




ARTICLE

Environmental variation structures reproduction and recruitment in long-lived mega-herbivores: Galapagos giant tortoises

Stephen Blake^{1,2,3,4,5,6}  | Freddy Cabrera⁶ | Sebastian Cruz⁶ |
 Diego Ellis-Soto^{2,7} | Charles B. Yackulic⁸  | Guillaume Bastille-Rousseau^{5,9}  |
 Martin Wikelski^{2,7} | Franz Kuemmeth¹⁰ | James P. Gibbs⁵ | Sharon L. Deem¹¹

¹Biology Department, Saint Louis University, Saint Louis, Missouri, USA

²Max Planck Institute for Animal Behavior, Radolfzell, Germany

³WildCare Institute, Saint Louis Zoo, Saint Louis, Missouri, USA

⁴Whitney Harris World Ecology Center, University of Missouri-St. Louis, Saint Louis, Missouri, USA

⁵Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, USA

⁶Charles Darwin Foundation, Galapagos, Ecuador

⁷Department of Biology, University of Konstanz, Konstanz, Germany

⁸US Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona, USA

⁹Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, Illinois, USA

¹⁰E-obs GmbH, Grünwald, Germany

¹¹Institute for Conservation Medicine, Saint Louis Zoo, Saint Louis, Missouri, USA

Correspondence

Stephen Blake
 Email: sblakewcs@gmail.com

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Abstract

Migratory, long-lived animals are an important focus for life-history theory because they manifest extreme trade-offs in life-history traits: delayed maturity, low fecundity, variable recruitment rates, long generation times, and vital rates that respond to variation across environments. Galapagos tortoises are an iconic example: they are long-lived, migrate seasonally, face multiple anthropogenic threats, and have cryptic early life-history stages for which vital rates are unknown. From 2012 to 2021, we studied the reproductive ecology of two species of Galapagos tortoises (*Chelonoidis porteri* and *C. donfaustoi*) along elevation gradients that coincided with substantial changes in climate and vegetation productivity. Specifically, we (1) measured the body and reproductive condition of 166 adult females, (2) tracked the movements of 33 adult females using global positioning system telemetry, and monitored their body condition seasonally, (3) recorded nest temperatures, clutch characteristics, and egg survival from 107 nests, and (4) used radiotelemetry to monitor growth, survival, and movements of 104 hatchlings. We also monitored temperature and rainfall from field sites, and remotely sensed primary productivity along the elevation gradient. Our study showed that environmental variability, mediated by elevation, influenced vital rates of giant tortoises, specifically egg production by adult females and juvenile recruitment. Adult females were either elevational migrants or year-round lowland residents. Migrants had higher body condition than residents, and body condition was positively correlated with the probability of being gravid. Nests occurred in the hottest, driest parts of the tortoise's range, between 6 and 165 m elevation. Clutch size increased with elevation, whereas egg survival decreased. Hatchling survival and growth were highest at intermediate elevations. Hatchlings dispersed rapidly to

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100–750 m from their nests before becoming sedentary (ranging over <0.2 ha). Predicted future climates may impact the relationships between elevation and vital rates of Galapagos tortoises and other species living across elevation gradients. Resilience will be maximized by ensuring the connectivity of foraging and reproductive areas within the current and possible future elevational ranges of these species.

KEYWORDS

body condition, chelonian, early life history, elevation gradient, migration, natal dispersal, reproductive trade-off, the lost years

INTRODUCTION

Quantifying patterns in vital rates (e.g., fecundity and survival) is fundamental to understanding and predicting population dynamics, community ecology, and the evolutionary trajectories of species (Murdoch, 1994; Williams et al., 2002). The magnitude of variation in vital rates at different life-history stages depends on the evolutionary consequences of trade-offs in demographic traits including recruitment rate, recruiting age, adult survival, fecundity, and reproductive longevity (Gaillard et al., 2000; Zera & Harshman, 2001). Species that live in variable environments may be subject to a variety of competing trade-off optima over time, such that vital rates are dependent on the ecological context of populations through time and space (Childs et al., 2010; Wilbur & Rudolf, 2006).

Organisms that occur along elevation gradients are often exposed to rapid change in environmental conditions over small geographical distances that are manifested by considerable variation in vital rates (Johnson et al., 2006). As such they are useful targets for study to understand how vital rates depend on a population's ecological context. Among animals, bird responses to elevation have been extensively studied (Boyle et al., 2016). For some species, such as yellow-eyed juncos (*Junco phaeonotus*), egg survival and hatchling growth may increase with elevation, while the length of the breeding season and adult survival decrease (Lundblad & Conway, 2020b). General trends among birds include an overall reduction in fecundity as elevation increases because of smaller clutch sizes and fewer breeding attempts, shorter and later breeding seasons, and longer development times (Boyle et al., 2016). Elevational migration and partial migration may have evolved under selection pressures from competition for breeding sites and other resources, predation risk, and, in the case of partial migration, niche variation among individuals within populations (Buchan et al., 2020; Chapman et al., 2011; Grayson

et al., 2011). Among mammals, partially migrant elk (*Cervus canadensis*) follow elevational shifts in the seasonal distribution of high-quality forage which increases both survival and reproductive success (Hebblewhite et al., 2008). However in partially migrating bighorn sheep (*Ovis canadensis*), fat deposition, not movement strategy, is the key determinant of survival in harsh environments for both residents and migrants (Denryter et al., 2022).

More generally, migratory species of birds and mammals exhibit a faster pace of life, with higher annual fecundity, earlier maturity, and shorter lifespans than resident species (Soriano-Redondo et al., 2020). Long-lived animals with primarily slow pace of life traits that can more efficiently obtain and use energy resources over large spatial extents via long-distance migration may acquire greater mean annual energy surplus than residents (Berg et al., 2019; Gaidet & Lecomte, 2013) allowing for greater allocation of resources for the fast pace of life traits such as reproduction and growth (Aikens et al., 2021). Whether these trends are a cause or consequence of migration is unclear, although the adaptive value of resource allocation away from survival and toward reproduction and development in variable environments is evident (Soriano-Redondo et al., 2020). These trade-offs may also apply to ectotherms despite their lower metabolic costs (Yackulic et al., 2014). For example, among partially migrating tortoises on Aldabra Atoll, migrant tortoises risk a higher probability of death, but achieve higher reproductive success than residents because they can access higher quality forage (Swingland & Lessells, 1979). Migratory Galapagos tortoises may have a higher annual energy surplus than residents in the same populations, potentially available to increase reproductive output (Yackulic et al., 2017). A combination of selective pressures that shape adaptation to either maximize survival or reproduction determines where on the slow-fast continuum of life histories individuals, populations and species occur (Hille & Cooper, 2015; Lundblad & Conway, 2020a).

Answering such questions and understanding the mechanisms of both adaptive and plastic responses to environmental variability along elevation gradients is urgently needed in the face of anthropogenic climate change (Hallman et al., 2022; Wiens, 2016).

Life-history data are unavailable for many species due to the technical and logistic difficulties of counting animals and estimating rates of birth, death, and movement characteristics (e.g., Holmes, 2001; Zimmerman et al., 2007). Quantifying survival of early life-history stages can be especially difficult because young individuals may be cryptic and/or sensitive to disturbance (Almany & Webster, 2006; Morin et al., 2016). These challenges compound in the many species that migrate over long distances (Berger, 2004; Harris et al., 2009; Wilcove & Wikelski, 2008). Migratory, long-lived species are of particular interest to biologists seeking to develop unified life-history theories because they present an extreme among trade-offs in vital rates that still permit population persistence: delayed sexual maturity, low fecundity, variable recruitment rates and long generation times (Brooks et al., 1991; Cayuela et al., 2016; Congdon et al., 1993; Lotze et al., 2011). However, long-distance migration often exposes individuals and populations to a suite of ecological drivers that are difficult to quantify (Congdon et al., 1993; Purvis et al., 2000).

Giant tortoises that live on volcanic slopes of the Galapagos Islands possess all these traits. Moreover, unlike birds and mammals on elevation gradients, Galapagos tortoises are ectotherms constrained by relatively restricted thermal limits (Blake, Parlin, et al., 2021), they provide no parental care, are subject to temperature-dependent sex determination (Deem et al., 2023), and vary over more than four orders of magnitude of body size from 0.06 kg hatchlings to 300 kg adults (Van Denburgh, 1914). In addition, the metabolic rate of tortoises is roughly one order of magnitude lower than that of endotherms (Schmidt-Nielsen, 1997). Thus, selective pressures imposed on giant tortoises by elevation gradients are likely to vary with body size and be different from those impacting mammals and birds. Low metabolic rate suggests that tortoises should be less sensitive to variable food and energy availability per unit mass than mammals and birds.

Despite their relatively low energy requirement and prodigious fasting ability (Van Denburgh, 1914), Galapagos tortoises on some islands display seasonal partial elevational migration following productivity gradients driven by climate mediated by elevation and topography (Bastille-Rousseau et al., 2017; Blake et al., 2013; Blake, Yackulic, et al., 2021). Tortoises migrate into arid areas, usually lowlands, during the hot-wet season when these areas “green up” and forage quality

is high. As rainfall and lowland vegetation quality and quantity decline, migrating tortoises return to humid, usually highland areas, where an abundance of lower quality forage is available year round. The migration is size-biased, with larger individuals having a higher propensity to migrate. Almost all adult males migrate, while among adult females some migrate while others do not although the proportion of the population that is migratory is unknown (Blake et al., 2013). Resident females remain in the arid zone year round, often close to nesting sites. The timing of the upslope migration is also size biased; large individuals initiate migration earlier than smaller ones, a pattern consistent within sexes (Bastille-Rousseau et al., 2019; Yackulic et al., 2017).

Yackulic et al. (2017) developed a theoretical model to test whether observations of the system could be explained by combining metabolic theory with spatiotemporal variation in the quality and quantity of forage. The bioenergetics model they developed suggested that size-biased patterns in the timing and probability of upslope migration were related to the ability of smaller individuals to tolerate declining forage levels in the lowlands for longer periods than larger tortoises due to their lower absolute energy requirements. However, unlike males, the timing of the upslope migration in females was also driven in part by nesting, with presumably strong selective pressure on the optimum timing and location of nests (Refsnider & Janzen, 2010). Optimal nesting conditions in terms of lifetime reproductive success and the evolution of life-history traits must incorporate diverse factors (Martin, 1995). These may be related to females such as energy balance, body condition and health, as well as to offspring, for example egg survival and hatchling survival and growth. The bioenergetics model suggests that migrants have better access to high-quality forage year round than sedentary individuals (Yackulic et al., 2017), promoting improved nutritional balance and body condition (Blake et al., 2015) and, as a consequence, higher reproductive condition (see Table 1, Hypothesis 1d). As migratory ectotherms living in a variable environment, Galapagos tortoises are likely to be capital breeders (Plot et al., 2013). Females are expected to produce the most eggs when body condition is high, and therefore migrants are likely to display a higher probability of being gravid than nonmigrants (see Table 1; Hypotheses 1a,b,c,d below).

