The Dominance of Introduced Plant Species in the Diets of Migratory Galapagos Tortoises Increases with Elevation on a Human-Occupied Island

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ABSTRACT

The distribution of resources and food selection are fundamental to the ecology, life history, physiology, population dynamics, and conservation of animals. Introduced plants are changing foraging dynamics of herbivores in many ecosystems often with unknown consequences. Galapagos tortoises, like many herbivores, undertake migrations along elevation gradients driven by variability in vegetation productivity which take them into upland areas dominated by introduced plants. We sought to characterize diet composition of two species of Galapagos tortoises, focussing on how the role of introduced forage species changes over space and the implications for tortoise conservation. We quantified the distribution of tortoises with elevation using GPS telemetry. Along the elevation gradient, we quantified the abundance of introduced and native plant species, estimated diet composition by recording foods consumed by tortoises, and assessed tortoise physical condition from body weights and blood parameter values. Tortoises ranged between 0 and 429 m in elevation over which they consumed at least 64 plant species from 26 families, 44 percent of which were introduced species. Cover of introduced species and the proportion of introduced species in tortoise diets increased with elevation. Introduced species were positively selected for by tortoises at all elevations. Tortoise physical condition was either consistent or increased with elevation at the least biologically productive season on Galapagos. Santa Cruz tortoises are generalist herbivores that have adapted their feeding behavior to consume many introduced plant species that has likely made a positive contribution to tortoise nutrition. Some transformed habitats that contain an abundance of introduced forage species are compatible with tortoise conservation.

Abstract in Spanish is available in the online version of this article.

ANIMAL FORAGING STRATEGIES ARE FUNDAMENTAL TO THE PHYSIOLOGICAL STATE AND LIFE HISTORIES OF INDIVIDUALS and to numerous higher order ecological processes (Spalinger & Hobbs 1992, De Roos *et al.* 2009). Forage abundance and patterns of consumption are key determinants of individual body condition, size, and fitness (Demment & Van Soest 1985, Belovsky 1987); movement strategies of individuals and populations (Mysterud *et al.* 2001, Thompson Hobbs & Gordon 2010); population dynamics of forage and forager (McNaughton 1984, Fryxell *et al.* 1988); inter- and intra-specific competition (Illius & Gordon 1992, Landman *et al.* 2013); and ultimately impact the evolutionary trajectories of species and ecosystems (Wikelski & Romero 2003).

The feeding ecology of 'megaherbivores' (Owen-Smith 1988) exemplifies these interactions. These animals are often described as ecosystem engineers; species that shape the structure and function of ecological communities (Owen-Smith 1988, Hester *et al.* 2006, Campos-Arceiz & Blake 2011). Megaherbivores are important conservation targets for their intrinsic value and because they can influence community diversity and stability (Augustine & McNaughton 2006, Blake *et al.* 2009, Terborgh 2013).

Our understanding of the ecology of large herbivores comes overwhelmingly from studies of mammals, the dominant vertebrates in most terrestrial ecosystems (Danell *et al.* 2006). An important exception occurs on tropical oceanic islands, where reptiles, particularly giant tortoises, were often the chief herbivores until their usually human-driven extinctions. Giant tortoises are the largest extant terrestrial reptiles, which survive in just two

sites; Aldabra Atoll in the Indian Ocean, and the Galapagos Archipelago in the eastern Pacific Ocean (Coe *et al.* 1979, Pritchard 1979), however, until the late Pleistocene (Hansen *et al.* 2010) they were widespread on all continents except Antarctica; thus extant giant tortoises are not island oddities, but rather the last examples of a once widespread lineage.

On Aldabra Atoll tortoises are grazers (Gibson & Hamilton 1983) that also feed on shrubs, herbs, fruit, and carrion (Hnatiuk *et al.* 1976). Aldabra tortoises impact their habitat through herbivory, which may transform scrub vegetation into taxonomically diverse grazing lawns (Gibson & Phillipson 1983), and through 'bulldozing' (Kortlandt 1984) which causes soil erosion and high mortality of trees and shrubs (Merton *et al.* 1976). These traits led Hansen and Galetti (2009) to argue that giant tortoises should be classified as 'megaherbivores' in island ecosystems. The important ecosystem role of giant tortoises (Gibbs *et al.* 2010) has led to recent calls for their introduction into degraded ecosystems to restore lost ecosystem functions (Hansen *et al.* 2010, Griffiths *et al.* 2011, Hunter *et al.* 2013).

The ecology of Galapagos tortoises has been less intensively studied. Preliminary research shows that they are also ecosystem engineers via selective feeding, seed dispersal, and trampling (Gibbs *et al.* 2008, Blake *et al.* 2012). Two different morphological types of Galapagos tortoise occur. Saddlebacked tortoises, found on relatively flat arid islands where ground vegetation is usually sparse, may have evolved elevated carapaces to facilitate browsing on *Opuntia* cacti. In contrast, domed-shelled tortoises, the carapaces of which descend low over the head, live on taller islands where humid highlands support year-round vegetation cover (Fritts 1984).

Galapagos tortoises undergo seasonal migrations driven by spatio-temporal gradients in vegetation productivity (Blake *et al.* 2013). On Santa Cruz, the migration takes adult tortoises from arid lowlands deep into upland agricultural zones that are dominated by introduced, sometimes invasive plant species (Guezou *et al.* 2010, Watson *et al.* 2010). While the diet of Galapagos tortoises has been intensively studied at a single site (Cayot 1987), and several shorter studies identified them as generalist herbivores (Rodhouse *et al.* 1975, Fowler 1983), the diet of tortoises over the range of their migration and the role of introduced species in the diet are unknown.

In summary, iconic, endangered, migratory Galapagos tortoises are subject to massive habitat transformation that is likely changing the nutritional balance and ecology of individuals and impacting population and ecosystem level processes. Unfortunately, we know little about what tortoises eat, or why, when and where they eat it. Here, we begin to respond to these apparently simple questions for two tortoise species found on Santa Cruz Island. Specifically, we sought to answer the following questions: (1) what are the characteristics of tortoise diets in terms of plant life form and species composition, diversity and dominance?, (2) How do the relative contributions of introduced and native plant species in tortoise diets vary over the elevation gradient of the tortoise migration?, and (3) What are the conservation implications of interactions between introduced plant food species and giant tortoises?

