

Chapter 16

Galapagos tortoises in a changing climate

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Chapter outline

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Introduction

Galapagos giant tortoise populations have declined since humans first arrived in the Archipelago in 1535 due to overexploitation, habitat destruction, and myriad introduced species, among other factors. In the mid-1900s, after over four centuries of destruction, conservationists began to turn the tide, restoring tortoise populations and eliminating some of the threats. Today a new threat is arising—climate change.

Climate change is unlike any previous threat. Although climate change has been anticipated, just what form it is taking in Galapagos and what its effect will have on tortoises are not clear. Unlike past threats and challenges, the extent of the crisis caused by climate change will not be determined by the people living and visiting Galapagos, but rather by the global community.

The far-reaching effects of climate change, even when hard to pin down at present, must now be considered. Even if tortoise poaching were ended, invasive tortoise predators and competitors eradicated, and all tortoise–human–habitat-related conflicts resolved, climate shifts could render the Galapagos environment unsuitable for self-sustaining tortoise populations, with tortoises becoming dependent for their continued persistence on zoos and breeding centers in perpetuity.

The fate of Galapagos tortoises under a changing climate is unclear for several reasons. Having evolved in island ecosystems driven by the cycles of El Niño and La

Niña, giant tortoises are preadapted for coping with a highly variable climate with occasional extreme conditions. Tortoises are also large and long-lived. Their large size provides a reservoir of stored resources to ride out periods of low food availability and water scarcity (Lindstedt and Boyce 1985; Lovich *et al.* 2014). Their long lifespan allows them to reproduce in years with favorable conditions for nesting, incubation, and survival of hatchlings, skipping years with unfavorable conditions (Lovich *et al.* 2014).

Yet large body size and longevity do not provide an inexhaustible buffer to all climate variation. If there is an increase in the frequency and severity of droughts associated with climate change, it could test the limits of Galapagos tortoises, as it has other tortoises, such as Agassiz's desert tortoise (*Gopherus agassizii*), which is suffering population declines throughout its range due to drought-triggered starvation, dehydration, loss of habitat, and possibly new predators (Barrows 2011; Lovich *et al.* 2014). Paradoxically, whereas long lifespan has probably helped buffer tortoises against climate variability for centuries, if not millennia, this very trait may become a liability given the rapidity of current climate change and all its ramifications. Long lifespans mean slow generation times (Chevin *et al.* 2010), such that any adaptive response may be too slow to keep up with the rapid pace of climate change. Furthermore, the geographic range of all species of Galapagos tortoises is small, both in area and elevation, and unlike many mainland species, if the

islands become unsuitable habitat, tortoises will have nowhere else to go.

Although how climate change will unfold in Galapagos is unknown and despite the lack of basic data needed for a full accounting of how tortoises might fare under altered climate conditions, there is enough knowledge to begin to predict potential outcomes and impacts on tortoises. Pairing outputs from current climate models with available data on tortoise population biology can help provide a sense of the opportunities and challenges that tortoises may face in the near to mid future. This chapter describes the past trajectory of the Galapagos climate and where it is expected to go in the future, the relationship between tortoises and climate, and the sensitivity of tortoise populations to climate impacts as climate change progresses.

Climate models and projections

Over long timeframes, the Galapagos climate has never been stable. Past climate changes, however, have unfolded slowly, over thousands of years, not at the rapid pace projected for this century. Looking at ocean sediment cores from the Galapagos region, David Lea and colleagues showed that local sea surface temperatures over the past 135,000 years have fluctuated by about 4.7°C (Lea *et al.* 2006). Sea surface temperatures were greatest about 130,000 years ago, at the start of the last interglacial period, when they reached about 2.7°C warmer than temperatures today. Temperatures slowly fell, over tens of thousands of years, reaching their coldest levels about 20,000 years ago, during the last glacial maximum, when they were about 2.3°C cooler than today. The climate then warmed until peaking again in the early Holocene. Then, over the past 6000 years, sea surface temperatures fell by about 1.5°C. In the 2000s the

expectation is that climate change will rapidly reverse this 6000-year cooling trend, driving sea surface temperatures upward by 1.5°C–3.5°C (Sachs and Ladd 2010).

As scientists around the globe work to understand climate change, a suite of global forecasting tools has been developed to chart possible trajectories, reflecting different emissions scenarios and climate models. The 2013 report by the International Panel on Climate Change (IPCC 2013) outlines four scenarios of anthropogenic greenhouse emissions; the Representative Concentration Pathways (RCP) denote four possible radiative forcing values for the year 2100 (2.6, 4.5, 6, and 8.5 W/m²). Working with these scenarios, dozens of different General Circulation Models (GCMs) have been run, each with varying complexity and assumptions about physical processes that impact the climate.

In the Galapagos, the GCM forecasts project that, on average, future climates will be warmer and wetter than current climates—in fact, under RCP 8.5, the archipelago-wide mean annual temperature is forecasted to be warmer than the current warmest location within the Archipelago (Fig. 16.1). Based on available downscaled data for current climates provided by WorldClim, the average annual temperature across all locations on the Galapagos is 22.3°C (SD = 1.6°C), with the average temperatures ranging from 15.2°C to 24.5°C at the coldest and warmest spots in the Archipelago. Looking at 17 GCM forecasts for 2070, under RCP 8.5, the archipelago-wide mean annual temperature is projected to be between 24.8°C and 27.2°C.

To fully understand the ground-level impacts of climate change, forecasting must be downscaled from the global climate simulations to ecologically relevant scales (Bao and Wen 2017; Eum *et al.* 2012; IPCC 2013; Potter *et al.* 2013). In global simulations, the entire Galapagos Archipelago is usually represented in just one or a few grid cells, which typically range from 50 to 300 km wide

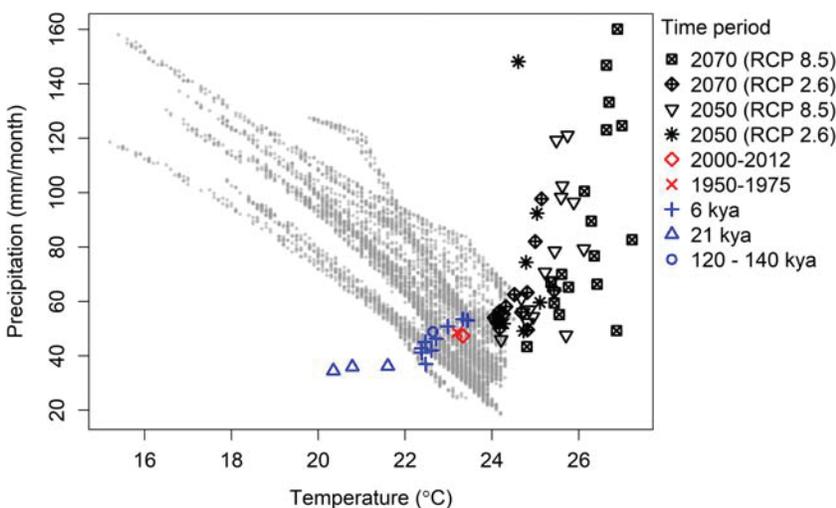


FIGURE 16.1 Galapagos climate over time. Gray points represent the current (2000–2012) mean annual precipitation and temperature at points across the Galapagos Islands. Archipelago-wide mean temperature and precipitation are plotted for all available Global Climate Models for seven different time periods. Data from WorldClim.