While forage quality and precipitation explain many of the patterns observed in adult Galapagos tortoises, it is likely that temperature also plays an important role in early life history. Ectothermic tortoises should be more vulnerable to temperature extremes and varying thermal environments than endotherms, and small tortoises are

TABLE 1 Questions and hypotheses concerning egg and hatchling survival of Western and Eastern Santa Cruz Galapagos tortoises (*Chelonoidis porteri* and *C. donfaustoi*) along an elevation gradient on Santa Cruz Island.

Questions	Hypothesis no.	Hypotheses
(1) How do movement strategies of adult female tortoises influence their body condition and egg production?	1a	Female body condition will peak at the end of the hot-wet season before nesting begins and decline thereafter.
	1b	Migratory females will display higher body condition (mass as a function of length) than nonmigrators.
	1c	If Galapagos tortoises are capital breeders, among adult females the probability of being gravid will be positively correlated with body condition.
	1d	Migratory females will display a higher probability of bring gravid than nonmigrators.
(2) How do the environmental conditions for nesting vary across the elevation gradient and is this related to egg survival and hatchling growth and survival	2a	Differences in temperature, rainfall and productivity exist between nesting areas, specifically rainfall and NDVI will increase, and temperature will decrease with elevation of area.
	2b	Because nesting occurs in the coolest months of the year, temperature within nests will increase over incubation.
	2c	Mean nest temperatures will decrease with elevation.
	2d	Clutch size is independent of nesting area.
	2e	Egg weight is independent of nesting area.
	2f	Egg survival will be positively correlated with temperature and negatively correlated with rainfall, thus highest at the lowest elevations.
	2g	Hatchling growth and survival are positively correlated with temperature, rainfall and NDVI, thus highest at intermediate elevations.
(3) What is the nature of natal dispersal?	3	Hatchlings will rapidly disperse from nesting sites upon occlusion.
(4) What are the implications of projected future environmental change for tortoise reproductive ecology on elevation gradients?		No a priori predictions.

more sensitive than large ones due to lower thermal inertia (Blake, Parlin, et al., 2021). Temperature is likely to have a bigger impact on egg survival than among endotherms such as birds that incubate their eggs. Furthermore, temperature is likely to play a more substantive role in the survival and growth of poikilothermic hatchling tortoises compared with homeothermic endotherm species. Temperature regimes outside the thermal optimum, both hot and cold, are expected to have a negative impact on the survival of eggs and the survival and growth of hatchlings.

Offspring survival and growth may be as important as fecundity in determining reproductive success and the trajectory of life-history trade-offs. Early investigations (Fowler De Neira & Roe, 1984; MacFarland et al., 1974) indicate that nesting in partially migratory species of Galapagos tortoises is usually restricted to lower elevations and occurs during the cool-dry season between July–October when forage quality is in decline (Yackulic et al., 2017). However, nesting can occur at elevations anywhere between 0 and 1000 m on some islands and the timing of nesting is highly variable between

and among individuals and species (S. Blake, personal observation). For example temperature and rainfall vary considerably with elevation and season on the Galapagos Islands (Bastille-Rousseau et al., 2017; Trueman & d'Ozouville, 2010), which can strongly influence egg survival (Refsnider & Janzen, 2010), offspring sex (through temperature-dependent sex determination; Ewert et al., 1994), and hatchling success and growth in turtles and tortoises (Winokur & Winokur, 1995; see Table 1; Hypotheses 2). On most islands of the Galapagos, gradients of rainfall and temperature are opposing: temperature decreases with elevation while rainfall and vegetation abundance increase with elevation (Cayot, 1987; Trueman & d'Ozouville, 2010). Adult female tortoises must navigate these gradients to optimize trade-offs between their own health, body condition, and fecundity against the survival of their offspring at the egg, hatchling, and juvenile stages (see Table 1; Hypotheses 2b–g). How the movement decisions of females and the timing and location of oviposition influence fecundity, the survival of eggs and hatchlings is poorly known (MacFarland et al., 1974) such that the “lost years”

(the period between leaving the nest and the late juvenile stage during which small cryptic chelonians are difficult to find and therefore to study, *sensu* Hamner (1988)) of Galapagos tortoises remain lost.

In addition to abiotic factors, predation by Galapagos hawks (*Buteo galapagoensis*) is a source of direct mortality of hatchlings (Darwin, 1839). Field observations show nesting sites to be relatively devoid of vegetation due to trampling and digging by tortoises (S. Blake, J. P. Gibbs, personal observation), potentially limiting protective cover from predators, thermal refuge, and forage for hatchlings. Furthermore, high concentrations of adult tortoises are likely to pose a mortality threat to hatchlings from trampling. Such conditions are expected to select for rapid dispersal of hatchlings from their nests into habitats that provide greater protection and lower competition for food (see Table 1, Hypothesis 3).

Here we report the results of a 9-year study on the nature of life-history trade-offs involving female egg production, clutch survival, and hatchling survivorship and growth among Galapagos tortoises along elevation gradients. We focused on two species of tortoises (*Chelonoidis porteri* and *C. donfaustoi*) on Santa Cruz Island in the center of the Galapagos Archipelago because they occupied the typical habitat types of Galapagos from arid lowlands, through a transition zone to humid highlands (Wiggins & Porter, 1971), they were relatively accessible for study unlike populations on more remote islands, and their reproductive ecology was largely unknown (Blake et al., 2013, 2015; MacFarland et al., 1974). Moreover, both species of Santa Cruz giant tortoises are critically endangered (IUCN, 2022); gaining a deeper understanding of their reproductive biology will assist conservation efforts.

Specifically, we addressed the following questions: (1) How do movement strategies of female tortoises influence their body condition and egg production? (2) How do the environmental conditions for nesting vary across the elevation gradient and are they related to egg survival and hatchling growth and survival? (3) What are the characteristics of natal dispersal? Based on current knowledge and expectations on the variation of dispersal, migration, and life-history traits of Galapagos tortoises along elevation gradients, specific hypotheses related to these questions (Table 1) are illustrated in a conceptual model (Figure 1).

METHODS

Study site

The Galapagos Islands straddle the Equator in the eastern Pacific ~1000 km west of continental Ecuador.

This volcanic archipelago consists of some 129 islands, including 13 large islands (more than 1 km²), the oldest of which are ~4 M and the youngest <0.5 M (Poulakakis et al., 2012). The climate is characterized by a hot-wet season from January to May, and a cool-dry season for the rest of the year (Trueman & d'Ozouville, 2010). However, during the cool-dry season, persistent cloud cover results in humid upland conditions on the windward (southern) slopes of the larger islands (Colinvaux, 1984). Vegetation patterns are driven by rainfall and substrate, which are largely determined by aspect, elevation, and lava flows.

Our study focused on Santa Cruz Island (Figure 2), which rises to 860 m elevation with a surface area of 986 km² (Snell et al., 1996), one of nine islands giant tortoises are believed to have currently or previously occupied (Caccone et al., 2002). The island hosts the largest human population on the Galapagos Islands, estimated at >15,000 in 2010 (León & Salazar, 2012). Most of the moist highland zone has been converted to agriculture and at least 86% of this area are now degraded by either agriculture or associated invasive plant species (Laso et al., 2019; Trueman et al., 2014).

Tortoises on Santa Cruz Island occur in two separate areas on the island's western and eastern flanks (Figure 1). Western Santa Cruz tortoises (WSCT), *Chelonoidis porteri*, are widely distributed from ~0–450 m elevation along the southwestern flank of Santa Cruz (labeled “El Chato” in Figure 2), and comprise several thousand individuals (Benitez-Capistros et al., 2018; MacFarland et al., 1974; Tapia et al., 2021). Eastern Santa Cruz tortoises (ESCT), *C. donfaustoi*, occur on the east of the island (labeled “Cerro Fatal” in Figure 2), between ~50–450 m elevation. Both species are of the “domed” morphotype and they display strong size dimorphism, with females weighing up to ~120 kg and males occasionally exceeding 260 kg (unpublished data). Both species are seasonal partial migrants along the elevation gradients, and females of each species use permanent nesting areas situated at different elevations with different environmental conditions that offer the potential to test our hypotheses. Some of our datasets come only from western Santa Cruz tortoises because we began our study in El Chato, before expanding to the eastern Santa Cruz tortoise species.

Environmental data collection

Rainfall and shade temperature across the elevation gradient of each species were quantified via a series of weather stations located at 50 m altitude increments from 50 to 400 m in El Chato and 100–400 in Cerro Fatal. Monthly rainfall was quantified by measuring the

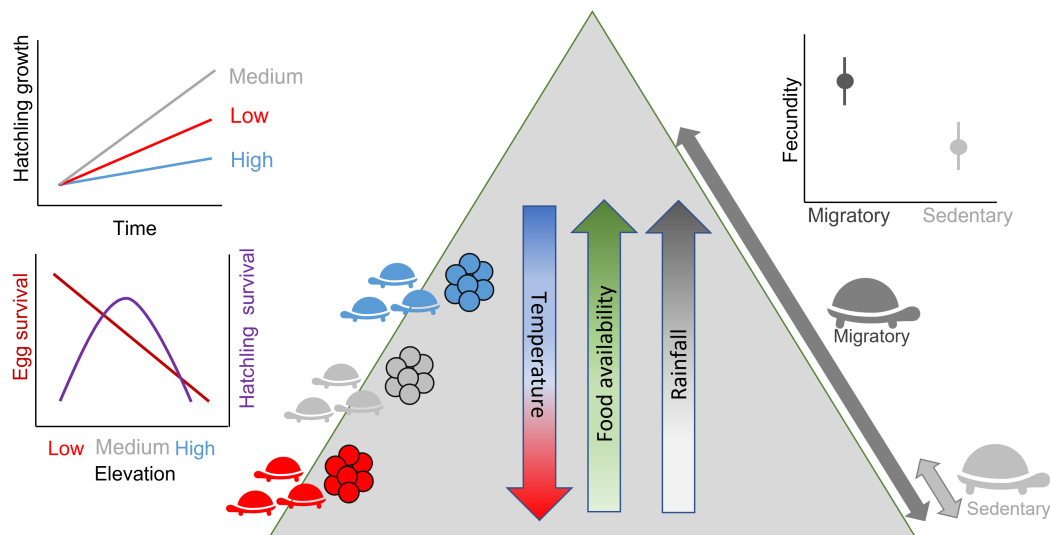


FIGURE 1 Conceptual model illustrating major environmental and abiotic gradients with elevation and core predictions of giant Galapagos tortoise life-history trade-offs related to adult fecundity and juvenile recruitment. We predict that 1. migratory female tortoises are more fecund than sedentary tortoises, 2. egg survival, and hatchling survival will be highest at intermediate elevations because of the effects of opposing gradients in temperature with rainfall and food availability (low elevations may be too hot and with lower food availability compared with higher elevations which have increasing food availability but are progressively colder and wetter). Hatchling survival is also predicted to be highest in intermediate elevations for similar reasons: food availability is higher at higher elevations but hatchling's ability to maintain optimal temperatures to exploit food efficiently is compromised by cooler, damper conditions, while low elevations are hotter but have lower food availability.

