

## Chapter 13

# Movement ecology

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### Introduction

At first glance, the decision to study movement in Galapagos tortoises seems curious. Given the slow speed of tortoises and their tendency to forage and rest as they move, it seems implausible that tortoises would string their slow bursts of activity together to accomplish large-scale movements. Nonetheless, as early as 1815 (Porter 1815) visitors to Galapagos noted the propensity for tortoises to walk long distances along well-used trails, leading to seasonal changes in the distribution of tortoises on the various islands of the Archipelago. In recent years, advances in the technology used to track animals have led to a better understanding of movement and the diversity of movement strategies among many animal taxa. This chapter focuses on the application of this technology to the study of movement in Galapagos giant tortoises. Recent work has shown not only the diversity of movement strategies employed by Galapagos tortoises but also illustrated how movement can both cause and be a consequence of the interaction between reproductive and foraging ecologies of tortoises and the presence of strong environmental gradients. Understanding that critical unimpeded movement is vital to the persistence of Galapagos giant tortoises also

informs efforts to maintain connectivity to, and suitable habitat within, tortoise range outside of protected areas.

### Galapagos tortoise movement ecology

Movement—a change in spatial location—is fundamental to all life. Patterns of movement throughout the lives of organisms impact the fitness of individuals, with cascading effects through populations, communities, and ecosystems (Alexander 2007; Chambers and Macmahon 1994; Travis *et al.* 2012). The interactions between organisms and their environment influence the evolutionary ecology of movement patterns, which feed back into the structure and function of ecosystems and of evolutionary processes. The discipline of movement ecology attempts to simplify this complexity into a unified mechanistic framework, within which predictions on the drivers of movement and how organisms and ecosystems may respond to environmental change can be made and tested (Nathan 2008). In a world dominated by anthropogenic change, such a framework is becoming increasingly critical for conservation (Tucker *et al.* 2018).

What does this have to do with Galapagos giant tortoises? The surprising answer, given the popular view of tortoises as slow, sedentary plodders, is “everything.” Galapagos tortoises move to find and exploit food resources, thermoregulate, find mates, locate nighttime resting sites, and much more. Charles Darwin spent many hours watching and following giant tortoises, which inspired him to ask some very basic questions (Darwin 1839): “Why do giant tortoise trails go up and down the slopes of the Galapagos Islands?” and “How far can a tortoise walk in a day?” To answer the first question, Darwin asked the locals, who told him that tortoises walked long distances on regularly used paths. To answer the second, Darwin followed a tortoise all day, methodically counting his steps to record distance. “At this pace, the animal would go four miles in the day & have a short time to rest” wrote Darwin. On occasion, he even rode tortoises but was disappointed by their lack of comfort and speed. But, thanks to Darwin, the study of Galapagos giant tortoise movement ecology was underway.

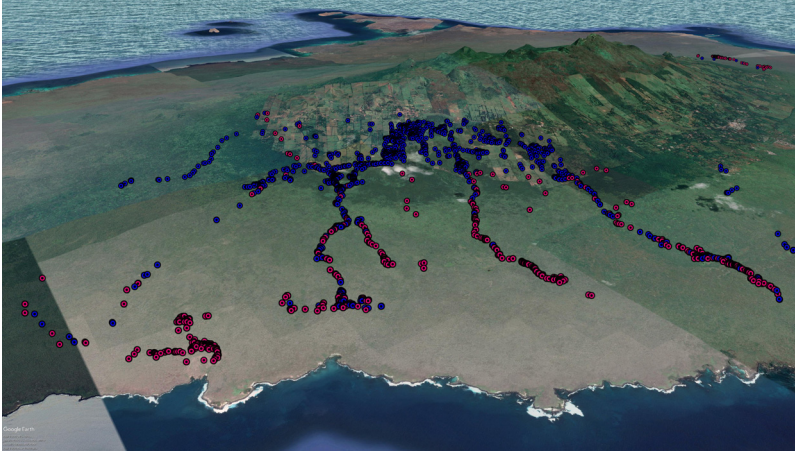
Darwin’s observations quickly inspired interest among zoologists in giant tortoises around the world, including Galapagos, The Mascarenes, and Aldabra (e.g., Günther 1874; Rothschild 1915, 1902). These early studies focused on morphology, taxonomy, and the origins of giant tortoises with little reference to ecology or movement. The first champion of Galapagos giant tortoises was John Van Denburgh, the Curator of Reptiles for the California Academy of Sciences, who described details of key tortoise populations on different islands and volcanoes, including notes on distribution, behavior, threats from people, and some clues on tortoise movements. Based on notes of members of the 1905–06 expedition of the California Academy of Sciences to Galapagos, he described tortoises using trails frequented by cattle and donkeys; however, it was unclear whether these trails were made by tortoises and used by the domestic animals or vice versa (Van Denburgh 1914).

It was not until the 1970s that research on the movement ecology of giant tortoises began in earnest. Studies on Aldabra Atoll under the auspices of the University of Oxford’s Zoology Department were completed on ecology, population dynamics, reproduction, and movement (Bourn *et al.* 1999; Coe *et al.* 1979; Eskildsen *et al.* 2004; Gibson and Hamilton 1984; Gibson and Phillipson 1983a,b; Grubb 1971; Merton *et al.* 1976; Swingland 1977; Swingland and Coe 1979; Swingland and Lessells 1979). Observations showed that during the dry season, Aldabra tortoises were concentrated toward the interior of the atoll where they foraged on ground vegetation (grasses, sedges, and forbs), locally called “tortoise turf,” where shade was available under dense shrubs. In the rainy season, coastal grass sward grew vigorously, and a proportion of the tortoises

migrated to these coastal areas to forage (Gibson and Hamilton 1983; Swingland and Lessells 1979). Large male and immature tortoises had a higher propensity than younger adults to migrate. It was postulated that the trade-offs between migrating and remaining sedentary were balanced—migratory tortoises had access to higher quality forage but risked mortality from overheating in the exposed coastal vegetation (Swingland and Frazier 1980; Swingland and Lessells 1979). Importantly, this body of work demonstrated migration in large terrestrial ectotherms, which seemed incongruous with their poor mobility and prodigious fasting ability.

Research on tortoise ecology and movements in Galapagos also began in the early 1970s and provided overviews of abundance, diet, and reproduction on several islands, which set the scene for conservation strategies (Fowler 1983; Fowler de Neira and Johnson 1985; Fowler de Neira and Roe 1984; MacFarland *et al.* 1974a,b). Some of the first quantitative data on tortoise movements came from members of the Cambridge and London University expeditions in 1972–73 (Rodhouse *et al.* 1975). Daily movements on Santa Cruz Island were described in which tortoises followed roughly circular routes often starting and ending at a sleeping site, with daily travel distance between 21 and 413 m. Rodhouse *et al.* (1975) also mentioned seasonal migrations from the uplands into lowlands, which they assumed were for egg laying in the arid zone. In the late 1980s Pinos (1990) recorded the locations of a cohort of 25 repatriated 1-year old tortoises on Española Island, observing that among the 14 individuals that could be relocated after 1 year, all but one remained within 100 m of their repatriation site.

The human residents of Galapagos have long known that there were seasonal swings in the abundance of tortoises with elevation on some islands. In the early 1980s, Cayot (1987, 1985) corroborated this local knowledge. During El Niño 1982–83, tortoise abundance declined dramatically at approximately 200 m elevation in the humid highlands of Santa Cruz Island; with the onset of El Niño rains, the majority of tortoises moved to lower elevations. Cayot surmised that the extreme rainfall triggered a migration as a survival mechanism to escape flooding, extremely dense vegetation, and much colder weather (Cayot 1987, 1985). Interestingly, there was no mass movement of tortoises on Pinzón Island during the same period, perhaps due to less of an elevational gradient, indicating that tortoises on different islands might have different movement strategies. Early use of individual recognition of tortoises combined with radiotracking on Alcedo Volcano provided equivocal results on tortoise movement patterns (Beaman 1985; Beaman and Harris 1987). Beaman was unable to relocate tortoises using radiotracking but noted that there was a seasonal shift in tortoise distribution.



