The Galapagos Tortoise Movement Ecology Programme: what have we learned about tortoise movement and what does it mean for conservation?

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Introduction

Today, natural populations of native giant tortoises occur in just two locations, and both are oceanic island sites: Aldabra Atoll in the Indian Ocean, some 400km northwest of Madagascar, and the Galapagos Islands, 1000km off the west coast of Ecuador in the eastern tropical Pacific. While these species have become icons of the biodiversity conservation movement and Darwin's Theory of Evolution by Natural Selection, the general view remains that giant tortoises are rather bizarre quirks of evolutionary processes that only occur on islands. This perspective is far from the truth, for rather than representing an evolutionary oddity only found at the ends of the earth, extant giant tortoises represent the last survivors of a once diverse lineage that occurred on all continents except Antarctica and then declined with the rise of predatory mammals. While direct evidence is rare (White et al. 2010), it is likely that human expansion out of Africa and around the world significantly contributed to the extinction of continental giant tortoises (Rhodin et al. 2015).

Giant tortoises on oceanic islands remained safe from mammalian and human predation until the colonization of the Indo-Pacific islands on which they occurred during the late Pleistocene and Holocene (Rhodin et al. 2015). The golden age of sail and global discovery saw the Mascarenes and Seychelles colonized by humans who killed large tortoises for food, while their introduced animals, including rats, pigs, dogs and cats, also ate eggs and young tortoises. Humans and the often-invasive species we introduced, led to the widespread extinction of giant tortoises and myriad other species.

Aldabra was not on the prevailing trade routes, but was visited often enough by hungry sailors to see the tortoise population at risk of extinction by the late 1800s (Bourn et al. 1999 and references therein). The Galapagos Islands, discovered in 1535, were abandoned for the next 250-plus years until whales were discovered there in fantastic numbers. The giant tortoise plunder there began to feed whalers, but expanded to a meat export trade that among other things fed the early days of the California gold rush (Conrad & Pastron 2014), and eventually provided oil for the street lamps of mainland Ecuador (Van Denburgh 1914). Several species of Galapagos tortoise became extinct and most other populations suffered dramatic declines (MacFarland et al. 1974a, b). Thanks to diminished demand for giant tortoise meat and oil and immense conservation efforts, giant tortoises remain on Galapagos and Aldabra today and bear witness to a former adaptive radiation that once spanned the globe.

Despite their iconic status, research on Galapagos tortoise ecology and reproductive biology has been limited. Pioneering research in the 1970s and 80s provided a general overview of the conservation status of Galapagos tortoises, from which management plans were developed and implemented (MacFarland et al. 1974a, b; MacFarland & Reeder 1975). Excellent research on the evolution and phylogeny of Galapagos tortoises followed, the outputs of which were of direct relevance to population management, including captive breeding (e.g. Caccone et al. 1999; Caccone et al. 2002; Russello et al. 2005; Russello et al. 2010; Poulakakis et al. 2015). Ecological research lagged somewhat behind, though some detailed work on Santa Cruz Island and Alcedo Volcano on Isabela Island provided valuable knowledge on diet and seasonal distribution, including analysis of competition between tortoises and introduced species (Fowler 1983; Fowler De Neira & Roe 1984; Cayot 1985; Fowler & Johnson 1985; Cayot 1987). However, by the turn of the new millennium many questions on the population dynamics, ecology and evolutionary biology of tortoises remained, including some posed by Darwin himself some 170 years previously.

One such broad question concerned the movements of Galapagos tortoises. Darwin wondered why tortoise trails went up and down the islands' volcanic slopes. Local people told him it was because tortoises walked long distances from lowlands to highlands on annual migrations. As the islands became colonized by humans, farmers and hunters were familiar with the seasonal shifts in tortoise abundance, but the phenomenon was largely ignored by scientists. Linda Cayot was a young PhD student during the El Niño cycle in 1982-83 which produced the most extreme weather event Galapagos had seen for a century, including record high temperatures and rainfall. Cayot noticed between the sheets of rain and ever more dense vegetation that all the tortoises she had been studying disappeared! She surmised that they

Fig. 1. Stephen Blake fitting a GPS tag to an adult male Galapagos tortoise in the highlands of Santa Cruz. Tags are attached with plumber's epoxy putty. Photo by Franz Kummeth.

had trudged into the lowlands to escape the torrential rains and potentially fatal flooding. This seemed to be one more tantalising tale of long-distance migration by Galapagos tortoises which have peppered legend and literature for centuries (Darwin 1839; Van Denburgh 1914; Townsend 1924, 1925; Rodhouse et al. 1975; Reeder & MacFarland 1978). Support for these stories also came from well-documented migrations by giant tortoises on Aldabra Atoll (Swingland & Lessells 1979; Gibson & Hamilton 1983).