accumulated depth of the water column in 10-cm diameter PVC pipe located in open vegetation. After measurement, the water column was siphoned out of each tube to allow refill during the next month. A 5-cm layer of engine oil above the water column prevented evaporation. The shade temperature was measured every 4 h with an iButton Thermochron data logger (iButton, DS1922L, Maxim Integrated, San Jose, CA) located in the shade and downloaded monthly. To measure vegetation productivity along the elevation gradient and also in nesting areas, we used the Normalized Difference Vegetation Index (NDVI) obtained from the NASA MODIS (Moderate Resolution Imaging Spectroradiometer) product of the Terra satellite, which reliably captures variation in vegetation growth, productivity, and resources available to herbivores (Huete et al., 2002; Mueller & Fagan, 2008; Pettorelli et al., 2005). MODIS vegetation indices are provided at 250 m × 250 m resolution every 16 days, yielding 23 composites per year. We calculated pixel values from raw data following methods described by Bastille-Rousseau et al. (2017). Pixel values averaged by month from 0 to 400 m along the elevation gradient within the range of tagged female tortoises were selected and projected onto a digital elevation model of Santa Cruz Island to assign elevation values to each pixel, and then binned at 25 m intervals. The NDVI within nesting areas and areas used by juveniles were obtained from values of pixels that touched minimum convex polygons formed from hatchling movement data collected in each area (see below).

Female tortoise movements, body condition, reproductive condition, and the timing of nesting

Between 2010 and 2021 custom-made GPS telemetry tags (e-obs GmbH, Munich, Germany) were fitted to a sample of adult female tortoises from both species ($n = 9$ in Cerro Fatal and $n = 16$ in El Chato; Bastille-Rousseau, Potts, et al., 2016; Bastille-Rousseau, Yackulic, et al., 2016; Blake et al., 2013, 2015). Tags were glued to the front of the carapace using a nontoxic plumber's epoxy (Fix-It Stick Epoxy Putty, Oatey, Cleveland, OH, USA). Tags collected fixes every hour.

Four times per year (November to December, March, June to July, and September) between 2013 and 2015 we attempted to locate all tagged female tortoises to determine their body condition and reproductive status. During these periods we also searched for nontagged females dispersed along the elevation gradient and recorded the same metrics. For each adult female encountered ($n = 166$) we recorded mass to the nearest 0.5 kg and curved carapace length to the nearest 0.5 cm with a tape measure. The body condition index (BCI) was calculated as:

$$BCI = m/CCL^{2.89},$$

where m = mass, and CCL = curved carapace length (Blake et al., 2015; $n = 238$, with some individuals measured repeatedly). The power coefficient was calculated

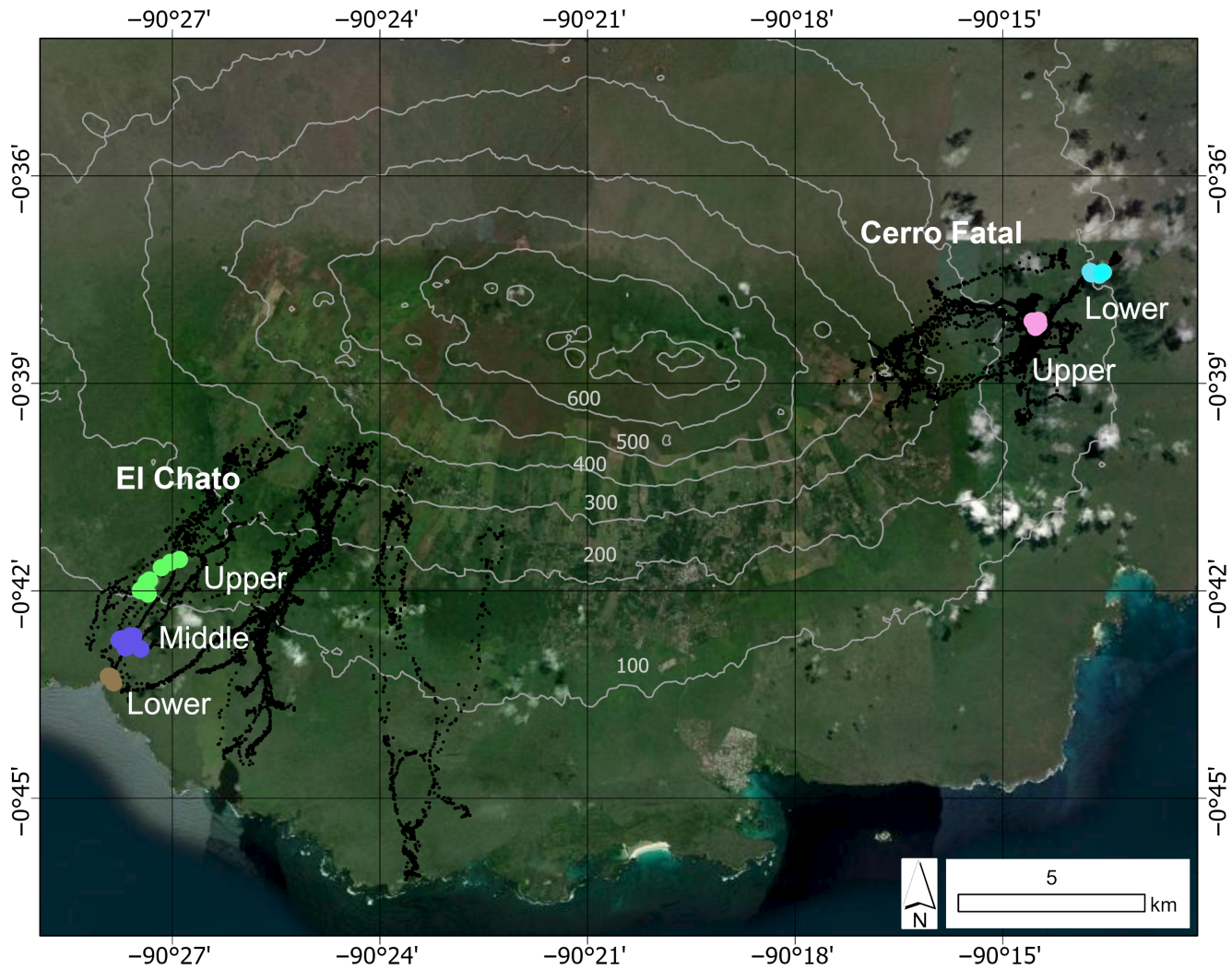


FIGURE 2 The geography of the study sites showing the location of Santa Cruz Island in the Galapagos Archipelago, the El Chato and Cerro Fatal regions, tracks of GPS-tagged adult female giant Galapagos tortoises (small black dots) and five monitored nesting areas (individually colored large dots for each nesting area); three in El Chato and two in Cerro Fatal.

based on the best fit for a large sample of length/mass measurements collected by Galapagos National Park Directorate (GNPS) rangers. We used a portable ultrasound machine (E.I. Medical Imaging Portable Ultrasound Ibex) with a curvilinear 3.8 MHz transducer probe to scan adult female tortoises for the presence of eggs and developing follicles following methods by Robeck et al. (1990) and Casares et al. (1997). Complete counts of follicles and eggs were not possible, so we recorded the presence/absence of follicles and/or eggs.

Monitoring of nesting areas and identification of nests

Studies on tortoise nesting were focused mostly on the three known nesting areas in El Chato, with supporting data from two areas in Cerro Fatal (Figure 2). Nesting

areas are distinguished by their open soil, evidence of existing and old nests and signs of intensive use by tortoises, and these concentration sites are well known to Galapagos National Park rangers. Mean elevation in the three El Chato nesting areas was 13, 58 and 107 m in the lower, middle, and upper areas respectively, and 90 and 165 m for the lower and upper areas in Cerro Fatal. Nesting areas are separated by extensive areas of lava rock unsuitable for nesting.

Between 2013 and 2016 from July to October, we searched for freshly made nests in the three El Chato nesting areas ($n = 98$) and in 2016 for the two Cerro Fatal areas ($n = 12$). We identified freshly constructed nests by signs of recent digging and the presence of moisture on the nest cap (tortoises often urinate and defecate in and on the nest site). On finding a fresh nest, we dug carefully under the hardened nest cap and removed it. We then removed all eggs, maintaining their

orientation and marking a unique ID number onto each egg with a pencil. We recorded breaks and cracks in each egg, weighed them to the nearest gram and, with calipers, measured the diameter to the nearest millimeter. Eggs were then carefully put back into the nest in the same position in which they had been found. For a sample of 41 nests, we estimated the center of the egg chamber where we placed the iButton ThermoChron data loggers (Maxim Integrated, San Jose, CA) as we replaced the eggs that recorded the temperature every 4 h. As we replaced the eggs back in their original location, we placed soil around each egg to secure the egg in its original configuration and packed surface soil to replicate the nest's cap as closely as possible.

It is the policy of the Galapagos National Park Directorate (GNPD) to protect tortoise nests in designated areas from feral pigs with wire mesh placed over nests and to open nests at the predicted end of incubation to extract hatchlings. This reduces the risk of entombment; however, it also means that hatchlings are liberated before they would naturally emerge. This precluded us from reporting on natural incubation times and emergence dates, as well as mortality caused by entombment. Following GNPD regulations, when incubation was estimated to be complete, we reopened the sample of nests. Hatchlings had either already exited the nest or had hatched but not emerged. When present, hatchlings were measured to the nearest millimeter, weighed to the nearest gram, visually inspected for abnormalities, and then released at the nest ($n = 105$). To quantify growth, survival, and movements, we selected a sample of hatchlings from randomly chosen nests to be fitted with very high frequency (VHF) radio tags (RI-2B, Holohil Ltd. Carp, ON, Canada). VHF tags weighed 5 g each; only tortoises that weighed >60 g were fitted with transmitters. The same attachment method as for adults was used, except that the tags were placed at the rear of the carapace only. A survival analysis revealed no effect of transmitter mass relative to initial body mass on hatchling mortality (Appendix S1: Table S11d). Thereafter, we identified the location of tagged hatchlings approximately bi-weekly, recording location obtained from a handheld GPS unit, weight, and length. Hatchlings found dead were usually in an advanced state of decay and the cause of death could not be determined.

All animal handling procedures followed the guidelines of the GNPD, the Max Planck Institute of Animal Behavior, and IACUC protocol no. 121202 of the State University of New York, College of Environmental Science and Forestry.

