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Frugivory and Seed Dispersal by Lizards: A Global Review

Alfredo Valido [1]* and Jens M. Olesen [2]

[1] Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (CSIC), La Laguna, Spain,
[2] Department of Bioscience, Aarhus University, Aarhus, Denmark

Birds and mammals are the only vertebrates which receive comprehensive attention in studies of dispersal of fleshy-fruited plant species. However, recently the importance of fleshy fruit in the diet of lizards (order Squamata: suborder Sauria), and their role as seed dispersers have been recognized in a number of studies, especially in studies from arthropod-poor habitats, such as oceanic islands. Here, we revisit the evidence of fruit-eating lizards on a global scale in order to test if fruit consumption is more common on islands than expected by chance. We constructed a database of 470 lizard species (from a global count of 6,515 species), that have been reported to consume fleshy fruits. This set of lizards belong to 27 families with Scincidae ($N = 78$ species), Gekkonidae (69), and Dactyloidae (55) having more frugivorous species than other lizard families. We found that 62.4% of these lizards inhabit islands, whereas only one third (35.3%) of all lizard species inhabit islands. These values support the presence of an "insular phenomenon," however; we also tested if this biogeographical pattern might be driven by body size and evolutionary history of lizards. Thus, we looked for any phylogenetic signals in the distributions of lizard body size, island-presence, and frugivory and calculated phylogenetically corrected correlations among the three variables on a global subset of 2,417 lizard species for which we had detailed phylogenetic information. Both lizard body size and island-presence were weakly influenced by phylogeny; whereas, frugivory was not. In addition, we found that (1) body size and frugivory were weakly positively correlated; (2) body size and island-presence were uncorrelated; and (3) island-presence and frugivory were strongly positively correlated. Thus, we conclude that the main driver of frugivory on islands is the specific island environment and not lizard body size *per se*. Islands are said to be poor in arthropods and predators, and this may force/allow island lizards to forage for additional food sources, such as fleshy fruits. We also suggest that modern lizards as well as their ancestors may potentially play an important role to many plants as seed dispersers. However, we do not known how tight the correlation is between frugivory and seed dispersal. Thus, lizards repeatedly inspire us to ask new ecological and evolutionary questions.

Keywords: frugivory, lizard, mutualism, plant-animal interaction, saurochory, seed dispersal, island, body size

Edited by:
Andy J. Green,
Estación Biológica de Doñana (EBD), Spain

Reviewed by:
Sean Thomas Giery,
University of Arkansas, United States
Daniel Wenny,
San Francisco Bay Bird Observatory, United States

***Correspondence:**
Alfredo Valido
avalido@ipna.csic.es

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INTRODUCTION

Birds and mammals are the principal seed dispersers of fleshy-fruited plant species (e.g., van der Pijl, 1982; Jordano, 2013). Fruit pulp is an important resource to these animals, which in return may promote an important ecosystem service, the dispersal of their seeds (e.g., Herrera and Pelmyr, 2002; Forget et al., 2011; Bascompte and Jordano, 2014; Wandrag et al., 2018). By dispersing seeds further away from the mother plants, seed mortality gets reduced and survival is favored if colonization happens to new microhabitats (e.g., Janzen, 1970; Howe and Smallwood, 1982; Cousens et al., 2008). In addition, seed dispersal promotes gene flow within and among plant populations (e.g., Rousset, 2004; Pérez-Méndez et al., 2018; Wandrag et al., 2018). Until recently, however, few studies have considered the role of other vertebrates as seed dispersers of fleshy-fruited plant species, e.g., fish, chelonians, crocodilians, and lizards (e.g., Olesen and Valido, 2003, 2004; Liu et al., 2004; Correa et al., 2007; Valido and Olesen, 2007; Platt et al., 2013; Falcón et al., 2018).

Here, we focus on lizards (order Squamata: suborder Sauria), because these animals are usually overlooked or dismissed as frugivores and seed dispersers. The main reason is that most are regarded as primarily feeding on small invertebrates (e.g., Greene, 1982; Cooper and Vitt, 2002; Pianka and Vitt, 2003), whereas only a few species bigger in size are herbivorous, i.e., folivorous (**Supplementary Material:** Herbivorous lizards). Thus, since Pough (1973) a relation between lizard body size and herbivory (specifically “folivory”) has been noted. In this respect, larger lizards would present some digestive and physiological modifications which favor an herbivorous diet (e.g., Iverson, 1982; Zimmerman and Tracy, 1989). This idea has also been extended to lizards with frugivorous habits, such as *Anolis*-like species whereas fruit intake has been related to large body size in some species (Herrel et al., 2004a). However, fruit pulp is an easily metabolized plant part, being low in fibers and proteins, and high in soluble carbohydrates (e.g., Valido et al., 2011; Jordano, 2013). Thus, lizards do not require large gape, strong bite or a large digestive system to process these items. In this respect, several studies have shown that small arthropod-eating lizards do consume fruit if their favorite arthropod food is scarce. This is most often observed on islands (e.g., Patterson, 1928; Vinson and Vinson, 1969; Schoener et al., 1982; Cheke, 1984; Whitaker, 1987; Pérez-Mellado and Corti, 1993; Valido and Nogales, 1994; Wotton, 2002; Valido et al., 2003; Hare et al., 2016; Wotton et al., 2016; Melzer et al., 2017; Parejo et al., 2018), where arthropods might be in short supply, but also in arthropod-poor habitats on mainland, such as high mountains and deserts (e.g., Fuentes, 1976; Mautz and Lopez-Forment, 1978; Hódar et al., 1996; Whiting and Greeff, 1997; Kiefer and Sazima, 2002; Espinoza et al., 2004; Valdecantos et al., 2012). By feeding from at least two trophic levels, these lizards become omnivorous. Generally, they do not have any morphological, digestive or physiological modifications related to their frugivorous diet (e.g., Valido and Nogales, 2003; Herrel et al., 2004b; Vidal and Sabat, 2010; but see Sagonas et al., 2015). Alongside their fruit diet choice, they may act as seed dispersers (e.g., Pérez-Mellado and Traveset, 1999; Olesen and Valido, 2003; Godínez-Álvarez, 2004; Valido and Olesen, 2007, 2010).

