6

The Importance of Lizards as Frugivores and Seed Dispersers

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Introduction

Despite the accumulation of a considerable body of literature about frugivory and seed dispersal of fleshy-fruited plants by vertebrates during the last decades (e.g. reviews in Howe and Smallwood, 1982; van der Pijl, 1982; Janzen, 1983; Howe, 1986; Howe and Westley, 1988; Stiles, 1989; Jordano, 2000; Herrera, 2002), and also previous editions of the *Frugivores and Seed Dispersal: International Symposium/Workshop* series (namely Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey *et al.*, 2002), the habits of reptiles as frugivorous animals and their role as seed dispersers have rarely been considered. At most, they are regarded as agents of the past (Labandeira, 2002; Tiffney, 2004).

Understandably, the literature has been dominated by studies on frugivorous birds, primates, ungulates and bats, which behave as important seed dispersers of vascular plants in many habitats. However, the pulp of fleshy fruits is also an important food resource for tortoises and turtles (MacDonald and Mushinsky, 1988; Milton, 1992; Jerozolinski, 2003) and for herbivorous and omnivorous lizards (Schoener *et al.*, 1982; Dearing and Schall, 1992; Valido *et al.*, 2003). Thus, one might expect that species included in both reptile groups would act as potential seed dispersers, but this has hardly ever been seriously considered. The exceptions are classic studies demonstrating the importance of herbivorous chelonians as seed dispersers (see Beccari, 1877; Borzí, 1911; Ridley, 1930; Rick and Bowman, 1961) and also some more recent publications (e.g. Racine and Downhower, 1974; Hnatiuk, 1978; Rust and Roth, 1981; Cobo and Andreu, 1988; Milton, 1992; Moll and Jansen, 1995; Varela and Bucher, 2002; Liu *et al.* 2004). In contrast to these animals, the reptile group upon which we focus in this chapter – the lizards (order Squamata: suborder Sauria), including around 4800 species worldwide – have received little attention as modern

plant mutualists although there is a growing interest in their role as seed dispersers, including both the herbivorous species (e.g. Klein, 1977; Janzen, 1982; Iverson, 1985; Traveset, 1990; Hartley *et al.*, 2000) and the omnivorous ones (e.g. Whitaker, 1987; Fialho, 1990; Valido and Nogales, 1994; Willson *et al.*, 1996; Lord and Marshall, 2001; Olesen and Valido, 2003; Valido *et al.*, 2003; Rodríguez-Pérez *et al.*, 2005).

Based on a large number of observations made by naturalists, many tortoises and turtles are regarded as herbivorous (25%; King, 1996) and most small, diurnal lizards as carnivorous. This commonly accepted wisdom is possibly related to the fact that most lizards primarily feed on small invertebrates (e.g. Greene, 1982; van Damme, 1999; Cooper and Vitt, 2002; Vitt and Pianka, 2005). However, a herbivorous diet is observed among lizards too. A strict herbivorous habit (70–100% plant volume in the diet; see Cooper and Vitt, 2002; Espinoza *et al.*, 2004) is generally associated with folivorous species, which are characterized by large body size, live in warm climates, and maintain high body temperatures (but see Espinoza *et al.*, 2004, for exceptions to this rule in small, cold-climate-living lizards). For example, all Iguanidae lizards (36 species) and also the 16 *Uromastyx* and three *Hydrosaurus* species (Agamidae), and some species and populations of skinks (e.g. *Corucia zebrata*, *Egernia* spp., *Tiliqua* spp., Scincidae) among others, are all specialized herbivores and possess the digestive specializations necessary for efficient foliage and stem processing (e.g. Iverson, 1982; Troyer, 1984). Thus, the conclusion is that an almost pure plant diet is uncommon in this widespread and large group of vertebrates. Estimates of the proportion of true herbivorous species are in the region of 1–3% (Iverson, 1982; Cooper and Vitt, 2002), although these values are slowly increasing as more data are becoming available on lizard diets (e.g. Espinoza *et al.*, 2004; O'Grady *et al.*, 2005). However, a number of small/medium-sized lizards regularly or occasionally eat some vegetable matter as well (i.e. they are omnivorous). For example, many insular species and also some mainland lizards from areas (or seasons) poor in arthropods are known to consume nectar, pollen and fruit (e.g. Pérez-Mellado and Corti, 1993; Valido and Nogales, 1994; Traveset and Sáez, 1997; van Damme, 1999; Cooper and Vitt, 2002; Olesen and Valido, 2003, 2004; Valido *et al.*, 2003; Espinoza *et al.*, 2004; O'Grady *et al.*, 2005). Fleshy fruits are, in general, low in fibre and protein, but high in soluble carbohydrates and water content (Jordano, 2000), and are thus easier to digest than foliage and stems. Therefore, these lizards can use such plant resources when other food resources, such as arthropods, are in short supply without any adaptive changes being required in the digestive tract, which is also typical of more folivorous species (Pearson, 1954; Rand, 1978; Búrquez *et al.*, 1986; Cooper and Vitt, 2002; Olesen and Valido, 2003; Valido and Nogales, 2003; O'Grady *et al.*, 2005).