METHODS

Study site.—The Galapagos Islands straddle the equator in the eastern Pacific *ca* 1000 km west of Ecuador (Fig. 1). This volcanic archipelago consists of some 129 islands, including 13 large islands (over 1 km^2), the oldest of which are *ca* 4 million years old (Poulakakis *et al.* 2012). Giant tortoises once apparently occurred on nine islands, but due to anthropogenic extinctions are now found on just six (Caccone *et al.* 2002). The climate is characterized by a hot wet season from January to May, and a cool dry season for the rest of the year. However, during the dry season, persistent cloud cover results in humid upland conditions on the windward (southern) slopes of the islands (Colinvaux 1984).

Vegetation patterns are driven by rainfall and substrate which are largely determined by aspect and elevation (Wiggins & Porter 1971). Five main natural vegetation zones are recognized on Santa Cruz. The coastal zone, characterized by salt resistant vegetation on sandy beaches, lava, and mangroves, is followed by the arid zone, dominated by xerophytic trees, shrubs and cacti on a mostly lava substrate. With increasing elevation comes the transition zone where soil and understory vegetation become more developed. The moist zone contains well-developed soil with vegetation characterized by an abundance of shrubs, herbs, ferns, and trees. Finally, the highland zone is dominated by ferns, sedges, and grasses with few trees.

Our study occurred on Santa Cruz Island which attains 860 m elevation with a surface area of 986 km^2 (Snell *et al.* 1996). Santa Cruz contains two species of giant tortoise, one of which is imperiled with extinction (Russello *et al.* 2005). The island also holds the largest human population in the Galapagos, estimated at >15,000 in 2010 (León & Salazar 2012). Farmers have converted most of the moist and highland zones to agriculture and at least 86 percent of these zones are now degraded by either agriculture or invasive species (Trueman *et al.* 2014).

Tortoises on Santa Cruz occur in two distinct areas on the island's southwestern and southeastern flanks (Fig. 1). A third population of three individuals to the northwest is likely the result of human-mediated transfer, and is not considered further here. The southwestern population, *Chelonoidis porteri*, which occurs in an area called *La Reserva* (Fig. 1) is widely distributed from 0 to 400 m elevation, and contains several thousand individuals (MacFarland *et al.* 1974). The eastern species, as yet undescribed, occurs in the *Cerro Fatal* region from *ca* 50 to 450 m (Fig. 1). The population is small, perhaps just several hundred individuals, due to hunting pressure until the recent past (Russello *et al.* 2005). Both species are of the 'domed' morphotypes, and both display strong size dimorphism, with females weighing up to *ca* 130 kg and males occasionally exceeding 260 kg (GNP, unpubl. data).

Field methods.—Fieldwork occurred between 2009 and 2013. To assess the elevational distribution of tortoises, we used
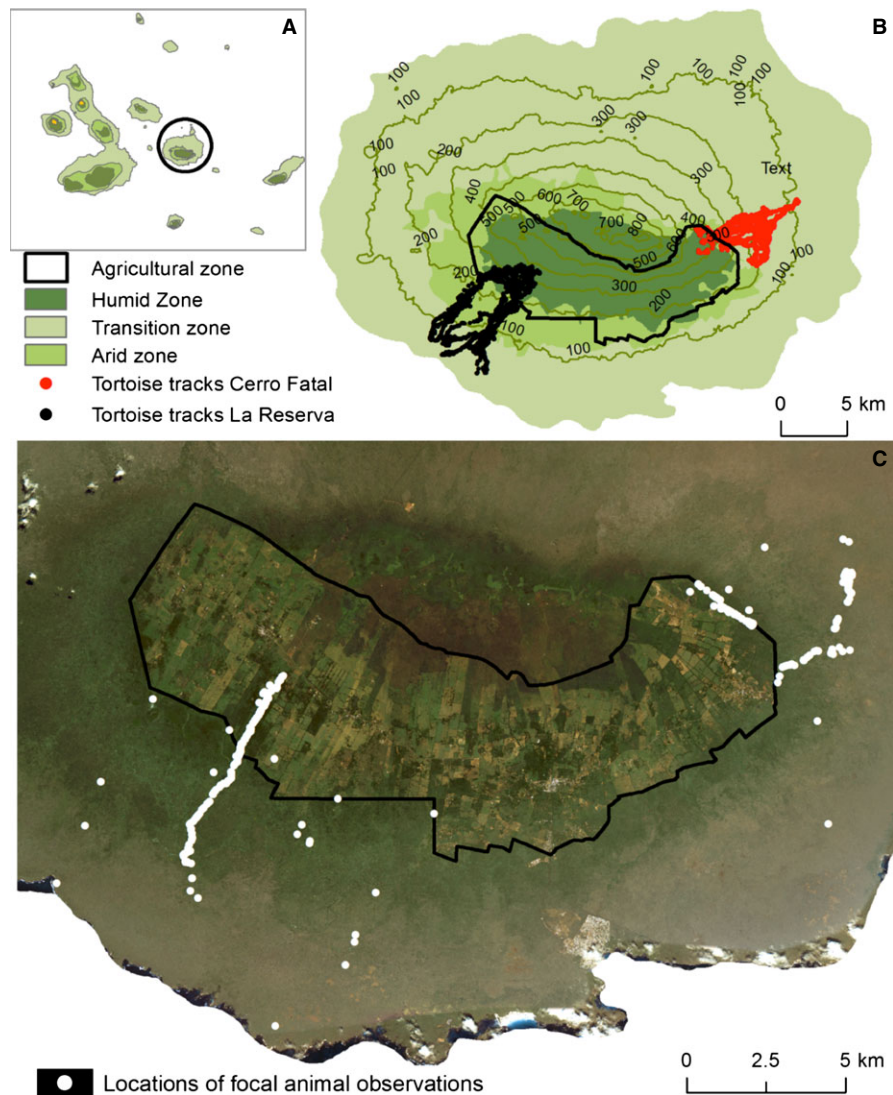
FIGURE 1. The study area on Santa Cruz Island showing (A) Santa Cruz in relation to the rest of the Galapagos archipelago; (B) Santa Cruz vegetation zones, agriculture zone, and the locations of GPS tagged tortoises from the two species; and (C) the locations of all focal animal sampling.