**FIGURE 13.1** Seasonal distribution of tortoises on Santa Cruz Island. Blue dots represent tortoise observations collected during October, November, and December (the cool season); red dots are observations made in March, April, and May (the hot season). Tortoises are concentrated at higher elevations in the cool (*garúa*) season and in the arid lowlands in the hot season.

Evidence for long-distance movements also began to accumulate. On Santa Cruz and other islands in Galapagos, researchers and park rangers conducted *ad hoc* surveys during which they recorded the location of every tortoise observed along with data on sex, size, and sometimes weight. Many tortoise observation data collected after 1998 were georeferenced using global positioning system (GPS) devices, and when these data collected on Santa Cruz Island are pooled and separated by season, the population scale shift in the distribution along the elevation gradient becomes clear (Fig. 13.1).

During the cool season, tortoises concentrate at higher elevations, whereas in the hot season, the population shifts to the arid lowlands. The early data, summarized by Torres (2002) and Guerra (2005), showed altitudinal and seasonal structuring of the tortoise population by body size and sex: juveniles occurred only at low elevations, females were most abundant at low and intermediate elevations, and large males dominated higher elevations during the cool season. Importantly, Torres (2002) recorded long-distance movements up to  $>5$  km in a single month (for a large male in the Cerro Fatal population on eastern Santa Cruz), and mean monthly linear displacement distances of approximately 1–2 km.

In aggregate, these observations were intriguing for at least three reasons. First, long-distance elevational migration was confirmed. Second, different populations and even different individuals within populations displayed different movement strategies suggesting that Galapagos could provide a window into the evolution of movement strategies. And lastly, long-distance movement by tortoises moving into and out of protected areas on inhabited islands might create conservation challenges. Might the study of Galapagos giant tortoise movement ecology provide insights into general rules governing the evolution of movement and impact of conservation strategies? Darwin's 170-year-old question of why the trails went up and down the volcanoes remained only partially answered. The time was right to use

state-of-the-art tracking technology to complement mud-on-the-boots ecological research to answer the “who, when, where, how, and why” of tortoise migration.

### Tracking tortoise movement using GPS

The Max Planck Institute for Ornithology, the Galapagos National Park Directorate, and the Charles Darwin Foundation began a study in 2009 called the *Galapagos Tortoise Movement Ecology Programme*. In an initial pilot study, eight adult and subadult tortoises from the two populations on Santa Cruz (four tortoises from each) were fitted with custom-made GPS tags (e-obs GmbH, Munich, Germany). The tags recorded every hour each tortoise's location, which was then stored in flashcards in the tags and eventually retrieved by handheld wireless base station (Fig. 13.2A). The tags incorporated a radio-tracking beacon to facilitate the relocation of the tortoises for visual inspection and data download. Tortoise location data over time provided answers to the “who, when, where, and how” of migration and other movement strategies but could not respond to the “why.” Understanding the evolutionary ecology of tortoise movements (“the why”) required data on a variety of explanatory variables, both intrinsic and extrinsic, that were hypothesized to influence movement.

Intrinsic variables studied were initially limited to body size and sex. Extrinsic variables included temperature and rainfall, which also drive patterns of primary (plant) productivity and thus food availability for herbivores. A series of weather stations was installed every 50 m in elevation between 50 and 400 m in both the western and eastern Santa Cruz tortoise populations (Fig. 13.3). Rainfall was measured monthly using rain gauges and shade temperature every 4 hours using iButtons (Blake *et al.* 2013). Satellite data in the form of the Normalized Difference Vegetation Index (NDVI) from NASA's Moderate Resolution Imaging Spectroradiometer instrument (Justice *et al.* 1998) were used





**FIGURE 13.2** The first GPS tags deployed on Galapagos giant tortoises were made by Franz Kummeth and weighed approximately 500 g (A). Tags were fitted to either the front (females) or rear (males) of the carapace using plumber's epoxy putty (B). Tags stored many months of data, which could be retrieved with a handheld base station (C). Randall Keynes (Charles Darwin's great-great-grandson) downloading movement data from an adult male who could very well have been alive and migrating when Darwin was writing his masterwork. *GPS*, Global positioning system. *Photos: Stephen Blake.*

as an index of vegetation productivity (Huete *et al.* 2002). These data characterized gross patterns in climate and food availability on Santa Cruz Island at spatial and temporal scales relevant to the interpretation of tortoise movements.

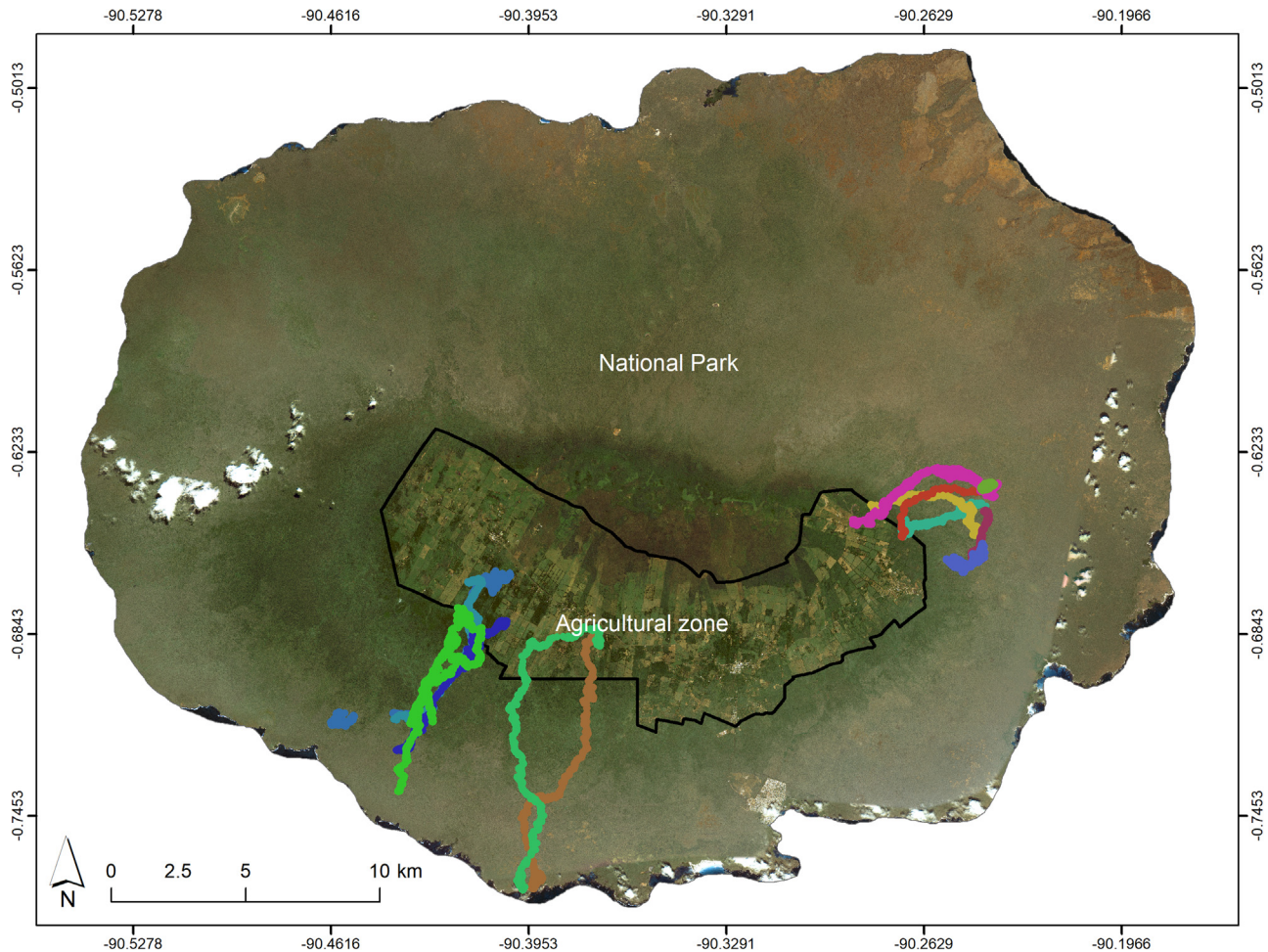
The first year of movement data demonstrated conclusively (Figs. 13.3 and 13.4) that Galapagos giant tortoises undergo stereotypic, long-distance seasonal migrations (Blake *et al.* 2013) in the same classic style as arctic terns, Serengeti herbivores, and myriad species around the globe (Bauer and Klaassen 2013; Dingle and Drake 2007; Milner-Gulland *et al.* 2011). Most tortoises migrated along well-used trails between arid lowlands and humid highlands, whereas some pushed their way through thick vegetation and scrambled over lava.

