Evolutionary Ecology, 1991, **5**, 272–290

The role of introduced species in shaping the distribution and abundance of island reptiles

TED J. CASE and DOUGLAS T. BOLGER

Department of Biology C-016, University of California at San Diego, La Jolla, CA 92093, USA

Summary

Species interactions, as revealed by historical introductions of predators and competitors, affect population densities and sometimes result in extinctions of island reptiles. Mongoose introductions to Pacific islands have diminished the abundance of diurnal lizards and in some cases have led to extinctions. Through these population level effects, biogeographic patterns are produced, such as the reciprocal co-occurrence pattern seen with the tuatara and its predator, the Polynesian rat, and with the tropical gecko competitors *Hemidactylus frenatus* and *Lepidodactylus lugubris* in urban habitats in the Pacific. Although competition has led to changes in abundance and has caused habitat displacement and reduced colonization success, extinctions of established reptile populations usually occur only as a result of predation.

These introductions, along with many manipulative experiments, demonstrate that present day competition and predation are potent forces shaping community structure and geographic distributions. The human introduction of species to islands can be viewed as an acceleration of the natural processes of range expansion and colonization. The immediate biotic consequences of these natural processes should be of the same intensity as those of the human introductions. Coevolution may subsequently act to ameliorate these interactions and reduce the dynamical response of one species to the other. The role played by coevolution in mediating interactions between competitors and predator and prey is highlighted by the susceptibility of predator-naive endemic species to introduced predators and the invalidity of species-poor communities.

Keywords: Introduced species; competition; predation; extinction; reptiles; island biogeography.

Introduction

One of the more controversial and fundamental questions in community ecology concerns the extent to which species affect the distributions and abundances of other species. The issue is not whether species interact; this is patently obvious, all heterotrophs eat other species and death is a strong interspecific effect. But do these interactions provide dynamic regulation and balance in the population dynamics of communities? Do they impart biogeographic interdependence of species' distributions? Or, alternatively are species' distributions largely independent of the distribution and abundance of any other species (Roughgarden and Diamond, 1986).

Here we synthesize a body of evidence, gained largely from species' introductions, that implies that predation and competition have set important constraints on the distribution, colonization and abundance of reptiles on islands. Islands provide sets of semi-replicate worlds that enable us to address these questions. We emphasize the qualifier 'semi'. Even within an archipelago, islands are not true replicates; they differ in size, elevation, habitat, geological age, history, distance to colonization sources, human land use and climate. These factors affect the number and identity of species on islands. For a biogeographic pattern caused by species interactions to

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be detectable, it must be strong enough to override any patterning caused by physical and historical differences among the islands.

The choice of reptiles (in fact, predominantly lizards) as our focal taxa is three-fold: (1) because the evidence may be less well known than for other taxa (e.g. birds, see Diamond, 1984); (2) because there have been particularly dynamic changes in their distribution in historical times and; (3) because reptiles are intermediate in oversea dispersal ability between most birds at one extreme and freshwater fish and amphibians at the other, so patterns in their biogeography will reflect both ongoing ecological processes affecting colonization and extinction, as well as remnants of ancient geophysical events (Case and Cody, 1983, 1987).

Our evidence is drawn from studies of the effects of introduced predators on native and introduced lizards and of competition among introduced lizards and between introduced and native lizards. The study of species introductions is especially revealing for two reasons. First, introductions are manipulative experiments, albeit only semi-replicated and partially controlled. Second, introduced species have not coevolved with the competitors and predators that they now encounter so that biotic interactions might be expected to be severe. In these situations we are not faced with the precarious task of interpreting what Mike Rosenzweig termed the 'ghost of competition past' (as cited in Connell, 1980).

Several interesting results emerge from this synthesis:

(1) Introduced predators cause extinctions and severe reductions in the abundance of native and introduced reptiles but their effect on the 'predator-naive' native species is more severe.

(2) Species-rich communities are more resistant to the invasion of introduced lizards than are species-poor communities.

(3) Competition between introduced species is more severe than competition between introduced and native species.

Predation

One of the most common patterns in lizard island biogeography is the association of high lizard density with low predator abundance. In the Sea of Cortez, small islands without mammalian predators have high densities of lizards compared to the mainland, or larger islands with mammalian predators (Case, 1983). A similar patern has been observed nearly world wide in areas as diverse as the Caribbean, the Aegean, Seychelles, Mascarenes, New Zealand, the Galapagos and elsewhere in the South Pacific (see below).

That it is predation that is responsible and not some other biotic variable, like a pathogen or competitors that might covary with island size and predator diversity, is tested by introducing lizard predators to some islands while not to others. Although strictly illegal in most places today, this 'experiment' was conducted historically many times with rats (*Rattus rattus* and *Rattus norvegicus*), housecats (*Felis domesticus*), and the Indian mongoose (*Herpestes auropunctatus*). The latter is one of the most potent predators on diurnal ground foraging lizards. Mongooses have been introduced to various islands around the world with the hope of controlling rats and other vertebrate pests. Although their success in this regard has been mixed, their impact on native bird and reptile populations, particularly ground foraging forms, like skinks, teiids, lacertids and snakes, has been devastating. In Puerto Rico reptiles and insects, not rats, form the bulk of the mongoose diet (Pimentel, 1955).

