Lizards as pollinators and seed dispersers: an island phenomenon

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Although it is well established that many insects, birds and mammals serve as important pollinators and seed dispersers of flowering plants, the role of lizards in these processes has traditionally been considered as rare and less important. However, recent work shows both that their role as mutualistic agents has been underestimated and also reveals a striking pattern – that pollination and seed dispersal by lizards is most common on islands. We argue that this island phenomenon occurs because island lizards reach very high densities (density compensation) and experience a lower predation risk than do those on the mainland and, consequently, can expand their diet to include nectar, pollen and fruit. Although further empirical evidence is needed to confirm this explanation, such relationships could be ideal systems with which to study fundamental ecological problems, such as niche shifts, ecological release and competition.

Lizards are usually ignored as mutualistic agents in the mainstream literature possibly because most are regarded as being carnivorous [15–17], and only ~1% are known to be truly herbivorous, (i.e. consuming substantial amounts of plant parts) [17]. However, many lizards have a broad diet, which can include fiber-poor components, (i.e. flowers, fruit, nectar and pollen) [17]. Published lists of lizard diet often include fruit, nectar and pollen into a general plant food category. Thus, our view about foraging in lizards, in general, is also changing.

Here, we consider recent studies of lizard–plant mutualisms and reach a surprising general conclusion: although they occur on the mainland, lizards as mutualistic agents are mainly confined to islands. Island lizards often drink nectar and eat fruit pulp in spite of the small amount of protein in these foods [1,18]. Why? Our answer...
is simple and straightforward. We use an argument based on density compensation, diet expansion and low predation levels to explain this phenomenon.

Evidence of lizards as nectar consumers and pollinators

In New Zealand, Hoplodactylus geckos visit flowers of several native plant species for nectar and pollen (Fig. 1b) [5]. More than 50 geckos, together with birds and bees, have been observed to pollinate flowers of a Metrosideros excelsa (Myrtaceae) tree. Experimentally increasing the volume of its viscous nectar (55% sugar) by 40–100% resulted in more geckos visiting the flowers [6]. Two-thirds of the geckos carried large amounts of pollen, suggesting that they might therefore act as pollinators [5]. However, since the arrival of humans in New Zealand, its lizard fauna has declined [5], and, today, the role of lizards as pollinators can only be assessed in unmodified habitats on offshore islets.

Lizard pollination is also known from the Balearic Islands. Both insects and the diurnal lacertid lizard Podarcis lilfordi, a Balearic endemic, visit flowers of the native Euphorbia dendroides (Euphorbiaceae) for its highly concentrated nectar. Traveset and Sáez [7] compared two sites with high and low lizard density. At the high-density site, lizards had a flower visitation rate that was eight times higher than that of the insects. Here, E. dendroides seed set was twice as high as at the site with a low density of lizards. Insect visitation was the same at both sites. Podarcis lilfordi is therefore regarded as an important pollinator of E. dendroides and has been recorded as a possible pollinator of at least 23 plant species [7,19,20].

In these examples, the lizards have a broad diet and thus it is probably incorrect to invoke a tight species—species coevolution. One recent study has, however, explicitly stressed the coevolutionary nature of a lizard—plant pollination system [8]. Above the timberline in Tasmania, the small, very abundant, endemic snow skink Niveoscincus microlepidotus visits one of the most abundant plants in its habitat, Richea scoparia (Proteaceae). Flower-visited skinks tear off the calyptra, a special floral structure covering the style, anthers and nectar. They then consume both the calyptra and nectar. Although the lizards never carry any pollen, their exposure of the style and anthers makes these accessible to insects, which then pollinate the flowers.

A more elaborate pollination system suggesting a common evolutionary history is that between day geckos Phelsuma and many different plants on islands in the Indian Ocean. These geckos spend much time consuming nectar, pollen and fruit [9]. Before the arrival of humans and a range of predators to the Indian Ocean islands, geckos must have been more frequent [21] and, consequently, several plant species might currently suffer from pollinator limitation.

Compiling these reports and personal observations, we find that flower visitation and/or pollination have been reported for 57 lizard species in seven families (Table 1). Thirty-five of these species are insular (17 islands and/or archipelagos), and only two are reported from the mainland (Baja California and Florida). Lizard—flower visits have been sampled intensively from both island and mainland sources, albeit not systematically, and we strongly believe that there is no serious sampling bias. Thus, we conclude that lizards as flower visitors are predominantly an island phenomenon.

Evidence of lizards as fruit consumers and seed dispersers

Ancient groups of lizards are recognized as important seed dispersers of the first gymnosperms and angiosperms [22]. Among more modern reptiles, however, only tortoises are regarded as important seed dispersers, because ~25% of tortoises today are herbivorous [23]. The first reference to the potential role of lizards as seed dispersers was possibly by A. Borzì [3] in 1911, who listed examples of lizards feeding on fruit, and also proposed the tentative (and early evolutionary) idea that a presence of fruits on trunks and branches (caulifrugy) could be an adaptation to frugivorous reptiles.

