THE RAFFLES BULLETIN OF ZOOLOGY 2000 **48**(1): 1-9

PERSPECTIVE:

EXTINCTION-PRONENESS OF ISLAND SPECIES - CAUSES AND MANAGEMENT IMPLICATIONS

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ABSTRACT.- After three centuries of anthropogenic insults, island species and communities are in the forefront of the precipitous decline in biodiversity that we face in the new millennium. The sorry plight of island biotas is often seen as resulting from an inherent weakness of island species, manifested particularly by how poorly they have fared in response to the many continental species introduced to islands. In fact, particular continental populations and communities have been similarly devastated. However, their larger geographic ranges tend to immunize them against the global extinction suffered by island species, many of which are endemic. The problems for island species are more those of restricted range than of minimum viable population size. Neither are the solutions to this insular hecatomb to be found in generalized attempts to avoid small populations. Rather, management must be tailored to the idiosyncrasies of particular threatened species and communities. The two key actions that would improve the prospects for many island biotas would be a lessening of the rate of introduction of nonindigenous species and a decline in the rate of habitat conversion. Prospects for activities to stem the impact of invasions are improving, though still not good. There seems little reason for optimism about lessening island habitat destruction, but improvements can be made in excluding potentially harmful species introductions, eradicating introduced species that nevertheless establish populations, and enhancing the ranges of very restricted island species through transplantation. Crucial to these efforts is a sound understanding of the natural history of island species.

KEY WORDS.- biodiversity, disharmony, endemism, equilibrium theory, extinction, impoverishment, islands, saturation.

INTRODUCTION

Biotas of islands, especially oceanic islands, characteristically differ from continental biotas in four ways. They are relatively impoverished, unsaturated, and disharmonic, and they harbor a disproportionately high number of endemic species. This last trait – high endemism – means that island species are crucially important to global biodiversity, while the first three traits are often seen as causing island species and communities to be particularly fragile. This is the island dilemma – great biodiversity, much of it not found elsewhere, but great danger. If New Guinea is taken as the largest island, islands comprise only 3% of the total land mass of the earth (Whittaker, 1998), while over 15% of plants, land snails, and birds are restricted to islands (Whittaker, 1998). This is because, for many taxa, even vagile ones like birds, isolated islands, even if depauperate in numbers of species, typically have very high proportions of endemics (Groombridge, 1992).

It is also true that a disproportionate fraction of all endangered and recently extinct species are island species. For example, island plants are 2.5 times as likely as continental ones to be endangered (calculated from data in Groombridge, [1992]; Whittaker [1998]), while island birds are 2.7 times as likely as continental ones to be endangered (calculated from data in Johnson & Stattersfield, [1990]; Groombridge, [1992]; Whittaker, [1998]). Thus, the fate of island species will disproportionately influence global biodiversity, and it is important to understand what threatens them and why they are disappearing so rapidly if there is to be any hope of effective activity to stem this loss.

Impoverishment, saturation, and disharmony

The single or combined influences of impoverishment, lack of saturation, and disharmony have long been seen

Received 8 Apr 2000 Accepted 10 Apr 2000

as rendering island communities particularly vulnerable. Impoverishment and lack of saturation are really parts of the same phenomenon. It is an ecological commonplace that, all other things being equal, an island will have fewer species than an equal-sized piece of the mainland, as is most readily seen by comparing species-area curves (e.g., Lawlor, 1986; Rosenzweig, 1995). However, the explanation for this commonly observed pattern is somewhat controversial.

The MacArthur-Wilson (1967) dynamic equilibrium theory of island biogeography sees the lower number of species on islands than on mainland as a consequence of both reduced area and increased isolation relative to the mainland: small islands have fewer species than large ones because they are smaller, and distant islands have fewer species than near ones because they are more isolated. Then, according to the dynamic equilibrium theory, the lower number of species on an island than on an equivalent mainland patch of equal area is due to the greater isolation of the island. On the mainland patch, there is a constant influx of propagules of species from the surrounding matrix, including propagules of species that might have no chance of long-term survival in the patch itself (e.g., if the patch were too small to support a viable population, or contained the wrong habitat). Island isolation prevents such an influx.