One of us (T. J. Case) quantified the impact of the mongoose on diurnal lizard abundance on islands in the South Pacific by censusing lizards on islands with and without the mongoose. Lizards were counted along 2–4 transects of about 1 km each per island. No attempt was made to capture any of the lizards so that a constant search speed could be maintained. Nearly all lizards

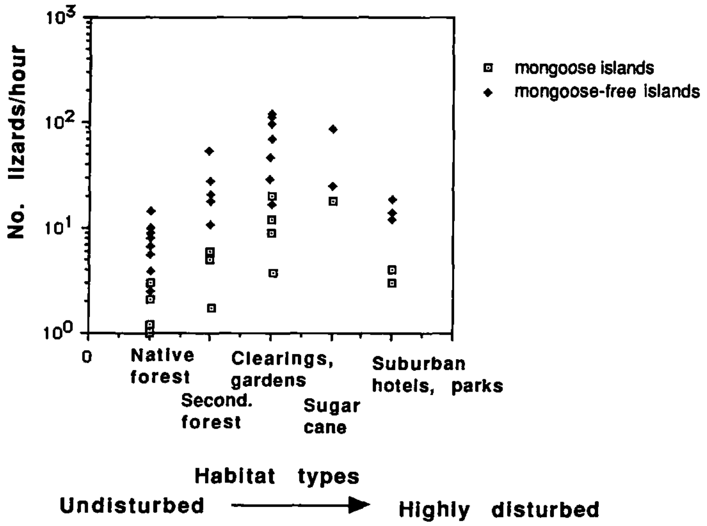

Figure 1. Crude lizard censuses (expressed as the average number of diurnal lizards seen per hour; also see Case, 1975) in natural and man-modified habitats on mongoose and mongoose-free islands in the tropical Pacific. All censuses were conducted during sunny days from 1984 to 1988 by T. J. Case. No attempt was made to capture any of the lizards so that a constant search speed could be maintained. Nearly all lizards seen were skinks and include both native and introduced species. Each point represents the average of 2–4 censuses. The islands and the number of habitats censused are: mongoose islands in Hawaii: Hawaii (2), Oahu (2), Molokai (2), Maui (1). Fiji: Vite Levu (5), and Rabi (2), Vanua Levu (1). Mongoose-free islands are New Caledonia (3), Kauai (3), Efate (2), Espiritu Santo (2), Tahiti (3), Moorea (1), Roratunga (1), Atiu (2), and in Fiji: Kadavu (4), Taveuni (3), and Ovalau (1).

seen were skinks and include both native and introduced species. Each point represents the average of 2–4 censuses. There is nearly a 100-fold increase in diurnal lizard abundance on islands without mongooses compared to islands with mongooses (Fig. 1).

The same qualitative pattern is evident in the West Indies. About 50 years after the introduction of the mongoose to Jamaica, Barbour (1910) noticed the 'almost complete extinction of many species which were once abundant . . . true ground inhabiting forms have, of course, suffered most . . . snakes have perhaps suffered more than lizards' (page 273). This effect on lizard abundance is also seen today on small cays off Jamaica and elsewhere in the West Indies: where the mongoose is absent, terrestrial lizards are much more common (Barbour, 1930; Schmidt, 1928; Pregill, 1986; Mittermaier, 1972).

On St Lucia island in the Lesser Antilles, for example, three reptile species have been extirpated in historical time coincident with the introduction of mongoose: one skink (*Mabuya mabuya*) and two colubrid snakes (*Liophis ornatus* and *Clelia clelia*) (Corke, 1987). *L. ornatus* is extinct on the main island but survives on the tiny offshore island of Maria Major along with the ground foraging lizard *Cnemidophorus vanzoi*. The latter has never been recorded from St Lucia itself. Although it seems likely that this lizard was once extant on St Lucia since Maria Major is so close inshore. Similarly, the colubroid snake, *Alsophis antillensis*, once occupied Barbuda and Antigua but today can only be found on mongoose-free offshore cays (Pregill *et al.*, 1988).

Domestic cats and dogs, and rats have also had devastating effects on island species. Cats and the tree rat (*Rattus rattus*), since they are more arboreal, affect prey species that the mongoose is less likely to capture. Gibbons and Watkins (1982) suggest that cats may have been even more damaging than mongooses to highly arboreal Fijian lizards and in particular to the now rare endemic Fijian iguanas. Today substantial populations can only be found on small islands lacking both mongoose and cats.

Thomson (1922) notes that New Zealand lizards became much less common after the mid-19th century and attributed the decline to loss of cover and predation by cats. Today on off-lying islands of New Zealand which lack mammalian predators, lizard numbers can be extraordinarily high (estimates reach 1390 lizards per acre or nearly one lizard every 3 m^2 (Crook, 1973; Whitaker, 1968, 1973). Islands with *Rattus exulans*, the Polynesian rat, support smaller populations of lizards and tuataras than do islands without rats (Crook, 1973; Whitaker, 1973).

In other parts of the world, one finds this pattern repeated. Up to 2074 diurnal lizards per acre have been reported for rat-free Cousin Island in the Seychelles (Brooke and Houston, 1983), and 1214 per acre for San Pedro Martir in the Sea of Cortez, Mexico (Wilcox, 1981).

Mammals are not the only taxa implicated in causing reptile extinctions. The introduced brown tree snake, *Boiga irregularis*, which has become infamous for eliminating 10 bird species on Guam (Savidge, 1987), has also severely impacted the lizard fauna there (Engbring and Fritts, 1988). Juvenile snakes prey predominantly on lizards and have apparently extirpated three species of skinks and two geckos (T. H. Fritts, personal communication). They have also severely reduced the numbers of *Gehyra oceanica*, *G. mutilata*, and *Lepidodactylus lugubris*, species which are abundant in the absence of the tree snake in other areas.

Introduced predators not only reduce reptile densities on islands, they also cause extinctions. The tuatara is the last remaining representative of a widespread Mesozoic order of reptiles, the Ryncocephalia. Today it is found only on uninhabited, predator-free landbridge islands off New Zealand, but subfossils (less than a thousand years old) are found on both the main islands (Cassels, 1984). Also in New Zealand, three species of lizards are extinct, a species of *Cyclodina* larger than any extant form and known only from subfossil deposits in Northland, and *Leiolopisma gracilocorpus* and *Hoplodactylus delcourti* known only from single museum specimens (Bauer and Russell, 1986; Worthy, 1987a; Hardy, 1977). *H. delcourti* is the largest known gecko with a snout-vent length of 370 mm. Nine reptiles today are found only on the off-lying islands (five skinks, three geckos and the tuatara). These include all the relatively large extant species (Hardy and Whitaker, 1979).

The time of disappearance of the tuatara and most of the lizards coincides well with the arrival of humans to New Zealand and the subsequent introduction of the Polynesian rat (*Rattus exulans*). On islands where the rat is present, the tuatara either is absent or not breeding (Crook, 1973). Similarly, the three largest of six species of frog (*Leiopelma*) have gone extinct in New Zealand in the Holocene (Worthy, 1987b) and the largest surviving frog (*L. hamiltoni*) occurs only on two rat-free islands.

