

Article

Small size does not restrain frugivory and seed dispersal across the evolutionary radiation of Galápagos lava lizards

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Abstract

Frugivory in lizards is often assumed to be constrained by body size; only large individuals are considered capable of consuming fruits, with the potential of acting as seed dispersers. However, only one previous study has tested the correlation of frugivory with body and head size at an archipelago scale across closely related species. All nine lava lizards (*Microlophus* spp.) were studied on the eleven largest Galápagos islands from 2010 to 2016 to investigate whether frugivory is related to body and head size. We also tested whether fruit abundance influences fruit consumption and explored the effect of seed ingestion on seedling emergence time and percentage. Our results showed that across islands, lava lizards varied considerably in size (64–102 mm in mean snout-vent length) and level of frugivory (1–23%, i.e., percentage of droppings with seeds). However, level of frugivory was only weakly affected by size as fruit consumption was also common among small lizards. Lava lizards consumed fruits throughout the year and factors other than fruit abundance may be more important drivers of fruit selection (e.g., fruit size, energy content of pulp). From 2,530 droppings, 1,714 seeds of at least 61 plant species were identified, 76% of the species being native to the Galápagos. Most seeds (91%) showed no external structural damage. Seedling emergence time (44 versus 118 days) and percentage (20% versus 12%) were enhanced for lizard-ingested seeds compared to control (uningested) fruits. De-pulping by lizards (i.e., removal of pulp with potential germination inhibitors) might increase the chances that at least some seeds find suitable recruitment conditions. We concluded that lizards are important seed dispersers throughout the year and across the whole archipelago, regardless of body size.

Key words: *Microlophus*, oceanic islands, plant–animal interactions, seed disperser size, seed dispersal effectiveness, seedling emergence

Lizards of different evolutionary lineages consume fruits on a regular basis (Olesen and Valido 2003; Traveset et al. 2016; Neghme et al. 2017), but the ecological and evolutionary drivers of such habit in these animals remain poorly understood. Body size has been considered a strong correlate of frugivory in lizards (Van Damme 1999; Herrel et al. 2004a). It is often assumed that large body and head size is required for lizards to efficiently process plant material (Pough 1973; Cooper Jr and Vitt 2002). Large lizards have more diverse prey-size range than smaller ones and are better adapted to coping with more generalist diets including plant material (Meiri 2008).

Frugivory by lizards is particularly common on islands. Insular lizards are more likely to consume fruits, since population densities tend to be higher whereas interspecific competition and predator pressure tend to be lower than on the mainland (Olesen and Valido 2003; Novosolov et al. 2018). This either allows or forces insular lizards to expand their trophic niche and explore novel food resources such as fruits (i.e., undergoing an “interaction release”, sensu Traveset et al. 2015). However, it is not clear whether such interaction release in lizards occurs regardless of their body sizes, especially on tropical islands where these animals are active year-round and have continuous access to fruit (Nogales et al. 2016). Specifically, only one study explored variation in lizard frugivory within a clade of closely related species showing a strong correlation between body size and frugivory (*Anolis* species in Jamaica; Herrel et al. 2004a).

The Galápagos islands host nine species of lava lizards (*Microlophus* spp., Tropiduridae). They constitute a remarkable vertebrate island radiation with only one species per island including seven single-island endemics (Benavides et al. 2009). Evolutionary radiations like this are valuable systems in our efforts to understand whether species interactions, including their food preferences, are the cause or the consequence of habitat-dependent shifts of morphological features (Calsbeek and Irschick 2007). Lava lizards are very common in the arid lowland of the Galápagos (Tanner and Perry 2007), where access to animal prey (arthropods) and water is often limited (Schluter 1984). Lizards on three Galápagos islands (Santa Cruz, San Cristóbal, Pinta) are known to consume fruits (Schluter 1984; Heleno et al. 2013). However, we do not know if this is a general pattern across both the entire lizard radiation and the archipelago. Variation in frugivory in relation to lizard size, and if there are seasonal differences in frugivory also remain unexplored. The latter could be expected since fruit availability has seasonal variations, and it is important to know whether fruit abundance is a driver of fruit selection (Pérez-Mellado and Corti 1993).

Many frugivores provide a highly valuable ecosystem service that may impact long-term vegetation dynamics due to their role as potential seed dispersers (Howe and Westley 1988; Traveset et al. 2013). Frugivores can reduce germination time by both removing fruit pulp, which often contains chemical inhibitors, and weakening physical barriers to germination, e.g. scarification (Traveset et al. 2008). Nevertheless, the effect of disperser gut passage on germination varies depending on both animal and plant identity (Wotton 2002; Nogales et al. 2017). Therefore, germination trials are needed to evaluate the viability of seeds after gut passage and the effect on germination time, in order to understand the ecological role of lizards towards plants.

Our aims were to assess at an archipelago level, whether (1) frugivory is related to body and head size; and whether (2) lizards consume fruits in proportion to the local fruit abundance. Lastly, (3) the effect of lizard ingestion on seedling emergence time and percentage was also investigated.

