning between tortoises and food crops.

Multiple lines of evidence from my research suggest abandoned agricultural land has the fewest benefits to tortoises of all the types of habitats available in the agricultural area. This finding was somewhat contrary to people’s perception, that farmland that had become ‘natural’ again, or that land left to return to nature would be favoured by tortoises (KP observation). However, the reality is that unmanaged land in highlands of the Galapagos tends to become degraded habitat easily colonised by invasive vegetation, which is often unfavourable to native species (Khatun 2018; Laso et al. 2020). Indeed, invasive vegetation is also implicated in the steep decline of populations of the vermillion flycatcher (*Pyrocephalus nanus*) from the agricultural area of Santa Cruz (Geladi et al. 2021). In Santa Cruz, 22% of the agricultural area is covered by invasive vegetation (Laso et al. 2020), my PhD research suggests that management of these areas should be a priority for increasing giant tortoises use of farmland areas, as well as for other wildlife. Options could include incentives to rehabilitate abandoned areas to become productive again, while allowing tortoise use (land sharing) or alternatively revegetation with native vegetation, followed by exclusive use by tortoises (land sparing). Manipulative experiments where plots of abandoned land are cleared and either assigned a land sharing (e.g., turned into coffee or livestock) or land sparing (revegetated with native vegetation) treatment and monitored over multiple seasons would go some way to answering this question. Monitoring the density of tortoises over time, as well as the costs of transforming and maintaining each treatment could help determine the overall effectiveness, economic and conservation value of either action in supporting critically endangered giant tortoises in the highlands. I recognise that to achieve a reduction in invasive species growth and spread requires a large input of resources and continued management, however, the results from my work provide evidence that it is likely to be beneficial to tortoise conservation, in addition to contributing to a number of other conservation objectives, and is therefore likely to be worthwhile.

My final recommendation for improving the management of critically endangered giant tortoises in farms would be to expand on some of this research to encompass more of the agricultural area both in space and time. I was limited in my ability to include all land-use types, and regions in the agricultural area due to logistical constraints, landholder permissions and limited tracking equipment. One of the strengths of the tracking dataset was that it allowed me to get a detailed look at tortoise farm use over time for the same individuals, however, as my research has demonstrated those individuals are also highly philopatric and thus only provide a view of their interactions with specific farmland areas. This led to a caveat in my research in that it was biased in particular to the south-west and far-east of the highlands of Santa Cruz and areas where we had no tagged tortoises such as the northern and central regions of the agricultural area were not included. This made it difficult in particular to capture the full spectrum of land-use types and continuum of roads and fences transecting the agricultural area. In our sample of tagged tortoises, very few travelled far north enough to interact with the main road making it difficult to draw a conclusion on how much of a barrier high-traffic roads are for giant tortoises. The regular flow of traffic and fewer observed tortoises to the north of the high-traffic road suggests that it is likely to limit tortoise movement, but more information is needed to determine the extent this road acts as a barrier and hazard to tortoises. Continuing this research, by extending the coverage of tortoise farmland interactions to encompass the areas I was unable to include either by tagging additional individuals or conducting a census in non-sampled regions, would be useful. I was able to draw conclusions that apply to the south-west and far-east of the agricultural area, however, assessing if these conclusions hold for the remainder of the agricultural area, especially in relation to the high-traffic road, and other land-use types would help to gather a more complete picture.

While the tortoise-farmer conflict on Santa Cruz is currently only an emerging problem (Benitez-Capistros et al. 2018), it is difficult to predict the nature of this relationship in the future. All accounts suggest that both tourism, and the local human population, are likely to increase, and these will inevitably place more demands on the fragile ecosystems of Galapagos (Epler 2007; Sampedro et al. 2018; Galapagos Governmental Council 2021). Concomitantly, populations of both species of giant tortoise on Santa Cruz are, fortunately, also increasing (Cayot et al. 2017a, b), however, if the Galapagos National Park Directorate are successful in restoring tortoise populations to their estimated original numbers, sharing land between tortoises and farmers will likely become more challenging. I would expect that the emerging conflict between tortoises and farmers would be exacerbated without mitigation measures being put in place that guide this interaction to positive outcomes for both farmers and tortoises. My research has provided several novel insights that can be used to inform tortoise conservation in non-protected areas, which occurs alongside farmer livelihoods. Furthermore, lessons learned from the scenario in Santa Cruz, can potentially inform the repatriation of tortoises to the agricultural areas of San Cristobal Island, and support tortoise conservation strategies in the highlands of southern Isabela, if both of these islands mimic the trajectories shown by Santa Cruz, into the future.

Lessons for land sharing and land sparing

Beyond the Galapagos, my research contributes several insights into the land sharing versus land sparing debate. Land sharing as a conservation strategy is sometimes discouraged, when compared to the conservation benefits protected areas can afford under a land sparing scheme (Green et al. 2005; Loconto et al. 2020; Balmford 2021). While land sharing may not be appropriate for some species with specialist ecological requirements or restricted geographical ranges, there still remains some species whose ecology can align with certain agricultural practices (Rosenzweig 2003b; Pywell et al. 2012; Linares and Eterovick 2013; Balmford 2021), that should not be overlooked. Additionally, while the option to intensify agricultural practices on existing land and spare natural areas from clearing is desirable, it is also not a viable option in all circumstances. As the discussion around land sharing and land sparing evolves, these strategies can be seen as two ends of a spectrum, rather than a dichotomy. This creates space for more context specific and intermediate strategies that can also provide some utility when the balance between agricultural needs and wildlife needs shift. Concepts such as "working lands conservation" recognises biodiversity conservation that relies on protected areas alone will not be enough to halt the biodiversity crisis and instead calls for landscape scale conservation practices that works for biodiversity and people (Kremen and Merenlender 2018). When a variety of biodiversity-based land management strategies are employed that include options along the land sharing and sparing spectrum at a landscape scale working lands can enhance protected areas and the production of resources (Kremen and Merenlender 2018).

The Galapagos provides an example in support of land sharing (in coffee and livestock areas) and land sparing (in touristic areas) complementing each other within agricultural areas. Here, I have shown that land sharing and land sparing are not only important for tortoise conservation now and into the future, but also that there are opportunities for both wildlife and farmers to benefit along the way. The presence of both approaches to conservation, in the same environment, highlights the need to use a diversity of tools to secure a future in which biodiversity and food production are not necessarily in an antagonistic relationship. I have also demonstrated that land-use types can differ in terms of the benefits and challenges they may confer to wildlife, and thus we need a nuanced approach to the discussion about options towards the land sharing end of the spectrum. Finally, my research has demonstrated there are some steps that can be taken to provide evidence-based recommendations for improving wildlife conservation in agricultural areas. In particular, I recommend including land-use type, and farmland infrastructure as a focus when considering important farm features to evaluate, especially within and among farms. To optimise wildlife conservation in agricultural contexts, we need a detailed understanding of the ecological requirements of wildlife using farmland, including research on their habitat preferences, behaviour, movement, and temporal and spatial patterns of farm use.

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Appendices

Appendix S2: Supplementary material for Chapter 2

Supplementary Table 2.1. Full model set to describe the relationship of factors influencing duration of time tortoises spent in the agricultural zone. Data are based on 113 farmland visits from 31 tortoises tracked during 2009–2018. The top models that were greater than 2 ΔAIC values than the null and within 5 ΔAIC values of the best model are denoted in bold. Models in the top set containing a parameter with CI that intersected zero are denoted by ΔAIC* and were not included in the top set of significant models.

