EVOLUTION AND ECOLOGY OF BIRDS ON ISLANDS: TRENDS AND PROSPECTS

J Blondel

EVOLUTION AND ECOLOGY OF BIRDS ON ISLANDS: TRENDS AND PROSPECTS

J. BLONDEL

CEFE/CNRS, 34293 Montpellier cedex 5, France

INSULAR SYNDROME
ISLAND BIOGEOGRAPHY
SPECIATION
TAXON CYCLE
EXTINCTION VORTEX
CONSERVATION
BLUE TIT

ABSTRACT. - This paper reviews ecological and evolutionary processes that operate among and within insular communities, species and populations. Being basically non-evolutionary the MacArthur and Wilson's paradigm of island biogeography holds well in explaining processes that operate on the short ecological time, and proved to be helpful in explaining such issues as colonisation-extinction processes, species richness at equilibrium and species turnover. But several limitations make it insufficient as a modern tool for explaining evolutionary changes on islands. Colonising an island necessarily entails rapid evolutionary changes as a response to both non-selective and selective evolution. This results in a cascade of changes of life history traits, the so-called insular syndrome. Components of this syndrome include changes in morphology (size and shape), demography (age-specific fecundity, survival, dispersal) and behaviour. Shifts in behaviour are among the most spectacular features in insular vertebrates. Surprisingly few systematic and broad-scale analyses of demographic changes on islands have been designed to document the classical tenet of evolutionary shifts from high reproductive rates and short life span towards the opposite combination of life history traits as a result of high intraspecific competition in crowded insular populations. Examples of shifts in life history traits are given from a detailed case study on the biology of Blue tits in the island of Corsica, and most of these changes fit the predictions of an insular syndrome. An interesting trend resulting from shift from dispersal to sedentariness and habitat fidelity in islands is the potential for population differentiation at much smaller spatial scales than on mainland regions. This results in enhancing within-species diversity which counterbalances the species impoverishment of insular biotas. Although ecological adjustments and evolutionary changes make insular communities self-regulating assemblages of species that are resistant face to the risks of spontaneous extinction and invasion, insular communities are among the most vulnerable biota on Earth. The most important threats to island birds are discussed and some directions are given for promoting studies that could contribute to fill the most important gaps in our knowledge on evolution on islands and contribute to conservation issues.

SYNDROME D'INSULARITÉ
BIOGÉOGRAPHIE INSULAIRE
SPÉCIATION
CYCLE DE TAXONS
VORTEX D'EXTINCTION
CONSERVATION
MÉSANGE BLEUE

RÉSUMÉ. - Cet article fait un bilan résumé de nos connaissances sur les processus écologiques et évolutifs qui caractérisent les communautés, espèces et populations d'Oiseaux en milieu insulaire. Le paradigme de biogéographie insulaire de MacArthur et Wilson s'est montré fort utile pour expliquer les processus qui opèrent à l'échelle relativement courte du temps écologique, notamment les processus de colonisation, d'extinction, de renouvellement d'espèces, ainsi que certains changements tels que l'élargissement des niches et différentes modalités de partage des ressources, de sélection de l'habitat et de densité de population. Mais il ne se prononce pas sur les processus évolutifs, ce qui en limite la portée. Lorsqu'une propagule réussit à s'implanter sur une île, des processus évolutifs de type non-sélectif (dérive, mutations) et sélectif (nouveaux régimes de sélection) entraînent de profondes modifications dans les traits d'histoire de vie, ces modifications caractérisant ce qu'on appelle le syndrome d'insularité. Les composantes de ce syndrome sont d'ordre morphologique (taille et forme), démographique (fécondité, survie, dispersion) et comportemental. Les modifications du comportement sont généralement spectaculaires chez les vertébrés insulaires. Peu de travaux se sont attachés à tester l'hypothèse classique selon laquelle les populations insulaires de vertébrés présentent un glissement démographique tendant à réduire la fécondité et augmenter la survie. Un exemple bien documenté de modifications de traits d'histoire de vie, celui de la Mésange bleue en Corse, révèle que la plupart des changements observés vérifient les prédictions du syndrome d'insularité. La tendance à la sédenta-

rité et à la fidélité de l'habitat, qui est un trait régulier en milieu insulaire, se traduit par une différenciation des populations à des échelles d'espace bien moindres que sur le continent. Cela favorise une diversité intra-spécifique élevée qui, d'un point de vue adaptatif, compense en partie le fait que les communautés insulaires soient appauvries en espèces. Bien que les ajustement écologiques et changements évolutifs qui caractérisent les communautés insulaires les rendent résistantes aux perturbations et invasions spontanées, ces communautés sont pourtant parmi les plus menacées de la planète. Les menaces les plus sérieuses sont examinées et quelques pistes de recherche sont données qui permettraient de combler certaines lacunes dans nos connaissances et favoriser la mise en œuvre de stratégies efficaces de conservation.

INTRODUCTION

The question why organisms are so diverse has been addressed by evolutionary biologists for more than a century and a half. This is especially true for bird diversity on islands which has been the object of a particular focus for two reasons. First, being conspicuous, mostly diurnal and popular as study models, birds are well known and suitable for observation, field studies and sometimes experiments. Second, being discrete small areas, islands have many advantages over larger mainland regions where shifts in distribution, geographical variation of populations and species, and problems of spatial scales complicate attempts to reconstruct evolutionary history and patterns of diversity. It is a commonplace since Darwin and Wallace to say that islands are natural laboratories for the study of evolution and it is true that whatever we learn about avian evolution on islands can be used as a basis for constructing explanations for diversification at larger spatial scales. By diversification, I not only mean taxonomic differentiation and speciation but also any evolutionary changes that occur at the level of populations and modify life history attributes in morphology, demography, physiology and behaviour.

Diversification on islands at the species level will not be considered further here (see Grant 1998). Suffice is to say that the main ideas inherited from the nineteenth century (e.g. Darwin 1859, Wallace 1871) have not been dethroned. Basically, speciation in birds is an allopatric process whereby natural selection causes divergence of geographically isolated populations. The most genetically similar populations are most often allopatric populations, not sympatric congeners (Grant 1998), which confirms the long-standing tenet that phenotypic resemblance reflects phylogenetic relatedness (Mayr 1942). These patterns are inconsistent with the theory of sympatric speciation which, on ecological and behavioural grounds, is unlikely in birds (Grant & Grant 1989). This is not to say that a deeper understanding of the mechanisms of species diversification did not occur during the twentieth century. Since the Perkins' (1903, 1913)

pre-genetical theory of insular differentiation applied to the radiation of the 36 forms of Drepanid honeycreepers on the Hawaiian archipelago, much insight has been given on the tempo and mode of species divergence. Recently, biochemical techniques such as electrophoresis (Hubby & Lewontin 1966) and then molecular data used to reconstruct phylogenies (Fitch & Margoliash 1967) made the new systematics shift from the mostly morphological (phenotypic) systematics of the first half of the century (Huxley 1942, Mayr 1942) to molecular systematics (Mindell 1997). Molecular data have the advantage to provide information on the temporal context of speciation as well as on the degree of genetic relatedness among the different taxa of a clade.

In this paper I will mostly focus on biogeographical, ecological and microevolutionary processes that operate among and within insular communities, species and populations. I shall try to show that combining the provinces of ecology and evolution in the field of evolutionary ecology is a prerequisite to answer fundamental questions on differentiation and adaptive radiation. Books on island biology are generally concerned with either evolution (e.g. Grant 1998) or ecology (e.g. Gorman 1979, Vitousek et al. 1995) but few encompass both ecological and evolutionary concerns (one exception is Williamson 1981). Islands are land masses isolated from others by water, but islands and mainland differ only arbitrarily in scale in relation to organisms: what is an island for birds may be a large mainland for ants so that investigating insular patterns involves to scale study areas to the dispersal range of organisms.

COLONISING AN ISLAND NECESSARILY RESULTS IN EVOLUTIONARY CHANGES

When a propagule, say a few individuals of a species, succeeds in colonising an island, both selective evolution resulting from new selection regimes in a new environment and non-selective evolution (founder effect and genetic drift because a

propagule is necessarily a genetic bottleneck) inevitably lead the new population to evolve rapidly and diverge from its mainland mother population. Molecular studies have confirmed that the founding of a new population by a few individuals involves a loss of genetic diversity (Mundy *et al.* 1997, Tarr *et al.* 1998), in an inverse proportion to the size of the founder group (Merilä *et al.* 1996) and that larger populations contain more genetic variation (Avise 1994). Since mutations inevitably arise and are subject to drift as well as selection, local environments do not have to differ for genetic divergence to occur in isolated populations (Grant 1998). The substitution at genetic loci of certain alleles for others from random drift is conducive to phenotypic change irrespective of any changes in selection regimes. However, selection regimes in the new insular environment of a colonising population inevitably differ from those on the source mainland because of differences in both abiotic (climate) and biotic (resources, competitors, predators, parasites) factors. Many comparisons of bird populations between islands and adjacent mainland regions or among islands within archipelagos have been used to infer differences in regimes of natural selection in different environments (Mayr 1940, Grant 1965a, Keast 1970, Alatalo & Gustafsson 1988, Roff 1994, Fitzpatrick 1998).

