# Speciation and Hybridization in Island Birds [and Discussion]

Peter R. Grant, B. Rosemary Grant and J. C. Deutsch

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# Speciation and hybridization in island birds

PETER R. GRANT AND B. ROSEMARY GRANT

*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544–1003, U.S.A.*

## SUMMARY

The process of speciation in birds can be inferred from the pattern of diversification on islands, especially in archipelagos. The basic model is one of initial differentiation of allopatric populations, with further differentiation taking place at the time that sympatry is established. Differences that evolve in allopatry are reinforced by a regime of divergent selection on the taxa in sympatry arising from ecological pressures and not from reproductive (genetic) incompatibility. A low level of interbreeding (hybridization) at the secondary contact phase and subsequently may occur with little or no fitness loss. Introgressive hybridization has the potential to play a creative role in evolution, facilitating further divergence by enhancing genetic variation and relaxing genetic constraints on particular directions of evolutionary change under natural selection. Hybridization potential may last for many millions of years after two taxa diverge, implying that post-zygotic isolation evolves slowly. The main alternative model of speciation in island birds is the peripatric model. It emphasizes major genetic changes taking place in the founding of a new population by a small number of individuals. There is no direct evidence that would make it preferable to the standard allopatric model for islands.

## 1. INTRODUCTION

Speciation is a process of lineage splitting, culminating in the formation of two or more non-interbreeding populations or species from an original one. We observe the results, i.e. species, and attempt to infer the process from their genetic, morphological, ecological and behavioural characteristics. At best only parts of the process are observed, which is why there is no universal agreement on how species are formed.

The most widely favoured is the allopatric model of speciation. Studies of island bird taxa have made important contributions to the development of the model, beginning with observations made by Darwin and Wallace, and extending into this century with the work of Rensch (1933) and Stresemann (1936) and especially Mayr (1942) and Lack (1947). In this article we illustrate the main features of the allopatric model by applying it to the Darwin's Finches of the Galápagos Islands. This application forms the basis of a discussion of four general issues or problems raised by the model, which are not restricted to finches, or even to birds.

The first problem is whether reproductive isolation evolves entirely in allopatry, or whether it is initiated in allopatry and completed in sympatry. The second is related to the first: are differences that evolve in allopatry reinforced by a regime of divergent selection on the taxa in sympatry, and if so does the reinforcement arise from ecological pressures or from a degree of reproductive (genetic) incompatibility? Third, does interbreeding (i.e. hybridization) at the secondary contact phase and subsequently simply eliminate the differences that arose in isolation, or does it play a creative role in facilitating further divergence? Fourth, does genetic restriction and reorganization embodied in the Founder Principle make a significant contribution to the divergence that leads to the formation of a new species?

Darwin's Finches are the most suitable group of island birds for addressing these issues, so we pay special but not exclusive attention to them. Other islands or groups of islands, such as West Indies, New Guinea, Hawaiian and western Pacific islands, are rich areas of avian speciation, but they have suffered more losses from human influences than have the Galápagos (Steadman 1995). None of the species of Darwin's Finches are known to have been driven to extinction. The Hawaiian archipelago, by contrast, lost almost half its species of honeycreeper-finches before the first western people arrived, and several more since then (James & Olson 1991; Steadman 1995). Therefore whatever can be learned about the evolution of Darwin's Finches on these islands can serve as a model for understanding speciation of birds on islands in general, and perhaps elsewhere. They serve less well as a model of long-term evolution on islands because they do not display some of the patterns, such as gigantism and flightlessness, manifested in other taxa or on older, larger, and more isolated islands.

## 2. SPECIATION

The essence of the speciation problem is to account for the generation of two species from one. In the dendrogram in figure 1, for example, there are 10 divisions or splits of a lineage, giving rise to 11 species (three other species are missing from the figure). If an explanation is found for any one branching point then the diversification of the entire group can be explained by combining the principles involved in the speciation

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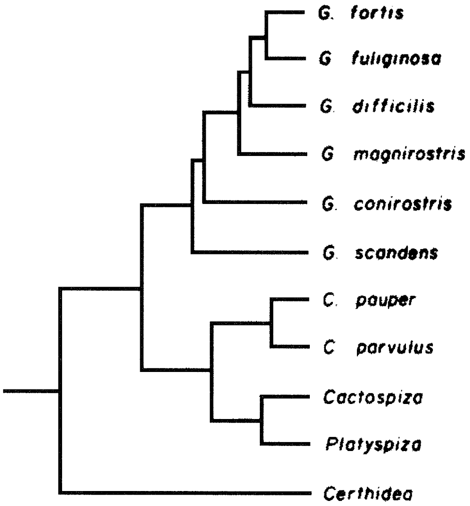