Model	K	AIC	ΔAIC	AIC weight
Size + species + month exit	**6**	**653.31**	**0***	**0.23**
Size + sex + month exit	**6**	**653.86**	**0.55***	**0.17**
Size	**4**	**654.86**	**1.56**	**0.1**
Size + species + month exit	**7**	**655.26**	**1.95***	**0.09**
Size + species	**5**	**655.58**	**2.27***	**0.07**
Sex + month exit + species	**6**	**655.77**	**2.46***	**0.07**
Sex × size	**6**	**656.46**	**3.15***	**0.05**
Size + month enter	**5**	**656.55**	**3.24***	**0.04**
Size + sex	**5**	**656.78**	**3.47***	**0.04**
Sex + species	**5**	**656.95**	**3.64***	**0.04**
Size × species	**6**	**657.35**	**4.04***	**0.03**

Size + species + sex	**6**	**657.53**	**4.22***	**0.03**
Sex	**4**	**658.11**	**4.81**	**0.02**
Month enter × size	6	658.38	5.07	0.02
Null	3	662.75	9.44	0
Species	4	663.12	9.81	0
Month enter	4	664.75	11.44	0
Month enter + species	5	665.04	11.73	0

Supplementary Table 1.2. The mean area of a tortoise's utilization distribution (UD) from their maximum likelihood occurrence estimate, the mean proportion of individual farms taken up by the utilization area, and the mean number of farms used, per utilization distrubtion. Data were taken from 23 individuals (eight *Chelonoidis donfaustoi* and 15 *Chelonoidis porteri*) tracked in the agricultural area during 2009–2018.

Occurrence estimate	Mean ± SE area of utilization (ha)		Mean ± SE proportion of farm used		Mean ± SE number of farms visited	
Chelonoidis donfaustoi						
Alison						
25% UD	0.1696	0.0434	0.0018	0.0004	1.6667	0.2887
50% UD	0.5170	0.1338	0.0054	0.0013	2.0000	0.0000
75% UD	1.1850	0.3583	0.0123	0.0034	2.3333	0.2887
95% UD	2.9935	1.0875	0.0304	0.0101	2.6667	0.2887
99% UD	4.8511	1.8367	0.0488	0.0170	2.6667	0.2887
Sandra						
25% UD	0.0396	0.0043	0.0010	0.0004	1.5000	0.3536
50% UD	0.0710	0.0336	0.0014	0.0006	1.2500	0.2500
75% UD	0.1861	0.0991	0.0034	0.0010	1.5000	0.5000
95% UD	0.6313	0.2986	0.0123	0.0041	1.5000	0.5000
99% UD	0.9653	0.4844	0.0180	0.0057	1.5000	0.5000
Connor						
25% UD	0.0426	0.0173	0.0004	0.0002	1.0000	0.0000
50% UD	0.0705	0.0275	0.0007	0.0003	1.0000	0.0000

75% UD	0.1077	0.0428	0.0010	0.0004	1.0000	0.0000
95% UD	0.2973	0.0605	0.0028	0.0006	1.0000	0.0000
99% UD	0.5537	0.1105	0.0053	0.0011	1.0000	0.0000
Dennis						
25% UD	0.0671	0.0151	0.0020	0.0011	3.6667	0.2887
50% UD	0.2255	0.0451	0.0076	0.0048	4.0000	0.5000
75% UD	0.5652	0.1044	0.0179	0.0107	4.6667	0.2887
95% UD	1.4530	0.3238	0.0399	0.0214	6.0000	0.5000
99% UD	2.6424	0.6345	0.0655	0.0311	6.0000	0.5000
Fredy						
25% UD	0.1027	0.0193	0.0065	0.0055	1.3333	0.2887
50% UD	0.3385	0.0584	0.0192	0.0156	1.3333	0.2887
75% UD	0.7308	0.2295	0.0275	0.0198	1.6667	0.5774
95% UD	1.5879	0.6858	0.0427	0.0251	2.6667	1.4434
99% UD	3.2346	1.4119	0.0734	0.0327	2.6667	1.4434

Occurrence estimate	Mean ± SE area of utilization (ha)		Mean ± SE proportion of farm used		Mean ± SE number of farms visited	
Helber						
25% UD	0.0712	0.0231	0.0016	0.0007	2.5000	0.3536
50% UD	0.1573	0.0548	0.0034	0.0015	3.5000	0.3536
75% UD	0.2780	0.0927	0.0056	0.0021	5.0000	0.7071
95% UD	0.8892	0.2539	0.0171	0.0049	5.5000	1.0607
99% UD	1.5092	0.4001	0.0323	0.0078	6.5000	1.7678
Herbert						
25% UD	0.0548	0.0125	0.0011	0.0004	2.2000	0.2236
50% UD	0.1794	0.0402	0.0036	0.0013	2.4000	0.2739
75% UD	0.5278	0.1010	0.0112	0.0036	2.4000	0.2739
95% UD	1.6170	0.2666	0.0337	0.0094	2.4000	0.2739
99% UD	2.7904	0.4646	0.0554	0.0141	2.4000	0.2739
Jumbo						
25% UD	0.1765	0.0608	0.0015	0.0005	1.3333	0.2887
50% UD	0.4713	0.1883	0.0043	0.0014	1.6667	0.2887
75% UD	1.2759	0.5066	0.0116	0.0038	1.6667	0.2887
95% UD	3.7233	1.4359	0.0345	0.0102	1.6667	0.2887
99% UD	6.2473	2.3791	0.0580	0.0168	1.6667	0.2887
Chelonoidis porteri						
Lore						
25% UD	0.1150	0.0335	0.0027	0.0008	1.2000	0.2236
50% UD	0.1906	0.0660	0.0053	0.0016	2.3333	0.5164

75% UD	0.5093	0.1397	0.0162	0.0043	2.8333	0.8612
95% UD	1.6473	0.4166	0.0530	0.0124	3.1667	0.8010
99% UD	2.8336	0.7895	0.0804	0.0198	3.5000	0.9354
Lucy						
25% UD	0.0651	0.0197	0.0020	0.0006	1.0000	0.0000
50% UD	0.2167	0.0818	0.0068	0.0024	1.2500	0.2500
75% UD	0.4209	0.1598	0.0202	0.0058	2.2500	0.9465
95% UD	0.8786	0.3070	0.0794	0.0457	4.0000	1.3540
99% UD	1.4385	0.4492	0.1128	0.0473	5.2500	1.6008
Mandy						
25% UD	0.0761	0.0195	0.0019	0.0005	1.5000	0.2887
50% UD	0.1823	0.0499	0.0045	0.0013	2.5000	0.2887
75% UD	0.5884	0.1271	0.0144	0.0036	2.5000	0.2887
95% UD	1.7319	0.4110	0.0410	0.0106	3.2500	0.7500
99% UD	3.1737	0.7514	0.0744	0.0198	3.5000	0.6455

SUPPLEMENTARY TABLE 2.2, *continued*

Occurrence estimate	Mean ± SE area of utilization (ha)		Mean ± SE proportion of farm used		Mean ± SE number of farms visited	
Mariposa						
25% UD	0.6251	0.2211	0.0031	0.0011	1.0000	0.0000
50% UD	1.6619	0.7474	0.0084	0.0036	1.2500	0.2500
75% UD	3.4362	1.5522	0.0204	0.0065	1.5000	0.2887
95% UD	11.9663	4.8434	0.0799	0.0184	1.5000	0.2887
99% UD	22.0129	7.6655	0.1476	0.0270	1.5000	0.2887
Patty						
25% UD	0.0206	0.0159	0.0007	0.0003	2.0000	0.0000
50% UD	0.0317	0.0149	0.0032	0.0017	3.5000	1.0607
75% UD	0.0790	0.0226	0.0133	0.0032	7.5000	2.4749
95% UD	0.3495	0.0899	0.0626	0.0132	9.5000	3.1820
99% UD	0.7263	0.1837	0.1176	0.0208	11.0000	4.2426
Veronica						
25% UD	0.0698	0.0231	0.0123	0.0063	1.3333	0.2887
50% UD	0.1901	0.0751	0.0325	0.0185	1.6667	0.5774
75% UD	0.2081	0.0929	0.0317	0.0202	4.0000	1.3229
95% UD	0.5104	0.1692	0.0585	0.0363	5.0000	1.3229
99% UD	0.9369	0.2165	0.0717	0.0365	6.0000	1.7321
Yvonne						
25% UD	0.0833	0.0381	0.0013	0.0006	1.3333	0.2887
50% UD	0.1917	0.0862	0.0029	0.0013	2.0000	0.8660
75% UD	0.3305	0.1412	0.0053	0.0021	3.0000	0.5000