Divergence may eventually lead to speciation and insular endemism if differentiation conducive to reproductive isolation of a first colonising propagule is attained before a second colonisation event by the same mother population occurs. This is the case of double invasion of pairs or more rarely triplets of species on several islands around the world (Grant 1968). A common feature of these sister species is a large difference in both ecological characters and morphology. On the Canary Islands, the Blue chaffinch *Fringilla teydea* evolved from a first colonisation event by the European chaffinch *F. coelebs*, and much later, the islands have been colonised again by the European chaffinch. In the meantime *F. teydea* achieved reproductive isolation, hence a full species status, so that the two species occur sympatrically without hybridising. This scenario, which had been proposed a long time ago from resemblance between the two species and common-sense, has been recently confirmed from molecular data (Marshall & Baker 1998). Whether species-specific adaptations to different habitats by the two species permits their coexistence or competitive interactions produced the divergence is difficult to assess (Grant 1998). Most non-oceanic islands are too close to the mainland, however, for differentiation having a chance to occur between two colonisation events, which explains why few species evolved as endemics in islands that are close to the mainland. For example very few birds evolved as endemic species in the Mediterranean archipelago because of the closeness of all islands to the mainland.

BIRD ASSEMBLAGES ON ISLANDS: A CASCADE OF ECOLOGICAL SHIFTS

Summarising the evidence from a great many studies on insular biology, Rosenzweig (1995) came to the conclusion that, in spite of much debate, controversies and shortcomings (see e.g. Blondel 1991), the MacArthur & Wilson's (1963, 1967) theory of island biogeography holds up well in explaining species diversity, immigration rates, extinction rates and turnover rates on islands. However, being basically non-evolutionary the theory captures only two of the three fundamental processes that determine biogeographic patterns, namely immigration, extinction and evolution although taken in a broader context the theory is not silent on evolutionary processes within the basic assumption of equilibrium (Whittaker 1998, 2000). Therefore the MacArthur & Wilson's paradigm has mostly been designed to explain processes that operate on the short ecological time and at relatively small-scale circumstances, which implies several over-simplistic assumptions (Heaney 2000, Lomolino 2000a).

What determines species richness on islands ?

Contrary to what is too often written, even in the best international journals, species impoverishment on islands is not an issue of the MacArthur & Wilson's model. The realisation that islands are depauperate in species in comparison with areas of similar size on the nearby mainland dates back to biogeographers of the nineteenth century (e.g. Wallace 1880) who noticed that the size of an island is the most important determinant of the size of the pool of species that coexist on it. The key point of MacArthur & Wilson is not species richness *per se*, but the existence of a turnover of species on islands as a result of an equilibrium between colonisation and extinction events in communities that are assumed to be more or less saturated in species. The role of island characteristics in shaping insular communities has received much attention from both theoretical and empirical studies (Hamilton & Armstrong 1965, Haila *et al.* 1980, Williamson 1981, Blondel 1991, Wiggins & Møller 1997). A positive relationship between island area and species richness has been so widely demonstrated that it became an universal law (Ricklefs & Lovette 1999 and references herein). However, disentangling direct from indirect effects of area on species richness has proven quite difficult. At least three factors interplay in determining species numbers on islands (see also Fox & Fox 2000). First, as the size of an island increases, so does the size of species' populations. Thus, the probability of extinction decreases as the island

area increases. Second, as the size of an island increases, so does its probability of encompassing a wider range of habitats that will be suitable for colonisation by a wider range of species. Watson (1964) on the Aegean islands, Greece, Haila *et al.* (1983) on the Aland archipelago, Finland, Martin *et al.* (1995) in the Queen Charlotte Islands, Canada, and Ricklefs & Lovette (1999) in the Lesser Antilles gave good illustrations that species-area curves are primarily determined by the diversity of habitats. Analysing 30 studies of bird species-area relationships that included some measure of habitat diversity, Ricklefs & Lovette (1999) reported that 22 studies found a significant area effect, 21 found a significant habitat-diversity effect, and 10 found both effects. Third, distance to the mainland source often explains a significant amount of the variance, especially in remote oceanic islands as first demonstrated by Diamond (1974) in a series of islands off New Guinea. For example, Reed (1987) found a significant relationship between the residuals of a regression that fitted island area to bird diversity and log distance to mainland for birds of the Bahama islands.

Insular communities are not a random sample of the source mainland pool of species

Besides the mere number of species, a point of major interest is whether or not the species present on an island are a random subset of the pool of species of the nearby source mainland, i.e. have all species of the mainland pool the same chance to successfully colonise the island as assumed in the MacArthur & Wilson's model ? Answering this question requires comparative studies on species-specific attributes in relation to colonising abilities. Species differ in their rates of immigration, dispersal abilities and aptitude to construct viable populations, which explains why islands include a non-representative sample of species from the mainland. Some species, the so-called tramps and supertramps (Diamond 1974), arrive at higher rates whereas others immigrate at imperceptible rates. Thus, the most successful colonists will on average be those species that arrive first on an island since rates of extinction are a function of the number of species already present. Successful island colonists are often small generalist species that are common, widespread and very mobile on the mainland, so to say flexible in habitat selection and in utilising resources. The smaller the island the more likely it will be colonised by a low number of small species that are common everywhere in the nearby mainland (Blondel 1991, 1995).

Another sorting process in colonisation probabilities is body size. For similar population sizes, large organisms need on average more space than small organisms. Hence a lower proportion of the larger species on islands in most taxonomic groups. This explains that predators are under-represented in most island biota. Predator populations being necessarily smaller than those of their victims, they are likely to become accidentally extinct with a much higher probability than their victims. Thus, island communities are 'disharmonic', a term which refers to changes in the relative proportions of different taxa or trophic levels on islands as compared with those on the nearby mainland. As a result, species richness alone is a poor characteristic of insular communities because the relation between species number and area is indirect. This relation is mediated by a chain of interrelated factors that include habitat structure, habitat size, and species-specific attributes (Haila *et al.* 1983).

In series of islands of different sizes not far from a mainland source, species assemblages are usually nested, which means that communities of lower species numbers (smaller islands) are non-random subsets of more diverse assemblages (larger islands). Each subset of species does not include species that are already absent from the next richer assemblage (Patterson & Atmar 1986, Simberloff & Martin 1991). In perfectly nested subsets one or several species are lost as species richness declines as a result of reduction of the size of the island, and none of the species lost from the richer communities reappears in any of the lower-rank communities once it has been lost. True biological nestedness requires that communities share a common biogeographic history, live in similar environments and have hierarchical niche relationships (Patterson & Brown 1991). Such situations are likely to occur in habitat islands resulting from forest fragmentation or in archipelagos not far from a same mainland source (Cutler 1991). Oceanic islands that were colonised from different mainland pools at different time intervals are much less likely to exhibit nested species assemblages (Patterson & Atmar 1986, Wright *et al.* 1998). Note that one approach to analyse sets of separate communities that are not independent, e.g. nested insular communities, is spatial autocorrelation (Koenig 1999).

Community structure and dynamics

What are the consequences of species impoverishment and disharmony on community dynamics and resource sharing ? Detailed bird censuses conducted at different scales of space in islands as compared to areas of similar size on the mainland frequently show that species impoverishment differ depending on scales and that impoverishment at the scale of the whole island does not necessarily translate at lower levels of the hierarchy, i.e. landscapes and habitats. For example 109 species of breeding birds occur in the whole island of

Corsica, as compared to 170 to 173 species in three mainland areas of similar size, a 37 % impoverishment, whereas there is hardly any impoverishment at the scale of a landscape including six habitat types ranging from a grassland to a mature forest (42 *versus* 43 species) (Blondel 1991). At the habitat level (the so-called alpha diversity), some habitats, especially old forests, are heavily impoverished on the island whereas other habitats, such as shrublands, have many more species than their mainland counterparts. Thus, there are on average higher alpha diversities on the island than on the mainland and lower beta diversities for a similar overall richness (gamma diversity) at the scale of a series of habitats combined. This results in a slow-down in turnover (beta diversity) among habitats on the island as compared to the mainland. This is because many species expand their habitat-niche and spill-over from their preferred habitat into other habitats (Blondel *et al.* 1988). In other words, species on an island recognise fewer habitats than on the nearby mainland. I will come back later on this process of 'niche expansion', first described by Lack (1969), which is a regular feature in island biota and results in a much looser structure of bird assemblages along habitat gradients.