In the rich herpetological literature, fruits are generally included within a category called 'vegetative or plant matter' and are rarely scored separately. Consequently, their importance in the diet of omnivorous lizard species has usually been underestimated. However, in the 'literature forest', the

understorey is rich in natural history reports of lizards feeding on fruits. The first testimonies we have at hand are painted motifs on pottery from northern Peru. These ceramics date back to the Mochica culture, which lasted from 200 to 100 BC to AD 700 (Larco, 2001). The first written evidence appears to relate to lizards inhabiting oceanic islands: the Canary Islands (Frutuoso, 1590, reprinted in 1964; Steindacher, 1891), the Mascarene Archipelago (Leguat, 1708, reprinted in 1981; Liénard, 1842), the Galapagos Islands (Darwin, 1845) and Jamaica (Gosse, 1851, cited in Schwartz and Henderson, 1991). These early references indicate that this phenomenon was already known by some of the naturalists of this time. We also wish to draw attention to a small specific report about the importance of lizards as seed dispersers published almost 100 years ago by Antonino Borzí (Borzí, 1911). In this first true review about saurochory, ten species of lizards were included as fruit eaters and potential seed dispersers. Recently, more than 200 examples of species of lizards feeding on fleshy fruit have been cited (Olesen and Valido, 2003); thus, we conclude that they may have a wide importance as seed dispersers. Unfortunately, most of these reports do not include any data on the quantitative importance of lizards as plant mutualists, and the accounts are rarely synthesized into generalizations of broader value to ecology and evolutionary biology. Based on a search of the literature, personal communications, and our own field research, we found that lizard–plant mutualistic interactions were much more frequent than hitherto realized (A. Valido and J.M. Olesen, unpublished results). However, quantitative information about fruit removal and seeds in scats, or quality data on dispersal of seeds to safe sites and subsequent germination are extremely scarce (see Table 2 in Godínez-Alvarez, 2004). Thus, in only a few cases do we have sufficient data to make valid comparisons with the more traditional modes of seed dispersal mediated by birds or mammals (Valido, 1999; Wotton, 2002).

Our main aim in this chapter is to revisit and synthesize the available evidence for fruit-eating lizards around the world in order to call attention to the fact that lizards need to be considered as frugivores and potential seed dispersal agents, especially in certain habitats and situations. In particular in this chapter we address:

1. The geographical distribution of saurochory;
2. The morphological characteristics of fleshy fruits consumed by lizards;
3. The taxonomic affiliation of both lizard and plant species;
4. The characteristics of their role as seed dispersers.

Inclusions and Exclusions from our Review

The available data about lizards using fleshy fruits as an alimentary resource vary in quality. Most reports and personal observations are only brief, qualitative observations of lizards feeding on fleshy fruits (e.g. *Uromastyx ornate*; Agamidae; see Bronstein *et al.*, Chapter 7, this volume). We have excluded all reports that did not explicitly mention fruit as a

separate food item. It is known that many lizards readily feed on fruit in captivity (e.g. Rogner, 1997). Such observations were also excluded if the report did not include additional field observations. Thus, only data on lizards observed feeding on fruit in nature were included. In some cases, we confirmed the presence of fruit in the diet of a lizard after personal communication with authors who only reported 'plant material' in their papers. In addition, reports without clear, unambiguous statements about the direct ingestion of fruits have not been included. For example, although infrequent fruit-eating has been reported for the tuatara (*Sphenodon punctatus*; Sphenodontidae) from Stephens and Middle Islands, New Zealand (Walls, 1981; Southey, cited in Whitaker, 1987; Ussher, 1999), based on seeds in droppings, we did not include these observations because the fruits may have originated indirectly from the fruit-eating *Hoplodactylus* gecko, which is commonly consumed by tuataras (Whitaker, 1968). A summary of our data is presented in Table 6.1 (the complete list will be published elsewhere). The systematic arrangement of lizards follows the March 2005 edition of the *European Molecular Biology Laboratory – EMBL – Reptile Database* (Uetz, 2005). We also classified lizards in relation to their geographical distribution: insular, mainland and mixed species (inhabiting islands and mainland) according to the EMBL database. Near-

Table 6.1. Taxonomic and geographical distribution of fruit-eating lizards.

Fruit-eating lizards	Number of species	Fruit-eating lizards	Islands	Mixed	Mainland	P	%
Scincidae	1306	63	36	3	24	***	4.8
Gekkonidae	1081	20	18	0	2	***	1.9
Polychrotidae	393	45	41	0	4	***	11.5
Agamidae	379	11	5	0	6	*	2.9
Tropiduridae	309	38	17	0	21	***	12.3
Lacertidae	280	27	17	2	8	***	9.6
Phrynosomatidae	125	7	1	0	6	ns	5.6
Teiidae	122	24	9	3	12	***	19.7
Anguidae	112	1	1	0	0	ns	0.9
Varanidae	59	2	2	0	0	*	3.4
Cordylidae	54	2	0	0	2	ns	3.7
Iguanidae	36	20	15	3	2	*	55.6
Gerrhosauridae	33	6	4	0	2	ns	18.2
Xantusiidae	24	3	2	0	1	**	12.5
Dibamidae	20	5	5	0	0	**	25.0
Crotaphytidae	10	2	0	1	1	ns	20.0
Corytophanidae	9	3	0	0	3	ns	33.3
Opluridae	7	1	1	0	0	ns	14.3
Total	4359	280	174	12	94	***	6.4
As percentage			62	4	34		

P, the probability that the sample of lizards differs from random (see Results). The last column is the percentage of the total of fruit-eating lizards.

shore islets were regarded as part of the adjacent mainland. For plant genera we followed Mabberley (1997). In the analysis we used MATLAB (Matworks, Natrick, Massachusetts, USA).

