

# Lizards as pollinators and seed dispersers: an island phenomenon

Jens M. Olesen and Alfredo Valido

Department of Ecology and Genetics, University of Aarhus, Ny Munkegade B540, DK-8000 Aarhus C, Denmark

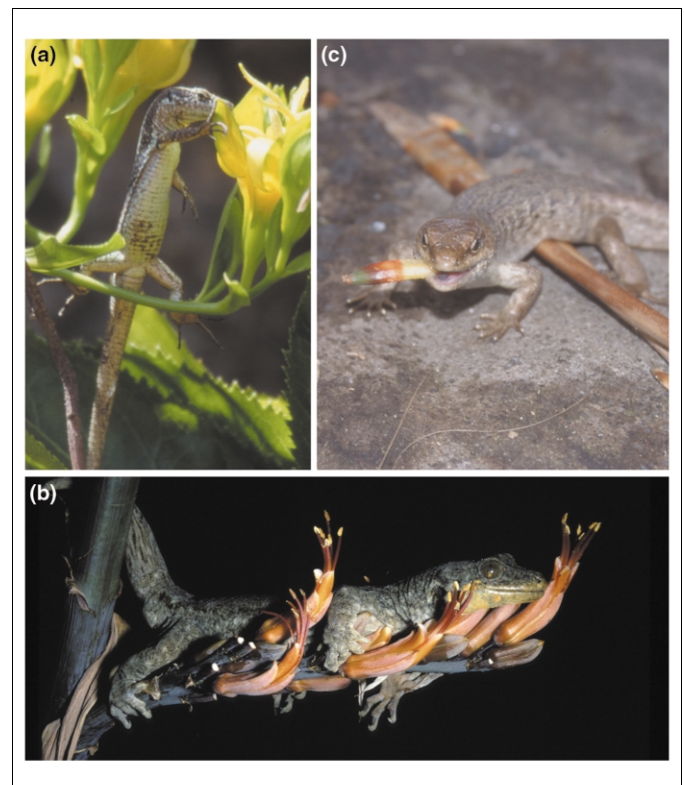
**Although it is well established that many insects, birds and mammals serve as important pollinators and seed dispersers of flowering plants, the role of lizards in these processes has traditionally been considered as rare and less important. However, recent work shows both that their role as mutualistic 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.**

Many insects, birds and mammals serve as important pollinators and seed dispersers of flowering plants, receiving, in return, floral food (i.e. nectar and pollen) and fruit pulp. Such mutualistic interactions between plants and animals occur in all kinds of ecosystem and their study has a long tradition [1,2]. In the past, lizards (i.e. Squamata: Iguania, Gekkota and Scincomorpha) have been suggested as plant mutualist agents (e.g. [3]), but the scientific establishment has generally regarded most of these observations of lizard–plant interactions to be rare and unimportant to an understanding of ecosystem functioning and to the evolution of flowers and fruits.

Ever since the beginning of the 20th century, lizards have been known to be seed dispersers [3], whereas the first observations of lizards as pollinators are more recent [4] (Fig. 1a). During the past decade, interest in the ecology of lizards has increased and studies from widely disparate regions now call for us to pay more serious attention to lizards as pollinators [5–9] and seed dispersers [5,10–14]. These new studies, using more rigorous experimental approaches, are now turning this subject into a promising and fascinating branch of mutualism research. The study of lizard–plant mutualisms might also have unexpected general value to a broad range of research areas in ecology and evolution, such as island biology, invasion biology and niche theory.

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



**Fig. 1.** Examples of lizards as pollinators and seed dispersers. (a) *Teira dugesii* (Lacertidae) drinking nectar in *Musschia aurea* (Campanulaceae), Madeira. This was the first lizard–flower interaction to be reported [4]. (b) *Hoplodactylus duvauceli* (Gekkoniidae) as a flower visitor on *Phormium tenax* (Agavaceae), New Zealand. Photograph reproduced courtesy of A.H. Whitaker. (c) *Leiolopisma telfairii* (Scincidae) consuming a fruit of *Pandanus vanderschmidii* (Pandanaceae), Round Island, Mauritius. Photograph reproduced courtesy of D.M. Hansen.