Seasonal migration by giant tortoises has some profound ecological and evolutionary implications. Why would these huge reptiles, well known for their ability to fast for long periods, undergo long distance migration? Why not stay put, and hunker down for the dry season when food becomes scarce? What would trigger migrations? How would tortoises navigate? What were the ecological impacts of these large, heavy, biological bulldozers (*sensu* Kortlandt 1984) pushing through vegetation, trampling, foraging, and perhaps dispersing seeds as they went? Importantly too, what might long distance migration mean for conservation? Some 97% of the land surface area of Galapagos has national park status. Of the remaining 3%, most is farmland in the humid highlands on human occupied islands. Long distance migrations could cause tortoises to leave protected areas for part of the year and live on private land. This presented an exciting opportunity to launch a study to discover whether tortoises really did migrate; and if they did, to learn which tortoises migrated, when, where, how, why, and what were the implications for conservation.

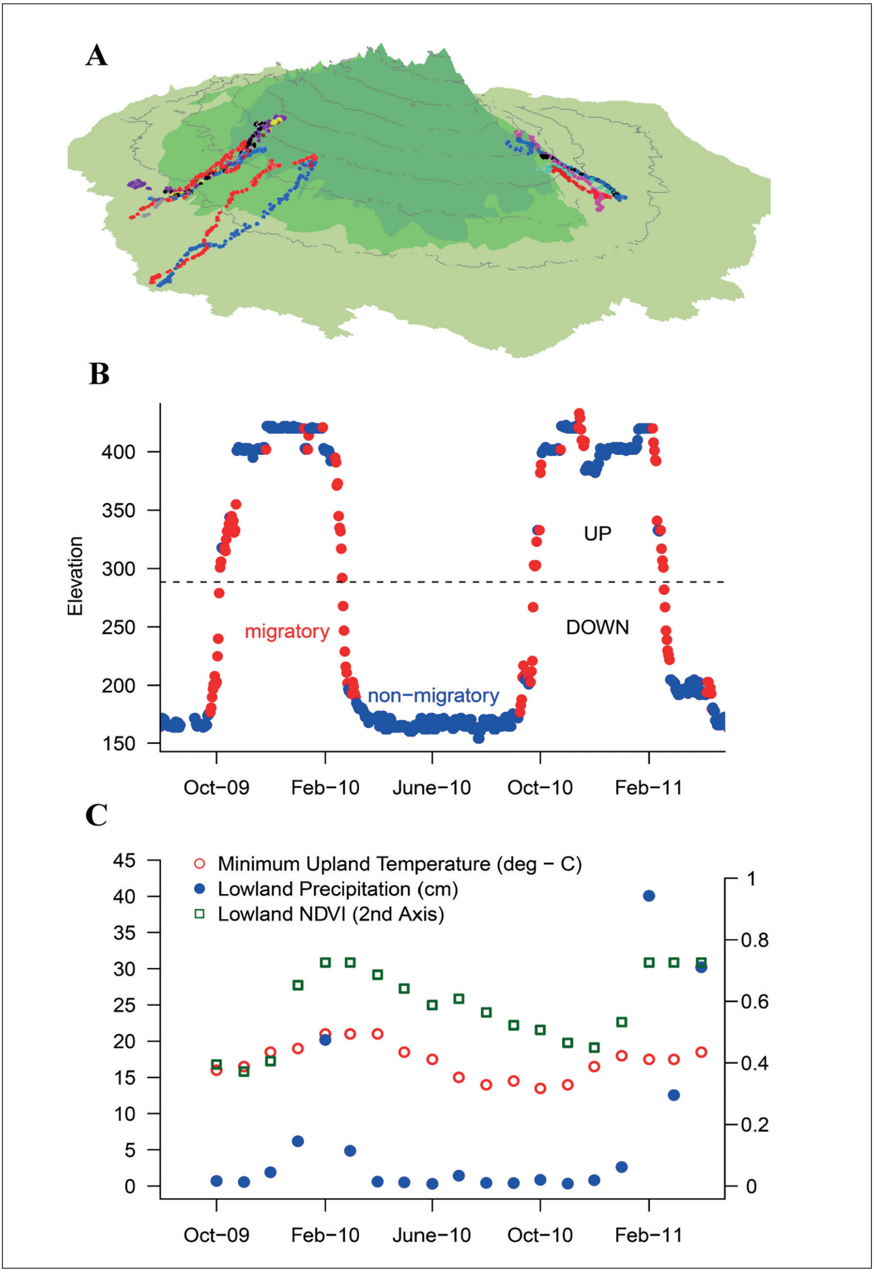

Fig. 2. (A) One year of GPS data from tagged tortoises on Santa Cruz Island. (B) The elevation of an adult male tortoise from Santa Cruz Island. (C) Environmental conditions along the elevation gradient of Santa Cruz.

In 2009, the Galapagos Tortoise Movement Ecology Programme (GTMEP) was initiated under the auspices of the Max Planck Institute for Ornithology, the Galapagos National Park Directorate, and the Charles Darwin Foundation. Ten custom made GPS tags (e-obs GmbH, Munich, Germany) were deployed (Fig. 1) onto adult tortoises on Santa Cruz Island, which rises to ca 860m, contains populations of two different tortoise species, and hosts the largest human population in the Galapagos Archipelago. The tags obtained a GPS fix every hour and stored the data on an onboard memory card. The data could be downloaded through Wi-Fi connection to a base station. The deployment of these tags spawned the productive period of research and discovery in movement ecology described in this article.

Galapagos tortoise movements