The combination of cats and mongoose on the two largest islands of Fiji, Viti Levu and Vanua Levu, has apparently resulted in the local extinction of the ground foraging skinks *Emoia nigra* and *E. trossula*. These are the two largest skinks in Fiji and they have not been seen on these islands in over 100 years (Zug, 1991), although they survive quite well on mongoose-free islands in the archipelago (e.g. Ovalau, Rotuma and Taveuni). Interestingly, nearly all these islands have rats (*Rattus rattus* and *R. exulans*) indicating that the mongoose is a more potent skink predator than *Rattus*.

The pattern of usually large, tame endemic lizards being restricted to smaller rat-free islands off-lying larger rat-infested islands is repeated in the Mascarenes (Vinson and Vinson, 1969). In the late 17th century, Rodrigues Island in the Indian Ocean was beginning a period of intensive European settlement. At that time there existed large numbers of some spectacular endemic geckos in the genus *Phelsuma*. *Phelsuma edwardnewtonii* was a large diurnal species, a stunning green with blue spots. It was described as being so tame that it inhabited houses and would eat fruits out of the owner's hands (Leguat, 1708). The species was devastated by rats and cats on the main island around the mid 19th century. It survived for a while on small outlying islets but finally disappeared from these too as they became rat-infested. An even larger species, *P. gigas* reached nearly a half metre in total length; it vanished from the main island before *P. edwardnewtonii* but, like it, disappeared from the off-lying cays later when rats were introduced (Vinson and Vinson, 1969).

Some huge skinks, *Leiolopisma mauritiana* (snout-vent length 300 mm), inhabited nearby Mauritius. They are known today only as subfossils and the causes and chronology of their extinction are not known. A likely guess is that they went the way of their contemporary, the dodo, for much the same reasons.

This pattern has been reported on islands throughout the world (Case *et al.*, 1991) including the Canary Islands (Klemmer, 1976), the Cape Verdes (Greer, 1976), Norfolk (Cogger *et al.*, 1983) and Lord Howe Islands (Cogger, 1971). On most of these islands, rats arrived so early historically that we do not have adequate pre-rat reptile records or census data. In the case of Lord Howe Island, however, the numerical decline of the only two native lizards *Phyllodactylus guentheri* and

Table 1. The number of terrestrial reptile species on various islands in Fiji, the Society Islands, Hawaii, Samoa, and Cook Islands. The presence of introduced mongooses is noted.

Island[1]	No. introduced reptile spp.[2]	No. native reptile spp.	Mongoose	Area (km²)	Maximum elevation (m)
Ovalau	8	7	0	103	626
Vanua Levu	8	5	1	5535	1032
Viti Levu	11	8	1	10387	1341
Kadavu	7	6	0	400	851
Taveuni	10	7	0	440	1241
Rotuma	7	4	0	45	300
Tahiti	10	0	0	1042	2241
Moorea	7	0	0	132	1207
Kauai	9	0	0[3]	1421	1598
Oahu	13	0	1	1535	1500
Hawaii	11	0	1	10456	4206
Molokai	6	0	1	676	1515
Maui	11	0	1	1886	3056
Upola	8	5	0	1554	1100
Tutuila	8	2	0	137	653
Rarotonga	7	1	0	67	652
Atiu	7	0	0	27	90

[1] The set of islands examined is limited to those where we have verified or added to lizard records by personal field surveys. A table listing the species present on each of these islands is available upon request from T. J. Case.

[2] Reptiles are considered introduced based on historical records, or for aboriginal introductions, the criteria listed in the notes to Appendix 2. Notice that a particular species may be exotic in many locations but self-introduced only recently to others, giving the appearance of being introduced. We therefore would not be surprised if some of our 'introductions' prove later to be natives. Much more palaeontological work is needed in the Pacific to distinguish these cases.

[3] The mongoose has entered Kauai very recently.

Leiolopisma lichenigerum on the main island seems to have occurred after the arrival of rats in 1918 (Cogger, 1971).

Most introduced predators arrive on an island shortly after it is settled, either by aborigines or Europeans. Pregill (1986) and Case *et al.* (1991) have correlated the settlement time of islands with the extinction times of a number of insular reptiles. The overall picture is quite convincing; the arrival of humans on an island is closely associated with increased reptile extinction rates, especially of large endemic species. The inference is that habitat destruction and predation by man and/or his entourage of introduced animals is responsible for these extinctions.

Further support for this scenario comes from studies by Richman *et al.* (1988). They found that small oceanic islands that have had extensive human disturbance have higher per species reptile extinction rates than relatively undisturbed islands off Australia and in the Sea of Cortez. Similarly, Whitaker (1973) finds that small islands off New Zealand with the introduced Polynesian rat have fewer lizard species (all natives) for their size, than islands without rats.

In cases where predators have been introduced relatively recently we have more direct evidence that predation is the cause of the extirpation, or decline of native reptile populations. The large herbivorous iguanine, *Cyclura carinata*, was nearly extirpated on Pine Cay in the Caicos islands during the three years following construction of a hotel and tourist facility (Iverson, 1978). Predation by cats and dogs introduced during the hotel construction resulted in the decline from about 5500 adults to only around five. Dogs and cats were frequently observed digging lizards out of their burrows and eating them. Iverson also presents evidence suggesting that population declines of *Cyclura* elsewhere in the Turks and Caicos Banks stems directly from cat and dog predation.

McCallum (1986) documents the changes to the herpetofauna following the colonization of Lizard Island off New Zealand by the Polynesian rat in 1977. Two lizard species appeared to become extinct and overall lizard densities dropped by at least one order of magnitude. Norway rats colonized Whenuakura Island in 1983–84 and by 1985 the previously thriving tuarara population had disappeared as had nearly all the lizards (Newman, 1986).