MICROEVOLUTIONARY CHANGES

Ecological characters of insular species cannot be dissociated from evolutionary changes to which they are intimately related. These changes are both idiosyncratic, that is specific to each particular organism or island, and general and widespread (Grant 1998). Similar characters in a group of organisms living in the same environment may be due to common inheritance and/or shared environmental pressures whereas similar trends among different unrelated organisms occupying different islands are more likely to reveal general evolutionary forces. One challenge is to disentangle which factors are responsible for the similarity of characters or trends.

The new environment of a colonising population is characterised by many changes including species impoverishment, new interspecific interactions, new genetic background, all resulting in a cascade of changes in the ecology and life history of that population. Many of them presumably evolved as mechanisms against extinction risks. They include higher population densities which reduce vulnerability to stochastic extinctions (Pimm *et al.* 1988, Tracy & George 1992), changes in body size and shape (van Valen 1973, Case 1978), broadening of several components of the niche (habitats, diet, foraging sites), modifications of fitness-related traits such as fecundity, survival, dispersal (Blondel 1991), and changes in social behaviour (Stamps &

Buechner 1985). All these characters are parts of a so-called insular syndrome (MacArthur *et al.* 1972a, Williamson 1981, Crowell 1983, Stamps & Buechner 1985, Blondel 1991, 1995). I will comment some of them.

Reduced dispersal

A common and repeated response of both plants and animals to new selective pressures in insular environments is a reduction in traits that allow them to disperse over long distances (Carlquist 1974). Hence is the paradox that the best long-distance immigrants are organisms with powerful dispersal abilities whereas the most efficient colonists are poor dispersers within the island. The response may be ecological, evolutionary, or both. At the level of ecology, bird communities in continental islands quite often include a disproportionate proportion of sedentary species, or species that become sedentary, which is repeatedly the case in remote oceanic islands (Blondel 1991). At the evolutionary level, a repeated trend is the reduction of morphological traits such as powerful wings in animals. Flightlessness is common in island populations of birds and insects because the advantages of sedentariness increase as the advantages of dispersal decrease (Darlington 1943, Carlquist 1974), including for winged organisms to be accidentally blown off islands by strong winds which often occur on islands. Flightlessness is also an energy saving mechanism in birds whenever a permanent habitat with a local year-round food supply and the absence of predation favour strong habitat fidelity (McNab 1994). Rails for example have evolved flightlessness many times (McNab 1994, Steadman 1995). Long-distance dispersal to find suitable habitats allowed this group of birds to colonise a large number of small islands sometimes quite remote as in the Pacific Ocean. Then walking while exploiting the habitats in the manner of large herbivores such as Dodos, Moas of Elephant-birds led to the progressive atrophy of wings which became useless because of the small distance to cover in the predator-free insular environments.

Size changes

A general trend on islands is changes in body size and shape which repeatedly evolved in most groups of plants and animals (Van Valen 1973, Carlquist 1974, Grant 1998). Plants usually evolved greater size and stature with herbs becoming shrubs and trees. In vertebrates, explanations for size trends are difficult because they involve interactions between many factors such as food resources, competition and predation (Case 1978, Heaney 1978, Lomolino 1985). Generalisation is

probably impossible because different size trends depend on species, islands and factors involved. In the absence of predators and competitors there is however a trend for mammals evolving large individual size in rodents (Foster 1964, Williamson 1981) and small individual size in carnivores which are supposedly food-limited (Klein 1968, Heaney 1978, Lomolino 1985, McNab 1994). In birds both gigantism in the case of large herbivorous species (Moas, Dodos, Elephant birds, *Sylviornis*), and dwarfism in many passerines are found on islands. However, the mechanisms that lead to either gigantism or dwarfism remain largely unknown and there are so many exceptions to this "rule" (e.g. Kikkawa 1976) that any generalisation would be premature. Ecological release from competitive and predatory constraints is often inferred from the measurement of ecologically significant morphological traits as a mechanism of changes in body size and/or shape. For example, island birds from a variety of taxonomic groups tend to have large beaks and long tarsi (Murphy 1938, Grant 1965b), and that independently of body size which does not necessarily follow the same trend.

High population sizes and niche expansion

The reduced species richness of island bird communities is often associated with higher population densities of species as compared to those in similar mainland habitats (Crowell 1962, MacArthur *et al.* 1972a, Yeaton 1974, George 1987, Blondel 1991, Ricklefs & Lovette 1999). Kikkawa (1976) reported on densities of the silvereye *Zosterops lateralis chlorocephaha* reaching an astonishing figure of 125 pairs per ten ha on Heron Island in the Great Barrier Reef, Australia. Such a density is higher that the highest recorded density of all land birds in a mainland rain forest of Australia ! In addition to higher population sizes, many island vertebrates (lizards, mammals, birds) expand the range of habitats occupied or dimensions of their feeding niche (MacArthur *et al.* 1972a, Williams 1972, Blondel 1991, Roughgarden 1995, Kikkawa 1976). A classical explanation of these patterns is a relaxation of interspecific competition for resources and different patterns of resource partitioning in species-poor islands. The rationale which follows from the niche theory and the dynamic equilibrium theory is that island habitats are saturated with fewer species than mainland ones with the result that extra-resources become available for more conspecifics. Several other hypotheses have been proposed to explain larger population densities, including reduced predation (Higuchi 1976, Abbott 1980, Nilsson *et al.* 1985, Williamson 1981), and reduced dispersal, the so-called "fence effect" (MacArthur *et al.* 1972b, Tamarin 1977). Reduced predation may also result in a release in

habitat selection because camouflage is less important in the absence of predators, favouring niche expansion in suboptimal habitats. Unfortunately, very few rigorous attempts have been made to test these hypotheses (Abbott 1980, George 1987), including the hypothesis of a causal relationship between species richness and population density. One exception has been provided by George (1987) who experimentally demonstrated that higher densities of small land birds on the Coronados islands, Mexico, resulted from lower predation rates than on the nearby mainland.

Responses of niche breadth and population density on islands are often called competitive release and density compensation respectively (MacArthur *et al.* 1972a). They have long been interpreted as a deterministic output of competitive processes in the framework of the assembly rules proposed by Diamond (1975). These rules assume the improbability of finding on the same depauperate island certain combinations of species, mostly species that overlap greatly in their ecological needs. Unfortunately they have rarely been tested and confronted to null hypotheses but one exception has been provided by Moulton & Pimm (1987) who elegantly demonstrated the likelihood of the role of competition in shaping insular bird assemblages. These authors showed that native species of the Hawaiian islands that were the most likely to be competitively wiped out by introduced species were those species that were morphologically and ecologically the most similar to the introduced ones.

However, changes in population sizes and niche breadth may also arise from other factors such as restricted dispersal or intraspecific spill-over, a neutral term to mean that increased niche breadth may be due to mechanisms other than competitive release. For this reason, the terms density inflation (Crowell 1983) has been proposed instead of density compensation because it does not imply any causal mechanism. In addition, comparing niche width of an insular population with that of a single mainland population may be misleading. A sound comparison should involve comparing insular niche width with the mainland niche width at the scale of the whole range of niches and habitats occupied by the species on the mainland, which is, of course, very hard to do.

Broadening of the niche and ecological generalisation on islands seem to contradict the tenet of a sharp specialisation of local endemics which is so characteristic of remote oceanic islands. The reason why niche broadening and ecological generalisation appear to be insular features is that there are many more small islands than large ones including clusters of small islands in large and well-isolated archipelagos. Populations on small islands are maintained in initial stages of evolutionary changes presumably because of limited ecological opportu-

Table 1. – Components of an insular syndrome in Corsican blue tits. Yes means that the trend fits the prediction of the insular syndrome. * P < 0.05; ** P < 0.01; *** P < 0.001.

