

by endemic mosquitoes in a human-modified landscape with relatively few native birds. Its original host remains unknown, but unlike many islands, New Zealand had endemic mosquitoes, which could have coevolved with viruses.

Another significant disease because of its pandemic potential is avian influenza. The normal hosts are waterfowl, shorebirds, and seabirds. Sampling for influenza antibodies in Australian seabirds shows variation between different species (wedge-tailed shearwaters *Puffinus pacificus* and black noddies *Anous minutus*) and local breeding islands, suggesting they may host local lineages of influenza.

THE FUTURE

Our understanding of the effects of introduced bird diseases on island avifauna has begun to lead to protective measures such as the removal of alien-host rock doves (*Columba livia*) in Galapagos and vector mosquitoes (*Culex quiquefasciatus*) on Midway Island in the Pacific, the implementation of quarantine systems of varying degrees of competence, the sterilization of boots in the Antarctic, and the institution of bans on importation of high-risk hosts. Despite these efforts, diseases such as Newcastle disease, West Nile, and avian influenza remain ever ready to make an appearance, facilitated by today's rapid forms of transportation and international trade.

The potential for emerging diseases from islands also continues and may even increase as ecotourism brings travelers onto ever more remote islands and then rapidly back to sophisticated medical facilities where their ailments can be diagnosed as something beyond "fever."

The study of bird diseases on islands remains one of the last frontiers for exploratory biology. It is likely to continue to provide unexpected insights into immunology, public health, community ecology, and conservation biology, as additional islands, their avifaunas, and their diseases are examined.

SEE ALSO THE FOLLOWING ARTICLES

Extinction / Honeycreepers, Hawaiian / Inbreeding / Seabirds

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BIRD RADIATIONS

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Bird radiations provide informative illustrations of ecological and evolutionary processes, including those that help to generate biodiversity as ancestral species radiate into multiple descendent species. Adaptive radiation involves initial phases of divergence among populations or incipient species, accompanied by or followed by the evolution of reproductive isolation. In this article, aspects of these two key processes—divergence and the evolution of reproductive isolation—are outlined and examined with specific reference to island bird radiations.

BIRD RADIATIONS ON ISLANDS: ECOLOGICAL AND EVOLUTIONARY INSIGHTS

Island habitats provide biologists valuable if not unique opportunities for the study of ecology, evolution, and animal behavior. Relative to continental habitats, islands tend to express low biological diversity, high abundance of constituent species, streamlined food webs, and environmental fluctuations that can be both marked and unpredictable. The simplified and dynamic profile of island biology has facilitated the study of a wealth of biological patterns and processes, with results gleaned from island studies often extrapolated to more complex and empirically less accessible habitats such as tropical rain forests.

Birds have taken center stage in many field studies of island ecology and evolution, following a tradition set by David Lack in the mid-twentieth century. Bird radiations have been numerous and varied, featuring outcomes such as flightlessness and robust variations in plumage, size, and beak form and function (Table 1). This entry provides a brief overview of some ecological and evolutionary processes that drive island bird radiations and then discusses recent findings from the authors' own studies of two island bird systems: introduced island populations of African weaverbirds, and Darwin's finches of the Galápagos Islands.

TABLE 1
Representative Examples of Bird Radiations on Islands

Bird Assemblage	Islands	Distinctive Features of the Radiation
Vangas (15–22 species) and Malagasy songbirds (9+ species)	Madagascar	The vangas' common ancestor presumably arrived on Madagascar about 25 million years ago and subsequently radiated into a group unusually diverse in both plumage and bill morphology. Another diverse group, Malagasy songbirds (previously placed into three different families of bulbuls, babblers, and warblers), represent a radiation from a single colonizing species 9–17 million years ago. At 587,000 km ² , Madagascar is the smallest single island in the world with a prominent bird radiation.
Moas (14 species)	New Zealand	Beginning about 20 million years ago, these herbivorous and flightless birds evolved in the absence of predators, radiating mostly within the last 10 million years into a variety of body forms and sizes.
Darwin's finches (14–15 species)	Galápagos and Cocos islands	A grassquit or warbler-like ancestral species colonized the Galápagos about 2–3 million years ago, followed by a pattern of island-hopping and speciation; descendant species eventually redistributed themselves throughout the islands without interbreeding. Bill morphology diverged by adaptation to available seed types, song subsequently diverged as a by-product; female preference for both traits is thought to have promoted reproductive isolation upon secondary contact.
<i>Myiarchus</i> flycatchers (five species)	West Indies	A single immigration to Jamaica from Central America about 4 million years ago, led to subsequent island-hopping and divergence. Several island-specific forms are designated as subspecies; thus this is apparently a radiation in process.
Honeycreepers (~52 species)	Hawaiian Islands	Beginning about 4–5 million years ago, the descendants of a single colonizing finch species radiated explosively; highly diverse feeding methods and bill types were facilitated by a broad range of vacant feeding niches.
Golden whistler <i>Pachycephala pectoralis</i> (66 forms, perhaps can be grouped into 5 species)	Northern Melanesia and New Guinea	Called the world's "greatest speciator" by Mayr and Diamond (2001), this bird has diverged greatly in color patterns, but species boundaries are difficult to determine. Some forms arose by divergence but others through hybridization (mixing) of existing forms.
Chaffinches <i>Fringilla coelebs</i> (four forms, designated as subspecies)	North Atlantic islands	DNA evidence has indicated the history of chaffinch expansion from an ancestral stock that ranges across Europe and Africa, to several nearby island groups: a Portuguese chaffinch population colonized the Azores, birds from the Azores colonized Madeira, and birds from Madeira then colonized the Canary Islands twice.