location data from 25 adult tortoises fitted with GPS tags between 2009 and 2013 (Blake *et al.* 2013). Only tortoises with more than 1 yr of movement data were used for this analysis. Each tag collected a GPS location fix every hour. The elevation of each location was obtained using ArcGIS 10.1 (Redlands, California, U.S.A.) by overlaying a shapefile of the GPS tracks onto a raster dataset from the Shuttle Radar Topography Mission (SRTM), (Rodriguez *et al.* 2005) of Santa Cruz, U.S.A.

We quantified the composition of native and introduced plant species in vegetation communities with elevation from a sample of replicated plots placed at 50 m elevation intervals from 50 to 400 m in *La Reserva* and 100–400 m in *Cerro Fatal*. At each 50 m interval along a predetermined survey line up the elevation gradients used for monthly tortoise population assessments (Blake *et al.* 2013), 4 × 200 m² circular plots were

established 50 m apart and perpendicular to the survey line. Within each 200 m² plot all trees (including adult cacti) over 5 cm diameter at breast height (dbh) were identified and measured. One 50 m² plot was placed in the center of each 200 m² plot, and within it, all vascular plant species were recorded and given a cover score on a five-point scale (1–20%, 21–40%, 41–60%, 61–80%, 81–100%). Five circular plots each of 5 m² were placed randomly within each 200 m circular plot, and within these all vascular plant species up to 1 m in height were recorded and given a cover score as previously described.

To quantify food selection, we conducted 10 min focal observations of tortoises recording every bite and the plant species and plant part consumed. A feeding bout was defined as all feeding on a given species during the focal observation, and bite rate was defined as the total number of bites on that

species during the 10 min focal observation. Tortoises were selected based on the first individual seen following a given time in the field to minimize selection bias based on individual attributes. The sex and age class (juvenile, sub-adult, adult) of the tortoise was recorded, as was location (using a handheld GPS) time, and weather conditions. Observations were made at distances between 3 and 10 m using binoculars when visibility was poor. Observations were stopped and duration noted if the observer judged that they had disturbed the tortoise's behavior. A total of 27.6 h of observations were completed in *Cerro Fatal*, and 28.5 h in *La Reserva*. *Ad hoc* observations tortoises while feeding completed the food species list but were not used in any analyses. Plant species identifications were made in the field, or, for doubtful observations, vouchers were taken for identification at the Charles Darwin Foundation herbarium. Nomenclature and classification of plant species origin (endemic, indigenous, introduced) followed Jaramillo Díaz *et al.* (2014), though for analytical purposes, we lump endemic and indigenous species together as 'native'.

Feeding on fruit was further quantified by analysis of 163 tortoise dung piles. During 2010–2013, we collected fresh, intact dung piles during the course of regular fieldwork. To avoid visually biasing our sample, we collected the first dung pile encountered each time we crossed an altitude level in multiples of 50 m (*i.e.*, 50 m, 100 m, etc.). All dung collections were geo-referenced using a handheld GPS and elevation was calculated as described above. Dung piles were washed with rainwater and sieved using a 0.5 mm mesh. All seeds were identified and counted, except for grass seeds that were identified where possible and their presence recorded. Poaceae seeds were therefore excluded from quantitative analysis of seed content in dung.

We investigated the relationship between diet composition and tortoise physical condition along the elevation gradient in November and December 2013 on 37 adult female tortoises (23 in *La Reserva* and 14 in *Cerro Fatal*). These months are near the end of the upland phase of the migration when most tortoises have spent several months at high elevations. We used three health metrics; body condition index (BCI), and from whole blood, packed cell volume (PCV) and total solids (TS). We calculated BCI as:

$$BCI = m/L^{2.89} \tag{1}$$

where m is mass (kg) of the tortoise, and L is curved length (cm) over the carapace. We measured tortoise mass to the nearest 0.5 kg by suspending each tortoise from a spring balance. We measured length from front to back of the tortoise carapace to the nearest 0.5 cm. The power coefficient was obtained from a regression analysis of log(mass) versus log(length) for sample of 196 tortoises measured on Santa Cruz. To estimate PCV and TS, we collected *ca* 5 ml of blood was from the left brachial vein using a 20 gauge 3.8-cm syringe, and dispensed directly into a vacutainer tube containing lithium heparin (Corvac, Sherwood Medical, Saint Louis, Missouri,

U.S.A.). In the field, we kept blood samples in a cooler with ice packs, and in the lab in a refrigerator until processed. All blood samples were processed <24 h after collection. Packed cell volume (expressed as %) was determined using a few drops of whole blood in capillary tubes that was spun for 5 min with a portable 12-V centrifuge (Mobilespin, Vulcan Technologies, Grandview, Missouri, U.S.A.), and then read using a Zipocrit reader card (LW Scientific, Inc., Lawrenceville, Georgia, U.S.A.). We measured plasma total solids (expressed as g/dl) using a handheld refractometer (Schulco, Toledo, Ohio, U.S.A.) temperature-calibrated at the site.