A year of relocation data from the tags (Fig. 2A) showed conclusively that Santa Cruz tortoises from both species underwent long distance one-way seasonal migrations up to 10km, from lowlands to highlands (Blake et al. 2013). These were stereotypic, seasonal, long distance migrations in the classic style of arctic terns, caribou, humpback whales and many other migrants (Milner-Gulland et al. 2011). The timing of the migration was closely correlated with environmental conditions along the elevation gradient of Santa Cruz, shown by the elevation of an adult male tortoise from Santa Cruz Island, characterized by long sedentary periods in the lowlands and highlands linked by rapid migratory movement up and downslope (Fig. 2B). Tortoise migrations are driven by oscillations in the spatiotemporal distribution of rainfall (Fig. 2C) which drives vegetation productivity. When lowland rainfall increases in January and February, it stimulates a rapid increase in vegetation productivity. Tortoises in the highlands begin migrating downslope to exploit this new nutritious growth rich in protein and low in non-digestible fibre. When the rain stops, productivity in the lowlands declines over coming months. At some point tortoises return to the humid highlands. There soils are always moist and the productivity is year-round, but vegetation quality is relatively low.

On Santa Cruz Island, tortoises start their lives in arid lowland nesting areas where temperature conditions are conducive to the incubation of eggs. When lowland vegetation becomes scarce during the cool dry season, the Santa Cruz highlands remain humid due to heavy cloud cover and foggy conditions, and the vegetation remains productive throughout the year. At this time, large tortoises migrate to the highlands to forage on the secure supply of available vegetation. They remain in the highlands until the onset of the hot rainy season when vegetation productivity increases again in the lowlands and both males and females migrate from humid highlands back to the arid lowlands.

As whalers and pirates knew well, Galapagos tortoises can fast for a year or more (Townsend 1925). So, why do adults bother to migrate into the highlands at all? Could an alternative strategy be to remain in the lowlands, and reduce activity and movements for the cool dry season, until vegetation growth begins again with the onset of high rainfall? The thermal environment along the elevation gradient and its impact on tortoise metabolism may hold part of the answer.