While it is apparent that introduced predators have severely affected native reptile species, they have not greatly affected the number of introduced reptile species on islands. We have compiled reptile species lists for a set of islands in the Tropical Pacific with and without mongoose (Table 1). We only included islands where we have personally conducted field work to be certain that faunal lists are reasonably complete (in the process we added at least 15 new records). We ask if there are fewer species on mongoose islands compared to mongoose-free islands. To perform the analysis it is first necessary to remove variation in species number due to uncontrolled variables, for example island area, isolation, and elevation which can greatly influence species number. We found that for introduced species only island area is a significant independent variable, but for native species both area and isolation are important predictors of species number. We used a *t*-test to compare the residuals from a single (in the case of introduced species) and multiple regression (in the case of native species) of log species number vs log island area and/or log elevation for mongoose and mongoose-free islands. The introduced species component showed no significant difference between the two island groups ($p > 0.8$) (but residual species number was slightly higher on mongoose islands). Native species also did not show a significant difference ($p > 0.4$) although residual species number was somewhat lower on mongoose-free islands. The native species analysis may not be valid for two reasons: (1) nearly half the islands considered have no native species whatsoever; (2) there is some doubt as to the continued presence of certain native species formerly common but not seen recently on some of the mongoose-islands (i.e., extinctions are hard to document).

We repeated this analysis for a single island group, the Seychelles, using species lists for islands with and without rats from Cheke (1984). We have totalled species numbers for introduced and native lizard species (Appendix 1). After performing a regression of species number vs log area, we compared the residuals for rat and rat-free islands for both the native and introduced lizard species components of the fauna. After correcting for island size (elevations are not available), there is a net excess of introduced species on rat occupied islands but a net deficit of native species relative to rat-free islands, however neither of these results are statistically significant between the rat categories ($p > 0.15$, using a t-test). The trend for both the Seychelles analysis with rats and the South Pacific analysis for mongoose runs counter to the naive prediction that predators make it harder for the rats to invade. Instead, if anything, introduced species are more common on predator-occupied islands. Because nearly all introduced species come originally from predator-rich contintental areas, they may be less susceptible to introduced predators than the endemic predator-naive species. Thus the introduced species are probably more resistant to the introduced predators than the natives. The presence of predators might even enhance the success of introduced species compared to predator-free islands by moderating the competive impact of natives.

Elsewhere (Case *et al.*, 1990) we have statistically compared the frequency of extinctions and extirpations in endemic and non-endemic components of the reptile fauna on various islands around the world with high levels of species endemism. Endemic species have significantly higher extinction rates than non-endemics. Endemic species have been isolated on islands lacking mammalian predators for long periods and have presumably become relatively defenceless to introduced predators. Similarly, Atkinson (1985) has found that on islands with native rodents or land crabs, introduced rats have caused fewer bird extinctions than on islands that were previously predator-free. Presumably the bird species on islands with native predators have evolved effective predator escape behaviours which enable them to evade the introduced rats. Few attempts have been made to quantify the 'predator naiveté' of species from predator-free islands although Shallenberger (1970) measured the flushing distance of insular and mainland iguanid lizards and found that a human can get up to 10 times closer to the insular varieties.

Competition

Competition between native and introduced lizards

Unlike birds, most lizards have been unable to colonize the remote islands of the world, such as those in the mid-Pacific. They reached these when the Polynesians and Melanesians inadvertently spread a set of geckos and skinks throughout much of the Pacific beginning about 3000 years ago. Additions to this set have occurred more recently during European settlement. These introductions, although unconscious and not as well controlled as a manipulative experiment, can be used to sort out competitive relationships among species because of the huge sample sizes involved, literally hundreds of island and mainland locations.

One of the most interesting features of these introduced lizards is their ability to penetrate native rainforest habitats on islands like Hawaii, the Cooks, Societies, and Marquesas, that lack an indigenous lizard fauna. In contrast on islands with even a modest number of native lizards as in Fiji, the Solomons, the New Hebrides, some of the introduced species are quite common in disturbed and agricultural habitats but few enter climax forest (McCoy, 1980; Medway and Marshall, 1975; Pernetta and Watling, 1979; Zweifel, 1979; personal observations). On islands with still richer native lizard faunas, like New Guinea, New Zealand, Australia, and New Caledonia, some lizards in the introduced species set are absent altogether and others are confined to small populations in or near cities (Robb, 1980; Cogger, 1983; Bauer and Russell, 1986; Scott *et al.*, 1977).

New Caledonia, which has a fairly rich endemic lizard fauna (31 native species), has only five of the nine lizards commonly introduced on smaller islands in the Pacific, and these are all geckos restricted to areas of human habitation. In contrast, the much smaller, nearby Loyalties which have only ten native species have seven introduced species. New Zealand has only one introduced lizard in spite of several putative invasions (Robb, 1980), Australia only three (Cogger, 1983).

The skinks *Emoia nigra*, *E. cyanura* and *Cryptoblepharus boutonii* are widespread and abundant on many small, species-poor islands in the Pacific (R. Crombie, 1988; personal observation) and Indian Oceans. However, they are rare or even absent from many large species-rich areas that lie within their ranges such as New Guinea, tropical Australia, the Philippines and New Caledonia. For example, *Emoia cyanura* which comprises the majority of the sightings detailed in Fig. 1, is rare in the Philippines and restricted to only a few small islands that lack competitors where it can be 'unbelievably common' (Taylor, 1922; Brown and Alcala, 1978). It is also extremely difficult to find in Guam (the Marianas) where it is largely replaced on the ground by *Carlia fusca* (introduced during the 1950s or 1960s from New Guinea) and by the native species *Emoia caeruleocauda* (M. McCoid, personal communication). In nearby Tinian, *E. cyanura* has never been recorded; instead until recently *E. caeruleocauda* was the most abundant lizard (Downs, 1948). Today *E. caeruleocauda* is rare on Tinian and instead the recent introduction *Carlia fusca* occurs in large numbers (Wiles *et al.*, 1989). On nearby Rota where *C. fusca* is absent, *E. caeruleocauda* is very common and found throughout the island (Wiles *et al.*, 1991). One finds a similar situation with the geckos *Lepidodactylus lugubris* and *Hemidactylus garnotti*. While common and widespread on islands in the mid-Pacific, these species are rare or absent on large islands in the Philippines, on Borneo, Thailand, and mainland Queensland (T. J. Case and D. T. Bolger, personal communications; Brown and Alcala, 1978, 1980; Taylor, 1922, 1963; Cogger, 1983). For example, out of over 400 individual geckos observed and/or collected in forest and urban habitats, we saw only five *Lepidodactylus lugubris* in the Philippines (Negros, Luzon, Mindanao, and Camiguin Islands). The individual from Los Banos on Luzon is the first record of a *Lepidodactylus* from that island.