Figure 1. Phenogram of Darwin's Finches, constructed from allozyme data (based on Yang & Patton 1981). A recent reanalysis of the data by cladistic methods shows that statistical support for the three major groups is moderately strong, but is weak for all other features of the reconstruction (Stern & Grant 1996).

process, which should be common to all, with the historical and ecological details which will differ from one lineage split to another. The main task is to identify those principles. Figure 2 was prepared to capture the essence and to explore the possible variations (Grant 1981).

In step 1, the archipelago is colonized from continental South or Central America. A breeding population becomes established, and its size increases. In step 2 some individuals disperse to another island and establish a new breeding population. Some evolutionary change is expected to take place through selection and drift in the new environment. Step 2 may be repeated several times. A single breeding population has become converted into two or more allopatric, partly differentiated, populations. Step 3 is the contact through dispersal of members of two populations; the secondary sympatric phase. The choice of islands to illustrate these steps in figure 2 is arbitrary.

Step 3 is crucial to the speciation process. If evolutionary divergence in allopatry has been minor, the members of the two populations are likely to treat each other as potential mates, interbreeding will ensue (without fitness loss) and panmixia will result. No speciation will have occurred. On the other hand evolutionary divergence might have proceeded to the point where members of the two groups do not recognize each other as potential mates, and do not even attempt to interbreed. Or they might interbreed but gain no fitness as a result of the inviability or perhaps sterility of the offspring. If this happened then the process of speciation will have been completed, in allopatry. This was Stresemann's view. Lack (1947) pointed out a third possibility. Speciation may have been initiated in allopatry and completed in sympatry as a result of natural selection against interbreeding.

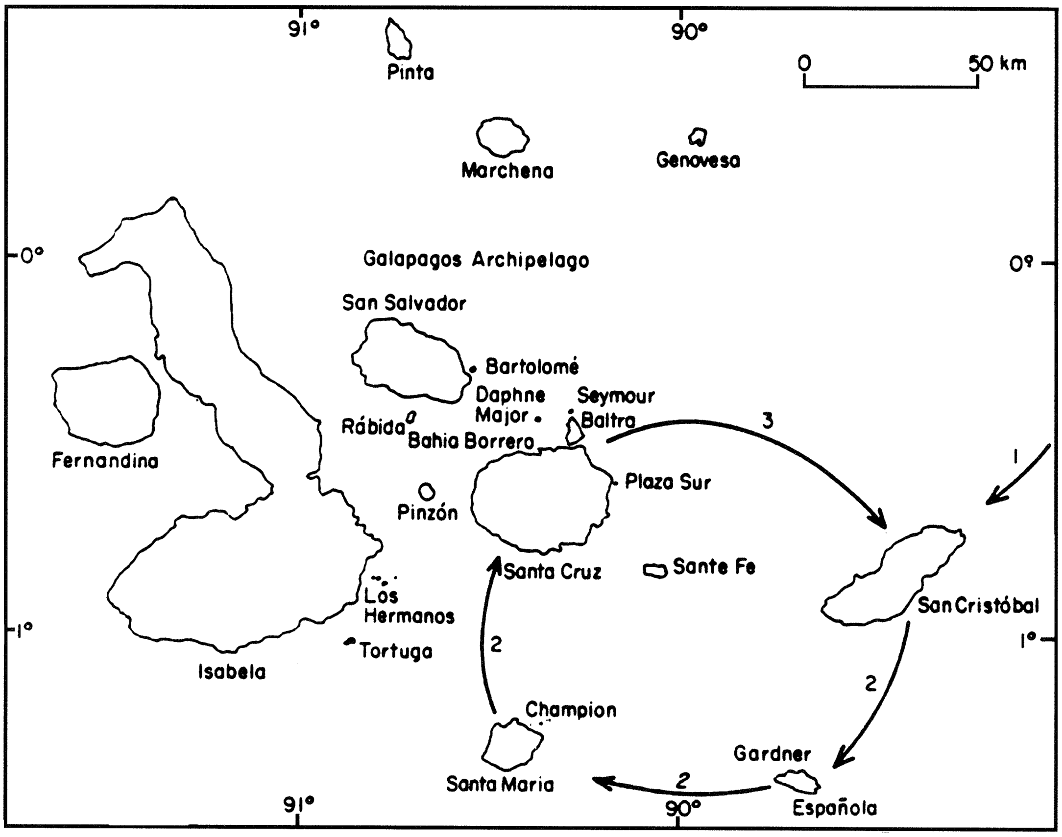

Figure 2. The speciation cycle applied to Darwin's Finches. Initially it comprises three steps: step 1, colonization of the archipelago; step 2, establishment of allopatric populations followed by; step 3, establishment of sympatry. Choice of the islands is arbitrary. Populations that are sympatric with little or no interbreeding are different species. Additional species are formed by evolution in a repetition of steps 2 and 3. From Grant (1981).