In ectothermic tortoises, high temperatures accelerate metabolism, which means high energy expenditure. When food is plentiful an accelerated metabolism is advantageous since food throughput and digestive efficiency are also high (Bjorndal 1989; Sadeghayobi et al. 2011); but when food is scarce, a warm tortoise will expend more energy than a cool one and may begin to use stored energy reserves. So, when food availability is limited in the relatively hot lowlands, it makes sense for a tortoise to move to the cooler highlands to reduce its internal temperature and energy costs. This migratory strategy will be adaptive over a year-round sedentary strategy if the energetic gains from migration are greater than the costs of the journey (Yackulic et al. 2017).

The migratory behaviour of tortoises is complicated, however, since not all tortoises migrate. Previous studies (Reeder & MacFarland 1978; Torres 2002) and observations from tortoise surveys on foot that accompanied the telemetry study showed that small tortoises do not migrate at all, and large tortoises migrate further upslope than smaller ones (Blake et al. 2013). Furthermore, anecdotal reports from other islands suggested that not all Galapagos tortoises migrate. It was time to expand the study to cover movements across the full ecological range of Galapagos tortoises, to investigate how the environment interacts with tortoise life history traits to drive the evolution of movement strategies.

In late 2010, 45 adult tortoises were tagged on three islands (Isabela, Española, and Santa Cruz) (Fig. 3).

Alcedo Volcano, located on Isabela Island, rises to 1100m, experiences little human impact, and hosts domed tortoises. Tortoises fitted with GPS tags on Alcedo (Figs 4 & 5) were all migratory. Migrations varied in their trajectories from some that followed the caldera, while others were elevational from lowlands in the hot wet season to the high caldera during the cool dry season.

Española is a small, relatively flat arid island which also has no human settlement, but hosts saddle-backed tortoises. Española tortoises were sedentary and nomadic, with nomadic periods often stimulated by the wet season when food and water were abundant. Española tortoises return to small home ranges centred around *Opuntia* cacti during the cool dry season.

Adult tortoises on Santa Cruz Island are mostly migratory, through some are sedentary and one tagged tortoise dispersed. Santa Cruz experiences the

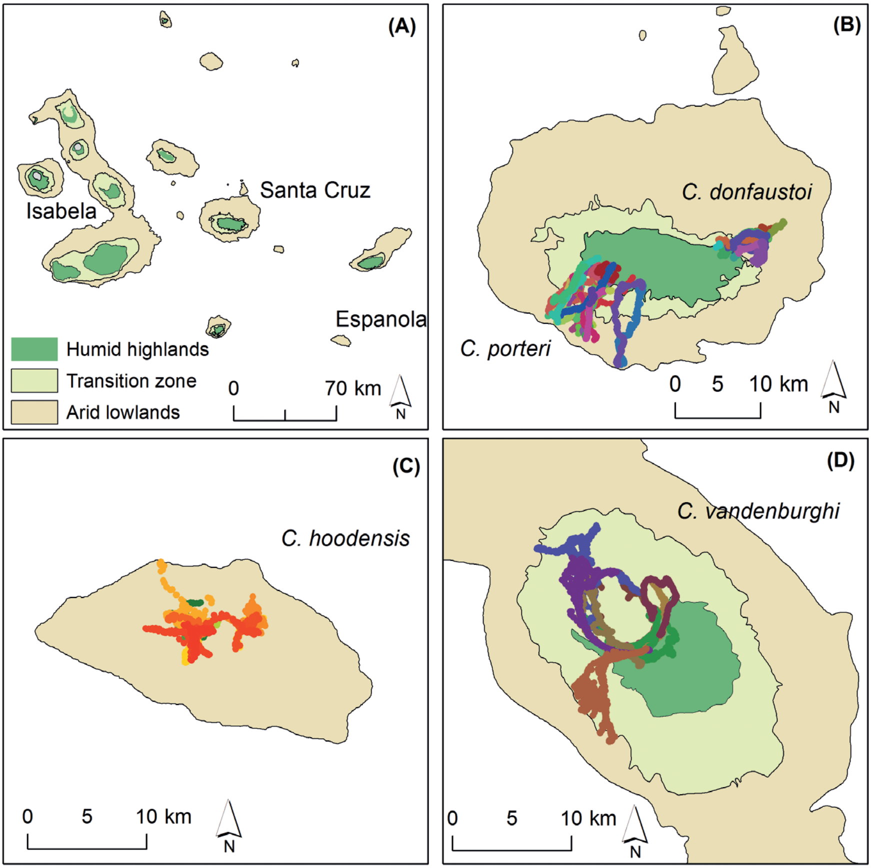

Fig. 3. (A) GTMEP operated on Isabela, Santa Cruz and Española Islands. (B) Migration patterns on Santa Cruz. (C) Migration patterns on Española. (D) Migration patterns on the Alcedo Volcano on Isabela.