The full extent of this mutualistic plant-lizard interaction is unknown, because fruit rarely is scored as a separate component in diet studies. In the literature, plant material consumed by lizards is often pooled into one diet component, notwithstanding the wide range in energy content and digestability of various plant parts, e.g., foliage, which is difficult to digest because of the presence of cellulose. In the past, however, mutualistic reptiles were also present in the past (**Supplementary Material**: Mutualistic reptiles in the past), and the natural history literature is rich in stories about fruit-eating lizards (**Supplementary Material**: Early records of lizard-fruit interactions), but this knowledge is still not integrated into general ecology and evolutionary biology (see Miranda, 2017). Consequently, most reviews about seed dispersal focus on birds and mammals (Traveset et al., 2013; e.g., Jordano, 2013).

Here, our aim is (1) to present a detailed global overview of the extent of fleshy fruit consumption and seed dispersal in lizards, by mapping their geographical and taxonomical distribution, and (2) to test if insularity favors plant-lizard mutualism, if we control for lizard body size and phylogenetic relationships.

MATERIALS AND METHODS

Collection Methods

Variation in collecting efforts and nomenclature changes make the global number of lizard species very dynamic, but on the 29th of August 2018, the number was 6,512 species (Uetz et al., 2018; **Table 1**). The taxonomy of lizards used here follows the *European Molecular Biology Laboratory Reptile Database*, EMBL. Two species were excluded from our analysis because their geographic range were missing in the EMBL, and, additionally, we included four new species from New Zealand and one from the Canary Islands (Hare et al., 2016; **Table S1**). Thus, our database included a total of 6,515 species sorted into 38 families, which further belonged to the infraorders Iguania, Gekkota, Scincomorpha, Diploglossa, Dibamia, and Platynota (Squamata: Sauria). Using this database, we classified lizards according to their geographical distribution, i.e., only island (*I*), only mainland (*M*), and both island and mainland (*IM*). We classified Australia as a mainland together with the other continents, whereas New Zealand, Madagascar, New Guinea, Borneo, Japan, and Taiwan were analyzed as islands. The borderline between island and mainland is obviously subjective. However, in island literature, Australia is most often regarded as a mainland, and here, we prefer to keep it that way. Several *IM*-species are introductions from their native islands to a mainland, e.g., from the Caribbean Islands to USA (e.g., *Anolis cristatellus,* Dactyloideae), from the Balearic Archipelago to the Iberian Peninsula (*Podarcis pityusensis*, Lacertidae), or *vice versa*, from USA to Japanese Ogasawara Islands (*A. carolinensis*), from North Africa to Menorca Island (*Scelarcis perspicillata*). Such species were here categorized as *IM.* Some lizard species are also island-to-island introductions (e.g., the lacertid *Teira dugesii* from Madeira to the Azores, and *Gallotia stehlini* from Gran Canaria to Fuerteventura). Finally, near-shore islets were regarded as part of their adjacent mainland or island. We also included the continuous variable lizard body size (maximum snout-vent length “max SVL”; Meiri, 2008, 2018), and the binary trait presence of fruits: 0 (absence) and 1 (presence) (see **Supplementary Material**: Quality of the data).

First, we compared species frequencies of fruit-eating lizards on islands and mainland. Our null hypothesis was that the frugivorous lizards had a geographical distribution similar to lizards in general. This was tested with a Chi squared

TABLE 1 | Number of lizard species (Sauria) in the families of the infraorders Iguania, Gekkota, Scincomorpha, Diploglossa, Dibamia, and Platynota, sorted according to their geographic distribution: *I*, island-only species; *M*, mainland-only species; and *IM*, species present on both island and mainland.