Synthesis of Data

Frugivorous lizards

From all the reports and observations included in our review, we found a total of 280 species of lizards from 85 genera and 18 families that consume fleshy fruits at least occasionally (Table 6.1). These observations originate from 45 islands/archipelagos and 30 mainland countries (e.g. Spain, Iran, Argentina). Fruit consumption is more often reported from islands (62%) than from mainland populations (34%). Species observed to eat fruit on both mainland and island regions only constituted 4% (see Fig. 6.1). Overall, there were many more frugivorous species on islands than would be expected by chance (Table 6.1; see below). Island species were significantly over-represented as fruit consumers in 11 out of the 18 lizard families, especially in Polychrotidae (91.1% of the registered cases), Gekkonidae (90.5%), Lacertidae (63%) and Scincidae (56.9%).

To test the null hypothesis stating that the observed distribution of frugivorous lizards is equivalent to the distribution of species between islands, islands + mainland, and mainland, we used a one-tailed Fisher's exact test for $N \times M$ contingency tables (Wells and King, 1980). Here we use as our database only the 18 lizard families (including a total of 4359

Fig. 6.1. The proportion of fruit-eating lizards (solid bars) compared with all other species (open bars) of lizard (Scincomorpha: Iguania, Gekkota, Scincomorpha) inhabiting islands, mainland or mixed. Data on geographical distributions of lizards from Uetz (2005).

species) in which frugivory is known. According to the EMBL Reptile Database, 30%, 7% and 63% of all species in these families are from islands (I), islands + mainland (IM) and mainland (M), respectively (Uetz, 2005). If we then draw a species randomly from the total pool of 4359 species, the probability of drawing an I-species must be $p_I = 0.30$, an IM-species is $p_{IM} = 0.07$, and an M-species is $p_M = 0.63$. The probability P of drawing two island species in a draw of two species is $P = p_I^2 = 0.30^2$. The probability P of drawing, for example, one I-species, two IM-species and two M-species from a trinomial random draw of five species is:

$$P = \left(\frac{5!}{1!2!2!} \right) p_I^1 p_{IM}^2 p_M^2 = 0.017$$

The general likelihood is

$$P = \left(\frac{n!}{r_I! r_{IM}! r_M!} \right) p_I^{r_I} p_{IM}^{r_{IM}} p_M^{r_M}$$

where n is sample size, r_I is number of I-species, r_{IM} is the number of IM-species and r_M is the number of M-species.

We have compiled a list of 280 species of lizards consuming fleshy fruits. Our review documented that 174 were island species, 12 occurred both on islands and mainland, and 94 were from mainland locations only (Table 6.1). We now want to know whether this is a random draw from the total species pool. To find out the exact probability, we computed the sum of P values by generating all tables that are more extreme than the table given, i.e. more island species. Exact p -values tend to be more conservative, since we are including all cell frequencies with the same fixed marginal totals as the observed one. The probability of getting our sample or one that is even more island-skewed was $P = 1.55 \times 10^{-29}$. Thus, many more frugivorous species occur on islands than would be expected by chance.

This pattern also holds true at the family level. We repeated the same calculations as above for each family (Table 6.1). Island species consuming fruit are highly over-represented in 11 of the 18 families. Exceptions are: Anguidae, Crotaphytidae, Cordylidae, Phrynosomatidae, Corytophamidae, Opluridae and Gerrhosauridae. However, in these families, the number of fruit-eating lizards was very small.

Lizard plants

Worldwide, a total of 414 species, 206 genera and 101 families of plants with fleshy fruits have been reported in the diet of these 280 species of lizards. This figure is clearly an underestimate, since many reports lack data about the identity of the species whose fruits are consumed (e.g. Auffenberg and Auffenberg, 1988; Beller and Avila, 2002). In spite of this shortcoming, these results reveal some interesting patterns that need to be considered in future studies. For example:

1. Lizards consume fruits that are very diverse in type, size and colouration.
2. Fruit consumption occurs on island and mainland areas from a wide latitudinal range.
3. Fruit consumption by lizards is recorded from all continents and many oceanic islands.

In short it is a very widespread phenomenon affecting plants with a wide range of fruit structures.

From this lizard–fruit database, five families: Moraceae (with 30 species), Palmae (27), Rubiaceae (25), Solanaceae (25) and Cactaceae (24) account for 34% of all species of plants that lizards feed on. Most species are scattered widely in the phylogenies of the angiosperms and gymnosperms. The fruit types consumed are highly diverse: including syconium (e.g. *Ficus* spp.; Moraceae); arcestd (e.g. *Juniperus phoeniceae*; Cupressaceae); berry (e.g. *Hippomane mancinella*; Euphorbiaceae); drupe (e.g. *Corynocarpus laevigatus*; Corynocarpaceae); polydrupe (e.g. *Rubus inermis*; Rosaceae); and arillate seed (*Annona araracuara*; Annonaceae).