Statistical analyses

We tested Hypothesis 1a (Female body condition will peak at the end of the hot-wet season and decline

thereafter) with a set of linear mixed models (LMMs) of the forms:

1. $\text{LogM} \sim \text{Constant} + \text{logCCL} + \text{Elev} + \text{Population}$
2. $\text{LogM} \sim \text{Constant} + \text{logCCL} + \text{Elev} + \text{Population} + \text{Month_numeric}$
3. $\text{LogM} \sim \text{Constant} + \text{logCCL} + \text{Elev} + \text{Population} + \text{Month_numeric} + \text{Month}^2$
4. $\text{LogM} \sim \text{Constant} + \text{logCCL} + \text{Elev} + \text{Population} + \text{Month_categorical}$

with individual as a random effect. Model fit was compared using the Akaike information criterion (AIC; Burnham & Anderson, 2002). Hypothesis 1b (Migratory females will display higher body condition than nonmigrators), could not be adequately tested with our population of GPS-tagged individuals because of small sample sizes. However, using data from the larger sample of tortoises, including tagged and un-tagged individuals, we were able to indirectly test Hypothesis 1b, under the assumption that, in November and December, all migrating tortoises had returned or were returning to the highlands (Yackulic et al., 2017). Thus, females in highlands during these months were considered migrants and we predicted that body condition would be positively correlated with elevation. We tested this hypothesis with a LMM of the form $\log(M)_{(\text{Nov-Dec})} \sim \log(\text{CCL}) + \text{elevation} + \text{population}$ with individual as a random effect, where $M = \text{mass}$ and $\text{CCL} = \text{curved carapace length}$. We used a Generalized Linear Mixed Model (GLMM) to determine the probability (P) of detecting eggs or follicles using a binomial distribution and logit link function of the form $P_{(\text{eggs/follicles})} \sim \text{BCI} + \text{month} + \text{elevation} + \text{population}$, with individual as a random effect to test Hypothesis 1c (Among adult females, the probability of being gravid will be positively correlated with body condition). Hypothesis 1d (migratory females will display a higher probability of being gravid than nonmigrators) also could not be evaluated using the small sample of GPS-tagged females. Rather, this was indirectly evaluated based on relationships between movement strategy and body condition, and body condition and the probability of being gravid (above).

Although we had a general understanding of gross trends in rainfall, temperature and plant productivity along the elevation gradient from data collected over several years (Figure 3; Bastille-Rousseau et al., 2017; Yackulic et al., 2017), we had little idea of their magnitude within nesting areas. Even small variations in temperature and rainfall conditions can have dramatic effects on the survival probability of eggs and hatchlings of turtles (Epperson & Heise, 2003; Spotila et al., 1994). We predicted that even over the small elevational range

of nesting areas, differences in temperature, rainfall, and productivity would exist between nesting areas, potentially of sufficient magnitude to impact recruitment. We tested Hypothesis 2a (across nesting areas, rainfall, and productivity increase with elevation, while temperature decreases with elevation) using LMMs of the form Environmental Response Variable ~ Month + Area, with Year as a random effect.

In general, ambient temperature conditions should govern the temperature of nests via conduction through

the soil. However local factors, such as the structure and composition of soils and vegetation cover, can influence conditions at individual nests and nest sites. We tested Hypothesis 2b (temperature within nests will increase over incubation) and 2c (mean nest temperatures will decrease with elevation) with an LMM of the following form: Mean Daily Nest Temperature ~ Incubation Day + Nesting Area + Year, with Nest as a random effect (with the nesting area defined over the three elevation levels, upper, middle, and lower). This analysis was restricted to

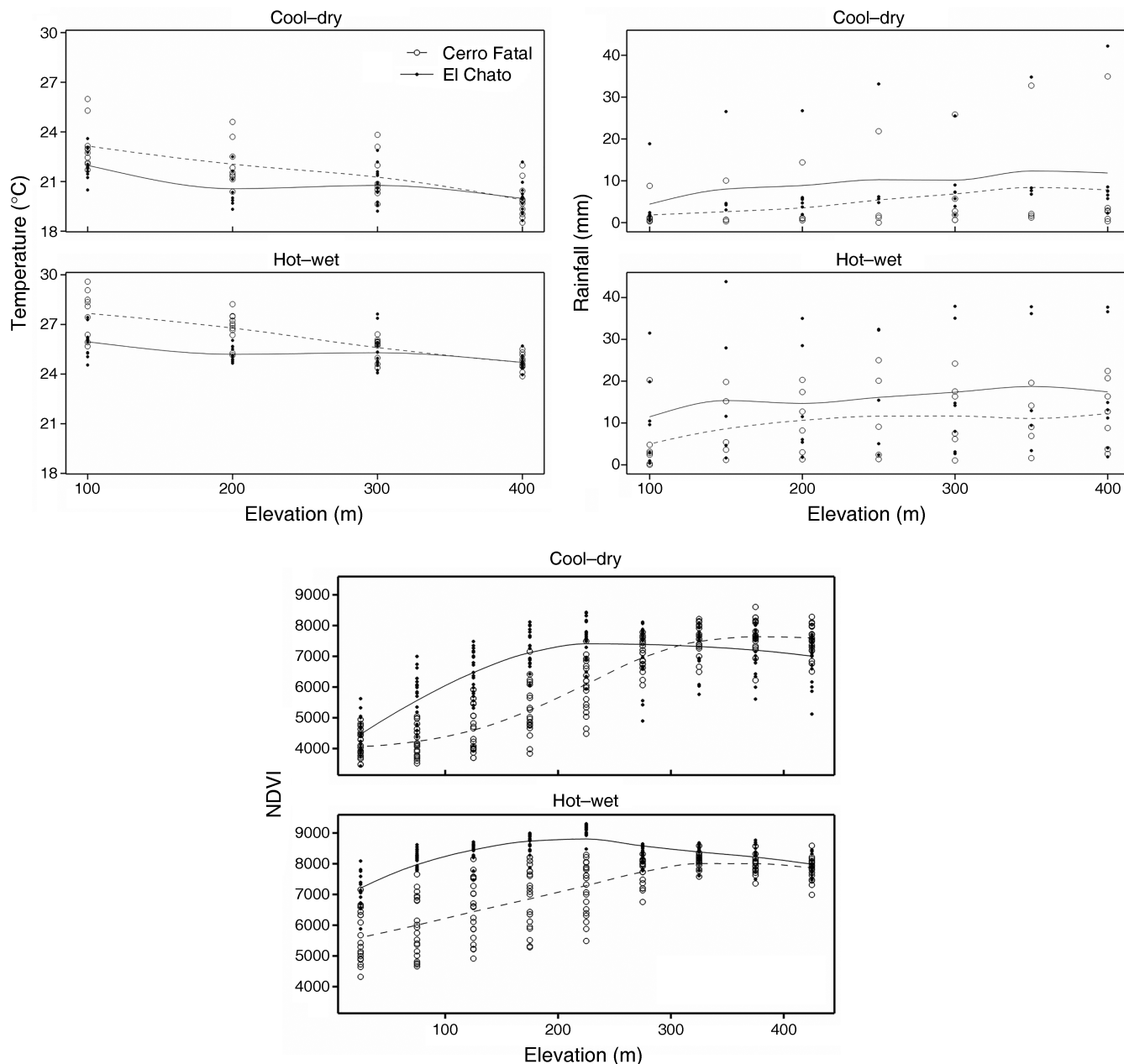


FIGURE 3 Gross patterns in temperature, rainfall, and vegetation productivity (NDVI) along the elevation gradients within the range of two species of Galapagos tortoise (*Chelonoidis porteri* and *C. donfaustoi*) in the El Chato and Cerro Fatal regions of Santa Cruz Island. Individual datapoints represent seasonal mean values (open circles represent Cerro Fatal values and black dots represent El Chato values). Curves are generated from splines with four degrees of freedom intended for illustrative purposes only. NDVI, Normalized Difference Vegetation Index.

nests in El Chato because we had no nest temperature data from the Cerro Fatal site.

Because we had no a priori knowledge of how clutch characteristics might vary along the elevation gradient, we assumed the null hypothesis that nesting area would have no effect on either (a) clutch size (Hypothesis 2d) or (b) egg weight (Hypothesis 2e). These predictions were tested with (1) a GLMM using a Poisson distribution and log link function of the form $N_{(\text{eggs})} \sim \text{Nesting Area} + \text{Population}$ and (2) an LMM using a normal distribution and identity link function of Mean Egg Weight Per Nest $\sim \text{Nesting Area}$ with Year as a random effect in both cases.

Opposing gradients of increasing rainfall/productivity and decreasing temperature with elevation within the nesting range suggest trade-offs in nest site selection. Low elevations with high temperatures and low rainfall should increase the probability of egg survival (Hypothesis 2f) because incubation is faster and eggs will be vulnerable for less time (tortoise eggs can be vulnerable when nest sites are saturated). Furthermore, hatchling survival and growth should be optimal at intermediate elevations due to opposing gradients of increasing food availability and decreasing ambient temperature (Hypothesis 2g) and, therefore, lower metabolic efficiency as elevation increases. We tested these predictions with:

1. a GLMM of the form Egg Survival Probability Per Nest $\sim \text{Elevation} + \text{Max. Monthly Rainfall} + \text{Mean Monthly Temperature}$ with Nest as a random effect;
2. GLMMs using a normal distribution and identity link function of the form $\Delta M \sim M_i + \text{NDVI} + \text{Rain} + \text{Temp}$, and $\Delta L \sim L_i + \text{NDVI} + \text{Rain} + \text{Temp}$, with VHF-tagged Individual as a random effect in both cases, and where ΔM and ΔL are daily change in mass and length between bi-weekly relocations, and M_i and L_i are initial mass and length (measured at the previous relocation) respectively;
3. a plot of Kaplan–Meier estimated survival functions by nesting area and nonparametric tests of equality of survival curves by nesting area;
4. a Cox regression of the form Survival Time $\sim \text{Nesting Area} + \text{Initial Hatchling Weight} + \text{Tag Weight}$ as a percentage of initial hatchling weight. The value of environmental variables was defined based on whether the time interval between relocations occurred entirely during a calendar month or straddled a month. When contained within a calendar month, the mean monthly values were used, and when the interval straddled 2 months, the mean of the values for each month was used.

We included rainfall in these models because hydration levels can strongly influence body mass which could

lead to an increase in mass during wetter months. Rainfall can influence rate of body length increases in reptiles (Grimm-Seyfarth et al., 2018) including tortoises due to rainfall effects on vegetation productivity rather than physiological limitations of dehydration. Hypothesis 3 (hatchlings will rapidly disperse from nesting sites upon occlusion) was examined semiquantitatively by plotting the linear distance from the nest over time for each radiotagged hatchling in each nesting area.