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 (53%[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-visiting 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 37 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

**Table 1. Island–mainland distribution of reported flower-visiting and fruit-eating lizard species<sup>a</sup>**

	No. of island spp.	No. of spp. on both island and mainland	No. of mainland spp.	Total
No. of flower-visiting spp.	35 (95%)	0	2 (5%)	37
No. of fruit-eating spp.	127 (63%)	11 (5%)	64 (31%)	202

<sup>a</sup>Data taken from [5,8,17,21,25,27,28,54–63] and personal communications.

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. Borzí [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

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 Cortéz [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. lilfordi* and *P. pityusensis* (Lacertidae), *Hoplodactylus* spp., *Phelsuma* spp. (Gekkonidae), *Mabuya* spp., *Cyclodina* spp. (Scincidae), *Cnemidophorus* spp. (Teiidae) and *Platysaurus broadleyi* (Cordylidae) ([5,9,13,19], A. Valido, PhD thesis, University of La Laguna). *Lepidophyma smithii* (Xantusiidae) 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 Cortéz 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  $1\text{ m}^{-2}$  in the Bahamas, 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  $2\text{ m}^{-2}$  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 *Liolaemus* 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.

### Acknowledgements

We thank Y.L. Dupont, D.M. Hansen and E.D. Parker for comments, and W.E. Cooper and L.J. Vitt for access to an unpublished manuscript [17]; H. Adersen, W.S. Armbruster, A. Bauer, D.G. Broadley, J. Cavalho, J. Davenport, J. Fedriani, G. García, D. Hall, J. Losos, R. Powell, J. Vitt van Sluys and A.H. Whitaker gave us unpublished information about lizard–flower and/or fruit interactions. The work was financed by the Danish Science Research Council (J.M.O.) and a Marie Curie grant (MCFI-2000–1995) from the European Union (A.V.).

### References

- Proctor, M. *et al.* (1996) *The Natural History of Pollination*, HarperCollins
- Fenner, M. ed. (2000) *Seeds, the Ecology of Regeneration in Plant Communities* CABI
- Borzi, A. (1911) Ricerche sulla disseminazione delle piante per mezzo di Sauri. *Mem. Soc. Itali. Sci.* 17, 97–115
- Elvers, I. (1977) Flower-visiting lizards on Madeira. *Bot. Not.* 130, 231–234
- Whitaker, A.H. (1987) The roles of lizards in New Zealand plant reproductive strategies. *New Zealand J. Bot.* 25, 315–328
- Eifler, D.A. (1995) Patterns of plant visitation by nectar-feeding lizards. *Oecologia* 101, 228–233
- Traveset, A. and Sáez, E. (1997) Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. *Oecologia* 111, 241–248
- Olsson, M. *et al.* (2000) Lizards as a plant's 'hired help': letting pollinators in and seeds out. *Biol. J. Linnean Soc.* 71, 191–202
- Nyhagen, D.F. *et al.* (2001) Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. *J. Trop. Ecol.* 17, 755–761
- Valido, A. and Nogales, M. (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70, 403–411
- Traveset, A. (1995) Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. *Acta Oecologia* 16, 171–178
- Willson, M.F. *et al.* (1996) Seed dispersal by lizards in Chilean rainforest. *Rev. Chil. Hist. Nat.* 69, 339–342
- Whiting, M.J. and Greff, J.M. (1997) Facultative frugivory in the Cape Flat lizard, *Platysaurus capensis* (Sauria: Cordylidae). *Copeia* 4, 811–818
- Lord, J.M. and Marshall, J. (2001) Correlations between growth form, habitat, and fruit colour in the New Zealand flora, with reference to frugivory by lizards. *New Zealand J. Bot.* 39, 567–576
- Greene, H.W. (1982) Dietary and phenotypic diversity in lizards: why are some organisms specialized? In *Environmental Adaptation and Evolution* (Mossakowski, D. and Roth, G., eds) pp. 107–128, Gustav Fischer
- van Damme, R. (1999) Evolution of herbivory in lacertid lizards: effects of insularity and body size. *J. Herpetol.* 33, 663–674
- Cooper, W.E. and Vitt, L.J. (2002) Distribution, extent, and evolution of plant consumption by lizards. *J. Zool.* 257, 487–517
- Jordano, P. (2000) Fruits and frugivory. In *Seeds, the Ecology of Regeneration in Plant Communities* (Fenner, M., ed.), pp. 125–165, CABI