This diversity in fruit types is also seen in their coloration. We looked for associations between fruit colour and consumption by lizards by comparing the colours of species consumed by lizards to the colour spectrum of the fleshy fruits available. We used data from three distant archipelagos, the Canary Islands (Fig. 6.2), the Balearic Archipelago (Fig. 6.3) and New Zealand

Fig. 6.2. A comparison of the proportion of colours of fleshy-fruited native plants from the Canary Islands (open bars) and those reported in the diet of the endemic lacertid species (*Gallotia* spp.) inhabiting these islands (solid bars). Data from Valido (1999).

Fig. 6.3. A comparison of the proportion of colours of fleshy-fruited native plants from the Balearic Archipelago (open bars) and those reported in the diet of the lacertid *Podarcis lilfordi* (solid bars). Data from Pérez-Mellado and Traveset (1999) and the Balearic Virtual Herbarium (<http://herbarivirtual.uib.es>).

(Fig. 6.4), which are all well represented in our lizard–fruit data set. We looked for any association between colour of fruit consumed by lizards and colour spectrum of fleshy fruits on these three archipelagos. Lord and Marshall (2001) and Lord *et al.* (2002) presented frequency distributions of colours of fleshy fruit for a large sample of New Zealand species. In our analysis, we used their data but lumped several of their colour categories (pink into red, yellow and orange; and purple into black). In addition, we introduced a ‘transparent’ fruit colour category, and placed the New Zealand *Muehlenbeckia* and the Canarian *Rubia fruticosa*, *Plocama pendula* (Rubiaceae) and *Jasminum odoratissimum* (Oleaceae) into this category. Canarian and Balearic data came from our own database and the Balearic ‘virtual herbarium’ (<http://herbarivirtual.uib.es/>), respectively. The numbers of species producing fleshy fruit were 77, 57 and 216, from the Canary Islands, the Balearic Archipelago and New Zealand, respectively. The numbers of fleshy-fruited species consumed by lizards in these three archipelagos were 41, 11 and 14, respectively.

The distributions of fruit colours in the flora from these distant areas were similar. As in most floras, colours such as red, yellow-orange and black constitute a majority of species (> 75%). Less well represented (12–16%) are white, blue and transparent colours. However, in spite of very similar fruit

Fig. 6.4. A comparison of the proportion of colours of fleshy-fruited native plants from New Zealand (open bars) and those reported in the diet of lizard species (solid bars). Data from Whitaker (1987), Lord and Marshall (2001) and Lord *et al.* (2002).

colour spectra from the three archipelagos, lizard preferences varied. For example, in contrast with data obtained from the New Zealand flora, there were no fruit colours particularly associated with saurochory in either the Canarian flora (Fig. 6.2) or the Balearic ones (Fig. 6.3). For example, unlike the New Zealand frugivorous lizards (see Lord and Marshall, 2001; Lord *et al.*, 2002), red (*Tamus edulis*; Dioscoreaceae), black (*Rhamnus crenulata*; Rhamnaceae), white (*Bencomia caudata*; Rosaceae), orange (*Canarina canariensis*; Campanulaceae) and translucent (*Plocama pendula*; Rubiaceae) fruits, which can be up to 27 mm in diameter (*Canarina canariensis*) with seeds up to 9 mm in diameter and the number of seeds per fruit up to 1395 (in *Canarina canariensis*) are heavily consumed in different habitats and islands by the Canarian lizards (*Gallotia* spp.; Lacertidae).

Lizards as Frugivorous Vertebrates

Our review and analysis reveal that fleshy fruits may be a more important food resource to some species of lizards than hitherto recognized in the specific literature about frugivores and seed dispersal. A remarkable result of our compilation of 280 fruit-eating species is that it is not only classical herbivorous lizards, such as the Iguanidae, that eat fruits. The omnivorous

and, surprisingly, many other species commonly considered to be truly insectivorous and/or carnivorous consume fruits as well. For example, within the Varanidae, which is usually considered a strictly carnivorous family, some species from Malaysia and the Philippines have been reported as feeding extensively (*Varanus olivaceus* – Auffenberg, 1988; Bennett, 2005), mostly (*Varanus mabitang* – Struck *et al.*, 2002) or sporadically on fleshy fruits (*Varanus* spp. – Yasuda *et al.*, 2005).

All major lineages of vertebrates use fruit as an alimentary resource, but birds and mammals are generally considered to be the only significant dispersers of seeds for vertebrate-dispersed plants. Fleming (1991) reported that 35.5% of bird and 19.6% of terrestrial mammal families contain species that, in some instance, use fruits as a food resource. However, among birds these values are lower (15.5%) if we only consider strictly frugivorous species with a nearly total fruit diet (Jordano, 2000). For lizards, we found that species from 69% of the 26 lizard families (at least 6% of all species) consume fleshy fruit in some quantity. However, since more attention is now being paid to this type of plant–animal mutualism, more cases are likely to be added in the near future. For example, there are records of lizards consuming flowers (e.g. *Sceloporus jarrovi* – Ballinger and Ballinger, 1979; *Liolaemus donosoi* – Ortiz, 1975), seeds (e.g. *Agama yemenensis* – Al-Johany, 1995), nectar (e.g. *Anolis conspersus* – Echternacht *et al.*, 2000; *Rhacodactylus auriculatus* – Bauer and Sadler, 2000), sap (e.g. *Gehyra australis* – Greer, 2005; *Phelsuma* spp. from Madagascar – Fölling *et al.*, 2001), pollen (e.g. *Phelsuma sundbergi* – Murphy and Myers, 1996; *Liolaemus platei* – Weiser *et al.*, 1975) and foliage (e.g. *Acanthodactylus erythrurus* – Busack and Jasick, 1982; *Podarcis milensis* – Adamopoulou and Legakis, 2002). At least some of these omnivorous species may be found to eat fleshy fruits as well. However, in order to make a more precise comparison of the relative importance of birds, mammals, reptiles and fish as frugivores, we need to know both the total number of frugivorous species in each group and also the quantitative importance of fruit in their diet. Unfortunately these data are not available for all groups.