We conducted all analyses in Genstat (Seventeenth Edition, VSN International Ltd., Hemel Hempstead, UK). In some cases, we presented coefficients and their associated standard errors for unscaled and scaled fixed effects data with scaled data (zero mean and unit standard deviation; Schielzeth, 2010) presented when comparing the magnitude of different effect sizes on the response variable.

RESULTS

Variation in environmental conditions experienced by tortoises at different life-history stages

GPS-tagged adult female tortoises from the two species showed different elevational distributions (Figures 2 and 4). In El Chato, WSCT occurred between 0 and 400 m, while in Cerro Fatal ESCT occupied elevations between 74 and 450 m. In both cases the gradient spanned the three major habitat types of the Galapagos Islands: from arid lowlands through the transition zone to humid highlands. The species' ranges extended well above the Galapagos National Park boundary into privately owned farmland where native vegetation has been heavily transformed by agriculture (Figure 2). Nests were recorded only in the arid and transition vegetation zones from 6 and 149 m in El Chato and 89 and 173 m in Cerro Fatal (Figure 2). Nest locations were clumped into distinct areas separated by extensive areas of lava rock, which dominate most of the land surface at these elevations. Nest sites were characterized by patches of soil embedded in otherwise continuous lava substrate, which provides the tortoises with limited opportunities to dig their nests.

Gross patterns in temperature, rainfall and vegetation productivity were generally predictable across the elevation gradient, although the magnitude of both climate and productivity variables varied annually (Figure 3). Temperature decreased with elevation at both sites and in both seasons, while rainfall and vegetation productivity increased, although vegetation productivity is an asymptote at higher elevations (~250–350 m). Seasonal comparisons followed the expected trends

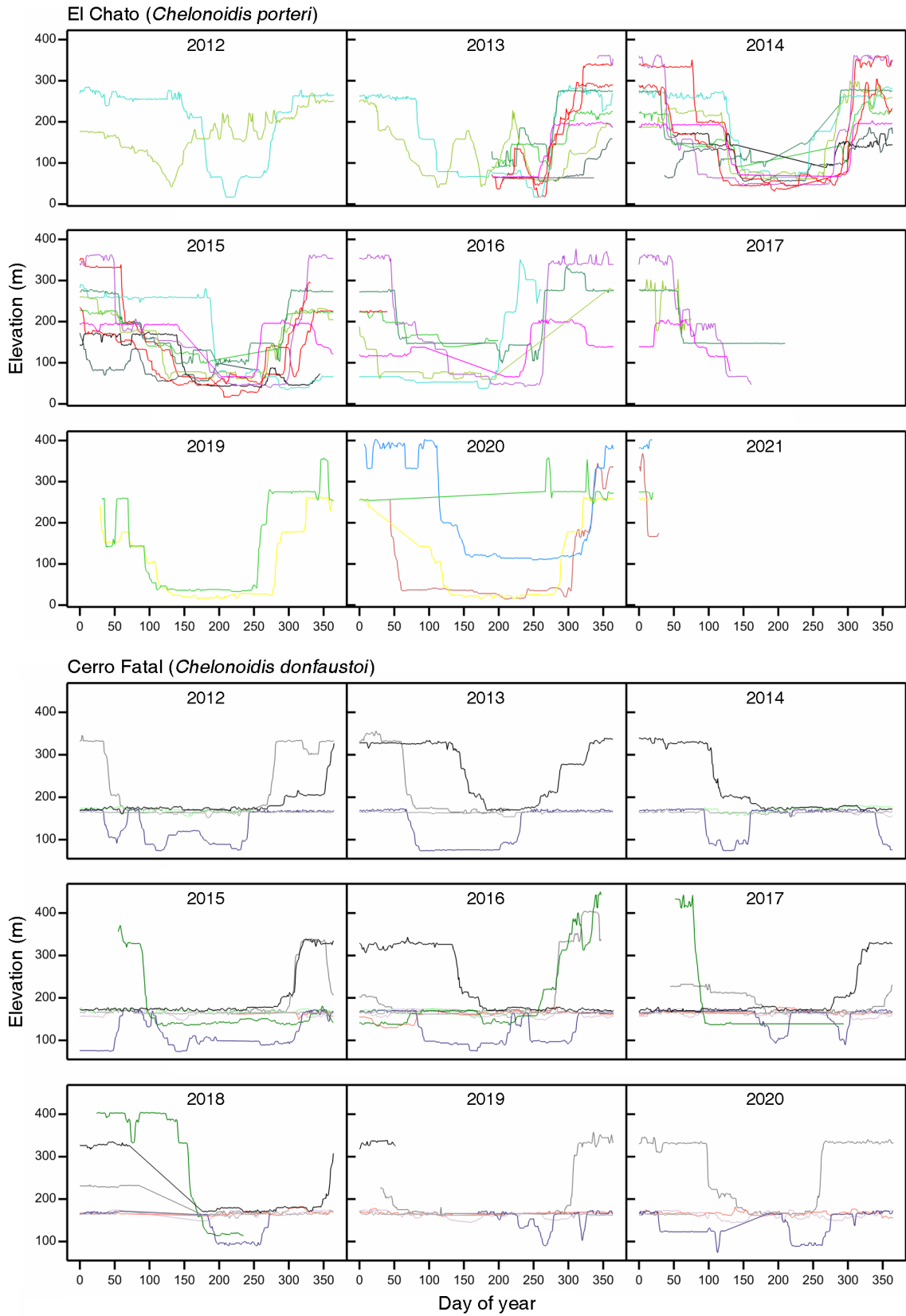


FIGURE 4 Elevation profiles over time of GPS-tagged female giant Galapagos tortoises from two different species on Santa Cruz Island. Presentation of years is inconsistent between the two species.

between “cool–dry” and “hot–wet.” In terms of site comparisons, El Chato was wetter than Cerro Fatal at all elevations and in both seasons. Cerro Fatal was hotter than El Chato to an elevation of ~300 m, above which temperatures were comparable between sites. Finally, vegetation productivity was consistently lower in Cerro Fatal than in El Chato at all elevations of less than ~300 m after which productivity was comparable between sites.

Adult female migratory propensity, the timing of nesting, body condition and reproductive condition

Of 16 GPS-tagged adult female WSCT in El Chato, 15 showed migratory behavior between highlands and lowlands. Of nine GPS-tagged adult female ESCT in Cerro Fatal, four were migratory (Figure 4). Three migrants (two in Cerro Fatal and one in El Chato, 12% of all GPS-tagged females) switched movement behavior between migration and residency. From 10 years of continuous tracking data, Allison (Cerro Fatal) was a resident for more than 3 years, Melina (Cerro Fatal, 3 years of data) was a resident for 1 year, and Mandy (El Chato, 5 years of data) was a resident for 1 year, with all resident periods spent in the lowlands. The five sedentary individuals remained in the lowlands, immediately around the Cerro Fatal upper nesting area throughout the year. The elevation of migration destinations and the timing of migration was inconsistent between individuals and years (Figure 4). The general trend was for downslope migration to occur between January and May, with most females remaining in the lowlands from June to September after which they began the upslope migration. Three ESCT migrants returned to the same nesting area (Cerro Fatal Upper), however the fourth migrant, Marilyn, used this hot–wet season “lowland” destination as her cool–dry season “upland” destination; her hot–wet season destination was the Cerro Fatal lower nesting area, and the timing of her migrations was extremely inconsistent.

We found no support for Hypothesis 1a that body condition was maximal at the end of the hot–wet season because model selection based on AIC favored the model that did not include the month or month² variables. (Appendix S1: Table S1). Body Condition Index was positively correlated with elevation (Appendix S1: Table S2, $p < 0.001$) during the upland migration, supporting Hypothesis 1b, and frequency of gravidity was positively correlated with BCI (Appendix S1: Table S3; $p < 0.01$) supporting Hypothesis 1c. These results indirectly supported Hypothesis 1d that migratory females had a higher probability of being gravid than sedentary individuals. Female WSCT had higher gravidity than ESCT females (Appendix S1: Table S3; $p < 0.05$).

Nesting area environmental conditions and nest temperatures

Ambient temperature was significantly different by both month and nesting area ($p < 0.001$). Modeled mean effect size varied more than 3.6°C across months, but by less than a degree overall between areas. In all sites, temperatures were highest between January and April (Appendix S1: Table S4; Figure 5), the time when few adult females are in the nesting areas, and lowest between July and October, when most nesting takes place. The annual variation in mean temperature within a site exceeded 5°C in some years. Mean temperature decreased with elevation within each region but with considerable variation by month and year (Figure 5; Appendix S1: Table S4).

Rainfall (Figure 5) differed by month and nesting area (Appendix S1: Table S4; $p < 0.001$). Rainfall was consistently highest during the time of peak hatchling emergence between February and April, and very low between June and December, the peak incubation months. Rainfall increased consistently with nesting area elevation within each region (Appendix S1: Table S4; Figure 5), but was lowest in the two Cerro Fatal nesting areas. Monthly trends in NDVI (Appendix S1: Table S4, Figure 5) were similar to trends for rainfall although the differences between El Chato and Cerro Fatal nesting areas were more extreme. The NDVI values remained high for some time after rainfall had peaked, well into June, before declining to low levels.

From the sample of 41 nests in which depth was measured, no difference was evident in the depth of the mid-point of the nest chamber by area (ANOVA; $F_{(2,40)} = 1.22$, $p = 0.307$). Over the entirety of incubation, mean nest temperatures in the El Chato Lower and Middle nesting areas differed by 0.2°C or less, however in the Upper area, nests were between 1.4 and 1.8°C cooler than in the other two areas (Appendix S1: Table S5). Across all sites, nest temperature ranged between 21.5 and 34.0°C. The temperature within nests monitored in the El Chato areas increased with incubation time (Figure 6; Appendix S1: Table S6; $p < 0.001$), supporting Hypothesis 2b. The effect sizes revealed by a LMM indicated that the mean temperatures of nests in the Middle and Upper areas were -0.2°C and -2.1°C cooler than in the Lower nesting area nests (Appendix S1: Table S6). The LMM also indicated that mean nest temperatures varied little among years ($p > 0.05$).