Family	Total no. spp.	I-spp (%)	M-spp. (%)	IM-spp (%)
IGUANIA				
Agamidae	489	106 (21.7)	340 (69.5)	43 (8.8)
Chamaeleonidae	210	94 (44.8)	113 (53.8)	3 (1.4)
Corytophanidae	9	0	9 (100)	0
Crotaphytidae	12	0	11 (91.7)	1 (8.3)
Dactyloidae	426	187 (43.9)	230 (54.0)	9 (2.1)
Hoplocercidae	19	0	19 (100)	0
Iguanidae	44	27 (61.4)	9 (20.5)	8 (18.2)
Leiocephalidae	31	31 (100)	0	0
Leiosauridae	33	0	33 (100)	0
Liolaemidae	307	0	304 (99.0)	3 (0.98)
Opluridae	8	8 (100)	0	0
Phrynosomatidae	156	12 (7.7)	133 (85.3)	11 (7.1)
Polychrotidae	8	0	6 (75.0)	2 (25.0)
Tropiduridae	137	11 (8.0)	125 (91.2)	1 (0.7)
GEKKOTA				
Gekkonidae	1181	388 (32.9)	720 (61.0)	73 (6.2)
Carphodactylidae	30	0	30 (100)	0
Diplodactylidae	153	58 (37.9)	92 (60.1)	3 (2.0)
Eublepharidae	38	8 (21.1)	25 (65.8)	5 (13.2)
Phyllodactylidae	146	44 (30.1)	96 (65.8)	6 (4.1)
Sphaerodactylidae	218	104 (47.7)	89 (40.8)	25 (11.5)
Pygopodidae	46	1 (2.17)	43 (93.5)	2 (4.4)
SCINCOMORPHA				
Cordylidae	68	0	68 (100)	0
Gerrhosauridae	37	19 (51.4)	17 (45.9)	1 (2.7)
Lacertidae	335	34 (10.2)	273 (81.5)	28 (8.4)
Scincidae	1,656	702 (42.4)	864 (52.2)	90 (5.4)
Xantusiidae	34	1 (2.9)	32 (94.1)	1 (2.9)
Alopoglossidae	23	0	22 (95.6)	1 (4.4)
Gymnophthalmidae	246	2 (0.8)	236 (95.9)	8 (3.3)
Teiidae	160	26 (16.3)	118 (73.8)	16 (10.0)
DIPLOGLOSSA				
Anguidae	78	2 (2.6)	69 (88.5)	7 (9.0)
Diploglossidae	51	26 (50.9)	25 (49.0)	0
Anniellidae	6	0	5 (83.3)	1 (16.7)
Xenosauridae	12	0	12 (100)	0
DIBAMIA				
Dibamidae	24	10 (41.7)	11 (45.8)	3 (12.5)
PLATYNOTA				
Helodermatidae	2	0	2 (100)	0
Lanthanotidae	1	1 (100)	0	0
Varanidae	80	36 (45.0)	30 (37.5)	14 (17.5)
Shinisauridae	1	0	1 (100)	0
TOTAL	**6515**	**1938**	**4212**	**365**
(%)		**(29.7)**	**(64.6)**	**(5.6)**

Number of species and their geographic range follow Uetz et al. (2018), update at 29 August 2018.

This table includes 6,515 species. In the analysis, we excluded two species with no information about their geographic range in the Reptile Database: Diploglossus microlepis (Diploglossidae) and Leiolopisma fasciolare (Scincidae), but we have included four new species from New Zealand, which were not in the Reptile Database: Oligosoma aff. polychroma (Scincidae), Dactylocnemis "Poor Knights," Woodworthia aff. brunnea, and W. "Southern Alps" (Diplodactylidae) (Hare et al., 2016). The extinct Gallotia goliath (Lacertidae) from Canary Islands was also included, because of available diet information.

test of data from each family separately and for the global count of lizards. Globally, 29.7% of all lizard species are *I*-species, 64.6% only *M*-species, and 5.6% are *IM*-species (**Table 1**; **Figure 1**).

We also tested if the variables body size, frugivory, and island-presence in their distribution among lizards had a phylogenetic signal (see below). As backbone lizard phylogeny, we used the one published by Pyron et al. (2013). This phylogeny only included 2,847 lizard species. We pruned the phylogeny for those lizard species without any information about their max SVL or geographic distribution, resulting in 2,417 lizard species, which were included in our phylogenetic analysis.

Phylogenetic Signal

The phylogenetic signal of a trait is a measure of the statistical dependency among values of this trait on the phylogenetic relationships among species in the study sample (e.g., Blomberg and Garland, 2002). If other factors than phylogenetical relatedness influence trait variation, for example convergence due to related ecology, this will reduce the phylogenetic signal.

The phylogenetic signal of a continuous trait (max SVL) can be measured by Blomberg's K and Pagel's λ (Pagel, 1999; Blomberg et al., 2003). Both measures react slightly different to number of species included in the phylogeny, amount of information about branch length and number of polytomies (Münkemüller et al., 2012). For both measures, the actual observed value is compared to a null model of trait evolution, a Brownian motion (*BM*) evolutionary model (Blomberg et al., 2003), which is based upon either pure genetic drift, randomly varying selection, or varying stabilizing selection, but not on directional selection. According to this *BM* model, trait evolution follows a random walk along the branches of the phylogenetic tree. To test this null hypothesis of no phylogenetic signal, the observed values of the focal trait was compared with values expected under random (1,000 permutations) value distribution by using a likelihood ratio test (Münkemüller et al., 2012).