Body Condition Index can provide an integrative index of physiological status in turtles (Bondi & Marks 2013, Lecq *et al.* 2014) and other species (*e.g.*, Green 2001 and references therein), but may be prone to several sources of bias, notably measurement error, non-linear relationships between body weight and structural size and rapid change in body weight (Schulte-Hostedde *et al.* 2005). We minimized measurement bias by utilizing the same technical staff and a standardized protocol for all estimates of mass and length, and reduced the possibility for structural size bias by calculating a power coefficient from field data (see Eqn. 1). Unlike small endotherms (Krebs & Singleton 1993), the body weight of large, ectothermic giant tortoises is relatively stable over short timescales. Nesting can reduce body weight rapidly in turtles, but our study occurred in the non-nesting season. The other metrics, PCV and TS are standard veterinary matrices used extensively as indicators of health in turtles (Deem *et al.* 2006, Grioni *et al.* 2014). When used together, PCV and TS provide an assessment of hydration and anemia; higher values may indicate dehydration, reproductive activity in females, or a higher nutritional status (Campbell 2006, Yang *et al.* 2014).

STATISTICAL ANALYSIS.—We tested hypotheses about how vegetative cover, feeding bouts, number of bites per bout, and number of seeds per dung pile varied between native and introduced plant species along an altitudinal gradient in two disjoint areas using a set of five models for each response variable and site. Specifically, we compared the Akaike's Information Criterion (AIC) values for five generalized linear models with the following forms: (1) response variable constant; (2) response variable varies in response to elevation; (3) response variable varies between plant types (native vs. introduced species); (4) response variable varies with elevation and plant type; and (5) response variable varies with elevation and plant type and there is an interaction between elevation and plant type. For all response variables, we assumed a log link, however error distributions differed based on whether the response variable was continuous or discrete and whether there was indication of overdispersion. We used the negative binomial distribution for analyses of bites per bout and seeds per dung pile, a poisson distribution for analyses of bout data, and a normal distribution for vegetative cover data. These analyses were completed in R v. x64 3.0.2 (R Development Core Team 2008) and negative binomial generalized linear models were fitted using the glm.nb

function in the MASS library. Additional analyses mentioned in the results were completed using Genstat 16th edition (VSN International Ltd. Hemel Hempstead, U.K.). Significant relationships between variables were defined in all cases as α < 0.05.

RESULTS

TORTOISE DIETS.—Tortoises ate leaves, stems, and fruits from at least 64 species in 26 families (Table 1). During focal animal observations, tortoises consumed 42 species from 20 families. Species accumulation curves approached an asymptote indicating that we have likely captured those species that form the majority of the diets of the two tortoise species.

Tortoises fed most frequently on graminoids that accounted for 32.6 percent of all feeding bouts, and together with forbs and herbs made up 73.2 percent of all feeding bouts. The diversity of tortoise diets recorded from focal sampling was higher in *Cerro Fatal* than *La Reserva* (27 and 20 species respectively); however, just a few species dominated the diet in each site. For example, *Paspalum conjugatum*, an abundant grass classified as 'questionably native' by (Jaramillo Díaz *et al.* 2014) and almost certainly introduced (P. Jaramillo, pers. comm.), was ranked first and second most frequently consumed in *La Reserva* and *Cerro Fatal*, comprising 14.6 percent and 31.8 percent of feeding bouts, respectively. *Tradescantia fluminensis*, an invasive herb, was ranked first in *Cerro Fatal*, comprising 16.5 percent of feeding bouts. The top five ranked species in *La Reserva* and *Cerro Fatal* accounted for 80.0 percent and 53.7 percent of all feeding bouts, respectively.

FOOD PLANT ORIGINS.—Of the 64 species recorded in tortoise diets, 8 (12.3%) were endemic, 27 (43.1%) were indigenous, and 28 (43.8%) were introduced, and one was unknown (Table 1). Seeds from 42 species of fruit were identified from 163 tortoise dung piles. The median and modal number of species per dung pile was two, with a range between 1 and 9 species. Excluding seeds from graminoids, the median number of seeds per dung pile was 212 (mean = 1208.0), and ranged from 1 to 9948. The mean number of species of seeds per dung pile was greater in *Cerro Fatal* tortoises than *La Reserva* (Mann–Whitney *U* test: $U = 608.0$, $P < 0.001$), but there was no difference in the number of seeds in dung piles between sites ($P = 0.338$). Fruit remains in dung piles were dominated by a few species, mostly pulp-rich drupes (*Psidium guajava*, *Psidium galapageium*, *Passiflora edulis*, *Opuntia echios*). Capsules, achenes, and schizocarps from several species were also well represented in dung piles, in particular *T. fluminensis* and *Sida* spp. Fruit feeding in these cases was most likely accidental ingestion when tortoises were feeding primarily on foliage.

Seeds from introduced species dominated fruit remains in tortoise dung (Table 1) comprising 58.5 percent and 63.2 percent of all fruit species recorded in dung piles in *Cerro Fatal* and *La Reserva*, respectively. Seeds from introduced species made up 71.6 percent of the total number of seeds found in dung piles in *Cerro Fatal* and 93.8 percent in *La Reserva*. Seeds from a single species

of highly invasive tree, *Psidium guajava*, were found in 17.8 and 24.6 percent of dung piles in *Cerro Fatal* and *La Reserva*, respectively, and comprised 55.1 percent and 82.4 percent of all seeds recorded.

VEGETATION COVER, SPECIES ORIGIN, AND TORTOISE FORAGING IN RELATION TO ELEVATION.—Dietary species richness tended to decline with elevation in both sites (Spearman's rank correlation coefficient: $\rho_{(Cerro\ Fatal)}$: = −0.600, $P = 0.044$, $N = 6$; $\rho_{(La\ Reserva)}$ = −0.387, $N = 8$, $P = 0.054$). Shannon–Wiener Diversity Indices (H') negatively correlated with altitude in *Cerro Fatal* but not in *La Reserva* ($\rho_{(Cerro\ Fatal)}$ = −0.600, $N = 6$, $P = 0.044$ and $\rho_{(La\ Reserva)}$ = −0.286, $N = 8$, $P = 0.115$). The Shannon Evenness Index (J') however was inconsistent. J' was negatively correlated with elevation in *Cerro Fatal* (ρ = −0.657, $N = 6$, $P = 0.034$) indicating low dietary diversity or greater specialization at higher altitudes, whereas a positive trend in J' was observed in *La Reserva* (ρ = 0.500, $N = 8$, $P = 0.049$).