This would happen, he suggested, if fitness loss was marked but not so profound as complete inviability or infertility of the offspring produced by interbreeding. He reasoned that divergence in sympatry would be produced by selection reinforcing the initial differences, culminating in a cessation of interbreeding. This has been referred to as the partial allopatric variant of the standard model (Grant 1986). The reinforcement process has been recently modelled and shown to be capable of completing the evolution of pre-mating isolation (Liou & Price 1994).

## 3. REINFORCEMENT

The reinforcement hypothesis makes two testable predictions. First, if we could find a situation similar to that in step 2 just before step 3 we could artificially combine partly differentiated allopatric populations with the expectation of observing mixed courtship and breeding. Second, if we could find a situation similar to that modelled in the early stages of step 3 we should observe interbreeding (hybridization) occurring, with relatively poor performance of the offspring (hybrids).

The first prediction was tested, not with live birds, which would be unethical, but with specimens of dead birds (females) prepared in a courting posture. The test was performed in two stages. First, the sympatric and morphologically similar species Small Ground Finch (*Geospiza fuliginosa*) and Sharp-Beaked Ground Finch (*G. difficilis*) from the island of Pinta were each tested with a pair of female models: one conspecific the other heterospecific. Males of each of the responding species made a clear discrimination between the models, directing far more attention, including copulations, to the conspecific than to the heterospecific model (Ratcliffe & Grant 1983*a*). Second, allopatric populations of the two species were tested in the same way, simulating the immigration of a closely related species. In agreement with the prediction of reproductive 'confusion', neither *G. difficilis* on Genovesa or *G. fuliginosa* on Plaza discriminated between the local conspecific model and the invader (Ratcliffe & Grant 1983*b*). Lack's reinforcement hypothesis is supported by these results (Grant 1986) and others (Ratcliffe & Grant 1983*a*, *b*).

The second prediction has been tested more recently by the accumulation of breeding data from a long term study on the island of Daphne Major. Hybridization occurs at a low frequency between the Medium Ground Finch (*G. fortis*) and two others; the Cactus Finch (*G. scandens*), a resident species, and the Small Ground Finch (*G. fuliginosa*), an uncommon immigrant. The natural hybridization of *G. fortis* and *G. fuliginosa* is as close to step 3 of the speciation model as we have been able to observe anywhere in the archipelago. Contrary to expectation from the reinforcement hypothesis, hybrids are both viable and fertile to a degree similar to that of the offspring of conspecific matings (Grant & Grant 1992), at least under the conditions prevailing after an exceptional amount of rain fell in 1983 (Grant & Grant 1993). Hybridization leads to introgression (Grant & Grant 1992, 1994). Supporting data have been obtained on the island of Genovesa, where the Large Cactus Finch (*G. conirostris*) interbreeds rarely with the Sharp-Beaked Ground Finch (*G. difficilis*) and the Large Ground Finch (*G. magnirostris*) (Grant & Grant 1989). Thus all six species of Darwin's Ground Finches (genus *Geospiza*) are known to hybridize with at least one other congeneric species. Some intergeneric crosses are known among the tree finches and warbler finch as well (Grant 1986).

Two conclusions follow from these tests. First, speciation does not run its full course in allopatry; at least in some cases, and perhaps all, the potential for interbreeding at the secondary contact exists. Second, the partial allopatric variant of the model is appropriate for the investigated species but not always for the reason identified by Lack. The lack of a fitness loss through interbreeding on Daphne means that the conditions for natural selection against interbreeding do not always exist. Both on Daphne and on Genovesa there have been times when hybrids have survived well, and backcrossed to the parental species, and other times when they have not survived well for ecological reasons (Grant & Grant 1989, 1993). The hypothesis of reinforcement is not supported.

