



SPECIAL  
ISSUE



## Seed dispersal by Galápagos tortoises

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### ABSTRACT

**Aim** Large-bodied vertebrates often have a dramatic role in ecosystem function through herbivory, trampling, seed dispersal and nutrient cycling. The iconic Galápagos tortoises (*Chelonoidis nigra*) are the largest extant terrestrial ectotherms, yet their ecology is poorly known. Large body size should confer a generalist diet, benign digestive processes and long-distance ranging ability, rendering giant tortoises adept seed dispersers. We sought to determine the extent of seed dispersal by Galápagos tortoises and their impact on seed germination for selected species, and to assess potential impacts of tortoise dispersal on the vegetation dynamics of the Galápagos.

**Location** Galápagos, Ecuador.

**Methods** To determine the number of seeds dispersed we identified and counted intact seeds from 120 fresh dung piles in both agricultural and national park land. To estimate the distance over which tortoises move seeds we used estimated digesta retention times from captive tortoises as a proxy for retention times of wild tortoises and tortoise movement data obtained from GPS telemetry. We conducted germination trials for five plant species to determine whether tortoise processing influenced germination success.

**Results** In our dung sample, we found intact seeds from > 45 plant species, of which 11 were from introduced species. Tortoises defecated, on average, 464 (SE 95) seeds and 2.8 (SE 0.2) species per dung pile. Seed numbers were dominated by introduced species, particularly in agricultural land. Tortoises frequently moved seeds over long distances; during mean digesta retention times (12 days) tortoises moved an average of 394 m (SE 34) and a maximum of 4355 m over the longest recorded retention time (28 days). We did not find evidence that tortoise ingestion or the presence of dung influenced seed germination success.

**Main conclusions** Galápagos tortoises are prodigious seed dispersers, regularly moving large quantities of seeds over long distances. This may confer important advantages to tortoise-dispersed species, including transport of seeds away from the parent plants into sites favourable for germination. More extensive research is needed to quantify germination success, recruitment to adulthood and demography of plants under natural conditions, with and without tortoise dispersal, to determine the seed dispersal effectiveness of Galápagos tortoises.

### Keywords

*Chelonoidis nigra*, digesta retention time, Galápagos, germination, giant tortoise, GPS telemetry, island ecology, megaherbivore, reptiles, seed dispersal.

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### INTRODUCTION

Megaherbivores often have dramatic roles in ecosystem function (Janzen & Martin, 1982; Owen-Smith, 1988; Dirzo

& Miranda, 1991). At natural densities in terrestrial systems they often comprise the majority of vertebrate biomass (Owen-Smith, 1988; White, 1994); they trample vegetation, killing trees and shrubs, thus increasing heterogeneity or retarding

ecological succession (Kortlandt, 1984; Chapman *et al.*, 1999; Terborgh *et al.*, 2008), which modifies community structure (van Aarde & Jackson, 2007; Ogada *et al.*, 2008). Megaherbivores may also be prodigious seed dispersers (Fragoso & Huffman, 2000; Guimarães *et al.*, 2008; Blake *et al.*, 2009), a major advantage of which is the movement of seeds away from parent plants (Howe & Smallwood, 1982; Levey *et al.*, 2002; Levin *et al.*, 2003; Terborgh *et al.*, 2008). Long-distance dispersal may be particularly advantageous (Cain *et al.*, 2000; Nathan, 2006) and, due to the strong correlation between vertebrate body size and ranging ability (Peters, 1983), large-bodied vertebrates are likely to move seeds further than do smaller-bodied ones.

A traditional definition of megaherbivores specifies animals over 1000 kg (Owen-Smith, 1988). However, Hansen & Galetti (2009) argue that a context-specific definition of the megafauna is more appropriate, when they state that 'one ecosystem's mesofauna is another ecosystem's megafauna'. By this definition, a 250 kg Galápagos tortoise (*Chelonoidis nigra*) should warrant classification as a megaherbivore because it is an order of magnitude larger than the next largest sympatric native vertebrate, the land iguana (*Conolophus subcristatus*). The large body size of giant tortoises may render them ecological keystones and/or ecosystem engineers in common with traditionally defined megaherbivores (Gibbs *et al.*, 2008, 2010; Hansen *et al.*, 2008, 2010; Griffiths *et al.*, 2010).

Despite their iconic status, the ecological role of Galápagos tortoises, including herbivory and seed dispersal, remains poorly understood. In the early 1960s, Rick & Bowman (1961) showed that Galápagos tortoise ingestion and defecation improves the germination of endemic tomatoes (*Solanum lycopersicum*). This observation was consistent with later research elsewhere which demonstrated that vertebrate digestion often enhances the germination success of seeds due to either mechanical or chemical alteration of the seed coat and/or removal of fruit pulp, which can inhibit germination (Barnea *et al.*, 1991; Cipollini & Levey, 1997; Traveset, 1998; Samuels & Levey, 2005; Traveset *et al.*, 2008). Furthermore, although the literature is sparse, the presence of dung may enhance seed germination and growth (Dinerstein & Wemmer, 1988; Traveset *et al.*, 2001). Large body size and a catholic diet should render Galápagos tortoises adept seed dispersers, particularly if they enhance seed germination, yet a recent literature review revealed only seven records of tortoise-mediated seed dispersal on the Galápagos (Heleno *et al.*, 2011), probably due to a dearth of research rather than ecological reality.

Given recent calls to use large-bodied tortoises as taxon substitutes in ecological restoration programmes for oceanic islands including the Galápagos (Griffiths *et al.*, 2010, 2011; Hansen *et al.*, 2010; Kaiser-Bunbury *et al.*, 2010), developing a better understanding of the ecological role of Galápagos tortoises is a research priority. This is particularly relevant in habitats invaded by introduced species, including much of the Galápagos (Gardener *et al.*, 2010), because generalist dispersers may move seeds from both native and introduced species.