Seed dispersal by reptiles was probably the most primitive condition (Tiffney, 2004). As birds and mammals evolved, they became the main dispersal agents in many habitats. However, the herbivory (or in some cases, frugivory) condition was retained in some chelonians and also in the most primitive extant lizard family, the Iguanidae (Estes, 1983). These two reptile groups are the two most commonly used examples of seed dispersers in the frugivory literature when reptiles are cited. However, some modern species of lizards, traditionally considered primarily carnivorous or insectivorous, ‘regain’ this relict function when other food resources (i.e. arthropods) are no longer available (see below).

Another interesting conclusion to be drawn is that frugivorous lizards are geographically widespread but occur disproportionately on islands. For example, although insular species constitute less than one-third of all recognized species worldwide (Fig. 6.1; Uetz, 2005), they are significantly over-represented in our lizard-frugivory database.

Why Islands?

Island food-webs are relatively more simple than those from the mainland areas. The difference arises because of a lower species diversity (Carlquist, 1974), taxonomic disharmony (some groups are absent or poorly represented; Baur, 1891), and high densities of certain taxa (i.e. density compensation: an increase in abundance in the absence of interspecific competitors; MacArthur *et al.*, 1972) on islands. In this respect, species-poor islands are generally characterized by the presence of an extremely high density of lizards (see Table 2 in Rodda and Dean-Bradley, 2002). For example, the terrestrial vertebrate with the highest recorded density is *Sphaerodactylus macrolepis* (Gekkonidae) from Guana Island (67,600 individuals ha^{-1} ; Rodda *et al.*, 2001). Only limited data are available on arthropods. It is known that island areas are likely to have relatively fewer species of insects than nearby mainland areas (Janzen, 1973; Ebenman and Nilsson, 1982). This pattern is evident in flower visitors; a lower number of pollinators have been detected visiting island plants compared with conspecific mainland populations (Barrett, 1998; Olesen and Jordano, 2002; J.M. Olesen and A. Valido, unpublished results). Thus, high densities in island lizards, together with arthropod scarcity and a reduced exposure to predation, may force predominantly arthropod-eating lizards to expand their trophic niche by exploiting other available resources: fruits being an important one (Olesen and Valido, 2003). Pulp from fleshy fruit is less energy-rich than other animal food items (i.e. insects), providing fewer calories and less protein per gram than animals do (see Table 6.3 in Jordano, 2000), but it is a food resource present in most island habitats.

In several families of lizards, frugivory (or omnivory) and insularity are significantly correlated (van Damme, 1999; Cooper and Vitt, 2002; see also Table 6.1). This pattern is also evident when comparing island-mainland populations within species. For example, in 1960 the large (> 500 mm snout-vent length) *Tupinambis merianae* (Teiidae) was introduced from the South American mainland to Fernando de Noronha Archipelago 345 km off the north-eastern Brazilian coastline (Péres, 2003). On the Archipelago it includes a higher proportion of plant material, especially fruits of both native and introduced species, into its diet than in its original mainland habitat (Mercolly and Yanosky, 1994; Kiefer and Sazima, 2002). Other known examples from omnivorous species are populations of *Podarcis hispanica* (Lacertidae) from the Iberian Peninsula (Mellado *et al.*, 1975) compared with populations from Columbretes Islands (Castilla and Bawens, 1991), and *Cnemidophorus lemniscatus* and *Ameiva ameiva* (Teiidae) from Providence Island (Janzen, 1973) which are more omnivorous than populations in several localities on the mainland (e.g. Vega *et al.*, 1988; Magnusson and da Silva, 1993; Vitt and Carvalho, 1995; Colli *et al.*, 1997). Although clearly more data are necessary, these intraspecific comparisons suggest that the increase in the use of fleshy fruits by island lizards is in part due to some common ecological factors occurring in these insular habitats. The use of phylogenetic contrast analysis or independent pair-wise comparisons (in the absence of a fully

resolved phylogeny) and controlling for lizard size variation would be the next step in testing this ecological pattern.

The arthropod-scarcity hypothesis can also be extended to other habitats characterized by a constant or seasonal scarcity of animal prey. For example, high mountains, arid regions and caves are lacking in arthropods compared with most other habitats (Mautz and Lopez-Forment, 1978; Pietruszka *et al.*, 1986). Several skinks (Scincidae) from arid regions consume plant material during dry periods when arthropods are scarce (Kuchling, 1970; Symon, 1979; Schleich *et al.*, 1996). In general, insects are scarcer in dry seasons than in the wet seasons (Churchill, 1994; Griffiths and Christian, 1996; Christian *et al.*, 2003), and such a seasonal scarcity of arthropod food may select for omnivory in lizards.