On the other hand, Lack (1976) did not believe that the equilibrium theory explained island distributions, at least for birds. Rather, he felt that islands typically lacked habitats present on the mainland, and distant islands on average had even fewer habitats than near islands. Thus, the fact that isolated islands had fewer species than near islands, which in turn had fewer species than the mainland, was explicable in terms of habitat differences.

When Lack's book was published, during the heyday of the equilibrium theory, it was generally panned. Nowadays, however, the equilibrium theory is seen as having quite limited application, especially to oceanic islands (Simberloff, 1994; Whittaker, 1998), and its role is more heuristic, focussing attention on the short-term causes of extinction (Haila & Järvinen, 1982), particularly the role of demographic stochasticity in small populations. And increasingly, observations that superficially would appear to support the equilibrium theory are more comfortably explained by habitat differences or changes, just as Lack had suggested. For example, the species-area relationship, that large islands have more species than small ones, is rationalized by the equilibrium theory as a consequence of lower extinction rates on larger islands (MacArthur & Wilson, 1967). However, it is also predicted without any turnover at all, simply on the basis that larger islands, on average, have more habitats than small islands, and each habitat adds a complement of species (Connor & McCoy, 1979). The habitat explanation seems usually to be the more cogent one, as few data demonstrate dynamic turnover on islands in the absence of habitat change (Simberloff, 1994).

Consider an observation from Socorro Island, ca. 600 km from the Mexican mainland (Jehl & Parkes, 1983). Between 1958 and 1978, the endemic dove *Zenaida graysoni* disappeared and the endemic mockingbird *Mimodes graysoni* declined towards extinction. At approximately the same time, the mainland mourning dove (*Z. macroura*) and mainland northern mockingbird (*Mimus polyglottos*) became established. This would seem to exemplify equilibrium turnover perfectly, with immigration balancing extinction. But Jehl & Parkes (1983) argue that it was actually biotic and abiotic habitat changes on the island that caused this turnover. Predation by recently introduced feral cats (*Felis catus*) caused the endemic species to decline, while the two new immigrants had been frequent transients on the island previously but had been unable to establish populations until freshwater became available when a military base was established.

The two hypotheses for island impoverishment and the species-area effect – the equilibrium theory and habitat differences – have very different implications for the idea that island communities are less saturated than mainland communities. Sometimes a low number of species on an island seems clearly to be related to the inability of some species to reach the island, and one would guess that the island could accommodate many more species if they could only disperse there. For example, Williamson (1981), following Wyatt-Smith (1953), pointed to the island of Jarak in the Straits of Malacca, 51 km from the nearest island and 64 km from the mainland. A 40-ha forested island, it lacks dipterocarps, the chief mainland dominant trees. Dipterocarps are believed to have poor long-distance dispersal abilities. In a 0.4 ha plot on Jarak, Wyatt-Smith found 34 tree species, compared to 94 and 102 for two mainland plots. In this instance, the island seems less saturated than the mainland, at least for trees, although experimental introductions would have to be performed to prove this hypothesis, against the alternative that some subtle habitat difference is precluding the dipterocarps from colonizing the island.

The wealth of successfully established introduced species on islands is also often seen as proof that islands are unsaturated (e.g., D'Antonio & Dudley, 1995). For example, Hawaii has about 2,500 introduced insect species (Funasaki et al., 1988; Nishida, 1992) and 5,000 native species (Nishida, 1992), while the continental United States has about 3,000 introduced insects (Anon., 1986) and 90,000 native species (Arnett, 1983). Again, it seems as if these islands are unsaturated relative to the mainland, and that perhaps this is why introduced species comprise such a large fraction of the total. But without information on how many propagules arrived in the two places and how many species failed to survive after introduction, it is difficult to make a definitive judgment (Simberloff, 1986, 1995). Also, many of these insects are found almost exclusively in agricultural habitats on these islands; this is an entirely manmade habitat and invasion into it says nothing about the degree of saturation of the original entomofauna.