In 2009 we initiated a study of seed dispersal by Galápagos tortoises to address the following questions and predictions:

1. *How many seeds from which species do tortoises disperse?* Large-bodied herbivores usually have more generalist diets than small-bodied ones (Owen-Smith, 1988; Woodward *et al.*, 2005), thus we expected Galápagos tortoises to consume more seeds from a wider variety of species than do smaller-bodied dispersers.
2. *What proportions of native versus introduced species are dispersed by tortoises in farmland and national park land?* We expected tortoises to disperse a higher proportion of introduced species in agricultural land compared with the Galápagos National Park (GNP) and that the proportion of introduced species per dung pile would decrease with distance into the park.
3. *How far do tortoises move seeds?* Due to the correlation between body size and ranging (Peters, 1983), we expected giant tortoises to disperse seeds over relatively longer distances than other vertebrate dispersers in the Galápagos.
4. *Does tortoise ingestion and processing influence the success of seed germination?* We predicted that ingestion and defecation by tortoises would increase seed germination success over seeds obtained from fallen fruits that were not processed by tortoises.

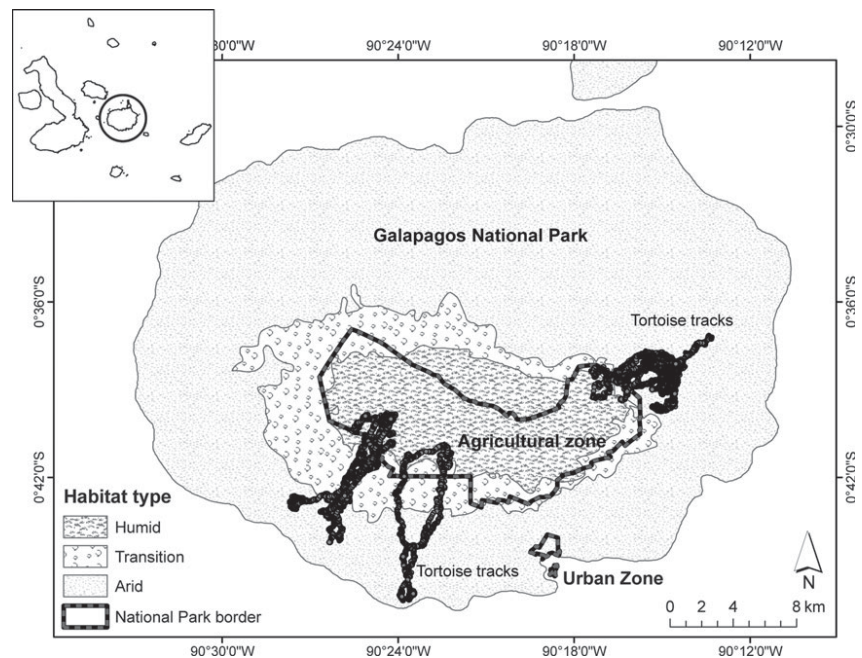
## MATERIALS AND METHODS

### Study site

Our study took place on the island of Santa Cruz near the geographic centre of the Galápagos Archipelago (Fig. 1). An extinct volcano, Santa Cruz rises to an elevation of c. 860 m a.s.l. Land use is divided into two main categories: agricultural land and the GNP. Agricultural land occurs mostly on upland slopes to the south and south-west in the island's rain shadow. The remainder of the island is part of the GNP, with the exception of several small urban areas. Agricultural vegetation is largely transformed and heavily dominated by introduced species, many of which are highly invasive (Gardener *et al.*, 2010). Natural vegetation occurs in three main zones that follow the island's elevation gradient (Fig. 1). The arid zone contains xeric vegetation such as *Opuntia* spp. cactus and arborescent and shrubby species, with annuals growing vigorously during periods of high rainfall. As elevation rises, the arid zone gives way to the 'transition zone', in which evergreen species are common. Grass abundance increases and large areas are covered in mono-dominant *Bursera graveolens* woodland. Finally the high-elevation humid zone is variable, and may be dominated by *Miconia* species or ferns, sedges and grasses (Wiggins & Porter, 1971; Jaramillo Díaz & Guézou, 2011).

Weather patterns are characterized by a hot wet season from January to May and a cool dry season for the remainder of the year. Annual precipitation is highly variable due to El Niño cycles (Trueman & d'Ozouville, 2010).

**Figure 1** Santa Cruz Island, Galápagos, illustrating land-use categories, main habitat types and a summary of tortoise (*Chelonoidis nigra*) movement tracks made over a 1-year period. The agricultural zone, a polygon enclosed by the national park border, lies in the centre of the island, primarily within the humid zone.



Our study site encompassed tortoises from two separate populations to the south-east and south-west of Santa Cruz, the taxonomy of which remains unclear (Chiari *et al.*, 2009; Poulakakis *et al.*, 2012). Here we refer to both populations as *Chelonoidis nigra* (Quoy & Gaimard, 1824) following the nomenclature suggested in version 2011.2 of the IUCN Red List of Threatened Species (Tortoise & Freshwater Turtle Specialist Group, 1996).

### Seed content of tortoise dung

During 2009–10, we collected fresh, intact dung piles during the course of regular fieldwork, which consisted of either monthly systematic tortoise population surveys (along a pre-defined survey trail that traversed the elevation gradient of Santa Cruz from 50 to 400 m a.s.l., and which traversed both agricultural land and GNP) or *ad lib* research conducted on tortoise behaviour. In an attempt to sample widely over the tortoise range and also to avoid visually biasing our sample (i.e. preferentially collecting piles containing many seeds), we collected the first dung pile encountered each time we crossed an elevation level in multiples of 50 m (i.e. 50, 100, 150 m). This approach also meant that it was unlikely that we collected multiple dung piles from the same individual, although we cannot be certain that every dung pile in our sample originated from a different individual. All dung collections were georeferenced. Fresh dung piles were defined as those which retained a mucus sheen, were damp and had a characteristic odour. Tortoise density, and therefore dung pile density, was highest in agricultural land, which resulted in a considerably higher encounter rate of dung, and therefore higher sample size, in farmland compared with the park (105 vs. 15 samples, respectively). Although this was suboptimal sampling coverage, the large difference between strata means and relatively

low variance within strata allowed us to make valid comparisons.