Lack changed his views about reinforcement, and concluded that ecological interactions at secondary contact are likely to have been primarily important in determining whether fusion or fission and coexistence would occur (Lack 1947). Our data are consistent with this alternative view. Thus divergence may have occurred under natural selection in step 3 of past speciation cycles, but it did so because the morphologically most similar individuals suffered greater effects from competition for food. Supporting evidence for this interpretation includes: (i) enhancement of beak size differences between species in sympatry; (ii) a positive correlation between beak size differences and dietary differences that is predicted from the distribution of seed sizes on each island; and (iii) the direct documentation of natural selection on genetically variable beak traits caused by a change in food supply (Grant 1986; Grant & Grant 1995*a*).

## 4. EVIDENCE FROM OTHER ISLANDS

Continental islands often support populations of birds that are morphologically different from mainland populations though clearly related to them. Populations on small satellite islands differ from those on nearby large oceanic islands in a similar way. They are treated as subspecies, occasionally species, and represent the early stage of speciation cycles (step 2). Divergence from presumed relatives is not random, but shows trends that can be interpreted as adaptations to the specific ecological conditions of the islands. For example the absence of ecological competitors has often been claimed as a key factor explaining a tendency for island birds to have large beaks (Grant 1965).

Step three of the speciation cycle on continental and satellite islands occurs when a second colonization takes place by members of the same ancestral species. The double invasion phenomenon has been inferred from several studies around the world of pairs, rarely triplets, of island species that resemble each other and only one mainland species (Mayr 1942). A feature of these island species is a pronounced ecological difference, often associated with a pronounced morphological difference (Grant 1968). The question of whether adaptation to the island environment permitted the establishment of a second, non-interbreeding, population, or whether competitive interactions were partly responsible for the divergence, is usually difficult to resolve (e.g. see Carrascal *et al.* 1992).

## 5. HYBRIDIZATION

Hybridization, the interbreeding of two species, could play a creative role in speciation in two ways: directly, simply by producing a new species; or indirectly, by providing genetic variation to each of the interbreeding species and thereby facilitating further evolutionary change in each.

The first possibility can be examined in the context of the allopatric model (figure 2) by noting a fourth possible outcome at step 3 of the model; the mixing of two, well differentiated, populations to form a new, hybrid, species, differing from all other allopatric populations. In other words fusion and speciation would occur instead of fission and speciation. If this happened it would be a manifestation of the creative role of hybridization in speciation. It is well known in plants, and usually involves polyploidy. Is it likely to happen in birds?

The possibility is very difficult to assess, given the allopatric status of the new species. Lack (1940) considered the highly variable Large Ground Finch on the island of Darwin (Culpepper) to have been formed in this way, by the mixing of *G. magnirostris* and *G. conirostris* to form *G. darwini*. He initially interpreted the Medium Ground Finch on Daphne in the same way. Mayr (1942, p. 270), despite recognizing that several species of different taxa show signs of being influenced by hybridization, could find no avian example of a clear hybrid origin of a new species. Recently *G. darwini* has been treated as a differentiated form of *G. magnirostris* (Grant 1986). We agree with Mayr that hybridization, by itself, is unlikely to produce a new species. There is no evidence of polyploidy in Darwin's Finches (Jo 1983).

On the other hand modern studies have confirmed the suspected but previously undemonstrated hybridization of Darwin's Finches. They have also shown that hybrids may be favoured by selection at times and disfavoured at others. Thus a population may be formed by the interbreeding of residents of one with immigrants of another, but is unlikely to remain a passive product of the interbreeding. Rather its characteristics will be moulded by natural selection to the local environment, with perhaps continuing input of genes from another species through hybridization. This leads to the intriguing second possibility that those genes could facilitate further evolutionary change by selection, perhaps along a new trajectory and culminating in the formation of a new species. New additive genetic variance introduced by hybridization (hybridizational variance) may be orders of magnitude greater than mutational variance (Grant & Grant 1994). Furthermore allometries can be altered by hybridization and backcrossing (Grant & Grant 1994). Thus hybridization could contribute to the speciation process, without being solely responsible for it, by enhancing genetic variation and relaxing genetic constraints on particular directions of evolutionary change.

## 6. IMPLICATIONS OF HYBRIDIZATION

Recent studies of introgressive hybridization have done more than point to a creative role in evolution while invalidating the reinforcement hypothesis applied to Darwin's Finches; they have cast doubt on previous attempts to use genetic data to reconstruct phylogenies (Avise 1989; Degnan 1993). Sympatric species may be genetically more similar than allopatric species pairs as a result of introgressive hybridization. In fact Yang & Patton (1981) found evidence of exactly this; at a locality on Santiago island and at another on Santa Cruz island *Geospiza fuliginosa* and *G. fortis* were more similar to each other in allozymes than either was to a conspecific elsewhere. The order of branching points may be incorrectly determined, and the accumulation of finch species may have occurred earlier than is shown in figure 1.