Throughout Oceania, the skink *Crptoblepharus boutonii (poecilopleurus)* is found primarily in rocky shoreline habitats. On small islands near New Guinea where many other skinks are found on rocky islands, *C. boutonii* is restricted to small sandy islets and *Emoia mirvata* from New Guinea takes over the rocky littoral zone (Heatwole, 1975). In the Solomons, *Emoia atrocostata* occupies the rocky littoral zone and *C. boutonii*, while present, is rare and found more often in sandy habitats (McCoy, 1980).

It appears that the large species-rich islands tend to be more invasion-resistant to the 'weedy' lizards that are so widespread elsewhere. Case (1991) shows how such invasion resistance can arise from multi-species competition communities, largely due to the emergence of multiple stable states and indirect effects. These impart a disadvantage to species which, although perhaps equally competitive with the residents, are late-comers and at low frequency. In this way a priority effect is produced for established residents giving them a competitive edge over invaders.

A telling exception to the usual priority effect among competitors involves the *Anolis* lizards of southern Florida. Subtropical and mainland south Florida has only two native anoles (*A. carolinensis* and *A. distichus*) but in recent years it has been a beachhead for at least six introduced anoles from the more anole-rich Greater Antilles. Most of these introductions are still highly localized in urban areas, but *Anolis sagrei* is successfully displacing the native *A. carolinensis* as the most common anole in urban areas and has penetrated into agricultural and even native habitats (Wilson and Porras, 1983). In the Greater Antilles anoles introduced from other islands have thus far been unable to invade native habitats (Schwartz and Thomas, 1975; Schwartz *et al.*, 1978), while on the anole-free island of Bermuda three introduced species have successfully invaded (Wingate, 1965).

These ideas are reminiscent of Elton's (1958) hypothesis that species-rich areas are more resistant to introductions than are species-poor areas. A prediction of this hypothesis is that islands with more native species should have fewer introduced species. Such an analysis is fraught with pitfalls for the statistically careless. It is not valid to simply plot the proportion of the fauna that is introduced as the ordinate versus total species number as the abscissa and determine whether a negative correlation results (e.g. Fox and Fox, 1986). The ordinate has the abscissa as its denominator, so the two variables are not statistically independent.

Ideally to experimentally test the hypothesis, we would construct islands identical in all respects but differing in the diversity of the resident fauna. We then would introduce a fixed set of species to each island and follow the course of events. Since this is obviously impossible at this biogeographic scale, we must rely on existing islands and past historical introductions. But a problem arises now because there are some places today which have no reptiles whatsoever, like the Antarctica, because the physical climate is inhospitable for all reptiles. If we were to introduce a collection of reptiles to such places, the introductions would obviously fail.

How then can we make a fair comparison? The conservative approach is simply to consider a wide collection of islands that are climatically capable of supporting reptiles and determining if a negative relationship exists between the number of resident species and the number of successful introductions. Since many of the places with few native species will also have had minimal human occupation and thus few introduction attempts, there will be a tendency to reject Elton's hypothesis even if it is correct. Similarly, since almost universally, the number of native species in an area increases with area, and since a priori there is no reason not to expect this same trend in introduced species, as well as native species, the numbers of both might be positively associated across islands. We test this hypothesis by performing a partial correlation between the number of native reptiles and the number of introduced reptiles (after the differences in island areas and elevations are removed by partial correlation) for island chains and three mainland sites around the world. We do not partial-out variation due to differences between islands' isolation distances, because isolation does not significantly affect introduced species number and its effect on native species' richness (highly significant) is immaterial to the hypothesis.

The island tallies are in Appendix 2 and the results appear in Fig. 2, which illustrates a significant negative partial correlation coefficient ($p < 0.012$) between numbers of introduced species and numbers of natives. There is a lot of scatter reflecting the very different human histories on these islands and the different species involved from place to place. Some places are outliers, like southern Florida, with high native and introduced species numbers. A rich native reptilian fauna will often be associated with a rich fauna of other taxa that might compete with or prey upon reptiles so it will be wise to test for other correlations. Could these other taxa be responsible for the major trend? The negative relationship in Fig. 2 cannot simply be explained by co-varying differences in these sites' mammalian predator species since their numbers do not significantly correlate with numbers of introduced lizard species ($p > 0.8$; partial correlation coefficients with introduced reptile numbers after partialling out log area and log elevation). The partial correlation between introduced reptiles and bird species number is negative but not quite significant ($p = 0.058$). The partial correlation between bird species number and native reptile species number is highly positive ($p = 0.305$) and significant ($p > 0.0001$). However, most of this correlation is because the richness of both native taxa decreases with island isolation (unlike the situation for introduced species where island isolation does not play a significant role). After partialling out the effect of log distance along with log area and log elevation, there is still a positive, although less significant, partial correlation coefficient between native reptile and native bird species number ($r = 0.329$; $p = 0.014$). Thus what ever factors (other than area, elevation, and isolation) are affecting species numbers in reptiles and birds, they are working jointly on both taxa.

