# Keynote Address

## Conservation Biology and the Unique Fragility
## of Island Ecosystems

### Daniel Simberloff

*Department of Biological Science, Florida State University, Tallahassee, Florida 32306*
*Tel. (904) 644-6739; Fax (904) 644-9829*

## Introduction

The term "island" has been used in recent conservation literature to denote oceanic islands, continental islands, and all manner of habitat islands. Generalizations and models referring to 1 kind of island are often applied inappropriately to other kinds, to the detriment of conservation. One needs an ecological definition of an island; Haila (1990) recognizes 4 scales of insularity.

On the individual scale, a habitat patch is an island for a species if a crucial stage of its life history (e.g., reproduction) occurs in 1 patch. But insularity at the individual scale does not have population or community consequences, except as it renders the entire locale a good or bad habitat for an entire population or community. Individuals, though restricted to single patches at certain times, are parts of larger, regional populations. At the population dynamic scale, populations on different islands are dynamically independent of one another. At a higher scale, populations may be genetically differentiated on different islands. (Though it is not completely clear that genetic differentiation must preclude population dynamic interaction, surely this must usually be the case.) And, if populations on different islands are completely isolated from one another, as on distant oceanic islands, the islands are insular at the evolutionary scale. Their evolutionary trajectories are independent.

All 4 scales of insularity are important to conservation. At the individual scale, habitat fragmentation may render an entire region increasingly unsuitable for a species because fragments suitable for individual use are too few and far between. The equilibrium and metapopulation theories that have dominated much of the conservation literature pertain to the population dynamic scale and are the bases for widely cited plans for refuge design and population recovery and transplant. Conservationists are interested in genetically different populations, of course, and are even more concerned to preserve independently evolving lineages (e.g., Vane-Wright et al.

1991). However, a confusion of scales will not help conservation, and models should be applied at their appropriate scales.

## The "New" Conservation Biology

### *The dynamic equilibrium island biogeography model*

Conservation biology is often viewed as a recent, burgeoning science, with a new, large professional society (the Society for Conservation Biology, founded in 1985), 2 new international journals (*Conservation Biology* and *Biodiversity and Conservation*), several recent edited collections of readings (e.g., Fiedler and Jain 1992), and a brand new textbook (Primack 1993). Certainly there has been a burst of research, with new emphases, during the last 2 decades, but scientific study of conservation problems is much older (Simberloff 1988). The "old" conservation biology focussed on habitat requirements of particular species. The "new" conservation biology originally focussed on 2 quite disparate subjects: (1) the dynamic equilibrium model of island biogeography as a metaphor for refuges, and (2) the genetic consequences of isolation of small populations. These foci both conceived of islands at the population dynamic scale.

These 2 new subjects were really quite distinct intellectually. Genetic happenings in small, isolated populations—particularly inbreeding depression and drift—pertain to populations, not communities. The equilibrium model is a community-level construct that aims to predict the number of species at a site in terms of ongoing immigration and extinction of component populations. Although 1 early mathematical model (Simberloff 1969, 1983) attempted to predict the equilibrium number of species for an island in terms of population characteristics of the individual species in the species pool, the focus of publications on the equilibrium theory remained on the community, not on the species. One wanted to

know such things as how the number of species on an island changes with island area, degree of isolation, elevational range, or other physical characteristics.

A flurry of almost simultaneous papers (Diamond 1975; Terborgh 1975; Wilson and Willis 1975) all propounded the idea (of disputed provenance [Willis 1984]) that the equilibrium theory of island biogeography has great import for conservation and the design of refuges, analogizing a refuge to an oceanic island. This was part of a general attempt to consider patches of distinct habitat as islands. Even in the early days after the publication of the key monograph on the equilibrium theory (MacArthur and Wilson 1967), researchers studied various kinds of habitat islands—lakes, forest patches in the midst of fields, and so forth—in the context of the theory. The peak of popularity of the dynamic equilibrium theory as a model and guide for conservation came in the wake of the publication in 1980 of *World Conservation Strategy* jointly by the United Nations Environmental Program, International Union for the Conservation of Nature, and World Wildlife Fund. This work propounded 6 rules for refuge design, ostensibly based on the equilibrium island model. The model and the rules quickly filtered into introductory textbooks and the popular press.