95% UD	0.6896	0.2588	0.0114	0.0037	3.6667	0.5774
99% UD	1.0073	0.3490	0.0171	0.0048	3.6667	0.5774
George						
25% UD	0.0327	0.0159	0.0004	0.0001	3.5000	0.3536
50% UD	0.0753	0.0260	0.0013	0.0004	7.5000	0.3536
75% UD	0.2275	0.0637	0.0039	0.0012	8.5000	1.0607
95% UD	0.9406	0.2060	0.0211	0.0084	9.5000	1.0607
99% UD	2.0320	0.3723	0.0422	0.0112	10.5000	0.3536
Harry						
25% UD	0.0833	0.0223	0.0015	0.0003	4.3333	1.2583
50% UD	0.2132	0.0610	0.0038	0.0009	6.0000	2.6458
75% UD	0.4573	0.1394	0.0091	0.0020	7.6667	3.1754
95% UD	1.4251	0.3835	0.0355	0.0082	8.3333	3.3292
99% UD	2.5742	0.5717	0.0672	0.0146	8.3333	3.3292

Supplementary Table 2.2, continued

Occurrence estimate	Mean ± SE area of utilization (ha)		Mean ± SE proportion of farm used		Mean ± SE number of farms visited	
Karlitos						
25% UD	0.0295	0.0061	0.0001	0.0000	1.0000	0.0000
50% UD	0.1175	0.0406	0.0006	0.0002	1.0000	0.0000
75% UD	0.5043	0.1639	0.0025	0.0008	1.0000	0.0000
95% UD	1.7495	0.4263	0.0087	0.0021	1.0000	0.0000
99% UD	4.8664	1.2428	0.0241	0.0062	1.0000	0.0000
Sebastian						
25% UD	0.0560	0.0162	0.0008	0.0002	3.6667	0.2887
50% UD	0.1598	0.0507	0.0023	0.0008	5.3333	0.7638
75% UD	0.4916	0.1534	0.0072	0.0023	5.6667	0.7638
95% UD	1.3898	0.4144	0.0203	0.0063	7.3333	0.2887
99% UD	2.8727	0.7329	0.0419	0.0110	7.3333	0.2887
Sepp						
25% UD	0.0528	0.0086	0.0003	0.0000	1.0000	0.0000
50% UD	0.2535	0.0443	0.0013	0.0002	1.0000	0.0000
75% UD	0.9485	0.2008	0.0047	0.0010	1.0000	0.0000
95% UD	3.7215	0.6605	0.0185	0.0033	1.0000	0.0000
99% UD	8.6047	1.2541	0.0427	0.0062	1.0000	0.0000
Sir David						
25% UD	0.1509	0.0682	0.0036	0.0020	4.0000	1.4142
50% UD	0.4072	0.1831	0.0120	0.0069	7.0000	2.1213
75% UD	0.9148	0.3810	0.0277	0.0100	10.5000	1.7678

95% UD	2.6503	1.1164	0.0780	0.0175	12.5000	1.7678
99% UD	4.3093	1.7079	0.1375	0.0261	14.0000	2.1213
Steve Devine						
25% UD	0.1709	0.0341	0.0008	0.0002	1.0000	0.0000
50% UD	0.7025	0.1161	0.0035	0.0006	1.0000	0.0000
75% UD	1.4574	0.3551	0.0073	0.0017	1.3750	0.2588
95% UD	4.2219	1.1246	0.0220	0.0053	1.6250	0.4581
99% UD	8.9403	2.2231	0.0489	0.0099	1.6250	0.4581
Wacho						
25% UD	0.0438	0.0164	0.0057	0.0035	4.0000	0.0000
50% UD	0.0720	0.0269	0.0093	0.0045	10.0000	1.4142
75% UD	0.1452	0.0502	0.0210	0.0065	15.0000	0.7071
95% UD	0.3910	0.1248	0.0612	0.0129	19.0000	1.4142
99% UD	0.7058	0.2173	0.1201	0.0226	21.0000	2.1213
All tortoises						
25% UD	0.0984	0.0118	0.0022	0.0004	1.8289	0.1400
50% UD	0.2501	0.0302	0.0059	0.0009	2.5432	0.2700
75% UD	0.5621	0.0621	0.0142	0.0017	3.2805	0.3700
95% UD	1.6191	0.1744	0.0437	0.0041	3.9268	0.4500
99% UD	2.9097	0.2885	0.0779	0.0060	4.2317	0.5000

SUPPLEMENTARY TABLE 2.2, continued

Supplementary Table 2.3. Mean overlap in space use among visits for each tortoise (± mean maximum likelihood and 95% CI for the mean estimate). The analysis is based on 83 fitted continuous time movement models from 23 tortoises tracked in the agricultural zone during 2009–2018.

Tortoise	Sex	Farmland visits	Low	Maximum likelihood	High
C. donfaustoi					
Alison	female	3	0.880	0.992	1
Sandra	female	4	0.648	0.874	0.992
Connor	male	5	0.850	0.932	0.981
Dennis	male	3	0.167	0.558	0.971
Fredy	male	3	0.414	0.742	0.935
Helber	male	2	0.848	0.997	1
Herbert	male	5	0.589	0.838	0.953
Jumbo	male	3	0.522	0.923	1
C. porteri					
Lore	female	7	0.236	0.532	0.843
Lucy	female	4	0.812	0.996	1
Mandy	female	4	0.767	0.984	1
Mariposa	female	4	0.703	0.989	1
Patty	female	2	0.635	0.978	1
Veronica	female	3	0.414	0.648	0.912
Yvonne	female	3	0.746	0.927	0.991
George	male	2	0.678	0.993	1
Harry	male	3	0.378	0.825	1
Karlitos	male	3	0.668	0.989	1

Sebastian	male	3	0.568	0.958	1
Sepp	male	5	0.659	0.984	1
Sir David	male	2	0.664	0.895	0.997
Steve Devine	male	8	0.710	0.971	1
Wacho	male	2	0.40	0.874	1
All tortoises		3.609	0.607	0.887	0.982
SD		1.525	0.189	0.137	0.037
SE		0.318	0.040	0.029	0.008

Appendix S3: Supplementary material for Chapter 3

Supplementary Table 3.1. Results for differences between species for their responses to human-modified vegetation and infrastructure in the agricultural area of Santa Cruz. We first estimated each individual tortoise's response using step-selection functions and then used univariate models to assess differences between the two species of tortoise. No significant species-specific differences were found for any of the environmental covariates in the models. Species differences gives the difference between the mean estimate of the Western Santa Cruz tortoise relative to the Eastern Santa Cruz tortoise with the standard error and p-value for the difference.

Model	**Term**	**Species difference**	**SE**	**t-value**	**p-value**	**Tortoises**
Vegetation class	pasture	-0.272	0.321	-0.848	0.407	21

(5hr timescale)	crop	0.539	0.295	-1.823	0.084	21
	invasive	-0.674	0.327	-2.058	0.054	21
Vegetation class (1hr timescale)	pasture: step length	0.030	0.197	0.153	0.880	24
	crop: step length	0.096	0.203	0.474	0.640	24
	invasive: step length	0.187	0.157	1.191	0.246	24
Ponds	pond distance	0.235	0.248	0.950	0.351	27
	pond distance: step length	-0.094	0.059	-1.605	0.121	27
Fence crossing	crossed complex fence	-0.386	1.110	-0.348	0.732	23
Low-traffic road	road distance	0.153	0.131	1.170	0.253	27
	road distance: step length	-0.014	0.053	-0.266	0.792	27
Medium-traffic road	road distance	-0.100	0.106	-0.946	0.353	27
	road distance: step length	-0.007	0.075	-0.095	0.925	27
High-traffic road	road distance	0.149	0.126	1.188	0.246	27
	road distance: step length	0.041	0.058	0.707	0.486	27

Supplementary Table 3.2. Overview of the number of tortoises, their sex, species, and the number of strata (the set of 1 used to 30 available GPS locations) that they contributed to each of the seven models (vegetation (one at 5 hours and another at the default 1 hour), pond, fence, low-traffic, medium-traffic and high-traffic). Not all tortoises interacted with each environmental covariate and thus could not be included in all models. F= female, J= juvenile, M= male