The scale of the problem in general for birds can be appreciated from two facts. First, almost one in ten species of birds is known to have hybridized at least once (Grant & Grant 1992). Admittedly hybridization with introgression is likely to be less common and widespread than hybridization without gene exchange. Second, the potential to hybridize remains for an extraordinarily long time after speciation in birds. Prager & Wilson (1975) calculated the length of the hybridization period to be 22 Ma on average, based on an analysis of albumin and transferrin immunological distances between 36 pairs of hybridizing bird taxa (more than half were different genera). Their maximum value was an estimated 50 Ma. This is truly remarkable, and put in perspective by noting that the most successful avian order, the Passeriformes (passerines), comprising more than half of the 9–10000 species of birds present today, have been in existence for little more than that (54 Ma; Boles 1995). A similarly long period of potential hybridization characterizes amphibia (Prager & Wilson 1975) and turtles (Bowen & Avise 1995), though not mammals (Prager & Wilson 1975).

An inference of the Prager and Wilson (1975) results is that prezygotic isolation arises much faster than postzygotic isolation, at least in birds and some other vertebrates, and that none of the Darwin's Finches have had time to evolve postzygotic isolation. Indeed no postzygotic isolation among Darwin's Finches is known. The scope for reinforcement is therefore restricted to those cases where little divergence has taken place over the long period before the evolution of post-zygotic incompatibilities. The evolution of prezygotic isolation may also take a long time, following a