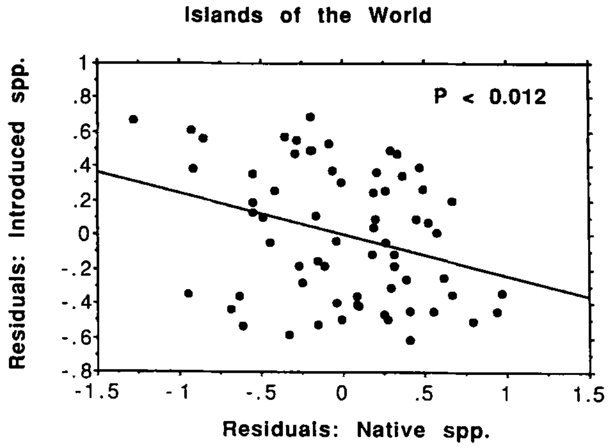

Figure 2. The partial correlation between introduced species richness and native species richness for reptiles on island chains worldwide. Both axes are the residuals of species number (log transform of S + 1) after the effects of log island area and log elevation are removed. The residuals are introduced lizard species are negatively correlated with those for native lizard species ($p < 0.012$). The data are in Appendix 2.

One problem with this analysis is that a single point, e.g. Fiji, includes many islands; not all of which have the full complement of introduced species present in the archipelago. Indeed one can imagine a situation wherein all the introduced species are confirmed to a single island that lacks any native species. In this case the two sets of species never see each other in the archipelago and it would be meaningless to examine species numbers for the archipelago as a whole. On the other hand, using individual islands as data points (rather than lumping into archipelagos) commits pseudoreplication since the native faunas and introduction histories of nearby islands are typically closely linked. Nevertheless, we expand this analysis with the data in Appendix 1 for individual islands in the Seychelles (which is only a single point in Fig. 2) and the data set for individual Pacific Islands in Table 1. The results are shown in Fig. 3 and Fig. 4. Islands of the Seychelles shows a significant negative partial correlation ($p < 0.0002$). (Recall that the presence or absence of rats is not significantly correlated with introduced species number and thus can not explain this trend.) On the other hand, we find that the partial correlation between native and introduced species number (after partialling out log area and log distance) for the Pacific islands data set although negative is not significant for these sample sizes (Fig. 4). Thus, here neither mongoose nor native species richness accounts for inter-island differences in introduced species richness for this small set of islands.

The invadability of many of the species-poor islands may not simply be a reflection of few native species *per se*, but of the competitive 'naiveté' of native species that have evolved in such isolation. In practice, it will be difficult to untangle the relative role of these two factors since species-poor islands tend to be isolated and thus have higher proportions of endemic species that have evolved in isolation.

Competition among introduced species

Because man has introduced lizards to various islands from different parts of the world and at different times we have semi-experimental conditions, complete with controls and replicates (albeit unconscious ones), to assess the strength and mechanism of interaction between species in these sets. Not enough time has elapsed for coevolution to reduce the intensity of interactions between introduced species so we might expect competition among them to be pronounced (Salzburg, 1984).

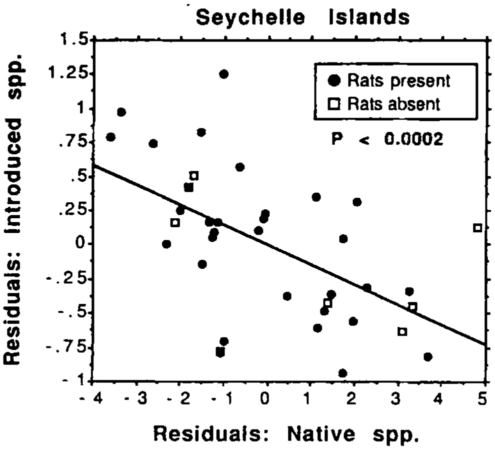

Figure 3. The partial correlation between introduced species richness and native species richness for lizards on islands in the Seychelles. Both axes are the residuals of species number after the effects of log island area are removed. The residuals for introduced lizard species are negatively correlated with those for native lizard species ($p < 0.0002$). The data are in Appendix 1.

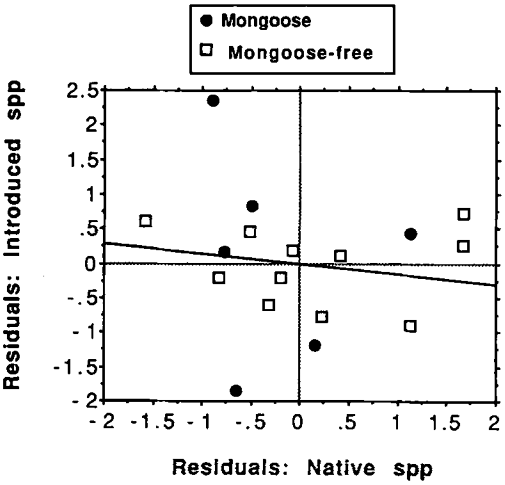

Figure 4. The partial correlation between introduced species richness and native species richness for reptiles on islands in the Tropical Pacific. Both axes are the residuals of species richness after the effects of log island area and log elevation are removed. The residuals for introduced lizards are not significantly correlated with those for native lizard species ($p > 0.5$). The data are in Table 1.

In Hawaii the most common skink until about 1940 was *Emoia cyanura*, which is still the most common skink in Fiji, Somoa, the Marquesas and nearly everywhere else in the Pacific where it occurs (Oliver and Shaw, 1953; McKeown, 1978; Jones, 1979). It is also common in subfossil deposits in Hawaii from the Polynesian period (G. K. Pregill, personal communication). This pattern changed around 1910 when *Leiolopisma metallicum* was accidentally introduced to Hawaii. Today *E. cyanura* along with the moth skink, *Lipinia noctua*, is extremely rare, while *Leiolopisma* is by far the most abundant skink on every island. Unfortunately, this lizard apparently was not introduced elsewhere in the Pacific so we have no replicates, but on the many 'control' islands in the Pacific *E. cyanura* and *L. noctua* are still very common. Moreover, in lizard-rich southeast Australia and Tasmania, where *L. metallicum* originated, it is neither particularly common nor widespread (T. J. Case, personal observations; Cogger, 1983).