- 19 Pérez-Mellado, V. and Corti, C. (1993) Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* 44, 193–220
- 20 Pérez-Mellado, V. and Traveset, A. (1999) Relationships between plants and Mediterranean lizards. *Natura Croatica* 8, 275–285
- 21 Checke, A.S. (1984) Lizards of the Seychelles. In *Biogeography and Ecology of the Seychelles Islands* (Stoddart, D.R., ed.), pp. 331–360, Junk
- 22 Tiffney, B.H. (1984) Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. *Ann. Missouri Bot. Gard.* 71, 551–576
- 23 King, G. (1996) *Reptiles and Herbivory*, Chapman & Hall
- 24 Salvador, A. (1986) *Podarcis pityusensis* (Boscá, 1883) – Pityusen-Eidechse. In *Handbuch der Reptilien und Amphibien Europas. Echsen III (Podarcis)* (Böhme, W., ed.), pp. 231–253, Aula-Verlag
- 25 Schwartz, A. and Henderson, R.W. (1991) *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*, University of Florida Press
- 26 Vinson, J. and Vinson, J.M. (1969) The saurian fauna of the Mascarene islands. *Mauritius Inst. Bull.* 4, 203–320
- 27 Auffenberg, W. and Auffenberg, T. (1988) Resource partitioning in a community of Philippine skinks (Sauria: Scincidae). *Bull. Florida State Mus. Biol. Sci.* 32, 151–219
- 28 Bauer, A.M. and Sadlier, R.A. (2000) *The Herpetofauna of New Caledonia*, SSAR Publications
- 29 Crombie, R.I. and Pregill, C.K. (1999) A checklist of the herpetofauna of the Palau Islands (Republic of Belau), Oceania. *Herpetol. Monogr.* 13, 29–80
- 30 Janzen, D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54, 687–701
- 31 Sokol, O.M. (1967) Herbivory in lizards. *Evolution* 21, 192–194
- 32 Pough, F.H. (1973) Lizard energetics and diet. *Ecology* 54, 837–844
- 33 Szarski, H. (1962) Some remarks on herbivorous lizards. *Evolution* 16, 529
- 34 Olesen, J.M. and Jordano, P. (2002) Geographic patterns in plant–pollinator mutualistic networks. *Ecology* 83, 2416–2424
- 35 MacArthur, R.H. et al. (1972) Density compensation in island faunas. *Ecology* 53, 330–342
- 36 Connor, E.F. et al. (2000) Individuals–area relationships: the relationship between animal population density and area. *Ecology* 81, 734–748
- 37 Ruesink, J.L. and Srivastava, D.S. (2001) Numerical and per capita responses to species loss: mechanisms maintaining ecosystem function in a community of stream insect detritivores. *Oikos* 93, 221–234
- 38 Case, T.J. (1983) The reptiles: ecology. In *Island Biogeography in the Sea of Cortéz* (Case, T.J. and Cody, M.L., eds) pp. 159–473, University of California Press
- 39 Andrews, R.M. (1979) Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora* 454, 1–51
- 40 Schoener, T.W. (1989) Food webs from the small to the large. *Ecology* 70, 1559–1589
- 41 Cox, G.W. and Ricklefs, R.E. (1977) Species diversity and ecological release in Caribbean land bird faunas. *Oikos* 28, 113–122
- 42 Cody, M.L. (1983) Bird diversity and density in south African forests. *Oecologia* 59, 201–215
- 43 Iverson, J.B. (1982) Adaptations to herbivory in Iguanine lizards. In *Iguanas of the World* (Burghardt, G.M. and Rand, A.S., eds) pp. 60–76, Noyes