Trait	Insular syndrome	Island/mainland
Ecology		
Body size	Yes	15% smaller ***
Population density	Yes	2.5 pairs *vs* 1 pair.ha^{-1}***
Habitat niche (e^H)	Yes	2.92 *vs* 1.0 ***
Feeding niche (H')	Yes	4.18 *vs* 3.72 ***
Breeding		
Laying date	Yes	11 May *vs* 15 April ***
Clutch size	Yes	6.6 eggs *vs* 8.6 ***
Breeding success	No	0.56 *vs* 0.57 ns
Nb. Fledglings/pair	Yes	3.5 *vs* 5.1 ***
Fled. Mass/ad. mass	Yes	1.14 *vs* 0.98 **
Nestling period	Yes	22 days *vs* 18.5 days *
Adult survival	No	0.56 *vs* 0.58 ns
Yearling survival	Yes	0.64 *vs* 0.48 **
Behaviour		
Territory size	Yes	0.94 ha *vs* 2.08 ha ***
Territory overlap	Yes	Circumstantial evidence
Aggressiveness	Yes	Much lower on Corsica

nities, and also possibly frequent extinctions (Mayr 1965). On large oceanic islands and archipelagos, ecological generalisation is far from being a necessary outcome of evolutionary trajectories. In fact the opposite is likely to be true whenever speciation can produce several efficient specialists from an original generalist. This happened for examples for Darwin's finches in the Galapagos (Lack 1947) and honeycreepers in the Hawaiian archipelago (Perkins 1913). The ultimate fate of such specialists is expected to be extinction from competition when a new generalist species colonises the island, which results in the end of a taxon cycle and the initiation of a new cycle of differentiation and specialisation (Wilson 1961, Ricklefs & Cox 1972).

Life histories

The large changes in community structure and species-specific attributes observed in insular biota result in large changes in life histories of species. One example of these changes has been provided by studies of insular and mainland populations of blue tits *Parus caeruleus* in the French Mediterranean region. As compared to their mainland counterparts, blue tits on Corsica strikingly differ in morphology, ecology, breeding patterns and behaviour. Most of the changes fit the predictions of an insular syndrome and are summarised in Table I (see also Higuchi 1976 for a study of insular populations of the varied tit *Parus varius*). In interpreting these changes, one problem arises: could the differences between island and mainland features

be simply different phenotypic expressions of the same genotypes raised under different environmental conditions ? Very few studies investigated whether differences between island and mainland populations have a genetic basis. Alatalo & Gustafsson (1988) demonstrated from cross-fostering experiments that the larger size of the Coal tit *Parus ater* on the island of Gotland is due to genetic factors, and Blondel *et al.* (1990) and Lambrechts *et al.* (1997) showed from common garden experiments that the large differences in laying date between a Corsican and a mainland population of blue tits were also genetically based.

Changes in fitness-related traits, i.e. breeding patterns and social structures, have often been interpreted as trade-offs among life history traits in response to high population densities in insular environments, especially between clutch-size and survival (Cody 1966, 1971, Ricklefs 1980). High population densities in insular environments were expected to result in high intraspecific competition, high adult survival, and hence low clutch-size. Reduction of clutch size in islands as compared to mainland has been reported in several species (Crowell & Rothstein 1981, Blondel 1991) including Darwin's finches (Grant & Grant 1989) and an extreme case is that of the predator- and competitor-free Seychelles warbler (*Acrocephalus sechellensis*) whose clutch size is only one egg while adult survival is as high as 83 % and life expectancy at the age of one year 3.9 years, which is extremely high for a small passerine (Komdeur 1994). However, a systematic and broad-scale analysis of reduced birth rates on islands controlling for latitudinal effects on clutch size has not yet

been performed (Grant 1998) and George (1987) found no difference in clutch size between conspecific island and mainland populations of three land birds on Coronados islands. If the trend of low birth rates combined with high adult survivorship is confirmed, it may reflect an evolutionary shift away from high reproductive rates and short life span towards the opposite combination of life history traits as a result of high intraspecific competition in crowded insular populations, that is an evolutionary shift from r-selection to K-selection (MacArthur & Wilson 1967, Boyce 1984).

Behavioural shifts

Shifts in behaviour are among the most spectacular features in insular vertebrates and many descriptions have been given of the tameness and apparent fearlessness of islands birds. Stamps & Buechner (1985) emphasised that the social behaviour of a variety of insular vertebrates (reptiles, mammals and birds) reveals a remarkable convergence in behavioural traits such as 1) reduced territory size, 2) increased territory overlap, 3) acceptance of subordinates, 4) reduced situation-specific aggressiveness, and 5) abandonment of territorial defence. A much lower aggressiveness of Corsican blue tits as compared to their mainland counterparts has been shown by Perret & Blondel (1993) to be associated with differences, probably genetically determined, in the ratio of sexual hormones. The higher the oestrogenous/androgenous ratio, the lower the level of aggressiveness because it has been demonstrated that both singing activity and aggressiveness depend on testosterone levels. Several hypotheses for explaining these shifts in behaviour have been proposed among which the "defence hypothesis" which predicts that a release in aggressiveness should be selected for if defence costs become exaggerated in crowded populations where encounters between territory contenders are frequent. Saving time and energy by reducing defence costs and decreasing territory size is expected to improve fitness payoffs per territory owners and result in the production of more competitive offspring. Breeding traits of Corsican blue tits and of an insular population of varied tits in Japan (Higuchi & Momose 1981) include higher ratio of fledging mass/adult mass, longer nestling period, prolonged infantile behaviour, higher survivorship of fledglings relative to adults, small territory size and large territory overlap. All these trends are consistent with the defence hypothesis. Kikkawa (1976) reported, however, that the insular silvereye of Heron Island, Australia, is more aggressive than its mainland counterpart, but interestingly, he noticed that the breeding success of dominant birds may not be as high as that of submissive birds in some years, which runs in the line of predictions from the defence hypothesis. Behavioural shifts on islands could have important consequences on genetic mating systems of socially monogamous birds, with lower levels of extra-pair paternity in insular populations than in their mainland counterparts (Griffith 2000, Petrie & Kempenaers 1998).

POPULATION DIFFERENTIATION ON ISLANDS

An evolutionary trend resulting from shift from dispersal to sedentariness is the differentiation from a single generalist species first colonising an island or archipelago to several locally adapted specialist species as a result of local adaptation. Radiation of such groups as Darwin's finches in the Galapagos or honeycreepers in the Hawaii islands are examples of such mechanisms which may eventually result in a taxon cycle of evolution leading to extinction of specialist species and their replacement by a new generalist species, which makes the cycle begin again (Wilson 1961, Ricklefs & Cox 1972, Pregill & Olson 1981, Grant 1998).

A consequence of low dispersal, sedentariness, high site fidelity and strong philopatry of insular birds is the potential for differentiation at smaller spatial scales than on mainland regions, even at a smaller scale than the dispersal range of organisms. This may seem surprising because in such highly mobile organisms as birds, the homogenizing effects of gene flow are supposed to preclude adaptive differentiation at spatial scales that are smaller than the dispersal range of individuals. However, theory predicts that such a differentiation can potentially occur if divergent selection pressures are strong enough.

Examples of large interpopulation differentiation at a small geographical scale are that of the white-eyes (Zosterops spp.) in the Mascarene islands (Cheke 1987), and, even more convincingly, the spectacular variation of bill size of Darwin's finches on the Galapagos islands in relation to the size and hardness of their seed food resources (Schluter 1996, Grant 1999). Food supply of the Darwin's finches has been found to differ on different islands in a way that is consistent with differences in the bill size of the birds, thus supporting the hypothesis that morphological differences result from different selection pressures acting on genetic variation (Schluter & Grant 1984). Evolutionary responses to oscillating natural selection on heritable variation in bill shape have been demonstrated when food supply changed after an El Niño event (Grant & Grant 1989, 1995).

One example of local differentiation of populations within an island as a result of resource-based divergent selection is that of the blue tit (*Parus caeruleus*) in Corsica. Two populations only 25 km-apart are highly specialised to their local habitats and differ so much in demographic and morphometric traits that they are apparently reproductively isolated (Blondel *et al.* 1999). These two populations responded to contrasting local selection regimes involving large differences in the timing and abundance of food resources, which resulted in divergent adaptive response of suites of life-history traits. Such a local adaptation to local environments at small spatial scales is a demonstration that selection can cause divergence, presumably in the face of substantial gene flow, giving support to the divergence-with-gene-flow model of speciation (Rice & Hostert 1993). Differentiation at such a small scale is really an insular feature because in a similar configuration of habitats on the mainland, much higher dispersal rates and gene swamping prevented local adaptation and resulted in local maladaptation (Dias *et al.* 1996, Dias & Blondel 1996). Thus strong habitat fidelity and reduced dispersal which are components of an insular syndrome (Diamond 1983, Blondel 1995, Grant 1998) explain that population differentiation of birds can occur at much smaller spatial scales on islands than on mainland. A somewhat similar case of incipient parapatric speciation has been suggested for *Neospiza* buntings on Inaccessible Island in the Tristan da Cunha archipelago (Ryan *et al.* 1994). Interestingly, the lower inter-species diversity which is so characteristic of island biota is to some extent counterbalanced by a higher intra-species diversity. These examples open the door to direct studies of observable evolution in natural populations which are surprisingly rare despite their interest to understand and interpret the rather static analysis of evolution in the past, and to predict evolutionary changes as responses to man-induced environmental changes.