However, the very popularity and exposure of the equilibrium island model led to much closer scrutiny of both the model and its applicability to conservation. The scrutiny, in turn, led to a sober re-evaluation of the theory itself (e.g., Gilbert 1980; Williamson 1981) and its relevance to conservation (e.g., Soulé and Simberloff 1986). Williamson (1989) has termed the underlying theory "true but trivial." With the advantage of many data gathered because of the theory, he suggested that there is rather little population extinction for most island and island-like systems, and what extinction occurs is restricted to a particular and relatively uninteresting set of species. Islands are often islands at the individual but not the population scale. In other words, most resident species on most islands, once established, go extinct so rarely that there is really no meaningful turnover rate to be measured. Other species may be recorded as present sometimes, absent others, but these are generally transient individuals of much larger, wide-ranging populations and their temporary disappearance from an island is not a population extinction. It is as if one were tallying the comings and goings of birds on a tree as immigration and extinction (Smith 1975). Neither does the equilibrium island model provide many direct insights into refuge design. In fact, most of the rules do not really follow from the model (Simberloff 1986a).

However, the model played a strong inspirational role (Haila and Jarvinen 1982; Soulé and Simberloff 1986). The powerful metaphor of a refuge as an island focussed attention on the fragility of both island and refuge biotas, and it also inspired a search for the causes of this fragility. If a refuge or an island does suffer extinc-

tions of its populations, why is this so? It seems evident that this process occurs more on small islands—why? What other processes threaten the communities of refuges and islands? Are they the same for refuges and islands?

## Extinction of isolated populations

The equilibrium island model had a restricted view of the cause of extinctions. Demographic stochasticity (references in Simberloff [1988]) was the only cause cited originally: the chance vicissitudes of mortality and natality that cause populations to fluctuate would, in a small enough population, be likely to bring the population all the way to zero, and this extinction would not be redressed except by new immigrants. This process would, of course, be more likely to cause extinction of a small population than of a large one, so this would explain why biotas of small islands and refuges are most vulnerable. However, demographic stochasticity is not the only conceivable cause of population extinction, nor the only one that is more likely to strike small populations.

Two sorts of genetic factors threaten small, isolated populations. Because of high rates of inbreeding, deleterious alleles may increase in frequency. The resulting loss of fitness is inbreeding depression. Genetic drift will also cause alleles to be lost from a population, and if these are not redressed by mutation or gene flow, eventually a population may be so genetically depauperate that it will be unable to evolve sufficiently rapidly in response to a changing environment. Both of these genetic threats were recognized in the early 1980s (references in Simberloff [1988]).

Another threat is that of singular catastrophes, like hurricanes or volcanic eruptions. Such events threaten all populations, of course, not only those on islands or in refuges. But if a species' entire population is restricted to an island or refuge assailed by such an event, an extinction may occur, whereas the existence of a well-distributed species is unlikely to be threatened; this point is discussed below. Even environmental stochasticity—fluctuation of environmental variables within their normal range—can drive a population to extinction.

The "new" conservation biology, then, has primarily been concerned with the dynamic equilibrium island model and has come to be dominated by the search for the forces that cause the ongoing population extinction that drives the model. In theory, demographic stochasticity is more likely than genetic factors to cause the disappearance of the very last individuals (Lande 1988). Further, for substantial populations, the risk from demographic stochasticity is theoretically less than that from catastrophes and environmental stochasticity (Lande 1993). In practice, when one looks at empirical data on the extinction of species, they often implicate several forces acting together. For example, the dwindling of the heath hen (*Tympanuchus cupido cupido*) through the disappearance of its last population on the island of Martha's Vineyard

in 1932 seemed to entail habitat destruction and hunting in the first instance to cause the geographic restriction to the island, then a series of chance catastrophes, demographic stochasticity, and perhaps inbreeding depression on the island (Simberloff 1986b).