Island Ecology

COMPETITION AND CHARACTER DISPLACEMENT

Any given habitat supports a diversity of species. Species that share habitats are thought to partition limited sets of resources such as space and nutrients. Shorebirds, for instance, have evolved to forage in distinct shoreline zones. Moreover, resource partitioning appears to be adaptive; sandpipers and plovers, to illustrate, are adept in extracting distinct food sources at particular depths within the sand or mud, by means of distinct bill lengths and shapes. Adaptive partitioning of resources among present-day species implies two historical processes: competition for limited resources, followed by selection favoring the occupation of divergent niches ("character displacement"). These processes are thought to be highly generalized, explaining, for example, how tropical rainforests can support a rich biota. However, these processes have proven notoriously difficult to study in field environments.

A clear demonstration of competition leading to character displacement has been reported by Peter and Rosemary Grant, who have been conducting field studies on Galápagos finches for over three decades. During an initial decade of study, beginning in 1973, the small central island of Daphne Major was found to support a large breeding population of the medium ground finch *Geospiza fortis*. This population featured birds of a wide range of beak sizes feeding on a diverse array of seed types, including the relatively hard seeds of caltrop *Tribulus cistoides*. Observations of feeding finches revealed that only the largest-beaked *G. fortis* were able to crack *Tribulus* seeds, a capability that served these large-beaked birds well during a severe drought in 1977. With exclusive access to this food resource, large-beaked *G. fortis* were able to survive and proliferate. In 1982, however, a breeding population of the large ground finch (*Geospiza magnirostris*) began to take root on Daphne, building slowly and peaking at about

350 individuals in 2003. *G. magnirostris* also feeds on the seeds of *Tribulus*, and thus introduced a competitive threat to large-beaked *G. fortis*. The effects of interspecies competition were realized during an intense drought in 2003, during which time the population of *G. fortis* crashed as a result of widespread starvation. Subsequent analysis revealed that large-beaked *G. fortis* had suffered disproportionately, presumably because of the depletion of the favored *Tribulus* seed resource by *G. magnirostris*. Smaller-beaked *G. fortis* survived and bred in disproportionate numbers, thus leading to an evolutionary reduction in *G. fortis* beak size in the next generation. The character of beak size had thus been displaced through competition from another species, through selection favoring those individuals that could avoid direct interspecies competition.

ISLAND BIOGEOGRAPHY

Given evidence of resource partitioning through competition and displacement, it follows that habitats with more ecological niches might support relatively greater levels of species biodiversity. This idea has received particular attention in the theory of island biogeography, which focuses on “rules” that might govern the diversity and evolution of species on terrestrial islands. A first rule is that large islands are expected to support more species than small islands, because of a greater abundance of ecological niches, resulting not only from their larger areas but also from broader elevational gradients. A tenfold increase in the size of an island is expected to lead to an approximate doubling of species number. A second rule of island biogeography is that more remote islands should be relatively depauperate, because chance immigrations of new species are less likely when mainland source populations are more distant. Larger and more isolated islands are also expected to support greater numbers of endemic species, because of increased opportunities for genetic isolation. Island species diversity can of course be influenced by other factors including the presence or absence of predators, the geological age of islands, the extent and diversity of appropriate habitats, and factors that can affect animal movement such as storm paths and migration routes. In modern times, humans have also imposed profound impacts on island species diversity through activities such as hunting, habitat conversion, and species introductions.