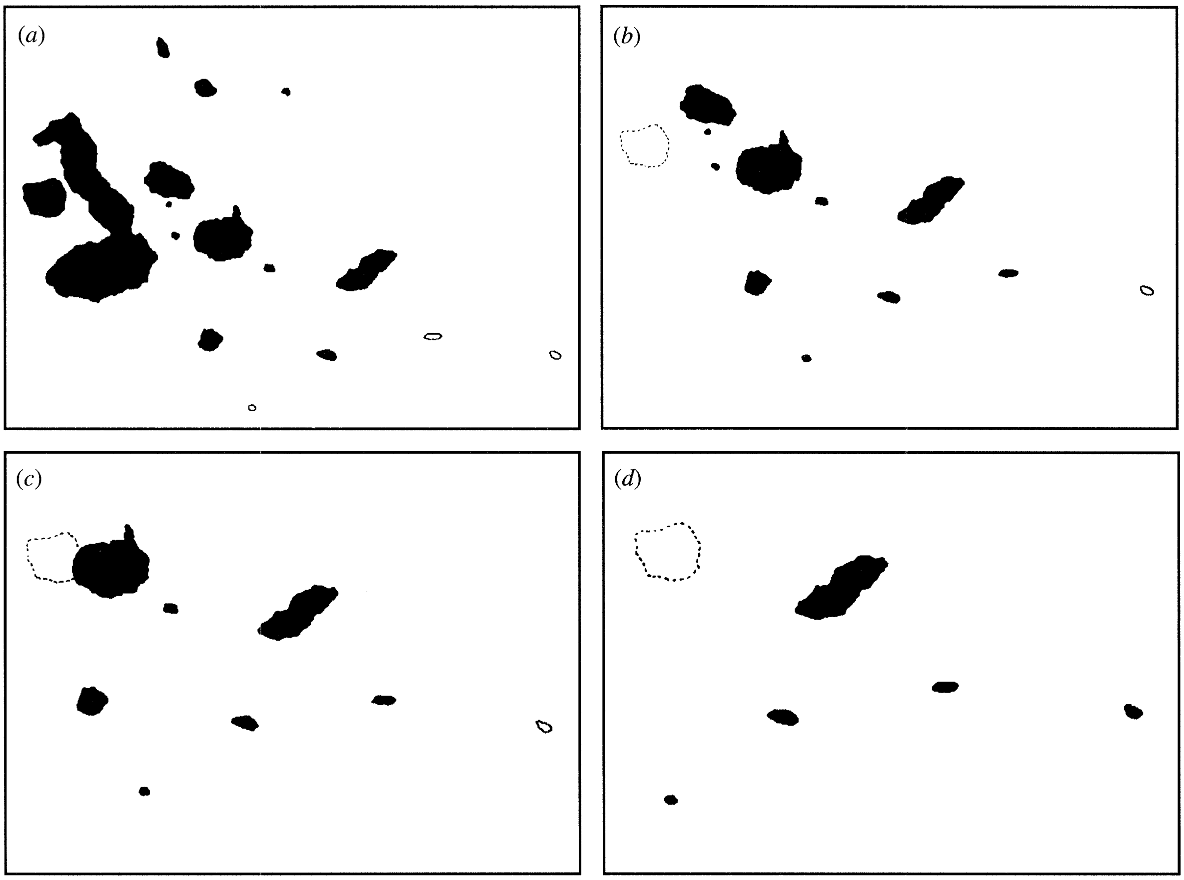

Figure 3. Geological history of the Galápagos archipelago over the last 3 Ma, since the time they were colonized by ancestral Darwin's Finches. (*a*) Present; (*b*) 1 Ma BP; (*c*) 2 Ma BP; (*d*) 3 Ma BP. The reconstruction is based on data in Christie *et al.* (1992), and assumes southeasterly plate movement of constant direction and speed over a fixed hotspot beneath modern Fernandina. The position of Fernandina is shown by a broken line. Submerged seamounts are shown in outline. Dates of submergence were calculated from current depths by a standard equation given in Kennett (1982, p. 147). The northern islands of Pinta, Marchena, Genovesa and two others not shown (Wolf and Darwin) were apparently formed from the Galápagos Spreading Centre trending irregularly east-west. Radiometric dating (White *et al.* 1993) suggests that Wolf is between one and 2 Ma old, whereas the rest are less than 1 Ma old.

period in which it occurs for non-genetic reasons, for example as a result of species-discriminatory mate choices that are formed through imprinting in early life on culturally inherited parental traits such as song (Grant & Grant, 1996).

The breeding of island birds elsewhere is not known well enough to permit confident generalizations about hybridization. The third species of *Zosterops* (White-eyes) to colonize Norfolk island hybridized with its predecessor (Gill 1970). Hybridization without fitness loss has been reported in *Nesospiza* buntings on Inaccessible Island in the Tristan da Cunha group (Ryan *et al.* 1994). Some degree of postzygotic isolation has evolved in *Ficedula albicollis* and *F. hypoleuca*, two species of flycatchers which hybridize on the Swedish island of Gotland. Apparently this has not led to reinforcement of preexisting differences in plumage, although the song sung by male *F. albicollis* may have diverged in sympatry (Alatalo *et al.* 1990). In accordance with Haldane's rule, female hybrids are sterile (Tegelström *et al.* 1990; Gelter *et al.* 1992). Mitochondrial DNA differences suggest the species shared a common ancestor 5 Ma BP (Tegelström & Gelter 1990). This puts an upper bound on the time to evolve partial sterility, at least in these two species. The whole of the radiations of Darwin's Finches ( ~ 3 Ma) and Hawaiian honeycreeper-finches (probably at least 50 species in ~ 4 Ma; Tarr & Fleischer 1995) occurred within this length of time.

## 7. FOUNDER EVENTS AND PERIPATRIC SPECIATION

Mayr (1992, and earlier) has written that speciation is likely to occur rapidly on islands through: (i) a loss of genetic variation in the founding of a new population by just a few individuals; (ii) the setting up of new epistatic balances in the early stages of population establishment when inbreeding is likely to be common and further genetic loss will occur; and (iii) selection on genes against altered genetic backgrounds.

This model of speciation, termed peripatric or founder speciation, was developed from the observation that peripheral (often insular) populations of a polytypic species tended to be the most distinct, and from the conviction that non-additive genetic factors were more important in evolutionary divergence than had been generally acknowledged (Mayr 1954, 1992).

The theory of peripatric speciation is difficult to test because the difference between it and the allopatric