(Fig. 16.2). Moving from coarse- to fine-resolution projections requires incorporating local elevation, slope, topography, wind patterns, vegetation structure, substrates, and other processes driving microclimate conditions. In island systems such as the Galapagos, complex local topography makes this particularly challenging (Khalyani *et al.* 2016; Lauer *et al.* 2013; Santos *et al.* 2004).

Two long-term weather stations at Puerto Ayora (coastal town) and Bellavista (inland town) on Santa Cruz Island in the Galapagos provide a window into the difficulties of downscaling from global climate models to local climate conditions. GCM models are often calibrated against a global data set created by the Climatic Research Unit (CRU) meant to capture observed conditions over the historic period (Harris *et al.* 2014). Puerto Ayora and Bellavista both fall within a single cell of the CRU data. Plotting these data sets against each other shows they generally correspond well but with substantial noise in the relationships between the regional and local trends (Fig. 16.3).

Beyond simply forecasting changes in the average temperature, average precipitation, and other averaged metrics, that is, the “mean climate state,” potential changes in the variability of these metrics, that is, extreme weather events, is of interest. In the Galapagos, data suggest that, although there has been no increase in average air temperatures over the past half century, seasonality has changed substantially (Box 16.1; Figs. 16.4 and 16.5).

At the global scale, the primary driver impacting weather extremes is the climate phenomenon El Niño-Southern

Oscillation (ENSO), which is especially relevant for Galapagos (Cai *et al.* 2015; IPCC 2013; Sachs and Ladd 2010; Wang and Picaut 2004). The ENSO phenomenon captures the oscillation among El Niño and La Niña events, and neutral climate conditions. Under neutral conditions, warm air rises upward from southeast Asia, travels eastward across the Pacific Ocean, and then descends as cool air in the Galapagos before returning with the trade winds blowing back westward. This cell of circulating atmospheric air, known as the “Walker Circulation,” drives ocean currents, which reinforce the temperature gradient driving the atmospheric circulation (Bjerknes 1969). The trade winds blowing westward across the ocean cause warm surface waters to pile up in the western Pacific, while drawing cold water up from the depths of the eastern Pacific. Thus the typical climate of southeast Asia is warm and moist, whereas the climate around the Galapagos is relatively cool and dry.

During an El Niño event, the Walker Circulation weakens or even reverses, causing warm water to drift eastward rather than westward. This brings warmer, wetter weather to the Galapagos. During La Niña, the Walker Circulation strengthens, causing the Galapagos to become cooler and drier than normal. The underlying mechanisms that cause the system to oscillate back and forth between El Niño and La Niña are not well understood, making forecasting how ENSO will respond to climate change difficult. Although the latest generation of models has improved the ability to capture observed ENSO dynamics, these models still have substantial shortcomings (IPCC 2013).

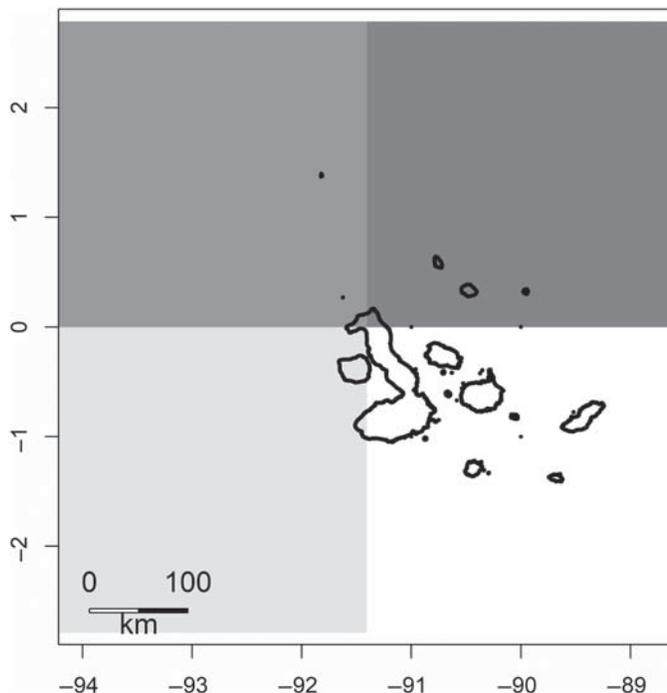


FIGURE 16.2 Scale of GCM grid cells. The Galapagos Islands fall entirely within four grid cells of this GCM, produced by the Canadian Center for Climate Modeling and Analysis. *GCM*, General circulation model.

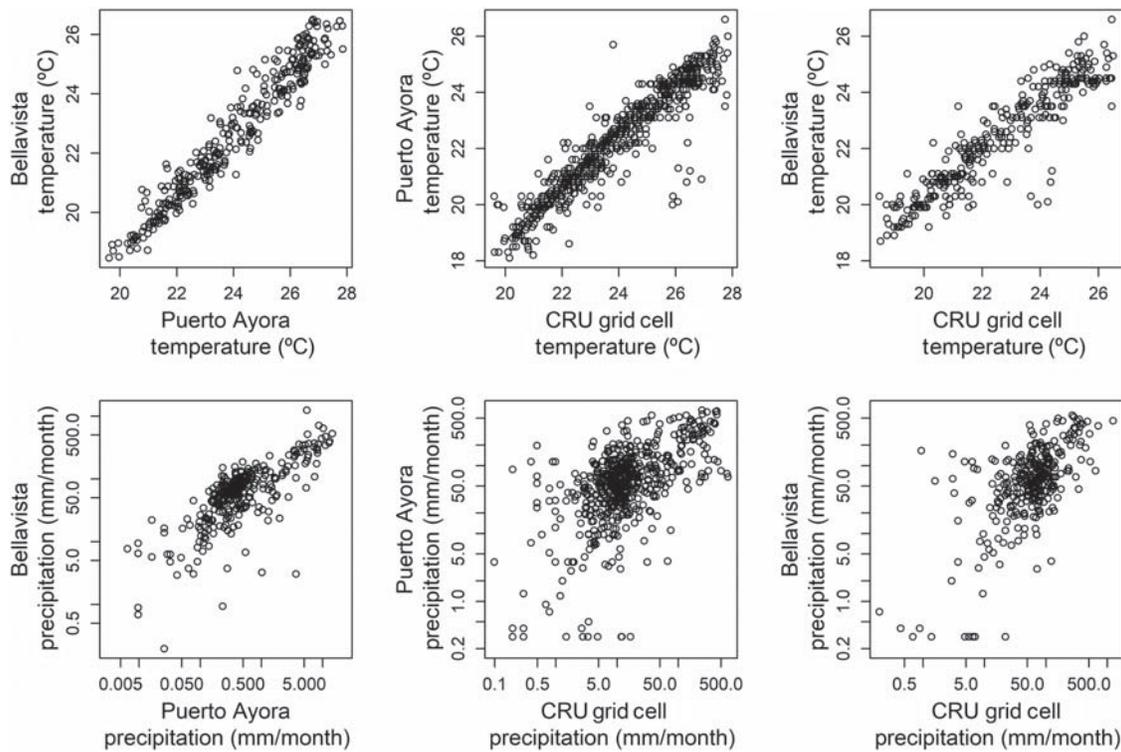


FIGURE 16.3 Monthly temperature and precipitation conditions on Santa Cruz Island in the Galapagos as reported from weather station data at Puerto Ayora (1981–2016), and weather station data at Bellavista (1987–2014), and corresponding data extracted from the CRU global climate grid cell. These indicate general correspondence but with considerable noise within modeled climate data and climate conditions on the ground in Galapagos. *CRU*, Climatic research unit.