A shortcoming of theories developed to date on the relative strength of different threats is that they do not account for the spatial arrangement of distinct populations and the likelihood of replacement of extinct populations by immigration from extant ones before an entire species is extinct. This matter is obviously important to the relative vulnerability of insular and mainland populations and will be discussed in the next section.

The disappearance of the very last individuals of a population or species is often viewed as not very exciting:

> The extinction problem has little to do with the death rattle of the final actor. The curtain in the last act is but a punctuation mark—it is not interesting in itself. What biologists want to know about is the process of decline in range and numbers. (Soulé 1983)

Certainly the restriction of species to increasingly isolated small refuges will be accompanied by massive extinction, but 2 considerations suggest that the fates of these small populations are interesting. First, this restriction is already occurring and will continue to do so for the foreseeable future. So if we intend to do something to prevent the extinction, we must understand exactly why it is occurring in the first place. Secondly, it is clear that small, isolated populations are not doomed to certain swift extinction, even if they are at increased risk. Many species and subspecies, even of vertebrates, have been so restricted to very small islands that they are neoendemics there. For example, the Socorro Island hawk (*Buteo jamaicensis socorroensis*) has had a stable population of ca. 20 pairs for many generations, if not for its whole existence (Walter 1990). Many such bird species and subspecies are now threatened, but this is invariably because of human activity (Johnson and Stattersfield 1990). So it is certainly possible for small populations to persist for very long periods.

## Metapopulations

As the dynamic equilibrium theory of island biogeography and its utility for conservation came to be questioned, metapopulation models began to replace the island model as a metaphor for refuges (Merriam 1991). The theoretical basis for this notion is much older, going back at least to Andrewartha and Birch (1954) and Levins (1969), who argued that single large populations that could not persist might do so as a metapopulation of small populations exchanging individuals at the right rate. One can easily imagine a network of small sites, each intermittently

occupied by a population of some species. Each site may function as an island in the equilibrium model, with ongoing extinction and reimmigration. However, given the right parameters in the metapopulation model, the likelihood that *all* populations of some species would be extinct at any one time could be vanishingly small. In other words, any local extinction of a population on one island will be redressed by immigration from other islands before all those latter populations themselves disappear. Refuges in a network are then different from islands, except perhaps islands in dense archipelagoes.

Many authors believe that most species in nature are distributed as in this metapopulation model (e.g., Carter and Prince 1988; Wilson 1992; Noss 1993). However, both theoretical and empirical considerations suggest that this conclusion is premature. Hanski and Gilpin (1991) defined a metapopulation as an ensemble of interacting populations, each with a finite lifetime, and a population as an ensemble of interacting individuals. One must then define "interacting": what kind and how much? Hanski and Gilpin (1991) suggested that individuals that interact during routine feeding and breeding constitute populations, while metapopulations consist of populations between which movement is infrequent, generally across inhospitable habitat. However, depending on how one defines "infrequent," this definition of metapopulation is problematic, because it is very close to the standard definition of species (Simberloff 1994a). That is, species are an interbreeding collection of populations, and one conceives of the breeding between populations as being much less than the breeding within populations (that distinction is what defines "population," in fact). So is the idea of the metapopulation a falsifiable hypothesis? Are all species metapopulations by definition? Evidently there is no dichotomy between metapopulations with true local extinction and aggregated populations in which the aggregations shift location. But if individuals typically occupy more than 1 aggregation in their lifetimes, the system would surely not be a metapopulation in the original sense.

Nevertheless, some ecologists apparently think all species *are* metapopulations, because all species show aggregation at some spatial scale. But aggregation alone does not say much about interaction and who is mating with whom. Such data are scarce, but Harrison (1991) reviewed many of the existing data and found very few that conform to the idea of a metapopulation. Rather, most species conformed to either of 2 models. One was species consisting of single, interbreeding populations, with so much movement between aggregates that no subdivision into separate populations was possible. The other was a different kind of metapopulation than that envisioned by Levins (1969) and described above. Boorman and Levitt (1973) suggested a different sort of structure— a large central population spawning small, ephemeral, peripheral populations. The peripheral populations owe

their existence to continued immigration from the central population, but the continued existence of the central population owes nothing to immigration from the peripheral ones. Pulliam (1988) termed the central and peripheral populations "sources" and "sinks" in a very similar model. Several of the cases Harrison (1991) examined conformed to this model. In other words, metapopulation dynamics was not key to the continued survival of the species.