Seeds were extracted from dung in the Charles Darwin Research Station (CDRS) 1–3 days after collection. Dung piles were washed with rainwater and sieved using standard soil sieves with a final mesh size of 0.5 mm. All seeds detected in each dung pile were identified and counted, except for grass seeds which were identified where possible and their abundance ranked (e.g. few, some, many). Grass seeds were therefore excluded from quantitative analysis of seed numbers contained in dung, which had the effect of considerably underestimating the total quantity of seeds dispersed by tortoises. It is possible that some seeds present in the dung evaded detection; however, our impression, due to our thorough and extensive searches for seeds, is that this was a minor source of bias if it did occur. All seeds detected and identified were intact, i.e. there was no physical evidence of damage such as fragmented or crushed seeds, probably because tortoises do not possess teeth. Throughout the study we did not find a single seed fragment, which suggests that, while it undoubtedly occurs, damage to seeds by tortoises is rare. During this study we did not assess seed viability. Seeds were identified by CDRS botanists (A.G. and P.J.) and vouchers were preserved.

We used logistic regression analysis (GENSTAT 14.0; VSN International Limited, Hemel Hempstead, UK) to test our prediction that the proportion of introduced species in dung piles would decrease with distance into the GNP.

### Estimation of the distances over which tortoises disperse seeds

Between May 2009 and May 2010, we fitted 14 adult Galápagos tortoises (eight males and six females) with global

positioning system (GPS) telemetry tags (custom built by e-obs GmbH, Munich, Germany), which recorded the position of each animal every hour. To estimate the tortoise-mediated seed dispersal kernel we first measured how long seeds remained in the digestive tract (for a full account of methods used see Sadeghayobi *et al.*, 2011). We fed small inert particles within the size range of seeds consumed by wild tortoises to captive tortoises held under semi-natural conditions by the GNP. Nineteen tortoises were fed a total of 15,200 particles (800 per individual) of four different sizes. Each tortoise was fed a unique colour combination of particles hidden in fruit and leaf foods, the different colours allowing dung piles to be associated with individual tortoises housed in the same enclosure. Dung was removed from the tortoise enclosures every 1–2 h during the day from 06.00 until 18.00 h, and the number of particles contained in each dung pile was recorded. The trials were stopped 5 days after the last particle was found. Mean seed recovery rate was over 90%, with some seeds lost in the substrate of the enclosure and in a small drinking pond, although it is possible that some seeds were retained in the tortoises beyond the 5-day limit. We considered our estimated digesta retention times from captive tortoises as a crude proxy for those in free-ranging tortoises, which may have biased our estimates of seed dispersal distances in the wild state.

Following these trials, we then calculated the average net linear displacement of a given tortoise over all possible pairs of GPS positions separated by the minimum, mean and maximum digesta retention times recorded during the trials (6, 12 and 28 days, respectively) (Sadeghayobi *et al.*, 2011). Lastly, in order to estimate a dispersal kernel (Cousins *et al.*, 2008) for seeds dispersed by tortoises, we calculated, from the GPS data, the average net displacement by tagged tortoise for the entire range of digesta retention times (from 6 to 28 days), resulting in a probability distribution of step lengths over time. We calculated the probability of seed defecation over time from the digesta retention experiment data, and combined these to estimate the probability distribution (the dispersal kernel) of seed dispersal with distance.

### Germination trials

Selection of species for germination trials was based primarily on the abundance of seeds by species in dung piles. The selection included endemic (*Psidium galapageium* and *Opuntia echios*), native (*Hippomane mancinella*) and introduced species (*Psidium guajava* and *Passiflora edulis*). Four of the five species were ranked highest in terms of both frequency of occurrence in dung piles, and mean number of seeds per dung pile (Table 1). The fifth species, *H. mancinella* was selected because we strongly suspected that the importance of this species had been under-represented in our sample of dung piles due to a high degree of spatial and temporal clumping in the distribution of its fruits. Fruit and seed characteristics varied widely among these species (Table 2), from large fleshy fruits containing high numbers of seeds

(*Psidium guajava*, *Passiflora edulis*), to small drupes with a low pulp to seed ratio (*Psidium galapageium*). Fruits of all species contain seeds embedded in a fleshy pulp, with the exception of *H. mancinella*, which has several seeds contained in a thick, copious endosperm resembling a nut that is embedded in the fruit pulp.

Germination trials involved four treatments, following the recommendations of Samuels & Levey (2005), namely: seeds taken directly from fruit and planted in pulp ('Fruit', F), ingested seeds planted in the tortoise dung pile in which they were found ('Dung', D); seeds taken from fallen fruit and washed in rainwater ('Washed Fruit', WF); and seeds from tortoise dung that were washed in rainwater ('Washed Dung', WD). Seeds were washed by gently removing traces of fruit pulp or dung with wet paper tissue, followed by thorough rinsing in rainwater.

Germination trials were conducted in a shade house in a randomized block design of four blocks  $\times$  four treatments to avoid potential bias due to local microclimate. Each treatment consisted of 10 seeds planted in plastic horticultural bags (12  $\times$  20 cm), in a consistent quantity of locally collected soil thoroughly mixed across all treatments. Ten seeds were planted in each bag, with the exception of *H. mancinella*, the woody nuts of which were planted one per bag due to their large size. For two species, *O. echios* and *Psidium guajava*, we planted 20 seeds per treatment (in two bags, 10 seeds per bag) per block because we had a surplus of seeds. In the 'dung' treatment, we planted each set of 10 seeds in a 50-g (wet weight) bolus of dung, with the exception of *H. mancinella*, for which each nut was planted in a 50-g dung bolus. During planting, we attempted to approximate the natural seed density in dung; however, the variation in seed numbers in tortoise dung is huge (0 to over 5000!), so our planting density should only be considered 'within the natural range'.