However, it was not until the 1980s that A.H. Whitaker [5] began to promote the importance of lizards as seed dispersers of many native New Zealand plants. He reported that four gecko species and nine skink species fed on fruit, and that the skinks, Oligosoma grande and Cyclodina alani, and the gecko Hoplodactylus maculatus, had high frequencies of fruit remains in their droppings. As many as 18 New Zealand lizard species are now known to feed frequently on fruit [14].

In the Canarian archipelago, ten endemic lizard species (seven lacertids and three skinks) feed on fruit, although the importance of fruit in their diet and their role as mutualistic agents have been studied in only a few cases. For Gallotia galloti inhabiting lowland xeric habitats in Tenerife, fleshy fruit is the principal component of its diet (>50% vol) during seven months of the year. In the smaller G. atlantica from Fuerteventura, 12% of its droppings include fruit remains (10], A. Valido, PhD thesis, University of La Laguna, 1999). Fleshy fruit is also an important food for two endemic Balearic lizards, P. lilfordi and P. pityusensis. Both consume high proportions of fleshy fruit, 38% and 53% (frequency of occurrence), respectively [19,24] and, during the year, they frequently eat fruit from at least 26 species [20]. Fruit is also often consumed by other insular lizards, such as those from the West Indies [25], Mascarenes [26] (Fig. 1c), Seychelles [21], Philippines [27], New Caledonia [28], and Palau Islands [29].

In total, fruit eating has been reported for 202 lizard species in 19 families (Table 1). Sixty-eight percent of these

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<th>Table 1. Island–mainland distribution of reported flower-visiting and fruit-eating lizard speciesa</th>
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<td>No. of flower-visiting spp.</td>
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aData taken from [5,8,17,21,25,27,28,54–63] and personal communications.
species are from islands (c. 50 islands and/or archipelagos). This provides strong evidence that lizards as fruit consumers are also mainly an island phenomenon.

Why are mutualistic lizards generally confined to islands?
From the literature, we found four potential reasons for why island lizards might include more floral resources and fruit into their diet compared with adjacent mainland species. Islands might have: (1) a surplus of floral food and fruit for lizards; (2) a scarcity of arthropod food (insects and spiders) for lizards [30]; (3) larger lizards pre-adapted to a herbivorous diet [31,32]; and (4) a reduced predation risk to lizards [33].

We are unaware of any evidence that plants on islands produce more nectar or fruit than do mainland species. Therefore, we suggest that when floral resources and fruit are more abundant on islands, it is because they are less harvested. Because most flower visitors are insects and most fruit consumers are birds and mammals, these groups might have lower densities on islands compared with similar-sized areas on the mainland.

A scarcity of arthropods on islands
A recent review [34] concludes that island plant species have fewer flower-visiting insect species than do comparable mainland plant species. However, the actual abundance of insects might be more important to unpollinated plants and hungry lizards than is the number of insect species alone. Classic niche theory suggests that a lower species density on islands means weaker interspecific competition potentially leading to a niche expansion and/or shift and subsequently an increase in density [a phenomenon termed density compensation (DC)], at least for some species [35].

However, based on current results, island insects do not show DC [30,36], either in nature or in experiments [37], but more data are needed. In 1973, Janzen commented that insect communities on islands received no attention in the literature [30], and this has not changed much. In an extensive study based on sweep-net sampling, Janzen [30] described species richness and abundance of Coleoptera (beetles) and Hemiptera (bugs) from the Costa Rican mainland and Caribbean island sites. Reanalyzing his data, we find that an average mainland sweep-net series contains eight times as many species and individuals of beetles overall as does an island series, suggesting that these island beetles do not demonstrate DC. Thus, we can conclude from this isolated study [30] that islands are potentially poor in insect species richness and abundance. In another study from Baja California, Case compared islands in the adjacent Sea of Cortez [38] with equivalent mainland areas and found that arthropod biomass was four times as low on islands. Habitat differences could explain the difference. However, comparing similar cacao plantations on Dominica Island and in Costa Rica, Andrews [39] showed that, even in these very similar habitats, the dry weight of arthropods on islands was one-third lower than that in Costa Rica. The general conclusion, albeit still poorly supported, is that island insects do not density compensate. The evidence for DC of spider species is less certain [40].

Thus, island plants might lack insect pollinators and island lizards probably suffer from a shortage of insect food. These two hypotheses could explain why lizards on islands include floral and fruit resources in their diet.

Is there a scarcity of frugivorous birds and mammals on islands?
Native mammals, except bats, are generally absent from islands and there are also fewer bird species found on islands [35]. Some bird species density compensate, whereas others do not [35,41]. If insectivorous rather than frugivorous birds show DC, competitive relaxation might facilitate a shift in the diet of lizards from arthropods to fruit. However, there is little evidence for such a guild-specific variation in DC. For example, in South Africa, in a series of increasingly smaller forest fragment ‘islands’, Cody [42] compared DC responses of insectivorous and fruit/seed/nectar-consuming birds, and found that the first guild demonstrated DC, whereas the last three did not.