Vegetative cover, feeding bouts and number of bites per bout, and number of seeds per dung pile all varied in response to elevation and plant origin (native vs. introduced). At both study sites native cover decreased with increasing elevation, while the cover of introduced species increased (Figs. 2A and B). In terms of number of feeding bouts, we observed similar significant trends at both sites (Figs. 2C and D). The number of bites per bout decreased with increasing elevation. According to a full model with interactions between elevation and plant origin, the number of bites per bout on native species decreased more steeply at both sites, (Figs. 2E and F), however the best model for *La Reserva* did not include an interaction suggesting similar declines in bite rates with elevation on both native and introduced species (Table 2). For the data from *Cerro Fatal*, the interaction was weakly supported over a model that did not include an interaction (ΔAIC = 1.5; Table 2). The number of native seeds per dung pile also decreased with increasing elevation, and the number of introduced seeds per dung pile increased dramatically (Figs. 2G and H). The best models for cover, bouts, and seeds included an interaction between elevation and plant type in both tortoise species and were strongly supported over a model without an interaction (ΔAIC > 6; Table 2).

The percentage of feeding bouts on introduced species was positively correlated with the percentage cover of introduced species along the elevation gradient in each site (Spearman's Rank Correlation Coefficient: $\rho_{(Cerro\ Fatal)}$ = 0.685, $N = 7$, $P = 0.022$, $\rho_{(La\ Reserva)}$ = 0.548, $N = 8$, $P = 0.030$). A crude preference index calculated as the percentage of feeding bouts on introduced species minus the percentage of vegetation cover of introduced species resulted in negative values at every elevation level in each site strongly suggesting that tortoises positively select introduced species over natives in all areas of their range.

TORTOISE FORAGING INTENSITY IN RELATION TO ELEVATION.—Tortoises tagged with GPS units ranged between 0 and 400 m

TABLE 1. *Plants by family and species recorded in the diet of Galapagos tortoises on Santa Cruz Island (CF and LR refer to the Cerro Fatal and La Reserva tortoise populations, respectively). N feeding bouts refers to the number of records of tortoises feeding on a given species during focal observations.*

Family	Species	Origin	N feeding bouts		N dung piles	
			CF	LR	CF	LR
Acanthaceae	Blechum pyramidatum	Indigenous	9	20		
Apiaceae	Centella asiatica	Indigenous	2	2		
Asteraceae	Bidens sp.	Unk.			1	
	Blainvillea dichotoma	Indigenous			3	
	Brickellia diffusa	Indigenous				1
	Pseudelephantopus spiralis	Introduced		4		
	Sonchus oleraceus	Introduced	2			
	Synedrella nodiflora	Introduced				1
Boraginaceae	Cordia lutea	Indigenous	1		1	1
Cactaceae	Opuntia echios	Endemic	11		19	8
Caesalpinaceae	Senna pistaciifolia	Indigenous		1		
Commelinaceae	Commelina diffusa	Indigenous	2			
	Tradescantia fluminensis	Introduced	27		24	4
Convolvulaceae	Evolvulus convolvuloides	Indigenous	16	4		
	Ipomoea triloba	Introduced			2	
Cucurbitaceae	Momordica charantia	Introduced	1			
Cyperaceae	Cyperus ligularis	Indigenous			1	
	Cyperus anderssonii	Endemic		1		
	Eleocharis maculosa	Indigenous				1
	Scleria distans	Indigenous				1
	Scleria hirtella	Indigenous			1	
	Kyllinga brevifolia	Indigenous	5	2		
Euphorbiaceae	Croton scouleri	Endemic				
	Hippomane mancinella	Indigenous		1		9
Fabaceae	Desmodium glabrum	Introduced	4	1		1
	Desmodium incanum	Introduced	4			1
	Rhynchosia minima	Indigenous				
	Tephrosia cinerea	Indigenous				
Malvaceae	Abutilon depauperatum	Endemic				
	Bastardia viscosa	Indigenous	1	1		
	Sida hederifolia	Indigenous	6	2	1	
	Sida rhombifolia	Introduced	2	21	17	20
	Sida spinosa	Indigenous	2	2	4	8
Mimosaceae	Acacia rorudiana	Indigenous				1
Myrtaceae	Psidium galapageium	Endemic	4	1	17	34
	Psidium guajava	Introduced	2	19	24	48
Nyctaginaceae	Pisonia floribunda	Endemic			1	
Passifloraceae	Passiflora edulis	Introduced	2	3	13	41
Plumbaginaceae	Plumbago scandens	Indigenous				
Poaceae	Anthephora hermaphrodita	Introduced			2	
	Axonopus micay	Introduced	10	1	4	
	Brachiaria mutica	Introduced				
	Cenchrus platyacanthus	Endemic				1
	Cynodon dactylon	Introduced				1
	Digitaria setigera	Introduced	1		6	13
	Eleusine indica	Introduced			1	1

(continued)

Table 1 (continued)

Family	Species	Origin	N feeding bouts		N dung piles	
			CF	LR	CF	LR
	Eragrostis cilianensis	Introduced	8		1	
	Eragrostis ciliaris	Indigenous	9	1		
	Eriochloa pacifica	Indigenous			1	
	Panicum dichotomiflorum	Indigenous			1	
	Panicum maximum	Introduced				1
	Paspalum conjugatum	Introduced	24	43	10	14
	Pennisetum purpureum	Introduced	4	5		
Polygonaceae	Polygonum opelousanum	Endemic				1
Portulacaceae	Portulaca oleracea	Introduced			1	
	Talinum paniculatum	Introduced				
Rosaceae	Rubus niveus	Introduced				5
Rutaceae	Zanthoxylum fagara	Indigenous				7
Solanaceae	Physalis pubescens	Indigenous			1	1
	Solanum americanum	Introduced			1	
Verbenaceae	Clerodendrum molle	Indigenous				4
	Lantana camara	Introduced	1			
	Phyla strigulosa	Indigenous	4			
	Stachytarpheta cayennensis	Introduced			1	
Total			164	135	58	89