Lizards as Seed Dispersers?

In 1985, the herpetologist John B. Iverson used this query to title a short note calling attention to the role of herbivorous lizards as seed dispersers. In the note, he analysed the percentage of germination for seeds removed from the droppings of the iguanas *Cyclura rileyi* and *C. carinata* from the Bahamas and the Turks and Caicos Islands. An increase (although not statistically significant) in seed germination in *Coccoloba uvifera* (Polygonaceae) seeds passing through the digestive tract (43.8%), compared with control seeds (27.5%), was observed. Although without control seeds for comparison, high levels of germination (85%) were obtained for *Casasia clusiaefolia* (Rubiaceae) seeds collected from *Cyclura* faecal pellets. In this pioneer contribution, the author pointed out that lizards can be considered as legitimate seed dispersers, since seeds were not damaged and germination was enhanced in some cases, even though the average passage time through a lizard gut is around 4 days (Iverson, 1985). As far as we know, this is the first published experimental evidence showing that lizards are legitimate seed dispersers. However, more examples are necessary in order to generalize Iverson's (1985) results and to compare them with results obtained from other frugivore groups (birds and mammals).

Fortunately, in recent decades there have been some studies undertaken, and about 25 papers dealing with the effects of seed passage through lizard guts have been published (reviewed in Traveset, 1998; Traveset and Verdú, 2002; A. Valido, unpublished results). They cover 40 plant species belonging to 17 families, and 17 lizards belonging to seven families. Although the number of experiments with lizards were much fewer than similar bird (153) and mammal (119) experiments, seeds consumed by lizards germinated just as well as seeds consumed by birds and mammals. The proportion of examples where germination of the seeds passing through the digestive tract of lizards was enhanced (25%), unaffected (57%) or inhibited (18%) was similar (χ^2 test; $P = 0.28$) to those observed when birds (36%, 48%, 16%, respectively), non-flying mammals (39%, 42%, 19%) and bats (25%, 67%, 8%) were the frugivorous species (Traveset, 1998).

A more interesting comparison would be to know the outcome of passage through a lizard digestive tract relative to other sympatric native frugivores (birds and mammals) for the seeds of a given species of plant. Greeff and Whiting (1999) observed no significant differences in germination success of *Ficus cordata* (Moraceae) seeds collected from lizard (48%; *Platysaurus broadleyi*; Cordylidae), bird (34%; mostly *Onychognathus nabouroup* and *Pycnonotus nigricans*) and rock hyrax (29%; *Procavia capensis*) droppings and controls (48%). In other tri-species comparisons, Morales-Mávila *et al.* (2005) showed that seeds being dispersed by *Iguana iguana* had a higher percentage of germination (86.7%) than those from spider monkey, *Ateles geoffroyi* (45%), toucan, *Ramphastos sulfuratus* (33.3%) or controls (20%). In contrast, Mandujano *et al.* (1994) showed that endocarps consumed by *Ctenosaura pectinata* (Iguanidae) germinated less successfully (35%) than those consumed by white-tailed deer (*Odocoileus virginianus*; 72%) or controls (63%).

In studies comparing the germination of seeds passed through lizards and birds, similar results were obtained. For example, seeds from *Plocama pendula* and *Rubia fruticosa* (Rubiaceae) dispersed by sylviid warblers (*Sylvia* spp.), lacertid lizards (*Gallotia* spp.) and control (Valido, 1999; Nogales *et al.*, 2005) all showed a similar percentage germination. An analogous result was also found by Rodríguez-Pérez *et al.* (2005) for several Mediterranean plant species being dispersed by lizards and birds. Reanalysing their data, we found that seeds obtained from blackbird (*Turdus merula*) and *Podarcis pityusensis* (Lacertidae) droppings and controls resulted in a similar germination success for *Rhamnus alaternus* (Rhamnaceae), *Rubia peregrina* (Rubiaceae), *Rubus ulmifolius* (Rosaceae), *Solanum luteum* and *Solanum nigrum* (Solanaceae). In addition, an increase in the germination success of seeds passed through lizards was obtained for *Rhamnus ludovici-salvatoris* (Rhamnaceae) compared with seeds that had passed through birds.

Thus, according to these comparisons, a cautious preliminary answer to Iverson's question would be 'yes': lizards can be regarded legitimate seed dispersers in the same way as frugivorous birds and mammals with regard to the effects on germination of the passage of seeds through the digestive tract.

Whether an animal is a legitimate disperser is just one of the aspects to take into account when we want to know the contribution of seed dispersers to plant fitness (seed dispersal effectiveness; *sensu* Schupp, 1993). To be effective as a seed disperser, lizards must transport viable seeds beyond the parent plant, and deposit them in a site where their chances of survival to adult plants are good. Accordingly, effectiveness can be analysed quantitatively (related to number of seeds being dispersed) and qualitatively (related to the probability that a seed will recruit a new adult individual) (Schupp, 1993; Jordano and Schupp, 2000; Schupp, Chapter 20, this volume). Only two studies (both from islands: Valido, 1999; Wotton, 2002) simultaneously included several aspects of the qualitative and quantitative components of lizard disperser effectiveness. The species studied were *Gallotia galloti* (Lacertidae) and *Plocama pendula*

(Rubiaceae) from the Canary Islands (Valido, 1999), and *Hoplodactylus maculatus* (Gekkonidae) and *Croprosma propinqua* (Rubiaceae) from New Zealand (Wotton, 2002). The studies showed that these omnivorous lizards appeared to be effective seed dispersal agents because: (i) the lizards removed a considerable proportion of fruits from plants; (ii) the ingestion of seeds had no detrimental effect on germination success; and (iii) the lizards tended to deposit seeds in microhabitats where the probability of germination and seedling establishment was improved more frequently than in hostile microhabitats. These results, although only based on two examples, demonstrate that lizards may be considered to be effective seed dispersers.