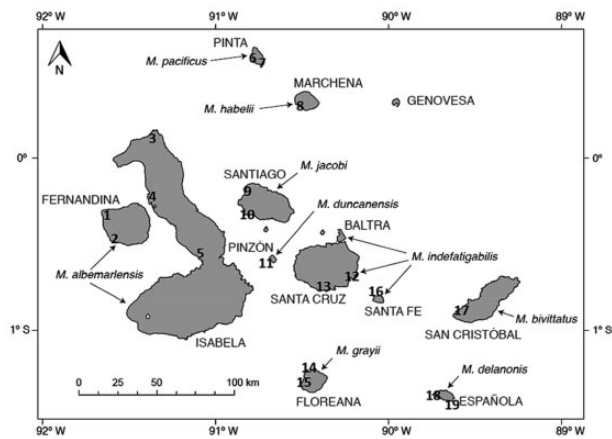


Figure 1. Distribution of the nine species of lava lizards across the Galápagos archipelago and location of the sites sampled on each island. Fernandina: 1–Cabo Douglas, 2–Cabo Hammond; Isabela: 3–Punta Albemarle, 4–Playa Tortuga Negra, 5–Bahía Elizabeth; Pinta: 6–*Barrancos, 7–Playa del Muerto; Marchena: 8–Playa Negra; Santiago: 9–Bahía James, 10–Bahía Ladilla; Pinzón: 11–Bahía de Pinzón; Santa Cruz: 12–Garrapatero, 13–Tortuga Bay; Floreana: 14–*Punta Cormorant, 15–Puerto Velazco Ibarra; Santa Fe: 16–Bahía de Santa Fe; San Cristóbal: 17–Punta Carola; Española: 18–Playa Manzanillo, 19–*Punta Cevallos. Sites marked with an asterisk were not included in the analysis of frugivory and body size due to a lack of biometric data.

Materials and Methods

Study site

This study was carried out on all main Galápagos islands ($n = 11$; Figure 1) with lava lizards (Table 1). Sampling was conducted in the arid zone (c. 0–300 m a.s.l.) where lizards are common (Tanner and Perry 2007). This zone is the largest (c. 60% of total land area) and most biodiverse of the archipelago (Guézou et al. 2010). This habitat is dominated by evergreen drought-tolerant shrubs, e.g., *Croton scouleri*, and fleshy-fruited species such as *Opuntia* spp., *Cordia leucophlyctis*, *C. lutea*, *Lantana peduncularis*, *Tournefortia psilostachya* and *Scutia spicata*. The arid zone becomes increasingly dry during the cold/dry season (June to December), until the first rains. Rainfall is extremely unpredictable spatially, varying considerably among islands (Trueman and d’Ozouville 2010). Arthropod abundance and activity and fruit production are highest in the hot/wet season (January–May) (Schluter 1984; Heleno et al. 2013).

Lizard body and head size

Between 2014 and 2015, ca. 30 adult individuals (15 males and 15 females whenever possible), from each island were captured by hand with noose poles. Snout–vent length (hereafter SVL), gape width (horizontal distance between commissural points), and skull length (rear of parietal bone to tip of upper jaw) were all measured using a digital calliper (precision 0.01 mm). This was normally performed by one observer (MN) in order to minimise potential biases. After measuring lizards, they were immediately released at the same place where they were captured.

Differences in body size (SVL) and head size (gape width and skull length) among islands were tested using Kruskal–Wallis analyses followed by Dunn’s *post-hoc* tests. Values from both sexes were pooled. Individuals from Santa Fe Island were not included in the analysis as only two individuals were captured (see sample sizes in Table 2).

Table 1. Characterisation of lizard droppings collected across the eleven largest Galápagos islands between 2010 and 2016

Species	Sites sampled (<i>n</i>)	Droppings analysed (<i>n</i>)	Droppings with seeds (%)	Seeds (<i>n</i>)	Seeds/Dropping (%)	Intact seeds (%)	Plant species dispersed (<i>n</i>)
<i>Microlophus albemarlensis</i>	2	195	6.2	58	29.7	96.6	5
	3	189	7.9	21	11.1	100.0	4
<i>Microlophus bivittatus</i>	1	97	1.0	1	1.0	100.0	1
<i>Microlophus delanonis</i>	2	235	14.9	109	46.4	77.1	14
<i>Microlophus duncanensis</i>	1	94	3.2	3	3.2	66.7	1
<i>Microlophus grayii</i>	2	97	4.1	7	7.2	71.4	2
<i>Microlophus habelii</i>	1	165	15.8	55	33.3	83.6	7
<i>Microlophus indefatigabilis</i>	2	137	23.4	79	57.7	84.8	9
	1	125	4.8	9	7.2	77.8	4
<i>Microlophus jacobi</i>	2	192	12.0	50	26.0	90.0	6
<i>Microlophus pacificus</i>	2	515	13.4	340	66.0	90.9	15
Total	19	2041		732			28