Male and female tortoises from both species migrated from elevations between approximately 300 and 400 m in the humid highlands during the cool season to arid lowlands in the hot season. Some western Santa Cruz tortoises migrated almost to sea level, whereas eastern Santa

Cruz tortoises usually stopped between 160 and 150 m elevation (Fig. 13.4). Tortoise migration downslope to the lowlands coincided with the “greening up” of the arid lowland vegetation at the onset of heavy rains. In the first year of study, peak lowland vegetation productivity occurred in February and March, exactly when most tagged tortoises arrived, and for a short time exceeded upland productivity (Fig. 13.5). Over subsequent months, rainfall and vegetation growth in the lowlands steadily declined. In contrast, vegetation in the humid highlands remained consistent throughout the year due to heavy stratus cloud cover and moist foggy conditions during the cool season.

If the Santa Cruz Island uplands remain productive year-round, why would adult Galapagos tortoises ever migrate to the lowlands? Alternatively, given their low metabolic rate, why would tortoises not remain in the lowlands year-round conserving energy by decreasing mobility? There are several potential explanations, including the interaction between





**FIGURE 13.3** One year of movement data from 10 adult giant tortoises on Santa Cruz Island revealed the extent of long-distance altitudinal migration, from 0 to 450 m elevation, and tortoises moving from the Galapagos National Park protected area into private agricultural land.

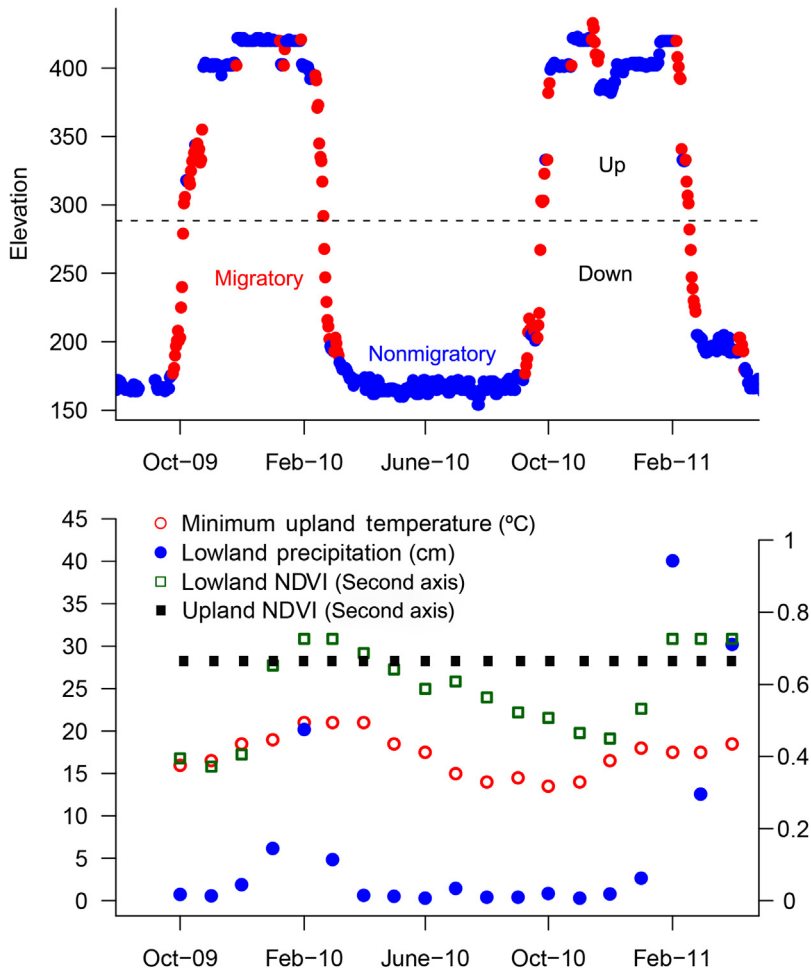
vegetation quality and quantity, tortoise body size, constraints of reproduction (e.g., mating, nesting, and offspring survival), temperature gradients and their impact on tortoise metabolism and energy balance, and the cost of movement, potentially a key determinant of migration (Sapir *et al.* 2011; Wikelski *et al.* 2003).

Based on the well-established “forage maturation hypothesis,” it is known that new vegetation growth is more nutritious than older plant tissues (Fryxell 1991; McNaughton 1985). Arid zone plants green-up rapidly with the onset of rains, producing tissues high in protein and digestible carbohydrates, and low in toxic antiherbivory compounds. As plant tissue matures, nutritional quality and digestibility decline while toxicity to herbivores often increases. Thus on Galapagos, although there is a more stable *quantity* of vegetation year-round in the humid highlands, the *quality* of this forage is relatively low. Tortoises with access to the lowlands during the period of “greening up” will find highly nutritious forage. With the onset of the cool season, tortoises can migrate

into the highlands and find reliable, abundant but low quantity forage. This pattern is consistent with migratory mammalian herbivores around the world (Augustine and McNaughton 2006; Frank *et al.* 1998; Fryxell *et al.* 2004; Hebblewhite *et al.* 2008; Middleton *et al.* 2018).

Migratory mammals and birds are endotherms that are obliged to maximize their energy budgets due to high metabolic costs (Weber and Houston 1997), and forage quality is paramount to both short- and long-term energy balance. Galapagos giant tortoises, on the other hand, are large ectotherms that can fast for a year or more (Townsend 1925). Given that tortoise nesting sites and all juveniles on Santa Cruz Island are found in the lowlands, why migrate into the highlands at all? Why not wait out the dry season in the lowlands and be ready to begin foraging as soon as the rains begin? The answer may lie in part in the thermal environment along the elevation gradient and its impact on tortoise metabolism.

Tortoise metabolic rate is related positively with internal temperature: high temperatures induce a high metabolic rate,



**FIGURE 13.4** After 1 year of movement data from tortoises fitted with GPS tags on Santa Cruz Island, coupled with environmental data from weather stations and satellite, a strong correlation emerged between tortoise migration and vegetation productivity. Tortoises migrated into lowlands as vegetation productivity peaked and returned to dependable year-round forage in the highlands when lowland vegetation abundance declined. *GPS*, Global positioning system.

irrespective of activity. High internal temperature means high energy expenditure, but it also means higher food throughput and efficient digestion are possible compared to low internal temperature (Bjorndal 1989; Sadeghayobi *et al.* 2011). If forage is plentiful, a warm tortoise can process large quantities of food but will be energetically penalized if food is scarce. During food scarcity, a tortoise can reduce energy consumption by selecting cool conditions. Thus on Santa Cruz Island during the cool season tortoises may be energetically motivated to migrate to the highlands to lower their metabolic costs, which would be adaptive if the energetic savings outweigh the costs of the journey.