Rainfall levels to which nests were exposed increased with elevation not only because of higher rainfall at higher elevations, but also due to the longer incubation times in the Upper area, which continued into March and April and thus included the heaviest rains of the hot–wet season. During incubation, the mean accumulated rainfall in the El Chato Lower, Middle and Upper areas was 16.5, 31.1,

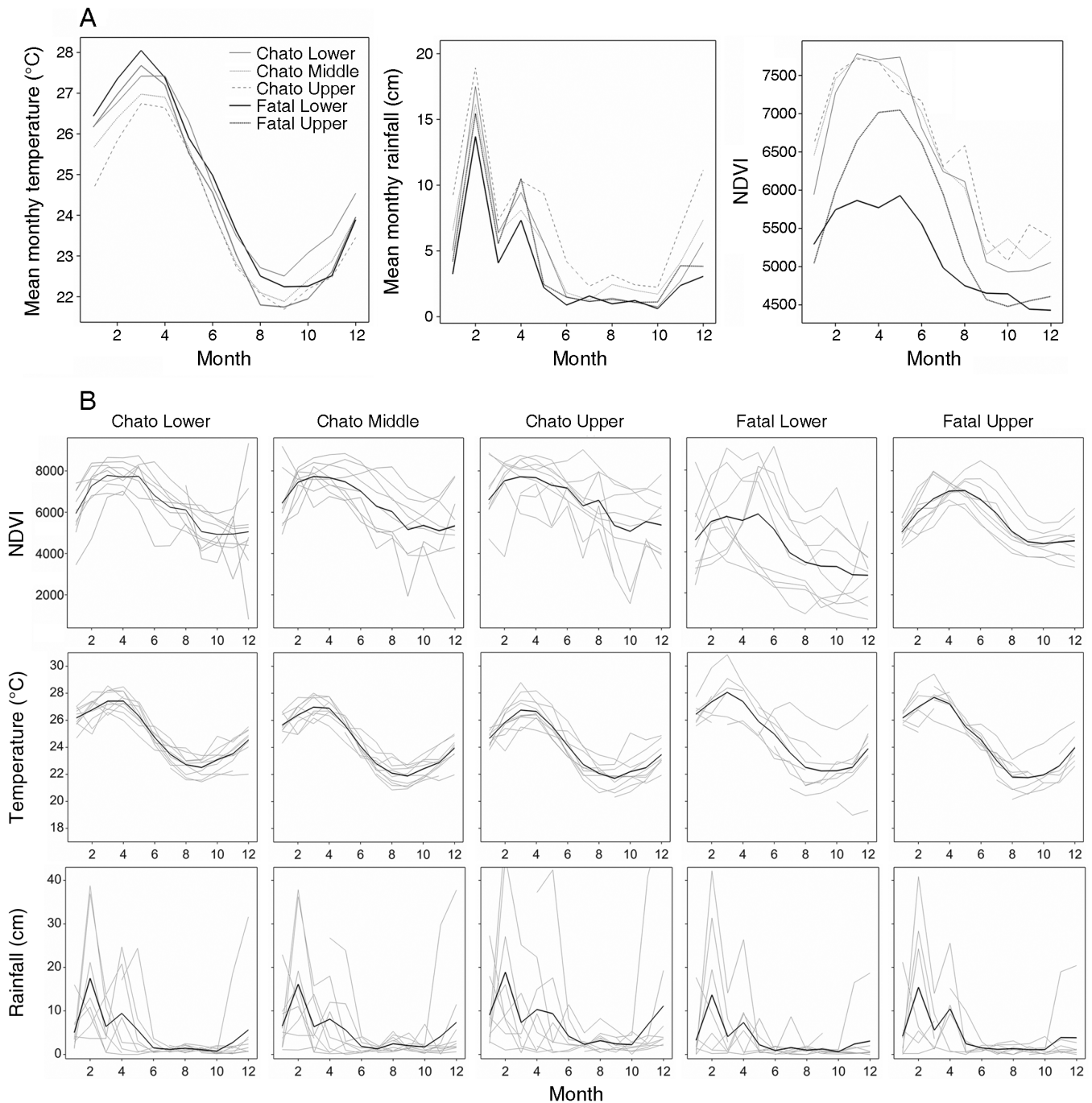


FIGURE 5 (A) Mean monthly environmental conditions (temperature, rainfall and NDVI) recorded between 2012 and 2020 in five Santa Cruz Island Giant Galapagos tortoise nesting areas: (B) Annual environmental conditions by nesting area (gray curves) and mean for all years (black curves) also recorded between 2012 and 2020. NDVI, Normalized Difference Vegetation Index.

and 64.7 cm, respectively, and 11.0 and 14.8 cm in the Cerro Fatal Lower and Upper areas, respectively.

Clutch characteristics, and egg and hatchling survival

Contrary to null Hypothesis 2d, clutch size increased with nesting area elevation in both tortoise populations

from 8.7 (SE = 0.56) to 9.1 (SE 0.55) and 10.3 (SE 0.56) in the El Chato Lower, Middle and Upper nesting areas, respectively, and 6.7 (SE = 0.71) to 10.0 (SE = 1.18) in the Cerro Fatal Lower and Upper areas, although sample size here was very low (Appendix S1: Tables S7 and S8). Egg mass was consistently higher in the El Chato Middle nesting area compared with other nesting areas refuting Hypothesis 2e for the El Chato region (Appendix S1: Table S9, Figure 7). No difference in egg mass by nesting

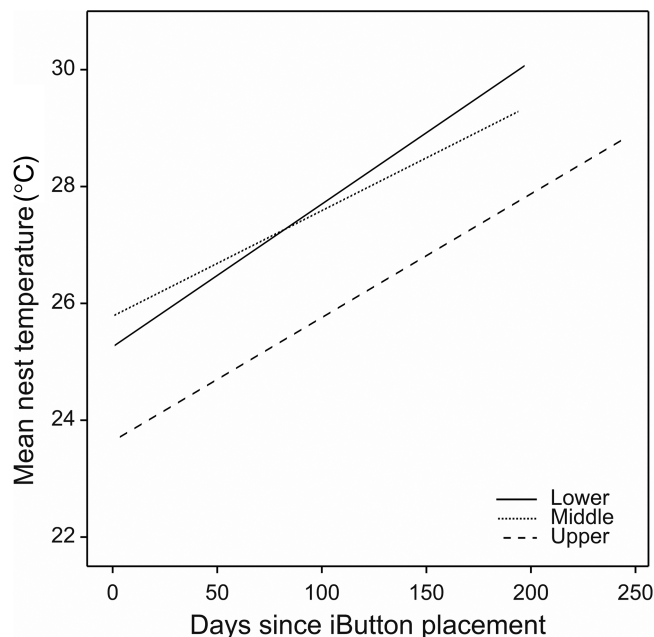


FIGURE 6 Mean daily temperature recorded in the center of giant Galapagos tortoise nests, in three nesting areas in El Chato, Santa Cruz Island, Galapagos, recorded between 2013 and 2017.

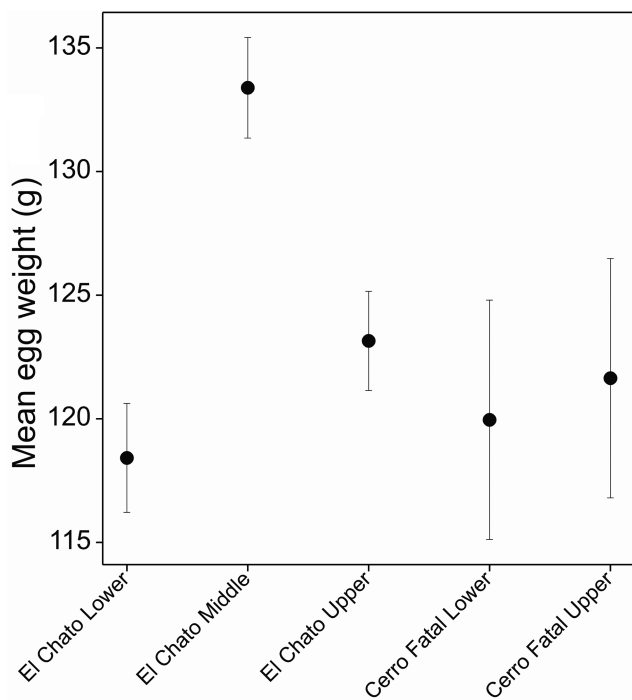


FIGURE 7 The mean mass of giant Galapagos tortoise eggs on Santa Cruz Island was consistently higher in the middle elevation nesting area of El Chato compared with eggs in the lower and upper areas, and both nesting areas in Cerro Fatal.

area was found in Cerro Fatal, however sample sizes were low.

The fate of eggs in 87 protected nests was monitored between 2013 and 2016. Of 609 eggs in total, 320 (52.5%)

were found dead upon opening the nests. Egg survival in El Chato decreased with elevation (59.4% in the Lower nesting area, 47.6% in the Middle area, and 40.3% in the Upper nesting area). However, in the Cerro Fatal site, egg survival was 18.5% and 56.7% and in the Lower and Upper nesting areas, respectively, although the sample size was low (Table 2). In partial support of Hypothesis 2f, maximum monthly rainfall during incubation was negatively correlated with egg survival probability (Appendix S1: Table S10; $p < 0.05$), whereas the mean incubation temperature and elevation were not. Rainfall is likely to account for the decrease in survival probability with elevation in El Chato because incubation is still ongoing throughout the hot-wet season in this area, whereas hatchlings had left most nests in the Middle and Lower areas before the February rains began.

Increasing rainfall, temperature, and NDVI had significant positive effects on hatchling growth in support of Hypothesis 2g, both in terms of mass gain and to some extent of length gain (Appendix S1: Tables S11a,b). The mass gain over time of hatchlings was highest in the El Chato Middle nesting area, moderate in the Lower area, and considerably slower in the Upper area, (Appendix S1: Table S11c; Figure 8A). Hatchling survival differed by nesting area (Appendix S1: Table S11d; $p < 0.01$; Figure 8B). In El Chato, hatchling survival was highest in the Middle area supporting Hypothesis 2g (Appendix S1: Table S11d). In this nesting area, the estimated survivor function stabilized after 1225 days at 55% with no further deaths until the end of data collection at 2900 days. The probability of survival dropped below 50% at 350 days and 600 days in the El Chato Upper and Lower areas respectively (Figure 8B). The highest hatchling mortality occurred in the Cerro Fatal Upper area with a Kaplan–Meier survival estimate of 16.8% compared with 42.9% in the hotter, drier, and less productive Cerro Fatal Lower nesting area. Initial hatchling weight had a significant positive effect on survival (Appendix S1: Table S11d; $p < 0.01$) while tag weight had no effect ($p > 0.05$) and reinforced the results of the Kaplan–Meier analysis on the strong effect of nesting area on survival.

Movements of hatchling tortoises

Hatchling tortoises undertook directed long-distance movements during the first weeks of leaving the nest, with daily linear travel distances of up to 30 m/day (Figure 9). Initially long step lengths and low turn angles resulted in rapid dispersal away from the nest, after which hatchlings maintained small, restricted ranges. The mean dispersal distance from nests was 236 m (SD 167.4), variation within areas was high and

TABLE 2 Egg and hatchling mortality for year 1 for giant tortoises recorded between 2013 and 2016 in the Tortoise Reserve of Santa Cruz Island, Galapagos.