Here is where disharmony comes in. Carlquist (1965, 1974) and others have pointed to the fact that island biotas tend to be disproportionately rich in some taxa, generally ones that are dispersive, and disproportionately poor in others. Berry (1998) objects that the term "disharmonic" is pejorative, implying that continents have some harmonious, "proper" sort of community and that island assemblages are somehow "wrong" or "out of balance." He is correct, but the fact remains that the distribution of species into higher taxa differs characteristically between islands and continents. Oceanic islands, for example, typically lack non-flying mammals.

It is perhaps disharmony rather than impoverishment per se that leads to less saturation on islands. Many island vertebrates, existing in impoverished and disharmonic communities, have expanded their ranges of habitats or feeding niches (references in Grant, 1998), so it is not as if many resources are unused on islands. Nevertheless, entire ways of making a living are absent (e.g., there are no grazing or predatory mammals), and it is probably these "niches" that are unfilled and render the entire biota less saturated than the mainland biota. About three times as many bird species and 1.6 times as many mammal species have been successfully introduced to islands than to continents (Atkinson, 1989). Without knowledge of how many attempted introductions were made and how many failed on islands and continents, one cannot be certain that the island communities were more invasible than the mainland ones, but I suspect that they were. It is possible that these successfully introduced species were largely filling roles that were vacant in the original disharmonic biotas.

Thus, to the extent that islands are relatively unsaturated, this feature is probably not linearly related to impoverishment – that is, to species richness – but rather to the more frequent absence of specific types of species on islands than on mainlands. At least this is an hypothesis, and it cannot be adequately tested without direct experiment or many more data on failed invasions than currently exist in the literature on invasions, which may be seen as unplanned and often uncontrolled experiments.

Biological resistance and island species as wimps

It is often claimed that island species are puny maladepts. For example, Yoon (1992: 88), speaking of the Hawaiian islands, said, "...the isolation of these gentle islands from mainland predators and diseases created a flora and fauna ill equipped to handle the rigors of competition with the outside world. Hawaii is home to thistles without prickles, blackberries without thorns and many flightless insects and birds." Greuter (1979) saw island plants as relicts, while Preston (1968) called islands evolutionary "backwaters and dead ends," inhabited by denizens whose relatives had long vanished on continents. Blondel (1995) depicts a "syndrome of insularity" in which typical island species have reduced fecundity, delayed sexual maturity, diminished territorial aggessiveness. The "taxon cycle" of Wilson (1959, 1961; cf. Ricklefs & Cox, 1972) rests on the notion that mainland species that colonize islands eventually evolve there to become less competitive when confronted with new colonists from the mainland, although whether a species on an island should really evolve to become less adapted to this environment than a new invader from the mainland is controversial (Pregill & Olson, 1981).

At the community level, island biotas are seen as presenting less "biological resistance" to invaders (e.g., Elton, 1958; Mayr, 1965). Partly this is simply because there are fewer species, the impoverishment already discussed (e.g., Elton, 1958; MacArthur & Wilson, 1967). Sometimes a related feature, simplified foodweb structure, is seen as making islands more invasible (e.g., Wilson & Bossert, 1971; Pimm, 1991). And often enhanced island invasibility is seen as caused by the inherent weakness of island species (e.g., Williamson, 1981). It is almost a wonder that any island species survives at all!