STRENGTH AND VULNERABILITY OF ISLAND BIOTA

Resistance of insular species to natural disturbance

The insular syndrome involves ecological adjustments as well as evolutionary changes that make insular communities self-regulating assemblages of species that are resistant face to the risks of extinction and invasion. The mechanisms whereby insular communities are highly integrated and resistant biological constructs remain obscure, and the vague concept of diffuse competition proposed by MacArthur (1972) to explain the resistance opposed by insular communities to potential colonists is not very helpful because it is impossible to test experimentally. The systems that control island diversity work by the principle of feedbacks. Low diversity causes diversity to grow and high diversity causes diversity to fall (Rosenzweig 1995). Although species turnover on islands is the keystone of the theory of island biogeography, there are few well documented case studies of turnover on islands and some classical examples are controversial because it is questionable whether observed changes in species composition between two census intervals are due to competition-mediated immigration-extinction mechanisms or to idiosyncratic habitat changes as a result of human action (Diamond & May 1977). Turnover can operate at long scales of time, thus remaining unnoticed, especially in remote oceanic islands where, on very long time scales, it turns to result in species replacement as exemplified by the taxon cycle (Ricklefs & Cox 1972). Indeed, even though islands are subject to natural disasters including drought, fire, severe storms and hurricanes which can devastate entire populations on smaller islands (Wiley & Wunderle 1994), to date the fossil record has revealed no major loss of species from natural causes (Steadman 1995). Even in some Galapagos islands where severe droughts such as those produced by El Niño events, may reduce population sizes to very few individuals, no extinction events seem to have occurred in the recent past in Darwin's finches (Grant 1986, Grant & Grant 1989). On the small six-ha Mandarte Island, British Columbia, Canada, heavy storms can reduce the population size of the Song sparrow (*Melospiza melodia*) to just a few individuals but no extinction of this small isolated population has been reported so far (Smith *et al.* 1991).

Yet, the lack of connection with larger areas with which populations could exchange propagules makes small insular populations potentially vulnerable to environmental, demographic and genetic stochasticity which together can precipitate them in an 'extinction vortex'. Stochastic fluctuations of life history traits may be conducive to demographic thresholds below which rare events may lead to extinction (Lande 1987).

There are critical factors of population size and structure below which inbreeding and loss of selectable variation could lead a population to extinction (Frankel & Soulé 1981, Soulé 1987). The "Allee effect" is a basic assumption underlying the so-called extinction vortex, stating that populations that become too small will inevitably be doomed to extinction as a result of the combined effects of demographic and genetic processes. Therefore, loss of genetic variability and reduced viability and fecundity due to inbreeding depression are probably a threat in small isolated populations. The relative impact of inbreeding on the viability of natural

populations has been questioned, however, because there is little evidence of deleterious effects of inbreeding depression in animal populations. Van Noordwijk & Scharloo (1981) demonstrated clear effects of inbreeding in a population of Great tit (*Parus major*) on the island of Vlieland, The Netherlands. Reduced hatching success has been shown in inbred zygotes and in clutches of inbred females. Both the average number of not hatching eggs (7.5 % for every 10 % increase in inbreeding coefficient) and the proportion of clutches in which any eggs fail to hatch increased with the degree of inbreeding. However, there were no indication of smaller clutch size or a reduced fertility in inbred adults. Moreover, the effects of inbreeding in early stages of the life cycle were compensated in later stages because successful young have been shown to have higher survival rates and higher recruitment rates (twice as many as expected). In fact continuous inbreeding probably exerts a strong selection against lethals. Purging of deleterious recessive alleles from the genome has been put forward as a potential effect resulting from periods of intense inbreeding following bottlenecks. In the small population of song sparrow on the Mandarte island that experienced a severe population bottleneck as a result of demographic crashes, those individuals that survived the crash were not a random subset of the pre-crash population in respect to inbreeding (Keller *et al.* 1994). After two crashes (1980 and 1989) the mean inbreeding coefficient in the breeding population was actually lower in the season after the crash than in the previous season. Natural selection clearly favoured outbred individuals which does not mean, however, that inbreeding does not affect survival in the wild. When there is a succession of crashes, serial bottlenecks cannot entirely purge the genetic load sufficiently to alleviate the negative effects of inbreeding. Thus environmental and genetic effects on survival may interact in such a way that their effects on individuals and populations should not be considered independently.

The holocaust of island birds

Islands are among the most threatened biota on Earth with more than two thirds of extinct avian species being insular endemics. Why are they so vulnerable in spite of them having evolved life history traits that successfully allow them to persist as explained above ? The answer is that insular biota became evolutionarily resistant to most natural disturbance events but they are ecologically sensitive to human-induced disruption. This explains that suddenly insularizing an area may have dramatic consequences on species which do not have the time to evolve the suite of life-history traits which would allow them to withstand new constraints of the recently isolated environment. An example is that of Barro Colorado Island (BCI). This artificial island has been created in 1914 when the canal of Panama has been built. Within some decades, as many as 60 species of birds became extinct. Extinction has been attributed to several causes including predation and a differential loss of species of undergrowth (Wilson & Willis 1975, Karr 1982). Interestingly, Karr *et al.* (1990) provided evidence that the species that were the most likely to disappear from the island were those that had the lowest survival rates. Among the 25 mainland species they analysed, survival rates of 8 species that vanished on BCI have been estimated as 0.50 ± 0.05 as compared to 0.59 ± 0.02 for the 17 species still present. Although the absolute difference may appear small, its demographic consequences are considerable.

Perhaps the most important threat to island birds is the disruption of interspecific interactions such as competition, predation and parasitism. As many as 49 different species of birds have been introduced in the Hawaiian islands between 1869 and 1963. In the meantime, a large proportion of the 36 endemic species of Hawaiian honeycreepers went extinct. From computer simulations on the morphological space of introduced and extinct species, Moulton & Pimm (1987) showed that competition must have happened among them at the expense of native species because extinct species were significantly closer to the introduced species in the morphological space than are the still existing native and introduced species among them. This strongly suggests that introduced species have been the direct cause of extinction for most of the native species. Additional causes of extinction of Hawaiian honeycreepers have been the disease from malaria (*Plasmodium*) which has been introduced with non-native bird species (Van Riper *et al.* 1986).

Release from predation pressure is one of the most conspicuous features of island communities. In communities that are naturally poor in predators, birds did not evolve defence mechanisms and are naïve and particularly tame and easy to approach and catch. At the time of European invasion of many islands, an incredible tameness of mammals and birds was reported in a number of so far uninhabited oceanic islands. Resident land birds on most oceanic islands are still remarkably tame, as illustrated for example by a photograph showing a Galapagos hawk sitting on the hat of Peter Grant (Grant 1998). In the Cousin island, the Seychelles warbler lacks natural predators and can be approached just a few metres (Komdeur 1994). New predators had catastrophic effects in such communities where introduced mice, cats and dogs become as harmful for defenceless prey as are weasels, lynxes and wolves, respectively, in mainland communities. The combination of tameness and flightlessness resulted in an unprecedented holo-

caust of thousands of species, especially in remote oceanic islands, as soon as man invaded them (Olson & James 1984, Steadman 1995). In the Hawaiian islands which are renowned for the radiation of Hawaiian honeycreepers, flightless ducks, geese and ibises, at least 60 endemic species of land birds have become extinct since human arrival at about 1500-2000 yr BP. Combining seabirds and land birds, Steadman (1995) conservatively estimated that an average of 10 species or populations in most families of Pacific island birds (rails, pigeons, doves, parrots, passerines) have been lost on each of the 800 major islands of the Pacific, yielding a total loss of 8000 species ! Most extinct species were flightless forest dwellers endemic to a single island. Flightless rails alone, with an estimate of one to four species per island, may account for 2000 species that have been doomed to extinction. In nearly all islands in the large archipelagos of the Pacific Ocean (Melanesia, Micronesia, Polynesia) birds have been decimated as soon as man reached them as early as 30,000 yr BP in Melanesia and much later, about 3500 yr BP in West Polynesia and Micronesia. Once people occupied an island, human predation, habitat loss, and introduced predators, competitors, or pathogens were responsible for mass extinction of native species within a very short period of time.