Nesting area	Mean elevation (m)	No. eggs	No. eggs dead in nest	Egg survival (%)	No. hatchlings tagged	No. hatchling deaths	Hatchling survival in first year (%)	Combined survival probability (eggs + hatchlings) to 1 year
EC Lower	13	124	48	59.4	19	5	73.7	43.8
EC Middle	58	187	98	47.6	13	3	76.9	36.6
EC Upper	107	211	126	40.3	15	9	40.0	16.1
CF Lower	90	27	22	18.5	7	3	57.1	10.6
CF Upper	165	60	26	56.7	26	19	26.9	15.3
Overall		609	320	47.5	80	39	51.3	24.3

Note: The combined survival probability to 1 year was calculated as follows: Combined survival probability = probability of egg survival × probability of hatchling survival.

Abbreviations: CF, Cerro Fatal; EC, El Chato.

there was no difference in dispersal distance by area ($p = 0.297$). In some cases, dispersal was particularly rapid; for example, one hatchling traveled over 600 m from the nest in the first 50 days (Figure 9). The terrain over which the hatchlings traveled was usually exposed lava, with many deep crevasses, sheer walls, and steep jagged undulations covered in dense woody vegetation. At the end of the dispersal events, hatchlings occupied restricted ranges, usually <0.1 ha in the area within which the hatchlings usually had two or three preferred resting sites, often under rocks, and several dispersed foraging sites. Hatchling fidelity to these sites was markedly high, with little sign of range expansion for at least 2000 days, and often beyond (Figure 9).

DISCUSSION

Elevation and latitude are key drivers of environmental conditions influencing biological systems (Mysterud et al., 2001; Qian, 2010; Swenson & Enquist, 2007). Because environmental conditions change over relatively small geographic distances, elevation gradients offer tractable systems in which to answer questions on the impact of environmental change on evolution and ecology, including life history. Here, we synthesized a comprehensive dataset on the movement and reproductive ecology of two closely related species of large-bodied, long-lived, ectothermic species, giant Galapagos tortoises, to test hypotheses related to the impact of environmental variation on life-history traits including egg production of adults and survival during early life stages. This synthesis allowed us to speculate on the impact of future environmental change on both the evolutionary ecology and conservation of these iconic megavertebrates, with wider implications for ectotherms living on elevation gradients.

How do movement strategies of adult female tortoises influence their body condition and the probability of being gravid?

A theoretical bioenergetic model of Santa Cruz Galapagos tortoise movement ecology predicted that elevational migration should be an optimal bioenergetic strategy for tortoises of more than ~70 kg (Yackulic et al., 2017). Upslope migration during the cool-dry season should allow tortoises to escape poor forage quality and minimize metabolic rate during periods of food scarcity by moving to cooler upland elevations where forage is available year round. Downslope migration during the hot-wet season was predicted to maximize access to high-quality forage in the lowlands. Despite small sample sizes and low temporal resolution, these theoretical predictions, and our hypotheses derived from them, are mostly supported by our empirical field data. Migratory females occupied lowlands during and after the hot-wet season, however the month did not predict adult female body condition as expected (Hypothesis 1a). A positive correlation between elevation and body condition at the peak of the upland migration also supported migration as an optimal energetic strategy (Hypothesis 1b). A positive relationship between body condition and gravidity indicated a capital breeding strategy (Hypothesis 1c) and indirectly supported Hypothesis 1d. Our results are strongly suggestive; however, small sample sizes and an inability to directly quantify fecundity (mean number of eggs produced per female) and offspring growth and survival of known females precluded a more conclusive exploration of trade-offs between movement strategy and life-history characteristics.

Support for Hypotheses 1a–d, and the Yackulic et al. (2017) theoretical model, provokes the question of why

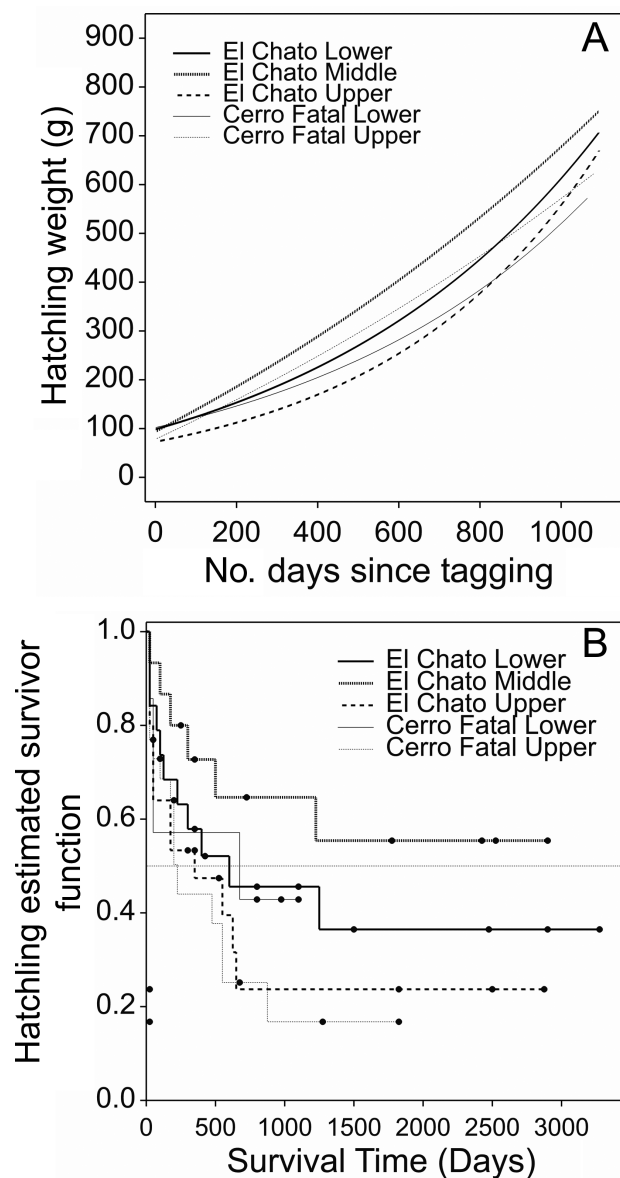


FIGURE 8 Santa Cruz Island Giant Galapagos tortoise hatchling weight over time (A) and the Kaplan–Meier survivorship function (B) of VHF-tagged hatchlings by nesting area.

some females remained resident, involving prolonged periods in energetically suboptimal conditions, while others migrated. Moreover, why did some females switch between resident and migratory mode of movement between years? Evolutionary ecologists have wrestled with these questions across taxa for at least four decades (Berg et al., 2019; Chapman et al., 2011; Lundberg, 1985, 1988; Lundblad & Conway, 2020a). That some individuals (12% of the sampled females) switched movement strategies is consistent with two hypotheses discussed by Berg et al. (2019) and references therein. First, an “environmental-genetic threshold” may result from gene-by-environment interactions, in which factors such as food availability or physiological conditions determine

whether a migratory genotype will be expressed. Second, state-dependent migration may exist in which decisions on movement tactics are plastic and depend on factors related to body condition. A third strategy may also be in play, proposed first based on the observations of Aldabra giant tortoises (*Aldabrachelys gigantea*) that maintain a partial migration because migrants face a balance of trade-offs between increased annual reproductive output and increased probability of mortality (Swingland & Lessells, 1979), later refined as a frequency-dependent mixed evolutionarily stable strategy (Swingland & Greenwood, 1983). It is noteworthy that all adult GPS-tagged male Santa Cruz Galapagos tortoises ($n = 25$ individuals) migrated annually during more than a decade of research (Blake, Yackulic, et al., 2021; S. Blake, unpublished data). Unlike adult males that are consistently of more than 200 kg (GNPD, unpublished data; Chiari, 2021), female body weight is closer to the 70 kg theoretical threshold at which migration becomes optimal, and males are therefore more sensitive to forage availability. Energetic gains of migration are maximized by optimally following vegetation productivity, which large male tortoises are able to achieve (Bastille-Rousseau et al., 2019) because they are unconstrained by reproductive considerations. However, females must balance trade-offs between their own current and future body condition with fecundity and recruitment success.

How do the environmental conditions for nesting vary across the elevation gradient and is this related to egg survival and hatchling growth and survival?

Despite the small elevational variation across nesting areas, elevation was negatively correlated with temperature and positively correlated with rainfall and NDVI (supporting Hypothesis 2a). Eggs were consistently larger and heavier in the El Chato Middle nesting area. Egg size is an important life-history trait among chelonians because individuals from larger eggs tend to have higher survival rates (Congdon & Gibbons, 1985; Wallis et al., 1999; Wilkinson & Gibbons, 2005). Moreover, female chelonians from large eggs may also reach sexual maturity more rapidly than those from smaller eggs (Roosenburg, 1996). Why eggs should be larger at mid-elevations is not clear, as several mechanisms contribute to egg size, including trade-offs between clutch size and egg size (Lovich et al., 2015; Shine, 2005; Wilkinson & Gibbons, 2005), and size and body condition of the female (Congdon & Gibbons, 1985; Nafus et al., 2015). On Aldabra Atoll, increased rainfall during the hot-wet season leads to larger egg size in giant tortoises because of improved nutritional balance of