Overall, global models project that a warmer ocean will trigger more extreme warm El Niño events in the future, which will in turn trigger a corresponding increase in extreme cool La Niña events, albeit to a lesser extent (Cai *et al.* 2015). The specifics of how this will play out in Galapagos, however, are difficult to predict. Although sea surface temperatures of the broader Pacific equatorial region have increased by about half a degree Celsius over the past half century, it appears that the area immediately surrounding Galapagos has not warmed during this same time (Sachs and Ladd 2010; Wolff 2010). Why this is and whether these divergent temperature trajectories will continue remains unclear. To answer these unknowns will require better models and better data.

The projected changes for physical parameters like precipitation and temperature in Galapagos will likely have significant ecological impacts. Most salient will be an increase in plant growth, which in Galapagos is strongly limited by and responds directly to moisture levels and ambient temperatures, particularly in the arid zones that dominate the terrestrial portion of the Archipelago. Variation in plant greenness is not just a phenomenon of differences over space as exemplified by the pronounced ecological zonation in Galapagos (Chapter 14: Habitats) but also occurs through time. Decades of work have shown

the far-reaching ecosystem impacts of fluctuating environmental conditions associated with El Niño and La Niña cycles in the Galapagos. For marine iguanas, El Niño events, with substantial increases in sea temperature, decrease the abundance of their preferred intertidal algae, resulting in high mortality and triggering the iguanas to shrink in length by up to 20% (Wikelski and Thom 2000). On land, El Niño brings excessive rains that cause a surge in vegetation growth (Box 22.2 in Chapter 22: Pinzón Island), generally benefitting higher level consumers (Trueman and d’Ozouville 2010). For instance, greater plant productivity in El Niño years results in rising caterpillar abundance, which in turn benefits cactus finch and medium ground finch populations (Grant *et al.* 2000).

In general, a wetter future for the Galapagos means greater plant productivity across the Archipelago. Simulating the vegetation response to future climates, Charney *et al.* (unpublished manuscript) forecast that, on average, the Galapagos will experience about one standard deviation higher plant productivity over the next 100 years in response to increased precipitation. Under the business-as-usual greenhouse gas emissions scenarios, RCP 8.5, the mean productivity across the Galapagos during the period 2080–2100 is projected by these models to be more productive than about 82% of the years during the 1900s. The future increase in

BOX 16.1 What is happening with the Galapagos climate?**Author: Harrison Goldspiel, Galapagos Conservancy**

Many projections of climate scenarios, using global and regional models, have been made for the Galapagos Islands (Sachs and Ladd 2010), but few analyses have examined recent trends in climate and weather extremes at archipelago- and island-level scales. The Galapagos is generally expected to become warmer, wetter, and greener (i.e., higher plant productivity) (Trueman and d'Ozouville 2010), with seasonality shifts occurring across ecological zones (Wolff 2010). However, it remains unclear if these changes have already begun and what the implications are for potentially vulnerable species such as Galapagos tortoises.

Local long-term climate records in Galapagos are largely limited to two weather stations on one island (Santa Cruz) that have collected data for over 50 years (from 1965 in coastal Puerto Ayora and from 1987 in inland Bellavista). Virtually all local assessments of climate change in Galapagos stem from these records, which may not accurately capture trends on other islands or be representative on an archipelago scale (Trueman and d'Ozouville 2010). In the absence of long-term data from other islands, open-access satellite data can be used to examine small-scale climate variation over a broad spatial scale. To this end, remote sensing climate data were acquired to examine recent trends in Galapagos from 1980 to 2020 in (1) quantity and seasonality of precipitation, and (2) occurrence of precipitation anomalies (e.g., drought) based on the Standardized Precipitation Index (SPI; CPC Global Unified Precipitation data provided by NOAA/OAR/ESRL PSL; Beguería and Vicente-Serrano 2016; McKee *et al.* 1993). Long-term precipitation records in Puerto Ayora were acquired from the Charles Darwin Research Station to provide a local reference against satellite data.

From the 1980s through the 2010s, there has been only a slight increase in average rainfall totals during the wet season and virtually no change during the dry season (Fig. 16.4). These trends in remotely sensed precipitation were similar among islands and ecological zones, but contrast with ground-level records from Puerto Ayora, which showed no change in the amount of precipitation during the wet season over the same period. By focusing solely on precipitation

totals averaged across years, we can overlook strong seasonality shifts that have occurred in Galapagos over the last 40 years. Recent seasonality changes are most clear from precipitation anomaly records, which show a transition to a more positive water budget, with a drastic decline in drought prevalence over time but no change in flood prevalence (Fig. 16.5). There was some variability in precipitation anomaly trends across the Archipelago, with islands containing large humid and transition zones, such as Isabela Island, experiencing no extended droughts in the last decade unlike the predominantly arid islands. The intensity of precipitation anomalies, both positive (wet) and negative (dry), has weakened in Galapagos over the last four decades, with “near normal” events ($-1.00 < SPI < 1.00$) becoming more frequent.

Galapagos has experienced a transition in climate over the last 40 years, exhibiting heightened overall wet season precipitation, fewer drought periods, and less extreme precipitation events. Precipitation anomalies in Galapagos are positively correlated with ENSO activity, yet while the frequency of severe El Niño events has increased globally (Wang *et al.* 2017), the frequency of severe precipitation (i.e., flood) events has been stable in Galapagos, possibly reflecting a decoupling between the current global presentation of ENSO cycles and local archipelago climate dynamics (Banks 2011; Yeh *et al.* 2009). There appears to be some variability in local drought dynamics among islands, in part due to the different scales of precipitation in arid and humid zones; but a general signature of recent climate change is apparent throughout the Archipelago. That these wet season precipitation patterns derived from remote sensing data contrast with local trends from the Puerto Ayora weather station highlights both the complexity of local and regional climate processes in the Galapagos and a potential caveat in exclusively relying on either instrumental or satellite-based climate data. Increases in wet season precipitation, and the near collapse of extended drought periods, carry important implications for Galapagos ecosystems, both marine and terrestrial. Understanding ecological responses to these trends is critical for future conservation planning for endemic Galapagos organisms, such as giant tortoises.

productivity is expected to be greatest during the wet season and in arid ecosystems, and to lead to a greater average “greenness” across the Archipelago that is more homogeneous, that is, there will be less distinction between arid, transition, and humid zones within and among islands.