highest human impact of any Galapagos Island with tortoises, and hosts two species of domed tortoise (Fig. 6).

To interpret relocation data from these tortoises, a variety of information on each animal was collected along with environmental data. Data from individual animals included sex, size, qualitative body condition, and in some cases quantitative health metrics (Blake et al. 2015; Sheldon et al. 2016). Environmental data were collected from both field weather stations and satellites. Weather stations provided hourly temperature and monthly rainfall. Satellite data quantified land surface temperature and an index of forage quality, (the Normalized Difference Vegetation Index [NDVI] from the MODIS products) described by Bastille-Rousseau et al. (2019). Local conditions vary

Fig. 4. This GPS tagged female tortoise (named Isabela) is in her dry season range to the southeast of the Alcedo caldera. When the rainy season kicks in, Isabela migrates around the caldera beyond the grey areas in the background. These open areas are sulphur springs which can provide warm soils. Isabela's total migration covers about 45km every year. Photo by Franz Kummeth.

both within and between islands, but the general pattern of seasonality remains the same – a cool dry season from June to December, and a hot wet season from January to May (Trueman & d'Ozouville 2010). El Nino Southern oscillations dramatically change weather patterns at irregular intervals every 6-10 years by increasing seasonal extremes (Colinvaux 1984).

Tortoises on different islands portrayed the gamut of movement strategies identified by ecologists, from stereotypical seasonal migration to nomadism in which animals move in an unpredictable fashion; dispersal, which involves movement to a distant location with no return trip; and sedentarism, which is prolonged use of a home range at a fixed location. Migration between spatially separated seasonal locations was the most frequent tortoise movement strategy on Alcedo Volcano and Santa Cruz, the two sites with humid highlands, while sedentarism was most common on flat, arid Española Island (Bastille-Rousseau et al. 2016a, 2017b). The reason for these patterns of movement may lie in the predictability of resource distributions through the archipelago (Bastille-Rousseau et al. 2017b). On Española there is little variation in the spatial distribution of resources through the year; however, there is considerable temporal variation. At the beginning of

Fig. 5. Downloading data from the tortoises' GPS tags from a hand-held base station. Due to limited range researchers must locate the tortoises using radio tracking. Here staff scientist Freddy Cabrera attempts to receive a radio signal from tortoises on Alcedo Volcano as a Galapagos hawk approaches overhead. Photo by Stephen Blake.

Fig. 6. Saddleback tortoises (left) occur on arid islands while domed tortoises (right) are found on islands with humid highlands. The morphology of these tortoises reflects the browsing ecology of saddlebacks and the grazer feeding ecology of domed tortoises. Photos by Stephen Blake.

the wet season vegetation grows profusely, and forage and water become relatively abundant for tortoises for a few short weeks. Annual variation is high, however. In some years rainfall is heavy and plant growth is vigorous; while in other years, rainfall is low and tortoises find little high quality forage. In general, however, on Española the dry season is always arid and food availability is poor. Thus, there are no reliable seasonal oscillations in the spatial distribution of resources to drive migration. On Alcedo Volcano and Santa Cruz however, where topography is varied, the seasonality of ocean and air currents interact with topography to drive predictable patterns in food distribution – peaks of productivity in lowland areas during the hot wet season and consistent upland vegetation production.

On Santa Cruz Island, rainfall increases with elevation except at the height of the wet season. The pattern on Alcedo Volcano, however, is more complicated. During the dry season prevailing winds from the south progress up the volcano causing dense cloud at the crater rim, but these quickly dissipate and much of the crater rim is bathed in sun. This leads to a distribution of vegetation around the rim similar to that along the elevation gradient on Santa Cruz. In other words, while the spatial distribution of vegetation on Santa Cruz increases with elevation, on Alcedo it increases on a gradient from north to south. In response to this pattern, Alcedo tortoises not only migrate between lowlands and highlands, but also from north to south.