Not all tortoises migrated in the first year of the pilot study, suggesting that these tortoises may be best characterized as partial migrants in which only a portion of the population migrates (Chapman *et al.* 2011; Lundberg 1988). The presence of migrating and nonmigrating adult tortoises within a single population offered an intriguing opportunity to study the effects of movement on fitness and identify the selective pressures that determined the evolutionary ecology of movement strategies. Furthermore, the upland destinations were different for

males and females: males generally migrated to higher elevations than females (Blake *et al.* 2013; Guerra 2005). Moreover, environmental conditions vary by island (Colinvaux 1984; Trueman and d'Ozouville 2010) and tortoises on different islands can display different movement patterns (Cayot 1985), providing an opportunity to study movement within and between different populations under different selective forces.

Understanding the variation in movement strategies among Galapagos giant tortoises also has profound implications for conservation. As barriers to movement proliferate and tortoise habitat at migration destinations are degraded, long-distance migration is a disappearing biological phenomenon worldwide, and migratory species are in dramatic decline (Harris *et al.* 2009; Sawyer *et al.* 2016; Wilcove and Wikelski 2008). Galapagos tortoises that migrate into and out of protected areas, as they do on Santa Cruz Island, are threatened by changing land use practices, infrastructure development, and invasive species, which combine to further modify the landscape. The pilot study then cracked open the window Darwin had peered through, to a vision for a larger research program





**FIGURE 13.5** Adult Galapagos giant tortoises were tagged on three islands: Alcedo Volcano on Isabela Island (left), and Española (top right) and Santa Cruz (bottom right) Islands. Photos: Christian Zeigler.

involving tracking multiple species on multiple islands over multiple years, using giant tortoises as a model system to better understand how environment, physiology, and life history interact to determine movement strategies.

### A decade of movement data: 100+ tortoises from four species on three islands

In 2010, 45 tortoises from four species on three islands were fitted with GPS tags. The sample attempted to span the range of ecological and human impact conditions experienced by Galapagos giant tortoises and included both dome and saddleback tortoises (Fig. 13.6). Adults of both sexes were tagged on: (1) Alcedo Volcano on Isabela, which ascends to approximately 1100 m with minimal human impact (with the exception of dramatic vegetation change in the 1990s and early 2000s caused by goats: Bastille-Rousseau *et al.* 2017a; Bellingham *et al.* 2010; Brewington 2013) and is home to dome tortoises (*Chelonoidis vandenburghi*); (2) Santa Cruz Island,

reaching an elevation of 860 m with extensive farming in the humid highlands and an abundance of introduced and invasive plant species, and home to two species of dome tortoises (*C. porteri* and *C. donfaustoi*), and (3) Española Island, a flat arid island rising to little over 200 m, with low current human impact, but a legacy of feral goat-related vegetation change (Gibbs *et al.* 2014) and home to saddleback tortoises (*C. hoodensis*).

An enormous dataset on tortoise movement has been amassed over the last decade, with additional GPS tag deployments on both species of Santa Cruz tortoises including juveniles and subadults. The dataset now consists of over two million locations from 107 different individuals. To complement the tortoise movement data, a variety of environmental datasets were collected to quantify the change in environmental conditions across the ranges of the four species, including satellite-derived data: (1) NDVI (plant productivity) as a proxy for forage quality at a temporal resolution of 16 days and spatial resolution of 250-m pixels; (2) nightly land surface temperature at a 1-km spatial resolution, and (3) daily temperature and monthly rainfall from field weather





**FIGURE 13.6** Variable topography and weather patterns on Alcedo Volcano promote vastly different environmental conditions and habitats, which provide the contrasting resource distributions in time and space that lead to the adaptive value of migration. *Photos: Christian Zeigler.*

stations on Santa Cruz Island (Bastille-Rousseau *et al.* 2019, 2017b; Blake *et al.* 2013; Yackulic *et al.* 2017).

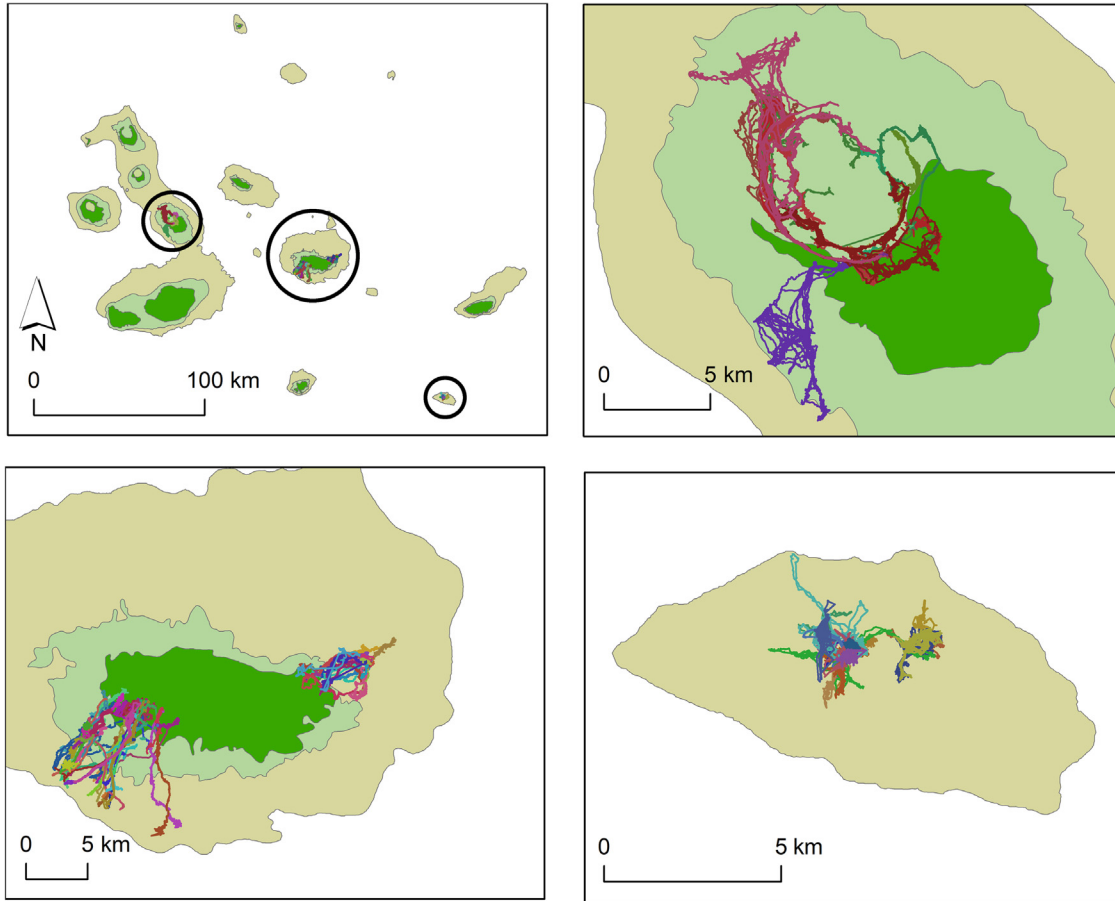
The landscapes and environmental conditions on each island where tortoises were studied are very different (Fig. 13.6). Española Island has the lowest vegetation productivity and highest temperatures, Santa Cruz has the highest productivity and intermediate temperatures, with Alcedo Volcano having the lowest temperatures. All islands followed the same underlying seasonal trends: highest temperature, rainfall, and productivity from January to June (the hot season), and lowest temperature, rainfall, and productivity from September–November (the height of the cool season). However, predictability of forage availability was highest on Alcedo Volcano, moderate on Santa Cruz, and lowest on Española (Bastille-Rousseau *et al.* 2017b). Variability in vegetation productivity was greatest on Alcedo Volcano and least on Española Island. The cone-like Alcedo Volcano imparts complex topographical patterns of weather conditions that generate much heterogeneity in forage availability, whereas the small size and low elevation of Española Island generate more homogeneous conditions.