Climate impacts on Galapagos tortoises**Rainfall, egg survival, and tortoise population growth**

In anticipating how climate change may impact Galapagos tortoises, an important area to begin the

investigation is reproduction, as many aspects of tortoise reproduction are directly tied to climate, including egg hatching success and sex ratios of offspring (Chapter 9: Reproduction). A Master’s thesis by Stephen Earsom (2000) provides a glimpse into the impact of moisture on Galapagos tortoise egg survival in the wild and in the laboratory. Under laboratory conditions, he found that tortoises’ eggs tolerate a relatively narrow range of soil moisture conditions. If the soil is too wet or too dry, tortoise eggs die. Monitoring tortoise nests in the field at Cinco Cerros, between Sierra Negra and Cerro Azul Volcanoes on southern Isabela Island, following the extremely rainy El Niño event of 1997–98, Earsom found

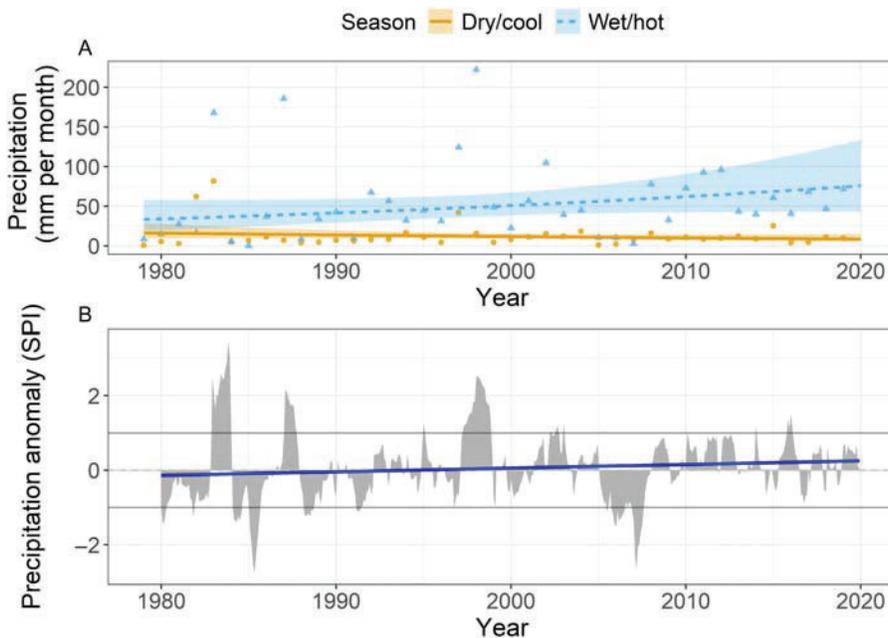


FIGURE 16.4 Trends in seasonal precipitation (top) and precipitation anomalies (bottom) in Galapagos from 1980 to 2020. Data and trends represent average recorded precipitation at the archipelago scale. Precipitation anomalies were calculated on a 7-month time scale. Anomaly periods with SPI values below -1 or above 1 represent drought and flood events, respectively. *SPI*, Standardized precipitation index.

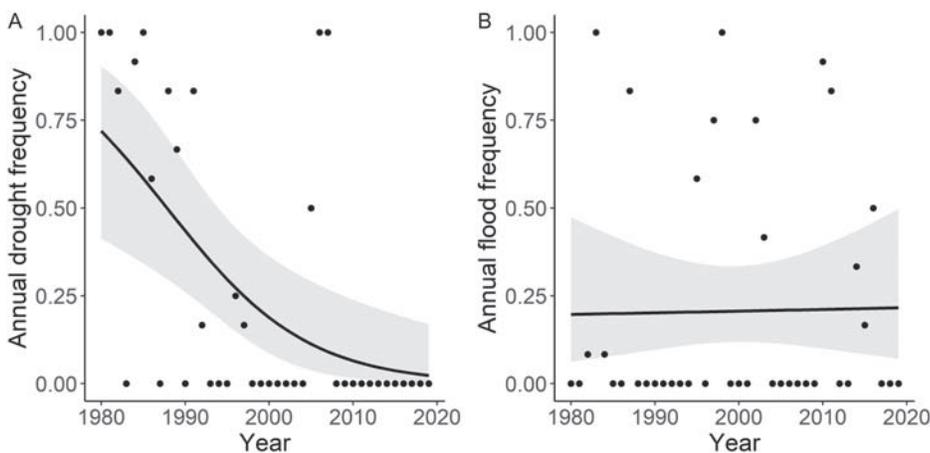


FIGURE 16.5 Trends in drought (left) and flood (right) events in Galapagos from 1980 to 2020. Drought and flood periods were delineated from the Standardized Precipitation Index values of archipelago-wide precipitation records, following [McKee *et al.* \(1993\)](#) and [World Meteorological Organization \(2012\)](#). Annual frequencies are based on the proportion of months in each year classified as drought or flood.

a single surviving hatchling out of 507 eggs in 37 nests. This mirrored the complete egg failure at Cinco Cerros after the extreme 1982–83 El Niño event ([Earsom 2000](#)).

If the amount of rain that fell in 1997–98 was enough to cause complete mortality of tortoise eggs, what will the future hold? El Niño events as extreme as 1997–98 occurred in the averaged climate models hindcast to the past at a rate of about 7% (SD = 4%) between 1970 and 2000, or about one in every 13 years ([Fig. 16.6A](#)). Under the business-as-usual climate change scenario (RCP 8.5), by the end of this century, such egg-killing rainfall totals are projected to occur in a majority of years, about 55% of all years (SD = 23%). Looking at outputs from all climate models, future projections indicate that from 20% to 90% of all years will experience extreme egg-killing rains. Under the most optimistic scenario (RCP 2.6), the probability of

egg-killing El Niño rains in any given year, averaged across all climate models, still increases to 19% (SD = 3%).

Providing a first glimpse at potential future impacts of climate on Galapagos tortoise reproduction, these forecasts of egg-killing moisture conditions paint a grim portrait. They suggest that all tortoise nests may suffer near-complete egg mortality in most years. But there is still a tremendous amount unknown. Perhaps the egg-laying site at Cinco Cerros is uniquely sensitive to moisture conditions, whereas in other populations the topography and substrate of nesting areas would allow eggs to survive extreme El Niño rains without such high mortality. Or, perhaps the physiology of the Cinco Cerros tortoise population makes for eggs that are more susceptible to moisture than other populations. On the other hand, other populations may be even more susceptible.

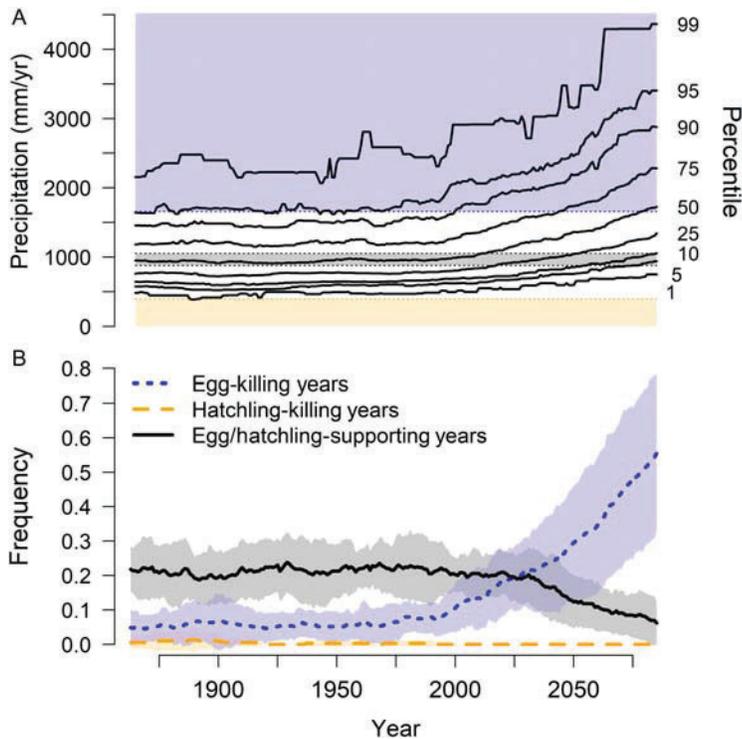


FIGURE 16.6 Projected changes in Galapagos precipitation over time. (A) The yearly rainfall totals associated with each percentile over time averaged across 14 GCM runs, averaged across a 30-year moving window. (B) The frequency of yearly rainfall amounts that exceed the amount observed in 1997–98, which was associated with complete egg failure at Cinco Cerros (“Egg-Killing Years”; Earsom 2000), are less than the amount observed in 1970, which was associated with near-complete hatchling mortality on Santa Cruz Island (“Young-Killing Years”; MacFarland *et al.* 1974), and are in between the amount observed in 1986, which was associated with successful egg hatching (Earsom 2000) and the amount observed in 1971, which was associated with successful hatchling survival (“Egg/Hatchling-Supporting Years”). In (A), the blue, orange, and gray shaded areas correspond to egg-killing, hatchling-killing, and egg/hatchling-supporting years. In (B), the shaded areas represent the standard deviation across model runs. GCM, General circulation model.