But a closer examination (Simberloff, 1994, 1995) suggests that the entire phenomenon of island species endangerment and loss plus island community invasibility does not arise simply because island species are inherently weaker or less adapted to their environments than continental species are. Indeed, occasionally an island species seems to do very well in encounters with continental ones, as does the New Zealand mud snail *Potamopyrgus antipodarum*. Since its arrival in 1994, it has exploded to comprise huge fractions of the snail community in the Greater Yellowstone region of North America (Kerans et al., 1999). But, even if all island species are not maladapted wimps, several factors do conspire against island species and favor mainland species.

Changed environment.- The Hawaiian islands, the Mascarenes, and other islands are often depicted as a mass of exotics with little of the native biota left. It is true, for example, that very little of the native forest remains in the lowlands of the Hawaiian islands (Schmitt, 1977). However, it is a far cry from this observation to a conclusion that the exotic species were in some sense "stronger". Rather, the lowland forests were cleared for agriculture, housing, and other human enterprises, and the species that now inhabit these regions are adapted to these anthropogenic habitats. Although I have seen no quantitative assessment of this proposition, I suggest that many continental habitats that have been deforested as exhaustively as certain islands are just as dominated in these areas as islands by exotic species. The consequences for biodiversity may often be greater on islands simply because islands are smaller, a point I will return to below.

The introduction of grazers and predators to islands, and the resultant devastation of plant and animal communities, is also a habitat change, and the fact that oceanic island species were not preadapted to this change does not mean they were somehow weak or maladapted. For example, feral goats have brought several endemic plant species in the Ogasawara Islands to the threshold of extinction (Shimizu, 1995), and there is every reason to think that the same process is now happening rapidly on Uotsuri-jima Island in the Senkaku Archipelago (Yokohata, 1999). However, even on continents, similar introductions have led to similar devastation. Perhaps citing Australia, the island continent, is not quite fair, but it is a continent and its biota is in no way impoverished or even disharmonic, yet grazers and predators have transformed the landscape. Feral cats probably eliminated many small mammals in the last century, and introduced foxes (*Vulpes vulpes*) today are a scourge with respect to numbats, bettongs, rock wallabies, and other small mammals (Low, 1999). Similarly, introduced rabbits (*Oryctolagus cuniculus*) transformed large parts of the Australian landscape (Myers et al., 1994). As another example, pigs (*Sus scrofa*) devastated plant communities of Auckland Island (Atkinson, 1989), but they also devastated plant communities of the Great Smoky Mountains National Park in the continental United States (Bratton, 1975; Singer et al., 1984). Mack (1986, 1989) has described the wholesale replacement of native plant communities of the North American intermountain West and their replacement by Eurasian plants as a consequence of the introduction of large, congregating grazers, to which American plant species were not adapted. And the domination of south Florida by the Australian paperbark tree (*Melaleuca quinquenervia*) and Brazilian pepper (*Schinus terebinthifolius*) (Schmitz et al., 1997) matches any island tale of woe. To my knowledge, no one has tallied the number of cases or total area of such damage on islands and mainland. I do not doubt that island communities are more devastated, as measured by various metrics, but the above examples make the point that many continental species and communities are equally poorly adapted to withstand the introduction of species with very different habits from any in the native biotas. They simply do not go extinct as readily as island species do, as will now be discussed.

Limited island size and lack of refuges.- Even if the total area transformed by invaders such as those just noted is greater on continents than on islands, the biodiversity consequences are greater on islands (Simberloff, 1994). This is because of the great number of island endemics and the fact that islands are much smaller than continents. Thus, a disturbance that strikes a rather small area on an island can imperil or even extinguish a species, whereas continental species are likely to be more widespread, thus to have at least some of their populations immune to a localized disruption. Persistence and subsequent recolonization are thus much more likely on continents.