Another apparent example of competitive exclusion has also occurred in Hawaii. After World War Two, a new gecko appeared in Hawaii: the common house gecko (*Hemidactylus frenatus*), native to Asia and the Indo-Pacific. It subsequently increased in numbers in urban/suburban habitats, while three other Polynesian-introduced geckos, the fox or Polynesian gecko (*Hemidactylus garnotii*), the mourning gecko, (*Lepidodactylus lugubris*), and the stump-toed gecko (*Gehyra mutilata*), formerly occupying this habitat became scarce (Oliver and Shaw, 1953). Today the most common association on lighted building walls is the house gecko alone or sometimes in association with the smaller and much less abundant mourning gecko (Case *et al.*, 1990). Frogner (1967) found that the house gecko could displace the mourning gecko from favoured shelter sites in laboratory experiments and that they would eat juvenile *Lepidodactylus*. The reverse is not true, however, since hatchling geckos are larger than the largest prey taken by *Lepidodactylus* in the field.

Elsewhere in the Pacific where the house gecko has yet to invade (e.g. most of the Societies, Tuamotus, Marquesas, most of the Cooks, and most of Fiji), *G. mutilata* or *G. oceania* with *Lepidodactylus lugubris*, and/or *Hemidactylus garnotii* have remained dominant in the 'human building' niche (Case *et al.*, 1990). This appears to be changing, however, on the main Fijian island, Viti Levu. Although unrecorded until recently, the house gecko has been in the Nadi area on the west for at least 20 years (D. Watling, personal communication) and now is the only gecko common in towns along the west. It appeared in the major port city of Suva in the southeast about 4 years ago and already has become the most frequent gecko on walls at the University of the South Pacific campus in Suva with the concomitant decline of the previous resident geckos (T. J. Case and D. T. Bolger, personal observations; J. Gibbons, personal communication; D. Watling, personal communication). Today the area around Suva is a mosaic with *H. frenatus* numerically dominant in some areas but absent in others where instead the other gecko species are found in high numbers. In areas where *H. frenatus* is present but not common, its numbers have been increasing over the last 2 years (Bolger and Case, unpublished). Transplantation experiments are underway to determine the mechanism behind the competitive interaction. Bolger and Case (in preparation) have shown that *H. frenatus* males are behaviourally dominant to the asexual *L. lugubris* and *H. garnotii*.

The house gecko fauna also changed rapidly in Vanuatu (New Hebrides). In 1971, the Royal Society did not find a single *H. frenatus* in Vanuatu (Medway and Marshall, 1975; A. G. Marshall, personal communiction). Today it is virtually the only urban gecko seen in the major city of Port Vila on Efate (although it is still restricted largely to that area on Efate) and is by far the most common gecko in the town of Santo on Espiritu Santo (Case *et al.*, 1990). Despite much recent work on the geckos of the Society Islands, Ineich (1987) did not find any *Hemidactylus frenatus*. In 1989 we recorded the presence of this species on Tahiti for the first time; it presently is restricted to the wharf area of Papeete where it is already the most common gecko on buidlings.

Despite these strong density effects we can find no documented case in the literature in which a native reptile species or a previously introduced species is reduced to complete extinction by the introduction of a reptilian competitor.

Acknowledgements

At various stages during the development of this paper many people contributed ideas, suggestions and useful unpublished information: Robin Andrews, Aaron Bauer, Ron Crombie, Tom Fritts, John Gibbons, Mike Gilpin, Gerald McCormick, Greg Pregill, Jon Roughgarden, Tom Schoener, Dick Watling, Ernest Williams, George Zug and Richard Zweifel. We thank them and we also thank Allison Alberts, Jared Diamond, Stuart Pimm, Greg Pregill and Tom Schoener for improving the presentation. NSF grant BSR 8805969 supported T. J. Case's work on Pacific gecko introductions.

Appendix 1: the number of lizards, species and island characteristics for the Seychelles and vic

The following species are considered introduced wherever they occur (Blanc, 1972): *Cryptoblepharus boutonii*, *Hemidactylus frenatus*, *H. brookii*, *Gehyra mutilata*, *Lepidodactylus lugubris*.

Island	No. introduced spp.	No. native spp.	No. extinct spp.	Area (km^2)	Total native spp.	Rats
Aldabra	2	2	6	155	8	+
Aride	0	6	0	0.683	6	–
Assumption	2	1	0	11.5	1	+
Astove	1	2	0	6.61	2	+
Bird	2	2	0	1.1	2	+
Cerf	0	2	0	1.27	2	–
Cerf (M)	1	3	0	1.3	3	+
Coetivy	2	0	0	9.32	0	+
Conception	0	4	0	0.6	4	+
Cosmoledo	1	1	0	3.5	1	+
Cousin	0	6	0	0.286	6	–
Cousine	0	4	0	0.257	4	–
Curieuse	1	5	0	3	5	+
D'Arros	1	2	0	1.7	2	+
Denis	1	3	0	1.5	3	+
Desnoeufs	1	1	0	0.35	1	–
Desroches	2	0	0	3.94	0	+
Farquhar	2	2	0	7.84	2	+
Felicite	0	5	0	2.68	5	+
Fregate	1	8	0	2	8	–
Glorieuses	1	2	1	–	2	+
Grande Soeur	1	5	0	0.84	5	+
La Digue	1	6	0	15	6	+
Long	0	3	0	0.21	3	+
Mahe	1	8	2	145	10	+
Marianne	0	2	2	0.95	4	+
Marie Louise	1	1	0	0.52	1	–
North	1	2	0	2.7	2	+
Petite Soeur	0	4	0	0.34	4	+
Platte	1	1	0	0.53	1	+
Poivre	1	1	0	1.11	1	+
Praslin	1	6	1	45	7	+
Providence	1	2	0	2.32	2	+
Remire	1	2	0	0.27	2	+
Round	0	4	0	0.2	4	+
Saint Anne	1	3	0	2.2	3	+
Silhouette	1	7	1	16	8	+
St. Joseph	0	2	0	1.39	2	+
St. Pierre	1	1	0	1.7	1	–
Thereese	1	4	0	0.74	4	+

Appendix 2: the number of introduced and native reptile species on various island groups