For a given species, all seeds were planted within a 2-h period on the same date, which was within 3 days of seed collection from the field whether from dung or intact fruit. Bags were watered three times per week with all pots receiving the same volume (50 mm) of rain water. Seeds were checked daily for signs of germination and we defined germination to be successful if cotyledons emerged. Trials continued for 6 months from the day of planting, with the exception of the *H. mancinella* trial, which terminated after 1 year because seeds of this species did not begin germinating until nearly 9 months after planting. At the end of the germination trials, we did not conduct a viability analysis for remaining non-germinated seeds.

### Analysis of germination trial data

To assess germination success, we conducted two separate analyses. We used the generalized linear mixed model (GLMM) procedure in GENSTAT 14.0 to test firstly for treatment effects on germination success per species, and secondly we combined the data from all species, and tested whether 'origin' (native/endemic or introduced) influenced the



**Table 1** Summary data indicating the frequency of occurrence of intact seeds in dung piles of tortoises (*Chelonoidis nigra*) found in farmland and in the Galápagos National Park on the island of Santa Cruz.

Family	Species	No. of dung piles	Percentage of dung piles*	Mean no. of seeds per dung pile	Origin
Asteraceae	<i>Bidens</i> sp.	1	0.83	21	?
	<i>Blainvillea dichotoma</i>	3	2.5	12	Na
	<i>Brickellia diffusa</i>	1	0.83	8	Na
	<i>Synedrella nodiflora</i>	1	0.83	1	Ac
Boraginaceae	<i>Cordia lutea</i>	3	2.5	1	Na
Cactaceae	<i>Opuntia echios</i> var. <i>gigantea</i>	17	14.17	156	En
Caesalpinaceae	<i>Crotalaria pumila</i>	13	10.83	40	Na
Commelinaceae	<i>Tradescantia fluminensis</i>	13	10.83	33	Es
	<i>Commelina diffusa</i>	3	2.5	10	Na
Convolvulaceae	<i>Ipomoea triloba</i>	4	3.33	3	Na
Cyperaceae	<i>Cyperus ligularis</i>	1	0.83	5	Na
	<i>Eleocharis maculosa</i>	1	0.83	1	Na
	<i>Kyllinga brevifolia</i>	1	0.83	2	Na
	<i>Scleria distans</i>	1	0.83	7	Na
	<i>Scleria hirtula</i>	1	0.83	4	?
Euphorbiaceae	<i>Hippomane mancinella</i>	5	4.17	10.8	Na
Fabaceae	<i>Desmodium incanum</i>	1	0.83	3	NaQ
	<i>Galactia striata</i>	1	0.83	1	Na
Malvaceae	<i>Sida rhombifolia</i>	32	26.67	48	Ac
	<i>Sida salviifolia</i>	1	0.83	3	Na
	<i>Sida spinosa</i>	5	4.17	4	Na
Mimosaceae	<i>Acacia rorudiana</i>	1	0.83	5	EnQ
Myrtaceae	<i>Psidium galapageium</i>	35	29.17	194	En
	<i>Psidium guajava</i>	38	31.67	931	Es
Nyctaginaceae	<i>Pisonia floribunda</i>	1	0.83	2	En
Passifloraceae	<i>Passiflora edulis</i>	34	28.33	177	Es
Poaceae	<i>Antheophora hermaphrodita</i>	2	1.67		NaQ
	<i>Cenchrus platyacanthus</i>	1	0.83		En
	<i>Cynodon dactylon</i>	1	0.83		Es
	<i>Digitaria setigera</i>	12	10		Ac
	<i>Eleusine indica</i>	2	1.67		Ac
	<i>Eriochloa pacifica</i>	1	0.83		Na
	<i>Panicum dichotomiflorum</i>	1	0.83		Na
	<i>Panicum maximum</i>	1	0.83		Es
	<i>Paspalum conjugatum</i>	2	1.67		NaQ
	Unknown	9	7.5		
	<i>Urochloa multiculma</i>	2	1.67		En
	<i>Urochloa mutica</i>	3	2.5		Es
	Polygonaceae	<i>Polygonum opelousanum</i>	1	0.83	4
Portulacaceae	<i>Portulaca oleracea</i>	1	0.83	4	NaQ
Rosaceae	<i>Rubus niveus</i>	1	0.83	1	Es
Rutaceae	<i>Zanthoxylum fagara</i>	8	6.67	2	Na
Solanaceae	<i>Physalis pubescens</i>	3	2.5	6	Na
	<i>Solanum americanum</i>	1	0.83	6	NaQ
Verbenaceae	<i>Clerodendrum molle</i>	2	1.67	2	Na
	<i>Stachytarpheta cayennensis</i>	1	0.83	3	NaQ

En, endemic; EnQ, questionably endemic; Na, native; NaQ, questionably native; Es, escaped; Ac, accidentally introduced.

\*The number of dung piles in which seeds of each species were recorded as a percentage of the total number of dung piles (120).

pattern of treatment effects. The GLMMs were fitted with a binomial distribution and logit link function and binomial totals of 10 reflecting the total number of seeds planted per pot (or group of pots for *H. mancinella*). For within-species analyses, treatment was included as fixed effect and block was

assigned as a random effect. In the test for an effect of origin, treatment, origin and their interactions were assigned as fixed effects and species as the random effect. We used Wald and *F* statistics to test for treatment effects on germination at the level of  $P = 0.05$ .

**Table 2** Fruit and seed characteristics for plant species included in germination trials (standard errors in parentheses).