Table 2. Sample sizes for the analyses performed to test whether: 1) lizard head and body size differ among islands (Kruskall–Wallis test); 2) body size influences level of frugivory (GLMM); 3) lizards eat fruit in proportion to its availability in the environment (Chi-squared test); and 4) seedling emergence time and percentage vary between treatments (GLM)

Species	Island	Kruskall–Wallis test		GLMM	Chi-squared test	GLM
		Females (<i>n</i>)	Males (<i>n</i>)	Sites (<i>n</i>)	Droppings (<i>n</i>)	Seeds in droppings (<i>n</i>)
<i>M. albemarlensis</i>	Fernandina	18	13	2		
	Isabela	18	16	3		
<i>M. bivittatus</i>	San Cristóbal	15	20	1	167	158
<i>M. delanonis</i>	Española	15	15	1		
<i>M. duncanensis</i>	Pinzón	15	15	1		
<i>M. grayii</i>	Floreana	13	16	1		
<i>M. habelii</i>	Marchena	15	15	1		
<i>M. indefatigabilis</i>	Santa Cruz	24	27	2	322	278
	Santa Fe	1	1	1		
<i>M. jacobi</i>	Santiago	13	16	2		
<i>M. pacificus</i>	Pinta	16	12	1		

Frugivory across islands

To compare frugivory across the archipelago, 11 islands were visited at least once from 2010 to 2016 between February and May. The number of sites sampled per island was selected according to island size (Figure 1, Table 1) and accessibility. A total of 2,041 lizard droppings were collected from the ground by five observers within an area of at least 1 km² per site. When an island was visited more than once, the same sites were sampled each time. Lava lizard droppings are long with round tips and easily distinguishable from those of the two coexisting families (Gekkonidae, Iguanidae). Droppings were dissected under a stereomicroscope in Petri dishes and all seeds and seed remains extracted, classified as either damaged or visually intact, and identified to species level using a reference collection at the Charles Darwin Research Station (CDRS) (Jaramillo and Heleno 2012). Results are expressed as the percentage of droppings with seeds, i.e. percentage Frequency of Occurrence (% FO), hereafter used as a proxy of frugivory level. This measure was selected as it provides a more realistic estimate of the real recruitment probability of dispersed seeds, while metrics based on the number of seeds are likely biased by high post-dispersal density-dependent mortality of many small seeds contained in a single dropping (López et al. 2016; Correia et al. 2017). Because our sampling included both fresh and old droppings, we experimentally estimated their persistence in the environment under natural conditions. Our sampling provided a

characterisation of the frugivorous activity during at least the previous seven weeks (see [Supplementary Material](#), data 1).

To examine if frugivory level is related to lizard body and head size across the different islands, three generalised linear mixed models (GLMMs) with a binomial distribution were built. Models included SVL, gape width or skull length (mean values per site) as explanatory variables. To account for non-independence in data structure (sampling the same sites in different years), the models included two random effects: site nested within island and year of sampling. Two additional models were constructed to examine the effect of head size relative to body size using the interaction ‘SVL*gape width’ or ‘SVL*skull length’ and including SVL as a third random effect to account for dependence among biometric data. The three biometric variables were highly correlated (all $P \leq 0.01$). Three of 19 sampling sites were excluded from the GLMMs because we were unable to collect biometric lizard measurements (Figure 1). In order to test whether the current lava lizard phylogeny (Benavides et al. 2009) could explain the variation in frugivory level, we used Pagel’s λ index as a measure of phylogenetic signal. The value of lambda (λ) ranges between 0 (the trait structure is not influenced by phylogeny) and 1 (the trait follows a Brownian Motion model). The lower and upper bounds of λ indicate which of the two scenarios is most likely. Correlation between frugivory level and body size was also tested using phylogenetic independent contrasts.

Fruit consumption and availability over a one-year period

Two large central islands (Santa Cruz and San Cristóbal) were visited monthly from March 2010 to February 2011. Droppings were collected along two randomly selected 50 × 2 m linear transects at four locations: Tortuga Bay (0° 45′ 03.449″ S 90° 19′ 26.566″ W) and the CDRS (0° 44′ 17.430″ S 90° 18′ 06.347″ W) on Santa Cruz; and west Galapaguera (0° 54′ 49.507″ S 89° 26′ 17.466″ W) and east Galapaguera (0° 54′ 51.354″ S 89° 26′ 08.394″ W) on San Cristóbal. A total of 489 droppings were found and analysed as described above. At each location, the abundance of fruits was estimated by monthly counts of all ripe fleshy and dry fruits within 1 m on either side of a fixed 50 m linear transect initially selected at random.

To test whether lizards ate fruits in proportion to their availability in the environment, Chi-squared tests were performed between relative fruit abundance per month and site (expected) and the occurrence of seeds in lizard droppings in that month and site (observed) (Table 2).