Birds on the islands of the Indian Ocean well illustrate some of the principles of island biogeography, particularly those related to endemism. Of fourteen islands, endemic species occur in much greater frequency on the larger islands. The two smallest islands (< 100 km² area)

support no endemics, whereas the three largest islands (> 1000 km²) support over a dozen each. A parallel pattern is observed across the four inhabited Comoro Islands. The largest of these islands, Grande Comore, supports 14 endemic species, whereas the other three islands support only two or three endemics each. The Comoro Islands also highlight the importance of elevation to bird diversity; all of the Grande Comore endemics can be found on its Mount Karthala, the only mountain of the archipelago. The Indian Ocean Islands also illustrate a relationship, albeit more subtle, between endemic species and degrees of island isolation. Very small and distant islands have no endemics at all, as predicted given that they are only seldom visited and that any occasional founding population is likely to go extinct. Of islands with at least one endemic species, the more remote ones tend to have higher proportions of endemics. For instance, Rodrigues, Mauritius, and Réunion make up the Mascarenes, the most remote archipelago in the Indian Ocean. Not surprisingly, none of the birds native to these islands are found anywhere else. The small, isolated island of Rodrigues illustrates both predictions of low total species and a high proportion of endemism. Before it was inhabited by humans, 13 landbird species lived on the island, 12 of which were endemic. Today there are only two native landbird species on the island, both of which are endemic (the Rodrigues fody and the Rodrigues warbler). The sharp decline in species on Rodrigues highlights the often overwhelming influence of human impacts, which usually affect species diversity to at least as great a degree as island biogeographic processes and thus interfere with our ability to detect those processes. The Indian Ocean islands are unusual in that anthropogenic extinctions and introductions apparently have not yet obliterated the effects of island size and distance.

Evolution on Islands

POPULATION DIVERGENCE

Populations that colonize island habitats can undergo rapid evolutionary change, through any number of evolutionary mechanisms. Colonizing populations are small (normally comprising a small fraction of individuals from source populations) and thus normally experience severe population bottlenecks, with subsequent trajectories of evolution altered by founder effects. Founder effects may be sustained in “island hopping” scenarios, because of multiple sequential bottlenecks. Small population sizes also amplify the effects of genetic drift, which can theoretically result in the elimination or the fixation of genetic traits. Evolutionary change may also be facili-

tated by the fact that island habitats often differ substantially from mainland habitats in resource structure and competition regimes. The genetic profiles of different populations can diverge even as they adapt to similar environmental challenges, because evolutionary changes in phenotypes can be achieved through distinct, parallel genetic modifications.

A well-known, comprehensive illustration of adaptive divergence is found again in the research of the Grants and colleagues. Comparative and phylogenetic analysis of Galápagos finches and sister taxa suggests that the common ancestor of Darwin's finches was relatively small-bodied and small-beaked, akin to present-day warbler finches. The radiation of Darwin's finches toward mostly larger-beaked forms reflects a general trend in island radiations toward larger beak sizes, which may be powered both by "release" from competition in low-diversity environments and by a relative abundance of hard foods in ocean island habitats. The microevolutionary process of adaptation through natural selection has been documented several times for the Daphne finch populations. During the severe drought of 1977 (mentioned previously in the discussion of competition and character displacement), large-beaked members of the *Geospiza fortis* population held a relative survival advantage in being able to crack *Tribulus* seeds, which were available in quantity at that time. The softer, smaller seeds on which smaller-beaked *G. fortis* relied had become depleted, both because of a lack of rain and new seed growth and because of high demand for seeds given the relatively large *G. fortis* population resident on Daphne at the time. As the *G. fortis* population crashed, large-beaked *G. fortis* thus survived to breed in greater numbers, and the subsequent generation exhibited larger beaks than their parental generation.

REPRODUCTIVE ISOLATION

Divergence is a prelude to radiation. In the opinion of many biologists, the currency of radiation—the generation of new species—is achieved only when divergence causes populations to become reproductively isolated from each other. Consider an ancestral population that colonizes multiple island habitats. If offshoot populations remain geographically isolated, they will accumulate, via divergent trajectories of drift or selection, differences in genetic and phenotypic traits. On secondary contact, insufficient reproductive isolation among offshoot populations would result in cross-breeding and reunification of gene pools, thus obstructing speciation. Alternatively, limited cross-breeding success would prevent mixing of

gene pools and thus foster continued interpopulation divergence.