Species	Mean fruit length (mm)	Mean fruit weight (g)	No. of seeds per fruit	Seed length (mm)
<i>Hippomane mancinella</i>	29.0 (0.9)	7.7 (0.8)	5 (1)	25.0 (0.9)*
<i>Passiflora edulis</i>	71.0 (3.8)	76.7 (4.7)	284 (15)	5.3 (0.1)
<i>Opuntia echios</i>	65.4 (2.1)	62.1 (2.9)	64 (3)	2.6 (0.1)
<i>Psidium galapageium</i>	16.8 (0.8)	2.7 (0.3)	4 (1)	5.0 (0.1)
<i>Psidium guajava</i>	48.4 (1.3)	59.8 (4.0)	226 (10)	2.4 (0.1)

\*Nut length.

## RESULTS

### How many seeds from which species do tortoises disperse?

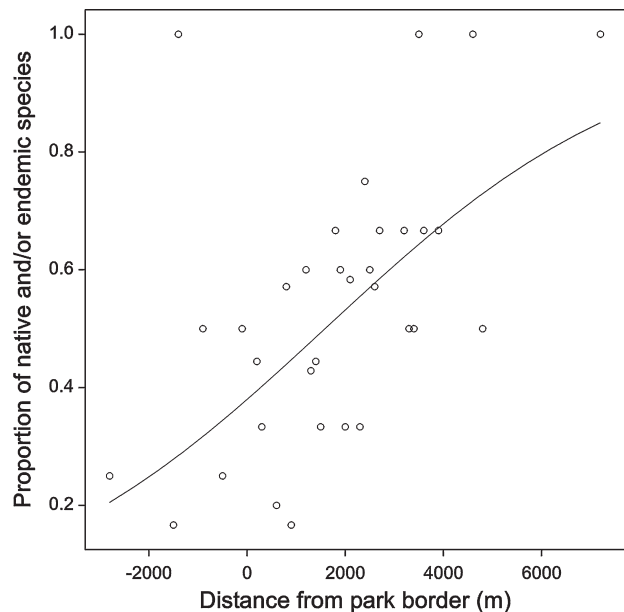
In the sample of 120 dung piles collected over 15 months we found an average of 464 (SE 95) seeds (excluding grass seeds) per pile; however, the statistical distribution of seeds per pile was highly variable and skewed. As a consequence, the median number of seeds per dung pile was only 122, and 28% of dung piles contained < 40 seeds, including a single dung pile with no seeds. These non-grass seeds came from at least 45 species, of which 11 species have been introduced to the Galápagos (Table 1). The number of species per dung pile (mean 2.8, SE 0.17; median 2, range 0–9) was modest and much less variable and skewed than the quantity of seeds. Introduced species overwhelmingly dominated the total volume of seeds dispersed by Galápagos tortoises. Throughout our sample, irrespective of location, an average dung pile contained 336 (SE 98) seeds from introduced species, compared with 64 (SE 46) from endemic species, and 7 (SE 4) from native non-endemic species. Four species of seed occurred in more than 25% of dung piles, of which three species are introduced (*Passiflora edulis*, *Psidium guajava*, *Sida rhombifolia*) and one is endemic (*Psidium galapageium*). Dung piles with higher numbers of individual seeds did not necessarily contain the greatest number of species. Twelve dung piles contained more than 1000 seeds from a single species (*P. guajava* 10 piles, *Passiflora edulis* 1 pile, and *O. echios* 1 pile). Sixteen species were recorded only once. The 45 non-grass species represent 21 families. Poaceae was the most represented family with 14 species identified, followed by Asteraceae (five species) and Cyperaceae (four species).

### What proportions of native versus introduced species are dispersed by tortoises in farm land and national park land?

Seeds from dung piles in farmland were dominated by introduced species, which comprised nearly 76% of seed occurrences, while in the park, endemic + native and introduced species occurred in approximately equal proportions (Table 3). The proportion of native/endemic species per dung pile increases as one moves from areas within agricultural land (negative distance values in Fig. 2) to areas within the park

**Table 3** Percentage occurrence of seeds by origin for dung piles of tortoises (*Chelonoidis nigra*) found in farmland and in the Galápagos National Park on the island of Santa Cruz.

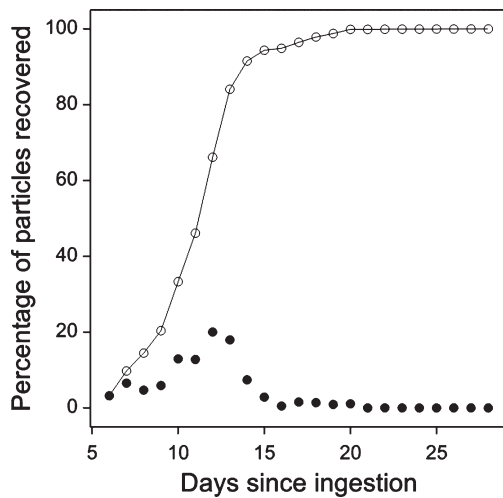
Origin	Park (n = 15)	Farm (n = 105)
Endemic	21.5	3.4
Native	26.9	20.7
Introduced	50.7	75.9

**Figure 2** Trend in the proportion of native/endemic plant species versus introduced plant species per tortoise (*Chelonoidis nigra*) dung pile (from a sample of 120 dung piles) with distance from the Galápagos National Park border (negative values on the x-axis indicate distances inside the agriculture zone, i.e. distance outside the national park).

(positive values in Fig. 2) (logistic regression: deviance ratio<sub>(1,38)</sub> = 16.90,  $P < 0.001$ ) (Fig. 2).