Even within Cinco Cerros, the threshold rainfall amount that causes complete egg mortality is unknown. Although 1997–98 was associated with 1658 mm of rain in the CRU data, Earsom reported successful hatching in years such as 1986, which had 1056 mm of rain. Where, between 1056 and 1658 mm of precipitation, is the threshold at which all eggs die? By the end of this century, this threshold represents the difference between egg-killing rains occurring in 10% or 50% of the years in the model-averaged forecasts (Fig. 16.6A). To answer these questions and better predict the future, additional field studies are needed.

Given that egg mortality is likely to increase, what will this mean for the future of tortoise populations? If tortoise populations are limited primarily by survival at later life stages, it is possible that high egg mortality will be of little significance. In a classic study, Deborah Crouse and colleagues showed that management of loggerhead sea turtle populations should not focus on protecting nests, as the survival of individuals at later stages is more important to population growth (Crouse *et al.* 1987), a pattern since demonstrated in most species of turtles.

To understand how high levels of egg mortality may impact populations, estimates for the rate of egg-killing rains can be incorporated into a standard population model developed for Galapagos tortoises. This model, technically a demographic projection matrix, partitions survival and fecundity rates for the various life stages.

Assuming that all eggs survive in any year when precipitation does not exceed the egg-killing threshold and all other factors are conducive to egg survival, then,

$$S_0 = (1 - M_0) \times S_a$$

where S_0 is the current combined survival probability, M_0 is the current probability of egg-killing precipitation, and S_a is the probability that all other factors are conducive to egg survival. If the future annual probability of egg-killing rains changes to M_1 while all other factors contributing to egg survival remain the same, then the future egg survival, S_1 , becomes:

$$S_1 = \frac{(1 - M_1) \times S_0}{(1 - M_0)}$$

Incorporating these equations into demographic models parameterized from a combination of studies of Galapagos tortoises on Santa Fe, Española, and Santa Cruz Islands (Table 16.1; Chapter 12: Population Biology) provides rough estimates of the sensitivity of tortoise populations to increased egg mortality due to increases in precipitation. As parameterized, the base demographic model projects a population growth rate, λ , of 1.05. This means that under current conditions, when egg-killing rains are estimated to occur at a rate of 7%, the population would double every 9.4 years (Fig. 16.6B). Incorporating mean and extreme estimates for future rates of egg-killing rains, of 20%, 55%, and 90%, λ would become 1.04, 1.02, and 0.99, respectively. These equate

TABLE 16.1 Transition probability estimates for a stage-based model of Galapagos tortoise population dynamics based on combined data from tortoises on Santa Fe, Española, and Santa Cruz Islands (GTRI unpubl. data; Chapter 12: Population Biology).

		Age this year			
		0–1	1–4	4–17	17+
Age next year	0–1	0	0	0	3
	1–4	0.198	0.568	0	0
	4–17	0	0.182	0.895	0
	17+	0	0	0.051	0.979

to growing populations that double in 16 and 29 years for the first two scenarios and a declining population with a half-life of 104 years in the last scenario (Fig. 16.6B). These estimates are tentative, as they are based on mixing demographic and survival data from different species, but they demonstrate the basic nature of the relationships. It would take a 12-fold increase in the frequency of egg-killing rains, up to 84%, to turn the hypothetical growing population into a declining population. This is approximately the point at which increased survival of hatchling, juvenile, and adult tortoises cannot compensate for increased egg mortality. Merely increasing survival at all older stages to 100% is not sufficient to overcome the impact of egg-killing rains on egg survival.

Egg incubation temperatures and hatching success

In addition to the importance of soil moisture conditions, tortoise eggs require a certain range of incubation temperatures for embryos to develop and survive. Eggs of Española tortoises (*Chelonoidis hoodensis*) incubated in the laboratory at three temperatures—25.5°C, 29.5°C, and 33.5°C—resulted in mortality of eggs incubated at 33.5°C, suggesting the potential for heightened mortality under future, warmer climates (Sancho 1988; Sancho *et al.* 2017). However, without data on how regional temperatures correlate with nest temperatures in the field, it is difficult to predict these effects on tortoise populations.

Egg incubation temperatures and hatchling sex ratios

Incubation temperatures also determine the sex of tortoise hatchlings (Chapter 9: Reproduction). Eggs of Española Island tortoises incubated below 28.3°C were shown to produce primarily males whereas eggs incubated at higher

temperatures produced primarily females (Sancho 1988; Sancho *et al.* 2017). Will temperature-dependent sex determination pose another challenge to the long-term survival of tortoise populations as the climate warms? Notably, the Sancho *et al.* (2017) model predicts that nests of Española tortoise eggs incubated between 25.2°C and 31.4°C would produce both males and females; this 6°C transition range of temperatures that produces both males and females is broad and may allow Galapagos tortoises greater scope to adapt to a changing climate (Hulin *et al.* 2009; Mitchell and Janzen 2010). The experiments of Sancho *et al.* (2017) are very limited, yet they do not suggest that profound shifts in sex ratios resulting from climate change are likely to occur.

To the extent that warming of nests may result in more female than male tortoises, this has the potential to impact tortoise population dynamics. Females generally contribute more to population growth than males, because the loss of each female generates a direct and proportional reduction in the number of eggs produced. In contrast, a single male can fertilize many females, so the loss of one male can usually be compensated for by another. Skewing reproduction toward more males—as may be the case with New Zealand’s tuataras under climate change (Mitchell *et al.* 2008)—is more problematic than if reproduction is skewed toward more females, as would be the more likely case with Galapagos tortoises. Still, from a genetic perspective, unequal sex ratios will result in smaller effective population sizes, raising risks of inbreeding depression and genetic bottlenecks that erode genetic diversity (Frankham 1995). However, inbreeding depression and genetic bottlenecks would only be important for population segments with genetically effective population sizes of less than 50 individuals (i.e., 10% of standing populations in the wild, Frankham 1995), which is far less than most current populations of Galapagos tortoises (Chapter 20: Population Status).

Site selection by female tortoises can also provide turtles with a behavioral option for responding to climate change through adjustment of nest-site choice (Refsnider *et al.* 2014). More specifically, females can choose to place their eggs in cool, shaded nesting sites (producing more males) versus warm, sunny sites (producing more females). Although intentionality of choice of offspring sex by female turtles through nesting site selection is speculative, it is clear that female turtles, including Galapagos tortoises, have a considerable behavioral repertoire for manipulating the sex ratios of their offspring as a means of responding to climate change (Refsnider *et al.* 2014).