This criticism of the metapopulation model is, in fact, very similar to Williamson's (1989) assessment of the equilibrium island model. In both instances, the key is whether there is a real population process of extinction going on or whether, instead, the sequence of presences and absences of a species at a site simply reflects the comings and goings of individuals in widely ranging single populations or perhaps peripheral populations in a source-sink system. It is interesting that, though the metapopulation model is said to be a successor to the equilibrium island model, the scarce empirical data on who goes where and mates with whom suggest that the spatial dynamics of most species conform to neither model.

Conservation strategy can be very misguided if based on an incorrect attribution of population dynamics to the movements of individuals within populations. For example, Pimm et al. (1988) estimated a risk of population extinction for birds with different body size and population size based on an analysis of bird censuses on small islands off the British coast. Statistical and logical problems beset this study (Tracy and George 1992, 1993; Diamond and Pimm 1993), but the greater problem is that these data are not about populations or extinctions at all, but about movements of individuals within much larger populations (Haila and Hanski 1993). Nevertheless, this model was taken at its face value and used to estimate extinction probabilities and to support conservation strategies for situations as diverse as the translocation of populations of threatened vertebrates to small New Zealand islands (Craig and Veitch 1990; Towns et al. 1990) and the design of a refuge system to save the northern spotted owl (Thomas et al. 1990). It is interesting that this controversy is a reprise, 20 yr later and at the metapopulation level, of the heated dispute about whether there is substantial turnover, in the equilibrium theory sense, for bird species of the Channel Islands (Lynch and Johnson 1974; Jones and Diamond 1976). As Williamson (1981) concluded, there is little reason to think that most recorded "extinctions" of Channel Islands birds are of populations as traditionally defined, so application of the theory for specific conservation plans for these species is not likely to be useful.

## The Peculiarities of Island Communities

Islands are widely known to be heavily represented among conservation basket cases. Peculiarities of island physical characteristics, species and communities have combined with attractiveness of islands to humans to make islands the heralds of the global biodiversity crisis (Carlquist 1974; Soulé 1983). For example, fewer than a fifth of all bird species are insular, but more than 90% of bird extinctions in historic times have occurred on islands and 39% of all threatened bird species are restricted to islands (Johnson and Stattersfield 1990). But what are these peculiarities that have generated this crisis?

### Ecological vulnerability to invasion

It is widely asserted that introduced species are more likely to survive and to wreak great ecological damage on islands than on mainland because island communities are especially fragile and island species especially weak (references in Simberloff [1994b]). The underlying reason is that selective pressures are believed to be less intense on islands because there are fewer species. Thus Preston (1968) saw islands as evolutionary "backwaters and dead ends," while Greuter (1979) described islands as the last redoubts of old relicts, and Carson (1981) termed island species less "aggressive," on average, than continental ones. Not only are island species felt to be inherently "weak," but the communities and ecosystems are felt to be less "stable" by virtue of the small number of species and consequent simple food-web structure (Wilson and Bossert 1971). One way this instability is said to manifest itself is the propensity for introduced species to survive and to have disastrous consequences.

As with most big biological generalizations, insular vulnerability to invasions is more complicated and less categorical when examined critically (Simberloff 1994b). A close examination is hindered by bias in reporting. Surviving invasions on both island and mainland are more likely to be reported than failed ones, and invasions that produce widespread ecological change are more likely to be reported than innocuous ones. Nevertheless, the empirical record casts doubt on the generalization.