PERSPECTIVES FOR FUTURE STUDIES

Despite an impressive body of knowledge accumulated on island biology since the time of Darwin and Wallace, there are still much ignorance and controversies about both ecological and evolutionary matters in island biota, including the very first step of describing their biological diversity. The equilibrium theory of island biogeography has undoubtedly been very useful to revitalise and rejuvenate insular studies by providing a novel and unifying theory that stimulated hundreds of studies for nearly 35 years. However, several limitations and new insights in the biology of isolates make the theory insufficient as a modern tool to explain patterns that span over a broad range of spatial, temporal and ecological scales, including habitat islands resulting from habitat fragmentation (Fox & Fox 2000, see also the special issue of *Global Ecol Biogeogr* 6, January 2000). Time is ripe to replace the long-standing MacArthur and Wilson's paradigm by a more comprehensive theory taking into consideration scale effects as advocated in the spatial and temporal continuum proposed by Haila (1990). A new model, the general conceptual framework of which has been offered by Lomolino (2000b), should incorporate those features not included in the MacArthur & Wilson's theory but which have been shown to be important in deter-

mining insular communities: 1) the fact that basic biogeographic processes are not only immigration and extinction, but also evolution, 2) the importance of island-specific characteristics (physiography, climate, stochastic abiotic events) in basic biogeographic processes, 3) the role of feedbacks among components of insular systems, including both processes and species, and 4) the species-specific variation of life-history attributes which affects microevolutionary processes and explains the non-random variation among species on islands (Lomolino 1999, 2000b).

In this context evolutionary issues should be considered at both scales of phylogenetic diversification, i.e. speciation, and microevolutionary changes within populations and species which operate on the same time-scale as colonisation and extinction. Processes of phylogenesis can generate patterns of species richness almost independently of colonisation and extinction with not only endemic species, but also entire endemic clades including many species as in the Galapagos and Hawaiian islands (Heaney 2000). Many microevolutionary questions remained to be answered before broad generalisations can be made. Each island is a singular system with its own history, environmental characteristics and living communities so that processes that have a significant impact on one species or set of species on an island may be unimportant for others on another island. Evolutionary changes on islands that are assumed to be components of an insular syndrome too often received *ad hoc*, "panglossian" (Gould & Lewontin 1979) and circular interpretations. Such explanations cannot be accepted until they rely on measured selective forces producing adaptations and until it has been demonstrated that similar trends evolved among different organisms living in the same or different islands. Interpretations of evolution on islands are strongest whenever a trend is statistically demonstrable and/or known from phylogenetic analyses to have arisen independently and several times in unrelated taxa, and are repeated in geographically distant areas (Grant 1998). Such conditions are rarely met but could be so thanks to recent improvements in the comparative method (e.g. Felsenstein 1985, Harvey & Pagel 1991).

Given the present state of the art of our knowledge on bird evolution on islands, several points should deserve investigations in the future. I shall limit myself to mention only a few of them. For example no generalisation should be made on the balance between birth rates and death rates until much further insight is given on the overall demography and trade-offs between traits from long-term population studies. The link between loss of genetic variation due to founder effect and evolutionary change, which is assumed from conventional wisdom, remains to be determined because not all in-

sular populations, including small populations, are genetically depauperate (Merilä *et al.* 1996, Tarr *et al.* 1998). Addressing the challenge of what determines genetic variation on islands requires an answer on the time period over which evolutionary changes occurred, and hence how much the island's environmental history needs to be known. Modern molecular techniques using mtDNA or microsatellites for constructing phylogenies at the intraspecific level combined with quantitative genetics on fitness-related traits, that respond within a few generations to strong directional selective pressures, should give an insight on the response of populations to environmental changes. Coupling historical data on islands' environments with genetic data on extant populations should help interpret the microevolutionary history of island populations and predict their responses to man-induced environmental changes including the forthcoming changes due to global warming. Reconstructing past environments to interpret evolutionary changes is a great challenge, however. If geophysical history is not too complicated to reconstruct and should give cues to understand adaptive radiations in archipelagos at the species level, as shown for example by Carson & Clague (1995) for the Hawaiian honeycreepers, or by Grant & Grant (1996) for the Darwin's finches in the Galapagos, the ecological history of islands on time scales that are consistent with microevolutionary changes is a much more difficult task which requires a multidisciplinary approach involving disciplines of both earth and life sciences. Molecular approaches are quite promising to track the history of species. For example, the expectation of Ricklefs & Cox (1972) that the relative ages of island populations could be inferred from the degree of taxonomic differentiation among island populations has been confirmed by analyses of DNA sequence divergence among West Indian birds (Ricklefs & Bermingham 1999).

Finally the alarming number of bird species that have become endangered or extinct in recent years (Diamond 1989), especially endemic forms on islands (Collar *et al.* 1994), is much more than a mere impoverishment in biological diversity. Among the many arguments to be made for conserving our biological heritage (Reaka-Kudla *et al.* 1996), one of them is that missing species make it difficult to interpret both ecological processes and evolutionary pathways. Missing species from ecological communities or from evolutionary clades are like missing pages in a book. When too many pages are lost, the message becomes obscure, and finally unintelligible. This makes urgent a thorough assessment of the causes of species declines and an insight in the relative impact on the demography of species of various threats such as habitat loss and fragmentation, pollution, the introduction of exotic predators, competitors and disease, human impact, unexpected catastrophes and hu-

man-induced climate changes. This can be achieved through population viability analysis (PVA) which has been developed to assess extinction risks and to compare alternative management options (Brook & Kikkawa 1998). PVA computer simulations based on demographic, environmental and genetic parameters (Gilpin & Soulé 1986, Boyce 1992) are currently widely applied to conservation biology thanks to recent improvements in the parameterisation of the models. Current technical sophistication makes the PVA recognised by the World Conservation Union (UICN) as one of the five internationally accepted criteria for risk categorisation and development of management decisions (Clark *et al.* 1991), especially because PVA simulations allows to rank the relative severity of risks and develop potential management strategies accordingly.

REFERENCES

Abbott I 1980. Theories dealing with the ecology of landbirds on islands. *Adv Ecol Res* 11: 329-371.

Alatalo R, Gustafsson L 1988. Genetic component of morphological differentiation in coal tits under competitive release. *Evolution* 42: 200-203.

Avise J C 1994. Molecular Markers, Natural History and Evolution, New York, London, Chapman and Hall.

Blondel J 1985. Habitat selection in island versus mainland birds. *In* Habitat selection in Birds, ML Cody Ed. New York, Academic Press: 477-516.

Blondel J 1991. Birds in biological isolates. *In* Bird Population Studies, their Relevance to Conservation and Management, CM Perrins, J-D Lebreton & G Hirons Eds, Oxford, Oxford Univ Press: 45-72.

Blondel J 1995. Biogéographie. Approche écologique et évolutive. Paris, Masson.

Blondel J, Catzeflis F, Perret P 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *J Evol Biol* 9: 871-891.

Blondel J, Chessel D, Frochot B 1988. Bird species impoverishment, niche expansion and density inflation in Mediterranean island habitats. *Ecology* 69: 1899-1917.

Blondel J, Dias PC, Perret P, Maistre M, Lambrechts MM 1999. Selection-based biodiversity at a small spatial scale in an insular bird. *Science* 285: 1399-1402.

Blondel J, Perret P, Maistre M 1990. On the genetical basis of laying date in an island population of Blue Tit. *J evol Biol* 3: 469-475.

Boyce MS 1984. Restitution of *r*- and *K*- selection as a model of density dependent natural selection. *Annu Rev Ecol Syst* 15: 427-447.

Boyce MS 1992. Population viability analysis. *Annu Rev Ecol Syst* 23: 481-508.

Brook BW, Kikkawa J 1998. Examining threats faced by island birds: a populaton viability analysis on the Capricorn silvereye using long-term data. *J Appl Ecol* 35: 491-503.

Brown ME, 1996. Assessing body condition in birds. *Curr Ornitho* 13: 67-135.

Carlquist S 1974. Island Biology. New York, Columbia Univ Press.

Carson HL, Clague DA 1995. Geology and biogeography of the Hawaiian Islands. *In* Hawaiian Biogeography. Evolution on a hostspot archipelago, WL Wagner & Funk VA Ed, Washington, Smithsonian Press: 14-29.

Case TJ 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59: 1-18.

Cheke AS 1987. The ecology of surviving native land-birds of Réunion. III. The surviving Native Birds of Réunion and Rodrigues. *In* Studies of Mascarene Island Birds, AW Diamond Ed, Cambridge, Cambridge Univ Press: 301-358.