In the forests of the eastern United States, only about 1% of virgin forest now remains after three centuries of logging. Yet only three of about 70 forest bird species have gone extinct (of which two were hunted to extinction), and two are endangered (Terborgh, 1975, 1989). By contrast, about a third of the original forested area remains in the Hawaiian islands (and much more of moist and montane forest), but 14 of 38 forest bird species are extinct since European colonization, and another 15 are endangered (Berger, 1981; Scott et al., 1986; Ehrlich et al., 1992). The reason the eastern United States avifauna fared better is that the area is so large that not all forest was cut down at once, so there was always substantial suitable habitat left somewhere in their range for most forest species (Terborgh, 1989). Populations were reduced or even lost, but almost all species survived and eventually recolonized the regrowth. In Hawaii, destruction was more rapid, there has been little regrowth, and there was simply insufficient habitat left for many species. They had no refuges in space, no place to go. Because all these Hawaiian birds are endemic species or subspecies, these losses constitute global extinctions. Nothing in this history suggests that the Hawaiian birds were "weaker" than those of eastern North America. They simply had much smaller ranges.

As another example, the brown tree snake (*Boiga irregularis*) was introduced from the Admiralty Islands to Guam around 1950 in military traffic (Rodda et al., 1992). The area of Guam is a mere 541 km^2, originally mostly forest. Of the 12 native and one introduced forest birds, the snake has already eaten 10 of the native species to extinction, and the other two plus the introduced species are rare (Williamson, 1996). There is much concern about the possibility that the snake will eventually be transported to the continental United States (e.g., Fritts, 1994), and one individual was trapped and killed at Corpus Christi, Texas. However, even though I am certain it will be a scourge if and when it arrives, I doubt that the snake will be able to cause global extinctions, and certainly not as quickly as it has on Guam, if only because the eastern forest is thousands of times larger. This would not mean that North American birds were "stronger" and Guam birds puny. Rather, the birds of Guam had no place to hide.

In general, the biodiversity consequences of introduced species are far greater on islands than on continents. For example, for bird species listed as endangered under the United States Endangered Species Act, introduced species were listed as at least one cause of decline from 16 of 19 Hawaiian species but only 2 of 13 mainland species (D'Antonio & Dudley, 1995). The global endangered bird picture resembles that for the United States (MacDonald et al., 1989): of threatened island species, 38% have introduced species as at least one cause of imperilment, while the comparable figure for threatened mainland bird species is only 5%. D'Antonio & Dudley (1995) paint a similar picture for plants of the California mainland as opposed to the California Channel Islands. For 19 island plant species listed as imperiled, exotic species were at least a contributor to the problem for 17 of them. For the mainland, 21 of 134 imperiled species are threatened by exotic species. D'Antonio & Dudley (1995) suggest that both inherent characteristics, like limited powers of dispersal, and the greatly limited geographic range of island species may be responsible for the greater probability of extinction on islands. However, they present no quantitative data in support of either hypothesis. It is not clear that inherent traits of island species play any role in this tale; it may be that they simply have no place where they can escape from invaders.

The differing impacts of cyclones and hurricanes on islands and continents also suggest that the increased vulnerability of island species is due to their small geographic ranges. The Hawaiian islands, the Mascarenes, and the West Indies are all in cyclonic pathways, and recent storms have extinguished several species and endangered others. A hurricane eliminated a bullfinch (*Loxigilla portoricensis grandis*) on St. Kitts (Raffaele, 1977), while another devasted the only population of the Laysan teal (*Anas laysanensis*) on Laysan (Fisher et al., 1969). Hurricane Hyacinthe killed about half the individuals of several small endemic bird species on La Réunion in 1980 (Barré & Barau, 1982). Most striking is that Hurricane Iniki extinguished five endemic bird species and subspecies on Kauai in 1992 (Pyle, 1993). The reason for these disastrous losses is that these islands are all small to begin with and all these populations had already been reduced in size and range by habitat conversion (Simberloff, 1994). Four of the five extinct taxa on Kauai were believed to have fewer than 10 individuals when Iniki struck. The Laysan teal had already been eliminated from Lisianski Island in the nineteenth century (Berger, 1981). On La Réunion, only about a fourth of the original forest remains, of which only a few hundred ha are in the original lowland range of most of the forest bird species. Surely all of these species, having evolved in cyclone belts, would have been able to survive even major hurricanes if their ranges had not been so reduced by humans. Probably mainland species, had they been similarly restricted to small islands and had their ranges further reduced by habitat conversion, would have fared no better.