From the standpoint of species' inherent weakness, it is not a matter of all island species' automatically being maladapted, or less well-adapted than invaders, to the changes wrought by an introduction. Rather, the absence on some islands of entire suites of species means that certain introduced species are very likely to thrive there. Many introduced small mammalian predators—rats, mustelids, the small Indian mongoose—have thrived on islands where there had been no species occupying this role (cf., King 1984; Atkinson 1989). Further, the native birds that were so often devastated by these predators were not inherent maladepts. They were maladapted to this particular new stress because, in the absence of similar stresses during their evolutionary histories, they had not evolved responses to it. Many extinctions of island birds and mammals that can be firmly attributed to introduced species were caused by predation (Ebenhard 1988; Atkinson 1989).

Given the view of island species as inherent weaklings, it is perhaps surprising that there are few clear examples in which an invading species has replaced an island species by outcompeting it (Udvardy 1969; Ebenhard 1988). However, there are also few clear examples in which an invading species has replaced a native mainland species. Many cases show shared resource use by an introduced species and a declining island native, but shared resource use does not automatically translate into a competitive effect. One must also show that the shared resource is actually limiting the population of the native species and that the introduced species' use of the resource is limiting access to the resource by the native species. Such data rarely exist, and they are no more common for islands than for mainland.

Introduced diseases often devastate island species (Ebenhard 1988). For example, the decline of native Hawaiian birds was aided by avian malaria vectored by introduced Asian birds (Van Riper et al. 1986). Of course, introduced diseases have also devastated mainland species. Rinderpest from Asia so reduced some African ruminant populations that the effects are still manifest a century later (Barbault 1992; and references therein), and, in North America, one need only consider how elms have been almost eliminated by Dutch elm disease and chestnuts by chestnut blight (Von Broembsen 1989). And I know of no data that determine whether diseases are introduced to islands more or less frequently than to mainland, and how many have no effect. Still, I think it is probably true that, on average, island species are more likely to be devastated by introduced diseases. If it *is* true, a possible explanation would be that the total genetic diversity of island species is far less than that of mainland species (Carson 1981) by virtue of the smaller number of local populations. The probability that resistant genotypes already exist is then less, and they will arise and evolve more slowly once the disease arises (Simberloff 1994b).

Destruction of habitat by introduced species has probably led to more extinctions of island populations than have all the above interactions. Grazing and browsing by introduced mammals and replacement of native vegetation by introduced plants (often facilitated by the grazing) are the main means. However, though habitat destruction is perceived as greater on islands (e.g., Atkinson 1989), there is no comprehensive study of the data, and one can cite many counter-examples. Mack (1986, 1989) describes the destruction of the native plant communities of the intermountain West by domestic stock and their replacement by Eurasian plants. It is hard to imagine that island devastation was much more thorough. The destruction of south Florida native plant communities by Australian *Melaleuca quinquenervia* and South American *Schinus terebinthifolius* (Ewel 1986) is staggering. *Melaleuca* alone advances 50 a. per day.

### Vulnerability to genetic swamping

Island populations, by virtue of being small, are more prone than mainland ones to a kind of phylogenetic extinction by hybridization. In general, small populations that are interfertile with other taxa with which they come in contact run this risk. This was the last step in the extinction of the dusky seaside sparrow (*Ammospiza maritima nigrescens*), as the last "pure" individual mated with a 75% dusky individual (Kale 1987). One of the 2 populations of the endangered Florida panther (*Felis concolor coryi*), in fact, is not quite the Florida panther, as it has undergone extensive introgression with either Central or South American cats introduced in south Florida (O'Brien et al. 1990). Similarly, the prospects for the red wolf (*Canis rufus*) in the wake of reintroductions are bleak, as the wolf hybridizes with the coyote (*C. latrans*), which is already more numerous and is increasing in the East.