In many groups of birds, reproductive isolation is driven in large measure by the divergence of mating signals and mate recognition systems. As mating signals diverge among populations, individuals are less likely to mate erroneously with members of other populations. Hybrid offspring, if viable, may suffer disadvantages in survival and reproduction, thus depressing the fitness of the hybrid's parents. Selection is thus thought to favor individuals that breed within-population, a pressure that in turn favors the divergence of mating signals. In a recent review of this literature, Trevor Price finds that island bird populations show unusually wide divergence from both ancestral and sister species in signals used in mate and species recognition, including color patterns, feather ornaments, and vocal structure.

Reproductive isolation of diverging island birds has been documented by Peter Ryan and colleagues for *Neospiza* buntings of the Tristan da Cunha archipelago. Two species of bunting, *Neospiza acunhae* and *N. wilkinsi*, are recognized on two islands, Nightingale and Inaccessible. On Inaccessible Island, the two species interbreed regularly, as indicated by an abundance of hybrids within a specific habitat (coastal tussock grass) favored by both species. On Nightingale Island, by contrast, reproductive isolation appears to be complete, with the two species forms showing highly distinctive body and beak forms and habitat preferences. Genetic analyses suggest that the diversity of subspecies in this group of birds has emerged through parallel trajectories of within-island interpopulation divergence, with reproductive isolation building up over time within each island, but not yet having reached completion on Inaccessible Island. Divergence among these species appears to have been facilitated not only by habitat segregation but also by the evolutionary divergence of mating signals.

FOCUS EXAMPLE: EVOLUTION OF VILLAGE WEAVERBIRDS ON ISLANDS

The village weaverbird *Ploceus cucullatus*, a species that is common across subsaharan Africa, has been introduced to a number of different islands worldwide (Fig. 1). In the 1700s village weaverbirds were introduced from West Africa to the Caribbean island of Hispaniola (present-day Dominican Republic and Haiti). In the 1880s weaverbirds from South Africa were introduced to Mauritius and Réunion, two islands in the Indian Ocean. In the 1980s the village weaverbird also became established on the Caribbean island of Martinique. The Cape Verde and

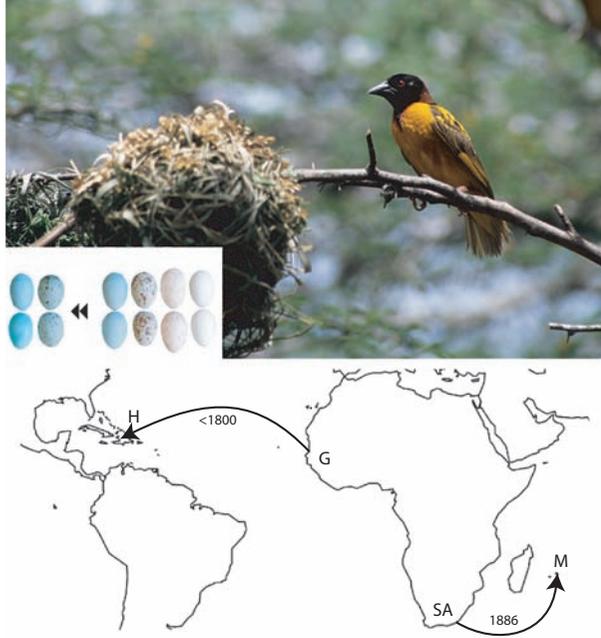


FIGURE 1 Egg color as an example of trait divergence on islands. The village weaver (*Ploceus cucullatus*) has been introduced from two African populations (G = The Gambia, SA = South Africa), to two islands (H = Hispaniola, M = Mauritius). Egg color has evolved in this species in both introduced populations. Variation in egg color and spotting between individuals has decreased, and variation within an individual's eggs has increased. Shown are an example of the range of egg colors in The Gambia (to the right of the paired arrows) and the reduced variation on Hispaniola over 200 years since introduction (to the left of the paired arrows). The pair of eggs in each column are from the same nest. Evolutionary theory predicts this divergence because of the presence of parasitic cuckoos in Africa but not on the islands (see text).

São Tomé Islands, off the coast of Africa, also appear to support small populations.