TABLE 2. *Delta AIC values for five models fitted to eight datasets. For all but one dataset, the models that allowed for different intercepts and relationships with elevation for plants of different origins were the best model and in most cases these models had moderate (ΔAIC's of 3–7) or very strong support (ΔAIC > 10).*

Model type	Number of parameters	Δ AIC values							
		Vegetative cover index		Number of feeding bouts		Bites per 10 min bout		Number of seeds in dung	
		La Reserva	Cerra Fatal	La Reserva	Cerra Fatal	La Reserva	Cerra Fatal	La Reserva	Cerra Fatal
Intercept only	1	136	340	41	49	10	5.3	51	7.5
Elevation (E)	2	111	342	43	51	1.4	6.3	43	6.9
Origin (O)	2	131	247	17	49	3.6	4.8	13	5.9
E and O—no interaction	3	112	226	18	51	0	1.5	15	7.4
E and O—interaction	4	0	0	0	0	0.7	0	0	0

elevation in *La Reserva* and 63–429 m in *Cerro Fatal*. Eight tortoises in *Cerro Fatal* and 12 in *La Reserva* undertook seasonal long distance migrations across the elevation gradient (Blake *et al.* 2013) (Fig. 1), though four individuals in *Cerro Fatal* and one in *La Reserva* were relatively sedentary in either the uplands or lowlands. If the GPS tagged tortoise movement behavior is representative of their populations, we estimate that 52.7 percent of all bites by *Cerro Fatal* tortoises are on introduced species, and 63.6 percent for *La Reserva* tortoises,

and 58.7 percent and 65.7 percent of bouts, respectively. Tortoises that remain in uplands year-round are likely to feed almost exclusively on introduced species. For example, the movement data of one adult male from *La Reserva*, indicated that some 92 percent of his bites and 83 percent of his feeding bouts were on introduced species. In contrast, the movement data from another individual, a female resident in the *Cerro Fatal* lowlands, suggested that 50 percent of her bites and 47 percent of her bouts were on introduced species.
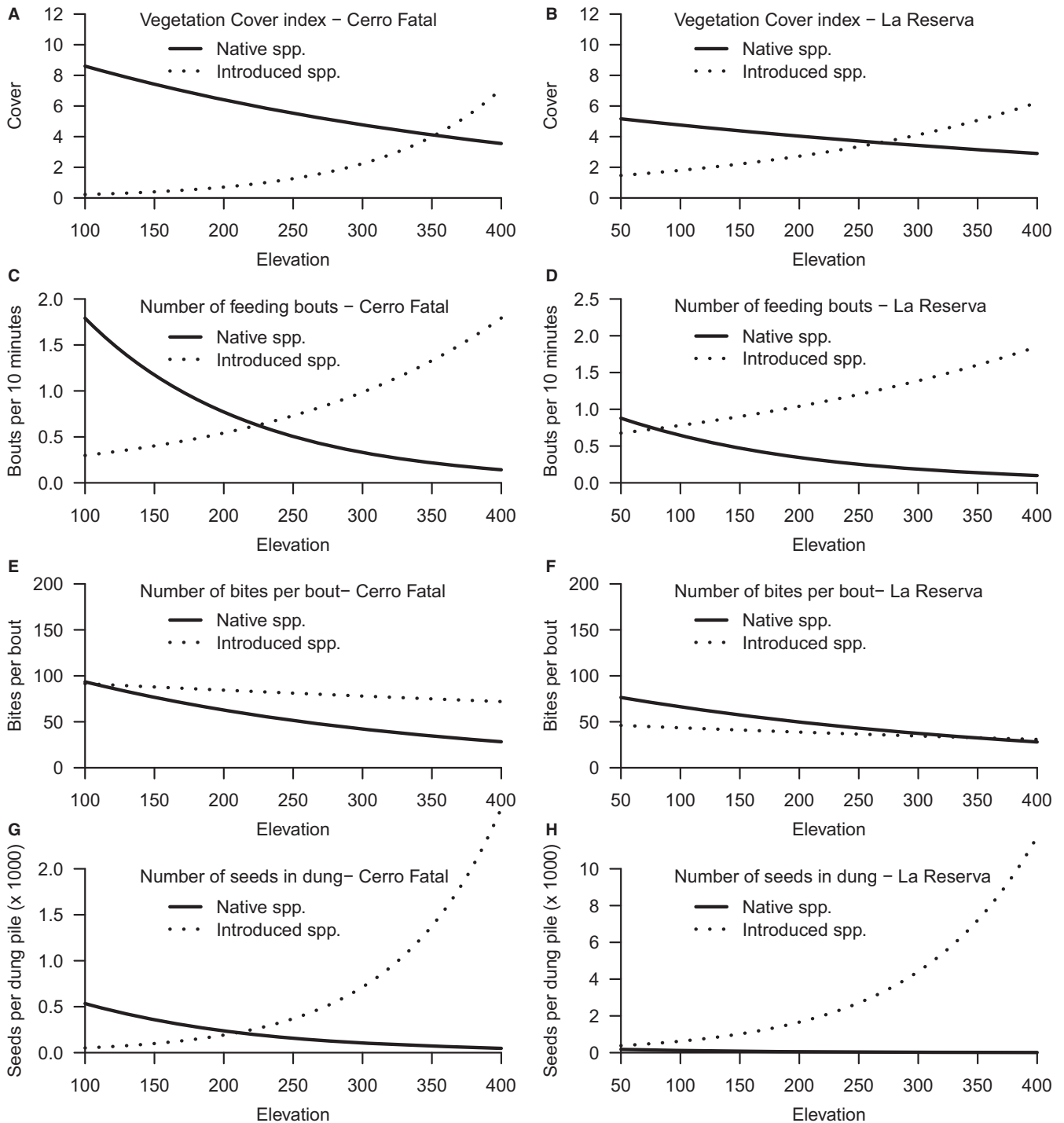
FIGURE 2. A visual summary of the relationships between elevation and properties of vegetation and tortoise diets. The cover of introduced species as a proportion of total vegetation cover increases with elevation in both *Cerro Fatal* and *La Reserva* (A, B). In both *Cerro Fatal* and *La Reserva*, the number of tortoise feeding bouts on introduced species increased with elevation while bouts on native species decreased (C, D). The number of bites on introduced species as a proportion of total bites increased with elevation, but the overall bite rate declined (E, F). Finally, consistently across both sites the number of seeds of introduced fruit species in tortoise dung piles increased with elevation, while numbers of seeds of native species declined (G, H).