The Seychelles turtle dove (*Streptopelia picturata rostrata*) has been eliminated by a century of interbreeding with the introduced *S. p. picturata* from Madagascar. The birds now present in the Seychelles appear to be a hybrid swarm phenotypically more similar to the Madagascar subspecies (Cade 1983). The Chatham Islands subspecies of the yellow-crowned parakeet (*Cyanoramphus auriceps forbesi*) probably no longer exists because of hybridization with the Chatham Islands red-fronted parakeet (*C. novaezelandiae chathamensis*) (Cade 1983). The yellow-crowned bird originally bred only on 2 small islands, in reproductive isolation from the sympatric red-fronted species. Deforestation, overgrazing, and predatory house cats greatly reduced both species, reducing the yellow-crowned parakeet to fewer than 100 birds on 1 island and none on the other. Reforestation and elimination of livestock and cats was followed by natural recolonization, but most birds were hybrids and very few were phenotypically recognized as yellow-crowned. Why the isolation broke down upon reintroduction is not known, but it may have to do with subtle habitat change allowing consistent mingling of the species. The yellow-crowned parakeet was most affected by the hybridization because its population is much smaller than that of the red-fronted parakeet. Now there is a heavy hunting program to reduce red-fronted and hybrid birds in an attempt to save some semblance of the yellow-crowned subspecies. A similar threat now faces the yellow-crowned subspecies on other islands, such as Little Barrier Island, a problem exacerbated by the release of captive-reared hybrids (Towns et al. 1990).

To some extent, concern over loss to hybridization of distinctive island forms may be dismissed as quibbling over racial purity, particularly where the island forms are subspecies rather than species. However, "biodiversity" is now generally defined to include genetic variants (e.g., Wilson 1992) and island forms are often among the most distinct genetic variants. The loss of morphologically and

genetically distinct birds of individual Channel Islands (Johnson 1972) or beach mice of the Channel Islands (Gill 1980) and Florida barrier islands would be tragedies, even if this loss were by hybridization rather than phyletic termination.

*Absence of network of suitable sites*

The fact that islands are much smaller than the mainland means that forces that might have simply reduced the numbers of a species on mainland can lead to species extinction on islands. The effects of introduced species are only some of these forces. The problem is that populations are fewer and more restricted geographically on islands than on mainland. It is therefore more likely that all representatives of a species will be affected by any detrimental force on an island than on the mainland. And local extinction on islands is global extinction, at least for endemic taxa, and cannot be redressed by reimmigration from unaffected populations. For widespread taxa, reimmigration can replace the population but will be more or less hindered by the expanse of water. On the mainland, the total area affected by an introduction can be staggering, and many species can be eliminated from wide areas, yet the species can remain extant, sequestered in isolated pockets. And if suitable habitat is restored, recolonization from adjacent areas is not as problematic as on an island.

An often cited statistic is that only 1% of the virgin forest of the eastern United States remained after about 3 centuries of logging, but only 2 of about 70 forest bird species went extinct (e.g., Terborgh 1975, 1989). Probably more accurate statistics are that 3 species have gone extinct (of which 2 were destroyed by hunting rather than deforestation), while 2 are endangered, but the point is well-taken. On the other hand, about a third of the original forests of the Hawaiian islands remains, and far more of moist and montane forest, but 14 of 38 forest bird species went extinct, and 15 are endangered (Berger 1981; Scott et al. 1986; Ehrlich et al. 1992). The reason for the difference is that the East is very large and eastern forest was not all cut down at the same time; the minimum forested area was probably never less than half of the original (Terborgh 1989). And there has been much regrowth (there is more forest now than a century ago), so that there was always substantial acceptable forest habitat left somewhere for most species. Populations were often lost, and numbers reduced, but almost all the species survived. In Hawaii, on the other hand, destruction was faster, there was little regrowth, and there was simply not enough habitat and not enough suitable areas for some species. Because these are all endemic species or subspecies, they constitute global extinctions.

The contrasting effects of cyclones and hurricanes on islands and mainland similarly betray the particular vulnerability to extinction of island species. Much of the world's most interesting avifauna resides in archipelagoes

in cyclonic pathways: the Hawaiian islands, the Mascarenes, the West Indies. Storms have caused some recent avian extinctions and numerous near-misses. A bullfinch on Saint Kitts (*Loxigilla portoricensis grandis*) was eliminated by a hurricane (Raffaele 1977), the only population of the Laysan teal (*Anas laysanensis*) was devastated by a hurricane on that island (Fisher et al. 1969), the recent Hurricane Hugo eliminated about half the single population of the Puerto Rican parrot (*Amazona vittata*), and Hurricane Hyacinthe killed about half the individuals of several small endemic bird species over large parts of Reunion Island in 1980 (Barré and Barau 1982). Perhaps most staggering is the apparent loss of 5 endemic species and subspecies of birds when Hurricane Iniki struck Kauai in 1992 (Pyle 1993).