It is particularly instructive in this regard to compare the impacts of Hurricane Hugo in 1989 on the Puerto Rican parrot (*Amazona vittata*) and the red-cockaded woodpecker (*Picoides borealis*). This hurricane eliminated about half the lone population of the parrot, that of the Luquillo Forest in Puerto Rico. The parrot had already been endangered, because it had been progressively restricted to this one site; in fact, when the hurricane struck, a plan was afoot to establish a second population on Puerto Rico specifically to lessen the threat of such a catastrophe. So the impact of the hurricane threatened the very existence of this species. The same hurricane then devastated the Francis Marion National Forest in South Carolina, home to one of the largest populations of the federally endangered woodpecker. However, the short-term existence of the woodpecker was never in doubt during this hurricane, even within the Marion Forest, because the Marion Forest is eight times as large as the Luquillo Forest, and its population is but one of six substantial populations of the woodpecker. Had the red-cockaded woodpecker been restricted to the Luquillo Forest when Hurricane Hugo struck, it might well have been even more gravely threatened than the parrot (Simberloff, 1994). The parrot was in no sense weaker than the woodpecker. By the same token, at almost the same time that Hurricane Iniki struck Kauai with devastating loss of bird species and subspecies, Hurricane Andrew struck south Florida. This hurricane was one of the largest and strongest ever to hit the United States mainland, yet no bird species went extinct or even suffered substantial population decline. This is because all the resident bird species in south Florida were much more widespread than those of Kauai, not because they were inherently stronger.

Disease.- Introduced diseases often devastate island species (Ebenhard, 1988), and some of these pathogens are vectored by introduced continental species that are resistant to them. A prime example is the decline of several native Hawaiian bird species. Originally, habitat conversion reduced all their populations and relegated them increasingly to upland forests. However, their decline was greatly exacerbated by avian malaria (*Plasmodium relictum capistranoe*) introduced with Asian songbirds and vectored by previously introduced mosquitoes (Van Riper et al., 1986). Perhaps the best known example of island populations devastated by diseases carried by introduced populations is the numerous island peoples worldwide who have fallen victim to diseases carried by human invaders, usually from Europe (Crosby ,1986; Whittaker, 1998). But there are many other pathogens, such as the North American pine wood nematode (*Bursaphelenchus xylophilus*), which reached Japan in timber and spread widely among the islands, killing more than 10 million pine trees and affecting 25% of Japanese forests (von Broembsen, 1989). On the other hand, mainland species and entire communities have also been devastated by introduced pathogens. African ruminant populations were so reduced by rinderpest (*Morbillivirus*) from Asia that the effects are still evident a century later (references in Barbault, 1992), while bubonic plague (*Yersinia pestis*) epidemics have killed millions of people on continents. Similarly, the transformation of forests of eastern North America by introduced plant pathogens such as chestnut blight (*Endothia parasitica*) matches any such devastation on islands (von Broembsen, 1989).

Thus, we cannot say that island species and ecosystems are uniquely affected by introduced pathogens and parasites, but I concede they are probably on average more susceptible (Simberloff, 1994). If there is indeed such a tendency, what might be the reasons? First, it is possible that any such propensity might be part of a larger trend, for Old World diseases to be more inimical to species of other regions than vice-versa (Simberloff, 1995). Almost all major human pandemics, including those that destroyed human populations of islands, originated in the Old World, especially Eurasia (Crosby, 1986). Only syphilis (*Treponema pallidum*) is a New World disease. Similarly almost all devastating plant pathogens have come from Eurasia (von Broembsen, 1989). I have yet to see a convincing general explanation for this trend.