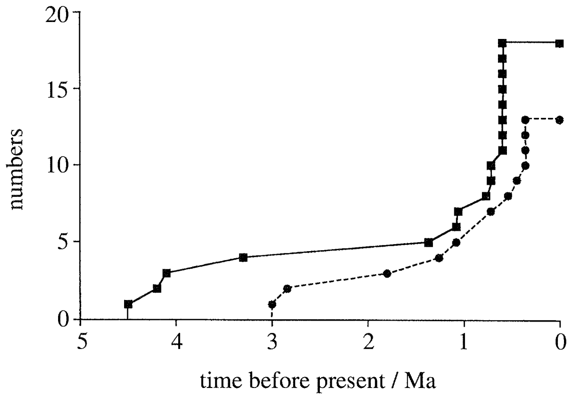

Figure 4. Accumulation of Darwin's Finch species in relation to the increase in number of Galápagos islands. Filled squares indicate cumulative number of islands; filled circles indicate cumulative number of species. Ages of the islands have been determined by a combination of methods: from sea floor spreading data and radiometric determination of the ages of rock samples from extant islands and submerged seamounts (see figure 3, and Christie *et al.* 1992; White *et al.* 1993). Ages of each of the species have been inferred from a molecular clock (Grant 1994) applied to their allozyme differences (see Yang & Patton 1981). Data in Polans (1983) were used for *Camarhynchus psittacula*, missing from the Yang & Patton analyses. *Cactospiza heliobates*, missing from both sets of analyses, is assumed to be as young as the youngest species on the basis of close morphological resemblance to *C. pallida*.

speciation we have articulated is one of genetic architecture (difficult to measure), epistasis and loss of recessive alleles being important in peripatric speciation and additive genetic variation being important in our version of allopatric speciation. In a sense it has been tested repeatedly, experimentally and unwittingly. Alien species have been introduced to islands around the world for over a century, usually in very small numbers. A few instances of rapid and substantial phenotypic change, indicative of incipient speciation, would be evidence in favour of peripatric speciation. None has been reported, although a systematic study of evolutionary change in the introduced populations has not yet been undertaken. The only direct study of a founder event from origin onwards provided evidence of non-random colonization, inbreeding and drift, but nothing that could be interpreted as reflecting a genetic reorganization (Grant & Grant 1995*b*).

The theory of genetic reorganization (founder effects) has been criticized on theoretical grounds (Lande 1980; Barton & Charlesworth 1984), and although it has its supporters it will remain conjectural until the genetic changes involved in speciation can actually be determined (Provine 1989).

Is the theory of founder effects necessary to account for speciation of birds on islands? It was developed because in Mayr's experience: (i) major evolutionary changes occur on islands that are not biotically or physically distinctive, yet; (ii) the majority of peripheral isolates show no evidence of major evolutionary change despite living in novel environments; and (iii) pronounced ecological shifts within widespread species are often not accompanied by phenotypic shifts (Mayr 1992). In other words evolutionary change does not always covary with ecological change. The lack of covariation undermines the claim that speciation can be explained solely in terms of selection pressures from the environment (exogenous factors). By default endogenous (genetic) factors take on special importance.

The reasoning may be flawed for three reasons. First, covariation may have been broken in the fairly recent past by the large human-induced changes in habitats and distributions of birds on both islands and continents (Steadman 1995). Second, the lack of covariation may have been over-emphasized. Observations that led Mayr to develop his theory were made in the era before ecological variables were measured. Evolutionary change may be interpretable in terms of current environmental factors when measurements of salient ecological and behavioural variables replace nonquantitative observations. Finally, covariation would not be expected if sexual selection had contributed to divergence in allopatry, as seems to have been the case in some avifaunas. The highly colourful and patterned *Tanysiptera* kingfishers on New Guinea and its satellite islands, which figured prominently in Mayr's (1954) development of ideas about founder effects, appear to be an example of divergence in allopatry under sexual selection.

In spite of this last objection, novel plumage traits in isolated populations offer the best evidence for a change in non-additive genetic variation during or shortly after a founder event. The new traits might be favoured by sexual selection. Nevertheless establishment of sympatry in the secondary contact phase of speciation (figure 2) would depend upon ecological divergence, in our view. An example is provided by the Hawaiian honeycreeper-finches. These display a diversity of (sexually selected) plumage patterns that may be under predominantly non-additive genetic control, and (naturally selected) bill sizes and shapes that are probably governed largely by additive genetic variation.

In conclusion, without rejecting peripatric speciation outright we see no reason why the standard allopatric model we have described cannot explain observed patterns of island differentiation and speciation, and why it is necessary to invoke founder events and genetic reorganizations. Similarly, sympatric (Grant & Grant 1989) and parapatric (Ryan *et al.* 1994) alternatives to the allopatric model appear to have at most limited applicability to the speciation of birds on islands.