TORTOISE PHYSICAL CONDITION BY ELEVATION.—Tortoise physical condition varied widely by species and elevation (Table 3). We found no increase in BCI with elevation in *La Reserva* (regression analysis; $F_{(1,25)} = 2.04$, $P = 0.166$). However, in *Cerro Fatal*, where we sampled at just two elevations, 150 m and 350 m, a one-way ANOVA suggested that tortoises in the uplands had

higher BCI values than those in the lowlands ($F_{(1,13)} = 6.05$, $P = 0.030$).

In *Cerro Fatal*, PCV and TS blood values for tortoises in the uplands were higher than those for tortoises in the lowlands, though TS just failed to reach significance (PCV: $F_{(1,12)} = 10.87$, $P = 0.007$; TS: $F_{(1,12)} = 4.51$, $P = 0.057$). In *La Reserva*, both PCV and TS tended to increase with elevation but not significantly (PCV: $F_{(1,20)} = 2.65$, $P = 0.119$; TS: $F_{(1,20)} = 4,25$, $P = 0.053$). The combination of BCI, PCV, and TS indicate that overall physical condition of tortoises was either consistent or positively correlated with elevation and the proportion of introduced species in the diet.

DISCUSSION

We have shown that Galapagos tortoises from two different species on Santa Cruz Island feed on a wide variety of plant forms, including grasses, forbs, and woody shrubs. Tortoises are also frugivorous, feeding extensively on drupes. In the only other intensive study on Galapagos tortoise diet conducted during the early 1980s in *La Reserva* at *ca* 150–200 m elevation, Cayot (1987) found that tortoises consumed some 40+ species with a small number comprising the bulk of the diet, and these were characterized primarily by high water content, with selectivity for these species increasing when environmental water was scarce.

In 1983, Cayot also recorded the presence of 145 plant species from opportunistic observations in her study site at *ca* 180–200 m in *La Reserva*, of which 21 (14.5%) were introduced species. At the same elevation, we recorded 29 species in replicated plots of which 17 (58.6%) were introduced, with 34 percent greater cover than native species. Comparing Cayot's exhaustive inventory over a large area and our small plot sample is fraught with problems, but the central point—that introduced species have increased in numbers and abundance—is well illustrated and supported by more recent observations (Trueman *et al.* 2010, 2013).

That over 50 percent of foods consumed by Santa Cruz tortoises are now from introduced species may represent a relatively rapid dietary change by giant tortoises. Introduced plants began to increase in abundance on Galapagos in the 1930s as native highland vegetation was cleared for agriculture (Restrepo *et al.* 2012), and the rate of introductions has been increasing dramatically ever since (Watson *et al.* 2010). On Santa Cruz, transformation of native vegetation accelerated in the 1950s before the creation of the Galapagos National Park, but dramatic increases in introduced species occurred after the *El Niño* of 1982 (L. Cayot, *pers comm.*). Tortoises have likely become exposed to introduced species in large quantities and have incorporated them into their diets well within the lifespan of most of the adults alive today.

Foraging herbivores usually select foods that have the highest digestibility and nutritional value (Hanley 1997) and the search for these resources has shaped the evolution of foraging strategies (Fryxell & Sinclair 1988, Mysterud *et al.*

2001). Given the abundance and nutritional quality of introduced species, it is no surprise that they now form a large part of tortoise diets and may be preferred over natives. The most frequently consumed forage species, *P. conjugatum* and *T. fluminensis*, occur in large dense patches, offering a super-abundance of forage in quantities rarely seen among native species assemblages. *Paspalum conjugatum* (buffalo grass) is widespread, copes well in droughts, is a preferred grass of cattle and goats (Heuzé *et al.* 2013), and on Galapagos is extensively used as cattle pasture. *Tradescantia fluminensis* contains high levels of nitrates (Maule *et al.* 1995), which can be an important source of nitrogen for herbivores (Mattson 1980), and also has high water content, a plant trait preferred by tortoises (Peterson 1996). The dominant fruit food species, *P. guajava* and *P. edulis* which are cultivated around the world, are large, sweet and contain abundant easily digestible pulp. Moreover, they occur in large dense fruit fall patches thus are easily acquired and processed by tortoises. Given the importance of tortoises and turtles as seed dispersers (Strong & Fragoso 2006, Kimmons & Moll 2010), the large quantities of seeds of introduced species dispersed by Galapagos tortoises may have important consequences for the competitive dynamics of plant communities on Galapagos and the spread of invasive species from farmlands into the national park (Blake *et al.* 2012). However, the converse is also true, and tortoises may also play a positive restoration role by repopulating degraded areas with native species (Griffiths *et al.* 2011).

The consequences of introduced species for the nutritional balance, movement patterns, fitness and population dynamics of tortoises are difficult to determine with few data on tortoise ecology and condition before the vegetation transformation on Santa Cruz, but it is likely that they have been positive. Our data on BCI, PCV, and TS were correlated with elevation suggesting that tortoises that migrate into the highlands maintain or improve body condition with increasing elevation. High PCV and TS values can indicate dehydration rather than high nutritional status, but we ruled out this conclusion as high values were found in tortoises in the humid highlands with moist soils and well hydrated vegetation and not in the arid lowlands where dehydration might be expected.