Survival of tortoise hatchlings

Whereas tortoise eggs generally do better in drier than wetter conditions, hatchlings do better in wetter than drier conditions, although they might not do well in extremely

wet seasons. In their first year of life, tortoise deaths are usually caused by lack of food and general desiccation during drought years (Caporaso 1989; MacFarland *et al.* 1974). On some islands, invasive mammals, such as pigs and rats, have killed many hatchlings, but this predation is increasingly under control. Prior to human arrival, aside from occasional predation by Galapagos hawks, hatchling tortoises had no predators. Therefore climate is likely the driving force in hatchling survival. In two back-to-back years, MacFarland *et al.* (1974) noted the impacts of drought stress on hatchlings. In 1970 they found starving hatchlings suffering near-complete mortality in a small area free of pigs and rats. The following year, they found high hatchling survival rates in the same area. They traced the difference to rainfall—in 1970 the CRU data from Galapagos show 397 mm of rain, whereas 881 mm of rain fell in 1971. If droughts as extreme as 1970 are sufficient to kill hatchlings, what do models project for the future?

As average conditions get warmer and wetter, the available model projections show fewer and fewer extreme drought years in the future, as does the analysis of rainfall data over the last two decades (Box 16.1). However, it is possible that the models do not sufficiently capture La Niña events, or that these modeled events are not well calibrated to regional conditions. The CRU data show two such extreme rainfall events occurred between 1961 and 2018, or in 3% of the years. But only one of 14 global climate models compiled by the Coupled Model Intercomparison Project (CMIP) projected such extreme years between 1961 and 2018 when hindcast to those years, for a total model-averaged annual probability of such events as 0.2%, or 1 in 500 years. Thus there is a misalignment between actual observations of extreme conditions and the ability of climate models to capture or predict these events. None of the CMIP model simulations show any major droughts after 2007. Yet, Cai *et al.* (2015) suggest that there will be an increase in the frequency of La Niña events in the future, compared to the past. It is not clear whether the current CMIP models fail to accurately capture these dynamics or whether the increased frequency of La Niña will occur in concert with an overall warming of the local sea surface (precipitation in Galapagos is closely tied to the temperature of the sea—with rainfall materializing as the sea surface temperature climbs), such that future global La Niña events will not produce the Galapagos drought conditions that past La Niña events did. As models are improved to better capture ENSO dynamics, the clarity of these projections should improve. For now, the models suggest that future hatchling tortoises will be at less and less risk of drought.

Tortoise fitness and physiology

What do these predicted shifts toward increased wetness, warmer temperatures, and more “greenness” mean for

individual tortoises navigating through the annual seasonal cycle? Seasonal change in vegetation productivity is the primary driver of migration in the species of Galapagos tortoises that occur on the larger islands with an elevational gradient that includes both lower, dry and upper, moist environments (Bastille-Rousseau *et al.* 2016; Chapter 13: Movement Ecology). Tortoises on small, arid islands, with minor elevation changes, do not migrate. On the larger islands, whereas smaller tortoises tend to stay in the lowlands year-round, larger juveniles and adults migrate to higher elevations during the dry season (Blake *et al.* 2012; Yackulic *et al.* 2017). Although small tortoises can maintain an energy surplus with much less food availability than larger tortoises, during severe droughts, small tortoises cannot survive on a deficit for as long as larger tortoises. With their greater stored resources, large individuals can survive long periods of low food availability, however, they may be operating on an energy deficit even when smaller individuals are operating at a surplus (Yackulic *et al.* 2017). Thus larger tortoises have more incentive to migrate in response to seasonal food availability in the lowlands.

Beyond larger tortoises being better able to meet their metabolic demands in more productive environments predicted for Galapagos in the future, the greater thermal mass of large individuals provides them more heat reserves to continue foraging through cold overcast days in the uplands (Fritts 1984, 1983; Yackulic *et al.* 2017). Meanwhile, smaller individuals are more able to escape excessive heating in the lowlands by making use of small amounts of shade and thermal refuges such as small caves and underneath shade-producing shrubs (Fritts 1983:1–16). The implications of climate change for heat balance in Galapagos tortoises are explored further in this volume (Chapter 10: Thermoregulation).

Tortoise growth and demography

Returning to the population model, the effect of increased foraging opportunities for tortoise populations can be incorporated by simulating faster juvenile growth rates, and thus shorter time to reproductive maturity. Juvenile tortoises grow substantially faster in wetter conditions (Chapter 12: Population Biology). Incorporating the frequency of droughts during the windows of growth observations, saddleback tortoises grew about 1.7 times faster when not in a sustained drought period compared to when a drought was occurring. During the period over which observations were made to develop the demographic matrix parameters, the Galapagos was experiencing drought approximately 27% of the time (Box 16.1). Future estimates suggest that there may be no more such droughts by the end of this century. Reducing the length of the juvenile stage (years 1–4) in the population

projection model by 1.8 years to capture the effect of reduced drought frequency on mean saddleback growth rates suggests tortoises would reach reproductive maturity at 14.2 years, instead of 16 years. This adjustment to the hypothetical generalized population increases the overall λ from 1.04 to 1.07, which equates to reducing the doubling rate of the population from 14 to 10 years. Incorporating the maximum effect of increased future juvenile growth rates with future rates of egg-killing rains of 20%, 55%, and 90%, λ would become 1.06, 1.04, and 1.00, respectively, which equate to growing populations that double in 11 and 18 years for the first two scenarios and one that does not grow in the third scenario. Thus increased juvenile growth rates may approximately counterbalance the impacts of the mean estimate for future egg-killing rains on overall population trajectories.

Tortoise habitat

The tens of thousands of records of adult and juvenile Galapagos tortoises matched to latitude/longitude coordinates (GTRI, unpubl. data) can be used to identify the environments where tortoises are found today and predict where suitable habitat might be in the future, using a standard niche-based species distribution modeling approach (Chapter 14: Habitats). Although widely used, the approach has limits, especially for forecasting, given that it is based on correlational data; the actual causal mechanisms may not be represented by the predictor variables selected, resulting in erroneous forecasts (Record and Charney 2016). Also, where Galapagos tortoises occur today is dictated somewhat by where populations were not destroyed and where people tend to look for them, that is, in more accessible areas (Chapter 20: Population Status). Rather than constructing a formal model here (but

see Chapter 14: Habitats), the Galapagos tortoise “niche” was examined in relation to an environmental variable that drives tortoise distribution and abundance: vegetation productivity, using the Normalized Difference Vegetation Index (NDVI) that indicates plant “greenness” measured across the landscape by satellites.

There are clear and strong links between plant productivity and tortoise occurrence (Fig. 16.7). Tortoises avoid unvegetated areas, most of which are open lava and cover 30% of the terrestrial landscape. When only the three dominant vegetated ecosystems that tortoises frequent (arid, transition, and humid zones) are included, plant productivity is significantly greater where tortoises are found than the overall average productivity of the available habitats (Fig. 16.7A and B). The average NDVI of vegetated ecosystems in the Galapagos is 0.51 (SD = 0.18), whereas the average productivity of NDVI in cells where tortoises have been observed is 0.65 (SD = 0.12) (Fig. 16.7C and D).