Body size determines energy trade-offs in tortoise migration

Animal movement patterns, like every other trait, evolved as a result of complex trade-offs between maximizing short term energy balance with longer term goals like growth and repair, annual reproductive rates, avoiding predation and other sources of mortality, the individual effects of which all combine to drive the lifetime reproductive output of individuals (Nathan et al. 2008). Energy relationships in biology are intimately linked to organism size (Schmidt-Nielsen 1997); building bodies requires organic material from food (in the case of animals) and energy to grow cells and tissues. Body size scaling relationships (allometry) are a key feature of the nature of trade-offs. For example, among animals, surface area to volume ratio declines with increasing size, which influences mass specific metabolic rate, which decreases as body size increases; cost of locomotion per unit mass declines, while the requirement for investment in support structures, like bone and muscle, increases. Evolution optimizes the combination of these trade-offs to determine physical and behavioural characteristics in relation to environment. In relation to movement, there is a clear relationship between ranging capabilities of animals and body size (McNab 1963) – large animals have larger home ranges than small ones, due both to the need to find greater absolute quantities of food and to more efficient movement.

Small tortoises do not migrate. This observation led to an investigation of how allometric scaling might govern movement strategies of Galapagos tortoises. Large tortoises move further compared to smaller ones than would be predicted based on a linear relationship (Bastille-Rousseau et al. 2016b).

Fig. 7. A small tortoise feeding. Photo by Stephen Blake.

Fig. 8. A large tortoise browsing. Photo by Stephen Blake.

Moreover a theoretical model developed by Yackulic et al. (2017) showed that, on Santa Cruz Island, whether tortoise migration is a more efficient strategy than remaining sedentary depends more on the relationship between body size and the benefits of food acquisition at the destinations than on the relationship between body size and the costs of the journey. This is in contrast to most mammal and bird migrants, in which the key factor in migration is the cost of the migratory journey (Wikelski et al. 2003; Hedenström et al. 2011).

Small tortoises are less sensitive to forage availability than large ones, primarily because they require only a small quantity of food to maintain their small bodies; thus they can always find enough plant material to maintain themselves, even during the dry season in the lowlands of Santa Cruz Island (Fig. 7). While large tortoises have lower mass-specific energy requirements, they do have big bodies to maintain and so require relatively large quantities of food. They can eat in a single mouthful enough food to sustain a smaller individual for days. Therefore, when the rains stop and vegetation productivity declines, large tortoises are more sensitive to food shortages, and migrate to the highlands where they can find secure stable food resources due to the permanently moist conditions. A small tortoise can survive in lowland habitats year-round because it can usually find a microclimate where a small but sufficient amount of food occurs. The quantity of food that sustains a small tortoise for the entire dry season might provide only a few mouthfuls of food for a large male tortoise.

Among the predictions of Yackulic et al. (2017) were that: 1) migration would become adaptive (the most favourable energetic balance) at a tortoise body mass of about 80kg; and 2) among migratory individuals large tortoises should leave the lowlands earlier than smaller individuals, because they would run out of food earlier in the season. Field observations very strongly supported these model predictions.

Migration and tortoise conservation

Long distance migrations around the world are disappearing as a result of habitat loss and degradation at destinations and barriers to movement along migration routes (Wilcove & Wikelski 2008; Harris et al. 2009; Holdo et al. 2011; Sawyer et al. 2016). The great aggregations of wildebeest and other ungulates in the Serengeti, single flocks of millions of sea and land birds on the wing traversing continents, and Arctic caribou and Mongolian gazelles trekking across endless grasslands may soon cease to exist. Galapagos tortoises hauling their heavy, cumbersome bodies up and down volcanoes may be less spectacular than these examples; but nevertheless represent a still intact long-distance migration, and one that is fundamentally important to tortoise ecology and energy balance. Unfortunately, even in Galapagos, some tortoise species face serious habitat problems on inhabited islands such as Santa Cruz, caused by human land use, development of infrastructure and introduction of invasive species. Two particularly aggressive introduced plant species, *Rubus niveus* (blackberry) and *Pennisetum purpureum* (elephant grass) grow in extensive, dense thickets in which they out-compete and eliminate tortoise food species and inhibit tortoise movements. The spread of these species can block tortoise migration routes.