The diet of small and large lizards
Vegetative plant parts, such as leaves and stems, vary significantly in their structure and composition. They have a high content of cellulose and are more difficult to digest than are nectar, pollen and fruit; therefore, the digestive system of truly herbivorous lizards is usually specialized [17,33,43]. For digestive and also antipredatory reasons, evolution of herbivory in general is correlated with an increase in body size [17]. Certain thresholds in jaw power, digestive efficiency and body temperature for microbial decomposition have to be exceeded. For this reason, it has been observed that only lizards >100 g in weight are successful vegetarians [32] and truly herbivorous lizards are the largest extant lizards (excluding the varanids), such as iguanas [17].

By contrast, lizards <100 g in weight eat arthropods [15,32]. However, to include the easily digestible nectar and fruit into their diet, they do not need any specific adaptations in their digestive tract [17]. Small lizards on islands, probably suffering from a shortage of arthropod food, consume nectar and fruit. Thus, these lizards do not fit into the classic lizard dichotomy of Pough: small, arthropod-eaters versus large, herbivores [32]. For instance, the Canarian lacertid G. galloti does not normally exceed 55 g but, in spite of that, fleshy fruit is the major component of its diet ([10], A. Valido, PhD thesis, University of La Laguna). Other, even smaller lizards, which also include nectar and/or fruit in their diet are G. atlantica, G. caesaris, P. tilfordi and P. pityusensis (Lacertidae), Hoplodactylus spp., Platsima spp. (Gekkonidae), Mabuya spp., Cyclodina spp. (Scincidae), Cnemidophorus spp. (Teiidae) and Platyurus broadleyi (Cordylidae) ([5,9,13,19], A. Valido, PhD thesis, University of La Laguna). Lepidophyma smithii (Xantusia) is an extreme case, weighing only 25 g, but has a diet comprising up to 91% fig fruit [44].
Are lizards more abundant on islands than on the mainland?

In general, islands only have a few lizard species, but they often show extreme DC [40], caused possibly by a lack of interspecific competition and predation [35,45]. For example, the density of the lizard Ctenosaura hemilopha is much higher on islands in the Sea of Cortez than on mainland California. There are predators on the islands, but the lizards live in predator-free crevices in rocky outcrops [38]. In the Caribbean, anoles are present on almost all islands and they are often very abundant [45,46] (e.g. reaching 1 m\(^{-2}\) in the Bahamian, which is several orders of magnitude higher than on the mainland [40]). This is also true to a lesser extent for other Caribbean lizards. Janzen [30] writes: The density of large insectivorous lizards...on Providencia Island was far higher than I have seen in any Central American...vegetation. He goes on to say that several hundred Costa Rican lizards examined had a gut filled with arthropods, whereas 83% of lizards sampled from Providencia Island had large amount of fruit and vegetable matter in their stomachs. The lizard Cnemidophorus murinus, from Bonaire Island, can only sustain its metabolic demands if it includes a more abundant resource than insects. Dearing and Schall [47] showed that fruit constituted 10–44% vol of its annual diet. The highest recorded lizard density is probably that of 2 m\(^{-2}\) on some Caribbean islands [48]. Thus many reports agree that island lizards show DC and use fruit as a major component in their diet.

A low predation risk and a shortage of arthropod food

According to Szarski [33], lizards on islands are more herbivorous than are those on mainland because predation risk in their island habitats is lower, thus enabling lizards to spend more time searching for and digesting plant matter. Although, we have no comparative data on predation levels on islands versus the adjacent mainland, we do know of several cases of lizards feeding on fruit in predator-rich mainland habitats, (e.g. Lacerta lepida in Spain [49], L. smithii in Mexico [44], Platysaurus capensis in South Africa [13] and several Australian lizards species [50]). These lizards, however, also live in habitats that are extremely poor in arthropods (i.e. deserts). Thus, when mainland lizards face food shortage in stressed environments, they expand their dietary niche to include fruit and nectar in the same way as do insular lizards. Intense herbivory was also observed in mainland Tropiduridae lizards living in arthropod-poor, but predator-rich habitats (e.g. species of Liolemaus inhabiting high-altitudinal zones in the Andes [51,52], and Tropidurus torquatus occupying Brazilian coastal restingas [53]). These cases indicate that food availability might be more important than is predation risk.

Conclusions

Recent data demonstrate that flower-visiting and fruit-consuming lizards are strikingly more common on islands compared with the mainland, making them a true island phenomenon. We believe that different DC responses of insular animals might create this phenomenon. However, to confirm this we need more systematic data sampling from mainland and island. Some lizard–plant interactions might be excellent systems with which to study mutualism and potential coevolution between interacting plants and animals, (e.g. Phelsuma–flower mutualisms and Gallotia–fruit mutualisms). In particular, we need more experimental studies to demonstrate lizards that could cause evolutionary changes in flower and fruit traits in island plants.

Many island lizard taxa are threatened by extinction or have already disappeared. The importance of mutualisms between plant-feeding lizards and flowering plants add very strong arguments to more joint conservation efforts for these groups of organisms.

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