Given Charney *et al.*'s (unpublished manuscript) forecast of an increase in plant productivity archipelago-wide over the next 100 years in response to increased precipitation (equal to about standard deviation higher of the current average value of NDVI), tortoise habitat availability in Galapagos is likely to increase both in terms of quality and extent. Considering the margins of suitability, currently, 95% of tortoise observations occur at cells with NDVI values greater than 0.46. Under the Charney *et al.* analysis, the area of the terrestrial portion of Galapagos at this level (or higher) of greenness by the end of the century will increase by 3.5% under RCP 8.5. Given a 90% threshold of tortoise occurrences, a 6.4% increase is projected in the land area at least this green. How might tortoise abundance respond? The current size of the tortoise population can be visualized as the area under the curve of the plant growth profile for tortoise observations (Fig. 16.7). To understand

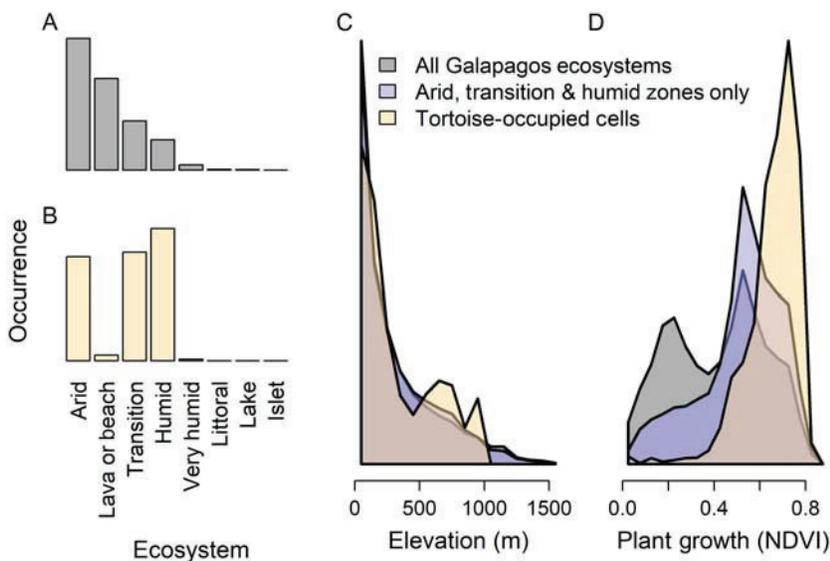


FIGURE 16.7 Ecosystems where Galapagos tortoises occur. (A) The extent of each ecosystem type. (B) The extent of each ecosystem type within 30-m grid cells where tortoises have been observed. (C) Elevation and (D) plant growth profiles for all areas in the Galapagos (gray), only the three vegetated ecosystems most frequented by tortoises (blue), and only the grid cells where tortoises have been observed (orange). Ecosystem data based on INGALA (1989).

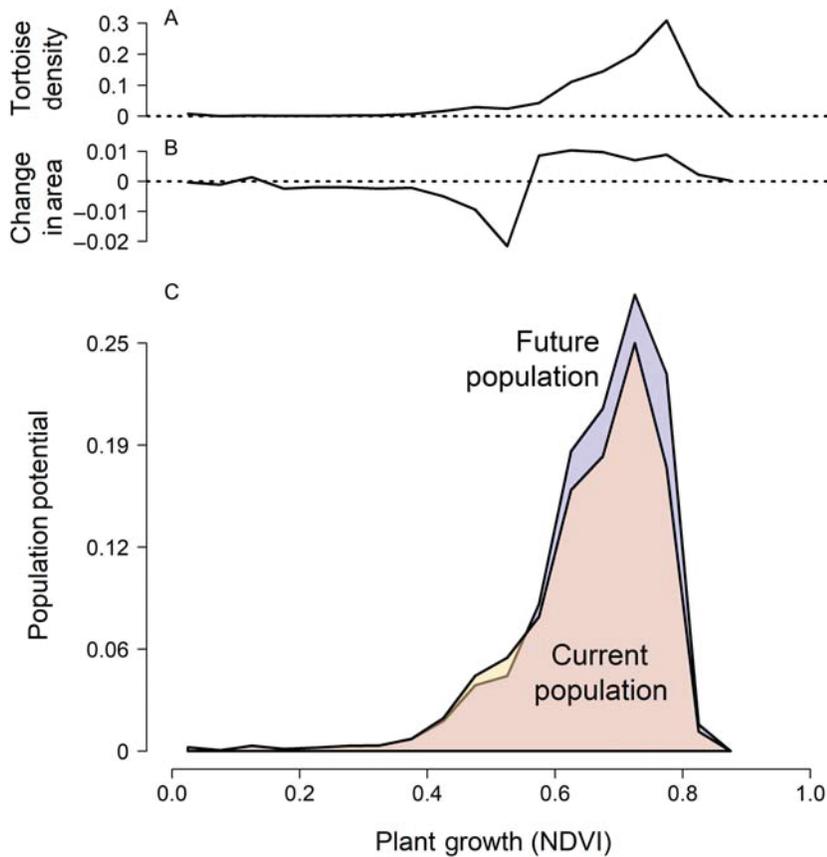


FIGURE 16.8 Projected impacts of future habitat suitability expansion on total tortoise populations. (A) Prevalence of tortoise observations relative to the amount of available land area within categories of plant productivity. (B) The relative change in the land area projected for each category of productivity by the end of the century under RCP 8.5. Combining (A) and (B) can be used to estimate the relative change (C) in the total population of tortoises across the system. *RCP*, Representative concentration pathways.

how changes in NDVI may impact the entire population, the plant growth profile of the tortoise observations can be divided by the profile of available habitat and then multiplied by the plant growth profiles projected by Charney *et al.* Comparing the areas under the current and future curves for RCP 8.5, and not including any other factors related to tortoise population dynamics or dispersal, total tortoise abundance is expected to increase by 13% by the end of the century (Fig. 16.8).

Tortoise—ecosystem interactions

In addition to increased plant productivity, species composition within plant communities will also change, with ramifications for Galapagos tortoises. Over the past 3000 years, plant community assemblages on the Galapagos have been relatively stable, despite slowly changing climate conditions. But in the past century, human activities caused dramatic changes to plant communities, largely through the introduction of nonnative species, both exotic mammals such as goats that transform tortoise habitats through herbivory and exotic plants that displace native species (Restrepo *et al.* 2012). In the coming century, it will be the interaction between climate and other biotic factors that will drive ecosystem change. Tortoises, as ecosystem

engineers, will play an important role in this unfolding process through herbivory, nutrient cycling, and seed dispersal (Falcón and Hansen 2018; Chapter 15: Role in Ecosystems). As moisture conditions increase, the areas within the Galapagos that provide suitable habitat conditions for invasive plants will likely expand (Trueman and d’Ozouville 2010), and tortoises will be one of the agents responsible for transporting invasive seeds to new habitats (Ellis-Soto *et al.* 2017). In some cases, the spread of invasive plants may be good for tortoises, as they forage on many invasive plant species (Blake *et al.* 2015; Chapter 11: Diet, Behavior, and Activity Patterns). In other cases, the spread of invasive plants that create barriers to migration could have a negative impact. Thus with increased overall rates of plant growth and more plant species to choose from, tortoises will likely play a major role through their foraging activities and movements that disperse plant seeds and change plant distributions in engineering novel ecosystems on the Galapagos, which will in turn impact the tortoises themselves.