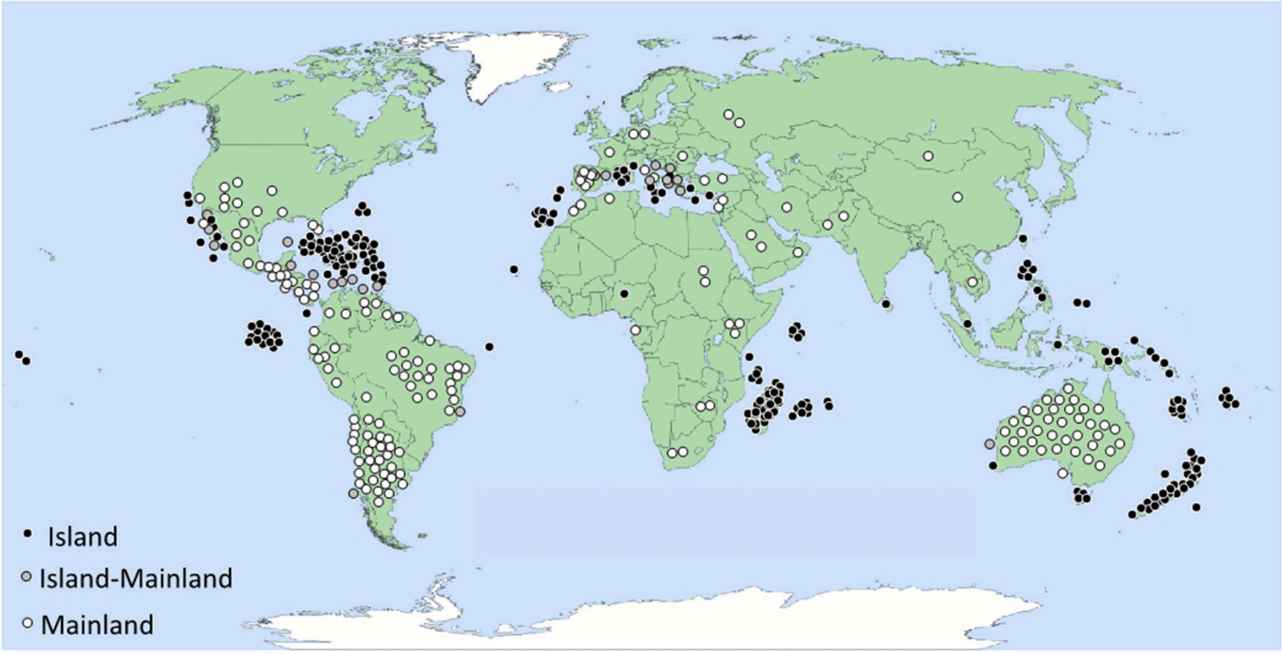

FIGURE 1 | Geographic distribution of 470 fruit-eating lizard species sorted as island-only species (*I*), mainland-only species (*M*) and species present on both island and mainland (*IM*). See also **Table S1** in Supplementary Material for a full list of frugivorous lizard species. The map shows not just the distribution of lizard frugivory, but also the heterogeneous sampling efforts. Note, for example, the absence of dots in Japan and Indonesia, which most likely is caused by insufficient field observation.

Both measures (K, λ) vary from 0 to 1, with values close to zero indicating lack of phylogenetic dependency, i.e., the trait has evolved in response to local selective processes. Whereas, a value close to 1 indicates an evolution according to the *BM*, i.e., a gradual accumulation of changes over time. K may also be larger than one, which indicates a strong phylogenetic signal. At least theoretically, λ might also become slightly larger than one (Münkemüller et al., 2012). The lower and upper bounds of K and λ indicate which of the two scenarios is the most likely.

The phylogenetic signal for binary traits (frugivory and island-presence) can be measured by D (phylogenetic dispersion) (Fritz and Purvis, 2010). $D = (d_{\mathrm{obs}}$ – mean $d_{\mathrm{b}})/($mean d_{r} – mean $d_{\mathrm{b}})$, where d_{obs} is the number of trait state changes needed to get the observed trait state distribution in our phylogeny, d_{b} is the expected distribution of d under a *BM* model (1,000 permutations) and d_{r} is the expected distribution of d, if trait states are randomly distributed among species. D typically varies from 0 to 1. $D = 0$ indicates that the trait evolves according to the Brownian model, *BM* (i.e., phylogenetic signal). $D = 1$ indicates that the trait evolves according to a random model (i.e., independent of the phylogeny), $D > 1$, if the trait is phylogenetically overdispersed, and $D < 0$, if the trait is more phylogenetically clustered than expected according to a *BM* model (Nunn, 2011).

The finding of a significant phylogenetic signal in some of these variables requires the use of comparative phylogenetic analysis to test for correlation between traits.

Phylogenetically Corrected Correlations

We tested for correlations between max SVL, island-presence and frugivory, using phylogenetically independent contrasts (*PIC*), i.e., any influence of statistical dependency among trait values was removed before the correlation analysis. The lizard body size (max SVL) data were log-transformed.

By using the lizard phylogeny (Pyron et al., 2013), and our compiled database including max SVL of lizards (Meiri, 2008, 2018), island-presence and frugivory (**Table S1**), we answered: 1. Is there, globally, any phylogenetic signal in the distribution of frugivory, body size, and island-presence in lizards; and 2. to what extent do island-presence and max SVL influence frugivory after correcting for any phylogenetical influence. For these phylogenetical analyses we used *picante* (Kembel et al., 2018), *geiger* (Harmon et al., 2016), *caper* (Orme et al., 2018), and *ape* (Paradis et al., 2018) R packages (R Core Team, 2014).

RESULTS

Fruit-Eating Lizards

We found reports of 470 lizard species from 27 families and 128 genera consuming fleshy fruits (**Tables 2**, **S1**). Thus, 7.2% of all lizards use fleshy fruits to some extent in their diet. These species are widely distributed taxonomically, since 71% of all lizard families included some frugivorous members; Scincidae ($N = 78$ species), Gekkonidae (69), and Dactyloidae (55) being most frugivorous. Other lizard families with a high percentage of frugivorous species are Iguanidae (54.5%), Corytophanidae

TABLE 2 | Taxonomic and geographical distribution of fruit-eating lizard families.