Tortoise ID	Sex	Species	Vegetation (5 hour)	Vegetation	Pond	Fence	Low-traffic	Medium-traffic	High-traffic
Alison	F	East	413	4166	4171	326	4171	4171	4171
Baronesa	F	West	-	136	148	26	148	148	148
Butternut	M	West	93	1215	1578	262	1578	1578	1578
Connor	M	East	126	1337	1337	1094	1337	1337	1337
Dennis	M	East	270	3017	4510	1791	4510	4510	4510
Destiny	F	West	56	655	657	18	657	657	657
Francisco	M	West	75	680	682	241	682	682	682
George	M	West	236	2427	2430	1378	2430	2430	2430
Harry	M	East	551	6293	6713	2916	6713	6713	6713
Herbert	M	East	834	10989	14210	11082	14210	14210	14210
Iggy	J	West	95	1197	1263	113	1263	1263	1263
Jack	M	West	71	746	746	172	746	746	746
Johnny	M	West	129	1417	1506	601	1506	1506	1506
Laura	F	West	-	-	219	-	219	219	219
Lore	F	West	259	2740	2769	789	2769	2769	2769
Lucy	F	West	364	4061	4327	312	4327	4327	4327
Melina	F	East	133	1620	2056	1068	2056	2056	2056
Randy	M	West	-	-	147	34	147	147	147
Roberto	M	West	75	928	1179	97	1179	1179	1179
Sandra	F	East	-	227	278	195	278	278	278
Sebastian	M	West	-	-	67	56	67	67	67
Sepp	M	West	200	2044	2044	-	2044	2044	2044
Sir David	M	West	652	6669	6674	882	6674	6674	6674
Speedy Gonzales	M	West	162	1786	1968	363	1968	1968	1968
Steve Devine	M	West	678	6968	6972	394	6972	6972	6972
Veronica	F	West	266	2686	2692	1564	2692	2692	2692
Yvonne	F	West	-	2368	2368	841	2368	2368	2368
Totals	**10F 1J 16M**	**7 East 20 West**	**21 tortoises 5738 strata**	**24 tortoises 66372 strata**	**27 tortoises 73711 strata**	**25 tortoises 26615 strata**	**27 tortoises 73711 strata**	**27 tortoises 73711 strata**	**27 tortoises 73711 strata**

Supplementary Table 3.3. Table of the original vegetation classification taken from Laso et. al. 2020 with the simplified classification of vegetation class used in this paper. Bare ground, bare environment and freshwater were removed due to their very low encounter rate.

Original categories from Laso et. al. 2020	**Simplified categories**	**Proportion of available locations**	**Proportion of used locations**
Bare ground	~~cleared~~	0.001	0.000
Built environment	~~cleared~~	0.005	0.004
Freshwater	~~cleared~~	0.004	0.006
Permanent crops (e.g. coffee, banana, other permanent crops)	crops	0.149	0.144
Transitory crops (e.g. watermelon, tomatoes, corn, etc..)	crops	0.023	0.027
Invasive (*Cedrela*-Cedar, *Cinchona*-Quinine, *Lantana*-Supriosa, mixed forest, *Psidium*-Guava, *Rubus*-Blackberry, *Syzygium*-Pomarosa)	invasive	0.293	0.288
Deciduous forest	native	0.004	0.003
Evergreen forest and shrubland	native	0.000	0.000
Evergreen seasonal forest and shrubland	native	0.070	0.064
Humid tallgrass	native	0.007	0.002
Pioneer	native	0.074	0.077
Pasture (Cultivated grasses, *Pennisetum*-Elephant grass, Silvopasture)	pasture	0.371	0.383
13 categories	4 categories (cleared removed)	1	1

Supplementary Figure 3.1. Examples of the three different road types used in our analysis of tortoise response to roads in Santa Cruz Island, Galapagos. The top left image is an example of a low-traffic road, top right shows an example of a medium-traffic road and the bottom image shows the high-traffic highway that dissects the agricultural area.

Supplementary Table 3.4. Model output for the influence of vegetation class on tortoise habitat selection (at a five-hour scale) with native vegetation as the reference factor. Tortoises preferred pasture to native vegetation and showed no significant difference in their preferences between native vegetation, crops, and invasive species.

Term	Estimate	SE	z	p-value
Pasture	0.380	0.139	2.730	0.006
Crop	-0.001	0.122	-0.010	0.993
Invasive	-0.078	0.131	-0.590	0.553
Step length	0.199	0.010	19.010	0.000
Cos(turn angle)	-0.595	0.019	-31.430	0.000

Supplementary Table 3.5. Model output for the influence of vegetation class on tortoise movement (at an hourly scale) with native vegetation as the reference factor. Tortoises travelled slower in pasture, and faster in invasive vegetation, with little difference in their step length between crop and native vegetation. An interaction is denoted with " : ".

Term	Estimate	SE	Z	p-value

Pasture : step length	-0.208	0.059	-3.500	>0.001
Crop : step length	0.023	0.057	0.400	0.684
Invasive : step length	0.098	0.050	2.000	0.050
Step length	0.028	0.049	0.600	0.566
Turn angle	-0.231	0.005	-42.100	>0.001

Supplementary Table 3.6. Model output for the influence of ponds on tortoise habitat selection and movement processes in the agricultural area of Santa Cruz Island, Galapagos. Tortoises preferred to be closer to ponds, and move slower when they near ponds. An interaction is denoted with " : ".

Term	**Estimate**	**SE**	**z**	**p-value**
Distance to pond	-0.475	0.066	-7.160	>0.001
Distance to pond : step length	-0.066	0.082	-0.800	0.425
Step length	0.037	0.005	8.100	>0.001
Turn angle	-0.252	0.005	-47.410	>0.001

Supplementary Table 3.7. Model output for tortoise response to crossing complex versus simple fences in the agricultural area of Santa Cruz Island, Galapagos. Tortoises preferred to cross simple fences.

Term	Estimate	SE	z	p-value
Crossed complex fences	-0.094	0.043	-2.200	0.029
Step length	0.011	0.006	1.800	0.074
Turn angle	-0.321	0.009	-37.00	>0.001

Supplementary Table 3.8. Model output for tortoise response to medium-traffic roads in the agricultural area of Santa Cruz Island, Galapagos. Tortoises showed no significant response to their proximity to the road or their step length when their proximity to the road changed. An interaction is denoted with " : ".

Term	Estimate	SE	z	p-value
Distance to medium-traffic road	0.173	0.094	1.840	0.0661
Distance to medium-traffic road : step length	-0.035	0.095	-0.370	0.714
Step length	0.049	0.006	8.520	>0.001
Turn angle	-0.254	0.005	-47.780	>0.001

Supplementary Table 3.9. Model output for tortoise response to high-traffic roads in the agricultural area of Santa Cruz Island, Galapagos. Tortoises showed no significant response to their proximity to the road or their step length when their proximity to the road changed. An interaction is denoted with " : ".