Clark TW, Backhouse GN, Lacy RC 1991. Report of a workshop on population viability assessment as a tool for threatened species management and conservation. *Australian Zoologist* 27: 28-35.

Cody ML 1966. A general theory of clutch-size. *Evolution* 20: 174-184.

Cody ML 1971. Ecological aspects of reproduction. *In* Avian Biology, DS Farner & JR King Eds, New York & London, Academic Press 1: 461-512.

Collar NJ, Crosby MJ, Stattersfield AJ 1994. Birds to whatch 2. *In* The World List of Threatened Birds. BirLife International, Cambridge.

Crowell KL 1962. Reduced interspecific competition among the birds of Bermuda. *Ecology* 43: 75-88.

Crowell KL 1983. Islands - insight of artifact ?: Population dynamics and habitat utilization in insular rodents. *Oikos* 41: 442-454.

Crowell KL, Rothstein SI 1981. Clutch sizes and breeding strategies among Bermudan and North American passerines. *Ibis* 123: 42-50.

Cutler A 1991. Nested faunas and extinctions in fragmented habitats. *Conserv Biol* 5: 496-505.

Darlington PJ Jr 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas and on atrophy of wings. *Ecol Monogr* 13: 37-61.

Darwin C 1859. On the origin of species by means of natural selection, London, Murray.

Diamond JM 1973. Distributional ecology of New Guinea birds. *Science* 179: 759-769.

Diamond JM 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science* 184: 803-806.

Diamond JM 1975. Assembly of species communities. *In* Ecology and Evolution of Communities, MLCody & JM Diamond Eds, Cambridge, Mass., Belknap Press Harvard Univ Press: 342-444.

Diamond JM 1983. Flightlessness and fear of flying in island species. *Nature* 293: 507-508.

Diamond JM 1989. Overview of recent extinctions. *In* Conservation for the Twenty-First Century, D Western & MC Pearl Eds, Oxford, Oxford Univ Press: 37-41.

Diamond JM, May RM 1977. Species turnover rates on islands: dependence on census interval. *Science* 197: 266-270.

Dias PC, Blondel J 1996. Breeding time, food supply and fitness components in Mediterranean blue tits, *Parus caeruleus*. *Ibis* 138: 108-113.

Dias PC, Verheyen GR, Raymond M 1996. Source-sink populations in Mediterranean blue tits: evidence using single-locus minisatellite probes. *J Evol Bio* 9: 965-978.

Felsenstein J 1985. Phylogenies and the comparative method. *Am Nat* 125: 1-15.

Fitch WM, Margoliash E 1967. The construction of phylogenetic trees - a generally applicable method utilizing estimates of the mutation distance obtained from cytochrome c sequences. *Science* 155: 279-284.

Fitzpatrick S 1998. Intraspecific variation in wing length and male plumage coloration with migratory behaviour in continental and island populations. *J Avian Biol* 29: 248-256.

Foster JB 1964. Evolution of mammals on islands. *Nature* 202: 234-235.

Fox BJ, Fox MD 2000. Factors determining mammal species richness on habitat islands and isolates: habitat diversity, disturbance, species interactions and guild assembly rules. *Global Ecol Biogeogr* 9: 19-37.

Frankel OH, Soulé ME 1981. Conservation and Evolution. New York, Cambridge Univ Press.

George TL 1987. Greater land bird densities on islands vs. mainland: relation to nest predation level. *Ecology* 68: 1393-1400.

Gilpin ME, Soulé ME 1986. Minimum viable populations: the process of species extinctions. *In* Conservation Biology: the science of scarcity and diversity, ME Soulé Ed, Sunderland, Mass, Sinauer Associates: 13-34.

Gorman M 1979. Island Ecology. Chapman and Hall, London.

Gould SJ, Lewontin RC 1979. The sprandels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc R Soc London B* 205: 581-598.

Grant P R 1965. A systematic study of the terrestrial birds of the Tres Marias Islands, Mexico. *Yale Peabody Mus Postilla* 90: 1-106.

Grant PR 1965a. Plumage and the evolution of birds on islands. *Syst Zool* 14: 47-52.

Grant PR 1965b. The adaptive significance of some size trends in island birds. *Evolution* 19: 355-367.

Grant PR 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations of islands. *Syst Zool* 17: 319-333.

Grant PR 1986. Ecology and Evolution of Darwin's Finches. Princeton NJ, Princeton Univ Press.

Grant PR 1998. Evolution on Islands. Oxford, Oxford Univ Press.

Grant PR 1998. Patterns on islands and microevolution. *In* Evolution on Islands, PR Grant Ed, Oxford, Oxford Univ Press: 1-17.

Grant PR 1999. Ecology and Evolution of Darwin's Finches. Princeton, Princeton Univ Press.

Grant BR, Grant PR 1989. Natural selection in a population of Darwin's Finches. *Am Nat* 133(3): 377-393.

Grant PR, Grant BR 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49: 241-251.

Grant PR, Grant BR 1996. Speciation and hybridization of island birds. *Phil Trans R Sc Lond B* 351: 765-772.

Griffith SC 2000. High fidelity on islands: a comparative study of extrapair paternity in passerine birds. *Behav Ecol* 11: 265-273.

Haila Y 1983. Land birds on northern islands: a sampling metaphor for insular colonization. *Oikos* 41: 334-351.

Haila Y 1990. Towards an ecological definition of an island: a northwest European perspective. *J Biogeogr* 17: 561-568.

Haila Y, Järvinen O 1983. Land bird communities on a Finnish island: species impoverishment and abundance patterns. *Oikos* 41: 255-273.

Haila Y, Järvinen O, Kuusela S 1983. Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *J Biogeogr* 10: 499-531.

Haila Y, Järvinen O, Väisänen RA 1980. Habitat distribution and species associations of land bird populations on the Aland islands, SW Finland. *Ann Zool Fenn* 17: 87-106.

Hamilton TH, Armstrong NE 1965. Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature* 207: 148-151.

Harvey PH, Pagel MD 1991.The Comparative Method in Evolutionary Biology. Oxford, Oxford Univ Press.

Heaney LR 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution* 32: 29-44.

Heaney LR 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecol Biogeogr* 9: 59-74.

Higuchi H 1976. Comparative study on the breeding of mainland and island subspecies of the Varied Tit, *Parus varius*. *Tori* 25: 11-20.

Higuchi H, Momose HG 1981. Deferred independence and prolonged infantile behaviour in young varied tits (*Parus varius*) of an island population. *Anim Behav* 29: 523-528.

Hubby JL, Lewontin RC 1966. A molecular approach to the study of the genetic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura*. *Genetics* 54: 577-594.

Hurlbert SH 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.

Huxley JS 1942. Evolution: the Modern Synthesis. London, Allen and Unwin.

Karr JM 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. *Am Nat* 119: 220-239.

Karr JR, Nichols JD, Klimkiewicz MK, Brawn JD 1990. Survival rates of tropical and temperate forest birds: will the dogma survive ? *Am Nat* 136: 277-291.

Keast A 1970. Adaptive evolution and shifts in niche ocupation in island birds. *Biotropica* 2: 61-75.

Keller L, Arcese P, Smith JNM, Hochachka WM, Stearns SC 1994. Selection against inbred song sparrows during a natural population bottleneck. *Nature* 372: 356-357.

Kikkawa J 1976. The birds of the great Barrier Reef. *In* Biology and Geology of Coral Reefs, 3, Biology 2, OA Jones & R Endean Eds, New York, Academic Press: 279-341.

Klein DR 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *J Wildl Mgmt* 32: 350-367.

Koenig WD 1999. Spatial autocorrelation of ecological phenomena. *Trends Ecol Evol* 14: 22-25.

Komdeur J 1994. Conserving the Seychelles Warbler *Acrocephalus sechellensis* by translocation from Cousin island to the islands of Aride and Cousine. *Biol Conserv* 67: 143-152.

Lack D 1947. Darwin's Finches. Cambridge, Cambridge Univ Press.

Lack D 1969. The number of bird species on islands. *Bird Study* 16: 193-209.

Lambrechts MM, Blondel J, Maistre M, Perret P 1997. A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc Natl Acad Sci USA* 94: 5153-5155.

Lande R 1981. Models of speciation by sexual selection on polygenic traits. *Proc Natl Acad Sci USA* 78: 3721-3725.

Lande R 1987. Extinction thresholds in demographic models of territorial populations. *Am Nat* 130: 624-635.

Lomolino MV 1985. Body size of mammals on islands: the island rule reexamined. *Am Nat* 125: 310-316.