- 44 Mautz, W.J. and Lopez-Forment, W. (1978) Observations on the activity and diet of the cavernicolous lizard *Lepidophyma smithii* (Sauria: Xantusiidae). *Herpetologica* 34, 311–313
- 45 Schoener, T.W. and Schoener, A. (1980) Densities, sex ratios and population structure in four species of Bahamian *Anolis* lizards. *J. Anim. Ecol.* 49, 19–53
- 46 Thorpe, R.S. and Malhotra, A. (1998) Molecular and morphological evolution within small islands. In *Evolution on Islands* (Grant, P.R., ed.), pp. 67–82, Oxford University Press
- 47 Dearing, M.D. and Schall, J.J. (1992) Testing models of optimal diet assembly by the generalist herbivorous lizard *Cnemidophorus murinus*. *Ecology* 73, 1
- 48 Bennett, A.F. and Gorman, G.C. (1979) Population density and energetics of lizards on a tropical island. *Oecologia* 42, 339–358
- 49 Hódar, J.A. et al. (1996) Trophic ecology of the ocellated lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey. *J. Arid Environ.* 33, 95–107
- 50 Brown, G.W. (1991) Ecological feeding analysis of South-eastern Australian scincids (Reptilia: Lacertilia). *Aust. J. Zool.* 39, 9–29
- 51 Fuentes, E.R. and di Castri, F. (1975) Ensayo de herbivoría experimental en especies de *Liolaemus* (Iguanidae) chilenos. *Ann. Mus. Hist. Nat. Valparaíso* 8, 66–75
- 52 Jaksic, F.M. and Fuentes, E.R. (1980) Observaciones autoecológicas en *Liolaemus nitidus* (Lacertilia: Iguanidae). *Studies Neotrop. Fauna Environ.* 15, 109–124
- 53 Fialho, R.F. et al. (2000) Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. *J. Herpetol.* 34, 325–330
- 54 Bischoff, W. (1998) *Handbuch der Reptilien und Amphibien Europas. Band 6. Die Reptilien der Kanarischen Inseln und des Madeira-Archipels*, Aula
- 55 Böhme, W. (1981) *Handbuch der Reptilien und Amphibien Europas. Band 1. Echsen I*, Akademische Verlagsgesellschaft
- 56 Böhme, W. (1984) *Handbuch der Reptilien und Amphibien Europas. Band 2/I Echsen II (Lacerta)*, Aula
- 57 Böhme, W. (1986) *Handbuch der Reptilien und Amphibien Europas. Echsen III. (Podarcis)*, Aula
- 58 Cogger, H.G. (1992) *Reptiles and Amphibians of Australia*, Reed Books
- 59 Henkel, F.W. and Schmid, W. (2000) *Amphibians and Reptiles of Madagascar and the Mascarenes, Seychelles and Comoro Islands*, Krieger
- 60 McCoy, M. (2000) *The Reptiles of Solomon Islands* (CD), ZooGraphics
- 61 Schleich, H.H. et al. (1996) *Amphibians and Reptiles of North Africa*, Koeltz
- 62 Stebbins, R.C. (1966) *A Field Guide to Western Reptiles and Amphibians*, Houghton Mifflin
- 63 Valido, A. (2003) *Records of Fruit-eating Lizard Species*, University of Aarhus

### Articles of interest

Articles of ecological or evolutionary interest in recent issues of other *Trends* journals

#### The mosquito genome: perspectives and possibilities

Kirkwood M. Land, *Trends in Parasitology* 10.1016/S1471-4922(03)00021-7

#### Human migration, mosquitoes and the evolution of *Plasmodium falciparum*

Jennifer C.C. Hume, Emily J. Lyons and Karen P. Day, *Trends in Parasitology* 10.1016/S1471-4922(03)00008-4

#### Why are the genomes of endosymbiotic bacteria so stable?

Francisco J. Silva, Amparo Latorre and Andrés Moya, *Trends in Genetics* 10.1016/S0168-9525(03)00041-6