Against this backdrop of dynamic environmental conditions, it was not surprising that tortoise movements varied strongly among islands. Where seasonal resource distribution

shifts predictably over large spatial scales (Alcedo Volcano and Santa Cruz Island), tortoises were usually migratory. On Alcedo Volcano, with the most predictable environment, all tortoises migrated between a cool season range at the south-east of the caldera centered around the heaviest and most consistent cloud cover (the rim), and a hot season range usually on the northern and western flanks of the volcano including inside the caldera (Fig. 13.7). The movement range of most tortoises in the hot season was larger and more variable than during the dry season (Fig. 13.8). The dry season movement range often consisted of a core, densely vegetated area tortoises used to avoid the moisture-laden prevailing winds, around which tortoises foraged during the day. This behavior could last for months until the next migratory journey began. The cool season range, concentrated on the southern rim, was consistently colder and more humid than any other part of the volcano. Most Alcedo Volcano tortoises migrated around the rim of the caldera on large trails, often the same route over many years, whereas others used different routes for the outward and return journeys. A full annual migration for an individual could cover 45 km.

On Santa Cruz Island, most tortoises from both species, particularly larger individuals of each, were migratory (69% and 77% for eastern and western species, respectively). Migrations of western Santa Cruz Island tortoises followed





**FIGURE 13.7** Movements of Galapagos giant tortoises on different islands. Lines of different colors reflect movements of different individual tortoises. Migration was the dominant strategy on islands with an extensive elevation gradient and predictable seasonal shifts in temperature, rainfall, and vegetation productivity (top right map – Alcedo Volcano on Isabela; bottom left map – Santa Cruz Island). Most tortoises on the only relatively flat, arid island included in the study, Española – bottom right, were sedentary.

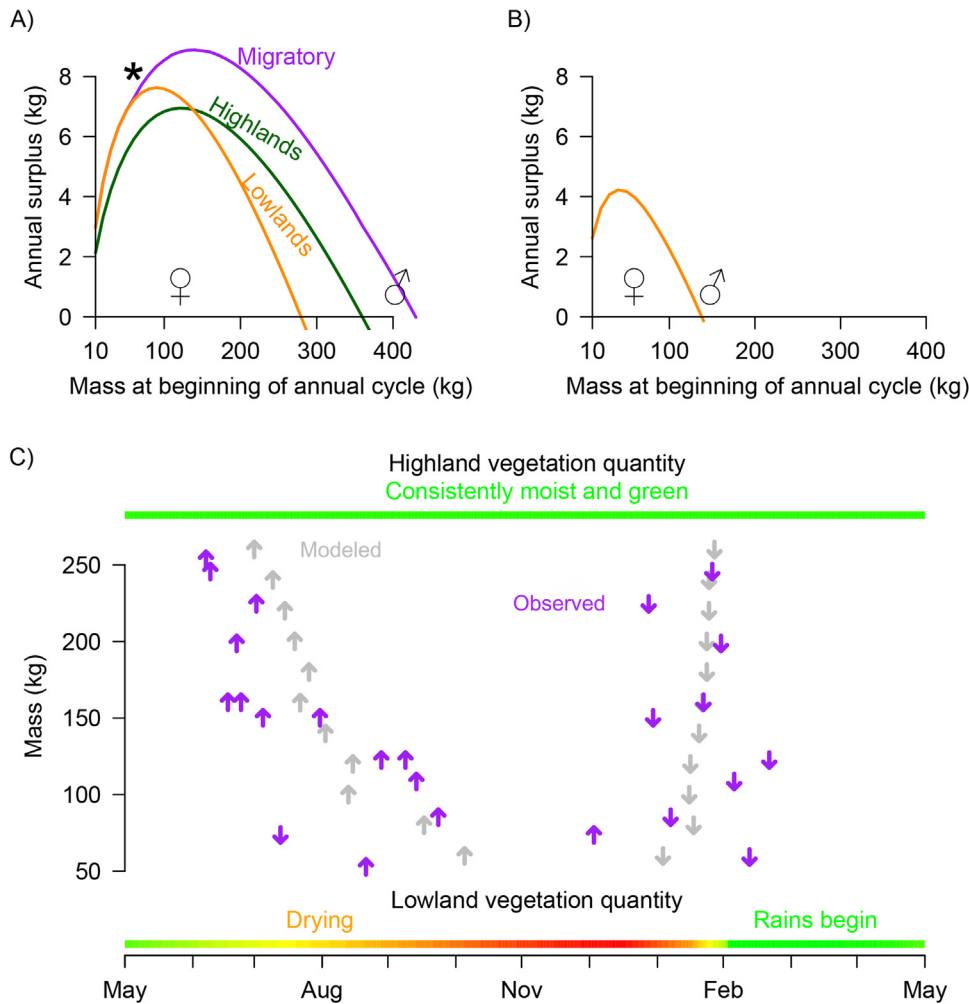
linear trajectories up and down the elevation gradient, up to approximately 10 km one way. Eastern Santa Cruz Island tortoises had curvilinear and shorter migrations, to a maximum of 7 km one way. Most tortoises migrated along the same trajectory (Bastille-Rousseau *et al.* 2019), often taking advantage of gullies, in which occasional flash floods denude much of the vegetation and provide a more open movement path. In both species the limit of the upland migration was approximately 450 m in elevation; the lower limit differed between species, with some western Santa Cruz tortoises migrating all the way to the coast, whereas the lower limit of eastern Santa Cruz tortoises was approximately 70 m in elevation.

Española Island tortoises did not migrate. Nine of the eleven tortoises remained sedentary within small ranges, and two (one male and one female) were nomadic. Many Española tortoises were “central place foragers” meaning that they were usually located at a small point location but foraged over short distances around the site before returning. Most of these point locations were at the foot of a large *Opuntia* cactus. Despite not migrating,

Española tortoises did respond to seasons. During the cool season, the tortoises ranged over very small areas and were concentrated at favored point locations. As the hot season rains began, they expanded their ranges, foraging nomadically, before either returning at the end of the rains or finding a new point location for the impending dry season. Conditions on Española Island can be particularly dry and hot. Shade and access to occasionally falling cactus pads and fruits are important resources when food and water are sparse. At the onset of the hot season, forage abundance increases dramatically, standing water is abundant, and tortoises may be unconstrained for a few short weeks to wander.