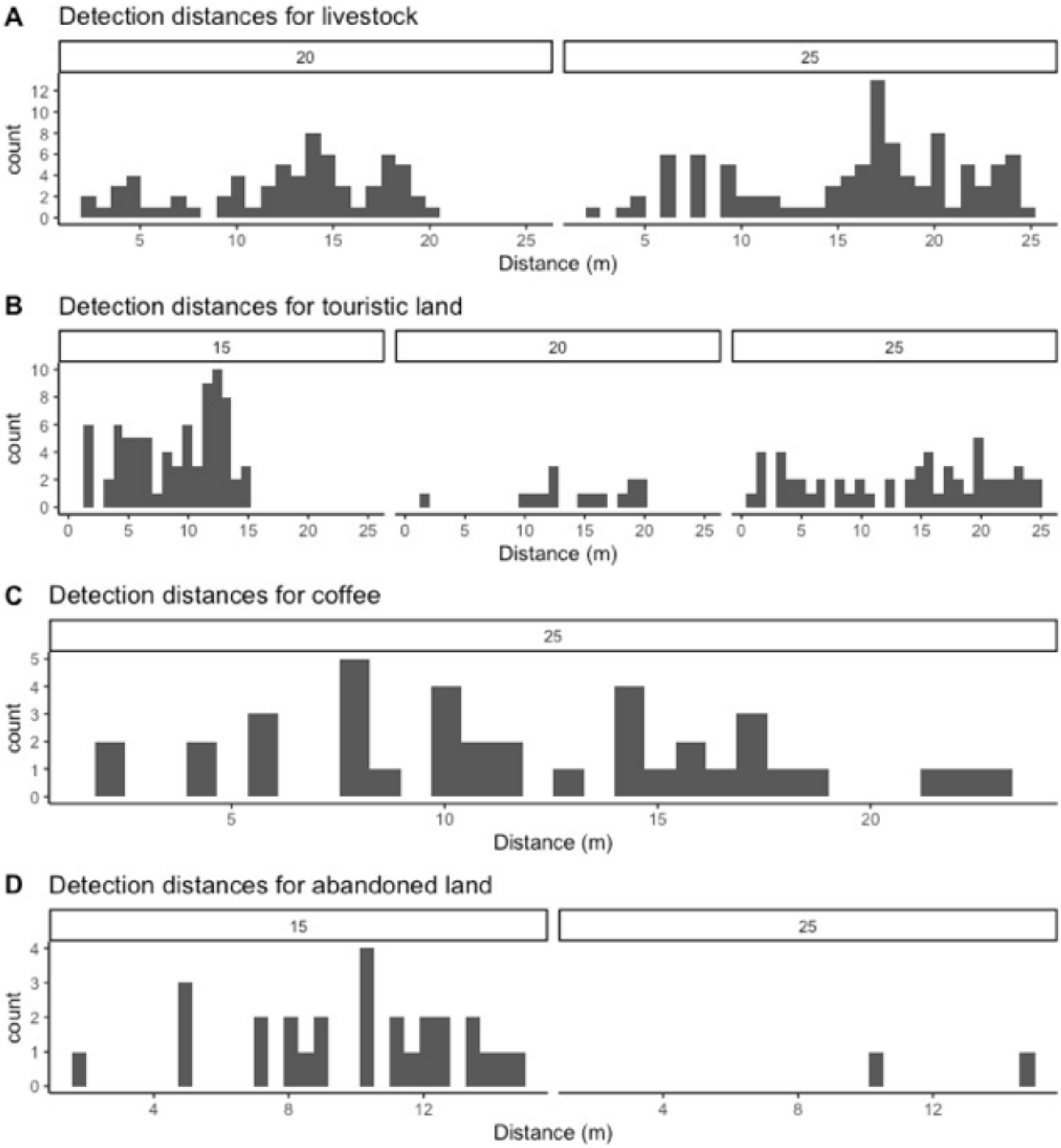
Term	Estimate	SE	z	p-value
Distance to high-traffic road	-0.105	0.061	-1.720	0.086
Distance to high-traffic road : step length	0.063	0.171	0.370	0.714
Step length	0.152	0.005	29.840	>0.001
Turn angle	-0.249	0.005	-46.810	>0.001

Appendix S4: Supplementary material for Chapter 4

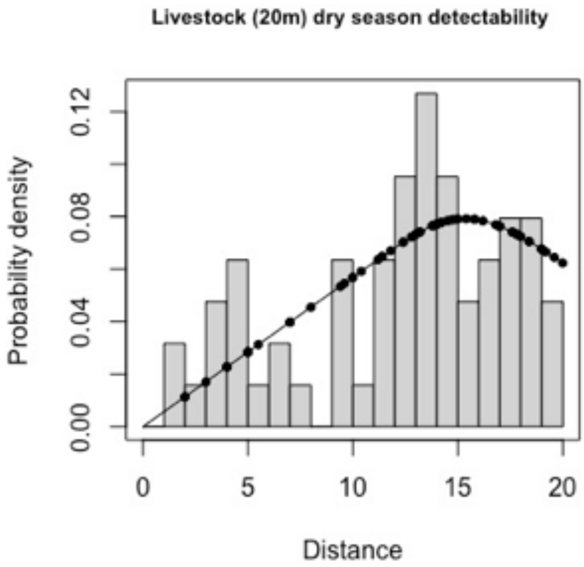
Supplementary Table 4.1. Differences in the detectability of giant tortoises among land-use types on Santa Cruz Island, Galapagos. Detection probabilities estimated using distance sampling methods.

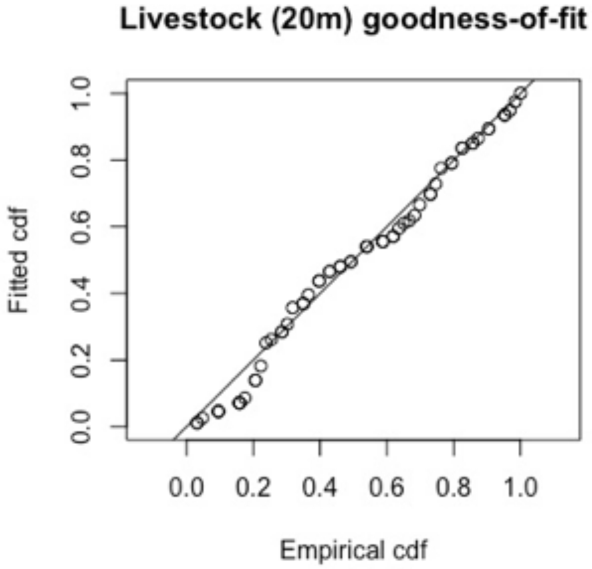
Land-use type	Detection probability	SE	Coefficient Variation	Distance function
Livestock 20m radius points	0.929	0.103	0.111	hazard rate
Livestock 25m radius points	0.879	0.118	0.135	hazard rate
Touristic 15m radius points	0.738	0.141	0.191	half normal
Touristic 20 & 25m radius points	0.624	0.105	0.168	half normal
Coffee 25m radius points	0.429	0.094	0.220	half normal

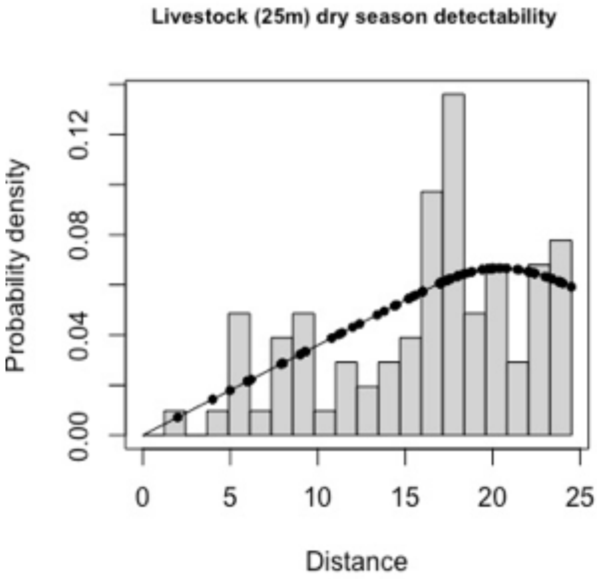
Abandoned 15 & 25m radius points	0.954	0.174	0.182	hazard rate

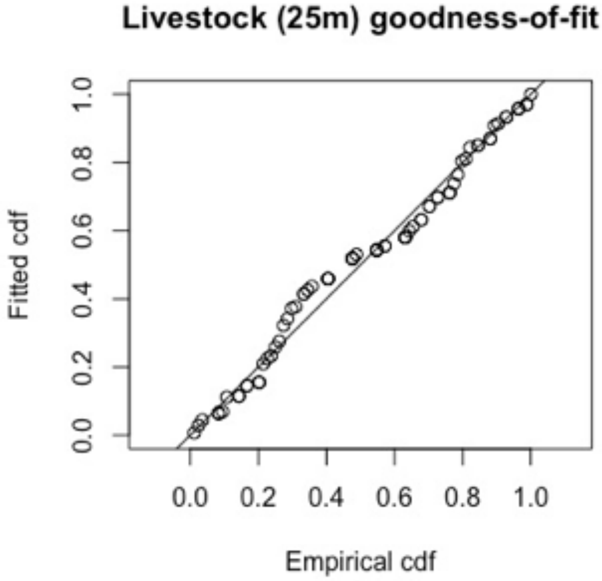


Supplementary Figure 4.1. Histograms of tortoise counts during the dry season in different plot sizes for each land-use type (A-D). The radius of the survey point differed depending on the size of the farm and was either 15m, 20m or 25m (shown by the numbers in each banner). Detectability was calculated for each land-use type and where possible (i.e. given sufficient data) the different plot sizes within each land-use type using distance functions.