Body condition is an important determinant of reproductive performance and survival across many taxa (Langvatn *et al.* 1996, Hayes & Shonkwiler 2001), including turtles and tortoises (Litzgus *et al.* 2008). Though weight gain is common in altitudinally migrating species during the upland phase of migration, and likely a primary reason for the evolution of these migratory systems across taxa (Lundberg 1985, Sztatecsny & Schabetsberger 2005), ours is the first such system reported in which introduced species dominate food selection. During the least biologically productive season on Galapagos, tortoises whose diets are the most dominated by introduced species can maintain or improve body condition.

Most research on the role of introduced species of plants and animals stresses the negative ecological impacts (*e.g.*, Mack *et al.* 2000, Mooney & Cleland 2001, Myers & Bazely 2003), and only

TABLE 3. *Galapagos tortoise body condition index (BCI), packed cell volume (PVC) and total solids (TS) by site and elevation (CCL = curved carapace length, CCW = curved carapace width).*

Tort. ID	Site	Elev. (m)	CCL (cm)	CCW (cm)	Wt. (kg)	BCI	PCV	TS
1701	*Cerro Fatal*	163	98.8	120.5	78	0.134	18	6.1
SB44	*Cerro Fatal*	163	101.5	112.5	73.5	0.117	17	5.8
1408	*Cerro Fatal*	164	92.7	104.5	68.9	0.142	23	7.1
1410	*Cerro Fatal*	164	90.5	107.6	69.4	0.154	14	6.8
Nigrita	*Cerro Fatal*	164	96.2	111.7	72.5	0.135	18	6.1
SB45	*Cerro Fatal*	164	105	120.4	80	0.115	20	8.0
Karla	*Cerro Fatal*	311	99.5	111.6	90.5	0.152	22	8.0
925	*Cerro Fatal*	311	102.7	114.5	96.5	0.148	25	9.2
SB46	*Cerro Fatal*	311	91.7	109.6	80	0.171	24	7.4
SB48	*Cerro Fatal*	312	102.7	111.1	85	0.131	24	9.2
SB49	*Cerro Fatal*	321	96.8	107	83	0.151	22	10.6
SB50	*Cerro Fatal*	321	108	118.7	107.5	0.143	20	6.8
SB51	*Cerro Fatal*	323	90	103.2	64.5	0.145	24	6.2
Alison	*Cerro Fatal*	326	102	112	106.4	0.167	22	8.6
1142	*La Reserva*	64	101.2	115.5	106.5	0.171	21	10.7
SB31	*La Reserva*	67	86	100	48	0.123	18	6.8
SB40	*La Reserva*	103	95.2	98.4	62	0.119	23	6.5
SB39	*La Reserva*	111	99.2	107	68	0.116	19	5.6
SB30	*La Reserva*	126	94	110.2	87	0.173	20	7.6
SB38	*La Reserva*	133	97.6	112	69.5	0.124	18	8.2
SB33	*La Reserva*	146	103	119.2	76	0.116	22	7.7
3159	*La Reserva*	159	90.3	105.9	66.2	0.148	20	6.7
SB41	*La Reserva*	160	76.7	96	56	0.200	20	7.8
SB42	*La Reserva*	178	86	91	63	0.162	14	6.7
2316	*La Reserva*	178	95	106.6	81.5	0.157	19	8.7
3148	*La Reserva*	195	90.5	96.2	65.2	0.144	24	10.1
SB43	*La Reserva*	203	92.2	102.2	79	0.166	26	8.6
SB36	*La Reserva*	206	102.1	115.8	109	0.170	22	9.6
SB37	*La Reserva*	206	89.9	104.6	78	0.176	20	9.8
1757	*La Reserva*	210	100.4	117	85.5	0.140	20	8.0
SB35	*La Reserva*	242	86.7	96	57	0.143	30	8.6
SB1	*La Reserva*	246	95.5	106	89.5	0.170	22	8.4
3143	*La Reserva*	255	83.5	94	54.7	0.153	20	6.6
1406	*La Reserva*	274	98.3	112.4	95.4	0.166	25	9.6
1400	*La Reserva*	276	106.5	117	122.9	0.170	22	10.0
3150	*La Reserva*	292	100	112	87.5	0.145	23	9.4
1398	*La Reserva*	323	105	114	108.2	0.156	24	8.9
3157	*La Reserva*	352	101.2	0	94.7	0.152	18	6.9
	Summary							
	Cerro Fatal	Mean	98.4	111.8	82.6	0.100	20.9	7.6
		Min.	90	103.2	64.5	0.100	14	5.8
		Max.	108	120.5	107.5	0.200	25	10.6
	La Reserva	Mean	94.8	102	79.6	0.200	21.3	8.2
		Min.	76.7	0	48	0.100	14	5.6
		Max.	106.5	119.2	122.9	0.200	30	10.7

recently has the concept of neutral or even positive impacts associated with introduced species been discussed (Richardson *et al.* 2000, Goodenough 2010). Undoubtedly, the ecology of the Galapagos Islands has been and is being severely negatively affected by numerous introduced species (Schofield 1989, Cruz *et al.* 2005, Causton *et al.* 2006), and many eradication programs have been

implemented with varying success (Gardener *et al.* 2010). The costs of eradication attempts and the likelihood of success has led to a re-evaluation of management objectives of introduced species on Galapagos (Gardener *et al.* 2010, Trueman *et al.* 2014) and around the world (Hobbs *et al.* 2006). A return to 'pristine nature' is unlikely for much of Galapagos. Fortunately, this may not be all bad news for the conservation of Santa Cruz tortoises, which have readily adopted introduced species into their diets, though further research is necessary to better understand the relationships between plant community composition and tortoise ecology and conservation. Priorities include (A) determining the nutritional contribution of native and introduced species on energy balance for tortoises under current conditions and predicted future conditions of vegetation communities under different land-use and climate scenarios; (B) an assessment of the impact of introduced non-food species, such as *Pennisetum purpureum* (elephant grass) and *Rubus niveus* (blackberry or Ceylon raspberry), on forage availability and their potential to block tortoise migrations; and (C) understanding the ecological role of tortoises themselves on competitive dynamics between introduced and native species.

ACKNOWLEDGMENTS

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