Family	Total no. spp.	No. fruit-eating lizards	I (%)	M (%)	IM (%)	*P*	%
IGUANIA							
Agamidae	489	19	7 (36.8)	12 (63.2)	0	ns	3.9
Chamaeleonidae	210	2	1 (50.0)	1 (50.0)	0	ns	0.9
Corytophanidae	9	4	0	4 (100.0)	0	–	44.4
Crotaphytidae	12	2	0	1 (50.0)	1 (50.0)	–	16.7
Dactyloidae	426	55	47 (85.5)	5 (9.1)	3 (5.5)	***	12.9
Iguanidae	44	24	16 (66.7)	3 (12.5)	5 (20.8)	ns	54.5
Leiocephalidae	31	13	12 (92.3)	0	1 (7.7)	–	41.9
Leiosauridae	33	1	0	1 (100.0)	0	–	3.0
Liolaemidae	307	34	0	34 (100.0)	0	–	11.1
Opluridae	8	2	2 (100.0)	0	0	–	25.0
Phrynosomatidae	156	8	1 (12.5)	6 (75.0)	1 (12.5)	ns	5.1
Polychrotidae	8	4	0	4 (100.0)	0	–	50.0
Tropiduridae	137	24	9 (37.5)	14 (58.3)	1 (4.2)	*	17.5
GEKKOTA							
Gekkonidae	1,181	69	66 (95.7)	3 (4.3)	0	***	5.8
Diplodactylidae	153	17	17 (100.0)	0	0	***	11.1
Phyllodactylidae	146	2	1 (50.0)	1 (50.0)	0	–	1.4
Sphaerodactylidae	218	2	1 (50.0)	1 (50.0)	0	–	0.9
Pygopodidae	46	17	0	17 (100.0)	0	–	37.0
SCINCOMORPHA							
Cordylidae	68	3	0	3 (100.0)	0	–	4.4
Gerrhosauridae	37	7	4 (57.1)	3 (42.9)	0	ns	18.9
Lacertidae	335	38	21 (55.3)	11 (28.9)	6 (15.8)	***	11.3
Scincidae	1,656	78	45 (57.7)	32 (41.0)	1 1.3)	ns	4.7
Xantusiidae	34	3	2 (66.7)	1 (33.3)	0	ns	8.8
Teiidae	160	36	15 (41.7)	19 (52.8)	2 (5.6)	*	22.5
DIPLOGLOSSA							
Anguidae	78	1	0	1 (100.0)	0	–	1.3
Diploglossidae	51	2	2 (100.0)	0	0	ns	3.9
PLATYNOTA							
Varanidae	80	3	3	0	0	ns	3.7
TOTAL	**6113**	**470**	**272**	**177**	**21**	***	**7.7**
(%)			**(57.9)**	**(37.6)**	**(4.5)**		

*I, island-only species; M, mainland-only species; and IM, species present on both island and mainland. P, probability that the geographical distribution of the fruit-eating lizards in a given family differed from a random draw of the same number of species from the world pool of lizards (see Methods). %, percent fruit-eating lizard species out of total count. Number of species and their geographical range follow Uetz et al. (2018), update at the 29 August 2018 (**Table 1**). See also **Table S1** in Supplementary Material for a full list of frugivorous species. *P < 0.05; ***P < 0.001.*

(44.4%), and Leiocephalidae (41.9%) (**Tables 2**, **S1**, Importance and examples of fleshy fruit to the diet of lizards).

Geographic Distribution of Frugivorous Lizards

64.6%, 29.7% and 5.6% of the 6,515 lizard species in the world inhabit mainlands, islands, and both, respectively (**Table 1**). However, frugivory in lizards were much more frequent among only island species (57.9% of all frugivorous lizards) than among only mainland species (37.6%). Only 4.5% of all frugivorous lizards were found on both island and mainland (**Tables 2**, **S1**). First, we tested the null-hypothesis H_0: the frequencies of fruit-consuming lizard species on islands, mainland and both could be explained by the global geographical distribution of lizards. In this analysis, only the 27 lizard families with reported frugivory were included ($N = 6{,}113$ species). H_0 was rejected ($P << 0.001$; **Table 2**). Thus, the high frequency of fruit-consuming lizards on islands could not be explained by the general biogeography of the group. This analysis was repeated at family level. Island species were significantly overrepresented as fruit consumers in Dactyloidae, Gekkonidae, Diplodactylidae, and Lacertidae (**Table 2**). In contrast, in the Tropiduridae, frugivory was significantly more frequent on mainland than on islands (**Table 2**). Thus, worldwide fruit-consumption among lizards is almost twice as common on islands than on mainland, but on the family level there is some variation.

Phylogenetic Correlations

The distribution of max SVL showed a significant, but weak phylogenetical signal ($K = 0.291$; **Table 3**). Pagel's λ was closer to 1 than 0, but it was still significantly different from both values (95% confidence interval = [0.911; 0.941], and both the lower and upper bound were strongly unlikely; **Table 3**). Thus, *K* and λ showed that phylogeny, but also other factors, were important as drivers of body size variation in lizards. That lizard body size, in general, is influenced by both phylogenetic relationships and other factors (ecology) is certainly also what one would expect.

Our null hypothesis, stating that any presence or absence of lizards on islands is influenced of phylogeny, was not rejected ($P = 0.80$; **Table 3**), and this binary trait was distributed according to a Brownian motion model ($D \approx 0$; **Table 3**). We would also expect evolution to have played a role here, especially because many lizard radiations are endemic to islands.