In other cases, farmers construct dense fences of tightly spaced trees spanned by barbed wire to keep tortoises off their pastures. The fencing of small areas to protect vegetables and fruit may not be detrimental to tortoises; but if large areas of upland habitat are blocked by fences, the tortoises may be unable to find food and maintain good body condition in their upland phase.

The current impact of roads and urbanisation on tortoise movements and migrations is difficult to assess with current data, principally because studies of migration began long after much infrastructure was already in place. Some roads pose formidable barriers to movement, while less well-used roads, particularly tracks, are used frequently by tortoises. Often, however, these dirt roads have barriers along much of their length which compromises the ability of tortoises to move off the road into surrounding vegetation, also exposing them to new threats such as car impacts and plastic ingestion.

Management implications

Pending the results of more detailed analysis of tortoise movements some pragmatic management actions are appropriate.

Remove or reduce barriers to migration

Cattle farmers who attempt to protect their farms from tortoises should be encouraged to make their pasture lands available to these animals which have relied on such areas for millennia. This can be achieved by maintaining multiple openings within otherwise dense fences through which tortoises can pass, but which are too small to allow the passage of cattle. Unless pastures are marginal or cattle stocking densities are close to carrying capacity, moderate densities of tortoises are unlikely to cause economically significant reductions in forage availability for cattle; indeed, the presence of tortoises may increase the productivity of grasslands (Hamilton & Coe 1982; Bastille-Rousseau et al. 2017a).

No successful methods have yet been devised on Galapagos for the eradication of either blackberry or elephant grass, which represent two significant barriers to tortoise movement that are also catastrophic to native species. In lieu of effective eradication, pathways should be made through extensive thickets of these species in known tortoise migration areas. Some farmers do this every year already to facilitate tortoise access into viewing areas for tourists.

Road development plans for the Galapagos highlands are not publicly available, but as the economy continues to grow, infrastructure development becomes more likely. Ideally, further road construction should be avoided due to their myriad negative ecological impacts (Forman & Alexander 1998), not just on migratory species. If road developments must occur, tortoise movements should be taken into account, and include the following features:

- ❑ Highland to lowland orientation, rather than running parallel to elevation contours.
- ❑ Road verges that are permeable to tortoises.
- ❑ Development and enforcement of strict rules to minimize urbanisation along roads.
- ❑ Traffic control.
- ❑ Tortoise overpasses or underpasses at critical intersections between major roads and tortoise migration routes (as is done commonly around the world for other migratory species).

Maintain high-quality habitat at both ends of the migration

Various options are under consideration for further development of the Santa Cruz highlands. These include re-invigorating agriculture for cattle, boosting fruit and vegetable production, creating multiple use areas that integrate agriculture with ecotourism, and attempts at large-scale restoration of native habitats within agricultural zones. Whatever actions are taken, tortoise conservation must be included as a planning priority if tortoises are to thrive. Tortoises may not be compatible with production of succulent vegetable and fruit crops, since failure to protect these crops in areas with large numbers of tortoises will lead to crop damage and potentially significant economic losses to farmers. Applied research is necessary to explore management options, but crop production in protected plots within a matrix of pasture and native/semi-native habitats is likely be compatible with tortoise conservation. Crops such as coffee, the production of which is expanding rapidly on Santa Cruz, may require protection during the establishment phase. Careful consideration of how to protect large areas under cultivation without creating major barriers to tortoise movement is needed.

Failure to maintain critical tortoise habitats and migratory corridors is likely to result in serious negative consequences for both tortoise species on Santa Cruz and perhaps also for those on other inhabited islands. Careful land use planning is needed. The above recommendations and other ideas need to be elaborated and refined through discussions amongst farmers, citizens, professionals and scientists. Implementation of such actions can provide simple, inexpensive, and effective ways to sustain tortoises and their migrations.

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