### A bioenergetic model of tortoise migration

Understanding why some tortoises migrate and others do not is difficult. Migration is driven at least in part by the distribution of food resources, but why then do some adult tortoises in predictable environments not migrate, and

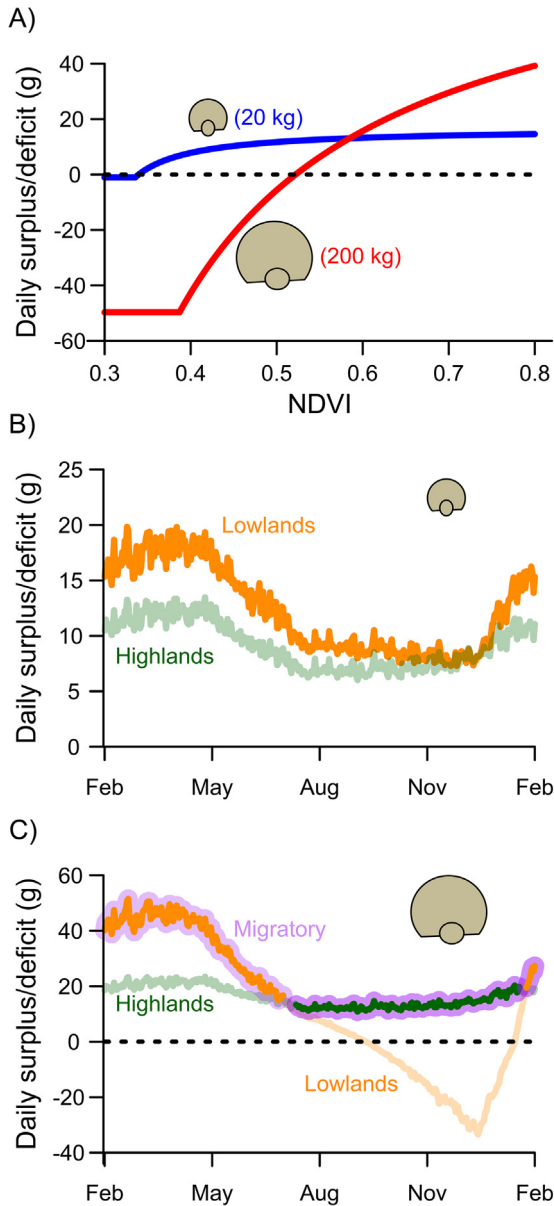


**FIGURE 13.8** Predictions from the Galapagos tortoise movement model are generally validated by the field data. (A) For migratory species of Galapagos tortoises, the model predicts annual energetic surplus as a function of body size for three potential strategies: a sedentary lowland-only tactic (orange), a sedentary highland-only tactic (green), and a migratory tactic (purple). The body size of the largest adult female (♀) observed during long-term monitoring aligns with model predictions of maximum annual surplus—a sensible pattern if female maximum body size evolved to maximize the energy available for reproduction. In contrast, the body size of the largest observed adult male (♂) is much larger (males compete for mates and larger body size likely confers an advantage). Predictions and data were pooled between the two migratory species because predictions were similar and data were sparse. (B) For the nonmigratory species of Galapagos tortoises found on Española Island, predicted growth also aligns well with observations of maximum male and female body size derived from long-term monitoring. (C) Timing of modeled (gray) migrations upslope (upward-pointing arrows) and downslope (downward pointing arrows) is consistent with observations of GPS-tagged individuals (purple), with the exception of a 70-kg female that migrated downslope in July and upslope in December. Color ramps at the top and bottom of the panel illustrate seasonal changes in vegetation quantity in the highlands and lowlands respectively, with green and red representing high (0.8) and low (0.4) NDVI. *GPS*, Global positioning system; *NDVI*, Normalized Difference Vegetation Index.

why is migration biased toward larger individuals, with smaller tortoises never migrating (Blake *et al.* 2013)? The answer potentially lies in the energetic costs of movement. A greater propensity for Galapagos giant tortoises to migrate as body size increases is consistent with observations of other terrestrial systems (Alerstam *et al.* 2003) and well-established physiological and biomechanical rules (Schmidt-Nielsen 1997). The ability to adequately process food at the migratory destination could also influence the energetic reward of migration. Under generalizable foraging rules, larger animals use more time in

acquiring and processing food than smaller ones, and larger bodied animals are more sensitive to declining forage availability than smaller ones (Yodzis and Innes 1992). Large-bodied animals are better able to exploit poorer quality foods because of their lower mass-specific energy costs, and their more efficient digestion (Belovsky 1997). Early data from tagged Santa Cruz Island tortoises indicated that tortoises left the hot season range (the arid lowlands) as forage quality declined to low levels, yet small tortoises remain there throughout the year (Blake *et al.* 2013). Was this because small tortoises could not





**FIGURE 13.9** Predicted energetic balances of small (20 kg) and large (200 kg) Galapagos giant tortoises respond differently to seasonal changes in food availability, explaining migratory patterns. (A) Energetic balances of small, as opposed to large, tortoises are less sensitive to seasonal changes in forage availability. (B) For most of the year, the energetic surpluses of small tortoises are higher in the lowlands, which are characterized by higher vegetation quality and temperatures. (C) Daily energetic balances for large tortoises in the lowlands are high during the wet season but decline rapidly during the dry season. A 200-kg individual is predicted to migrate upslope in July.

afford the energy-demanding journey, or because there was enough food remaining in the lowlands to meet their energetic needs year-round, or a combination of both?

To answer these questions, a theoretical model was developed from basic biophysical and biomechanical principles to explore these scenarios, and empirical tortoise

movement data were then used to test the model's predictions. Yackulic *et al.* (2017) first modeled forage intake rate at both destinations over the full annual range of local climate conditions and tortoise body sizes (from 10 to 400 kg) to calculate metabolic rate over a year. Second, migration travel time and energetic cost were modeled based again on environmental conditions and body size. The optimum movement tactics could then be calculated by cost/benefit analysis of migration versus sedentarism. The model made three key predictions (Figs. 13.9 and 13.10): (1) sedentary tortoises below approximately 80 kg have a larger annual energy surplus if they remain year-round in the lowlands versus the highlands; (2) migration becomes the optimal energetic tactic for tortoises above 80 kg; (3) the timing of migration from the hot seasonal range (lowlands on Santa Cruz Island) to the cool seasonal range (highlands on Santa Cruz Island) should be progressively earlier in the year (when forage quality is still relatively high) as tortoise body size increases. The timing of the downslope migration was predicted to coincide with lowland “green-up” with little variation due to body size.

When model predictions were compared to empirical data, congruence was remarkably high (Figs. 13.9 and 13.10). Tortoises begin to migrate at roughly 70–80 kg as predicted, with few tortoises occurring in the highlands below this body mass (Blake *et al.* 2013). The predicted size-biased timing of the upslope migration was also supported: the largest tagged tortoises left the lowlands up to 4 months before the smallest, whereas no discernable pattern was observed in the timing of the downslope migration with body size. The model was then used to test whether body size patterns in migratory behavior were primarily driven by body size effects on foraging and metabolism (forage hypothesis) or impacts on the cost of locomotion. Surprisingly, the model predicted that the costs of locomotion had little impact on the energetic efficiency of migration while forage efficiency had a dramatic impact.

Preliminary field data support the prediction of negative fitness consequences if large tortoises fail to migrate. Blake *et al.* (2015) found that during the cool season (the upland phase of the migration), body condition, red blood cell count, and total blood protein were all higher in tortoises sampled in uplands compared to lowlands. Although not a direct fitness measure, these indirect indices of health status suggest a benefit for migrants. If this is the case, an important question is: why do not all tortoises migrate? While interpretations of behavior over several years in long-lived species such as tortoises are fraught with problems, several explanations seem plausible. First, body condition may determine migration ability, thus our sampling of migrants was already biased toward those individuals in good enough condition to



**FIGURE 13.10** The highlands of Santa Cruz Island present many challenges for free-ranging tortoises. Fences separating farmer's fields often present impenetrable barriers for tortoises. Roads can be traversed but tortoises tend to avoid them, and as vehicular traffic increases roads are dangerous for both tortoises and drivers. *Photos: Stephen Blake.*

migrate. Second, our indicators, although useful, are indirect short-term metrics, whereas fitness is best measured in terms of lifetime reproductive success, which may be different, especially in long-lived species like tortoises. Third, nonmigrants may be poor competitors that remain in lowlands year-round to minimize energy expenditure and maximize foraging opportunities before migrants arrive. Fourth, migration is adaptive under current conditions and is increasing in frequency. Fifth, if the penalty for suboptimal decisions is small, selection pressure for migration may be low.