Location	No. introduced spp.	No. native spp.	Island area (km^2)	Maximum elevation (m)	Mammal predators	No. bird spp.
Aldabra	2	3	155	100	3	21
Ascension	2	0	90	860	3	0
Australia	2	477	7 680 000	2228	5	466
Azores	0	1	2 304	2320	3	20
Balearic	0	12	5 014	1445	5	119
Bermuda	3	1	49	73	3	13
British Isles	1	6	307 702	1343	5	170
Calif. Channel Islands	0	12	904	753	4	56
California (Southern)	3	64	137 016	3963	5	213
Canaries	1	9	7 273	3720	3	48
Cape Verde	—	9	4 033	2829	3	26
Chagos	4	0	65	20	3	3
Chatham	0	1	973	213	2	20
Christmas (Ind. Ocean)	4	6	135	357	0	8
Clipperton	1	0	12	29	3	—
Cocos	0	2	47	854	4	7
Comoros	5	20	1 958	2361	4	52
Cook Islands	9	1	240	652	3	13
Corsica-Sardinia	0	17	32 771	2771	5	120
Cozumel	0	15	324	24	5	75
Crete	1	11	8 332	2457	4	51
Curaçao	1	11	425	372	3	40
Easter	3	0	116	530	2	0
Fiji (excludes Rotuma)	10	13	18 300	1300	4	58
Florida (Southern)	12	52	30 388	40	5	133
Galapagos	3	24	7 855	1524	3	36
Guam	14	3	541	406	3	23
Hawaii	13	0	16 344	4206	4	43
Henderson	2	0	37	33	1	4
Jamaica	0	32	11 424	2256	4	92
Kangaroo	2	20	3 890	190	4	79
Lord Howe	0	2	13	853	3	14
Loyalties	7	10	2 070	129	–	—
Madagascar	4	247	587 000	2881	5	186
Malpelo	0	3	85	377	0	2
Margarita	0	17	850	990	3	—
Marquesas	9	0	910	1260	2	14
Mauritius	10	4	1 865	826	4	15
New Caledonia	5	31	16 912	1815	3	62
New Hebrides (Vanuatu)	10	14	12 000	1889	3	56
New Zealand	1	30	266 800	3765	4	65
Norfolk	0	2	40	310	2	20
Palau	7	17	440	240	3	31
Pemba	2	17	984	85	4	68
Pitcairn	4	0	5.2	347	–	3
Poor Nights	0	7	2	152	0	7
Puerto Rico	2	29	8 897	1350	4	86

Location	No. introduced spp.	No. native spp.	Island area (km^2)	Maximum elevation (m)	Mammal predators	No. bird spp.
Reunion	7	4	2512	3040	3	16
Revillagigedo	0	3	233	1113	0	—
Rodriguez	5	0	109	396	3	13
Rotuma	7	4	45	300	3	15
Samoa	8	6	3150	1858	3	34
Sea of Cortez (LB)	0	58	1713	620	1.5	34
Sea of Cortez (Oc)	0	68	1236	1316	2	26
Seychelles	4	16	414	913	3	19
Societies	10	0	1550	2322	3	24
Solomons	9	55	35800	3100	4	143
Sri Lanka	1	136	65610	2528	5	225
Taiwan	3	72	36125	3998	5	132
Tasmania	0	15	67900	1520	5	104
Three Kings	0	5	7	300	1	11
Très Marias	0	18	350	613	4	34
Trinidad	4	59	4542	1250	5	235
Tristan da Cunha (Archi)	0	0	259	2329	3	6
Tuamotu	8	0	855	113	3	8
Wake	6	0	23	6	3	1
Zanzibar	3	38	1658	125	5	102

(1) LB = Recent landbridge islands; Oc = Oceanic islands not connected to the mainland or source islands during the Pleistocene.

(2) The number of introduced species includes those thought to be introduced by aboriginal peoples as evidenced by: (a) a lack of subspecific differentiation; (b) anthophilic habits; (c) no appearance in middens or subfossil deposits dated earlier than man's appearance on the island group. For the Pacific we consider the following species as introduced: *Hemidactylus frenatus*, *H. garnotii*, *Lepidodactylus lugubris*, *Nactus pelagicus*, *Gehyra oceanica*, *G. mutilata*, *Emoia cyanura*, *Lipinia noctua*, *Cryptoblepharus boutonii*. Some of these species also occur on New Guinea but since they may or may not be native to that large island we exclude New Guinea from consideration.

(3) An introduced species must present be maintained a breeding population.

(4) For island archipelagos like Hawaii or Fiji the number of species is totalled over all islands in the group. The definition of an archipelago does not always follow geo-political boundaries. Here, islands are lumped when the islands share species, are similar in area, geological age, and distance to colonizing sources. Islands whose distance apart is greater than the distance to the mainland or other major faunal source island are not lumped. For example, 'New Zealand' includes only the two major islands, not the many small off-lying islands; The Mascarenes: Reunion, Rodrigues, and Mauritius, are considered separately because they are about as far apart from one another as they are to their major source. Rotuma is considered separate from the rest of Fiji. The Sea of Cortez is separated into two groups: landbridge and older oceanic islands. We do not consider the geographically diffuse Bahamas at all.

(5) The choice of islands is constrained by the following considerations: (1) islands should occur at latitudes less than 36 degrees and no oceans or seas should be excluded if in the correct latitudinal band; (2) islands should be well surveyed for reptiles.

(6) Only land and freshwater reptiles are considered and only those presently extant.

(7) The species diversity of mammalian predators is categorized as follows: (0) None; (1) Polynesian rat (*Rattus exulans*) or other native rats but no introduced rats (*R. rattus* or *R. norvegicus*) or other predators; (1.5) feral domestic cats but no rats; (2) *Rattus rattus* and/or *R. norvegicus* but no feral cats or other predators; (3) introduced rats and feral cats with or without native rats and feral domestic dogs (but no other predators); (4) introduced rats, feral cats and dogs, plus a mongoose, and/or a stoat or weasel, or any other mustelid or viverid; (5) a rich mainland fauna that includes rats, feral cats, and dogs plus several native carnivore species and other lizard predators such as primates and large insectivores.

(8) The number of bird species includes all land and freshwater species living or extinct since 1600 but not prehistoric extinctions whose existence is based solely on fossils.

(9) References for reptiles, birds and mammals on each archipelago are from Case (unpublished).

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