Effects of seed ingestion on seedling emergence

In order to determine the role of lizards as seed dispersers, germination trials were setup in April 2011, testing the effect of three treatments: (1) seeds from the 17 most common plant species retrieved from droppings collected on Santa Cruz ($n=278$ seeds) and San Cristóbal ($n=158$); (2) manually de-pulped seeds (hereafter de-pulped, $n=799$), from the same plant species to simulate the effect of internal processing by the lizards' digestive tract; and (3) control fruits also from the same plant species but without de-pulping ($n=930$). Fruits for treatments 2 and 3 were collected from at least ten individuals of each species on Santa Cruz, following the biosafety rules of the Galápagos National Park. Approximately 50 seeds per species and treatment were sown individually in 40 cm³ (3.5 × 2.5 × 4.5 cm) plastic plant pots filled with farmland soil, volcanic lapilli and peat (2: 1: 1 ratio), randomly arranged in space and under the same conditions at the greenhouse of the CDRS in Puerto Ayora (Santa Cruz). Seeds were watered regularly every day to keep soil moisture as constant as possible. Because the life-span of buried seeds can exceed 1 year (Bewley and Black 1982), seedling emergence was recorded for two consecutive years, every other day during the first year and once a week during the second year. Results are expressed as seedling emergence time (days) per species (a proxy for germination time, which cannot be directly measured as seeds are buried), and percentage of seedling emergence per species (a proxy for germination percentage) (Robertson et al. 2006).

Differences in seedling emergence time and percentage between treatments were examined using generalised linear models (Poisson and binomial distribution, respectively), in this case including treatment and plant species as explanatory variables and pooling values from Santa Cruz and San Cristóbal. We also tested if the effect of treatment in seedling emergence time and percentage differed among plant species by including the interaction “treatment*plant species” (Table 2).

Analyses were conducted using the packages “dunn.test”, “Hmisc”, “lme4”, “r2glmm”, “geiger”, and “ape”, while plant-lizard seed dispersal networks were visualised using “bipartite” in R 3.3.1 (Dormann et al. 2008; R Core Team 2016). The support for each model was quantified by providing AIC weights. Values are mean ± SD.

Results

Body size and level of frugivory

Galápagos lizards varied across islands in body size (SVL $H_8 = 121.7$, $P < 0.001$), head size (gape width $H_8 = 80.1$; and skull length $H_8 = 113.5$; both $P < 0.001$; Table 3 and Additional Figure 1), and in the percentage of droppings with seeds (1–23%). However, variation in frugivory level was not significantly explained by differences in lizard size. The models with “SVL”, “skull length”, and “gape width” received no support from the data (Table 4).

Frugivory level showed no significant phylogenetic signal, i.e., the lambda value (0.44) differed from 1 ($P_{\lambda=1} = 0.03$). Even when using phylogenetically independent contrasts, frugivory level and lizard size were not correlated ($r^2 = 0.01$, $P = 0.762$).

Microlophus delanonis on Española was the largest of all lizards, being 33% in SVL, 27% in gape width and 34% in skull length larger than the smallest, *M. bivittatus* on San Cristóbal. However, despite its greater size, *M. delanonis* was only the third most frugivorous lizard (15% of the droppings with seed remains). Notably, the most frugivorous lizards, *M. indefatigabilis* on Santa Cruz (23% FO), and the least frugivorous, *M. bivittatus* on San Cristóbal (1% FO), were similar in size (Table 1, Supplementary Material Figure 1).

Fruit consumption and availability over a one-year period

Lizards consumed fruits throughout the year, with consumption peaking in May on Santa Cruz and in August and November on San Cristóbal (Supplementary Material, Table 1). The highest fruit abundance was recorded between March and June and the lowest from October to January on both islands (Supplementary Table 2). Lizards did not consume fruits proportionally to their availability in the environment (Figure 2; Tortuga Bay: $\chi^2_8 = 47.4$, $P < 0.001$; CDRS: $\chi^2_9 = 33.9$, $P < 0.001$; west Galapaguera: $\chi^2_{11} = 43.0$, $P < 0.001$; east Galapaguera: $\chi^2_{11} = 40.9$, $P < 0.001$). *Tournefortia psilostachya* was the most consumed species on Santa Cruz, and *L. camara* (introduced) and *Zanthoxylum fagara* the most consumed on San Cristóbal.

Effects of seed ingestion on seedling emergence

The vast majority of seeds (91%, $n=1,714$ total seeds) showed no external signs of structural damage. Lizards consumed fruits of at least 61 species, most of them native (76%), and 44% of these endemic to the Galápagos. Ten species were introduced into the archipelago, including the invasive *Rubus niveus*, *L. camara*, and *Psidium guajava*. The four most commonly dispersed plant species (*T. psilostachya*, *S. spicata*, *L. peduncularis*, and *L. camara*) were present in 50% of all droppings with seeds. Fleshy-fruits represented 52% and dry-fruits 48% of the dispersed species. The whole seed dispersal network, representing all fruit species dispersed by lizards is depicted in Figure 3. In order to allow a more direct comparison of the importance of each lizard population as seed disperser, a standardised network is provided in Supplementary Figure 2, based on a random selection of the same number of samples for all populations ($n=94$ droppings).