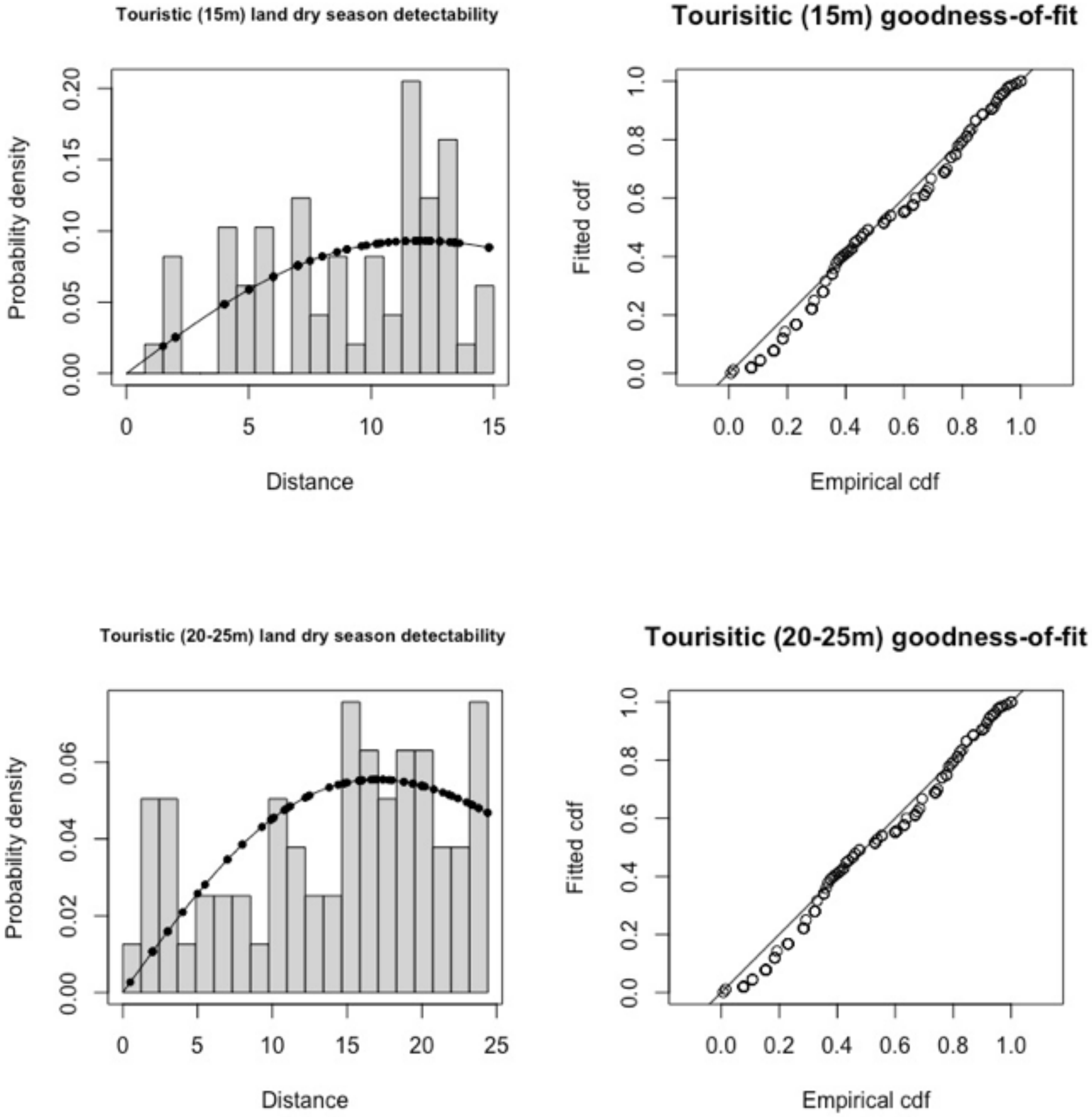

Livestock (20m) dry season detectability


Livestock (20m) goodness-of-fit

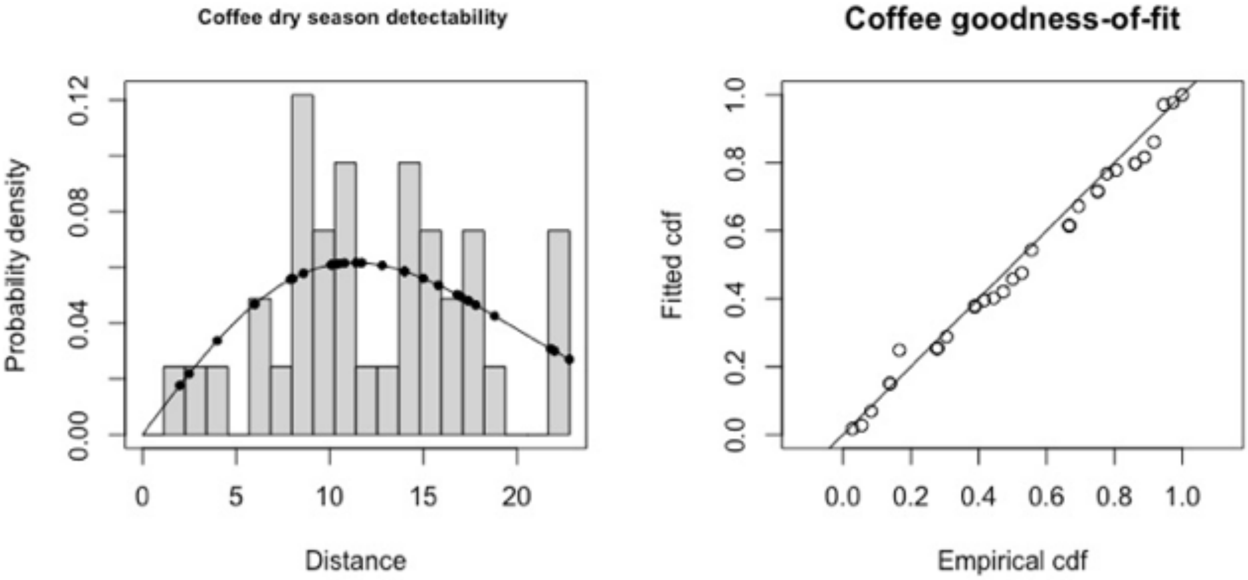

Livestock (25m) dry season detectability


Livestock (25m) goodness-of-fit

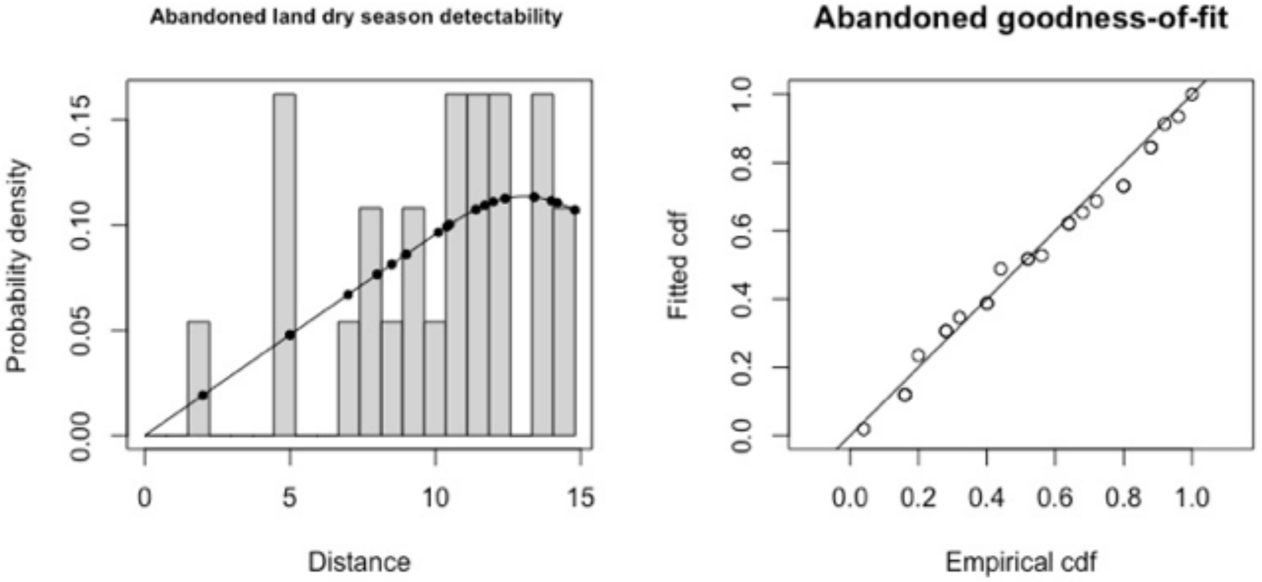
Supplementary Figure 4.2. Detection probabilities for tortoises in livestock farms sampled at survey points with a 20m radius (top) and 25m radius (bottom). On the left are the detection probability curves fit to observations of tortoises from our distance sampling and the model's goodness-of-fit on the right.