### How far do tortoises move seeds?

Digesta retention time ranged from 6 to 28 days, with a mode of 12 days (Fig. 3). The mean retention time was also 12 days. Telemetry data revealed that tortoise movement was characterized by prolonged sedentary phases followed by rapid

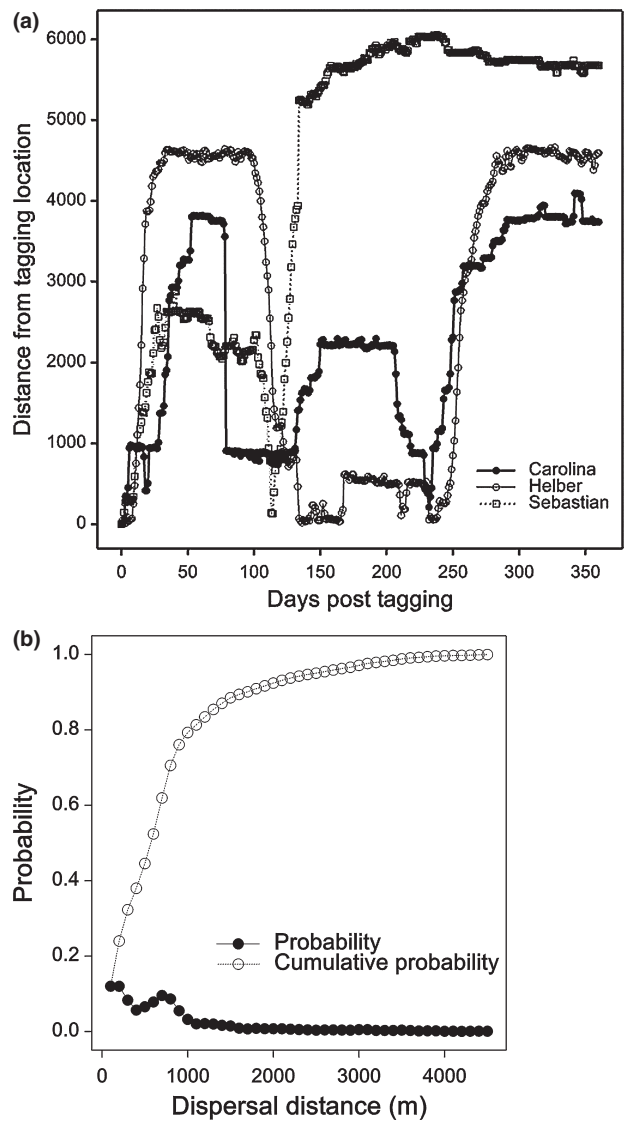


**Figure 3** The percentage of inert particles recovered following ingestion by Galápagos tortoises (*Chelonoidis nigra*) in the Galápagos National Park captive breeding facility. Closed circles represent the percentage of total seeds recovered per day, and open circles represent the cumulative percentage of seeds recovered.

displacements (Fig. 4a). Tortoise displacement varied considerably over the range of estimated digesta retention times, from < 1-m displacements over 6 days to 4355 m over 28 days. Over the shortest digesta retention time (6 days), mean dispersal distance by tortoises was 245 m with a maximum of 2610 m. Over the mean digesta retention time (12 days) the mean and maximum distances moved were 394 and 3262 m, respectively, with 50% of displacements > 200 m, 10% > 1000 m and 5% > 1700 m. One per cent of displacements over 12 days were > 2800 m. Thus, despite prolonged sedentary periods, relatively long distance displacements were the norm; for example 81.6% of all displacements over 12-day intervals were > 50 m. The estimated seed dispersal kernel (Fig. 4b), which incorporates the probability of seed deposition by digesta retention time, illustrates that long-distance seed dispersal by tortoises is not a rare event, but rather occurs on a regular basis; for example, we estimate that over 47% of ingested seeds are dispersed > 500 m from the parent plant, and 3% are expected to travel beyond 3000 m.

### Does tortoise ingestion and processing influence the success of seed germination?

We found no consistent pattern in treatment effects on seed germination success when species data were analysed individually (Table 4). For three species (*Psidium guajava*, *O. echios* and *P. galapageium*) treatment did not influence germination success. In the case of *Passiflora edulis*, treatment effects were highly significant (Table 4), driven by the extremely low germination success for treatment F, and high success for seeds under treatment WF (Table 4). Significantly different treatment effects were also found for germination success in *H. mancinella* (Table 4), with mean germination success for both 'washed' treatments (WF and WD), higher than treatments D and F.



**Figure 4** (a) Linear displacements from tagging location over time of three GPS tagged Galápagos tortoises (*Chelonoidis nigra*) reveal the propensity of tortoises for rapid long-distance movements, during which they are capable of moving ingested seeds far from the parent plant. We have plotted the data for only three out of the 14 tagged individuals for clarity of presentation (names of each individual are provided in the legend). (b) Dispersal kernel, with both probability and cumulative probability of dispersal distance for seeds dispersed by tortoises based on estimated travel distances and the number of seeds dispersed by estimated digesta retention times.

The GLMM on the combined dataset did not support our hypothesis that tortoise processing would improve germination success (Wald = 5.03, n.d.f. = 3,  $F = 1.68$ , d.d.f. = 101.0,  $P = 0.117$ ), nor was there evidence that origin influenced germination success any more than did species (Wald = 0.58, n.d.f. = 1,  $F = 0.58$ , d.d.f. = 103.0,  $P = 0.503$ ). The interaction term (origin  $\times$  treatment) was significant (Wald = 8.41, n.d.f. = 3,  $F = 2.80$ , d.d.f. = 101,  $P = 0.044$ ); however, this appeared to be driven by the very high germination success of

**Table 4** Generalized linear mixed model (GLMM) output: significance tests of treatment effects on germination success. The GLMM used a binomial distribution and logit link function, and included number of germinations per pot as the response variate, treatment as a fixed factor, block as a random factor and 10 (number of seeds planted per pot) as the binomial total.

Species	Origin	Wald	n.d.f.	<i>F</i>	d.d.f.	<i>P</i>	Treatment means			
							Dung	Washed dung	Washed fruit	Fruit
<i>Passiflora edulis</i>	Es	27.62	3	9.21	9	0.0004	4.8 (0.8)	5 (1)	7.8 (0.5)	1.0 (0.4)
<i>Psidium guajava</i>	Es	6.13	3	2.04	28	0.131	2.6 (0.8)	3.9 (0.5)	4.3 (0.3)	4.4 (0.4)
<i>Hippomane mancinella</i>	Na	19.36	3	6.45	9	0.013	6.0 (0.9)	8.5 (0.6)	7.5 (0.3)	5.0 (0.4)
<i>Opuntia echios</i>	En	3.94	3	1.31	28	0.293	4.3 (0.8)	4.4 (0.3)	2.9 (0.6)	3.5 (0.6)
<i>Psidium galapageium</i>	En	1.39	3	0.46	9	0.715	5.5 (0.7)	4.5 (0.9)	4 (1)	6 (2)

En, endemic; Es, escaped; Na, native.