Twelve out of the 17 most common species retrieved from the droppings germinated in the greenhouse. On average, seeds from droppings (44 days ± 83 SD) and de-pulped seeds (42 ± 90) germinated earlier than control fruits (118 ± 168) ($Z = -10.7$ and

Table 3. Mean values \pm SD for snout–vent length (SVL), gape width and skull length of lizards (*Microlophus* spp.) and number of lizards captured on each island F = female, M = male, NA = not applicable.

Species	Island	SVL		Gape width		Skull length	
		F	M	F	M	F	M
<i>M. albemarlensis</i>	Fernandina	64.26 \pm 5.20	85.67 \pm 14.83	10.33 \pm 0.66	13.60 \pm 1.73	14.41 \pm 0.93	18.71 \pm 2.26
	Isabela	61.95 \pm 7.83	78.69 \pm 9.57	9.53 \pm 0.74	12.39 \pm 1.41	14.05 \pm 1.02	17.42 \pm 1.67
<i>M. bivittatus</i>	San Cristóbal	57.10 \pm 5.10	68.61 \pm 8.17	9.55 \pm 0.92	11.32 \pm 1.19	12.55 \pm 0.67	14.36 \pm 0.99
<i>M. delanonis</i>	Española	83.61 \pm 7.67	119.70 \pm 7.06	13.06 \pm 1.01	15.94 \pm 1.25	17.36 \pm 1.21	21.92 \pm 1.02
<i>M. duncanensis</i>	Pinzón	71.02 \pm 4.04	85.96 \pm 4.29	11.09 \pm 0.66	13.45 \pm 1.06	15.22 \pm 0.83	17.33 \pm 1.22
<i>M. grayii</i>	Floreana	70.37 \pm 4.19	88.02 \pm 9.16	11.33 \pm 0.74	13.44 \pm 1.09	15.50 \pm 0.68	18.53 \pm 1.40
<i>M. habelii</i>	Marchena	75.17 \pm 4.33	90.87 \pm 9.70	11.39 \pm 0.80	12.87 \pm 1.21	15.69 \pm 0.73	17.89 \pm 1.10
<i>M. indefatigabilis</i>	Santa Cruz	63.23 \pm 3.65	76.26 \pm 8.04	10.79 \pm 1.01	13.05 \pm 1.90	13.57 \pm 0.57	15.47 \pm 1.89
	Santa Fe	67.96 \pm NA	95.82 \pm NA	14.35 \pm NA	14.87 \pm NA	10.98 \pm NA	18.73 \pm NA
<i>M. jacobi</i>	Santiago	63.62 \pm 2.07	80.13 \pm 8.99	9.69 \pm 0.91	12.11 \pm 1.14	14.21 \pm 0.73	17.26 \pm 1.31
<i>M. pacificus</i>	Pinta	78.10 \pm 5.68	94.28 \pm 4.62	11.02 \pm 0.61	13.05 \pm 1.12	16.14 \pm 1.11	19.15 \pm 0.75

Table 4. Model selection summary of the five models constructed to explain variation in frequency of seeds in lizard droppings collected on the eleven largest Galápagos islands from 2010 to 2016. SVL is the snout-vent length, skull length is the distance from the back of the parietal bone to the tip of the upper jaw, and gape width is the horizontal distance between commissural points.

Model	K	logLik	AICc	Δ AIC	ω AIC
Null	4	-562.27	1132.56	0.00	0.378
SVL	5	-561.66	1133.36	0.79	0.254
Skull length	5	-561.97	1133.97	1.41	0.187
Gape width	5	-562.24	1134.51	1.94	0.143
Gape width*SVL	8	-562.08	1138.25	5.68	0.002
Skull length*SVL	8	-561.36	1138.81	6.24	0.017

$Z = -21.6$, respectively, $P < 0.001$). This effect of treatment varied among plant species and was significant for *Chiococca alba*, *T. psilostachya*, *T. pubescens*, and *T. rufo-sericea*. Overall, 25% of the seeds from the droppings and 28% of the de-pulped seeds germinated, compared with only 18% of those from the control treatment ($Z = 4.1$ and $Z = 5.6$, respectively, $P < 0.001$), and the effect of treatment did not vary across plant species, as denoted by the non-significant interaction “treatment*species”. No differences were observed between seeds from droppings and de-pulped seeds (Figure 4 and Supplementary Table 3).

Discussion

This study reveals that even small Galápagos lizards consume fruits. Thus, our findings do not support the general view that size is the strongest factor facilitating fruit consumption (Van Damme 1999; Cooper Jr and Vitt 2002; Herrel et al. 2004a). Interestingly, lizards consumed fruits independently of their abundance and throughout the year. Lizards acted as legitimate seed dispersers enhancing both seedling emergence time and percentage.

Does body size influence frugivory on oceanic islands?