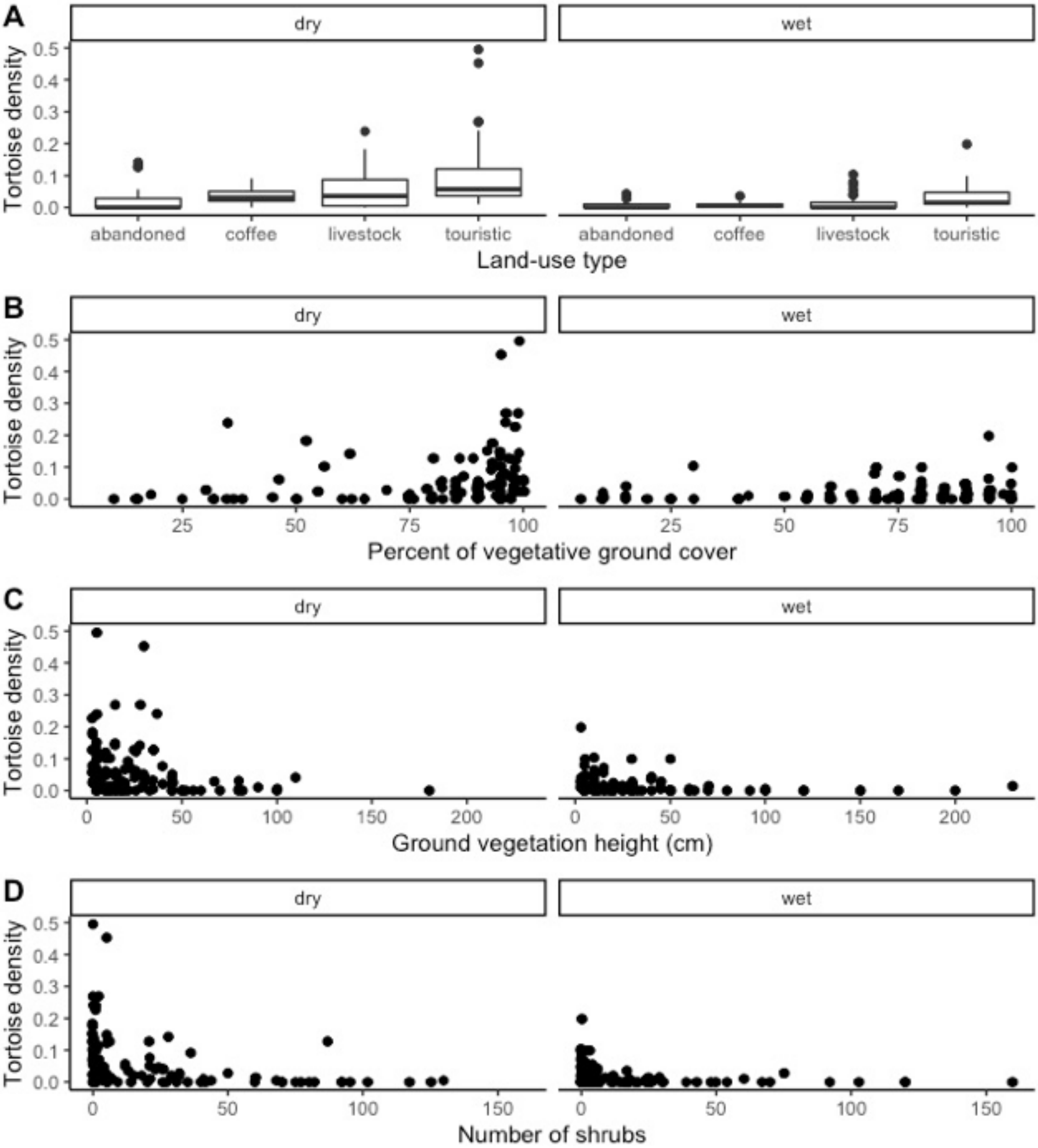
Supplementary Figure 4.3. Detection probabilities for tortoises in touristic land sampled at survey points with a 15m radius (top) and 20-25m radius (bottom). On the left are the detection probability curves fit to observations of tortoises from our distance sampling and the model's goodness-of-fit on the right.



Supplementary Figure 4.4. Detection probabilities for tortoises in a coffee plantation sampled at survey points with a 25m radius. On the left is the detection probability curve fit to observations of tortoises from our distance sampling and the model's goodness-of-fit on the right.



Supplementary Figure 4.5. Detection probabilities for tortoises in abandoned land sampled at survey points with a 15-25m radius. On the left is the detection probability curve fit to observations of tortoises from our distance sampling and the model's goodness-of-fit on the right.



Supplementary Figure 4.6. Raw data differences in the patterns of giant tortoise density (per m^2) between seasons on Santa Cruz Island, Galapagos, showing that for land-use type (A), ground cover (B), ground cover height (C) and number of shrubs (D) both the dry season and wet season follow the same overall patterns. However, during the wet season many tortoises return to the lowlands so the dataset for wet season contains many more 0 values for tortoise density making it harder to tease apart which habitat characteristics tortoises like and dislike.

Supplementary Table 4.2. Results from the model testing the impact of land-use type on giant tortoise density in the agricultural area of Santa Cruz Island, Galapagos. Abandoned land had the lowest level of tortoise density (number of tortoises per survey point), livestock, coffee, and touristic land had higher tortoise densities, but only touristic land was significantly higher. Coefficients estimated using a negative binomial zero-inflated regression model. Model estimates have been back transformed and show the multiplicative impact of each land-use type on tortoise density in the count model and the probability of zero-inflation of in the zero-inflation model n = 108.

Term	**Estimate**	**SE**	**z-value**	**P value**	**Low CI**	**High CI**
Count model						
(Intercept)	1.815	0.305	1.956	0.051	0.999	3.298
coffee	1.556	0.439	1.008	0.314	0.659	3.676
livestock	1.301	0.344	0.764	0.445	0.663	2.553
touristic	2.817	0.353	2.936	0.003	1.411	5.624
Zero-inflation model						
(Intercept)	0.395	0.446	-2.084	0.037	0.165	0.946
coffee	0.021	5.128	-0.750	0.453	0.000	494.616
livestock	0.128	0.610	-3.374	0.001	0.039	0.422

touristic	0.000	2273.254	-0.008	0.993	0.000	Inf

Supplementary Table 4.3. Results from the Boosted Regression Trees evaluating which habitat structure variables were good candidates for modelling habitat preference of giant tortoises on Santa Cruz Island, Galapagos, based on their relative influence scores. Variables in bold were indicated to have a greater contribution to characterising the data than by chance alone and chosen for further modelling.

Variable	Relative influence
Ground cover	**34.626**
Number of shrubs	**17.421**
Ground cover height	**12.545**
Canopy cover	**11.052**
Mean shrub height	**9.362**
Trees 1 to 4m	**9.005**
Shrub cover	4.586
Trees 4m to 8m	0.889
Number of fruit trees	0.463
Trees 8m	0.052
Wallow present	0.000
Fruit fall	0.000

Supplementary Table 4.4. Full list of models used to determine the top model of habitat structure against giant tortoise density on Santa Cruz Island, Galapagos. The highest-ranking, most parsimonious model was chosen based on AICc value and is denoted in bold.