However, the key fact in all these cases is that the populations had already been greatly reduced in numbers and range by habitat destruction. Four of the 5 taxa on Kauai were believed to have fewer than 10 individuals when the storm struck. The Puerto Rican parrot had already been reduced to about 50 individuals in a single forest that happened to be in the hurricane's path. The Laysan teal was eliminated from Lisianski Island in the 19th century (Berger 1981). On Reunion, only about a fourth of the forest that had covered almost the entire island remains, and only a few hundred ha is in the lowlands. Surely all these taxa, having evolved in areas frequently struck by cyclones, would have been able to survive even severe storms that had not humans so reduced their range and numbers. Otherwise they would not have been on these islands for us to record them! But, on an island, a reduction in range and numbers can reduce a species to a point where extinction is highly probable from inevitable disasters. It is not that these island species were weaklings; probably mainland relatives, had they been so reduced in numbers and range, would have suffered the same fate.

On the mainland, however, no bird species or subspecies have been eliminated by hurricanes. The same Hurricane Hugo that devastated the Puerto Rican parrot struck the Francis Marion National Forest in South Carolina, home of one of the largest populations of the endangered red-cockaded woodpecker (*Picoides borealis*). However, that woodpecker population has since largely recovered in spite of massive destruction of its habitat in the hurricane's path. Small wonder! The Marion forest is 8 times as large as the Luquillo Forest, last redoubt of the Puerto Rican parrot. And the Marion Forest is only 1 of 6 substantial populations or clusters of populations of the woodpecker. If the red-cockaded woodpecker had been restricted to the Luquillo Forest when Hurricane Hugo struck, it might well have been affected even more than the parrot was. Similarly, Hurricane Andrew struck Florida with tremendous habitat damage approximately at the same time that Iniki struck Kauai, but no bird went extinct or even declined

precipitously. If Florida birds had been restricted to tiny forest refuges on Kauai, I doubt they would have outperformed the Hawaiian species.

## The "Old" Conservation Biology and its Relevance to Islands

The "old" conservation biology emphasized autecology, particularly the detailed study of habitat use by species of interest. This kind of research is not popular at the highest levels of academia. It does not seem to lead to ready generalizations, it is very labor-intensive, it is part of an old tradition. In short, it is not flashy. Though intensive autecological research is still performed, it is distinctly subsidiary in the "new" conservation biology to the community theory, population genetics theory, and metapopulation research described above (Simberloff 1988). However, very intensive study of particular island species and their interactions with the habitat can lead to more accurate understanding of the particularities of island ecology, and attempts to match island observations to general theory can be misleading. I will give 2 recent avian examples.

The endemic dove *Zenaida graysoni* disappeared from Socorro Island between 1958 and 1978, while the endemic mockingbird *Mimodes graysoni* declined towards extinction during the same period (Jehl and Parkes 1983). The mainland mourning dove (*Z. macroura*) and mainland northern mockingbird (*Mimus polyglottos*) became established there approximately during the same period. At first glance, these facts would seem perfectly explained as competitive replacement of "weaker" island species by "stronger" mainland competitors, and would further seem to exemplify the equilibrium theory of island biogeography, with extinction balancing immigration to maintain species richness. However, Jehl and Parkes (1983) convincingly argue that such an interpretation would be a complete misreading. Predation by recently introduced feral cats is much more likely to have generated the decline of the endemics, while the 2 immigrants had been frequent transients on the island but were probably able to colonize only after fresh water became available with the establishment of a military base. There is no evidence that the introduced species outcompeted the natives in any way. There are not many detailed studies such as this of particular extinctions on islands; those that exist do not suggest a dynamic equilibrium explanation (references in Simberloff [1986b, 1994a]).