Despite the inter-island differences in size and in level of frugivory, neither body size nor head size were relevant predictors of frugivory in Galápagos lava lizards. To the best of our knowledge, level of frugivory within a species radiation with an interspecific variation in size had only been examined in Jamaican *Anolis* lizards (Iguanidae)

by Herrel et al. (2004a). These authors found a strong correlation between body size and the prevalence of fruits in diet. In order to compare our results to those of Herrel et al. (2004a), we tested whether a linear or polynomial regression linked body size to level of frugivory in Galápagos lizards. Even considering Santa Cruz as an outlier, frugivory level does not seem significantly affected by differences in size on any regression models (see Supplementary Figure 3 for details). A relatively lower interspecific competition in lava lizards (single island species), compared to Jamaican *Anolis* lizards (four syntopic species), might create a weak selective pressure on Galápagos individuals to diverge in the use of food resources (niche variation hypothesis) (Bolnick et al. 2010; but see Novosolov et al. 2018). Thus, Galápagos lizards living in arid environments with a shortage of arthropods, high-population densities and low interspecific competition consumed fruits independently of body size. These results are in line with a massive diet shift typical of the insular interaction release phenomenon observed in Galápagos birds (Traveset et al. 2015). However, dietary studies on the congeneric mainland species are needed to further support this hypothesis. Another example is found on the Canarian lizards, where all species of the endemic genus *Gallotia* (Lacertidae) show evolutionary diet shifts towards frugivory (Van Damme 1999; Herrel et al. 2004b).

Island-intrinsic factors such as climatic conditions are likely to influence the level of frugivory across the archipelago and certainly deserve further investigation. Rainfall and cloud cover play an essential role in determining Galápagos plant growth and reproduction, and thus fruit and arthropod availability (Grant and Grant 2002). Climate is known to vary drastically among islands (Trueman and d'Ozouville 2010), and possibly affects frugivory in lizards. Unfortunately, we could not test this hypothesis as climate data are available only from a few islands. Furthermore, mammalian predators introduced to the four inhabited islands (Santa Cruz, San Cristóbal, Floreana, Isabela) may prevent lizards from foraging on fruits for longer periods (Case and Bolger 1991). For instance, it is possible that cats are responsible for the low frugivory level by lizards on San Cristóbal where they are known to prey upon them (Carrión Avilés 2012). Cats are also thought to have depleted the populations of several native species to the verge of extinction on Floreana (Grant et al. 2005), where frugivory level by lizards was relatively low. With the available information, we cannot infer drivers of the high frugivory of lizards observed on Santa Cruz. It might be related to differences in predation pressure, or to alternative food sources due to the more intense human occupation of the island.

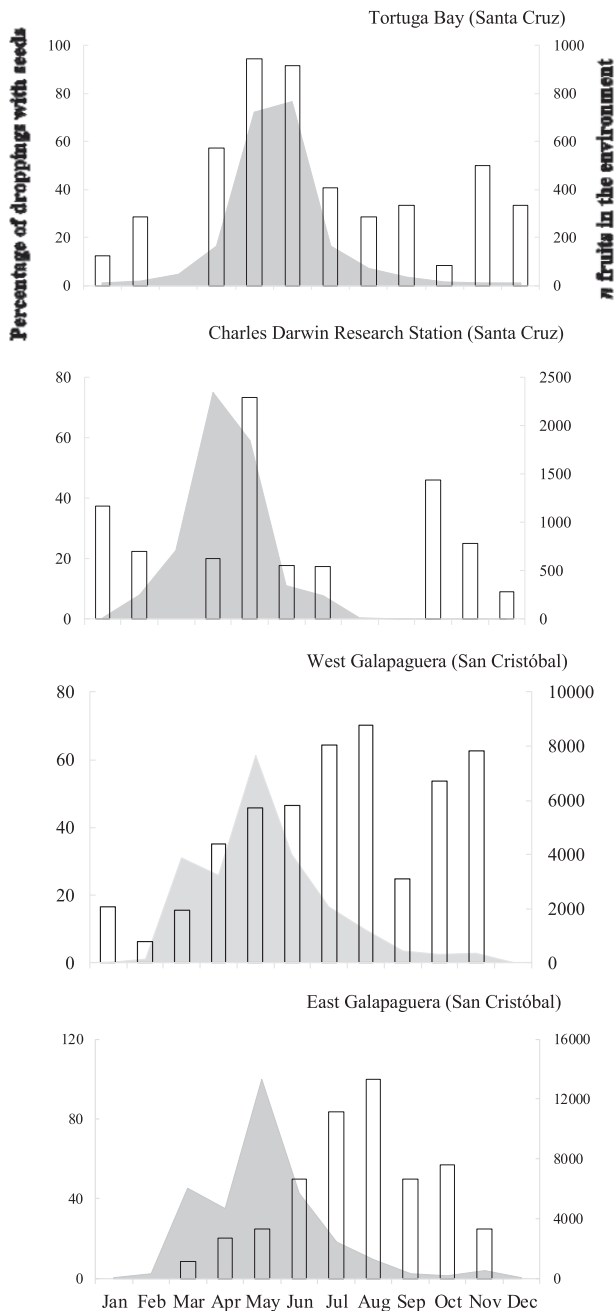


Figure 2. Mean number of available fruits (area) and proportion of lizard droppings with seeds (bars) recorded monthly from March 2010 to February 2011 at four locations on Santa Cruz and San Cristóbal islands.