For the binary trait frugivory, the null model was rejected ($P = 0.003$). Thus, the trait was not distributed according to a Brownian motion model of evolution ($D \approx 1$). However, $D \approx 1$ (no influence of phylogeny) was also rejected ($P < 0.001$). Thus, both phylogeny and other factors (ecological) play a role in the distribution of frugivory among lizards.

After correcting for any influence of phylogeny (*PIC*, phylogenetically independent contrasts; **Table 4**), we found (1) that body size (max SVL) and frugivory were positively, but weakly correlated; (2) that body size and island-presence were uncorrelated; and (3) that island-presence and frugivory were strongly positively correlated. Thus, in our database, frugivory was significantly associated with insular species after correcting for any influence of evolutionary relationships.

DISCUSSION

In this review, we reported that 470 lizard species consume fleshy fruit, many more than previously thought (Cooper and Vitt, 2002; Olesen and Valido, 2003; Godínez-Álvarez, 2004; Valido and Olesen, 2007; Meiri, 2018). However, it is still low compared to equivalent estimates for birds (around 4,000 bird species consume fleshy fruit, Wenny et al., 2016), but similar to mammals (460 species are primarily frugivorous, Fleming and Sosa, 1994). In addition, 182 Neotropical freshwater fish are fruit eaters (Correa et al., 2007), and recently Falcón et al. (2018) reported that up to 72 species of turtles include fleshy fruits in their diet.

However, for several reasons our number of frugivorous lizards is clearly an under-estimate: For example: (1) modern researchers have just recently begun to pay more attention to lizards as frugivores/plant mutualists; (2) many omnivorous (i.e., with 10–90%volume (V) plant matter in their diet) and herbivorous (>90%V) lizard examples reported in e.g., Cooper and Vitt (2002) were not incorporated in our database since the original reports did not specify which vegetative parts were consumed, and these species may use fleshy fruit as well; (3) lizard diet sampling conducted outside the fruiting period will not detect frugivory, and (4) for most lizards we did not find any data about their diet, particularly for endemics inhabiting remote islands, although some of their congenerics are in our database. Thus, we believe that many more fruit-eating and seed-dispersing lizards are waiting to be discovered.

Evolution of Frugivorous Lizards

Irrespectively of recent finding of an herbivorous lizard from early Cretaceous (Evans and Manabe, 2008), carnivory is the ancestral feeding mode in modern lizard species and most species are still exclusively or mainly carnivorous (e.g., Cooper and Vitt, 2002). However, trends toward true herbivory are seen repeatedly (Iverson, 1982; King, 1996; Cooper and Vitt, 2002), e.g., ∼18 herbivory origins within the South American

TABLE 4 | Phylogenetic independent contrasts (*PIC*) correlations between "max SVL," "frugivory," and "island-presence" of 2,417 lizard species, based on the phylogeny of Pyron et al. (2013).

Correlation	$F_{\mathrm{phy}\ 1,2414}$	P_{phy}
Max SVL × island-presence	0.029	0.86
Max SVL × frugivory	8.793	0.004
Island-presence × frugivory	52.31	0.001

"Island-presence" and "frugivory" were categorized as binary variables (0, 1) (see Methods for details). P_{phy} *is the probability that there is no correlation between two variables.*

TABLE 3 | Size of phylogenetic signal in the distribution of the continuous trait "max SVL" (*K*, λ), and the binary traits "island presence" and "frugivory" (*D*) of 2,417 lizard species, according to the phylogeny of Pyron et al. (2013).

Trait	*K*	*P*(*K*)	λ	Confidence interval of λ	*P*(λ) (lower bound)	*P*(λ) (upper bound)
Max SVL	0.291	<0.001	0.927	[0.911; 0.941]	0.001	0.001
	D				***P* (*D* ≈ 0)**	***P* (*D* ≈ 1)**
Island presence	−0.080				0.80	0.001
Frugivory	0.314				0.003	0.001

P of null model of Brownian motion (BM) (see Methods for details).
$K \approx 0$ no influence of phylogeny; $K \approx 1$ trait evolution according to BM model; $K > 1$ trait is phylogenetically clustered; $\lambda \approx 0$ no influence of phylogeny; $\lambda \approx 1$ trait evolution according to BM model; $D < 0$ trait values are phylogenetically clustered; $D \approx 0$ trait evolution according to BM model; $D \approx 1$ no influence of phylogeny.

Liolaemus (Espinoza et al., 2004). These lizards are smaller (max. SVL <100 mm) than other herbivorous species, and also inhabit mainland cold areas. Thus, small montane lizards may keep a higher body temperature (Vitt, 2004), being necessary for microbial hindgut endosymbionts, by digesting plant fibers. Cooler habitats have fewer insects and selection may favor a switch to herbivory (Pearson, 1954; Fuentes and Di Castri, 1975; Jaksic, 1978). However, the rarity of plant-eating lizards also suggests that herbivory in lizards is constrained (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; Espinoza et al., 2004). Here, we demonstrate that the use of easily digestible plant matter (i.e., fleshy pulp) is relatively frequent, occurring in several lizard lineages. However, the extent of this shift to frugivory in lizards is affected by insularity and body size.