Many authors have commented on the expansion of habitat range by island populations relative to conspecific or related mainland ones. Such observations are almost always attributed to release from interspecific competition in the newly occupied habitat on the depauperate island, following a theoretical argument by MacArthur (1972). This shift is sometimes also seen as being partial-

ly generated by release from competition in the normal habitat. The normal habitat on the island, occupied by fewer species than on the mainland, allows those species that are present to have higher population densities than on the mainland. The higher densities in the normal habitat are believed to lead to "spillover" (Blondel 1993) into other habitats.

However, habitat or other environmental differences between island and mainland may provide compelling alternative hypotheses. For example, at least 10 bird species restricted to forest on the mainland occupy both forest and matorral (shrublands dominated by broadleaved evergreen plants) on Corsica (Martin 1992). One could easily imagine that they are responding to absence of some mainland competitors on the island. However, the matorral habitat is not exactly the same on mainland and island. In particular, the matorral on the mainland is closely juxtaposed with deciduous forest, whereas on Corsica such forest covers less than 5% of the area. Thus, it is quite possible that birds that occupy both forest and matorral cannot adapt to matorral on the mainland because of gene-flow from forest conspecifics, while they can do so on the island (Martin 1992). There is much about this system that is not yet explained (Blondel 1993; Martin 1993), but it is clear that a simple model of ecological release does not capture the key aspects of the problem and that an understanding of the differences between these mainland and island birds is impossible without very detailed study of the habitat and its use.

The idea that subtle habitat differences between islands and mainland explain differences in species composition and habitat use was most strongly propounded by the avian ecologist David Lack (1976), who saw his views as an alternative to the dynamic equilibrium model. Lack felt that, for birds, which species were found on islands was almost entirely determined by the ecology of individual species and the suitablility of habitat on the individual island. He felt that the depauperation of distant islands was generally *not* due to failure of species to disperse there, but to the fact that distant islands were generally also small and poor in habitats. However, he even viewed communities on large islands in this light. For example, Ireland lacks several bird species found on Great Britain (e.g., woodpeckers), and Lack convincingly explained almost all these absences by habitat and climatic differences between the 2 islands. He saw little reason to invoke dispersal failure as a reason for absence of taxa as vagile as most birds. Of course, one might have a very different view for less mobile species, but one must still study habitat requirements of species and habitat differences among sites closely before invoking dispersal failure, interspecific interactions, and equilibrium dynamics as an explanation of species composition and habitat use. In fact, given the wealth of venerable literature on the universality of habitat restrictions, often subtle ones, for various species, Lack's hypothesis should probably be the

null hypothesis for any observed pattern. It may often be falsified, especially on very distant islands and/or for species with particularly poor dispersal abilities, but one should at least consider it at the outset.

Lack's views met with a resounding thud; his book received generally bad reviews (e.g., Grant 1977, Ricklefs 1977). Probably its rejection was more because it was qualitative, rested on species' idiosyncrasies, and was generally boring in contrast to the dynamic equilibrium theory, which promised to explain by simple general laws all manner of island communities, than that it was wrong. Also, it was an extreme statement, attributing virtually every pattern to species' biology and habitat differences; probably Lack was extreme because he was writing at a time when the equilibrium theory was an ecological and biogeographical juggernaut, applied willy-nilly to almost every situation and almost always without critical data on turnover.

But the reviews did not really show that Lack was wrong, particularly in the specific island patterns that he addressed. Now, with the hindsight of a quarter century, the general view that the equilibrium theory has a much more limited domain than originally proposed, and the recognition that islands at the individual scale need not be islands at the dynamic scale, it seems to me that Lack's ideas deserve reconsideration. For example, Case and Cody (1983) criticized Lack for failing to account for "observed" turnover and for the rapid relaxation of landbridge avifaunas. However, the specific turnover to which they referred, including that on the Channel Islands, has been challenged, as noted above, on the grounds that it is just intrapopulation movement rather than a population-scale process. And the relaxation of landbridge avifaunas is only hypothesized and has been equally disputed (e.g., Abele and Connor 1979). At the very least, a conservation strategy for island species should rest on detailed study of threats to resident species, and one should not rely on overarching theories of questionable validity and even more questionable relevance to management.

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