The small lizards on Santa Cruz, previously considered to be almost entirely insectivorous (Stebbins et al. 1967), are now well established as also being frugivores (23% FO), consuming fruits from at least 22 plant species (Figure 3). In fact, our frugivory values should be regarded as conservative since some of the sampled droppings might date from a few weeks before the fruiting peak for most Galápagos plants (Heleno et al. 2013).

Temporal variation in frugivory

We studied frugivory on Santa Cruz and San Cristóbal for an entire annual cycle to assess whether fruit consumption was linked to fruit

abundance. Our findings supported previous suggestions that lizards do not eat fruits in direct proportion to their abundance (Dearing and Schall 1992; Diaz 1995). Thus, lizards on these two islands may prefer fruits of some plant species to others. The three plant species most consumed by lizards (*T. psilostachya*, *L. camara* and *Z. fagara*, Supplementary, Table 1) on Santa Cruz and San Cristóbal have different origin, fruit type and colour, and number of seeds, but relatively similar fruit size (3–6 mm in mean diameter) (McMullen 1999). Further effort is needed to fully disentangle the factors driving fruit selection by Galápagos lizards, such as energy content, pulp nutritional composition, accessibility, and fruit crop (Jordano 1995; Brodie 2017).

Fruit consumption by lizards throughout the year indicates the importance of this under-recognised food resource. On the Galápagos, the highest abundance of arthropods and fruits occurs in the wet season (Schluter 1984; Heleno et al. 2013). According to the moderate level of frugivory in the Galápagos lizards, they might vary their diet depending upon seasonal abundances of animal prey and be forced to increase frugivory in months of greater arthropod shortage (Rand 1978). In support of this hypothesis, Schluter (1984) found that the herbivory ratio (leaves, flowers, and fruits) in the diet of *M. pacificus* on Pinta depends primarily on arthropod availability. It is therefore possible that the temporal variation in frugivory is inversely related to changes in arthropod availability (Pérez-Mellado and Traveset 1999), although this needs further testing at the population level.

Quality of seed dispersal by insular lizards

Lizards are important seed dispersers in the arid zone across the archipelago, where native plants are particularly abundant and diverse (Guézou et al. 2010), particularly for: *T. psilostachya*, *L. peduncularis*, and *S. spicata* (Figure 3). Although most plant species have broad distributions across the archipelago (Heleno and Vargas 2015), there was only a small overlap in the fruit species consumed on each island (Supplementary Figure 2). This might be explained by differences in rainfall patterns and thus fruit phenology during our sampling over a seven-year span (Grant and Grant 2002). The vast majority (76%) of dispersed seeds belong to the group of native plants to the Galápagos, but lizards also dispersed seeds of highly invasive species (*R. niveus*, *L. camara*, *P. guajava*). Despite the low presence of these invaders in the arid zone of the inhabited islands, their fruits were an important food resource to lizards that are likely contributing to their expansion. Ten fruit species identified in this study (Figure 3) were not previously known to be dispersed by either mammals (Heleno et al. 2011), birds (Heleno et al. 2013), land iguanas (Traveset et al. 2016), or giant tortoises (Blake et al. 2012) in the archipelago.

Previous studies showed no effect of lizard fruit consumption on seedling emergence or opposite effects for several lizard families (reviewed in Traveset and Verdú 2002; Godínez-Álvarez 2004). For instance, Lacertidae, Liolaemidae, and Tropiduridae tend to increase germination percentage, whereas others such as Iguanidae tend to reduce it. In our study, lizards legitimately dispersed at least 12 species, increasing seedling emergence percentage by 39%, and reducing seedling emergence time by 62%. When compared to control fruits, this finding confirms previous suggestions that Galápagos lizards are legitimate and highly effective seed dispersers (Heleno et al. 2013). As no differences between seeds from droppings and de-pulped seeds were found, it appears to be primarily related to the removal of fruit pulp by lizard ingestion, as reported for other frugivorous animals (Traveset et al. 2008). In an unpredictable