Model	**df**	**AICc**	**Delta AICc**
Ground cover + ground cover height + number shrubs + canopy cover	11	628.153	0
Number of shrubs * canopy cover	9	629.956	1.803
Ground cover + ground cover height + number shrubs	9	632.060	3.907
Ground cover + ground cover height + number shrubs + canopy cover + mean shrub height + tree 1m to 4m	15	635.681	7.528
Number of shrubs	5	636.952	8.800
Ground cover * ground cover height	9	639.654	11.501
Number of shrubs * mean shrub height	9	639.660	11.507
Canopy cover + ground cover	7	643.792	15.639
Ground cover	5	644.215	16.062
Ground cover height	5	657.455	29.303
Ground cover : ground cover height + tree 1m to 4m	7	660.754	32.602
Mean shrub height	5	661.543	33.390
Canopy cover	5	663.545	35.393
Trees 1m to 4m	5	664.967	36.814
Null	3	665.735	37.582

Supplementary Table 4.5. Output from the zero-inflation component of our best-ranking, most parsimonious model determining which habitat structure variables have the strongest impact on tortoise density in the agricultural area of Santa Cruz Island, Galapagos. Model estimates have been back transformed and show the multiplicative impact of each habitat variable on probability of zero-inflation of tortoise density in the agricultural area n = 108.

Term	Estimate	SE	z-value	P value	Low CI	High CI
(Intercept)	0.053	0.376	-7.536	0.000	0.026	0.107
Ground cover	0.970	0.017	-1.648	0.099	0.941	1.000
Number of shrubs	1.022	0.012	1.457	0.145	0.999	1.046
Height of ground cover	1.014	0.015	0.695	0.487	0.989	1.041

Appendix S5: Supplementary material for Chapter 5

Supplementary Table 5.1. Ethogram of all behaviours recorded during the 30-minute focal observation. The three vegetation characteristics (ratio of live vegetation, vegetation height and vegetation density) were recorded every 5 minutes during each focal observation and matched with the tortoise's behaviour when the vegetation characteristics were estimated.

Code	Type	Description

eat	State	when a tortoise is consuming, handling or searching for food
drink	State	when a tortoise is observed drinking
hiss	Point	when a tortoise makes hissing sound
withdraw head	State	when a tortoise withdraws their head into their carapace until they poke their head back to a regular position
walk	State	when a tortoise is walking
bite	Point	when a tortoise bites a conspecific
rest	State	when a tortoise is remaining motionless with their plastron on the ground
wallow	State	when a tortoise is submerged in water, wallowing
pursue	State	when a tortoise is acting aggressively to a conspecific and is pursing another individual
mounting	State	when a tortoise mounts a conspecific as part of mating behaviour
scan	State	when a tortoise raises head above carapace and remains vigilant, looking around at surroundings
groom	Point	when a tortoise is groomed by a bird on their carapace or skin
defecate	Point	when a tortoise defecates
cross fence	Point	when a tortoise crosses a farm border structure
copulation	State	when a tortoise is engaged in copulation when mounting is successful and cloacas are in contact
grunt	Point	when a tortoise makes grunt sounds from low slow exhalations
yawn	Point	when a tortoise opens mouth wide to yawn
approach	State	when a person e.g. tourist is within 5m of animal
veg height	Point	estimated vegetation height within 1m radius of in front of tortoise
veg density	Point	estimated vegetation density within 1m in front of tortoise
full sun	State	when a tortoise is in full sun during observation

full shade	State	when a tortoise is in full shade during observation
In between	State	when a tortoise is not in full sun or shade
defence posture	Point	when a tortoise raises its body off the ground and angles its carapace or head forwards into a defensive posture
ratio g:b	Point	estimated ratio of green to brown material within 1m radius in front of tortoise

Supplementary Figure 5.1. From top left to bottom right, an example of very low density, low density, dense, very dense ground vegetation.

Supplementary Table 5.2. Full list of models used to determine the top model of factors impacting the relative proportions of eating, walking and resting behaviour on farms on Santa Cruz Island, Galapagos. The highest-ranking, most parsimonious model was chosen based on delta AIC$_c$ value and is denoted in bold. An interaction is denoted with '*'.

Model terms	dAIC$_c$	df
Land-use type	0	9
Land-use type + carapace temperature	**2.4**	**12**
Land-use type + ground temperature range	2.7	12
Land-use type + curved carapace length	3.2	12
Land-use type + mean carapace temperature*mean ground temperature	4.8	18
Land-use type + ground temperature range* mean carapace temperature	5.6	18
Land-use type + curved carapace length + mean carapace temperature	5.8	15
Land-use type + mean carapace temperature + ground temperature range	5.9	15
Land-use type + ground temperature range	6.6	12
Land-use type * mean carapace temperature	10.5	18
Land-use type * ground temperature range	12	18
Land-use type + curved carapace length* mean carapace temperature	12.7	18
Land-use type * curved carapace length	14.6	18
Ground temperature range	23.5	6

Mean carapace temperature + ground temperature range	26.4	9
Mean carapace temperature	26.7	6
Null	28.3	3
Curved carapace length	31.7	6
Mean ground temperature	32.9	6
Sex	33	9
Hour	33.8	6
Season	34.4	6

Supplementary Table 5.3. Full list of models used to determine the top model of vegetation characteristics influencing the probability of a tortoise eating in the agricultural area on farms on Santa Cruz Island, Galapagos. The highest-ranking, most parsimonious model was chosen based on delta AIC$_c$ value and is denoted in bold. An interaction is denoted with ‘:’.

Model terms	**dAIC$_c$**	**df**
percent vegetation : vegetation density + vegetation height	**0**	**7**
percent vegetation : vegetation density	0.6	6
vegetation height + percent vegetation + vegetation density	4.5	7
percent vegetation + vegetation density	6.5	6
percent vegetation + vegetation height	9.8	4

vegetation height : vegetation density + percent vegetation + vegetation density	10.4	5
vegetation height : vegetation density + percent vegetation	10.5	4
percent vegetation	11	3
vegetation height + vegetation density	25.9	6
vegetation density	27	5
vegetation height	52.3	3
Null	59.2	2

Supplementary Table 5.4 Full list of models used to determine the top model of vegetation characteristics influencing the probability of a tortoise walking in the agricultural area on farms on Santa Cruz Island, Galapagos. The highest-ranking, most parsimonious model was chosen based on delta AIC$_c$ value and is denoted in bold. An interaction is denoted with ‘:’.

Model terms	**dAIC$_c$**	**df**
vegetation height + vegetation density	**0**	**6**
vegetation height + percent vegetation + vegetation density	0.9	7
vegetation height	3.2	3
percent vegetation + vegetation height	3.7	4
vegetation height : vegetation density + percent vegetation + vegetation density	4.8	5
vegetation density	6.9	5

percent vegetation : vegetation density + vegetation height	7.4	7
percent vegetation + vegetation density	8	6
percent vegetation	10.1	3
vegetation height : vegetation density + percent vegetation	11.8	4
percent vegetation : vegetation density + percent vegetation + vegetation density	13.2	9
Null	13.4	2
percent vegetation : vegetation density	15.2	6

Supplementary Table 5.5. Full list of models used to determine the top model of vegetation characteristics influencing the probability of a tortoise resting in the agricultural area on farms on Santa Cruz Island, Galapagos. The highest-ranking, most parsimonious model was chosen based on delta AIC$_c$ value and is denoted in bold. An interaction is denoted with ‘:’.

Model terms	**dAIC$_c$**	**df**
vegetation density	**0**	**5**
vegetation height + vegetation density	1.9	6
percent vegetation + vegetation density	2	6
Null	3.5	2
vegetation height + percent vegetation + vegetation density	3.8	7
percent vegetation	4.1	3

vegetation height	4.9	3
percent vegetation + vegetation height	5.8	4
vegetation height : vegetation density + percent vegetation	5.8	4
vegetation height : vegetation density + percent vegetation + vegetation density	7.7	5