Treatments are as follows: Dung – seeds ingested by Galápagos tortoises (*Chelonoidis nigra*) planted in the dung pile in which they were found; Washed dung – seeds from tortoise dung that were washed in rainwater; Washed fruit – seeds taken from fallen fruit and washed in rainwater; Fruit – seeds taken directly from fruit and planted in pulp. Values in parentheses are standard errors of treatment means.

n.d.f., numerator degrees of freedom for an approximated *F* distribution; d.d.f., denominator degrees of freedom for an approximated *F* distribution.

the WF treatment for *P. edulis* rather than by consistent differences in germination success across treatments.

## DISCUSSION

### Number of seeds dispersed

Several recent studies have shown that small and medium-sized tortoises can be prolific seed dispersers (Birkhead *et al.*, 2005; Guzman & Stevenson, 2008; Jerolimski *et al.*, 2009). Aldabra giant tortoises also disperse large numbers of seeds and may have been responsible for introducing novel plant species to Aldabra and the Seychelles when tortoises first colonized these islands as a result of accidental oceanic voyages from Madagascar (Hnatiuk, 1978; Hamilton & Coe, 1982). With the exception of their role as dispersers of tomatoes (Rick & Bowman, 1961), reports of Galápagos tortoises as seed dispersers have been largely anecdotal until now. Our analysis of 120 tortoise dung piles has increased the estimates of species dispersed by Galápagos tortoises cited by Heleno *et al.* (2011) by over sixfold to a total of at least 45, with some seeds still awaiting identification. In their review, Heleno *et al.* (2011) found that of all the Galápagos terrestrial and avian fauna, only two species are known to disperse more than 10 species of seeds: the black rat, *Rattus rattus* (16 species), and the small ground finch, *Geospiza fuliginosa* (13 species); and there are records of only 26 animal species dispersing any seeds at all. Most likely this does not indicate the extent of zoochory on the Galápagos, but rather the dearth of information on the subject. Among birds, Darwin's finches may be significant dispersers, despite their primary role as seed predators. Eight of nine species of Darwin's finches studied by Guerrero & Tye (2009) disperse seeds either through regurgitation or defecation or both, and 23% of faecal samples in their study contained intact seeds, of which 50% were viable. Other potentially important seed-dispersing reptiles include lava lizards (Schluter, 1984) and land iguanas (Carpenter, 1969), although few data are available (Heleno *et al.*, 2011). It is likely that, given their size, generalist

diet (Cayot, 1987) and relatively benign food processing (Bjorndal, 1989; Hailey, 1997), Galápagos tortoises are the most prolific native vertebrate seed dispersers on the archipelago.

It is important to recognize that the number of seeds dispersed is but one aspect of seed dispersal effectiveness; the quality of dispersal also matters, including dispersal into appropriate environments for germination, growth and subsequent survival as reproductive adults (Schupp, 1993, 1995). High seed densities in dung piles may even be detrimental to germination and seedling survival because of density-dependent mortality effects (e.g. Harms *et al.*, 2000). A comprehensive *in situ* study that quantifies recruitment and subsequent fitness of adult plants over a range of dispersal scenarios is necessary to understand the role of tortoise dispersal in plant dynamics on the Galápagos.

In recent history, the number of seeds dispersed by non-native vertebrates may rival or exceed that of Galápagos tortoises. Goats (*Capra hircus*), cattle (*Bos taurus*) and donkeys (*Equus asinus*) are known to be important seed dispersers in arid and semi-arid environments, often of invasive species (Constible *et al.*, 2005; Baraza & Valiente-Banuet, 2008; de la Vega & Godínez-Alvarez, 2010; Vignolio & Fernandez, 2010), and all may play or have played an important role in seed dispersal on the Galápagos Islands where they occur (Thornton, 1971). However, successful eradication programmes (Campbell & Donlan, 2005; Carrion *et al.*, 2007) have either eliminated or greatly reduced dispersal by these species.

### Distribution of seeds of native/endemic versus introduced species by land use

We have shown that Galápagos tortoises disperse large numbers of seeds from introduced plants, particularly in agricultural land. Consumption of fruits of these species, coupled with long-distance movements, may make tortoises formidable allies for invasive species, allowing them to spread rapidly from agricultural lands into the GNP. Importantly, however, tortoises also vigorously disperse native species,



possibly enhancing their re-establishment in degraded habitats. The trade-off between tortoises as agents of invasion and/or restoration will depend on many factors, including the quantity and quality of dispersal, the competitive dynamics among species, tortoise diet and ranging patterns over time, differential impacts of tortoise processing of seeds and the availability of native versus introduced fruits.

### Tortoise transport of seeds

Seed dispersal distance is a strong determinant of the structure, dynamics and evolution of plant populations (Nathan & Muller-Landau, 2000; Levey *et al.*, 2002; Levin *et al.*, 2003). Dispersal may help germination and survival as it takes seeds away from density-dependent mortality factors such as predators and pathogens (Janzen, 1970; Connell, 1971), reduces kin competition (Howe & Smallwood, 1982) and allows for bet hedging in heterogeneous environments such that the likelihood of finding suitable germination sites will increase with increasing rates of dispersal (Levin *et al.*, 2003).