Although more the study of cases is necessary before we can conclude that lizards are generally effective dispersers, additional evidence, including some of the aspects of the quantitative component of effectiveness, have been found with different species of lizards which may support this conclusion. Extensive use of fleshy fruits (high frequency of occurrence or volume; > 40%) in the diet has been found in: *Ameiva exsul* (Patterson, 1928), *Ameiva ameiva* and *Cnemidophorus lemniscatus* (Janzen, 1973), *Anolis equestris* (Brach, 1976), *Liolaemus nigromaculatus* (Ortiz and Riveros, 1976), *Podarcis* spp. (Salvador, 1986; Pérez-Mellado *et al.*, 2005), *Leciocephalus carinatus* (de Armas, 1987), *Darevskia rudis* (Franzen, 1991), *Klentropyx striatus* (Magnusson and da Silva, 1993), *Tropidurus torquatus* (Côrtes-Figueira *et al.*, 1994), *Lacerta lepida* (Hóðar *et al.*, 1996), *Cnemidophorus lemniscatus* (Vitt *et al.*, 1997), *Gallotia* spp. (Valido *et al.*, 2003; Valido and Nogales, 2003), *Anolis garmani* (Herrel *et al.*, 2004) and *Psammotromus algirus* (Calviño-Cancela, 2005), among others.

Although most lizards are not as mobile as many birds and mammals, and long-distance seed dispersal is uncommon, lizards can be effective in transporting seeds sufficiently far away to avoid density-dependent mortality, which may occur below the parent plants. For example, Greeff and Whiting (1999) observed dispersal distances up to 187 m in the case of seeds of *Ficus cordata* (Moraceae) being dispersed by *Platysaurus broadleyi* (Cordylidae) from South Africa. Whitaker (1968) recorded 73 m as the maximum distance movement by *Hoplodactylus duvaucelli* (Gekkonidae) in New Zealand. This author also found dispersed seeds 12 m away from the nearest fruiting plants (Whitaker, 1987). Barquín and Wildpret (1975) cited up to 50 m for seeds of *Plocama pendula* (Rubiaceae) being dispersed by *Gallotia galloti* from the nearest potential parent plant. Côrtes-Figueira *et al.* (1994) reported 6.9 m as maximum dispersal distance of *Melocactus violaceus* (Cactaceae) seeds by *Tropidurus torquatus* (Tropiduridae). Using spatial distribution of seedlings of *Daphne rodriguezii* (Thymelaeaceae) from a population where seeds of this species are only being dispersed by lizards (*Podarcis lilfordi*), Traveset and Riera (2005) estimated dispersal distances up to 4 m away from any reproductive adult. However, longer seed dispersal distances would be possible because a gut passage time of 4 days has been reported for this species (Traveset and Riera, 2005). These different seed dispersal distances may be due to differences in lizard body size, gut passage time, alternative

food sources, environmental temperature, foraging patterns and social behaviour, among others.

Another important aspect to consider in relation to quality of seed dispersal is that lizards may also deposit considerable quantities of seeds in places suitable for germination and subsequent plant recruitment for the plants they are dispersing, including cracks and crevices in rocks, or sheltered places adjacent to stones (e.g. Whitaker, 1987; Valido and Nogales, 1994; Valido, 1999; Wotton, 2002; Benítez-Malvido *et al.* 2003; but also see Fialho, 1990). Generally, these areas show some common characteristics, for example they have relatively high humidity, low aridity and low predation rates. Lizards may potentially also be responsible for vegetation composition and distribution in such habitats (Valido and Nogales, 1994).

A Lizard Fruit Syndrome?

Fruit syndromes (correlated fruit traits associated with some particular group of frugivores) have been a classical topic in the frugivory literature. For example, small brightly coloured fruits persisting on plants after ripening have generally been associated with birds, while large green/brown-coloured fruits that fall to the ground after ripening are associated with mammals (e.g. Herrera, 2002). A fruit syndrome for reptiles was first proposed by Borzí (1911), possibly based on earlier observations by Beccari (1877). He proposed three tentative types of saurochorous fruits based on what was known at that time: (i) the *Scioide* (which included *Ficus*, *Capparis* and *Opuntia* fruits); (ii) the *Arum*; and (iii) the *Viola* types. In addition, Borzí formulated the idea that the presence of fruits on the trunk near the ground (caulicarpy) could be an adaptation to seed dispersal by reptiles. Later, van der Pijl (1969, re-edited in 1982) proposed that reptile-fruits are aromatic, coloured, and may be borne near the ground on a trunk or dropped to the ground when ripe. This description is probably based on the fact that the classical reptile-fruit known in van der Pijl's time, *Ginkgo biloba* (Ginkgoaceae), clearly fits this description: 'greenish drupe-like ovule-seeds with a faint smell which fall to the ground' (p. 131; van der Pijl, 1982). Nowadays, many examples are known that do not fit this syndrome; many lack odour and colours vary widely. For example, Varela and Bucher (2002) found that the odourless fruit of *Celtis pallida* (Ulmaceae) and *Capparis atamisquea* (Capparaceae) had a high frequency of occurrence (59%) in *Teioudon teyoudon* (Teiidae) droppings. Several odourless lizard-fruits are known from the Balearic Archipelago (Pérez-Mellado and Traveset, 1999) and the Canary Islands (Valido *et al.*, 2003) as well.