Lomolino MV 2000a. A call for a new paradigm of island biogeography. *Global Ecol Biogeogr* 9: 1-6.

Lomolino MV 2000b. A species-based theory of insular zoogeography. *Global Ecol Biogeogr* 6: 39-58.

MacArthur RH 1972. Geographical Ecology. New York, Harper and Row.

MacArthur RH, Diamond JM, Karr JR 1972a. Density compensation in island faunas. *Ecology* 53: 330-342.

MacArthur R, MacArthur J, MacArthur D, MacArthur A 1972b. The effect of island area on population densities. *Ecology* 54: 657-658.

MacArthur RH, Wilson EO 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387.

MacArthur RH, Wilson EO 1967. The Theory of Island Biogeography. Princeton, NJ, Princeton Univ Press.

Marshall HD, Baker AJ 1998. Rates and patterns of mitochondrial DNA sequence evolution in Fringilline finches (*Fringilla* spp.) and the Greenfinch (*Carduelis chloris*). *Mol Biol Evol* 15: 638-646.

Martin JL, Gaston AJ, Hitier S 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). *Oikos* 72: 115-131.

Mayr E 1940. Speciation phenomena in birds. *Am Nat* 74: 249-278.

Mayr E 1942. Systematics and the origin of species. New York, Columbia Univ Press.

Mayr E 1965. The nature of colonizations in birds. *In* The Genetics of Colonizing Species, HG Baker & GL Stebbins Eds, New York, Academic Press: 29-43.

McNab BH 1994. Energy conservation and the evolution of flightlessness in birds. *Am Nat* 144: 628-642.

Merilä J, Björklund M, Baker AJ 1996. The art of successful bottlenecking: genetics of introduced Green-

finch (*Carduelis chloris*) populations in New Zealand. *Heredity* **77**: 410-422.

Mindell DP 1997. Avian molecular Evolution and Systematics. San Diego, Academic Press.

Moulton MP, Pimm SL 1987. Morphological assortment in introduced Hawaiian passerines. *Evol Ecol* 1: 113-124.

Mundy N, Winchell CS, Burr T, Woodruff DS 1997. Microsatellite variation and microevolution in the critically endangered San Clement Island loggerhead shrike (*Lanius ludovicianus mearnsi*). *Proc R Soc Lond B* 264: 869-875.

Murphy RC 1938. The need for insular exploration as illustrated by birds. *Science* 88: 533-539.

Nilsson SG, Björkman P, Forslund P 1985. Egg predation in forest communities on islands and mainland. *Oecologia* 66: 511-515.

Olson SL, James H 1984. The role of Polynesians in the extinction of the avifaunas of the Hawaiian Islands. *In* Quaternary extinctions: a prehistoric revolution, PS Martin & RG Klein Ed, Tucson, Univ Arizona Press.

Patterson BD, Atmar W 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol J Linn Soc* 28: 65-82.

Patterson BD, Brown JH 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. *J Biogeogr* 18: 395-402.

Perkins RCL 1903. Vertebrata. *In* Fauna Hawaiiensis, D Sharp Ed, Cambridge, Cambridge Univ Press: 365-466.

Perkins RCL 1913. Introduction. *In* Fauna Hawaiiensis, D Sharp Ed, Cambridge, Cambridge Univ Press, xv-ccxxviii.

Perret P, Blondel J 1993. Experimental evidence of the territorial defense hypothesis in insular Blue Tits. *Experientia* 49: 94-98.

Petrie M, Kempenaers B 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends Ecol Evol* 13: 52-58.

Pimm SL, Jones HL, Diamond JM 1988. On the risk of extinction. *Am. Nat.* 132: 757-785.

Pregill GK, Olson SL 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annu Rev Ecol Syst* 12: 75-98.

Reaka-Kudla ML, Wilson DE, Wilson WO eds 1996. Biodiversity II. Understanding and protecting our biological resources. Joseph Henry (National Academy) Press, Washington, D.C.

Reed TM 1987. Island birds and isolation: Lack revisited. *Biol J Linn Soc* 30: 25-29.

Rice WR, Hostert EE 1993. Laboratory experiments on speciation: what have been learned in 40 years ? *Evolution* 47(6): 1637-1653.

Ricklefs RE 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *The Auk* 97: 38-49.

Ricklefs RE, Cox GW 1972. Taxon cycles in the West Indian Avifauna. *Am Nat* 106: 195-219.

Ricklefs RE, Bermingham E 1999. Taxon cycles in the Lesser Antillean avifauna. *Ostrich* 70: 49-59.

Ricklefs RE, Lovette IJ 1999. The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *J Anim Ecol* 68: 1142-1160.

Roff DA 1994. The evolution of flightlessness: is history important ? *Evol Ecol* 8: 639-657.

Rosenzweig ML 1995. Species diversity in space and time. Cambridge, Cambridge Univ Press.

Roughgarden J 1995. Anolis lizards of the Caribbean: ecology, evolution and plate tectonics. Oxford, Oxford Univ Press.

Ryan PG, Moloney CL, Hudon J. 1994. Color variation and hybridization among *Nesospiza* buntings on Inaccessible islands, Tristan da Cunha. *Auk* 111: 314-327.

Schluter D 1996. Ecological causes of adaptive radiation. *Am. Nat.* 148: S40-S64.

Schluter D, Grant PR 1984. Determinants of morphological patterns in communities of Darwin's Finches. *Am Nat* 123: 175-196.

Simberloff D, Martin JL 1991. Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fenn* 68: 178-192.

Smith JNM, Arcese P, Hochachka WM 1991. Social behaviour and population regulation in insular bird populations: implications for conservation. *In* Bird Population Studies. Relevance to Conservation and Management, CM Perrins, JD Lebreton, GJM Hirons Eds, Oxford, Oxford Univ Press: 148-167.

Soulé ME 1987. Viable Populations for Conservation. Cambridge, Cambridge Univ Press.

Stacey PB, Taper M 1992. Environemental variation and the persistence of small populations. *Ecol Applic* 2: 18-29.

Stamps JA, Buechner M 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quart Rev Biol* 60: 155-181.

Steadman DW 1995. Prehistoric extinctions of Pacific island Birds: Biodiversity meets zooarcheology. *Science* 267: 1123-1131.

Tamarin RT 1977. Dispersal in island and mainland voles. *Ecology* 58: 1044-1054.

Tarr CL, Conant S, Fleischer RC 1998. Founder events and variation at microsatellite loci in an insular passrine bird, the Laysan finch (*Telespiza cantans*). *Mol Ecol* 7: 719-731.

Tracy CR, George TL 1992. On the determinants of extinction. *Am Nat* 139: 101-122.

Van Noordwijk AJ, Scharloo W 1981. Inbreeding in an island poulation of the Great Tit. *Evolution* 35: 674-688.

Van Riper IC, Van Riper SG, Lee Goff M, Maird M 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol Monogr* 56: 127-144.

Van Valen L 1973. A new evolutionary law. *Evol Theory* 1: 1-30.

Vitousek PM, Loope L, Anderson N 1995. Islands: Biological diversity and ecosystem function. Springer-Verlag, New York.

Wallace AR 1871. Contributions to the theory of Natural Selection. A series of essays. London, Macmillan.

Wallace AR 1880. Island Life. London, Macmillan.

Watson GE 1964. Ecology and evolution of passerine birds on the islands of the Aegean Sea, Yale Univ.

Whittaker RJ 1998. Island biogeography. Ecology, evolution and Conservation. Oxford, Oxford Univ Press.

Whittaker RJ 2000. Scale, succession and complexity in island biogeography: are we asking the right questions ? *Global Ecol Biogeogr* 9: 75-85.

Wiggins DA, Moller AP 1997. Island size, isolation, or interspecific competition ? The breeding distribution of the *Parus* guild in the Danish archipelago. *Oecologia* 111: 255-260.

Wiley JW, Wunderle JM Jr 1994. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conservation International* 3: 319-349.

Williams EE 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evol Biol* 6: 47-89.

Williamson M 1981. Island Populations. Oxford, Oxford Univ Press.

Wilson EO 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am Nat* 95: 169-193.

Wilson EO, Willis EO 1975. Applied biogeography. *In* Ecology and Evolution of Communities, M L Cody, JM Diamond Eds, Cambridge, Mass, Harvard Univ Press: 522-534.

Wright DH, Patterson BD, Mikkelson G, Cutler AH, Atmar W 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113: 1-20.

Yeaton RI, Cody ML 1974. Competitive release in island song sparrow populations. *Theor Pop Biol* 5: 42-58.