As for why island populations might be particularly vulnerable to introduced pathogens, perhaps the smaller size of island populations lowers the probability that genotypes exist that are resistant to a new pathogen and retards the evolution of new resistant genotypes (Simberloff, 1995) because it takes longer for resistant mutations to occur. This hypothesis is consistent with Carson's (1981) suggestion that total genetic diversity is far greater in mainland populations than island populations because the former are so much larger. Similarly, Kilpatrick (1981) and Berry (1998) found island mammal populations to have less genetic variation than mainland ones, with the former having lower overall heterozygosity. They saw this pattern as consistent with loss of alleles during founding events consisting of small propagules. Carson (1981) also saw lower total genetic diversity on islands as responsible for a tendency for island genotypes to lack well-adapted "general purpose genotypes" that characterize invaders from continents.

Hybridization.- In general, populations in contact with introduced species with which they are interfertile can undergo hybridization and introgression; this is a major global conservation problem (Rhymer & Simberloff, 1996). If sufficient gene flow occurs, a species can even undergo a sort of genetic extinction. This threat is particularly great where a small population is in contact with a much larger one with which it can exchange genes, and many island populations fall in this category. For example, the Seychelles turtle dove (*Streptopelia picturata picturata*) has been transformed into a hybrid swarm by a century of interbreeding with *S. p. picturata*, introduced from Madagascar (Cade, 1983). Similarly, the endemic Hawaiian duck (*Anas wyvilliana*) and New Zealand grey duck (*A. superciliosa superciliosa*) are both threatened with extinction by hybridization with burgeoning introduced populations of North American mallards (*A. platyrhynchos*) (references in Rhymer & Simberloff, 1996). Likewise, the Catalina Island mountain mahogany (*Cercocarpus traskiae*) is in danger of being genetically swamped by introgression with the more widespread and common island mountain mahogany (*C. betuloides* var. *blancheae*) (Rieseberg & Gerber, 1995).

There are myriad examples of this sort of genetic swamping of both island and mainland species (Rhymer & Simberloff, 1996), and it is not clear that the phenomenon is more prevalent on islands than on continents. However, I know of no instances in which an island species invading a continent has thus threatened a native species. In many cases, an invader from one island threatens a population on another island – e.g., the turtle dove example above, or the gradual transformation of Scottish red deer (*Cervus elaphus*) by hybridization with sika deer (*C. nippon nippon*) introduced from Japan (Abernethy, 1984).

Conservation implications

It is clear from the above catalog of threats that island species are not doomed to extinction by inherent weaknesses. Their small geographic ranges and concomitant small population sizes may make them more prone to extinction than the average mainland species when a disaster strikes or the biotic or abiotic habitat changes, but continental species of greatly restricted range and numbers are equally at risk. The small population sizes of island species do not automatically doom them to swift extinction. For example, the Socorro Island hawk (*Buteo jamaicensis socorroensis*) has had a stable population of no more than ca. 20 pairs for many generations, and probably for its entire existence (Walter, 1990). So long as its island environment does not change rapidly, especially by human actions, there is no reason to think it cannot persist indefinitely. Thus, for this species as for other island inhabitants, the key to conservation is not to change the island habitat. At least for some taxa, in the recent historical past, introduced species have been the single biggest cause of island species loss (e.g., birds; Johnson & Stattersfield, [1990]). Nowadays, although introduced species are still the second most important threat, habitat conversion is the single biggest factor. For example, for endemic island bird species, habitat conversion is a principal cause of decline three times as frequently as introduced species are (Johnson & Stattersfield, 1990), although often these phenomena both contribute to the decline. Unfortunately, habitat destruction is probably the single most intractable worldwide trend, bound up as it is with socioeconomic and political issues. However, even before a solution evolves to this global change, several possibilities for positive action to preserve island biodiversity suggest themselves.