Recently, and using a comprehensive database of fruit characters from the New Zealand flora ($n = 246$ plant species), Lord and Marshall (2001) and Lord *et al.* (2002) found some support for a lizard-fruit syndrome. They suggest that lizards may be of importance in the evolution of fruit

from shrub species with divaricated branches, growing in open, dry habitats. They also proposed that fruit-eating lizards favour small, elliptically shaped, white or pale-blue to sky-blue fruits. Captive *Oligosoma* lizards prefer blue and white *Coprosma* fruit to white and red ones. However, as Lord *et al.* (2002) also point out, this lizard dispersal syndrome cannot be applied to other floras, and differences can be related to the taxonomic composition of the lizard fauna. The guild of frugivorous lizards from New Zealand consists of six species of Gekkonidae and 13 species of Scincidae (Whitaker, 1987, and references therein; Patterson, 1992; Cogger *et al.*, 1993; Spencer *et al.*, 1998). Many of these lizards (e.g. the geckos *Hoplodactylus* spp.) are nocturnal, whereas practically all the *Oligosoma* skinks are diurnal. It is likely that this lizard-fruit syndrome described for New Zealand is location-specific and cannot be applied to other areas. For example, a comparison of the frequency of fruit colours in lizard diets from the Canary Islands (Fig. 6.2) and the Balearic Archipelago (Fig. 6.3) floras with the New Zealand flora (Fig. 6.4) show distinct differences. This is likely to be caused (in part) by practically all the frugivorous lizards from the Canaries and the Balearic Archipelago being diurnal lacertids.

In addition, we need to incorporate information about the evolution of Squamata feeding strategies (Vitt, 2004) and plant phylogeny (Jordano, 1995), in order to test for any association of fruit traits with frugivory in lizards. For example, the Iguania lizards use visual signals to detect prey and their tongue to capture it. Gekkota species, on the other hand, use visual and olfactory prey discrimination, and use their mouth for capture and tongue for cleaning face and eyes. Scincomorpha use visual cues and their vomeronasal organs in chemical discrimination. Visual prey detection may be the primitive state (see Fig. 1 in Vitt, 2004). This means that plants whose fruits are consumed and seeds dispersed by different lizard clades are under very different selection pressures according to the predominant cues used by different lizard taxonomic groups for food selection. With respect to plants, Jordano (1995) found that the evolutionary history of lineages accounts for a great proportion of the variation in fruit traits, and only fruit size (diameter) showed an important interspecific variability independent of phylogeny. Thus, if lizards are important selective agents on fruit traits, we may one day discuss a gecko fruit syndrome and an iguanid fruit syndrome, among others, similar to the distinction between different mammal groups, such as bat-fruit and primate-fruit syndromes.

Avenues for Future Research

Although lizard frugivory and seed dispersal are of particular relevance in some specific geographical situations (principally islands, but also xeric habitats), this topic is a slowly emerging research focus within mutualism studies in general, and seed dispersal research in particular. However, since little has been published on the topic of seed dispersal by lizards, any current

interest on ecological and evolutionary plant–frugivore interactions (e.g. Herrera, 2002), including some aspects already published in this volume (e.g. digestive treatment (Traveset *et al.*, Chapter 4), spatial patterns of seed shadows (Dennis and Westcott, Chapter 9), demographic consequences (Godínez-Alvarez and Jordano, Chapter 17) and consequences of frugivore extinction (Silva *et al.*, Chapter 26)) are also relevant for studies focusing on lizards. We have shown that a frugivorous diet is more common in lizards than previously appreciated, but at the same time, many information gaps (e.g. lizard diet) have hampered our efforts to make solid generalizations, especially in relation to island species (see a compilation of the herpetological literature at <http://www.herpllit.com/>).

Apart from this necessary basic natural history information, the next step is to compare patterns of frugivory and the process of seed dispersal by lizards to that by birds and mammals in an attempt to establish the importance of lizards for plant regeneration. Earlier we highlighted several future research directions and several key questions that have emerged from our analyses, which focus on the interactions between frugivorous lizards and plants. When more data become available from more sites, a clearer understanding of the importance of lizards as seed dispersers will emerge. Particularly important is their relevance to conservation, since lizards may be the only seed dispersers of some species of plants, for example *Withania aristata* (Solanaceae), *Neochamaelea pulverulenta* (Cneoraceae), and *Kunkeliella subsuculenta* (Santalaceae) from the Canary Islands (A. Valido, personal observation), and *Daphne rodriguezii* (Thymelaeaceae) from the Balearic Islands (Traveset and Riera, 2005), among others.

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