In summary, the theoretical model provides a mechanism to evaluate the energy balance of migration versus sedentarism for tortoises on Santa Cruz Island that has been largely validated by field data. The interaction between energetic balances and body size was identified as the key determinant of the efficiency of migration over sedentarism. Although the model outputs correlated well

with field data, the model did not consider energetic constraints imposed by reproduction—specifically nesting and egg-laying by females. There is strong selective pressure among oviparous (egg-laying) species in seasonal environments to time egg-laying and incubation for maximum survival of eggs, and growth and survival of hatchlings. Incorporating sex into the model was the next important step in refining its utility.

### **Migratory behavior: Timing, cues, and differences between sexes**

Migration is a complex behavior in which cognitive, physiological, and locomotory processes must be timed appropriately to match the distribution of resources or other factors governing movement. Failure to match movement with ecological conditions can result in



suboptimal or even catastrophic energy balance among migrants (Burrows *et al.* 2011; Fox and Walsh 2012; Tomotani *et al.* 2016). Selection pressure exists for optimal timing of migration, but the triggers that govern migratory behavior are poorly known, including how animals sense, evaluate, and/or predict important environmental factors. An increasingly climatically variable world may render it difficult to match the timing of movements with seasonal patterns (Edwards and Richardson 2004; Saalfeld *et al.* 2019). Although the fitness consequences of poor timing may be relatively modest for large ectotherms like Galapagos giant tortoises compared to smaller endotherms (e.g., migratory songbirds), failure to access high-quality resources over multiple years may nevertheless incur a fitness cost.

Variation in the timing of migration in relation to environmental conditions and the energetic consequences of this variation were investigated using a subset of the movement dataset including 34 tortoises from Alcedo Volcano and Santa Cruz Island (Bastille-Rousseau *et al.* 2019). Individual tortoises showed strong variation in the timing of their migrations that were not correlated with the prevailing environmental conditions. Rather, the timing of migration was best predicted from an average of the conditions experienced over the 7 preceding years. This suggests that tortoises are collecting, storing, and integrating multiyear information to make decisions about the timing of migration. It is difficult to imagine how such a complex mechanism may have evolved; however, recently it has been shown that tortoises have strong learning and discriminating abilities coupled with a prodigious memory, thus the potential for such a mechanism may exist (Gutnick *et al.* 2019).

The trigger for migration depends on the direction of the journey. Departure from the warm range occurred as the temperature was decreasing both in the current year and the mean trend over the previous 7 years. Temperature and productivity both increase together. Tortoises began their migration from the warm range as mean multiyear temperature declined but notably they did not respond to temperature in the current year of movement. Male departures from their hot season ranges were more related to environmental conditions than those of females. Departure from the cool season range was correlated with 7-year average trends in both plant productivity (NDVI) and temperature, with tortoises initiating migration based on increasing NDVI and temperature in the 7-year window and not conditions in the current year. Again, the timing of movement was less predictable for females than males. When the timing of migration of tagged individuals was compared to the modeled optimum timing (Yackulic *et al.* 2017), the mean efficiency was 85%, that is, mean departure date resulted in a 15% loss in net energy gain compared to the theoretical optimum

departure date for a given year. Differences in departure dates of  $\pm 60$  days from the theoretical optimum only led to an estimated 20% loss of efficiency. This is consistent with the large variability of actual departure dates observed and the slow metabolic rate of these large ectotherms. Optimal timing of migration is likely under weak selective pressure since the consequences for annual energy balance are low. Nevertheless, in a world of increasingly unpredictable climates, tortoises that respond to average conditions over several years may face difficulty in correctly timing their migrations. This may not have a major impact on the energy budget of individuals in any given year, but continued mismatch of migration to resource distribution could have cumulative effects over longer time scales.

That migration timing depended on both body size and sex across populations demands an explanation. Male movements more closely related to food availability than females' makes ecological sense because males are not constrained by nesting. Females must compromise access to high-quality resources for their own annual energy balance with other fitness constraints, such as offspring survival. The consequences of the timing of female migratory movements may be considerably more important than for males. Females nest at the beginning of the cool season, which delays their departure from their hot season range as predicted based on body mass. Data on egg and hatchling survival (Blake *et al.* unpubl. data) show that poor timing and or location of nests can have highly negative fitness consequences: high rainfall increases egg mortality and low temperatures increase incubation times, which can expose eggs and hatchlings still in the nest to the hot season rains and potential drowning. These strong selective forces may influence the evolution of migration timing among females (Box 13.1).

## Tortoise movements, conservation, and management

The consequences of the movement strategies of Galapagos giant tortoises for conservation vary widely across the Archipelago. Among terrestrial species around the world, mobility is often a strong predictor of conservation status (Woodroffe and Ginsberg 1998), because the larger the area over which an animal ranges, the higher the probability that it will encounter anthropogenic threats (Blake *et al.* 2008). Large terrestrial predators and herbivores within diminishing ranges frequently encounter fences, poachers, livestock, and settlements, which lead to conflict with humans with consistently negative consequences for wildlife (Blake *et al.* 2008; Creel *et al.* 2013; Woodroffe *et al.* 2005). Species that range or migrate outside of protected areas into private



**BOX 13.1 A day in the life of a tortoise tracker****Author: Freddy Cabrera**

My name is Freddy Cabrera, and I am a tortoise tracker. It is 4:30 a.m., well before sunrise, in Bellavista, an inland village on Santa Cruz Island in Galapagos. I am already making breakfast before I start a long day of field work. Today I'm going to one of my favorite places, the nesting zone below El Chato. I first began tracking hatchling tortoises, fresh out of the nest, in 2013. It has been seven years but, even today when I visit the hatchlings, I am still so excited I don't need an alarm clock. After cooking some "humitas" for breakfast and gathering my equipment, I jump on my motorbike and am off. By 6:15 a.m., I have left my motorbike behind and am heading down the muddy trail. My father taught me to walk fast; that's how I got the nickname "wind."

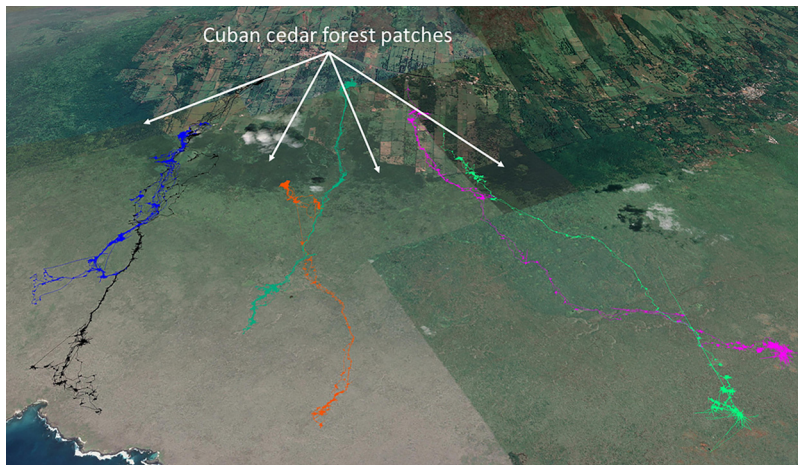
After 90 minutes of hard walking, I reach the nesting zone and start searching for radio-tagged tortoises. Finding a hatchling can take anywhere from minutes to hours. The lava terrain often impedes our radiotracking, limiting it to a very short range, and small hatchlings are often hidden in deep crevices. Although newly hatched tortoises weigh less than 100 g, they immediately disperse from the nest, sometimes walking hundreds of meters during the first month before settling into a small home range — an amazing feat of endurance.