## 8. THE TIMESCALE OF EVOLUTION

The starting point of the Darwin's Finch radiation was a splitting of the ancestral stock into a lineage leading to the modern Warbler Finch (*Certhidea olivacea*) and all of the rest (figure 1). This was dated by Yang & Patton (1981) to little more than 0.5 Ma BP, using Nei's method of equating genetic distance to time on the basis of clock-like behaviour of the substitution of neutral alleles. Thus Darwin's Finches are young, and their radiation was rapid. However recent work with other groups of birds suggests that the calibration of the clock was in error in this calculation, and that the period over which Darwin's Finches have diversified is much longer than originally thought. On the basis of the new information the first split occurred about 2.8 Ma BP (Grant 1994).

This new finding has an important implication. For as long as the radiation was thought to be confined to the last 0.5 Ma the geological history of the islands could be ignored (Grant 1986; Cox 1990). With this greater period, however, it cannot be ignored. At the time of arrival of the first finches, approximately 3 Ma BP, there were only five islands in existence (figure 3); San Cristóbal (possibly split into two or more at that time), Española and three others that are now submerged (see Christie *et al.* 1992). The initial colonization may have been influenced by climate, as a global cooling period began about 3 Ma BP (deMenocal 1995).

Figure 4 maps the finch species diversification onto the pattern of island diversification. Ignoring possible but unknown extinctions, the number of islands has apparently always exceeded the number of species. One can interpret the relation to mean that the increase in number of islands facilitated an increase in number of species through speciation. This gives a new twist to the old idea of the role of ecological opportunity in governing adaptive radiations (Lack 1947). For example, the slow initial diversification (figure 1) can be explained by the small number of islands. The scheme in figure 2 is therefore not strictly correct, and should be modified, although fortunately two of the islands arbitrarily chosen to illustrate the initial cycle of speciation happen to be ones in existence when the ancestral species arrived. The archipelago was not a fully formed ecological theatre, passively waiting for the arrival of the finch evolutionary play. The two developed together. The same applies to Hawaiian evolution (see Tarr & Fleischer 1995).

## 9. CONCLUSIONS

The allopatric model of speciation fits the facts of Darwin's Finch evolution on the Galápagos islands, and the evolution of other species of birds on islands elsewhere. Evolutionary change is initiated in allopatry and continues in sympatry, the driving force is directional natural selection arising from ecological factors, principally food factors, and a low level of introgressive hybridization without appreciable fitness loss occurs during and after the initial secondary contact for an unknown, but probably long, time. Thus species, perhaps for millions of years, are not completely reproductively isolated from each other, isolating mechanisms do not set up impregnable barriers to gene exchange and so the integrity of the species is not preserved by them.

Our proposal makes no allowance for several other factors or processes held to be important in the speciation of other groups (e.g. see Endler 1989). There is no explicit statement on the evolution of post-zygotic barriers to gene exchange through inviability or sterility factors, no provision for coadapted gene complexes and epistatic gene interactions being perturbed by interbreeding, and no provision for genetic reorganization occurring through founder-flush demographic cycles. We have invoked no founder effects or loss of genetic variation in colonization events. All could play a role in the speciation of birds on islands. None appear to be necessary.

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## *Discussion*

J. C. DEUTSCH (*Imperial College, Silwood Park, Ascot SL5 7PY, U.K.*). I did not understand the relation between the first three points of your talk: that females from sympatric species are more accurate in choosing males of their own species; that hybrids are not less fit than pure breds; and that environmental conditions select against hybrids. Could you explain how these points fit together?

P. R. GRANT. The experimental tests show that females of sympatric species discriminate between conspecific and heterospecific models. Outside the experimental setting females generally avoid heterospecific males. Occasionally a male will be seen to court a heterospecific female, and the usual outcome is that the female flies away. These observations, experimental and non-experimental, are consistent with our finding that hybridization is a rare event, affecting no more than one or two percent of breeding individuals. Nevertheless hybrids on Daphne Major island were no less fit than the pure breds after 1983 when an exceptionally severe El Niño event resulted in a long-lasting change in the composition of the vegetation and the dry season food supply of the finches. Why, then, should the finches court and mate assortively if interbreeding carries no fitness penalty? There are two complementary answers. First, mate choice is based on sexual imprinting. Early in life offspring learn conspecific features from their parents, and use those features (song and morphology) in choosing a mate. Very rarely the normal imprinting process is perturbed, individuals learn heterospecific features, and hybridize as a result. Second, hybrid fitnesses are not constant. For example, before 1983 hybrids formed by the interbreeding of *Geospiza fortis* and *G. fuliginosa* on Daphne Major did not survive long enough to breed. Thus species discrimination is maintained partly because sexual imprinting constrains mate choice, and partly because under some environmental conditions interbreeding individuals produce few or no recruits.