Insularity

One third of all lizard species live on islands, but two thirds of all the fruit-consuming lizards are reported from islands. This geographical pattern is not caused by a higher number of scientists working both on seed dispersal (e.g., Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002; Dennis et al., 2007; and references therein) or diet of lizards on islands compared to mainland habitats (Meiri, 2018). In addition, the pattern is not caused by a presence of more fleshy-fruited plant species on islands compared to mainland habitats; on the contrary, islands have fewer fleshy-fruited plant species than comparable mainland habitats (e.g., Heleno and Vargas, 2015). Herrel et al. (2004a) compared the geographic distribution of frugivory among 45 island and 16 mainland *Anolis* species and also demonstrated that fruit in the diet of lizards is more common on islands (90% of all cases) than on mainland (10%). Analyzing many lizard species, but pooling all dietary plant parts, earlier studies also found this relationship (e.g., van Damme, 1999; Cooper and Vitt, 2002). However, island lizards include fleshy fruit, but also other vegetable food items, into their diet because they may be food limited (Janzen, 1973; Andrews, 1979; Schluter, 1984; Pérez-Mellado and Corti, 1993; van Damme, 1999; Cooper and Vitt, 2002; Polis et al., 2002; Olesen and Valido, 2003; Barret et al., 2005). This recurrent island phenomenon is an example of "niche expansion" or interaction release (*sensu* Traveset et al., 2015) and was first demonstrated for island birds (Grant, 1966; MacArthur et al., 1972). This pattern is possibly caused by a three-step process: 1) Compared to mainland, islands usually support fewer insect taxa (Gulick, 1932; MacArthur and Wilson, 1967) of a lower overall abundance (Allan et al., 1973; Janzen, 1973); 2) island lizards are less exposed to interspecific competition and predation because of a general low species density (MacArthur et al., 1972; Case, 1975; Andrews, 1979), and 3) some island lizard species respond to 2) by density compensation (MacArthur et al., 1972; Case, 1975; Rodda et al., 2001), resulting in intense intraspecific competition and consequently an expansion of their feeding niche toward the use of alternative resources, such as fleshy fruits (Olesen and Valido, 2003). However, only scant information is available on island arthropod abundance (Allan et al., 1973; Janzen, 1973; Andrews, 1979; Case, 1982; Faeth, 1984), but the impression from the general island biology literature is that arthropods are less abundant on islands and that they do not density compensate. On tiny islets, however, where coastline habitats dominate, flies functioning as decomposers of algae may be so abundant (Polis et al., 2002), that, at least theoretically, arthropod-eating lizards may be less inclined to shift to fruit.

On many islands, lizards have higher densities than related groups from adjacent mainland (Rodda and Dean-Bradley, 2002; Buckley and Jetz, 2007). Exceptionally high densities of lizards on islands have attracted considerable attention (Case, 1975; Case and Bolger, 1991; Rodda et al., 2001; Buckley and Jetz, 2007). The world record seems to be >5 *Sphaerodactylus macrolepis* individuals/m^2 in the Virgin Islands (Rodda et al., 2001). Insular founders may reach such high densities in just 3 years (Schoener, 1989). Density compensation in island lizards is a ubiquitous and global phenomenon, and total island lizard density is an order of magnitude higher than on mainland (128 *vs.* 1,920 individuals/ha) (Rodda et al., 2001; Buckley and Jetz, 2007). Many of these density-compensating island lizards are also present in our database (genera *Anolis*, *Gallotia*, *Gehyra*, *Hemidactylus*, *Lepidodactylus*, *Oligosoma*, *Phelsuma*, *Podarcis*, *Xantusia*, etc.). Reduction in species richness of predators (e.g., birds of prey) and number of competitors (insectivorous birds) may be the dominant drivers of lizard abundance on islands (Schoener and Schoener, 1978; Andrews, 1979; Wright, 1979; Buckley and Jetz, 2007). Density compensation in fruit-consuming lizards may thus be of high importance to seed dispersal in many plant species, influencing their chance of colonization and establishment on small islands, and their general population structure. Besides, the poor ability of mammals to reach remote islands will leave part of the diet niche dimension empty for other animal groups to explore (Whittaker and Fernández-Palacios, 2007).

Fruit -eating lizards are also observed in mainland habitats poor in arthropods. Frugivory in lizards inhabiting desert-like habitats (e.g., Clark and Comanor, 1976; Vitt et al., 1981; Hódar et al., 1996; Whiting and Greeff, 1997; Belver and Avila, 2002), high mountains (e.g., Hurtubia and Di Castri, 1973; Fuentes, 1976), cerrado habitats (e.g., Vitt, 1993; Mesquita and Colli, 2003) and caves (Mautz and Lopez-Forment, 1978) make up most of the mainland observations. Seasonal scarcity of arthropods and frugivory in lizards are also reported (e.g., Schleich et al., 1996; Duffield and Bull, 1998; Fialho et al., 2000). Thus, the arthropod-scarcity hypothesis can also explain mainland observations of lizards as fruit eaters.

Lizard Body Size

Since the review by Pough (1973) about lizard body size and herbivory diet, the generalization that only lizards >300 g (>217 mm SVL) are truly herbivorous and that medium-sized lizards, 100–300 g (150–217 mm SVL) are omnivorous have become a dogma in lizard ecology. It has been used to explain the paucity of modern, truly herbivorous lizards. However, a debate about this has also been running for more than 50 years (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; Iverson, 1982; van Devender, 1982; Auffenberg, 1988; King, 1996; van Damme, 1999; Cooper and Vitt, 2002; Cooper, 2003; Espinoza et al., 2004; Herrel et al., 2004a,b, 2008), including issues about predation risk, insularity, lizard body size, and digestive and physiological adaptative modifications. However, Espinoza et al. (2004), and more recently Vervust et al. (2010) demonstrated true herbivory in smaller species (max. SVL <100 mm) than in other known herbivorous species. These species were inhabiting insular (-like) habitats and true islands.