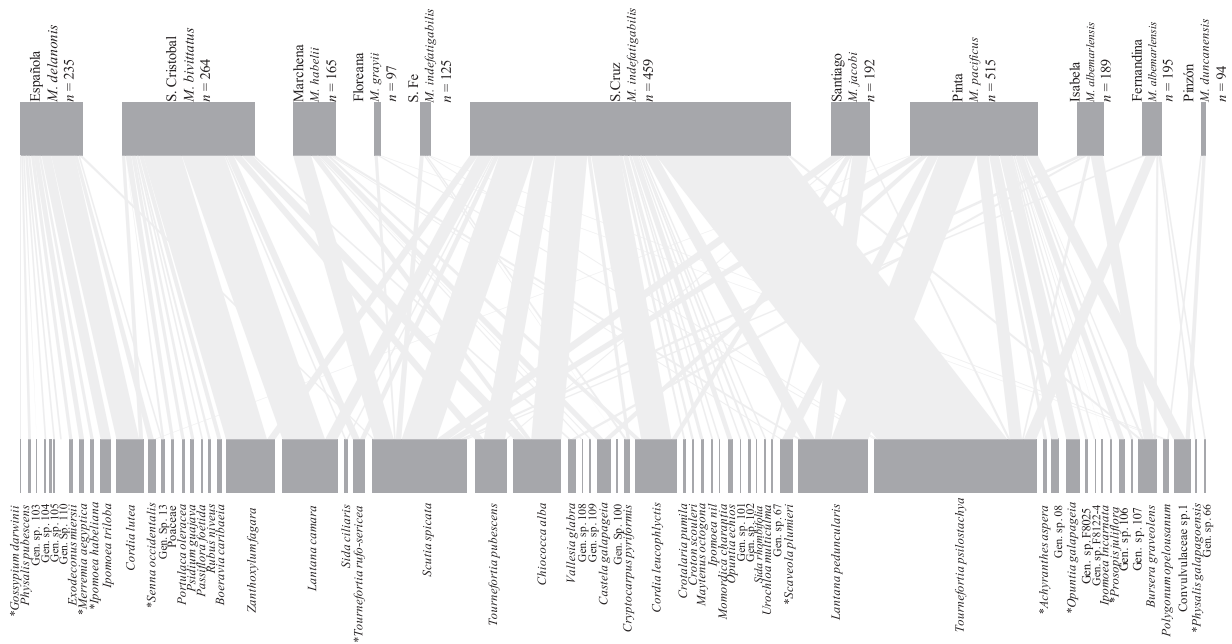


Figure 3. Quantitative plant–lizard seed dispersal network with all lizard droppings containing intact seeds ($n = 370$), collected from 2010 to 2016 in the eleven largest Galápagos islands. Interaction frequency was quantified as the number of droppings with at least one intact seed of any plant species. $n =$ number of droppings collected and examined for seeds on each island. *Species not known to be dispersed by any other animal on the Galápagos.

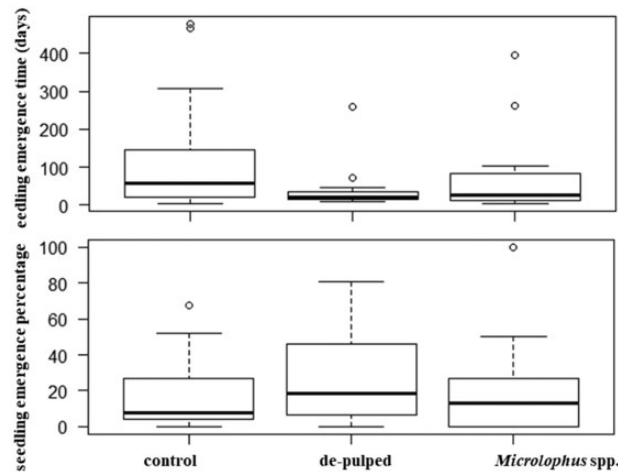


Figure 4. Median (solid horizontal bar), 25th and 75th percentiles (upper and lower horizontal boxes), $1.5 \times$ inter-quartile range (whiskers) and outliers (points) of seedling emergence time and seedling emergence percentage for seeds retrieved from lizard droppings, manually de-pulped seeds and control fruits collected from mature fruits, from March 2010 to February 2011 on Santa Cruz and San Cristóbal islands.

environment such as the Galápagos arid zone where rainfall patterns are extremely variable, taking advantage of different de-pulping agents is likely to be an important plant strategy to increase the probabilities of germination when the first rain falls, thus securing recruitment (Nogales et al. 2006).

Synthesis and limitations

This study represents the first assessment of frugivory and seed dispersal across the Galápagos lizard radiation and shows that small body size is not a limiting factor for fruit consumption in contrast to previous findings. It supports the hypothesis that island-dwelling lizards of all sizes undergo a release in their plant-lizard interactions,

taking advantage of available resources in simplified environments. Therefore, the role of small lizards as seed dispersers should not be neglected on islands and probably not on continents as well. In a nutshell, our study shows that Galápagos lava lizards play an important and legitimate role as seed dispersers of many Galápagos plants, across the entire year and across the whole archipelago.

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Authors' contributions

M.N. and R.H. conceived the study; M.N., R.H., B.R., B.G., P.V., J.O., A.T., C.V., and S.H.P. collected material and data; R.H., B.R., and S.H.P. performed seed identifications and germination experiments; S.H.P. analysed the data and led the writing with contributions from all authors.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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