Evidence suggests that recently established island populations of village weaverbirds are undergoing rapid divergence from their mainland ancestral counterparts. One major axis of divergence hinges upon interactions between weaverbirds and the diederik cuckoo *Chrysococcyx caprius*. Across the African continent, diederik cuckoos lay eggs in the nests of numerous “host” species, including the village weaverbird. Cuckoo chicks normally expel host eggs and nestlings, and unwitting host parents rear parasite chicks until they achieve independence. Given the obvious detriments of brood parasitism, it is not surprising that antiparasite adaptations are common in host species. One such adaptation in village weavers is their ability to identify and eject parasite eggs from their nests, based largely on the visual cues of egg color and spotting. Diederik cuckoos, in response, have evolved eggs that mimic weaver eggs. As a coevolutionary response, weavers

have evolved unusually high individual distinctiveness of egg color and spotting, by means of an increased consistency of eggs within clutches, and by means of diverse color patterns among females in a given population. These counteradaptations ensure that cuckoo eggs rarely present a perfect match to a host's eggs, thus helping the weaver to detect and evade the fraud.

In at least two weaver island populations, Mauritius and Hispaniola, there are no diederik cuckoos nor any other brood parasite that mimics weaver eggs. Thus the ancestral traits—wide population variation of egg spotting patterns, individual consistency of egg spotting patterns, and refined egg discrimination abilities—presumably no longer retain their original function. Traits that lose their original functions and attain no new functions are expected to decay through evolution, especially if there is some cost to their maintenance. After one hundred years in the absence of the cuckoo on Mauritius, and after more than two hundred years on Hispaniola, weavers have lost some of their egg spotting, have showed reduced within-bird consistency of egg color and spotting, and express comparatively reduced variation among individuals. As a result of these changes the efficiency of egg rejection has declined as well. Notably, these changes have been more pronounced on Hispaniola, where the weavers had about twice as much time to evolve in the absence of the cuckoo as on Mauritius. Thus in only about 75 and 150 generations, two island populations diverged from their respective source populations.

Other differences have arisen between the island and mainland populations. Egg color of village weavers on the islands of Mauritius and Hispaniola, for instance, are converging on a shade of medium blue-green that is roughly what would be expected if eggshell pigment were to evolve to optimally protect embryos from solar radiation, and ultraviolet (UV) rays in particular. This convergence suggests that in Africa egg colors tend to be determined mostly by the importance of avoiding cuckoo parasitism, whereas in the absence of the cuckoo the egg colors are determined by a weaker source of selection, possibly avoidance of damage from solar radiation. Some divergent behavioral traits might be learned or innovated rather than having evolved. For instance, weavers nest higher in trees on Mauritius than they do in South Africa, which makes sense because hawks are a dangerous predator of nests in South Africa but not on Mauritius. Also, weavers depend on rainfall and the proximity of water in order to breed in Africa, but on Hispaniola they were found to breed in a remarkably arid region, with the lack of nearby water mitigated by

the presence of a common juicy cactus fruit (“pitaya,” *Stenocereus*).

Further insights into the evolutionary divergence of island populations are being gleaned from genetic analyses. In village weaverbirds, DNA has been found to be more variable in a continental African population than in a similarly sized region of Hispaniola. More specifically, DNA sequences from weaver mitochondria, which are transmitted from mother to offspring, are identical in all Hispaniolan birds sampled, whereas their ancestral population in The Gambia shows a great deal of variation. This result suggests the action of a founder effect on Hispaniola, which might be partly responsible for some of the evolutionary changes observed in egg features, most plausibly the decrease in egg color and spotting pattern variation. On the other hand, variation in nuclear genes, which are inherited by offspring through both the mother and father, have declined to a lesser extent following introduction. This indicates that female-inherited mitochondrial DNA has experienced a stronger or more persistent founder effect than biparental nuclear DNA. The contrast here might be explained by genetic drift or, alternatively, might indicate genetic peculiarities of the species introduction. Given that only males sing and have bright plumage, it is likely that many more males than females were brought to Hispaniola. If so, then perhaps only a few forms of weaver mitochondrial genes were retained across generations, whereas the large number of males ensured that a greater variation in nuclear DNA were maintained in the introduced Hispaniolan population. In summary, these weaver studies illustrate how species introductions can drive ecological and genetic changes that underlie divergence of populations, the raw material for adaptive radiation.