First, the prominence of introduced species among the threats to island inhabitants is obvious. Predators, grazers, pathogens, and hybridizers have all been mentioned. To this list can be added species that change ecosystem properties to the detriment of natives, such as the nitrogen-fixing shrub *Myrica faya* on nutrient-poor Hawaii (Vitousek et al., 1987), the salt-depositing African ice-plant *Mesembryanthemum crystallinum* in the California Channel Islands (D'Antonio & Dudley, 1995), and fire-enhancing introduced grasses on many Pacific islands (D'Antonio & Vitousek, 1992). Thus, the single most important action that would enhance the prospects for conserving island biodiversity would be to prevent the importation of new invaders. In an era in which cargo and travel are rapidly increasing and free trade is a religion, limiting movement of new species to islands will be difficult, but there are rays of hope. The inclusion of the introduced species problem in the Rio Convention on Biological Diversity is a promising start (Simberloff, 2000a), and the Global Invasive Species Programme (Mooney, 1999) that will make this problem an action item seems well underway.

Further, introduced species can sometimes be eradicated, and islands have been the locus of some of the most important and inspiring successful eradications (Simberloff, 2000b), from the nutria *(Myocaster coypus)* eradication on Great Britain (Gosling, 1989) through many mammal removals on smaller islands (references in Simberloff, 2000b). The sterile-male technique has allowed insects to be eradicated, such as the the melon fly *(Bactrocera cucurbitae)* from the entire Ryukyu Archipelago, including Okinawa, between 1972 and 1993 (Iwahashi, 1996; Kuba et al., 1996). The very isolation that limits native species' ranges and re-immigration probabilities and enhances their vulnerability also enhances the vulnerability of introduced invaders to eradication campaigns. The key is to have early detection plus a rapid-response mechanism in place with a designated lead agency and sufficient funds and powers to see a campaign to completion (Simberloff, 2000b).

A second general lesson from the above catalog of threats is that, whenever possible, island species' ranges should be enhanced to lower the possibility that a single catastrophe will destroy the entire population. It would be best to be proactive in this matter, rather than trying to establish a new population from the remnants of a population that has already been devastated. Where an island species' range has been greatly restricted by habitat conversion and/or other forces, it is important to consider the possibility of establishing new populations even on islands that were not part of the original range. In New Zealand small islands have been widely used for the establishment of such "insurance populations" of birds (e.g., Craig & Veitch, 1990; Butler & Merton, 1992). However, much thought must be given to the possibility that introduction of a species to a new island for this purpose might affect one or more resident species. For instance, a second population of the endangered Laysan finch (*Telespiza cantans*) was established at Pearl and Hermes Reef, some 500 km northwest of Laysan, in 1967 (Ehrlich et al., 1992). It is thriving, but there is some indication of negative impact on native birds, as the finch preys on eggs of small seabirds (S. Conant, pers. comm., 1999).

Finally, the key role of habitat in the trajectory of island species, plus the recognition that island species are not inherent weaklings destined to disappear because of small population size or other peculiarities, imply that generic responses to small population size (e.g., the 50-500 rule [Franklin, 1980]) are unlikely to be very effective. Caughley (1994) has contrasted the small population paradigm of conservation biology, which sees a few general threats to any small population, to the declining population paradigm, in which concern is focused on populations actually undergoing a decline, and on the specific reasons for each decline, some of which may be highly idiosyncratic. He exemplifies the latter approach with the rescue of the Lord Howe Island wood hen *(Tricholimnas silvestris)*. At heart, a conservation program based on the declining population paradigm is simply sensitive natural history, so it lacks a set of general, quantitative, deductive rules of the sort that confer a scientific cachet on the small population paradigm, which has dominated modern conservation biology (Simberloff, 1988; Caughley, 1994). However, if it is sensitive natural history that is going to underpin most truly successful island conservation programs, then this is the course that conservationists will have to follow, scientific cachet or not.

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