Tortoise morphology and evolution

More productive ecosystems within the Galapagos—generally at higher elevations—tend to support larger

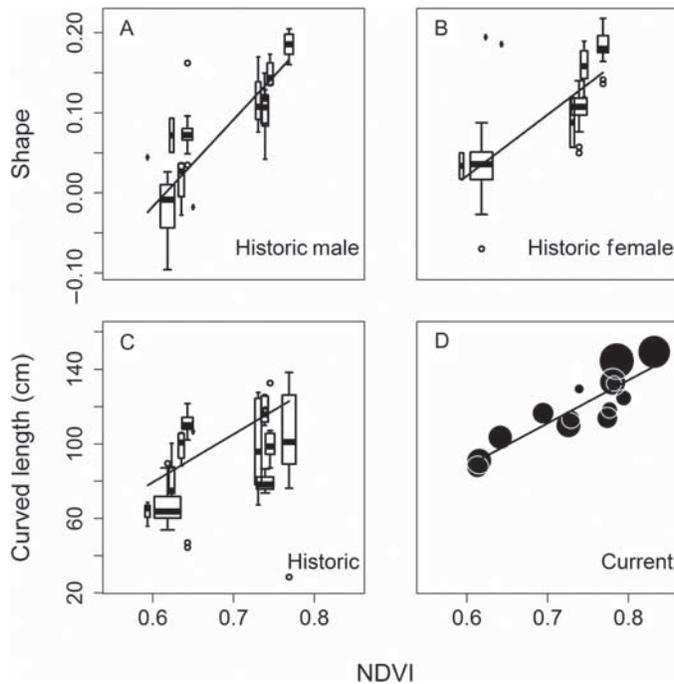


FIGURE 16.9 Relationship between size and shape of Galapagos tortoises in relation to plant productivity at the sites where tortoises occur. Carapace shape for (A) males and (B) females from 11 “historic” Galapagos tortoise populations reported by Van Denburgh (1914) versus vegetation productivity (NDVI) measured with recent satellite data. Positive carapace shape values correspond to dome forms, whereas negative values correspond to saddleback forms. Regressions were weighted by the number of observations at each site, with box plots representing the site-level distribution of shapes. (C) Histograms of curved carapace length of tortoises versus best available NDVI for 11 localities surveyed by Van Denburgh (1914). The solid line represents a linear regression between the 95th percentile of length and NDVI. Histogram width for each locality is proportionate to the square root of the number of samples, ranging from 1 to 86. The best available NDVI is calculated as the 95th percentile of NDVI within 10 km of the locality center. (D) The 95th percentile of length for adult tortoises observed during 1962–2014 versus best available NDVI for 14 localities, with the solid line representing a linear regression fit. The point area is proportionate to the square root of sample size, ranging from 41 to 7887. The solid line represents a linear regression between length and NDVI. NDVI, Normalized difference vegetation index.

bodied tortoises, whereas more arid environments—generally at lower elevations—support smaller tortoises (Chapter 8: Morphology; Chapter 14: Habitats). Turtle shape is also related to ecosystem productivity—saddleback forms predominate in arid lowlands (Fritts 1984). The reason for this correlation is not entirely clear (Chapter 8: Morphology), but the primary explanation is that the higher head extension provided by the saddleback form allows tortoises to compete better for scarce resources—both by allowing a higher reach in foraging and by providing an advantage in aggressive encounters with other tortoises (Fritts 1984, 1983). Examination of current and historic records of tortoise size and shape, linked to the plant productivity or “greenness” of where the tortoises were found, will help in addressing the question of how changes in ecosystem productivity may affect tortoise morphology. The size of adult tortoises increases with greater plant productivity (NDVI) in both the contemporary and historic data sets across sites (Fig. 16.9). Tortoises are more dome-shaped at higher NDVI values for both males and females. These patterns demonstrate that tortoise size and shape closely fit the environments in which they occur. With the Galapagos climate projected to change toward warmer conditions in the future, the saddleback form, unique to Galapagos among living turtles, is predicted to devolve toward the ancestral dome form from which it arose (Chapter 7: Evolution). This process may be further facilitated by climate change impacting select native plant species that are of vital importance to tortoises. More specifically a primary driver of the saddleback morphology is hypothesized to

be the climate-sensitive arboreal *Opuntia* cactus of Galapagos. Accessing cacti in arid zones during extended dry seasons is considered a primary selective force for the evolution of the saddleback shell and increased neck length (Fig. 8.7). *Opuntia* cactus experience elevated mortality from water logging and subsequent toppling during wet periods (Grant and Grant 1989). This selective agent for the distinct saddleback shell morphology may diminish under a wetter climate in Galapagos.

Conclusion

Despite knowledge gaps and an enormously uncertain future, there is enough knowledge to formulate important questions about Galapagos tortoises in a changing climate. Although current models suggest that climate change may generally increase the fitness of juvenile and adult tortoises foraging across Galapagos landscapes, a serious threat may be posed to the viability of future tortoise eggs during incubation. Continued efforts to eradicate invasive mammalian predators and competitors combined with increased future vegetation growth rates ought to provide expanded suitable habitat for tortoise populations. But whether populations can disperse into these areas will depend, in part, on their ability to reproduce. Future tortoise conservation efforts may require creative solutions, such as artificially modified egg-laying sites in the wild (e.g., Buhlmann and Osborn 2011), engineered to provide dry soils despite heavy rain, or perhaps harvesting eggs from wild nests for selective incubation in captivity at male-producing temperatures to manipulate

sex ratios in wild populations. Interventions are already being considered to equilibrate sex ratios in the Santiago Island tortoise population due to skewed exploitation in the past, albeit in this case to generate more females (Chapter 20: Population Status).

The possibility for high rates of egg failure in Galapagos tortoises in the future is concerning; however, these observations are based on monitoring a single nesting area. More research is needed, including data from nesting sites of several populations, to determine how weather, geology, and topography relate to soil conditions in the nest, and the variability and heritability of egg tolerance to these conditions. Demographic models for different populations need to be better parametrized to understand the sensitivity of all stages of tortoise growth and survival to ecosystem change.

Given that Galapagos tortoises frequent the most productive ecosystems in Galapagos, the forecasts for increased archipelago-wide productivity would seem to be good news. More plant growth means more food available in more places. Habitats that are currently too arid to support tortoises may become suitable. Larger, dome tortoises may be at a greater advantage in lowlands where smaller, saddleback tortoises were historically selected for. Tortoises may no longer need to migrate seasonally to maintain surplus energy budgets.

Whether, and over what timeframe, these changes in fitness result in actual changes in morphology, behavior, and distribution are separate questions. For instance, tortoises appear to migrate in anticipation of seasonal changes based on average conditions in the past, rather than responding to actual conditions (Bastille-Rousseau *et al.* 2019). If the cues for the timing of migration are learned over decades of experience, it may be difficult for individual tortoises to keep pace with rapidly changing conditions. To the extent that migratory instincts, habitat selection, morphology, and growth rates are controlled by genetics, it will take many, extended generations of tortoises before these aspects of tortoise ecology fall into “sync” with new climate conditions.

Many global-scale questions with strong Galapagos-scale implications remain unanswered. What will be the trajectory of future greenhouse emissions? Which predictive models best describe how the global climate will operate? What El Niño and La Niña dynamics will play out? How will the local sea surface temperatures shift and by extension alter patterns of precipitation on land? How will Galapagos microclimates respond?

Uncertainty is the overriding characteristic of climate change. Management strategies must be more flexible in the future to adapt to changes as they occur. While the tools to evaluate the fate of Galapagos tortoises in a changing climate exist, additional knowledge of tortoise reproduction and how tortoises interact with the ecosystems

they inhabit is needed to identify how to minimize the impact of a range of possible outcomes of climate change on Galapagos tortoises.

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