It is likely then that tortoise seed dispersal plays a strong role in vegetation dynamics, because not only do tortoises disperse a large diversity and quantity of seeds, but they frequently disperse these seeds over long distances. For example, our estimates suggest that tortoises may disperse seeds more than 4 km from the parent plant, and regularly disperse them over 100 m, which was used as general definition of 'long-distance dispersal' by Cain *et al.* (2000). Our digesta retention data were obtained from semi-captive tortoises fed regularly, and as such should be considered a first approximation of digesta retention times for wild tortoises, which may be considerably longer (Hansen *et al.*, 2008), potentially increasing our estimates of seed dispersal distances. The dispersal distances we obtained dwarf by one to three orders of magnitude those for herbs dispersed by wind, ballistic and non-specialized means cited in a review paper by Willson (1993) and for desert annuals recorded by Venable *et al.* (2008).

Among potential animal dispersers, few data are available on movements for terrestrial and avian species on the Galápagos, although short retention times and allometric scaling suggest that smaller vertebrate birds and terrestrial reptiles should disperse seeds over comparatively short distances (Sutherland *et al.*, 2000), as supported by several field studies on the Galápagos. For example, the endemic rodent (*Nesoryzomys swarthi*) may move up to 528 m between extremes of its home range (Harris & Macdonald, 2007); however, it is unlikely that these animals move over such large distances during digesta retention time, which in rats is usually between 22 and 25 h (Luick & Penner, 1991). Galápagos land iguanas move up to 10 km into the caldera on Fernandina Island for egg laying (Werner, 1983), thus may transport seeds over long distances during these migrations; however, gut retention time and routine movements are likely to be short compared with those of tortoises.

The importance of long-distance dispersal in ecology and conservation is widely accepted because of its impacts on

population structure, the dynamics of native plant migration and invasions of non-natives, the maintenance of metapopulations and regional survival of plant species (Clark *et al.*, 1999; Myers *et al.*, 2004; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005; Nathan, 2006). Undoubtedly, tortoise-mediated dispersal plays a role in these processes on the Galápagos; however, distance moved is only one component of dispersal effectiveness, and data on other factors influencing seed abundance, establishment, survival and lifetime reproductive success are necessary if the dispersal effectiveness of tortoises is to be adequately evaluated.

Two important caveats must be considered when interpreting these results. First, our estimates of digesta retention times for Galápagos tortoises used here and published by Sadeghayobi *et al.* (2011) were obtained from a study of captive tortoises rather than wild tortoises. Captive tortoises were fed on a regular basis and therefore did not experience the variation in food availability, quality and species composition experienced by wild tortoises. Therefore the digesta retention times we used to estimate seed dispersal distances should be seen as crude estimates of those of wild tortoises. The second caveat is that most very long dispersal events (> 200 m) were oriented along the elevation gradient of Santa Cruz (Fig. 1) rather than laterally and parallel to elevation contours. In these cases, seeds are transported across vegetation zones from arid, through transition vegetation and into the humid highlands, and vice versa, which may compromise seed germination (or subsequent establishment) success, compared to lateral dispersal.

### The influence of tortoise digestion on germination

Following the recommendations of Samuels & Levey (2005), our germination trials were designed to test whether digesta retention time, the presence of dung in the substrate and the presence of fruit pulp influenced germination patterns of the five focal species. Our results did not support the prediction that tortoise digestion and defecation improves seed germination success over seeds that are not exposed to tortoise processing. This is in contrast to the early work of Rick & Bowman (1961), who found that tortoise digestion improved the germination of Galápagos tomatoes. Similarly, in an unpublished report, Estupiñán & Mauchamp (1995) recorded an improvement in the germination success of *Opuntia* spp. following tortoise ingestion. In the only other study of the impacts of giant tortoises on germination that we know of, Hansen *et al.* (2008) found that Aldabra tortoise digesta retention time decreased germination success for *Syzygium mamillatum*, with success inversely proportional to digesta retention time.

### CONCLUSIONS

In response to the questions and predictions posed at the beginning of this article, our study supports the notions that: (1) Galápagos tortoises disperse large numbers of seeds from a wide variety of plant species of both native and introduced species; (2) the proportion of seeds from introduced species found in

dung piles decreases as distance into the GNP, and away from agricultural land, increases; and (3) Galápagos tortoises frequently move seeds over relatively large distances due to a combination of their considerable mobility and long digesta retention times. However, our fourth prediction was not supported, because ingestion and defecation of seeds by Galápagos tortoises did not improve germination, but nor did they suppress germination success. If it matters 'who defecates what where', as argued by Janzen (1986), then we have shown that giant tortoises are likely to have an important impact on the vegetation of the Galápagos although more extensive research is needed to quantify both the quantity and quality of tortoise seed dispersal on the dynamics of Galápagos' plant communities.

## ACKNOWLEDGEMENTS

This study was made possible by the excellent collaborative spirit of the GNP and the Charles Darwin Foundation (CDF). In particular, Edwin Naula of the GNP provided permission to conduct the study, and Washington Tapia gave administrative and technical support as well as friendship and encouragement. Mark Gardner of CDF facilitated all aspects of the study. James Gibbs freely shared his knowledge of Galápagos tortoises. e-obs GmbH provided excellent telemetry equipment. Funding was provided by the Max Planck Institute for Ornithology, National Geographic Society Committee for Research and Exploration, the Swiss Friends of Galápagos, the Galápagos Conservation Trust, and The Lonesome George & Company. C.Y. was supported by the National Science Foundation (NSF) under award no. 1003221. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the NSF. Roger Payne and the Genstat team provided free statistical software and advice. Dennis Hansen, James Gibbs, Ruben Heleno, Doug Levey and two anonymous referees provided valuable comments on earlier versions of the manuscript.

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## BIOSKETCH

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Author contributions: S.B. and M.W. conceived the ideas; S.B., F.C., A.G., M.S., E.S. and P.J. collected the data; S.B. and C.Y. analysed the data; S.B. wrote the paper.

Editor: Anna Traveset

This Special Issue arose from contributions presented at the symposium 'Seed Dispersal on Islands', which was part of the 5th International Frugivory and Seed Dispersal conference that took place from 13 to 18 June 2010 in Montpellier, France (<http://fsd2010.org>), and also includes contributions arising from several other relevant presentations at this conference.