Many small (<150 mm SVL) lizards are being classified as frugivorous, e.g., species of *Gallotia*, *Podarcis* (Lacertidae), *Anolis* (Dactyloidae), *Carinascincus, Trachylepis* (Scincidae), *Gehyra*, *Phelsuma* (Gekkonidae), *Platysaurus* (Cordylidae), *Ameiva, Cnemidophorus* (Teiidae), *Leiocephalus* (Leiocephalidae), *Microlophus* (Tropiduridae), and *Lepidophyma smithii* (Xantusidae). Large lizards have large gapes and a strong bite (e.g., Herrel et al., 1999, 2004a,b), and this may be advantageous if the diet is vegetarian, because it allows the lizards to crush the material efficiently (Szarski, 1962; Sokol, 1967). Fleshy fruits, on the other hand, do not require this.

Frugivorous Lizards as Legitimate Seed Dispersers

Lizards do not fully chew their food and seeds passing through their gut may remain intact. Reviewing experimental studies of 40 plant species and 17 lizard species, Traveset (1998) and A. Valido (*unpublished*) concluded that seeds dispersed by lizards germinated just as well as seeds dispersed by frugivorous birds and mammals. The proportions of experiments in which germination of seeds was enhanced (25%), unaffected (57%) and inhibited (18%) after lizard gut passage were similar to figures for seed-dispersing birds (36, 48, and 16%, respectively), non-flying mammals (39%, 42%, 19%), and bats (25%, 67%, 8%). Here, we summarize some of these results.

Iverson (1985) detected a 6% increase in seed germination of *Coccoloba uvifera* (Polygonaceae) after passage through the gut of *Cyclura* compared to controls. Studies of other rock iguanas gave similar results. Within Lacertidae, a significant increase in germination in *Gallotia*-consumed seeds of *Withania aristata* (Solanaceae) has been reported (Valido and Nogales, 1994). Other reports from the Canaries and Balearics show similar results (Nogales et al., 1998; Castilla, 2000; Pérez-Mellado and Riera, 2004; Pérez-Mellado et al., 2005; Rodríguez-Pérez et al., 2005). Thus, many of these island lizards may contribute to plant fitness. However, for *Cnemidophorus murinus* from Bonaire Island, Lesser Antilles, Schall (1996) did not find any germination response for *Erithalis fruticosa* (Rubiaceae).

In Brazilean *Melocactus violaceus* (Cactaceae), 36% of the seeds passing through *Tropidurus torquatus* germinated compared to no germination at all for controls (Côrtes-Figueira et al., 1994). Fruits of *Melocactus* species appear to be consumed by lizards only (Dearing and Schall, 1992). On Chiloé Island, Chile, Rubiaceae seeds defecated by *Liolaemus pictus* germinated better or to the same extent as controls (Willson et al., 1996). Seeds of *Genipa americana* (Rubiaceae) and *Cereus peruvianus* (Cactaceae) consumed by *Salvator merianae* germinated significantly better and or to the same extent as controls, respectively (De Castro and Galetti, 2004). Vasconcellos-Neto et al. (2009) showed that seeds of *Solanum thomasiifolium* (Solanaceae) were dispersed less frequently by lizards (4%) than by birds (77%) and foxes (19%), but with higher germination rate (80%) compared to birds (64%) and foxes (53%).

The digestive treatment of seeds seems to be quite similar among different frugivore groups (Valido and Olesen, 2007). Although examples are still scarce, lizards seem to be in the same seed disperser league as the classical and better studied frugivorous birds and mammals. However, the series of seed germination studies mentioned above suggests that frugivory may not just lead to dispersal of seeds, but also to dispersal of viable seeds, which may germinate and increase plant fitness. However, we do not know how strong frugivory is as a proxy for plant fitness, and we also lack an experimental comparison of seed germination after passage through sympatric native lizards, birds and mammals, with the control treatment of intact fruits (Samuels and Levey, 2005).

CONCLUSIONS

Many lizard species are potential seed dispersers, and fruit feeding among lizards is taxonomically and geographically widespread, including 7.2% of all lizard species. It is especially important in species and populations inhabiting islands (62.4% of all reported cases). Finally, compared to other, more classical vertebrate mutualists (birds, mammals) seed dispersal by lizards is relatively poorly documented, but may be just as effective in terms of the quantitative and qualitative component of the seed dispersal effectiveness (*sensu* Schupp et al., 2010).

We believe that the results presented here are only the tip of the "lizard-plant seed dispersal iceberg." Thus, we find that fruit is an important supplementary diet component for island lizards. Other easily digestable plant material, like nectar and pollen, may show the same difference between islands and mainland, whereas we expect consumption of fiber-rich plant parts to show a deviating pattern. In general, much about lizard diet and its ecological and evolutionary consequences remain unknown. Our review may encourage ecologists, herpetologists, island biologists and natural historians in general to pay more attention to this type of plant-animal interaction, which may expand our general understanding of the ecology and evolution of mutualisms. For several decades, lizards have offered us outstanding opportunities for many kinds of ecological and evolutionary study (e.g., Pianka and Vitt, 2003; Losos, 2009), and here a new research line about lizard-plant mutualisms is suggested.

DATA AVAILABILITY

The datasets analyzed for this study are available in Supporting Information (**Table S1**) and the lizard phylogeny in Pyron et al. (2013).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00049/full#supplementary-material

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