FOCUS EXAMPLE: EVOLUTION OF REPRODUCTIVE ISOLATION IN GALÁPAGOS FINCHES

Reproductive isolation and speciation in Galápagos finches have been facilitated by a diverse array of factors. The dispersed geography of the Galápagos archipelago, which contains some isolated peripheral islands, has caused cross-island immigration events to be relatively rare. Population sizes of these birds tend to be small, and population characteristics are thus subject to unusually rapid change via genetic drift or natural selection. A relative paucity of other terrestrial bird species has allowed Darwin’s finches to occupy a broad range of ecological niches. Despite the plethora of evolutionary pressures

driving populations apart, however, speciation in this clade remains a fairly rare occurrence, as can be observed in the propensity for diverging populations to undergo fusion via hybridization.

The regular occurrence and viability of hybrids indicates that species barriers in this group of birds are normally maintained through pre-mating rather than post-mating barriers. The question of whether populations in secondary contact will fuse or split thus depends largely on the behavioral processes by which Darwin’s finches choose their mates. As in many other songbird groups, male Darwin’s finches compete for access to females, who in turn choose mates. Towards this end, females attend to mating cues or signals expressed by males, in part to assess the potential quality of male partners as parents for their offspring. Such abilities result from a process of sexual selection. Females are also presumably under selection to be able to identify males that are of their own population of species, given that hybrid offspring production might be disadvantageous.

A primary cue by which females might recognize preferred mates is the size and shape of the beak. Studies on the responses of territorial males to taxidermic mounts provide indirect support for this idea. Females also appear to assess male identity and quality by attending to male vocal mating signals, or songs, which have been shown to vary across species and populations. Territorial male finches have been shown to respond more aggressively to playback of songs of their own species, population, and locality.

Recent research on vocal mechanics and performance in Darwin’s finches and other songbirds indicates a relationship between song structure and beak morphology. The beak and upper vocal tract of songbirds serve as a resonance chamber for sounds produced at the syrinx (the sound-producing organ of birds). As birds modify source frequencies, they often conduct parallel modifications of vocal tract structure, presumably in order to retain the resonance function across a wide range of frequencies. These modifications include (but are not limited to) changes in beak gape. For example, when birds produce high-frequency notes, they will often flare their beaks, thus reducing the volume of the vocal tract and maintaining an effective resonance function for the vocal tract. With respect to variation in beak morphology, it is thought that birds with large beaks should face relatively severe limitations in being able to rapidly adjust beak gape, whereas birds with small beaks should face fewer such limitations. This expectation is based on a predicted trade-off between bite force production



FIGURE 2 Evidence of assortative mating by beak morph in a population of Darwin's finches. The population of medium ground finches (*Geospiza fortis*) at El Garrapatero, Santa Cruz Island, shows distinctive small- and large-beaked morphs, with few birds of intermediate beak size. Breeding season observations reveal that females generally choose as mates males of similar beak size. The panels show representative pairs of breeding finches matched for being small-beaked (A) and large-beaked (B).

and the velocity by which birds can open and close their beaks while singing. The vocal tract constraint hypothesis posits that song structure should evolve as an incidental byproduct of beak evolution. These predictions have been borne out to some extent in field studies of Darwin's finches.

Correlations between vocal signals and visual cues would appear to provide a measure of redundancy for females attempting to assess male identity. This redundancy could potentially facilitate the process of reproductive isolation, by providing females with redundant information they could use to make "correct" mating decisions. This possibility has been raised in a recent study of *G. fortis* at El Garrapatero on Santa Cruz Island. This population features birds of either large beaks or small beaks, with few birds of intermediate beak size. These beak morphs produce distinctive songs, in a manner consistent with a vocal tract constraint hypothesis. Females of this population thus can rely on both visual cues and vocal signals when selecting mates. Indeed, females have been found to choose mates with similar beak sizes to their own (assortative mating, Fig. 2). Persistence of strong assortative mating in the absence of gene flow would presumably lead to further genetic divergence, further song divergence, and strengthened barriers to pre-mating isolation.

SEE ALSO THE FOLLOWING ARTICLES

Convergence / Ecological Release / Flightlessness / Fossil Birds / Founder Effects / Galápagos Finches / Island Biogeography, Theory of / Population Genetics, Island Models in

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BORNEO

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Straddling the equator between 7° N and ~4° S at the southeasternmost extremity of the Eurasian continental crust, Borneo, at ~740,000 km², is the third largest island after Greenland and New Guinea. Early explorers in the Indo-Malaysian archipelago encountered a Borneo that was cloaked in dense rain forests from coast to coast and inhabited by headhunting tribes. The original forests of Borneo have been reduced to about half their former extent but still hold an exceptionally rich biota teeming with endemics. Borneo's forests rank among the most diverse of the world's rain forests, and, as recently as 2005,