By mid-morning, I've located several hatchlings, but the sun is now high in the sky and the heat suffocating, so I find a

place under an incense tree to rest, and my thoughts take flight. I remember when Dr. Sharon Deem, a wildlife veterinarian on our team, taught me how to use ultrasound. It was incredible to see eggs inside the abdomens of female tortoises, and begin to understand which females produced eggs, which did not, and why these and other patterns of tortoise health and reproduction occurred in relation to movements and ecology.

Back to reality. There are still a couple of hatchlings to find before returning home. I make this hike every two weeks to track the baby tortoises and record their weight and measurements. It is fascinating to see how some grow and thrive, while others do not! We record temperature and rainfall. The results indicate that cold temperatures prevent hatchling growth while heavy rainfall can waterlog nests and kill eggs. I wonder what climate change will mean for the tortoises. After finding all of our radio-tagged babies healthy and alive, I start the long trek, uphill this time, back to my motorbike.

After a full day in the field, I return to the office to digitize the day's data. I'm tired, but still working hard. I'm motivated by the wish to see one or more of the tortoise babies that I tagged the day they hatched grow into adults and, like their parents, begin their annual migrations between the lowlands and highlands that may continue for well over 100 years.



**FIGURE 13.11** Tortoise migrations by western Santa Cruz tortoises appear to be restricted to a few small corridors through dense stands of Cuban cedar, an invasive tree species. For clarity, this image only shows six individual tortoise migration trails. Cuban cedar stands can be identified by dark patches of vegetation surrounded by lighter areas.

lands face enormous conservation challenges compared to sedentary species with small ranges that live in viable populations in small, protected areas (Berger 2004; Schuster *et al.* 2019; Yackulic *et al.* 2011). Thus conservation challenges for Galapagos giant tortoises are likely greatest for migratory species that share islands with humans, such as on Santa Cruz Island where an incipient tortoise–human conflict in farmlands has been reported (Benitez-Capistros *et al.* 2019, 2018, 2016, 2014). While conflict levels are currently low, and most landowners

have benign or favorable attitudes toward tortoises, infrastructure development, intensive farming, and the break-up of large farms into smaller production farms and housing developments all have significant negative implications for tortoise ecology.

In the early days of colonization of Santa Cruz Island, tortoises were heavily hunted for food. In 1959 tortoise hunting became illegal and since then farmers have usually tolerated tortoises, particularly because most farms within tortoise range were cattle farms where conflict was





**FIGURE 13.12** Tortoises in the highlands of Santa Cruz eat a wide variety of introduced species, which modify their annual energy budget and therefore the efficiency of different movement tactics in poorly known ways compared to original native vegetation. *Photos: Stephen Blake (A and B); Christian Zeigler (C).*

low. Some landowners saw economic opportunity in tourism and tortoise migration was encouraged. The period from the creation of the Galapagos National Park to the present saw an expanding tortoise population, after 150 years of rampant exploitation.

The future is less clear. The islands are under pressure to increase food production, and the stage is set for the widespread conversion to agriculture throughout the cool season range of migratory tortoises, most of which on inhabited islands is on private land outside the boundaries of the Galapagos National Park. The intensification of agriculture will be less compatible with the presence of tortoises compared to cattle farming. For example, coffee production on Santa Cruz has strongly increased over recent years, and because tortoises destroy young coffee plants, knock over adult plants, and undermine tree roots, farmers generally prevent tortoise access into coffee production areas. Similarly, production crops such as maize and succulent vegetables may be incompatible with free-ranging tortoises. Recent prolonged droughts (possibly due to anthropogenic climate change) have exacerbated conflict between tortoises and cattle as grass sward quality declined dramatically (F. Cabrera, pers. obs.).

In addition to changes in agriculture, the division of once large farms into small lots for housing developments is further fragmenting and reducing tortoise habitat and potentially blocking migration routes to important resources. Increases in roads, impenetrable fences, and other barriers pose a serious threat to tortoise migration. The consequences of blocking migration will involve negative annual energy balances for large tortoises with impacts on body condition and reproductive success, as they have for migratory species around the world (Harris *et al.* 2009; Shuter *et al.* 2012; Wilcove and Wikelski 2008).

Barriers to movement from invasive plant species are also increasing on Santa Cruz Island. Blackberry (*Rubus niveus*) and elephant grass (*Pennisetum purpureum*) proliferate rapidly and can form impenetrable thickets. A further threat is the rapid expansion of Cuban cedar (*Cedrela odorata*) into the protected area, because this species forms dense stands with extensive root systems that tortoises find difficult to traverse. Across much of the range of the western Santa Cruz Island tortoises, migration routes are restricted to a few small corridors where native vegetation has not been engulfed by cedar (Fig. 13.11). If these last corridors close, tortoise migration routes may become untenable. Invasive species may also play important roles on uninhabited islands such as Santiago and San Cristóbal Islands, where blackberry thickets have made large areas of the highlands inaccessible for tortoises (F. Cabrera, pers. obs.).

Unfortunately, the immediate effects of these habitat disturbances may not become evident for many years in

creatures such as long-lived tortoises with extended generation times. The increase in the energetic deficit in an adult tortoise unable to migrate may not be manifest for several years. But a decline in body condition over the years will lead to deteriorating physical condition and failure to realize reproductive potential. Reproductive failure itself may also not be detectable immediately—hatchling and juvenile tortoises are cryptic and monitoring methods are poorly developed and not currently implemented in a robust way. A potential conservation crisis for one of the Archipelago's largest tortoise populations may be largely going unnoticed as infrastructure and land use changes that inhibit migration become more and more permanent.

Even in the absence of direct human impacts, a combination of climate change and invasive species may change the energy balance of migratory Galapagos giant tortoises (Chapter 16: Climate Change). Body condition of tortoises that eat a high proportion of introduced and invasive species is similar or higher to those that do not (Blake *et al.* 2015). Large quantities of succulent fruit such as introduced guava (*Psidium guajava*) and grasses introduced for cattle could change the energetic balance in favor of year-round sedentarism in the highlands. Similarly, increasing rainfall, as predicted under climate change scenarios for Galapagos (Ellis-Soto *et al.* 2017; Sachs and Ladd 2010), may increase year-round productivity in the lowlands and render sedentarism more efficient than migration. Whether tortoises are able to modify their behavior to adapt to rapid environmental change remains to be seen (Fig. 13.12).

## Conclusions

The questions Darwin posed about tortoise movements as he ambled slowly behind them nearly two centuries ago, now have at least been partially answered. More than a decade of GPS data from over one hundred tortoises analyzed in conjunction with environmental data have revealed deep insights into tortoise movement ecology and animal movement generally. Tortoise movement strategies are diverse and complex; sedentarism, nomadism, dispersal, and long-distance migration have evolved under a diversity of environmental selective pressures shaped by the varied topography of each island, which interact with life history traits including body size and sex. Migration becomes adaptive on islands with humid highlands when adult body size is attained and is driven by the spatiotemporal distribution of forage. On islands inhabited by humans, migration brings tortoises into potential conflict with people in unprotected agricultural lands. Climate change, invasive species, and other anthropogenic disturbances, which are increasing under a dramatic economic boom, threaten the integrity of tortoise



migrations, with strong negative consequences for tortoise conservation. Private lands remain largely open and heavily utilized by tortoises, however, and human attitudes to tortoises are generally benign. A window exists to integrate research on the movement, health, and reproductive ecology of tortoises applied to future environmental and socio-economic development scenarios of the Archipelago to drive adaptive management of tortoises and their habitats.

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