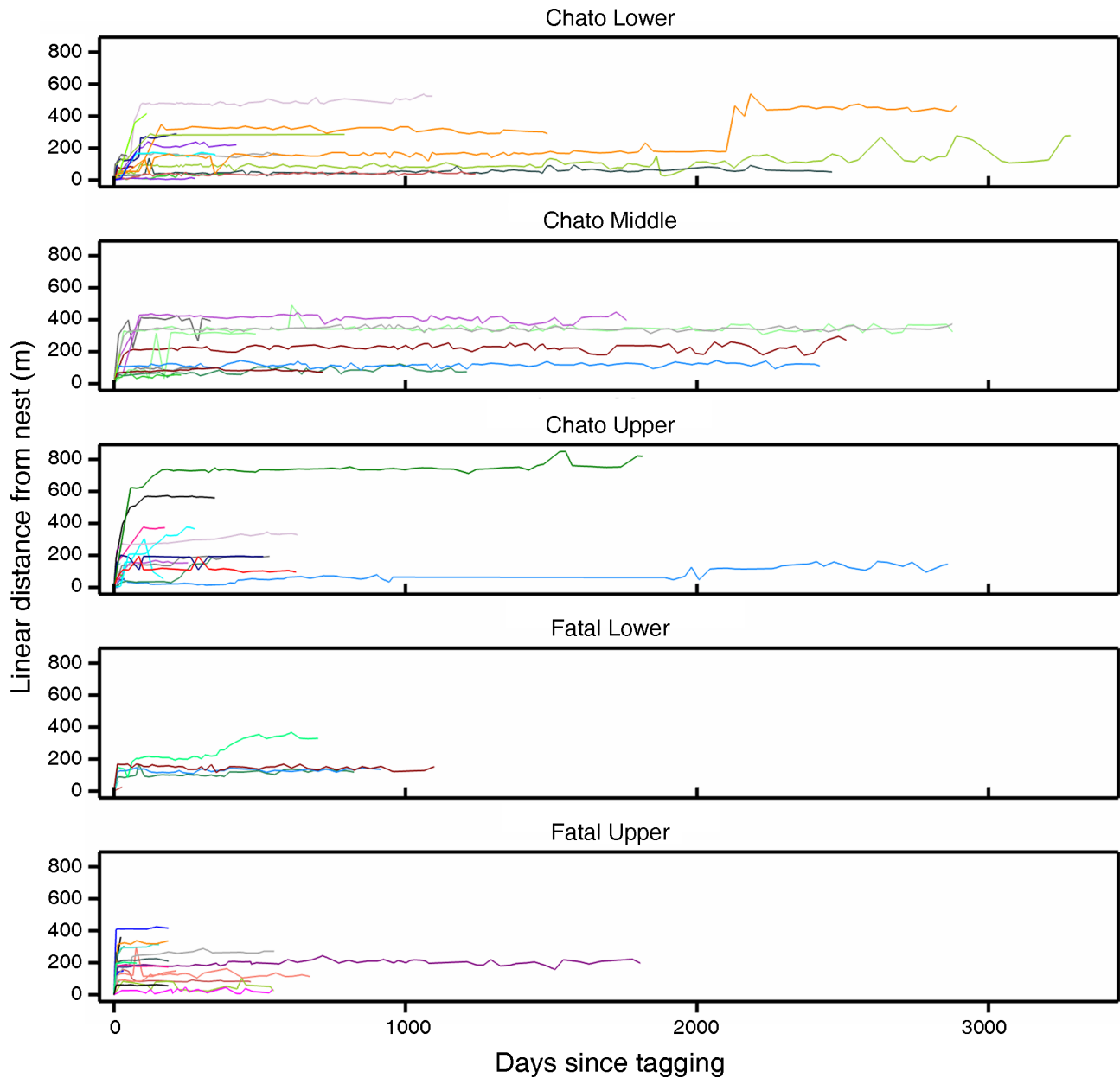


FIGURE 9 Santa Cruz Island Giant Galapagos tortoise hatchling dispersal illustrating the linear displacement of VHF-tagged hatchlings from their nest over time by nesting area.

females (Swingland & Coe, 1979). We found no evidence of higher body condition or larger body size of females in the El Chato Middle nesting area compared with the other areas. Clutch size increased slightly but significantly with elevation in both populations (refuting Hypothesis 2d). Possible explanations may include that (1) female tortoises continue to feed through the nesting season, and because productivity increases with elevation, tortoises at higher elevation nesting areas had better nutrition, and (2) migrant tortoises that nested in upper elevations had shorter, less energetically costly migration journeys. In combination, these factors could increase the energy

available for egg production compared with migrant and resident tortoises at lower elevations.

The small potential fitness advantage accrued by larger clutch size at higher elevations was offset by a decline in egg mass, and egg and hatchling survival in more upland areas. The timing of nesting and the location of the nest are important determinants of the rainfall regime that a clutch will experience. In the El Chato Upper nesting area, relatively cool incubation temperatures (Figure 5) extend incubation times, which exposes eggs to wetter conditions for longer periods than eggs at lower, drier elevations.

What are the characteristics of natal dispersal?

The scale of the natal dispersal was immense. Hatchlings weighing ~70–100 g and measuring ~75 mm long frequently walked for hundreds of meters in the space of a few weeks over uneven, sharp, and unstable terrain comprised of loose lava boulders, deep crevasses, and often dense vegetation. The energetic cost of this behavior must be enormous. At some point, hatchlings stop their dispersal and quickly adopt a small resident range measuring <0.2 ha. We do not know the cues that determine the cessation of dispersal and the adoption of the resident range; however, resident ranges usually include moderate vegetation cover, several preferred shady crevices in the lava, and areas with low-level forage availability (F. Cabrera & S. Blake, personal observation). Nine years of observations for some individuals indicated that hatchlings have high fidelity to their chosen site (Figure 9).

Long-distance natal dispersal is common among many animal species (Bowler & Benton, 2005; Howe & Smallwood, 1982; Ronce, 2007; Sutherland et al., 2000) including many chelonians such as sea turtles (Scott et al., 2014; Shillinger et al., 2012). However natal dispersal among tortoises is poorly documented (Epperson & Heise, 2003; Pike, 2006). Such consistent long-distance hatchling dispersal was surprising and underscored the importance of this energetically costly and potentially high-risk behavior (Clobert et al., 2009; Cote & Clobert, 2010). Factors including habitat quality, predation and competition may promote this behavior. Tortoise nesting sites are usually relatively devoid of vegetation, due to the concentrated mechanical damage from nest digging and trampling that makes them poor foraging habitats compared with surrounding areas. The high use of nesting areas by adult tortoises is likely to make them dangerous for hatchlings, which could easily be crushed or physically damaged. Predation is not often considered an important ecological factor for giant tortoises on oceanic islands (Itescu et al., 2014); however, Darwin (1839) observed numerous successful attacks on hatchling tortoises by Galapagos hawks, and rapid movement away from nest sites may have evolved as a predator avoidance strategy.

What are the implications of projected future environmental change for tortoise reproductive ecology on elevation gradients?

For egg-laying species, the importance of where and when to nest is well known (Refsnider, 2016; Refsnider & Janzen, 2010; Roosenburg, 1996; Wilson, 1998), and was

exemplified among Galapagos tortoise species in our study system. The location and timing of nesting determine not only egg survival, but also the temperature and vegetation productivity conditions to which hatchlings will be exposed. High incubation temperatures at lower elevations imply that incubation will be shorter, with the potential for hatchlings to emerge too early to take advantage of the onset of the hot-wet season and high plant productivity. Conversely, rapid incubation and emergence from nests at low elevations may save eggs and newly emerged hatchlings from inundation during the early hot-wet season, to which nests at higher elevations will be exposed. In El Chato, the 2.5-fold difference in combined egg and hatchling survival of up to 1 year occurred over a mean elevation gradient of just 94 m and a linear distance of 3.3 km. Why some females select what appears to be poor nest sites is unclear. First, intra-species competition may play a role because lowland areas with open soil in which to nest are rare (S. Blake & F. Cabrera, personal observation). Although we did not find evidence for larger, perhaps dominant, females occupying the lower areas, less competitive females may be obliged to nest in suboptimal sites. Second, our multiyear study is but a small window into the 100+ year reproductive life of female Galapagos tortoises over which lifetime reproductive success is accrued. The variable climate of the eastern Pacific that causes large interannual differences to the terrestrial climates on the Galapagos Islands (Colinvaux, 1984; Trueman & d'Ozouville, 2010) may generate nest location environments inconsistent over time scales relevant to the reproductive lifetime of female tortoises. We recorded considerable interannual variation in environmental conditions along the elevation gradient of Santa Cruz. The kinds of interactions described above may lead to spatial and temporal variations in optimal nesting conditions and favor variation in the distribution of nests, analogous to the scatter-nesting observed in sea turtles on beaches of variable quality (Mrosovsky, 2006).

The importance of migration for female energy balance and the large variation in egg and juvenile survival over such a small gradient raises the questions of how Galapagos tortoise reproductive success varies across the archipelago, and how it may change over time. Like much of the planet, the Galapagos Islands are projected to experience dramatic and rapid environmental change from a combination of land use change, invasive species, and climate change (Buddenhagen & Tye, 2015; Liu et al., 2013; Mejia & Brandt, 2015; Restrepo et al., 2012; Trueman & d'Ozouville, 2010; Watson et al., 2010). At the extent of Santa Cruz Island, expanding human populations and economic development are likely to lead to infrastructure development, agricultural intensification, and fragmentation of private lands in the highlands,

which are seasonal foraging areas for migratory tortoises and important for the maintenance of individual female body condition and fecundity (this study). If the upland terminus of migration becomes unavailable to tortoises, or habitats anywhere along the migration route becomes degraded, there will likely be a significant reduction in fecundity. Likewise if tortoises become trapped in or blocked from accessing lowland habitats because of barriers to movement either due to construction (such as fences, roads and ditches) or encroachment of invasive species (Guézou et al., 2010) access to nesting areas will become impossible.

However, island-wide precipitation is likely to increase dramatically by 2070, potentially tripling current levels according to some models, while mean temperature may increase by $>2.5^{\circ}\text{C}$ (Charney et al., 2021). This will result in unprecedented vegetation productivity and change the current relationships between elevation, movement, and energy balance of tortoises. Under such conditions, migration may become energetically suboptimal (Yackulic et al., 2017). In terms of recruitment, if predicted increases in rainfall are realized, egg survival will plummet. The combination of increasing rainfall and vegetation productivity may have a positive impact on hatchling survival and growth. Demographic models of long-lived Galapagos tortoises (Gibbs & Goldspiel, 2021) and sea turtles (Crouse et al., 1987) demonstrate that recruitment plays a limited role in population growth compared with female survival. However large, persistent recruitment decline, or failure, will inevitably lead to population reduction.

Whether Galapagos tortoises can modify their reproductive behavior in the face of climate change will be crucial to their future reproductive success and conservation status. Elevation gradients provide opportunities for mobile species and communities to adapt to climate change via shifts in their distribution in response to change (Hargreaves et al., 2015). Adult Galapagos tortoises have the physical ability to shift their distribution, but whether they have the behavioral flexibility to modify nest site selection based on environmental conditions remains unclear because many chelonians are highly philopatric (Lee et al., 2007; Reinhold, 1998; Stiebens et al., 2013). Long lifespans and generation times compared with projected rates of significant climate change (Cox et al., 2000) suggest that behavioral flexibility will be critical for the future reproductive success of Galapagos tortoises. If land use managers, government development agencies and private landowners maintain vertical connectivity of tortoise habitat in both protected areas and private lands well beyond the current upper limit of migratory tortoises, it will improve the conservation outlook by allowing the potential of range shifts of both giant tortoises and the biological communities that

they shape (Blake et al., 2012; Hunter et al., 2013) and upon which they depend.

AUTHOR CONTRIBUTIONS

Stephen Blake conceived the study. Sharon L. Deem, Stephen Blake, Freddy Cabrera, Sebastian Cruz, Martin Wikelski, Franz Kueemmeth, and Diego Ellis-Soto, collected data. Stephen Blake led data analysis with input from Charles B. Yackulic, Guillaume Bastille-Rousseau, and James P. Gibbs. Stephen Blake wrote the manuscript with review support from all authors.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Blake, 2023) are available in Dryad at <https://doi.org/10.5061/dryad.tx95x6b24>.

ORCID

Stephen Blake  <https://orcid.org/0000-0002-2220-1589>

Charles B. Yackulic  <https://orcid.org/0000-0001-9661-0724>

Guillaume Bastille-Rousseau  <https://orcid.org/0000-0001-6799-639X>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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