Sci. **75**, 259 (1988)] commented that "The relationship of these late granitoids to the collision process is obscure, and hitherto their ages and compositional variations have not accorded with those predicted by various plate models." B. W. Chappell and W. E. Stephens (*ibid.*, p.71), comparing granites of similar (Late Caledonian) age in Scotland and southeastern Australia with the Mesozoic continental margin batholiths of western North America, concluded: "The Paleozoic granites show little evidence of such a direct relationship to subduction." See also A. N. Halliday and W. E. Stephens, *Phys. Earth Planet. Inter.* **35**, 89 (1984); M. Owen and D. Wyborn, *Austral. Bur. Min. Res. Bull. No. 204* (1979).

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39. Evidence for many of the inferred plume heads is from [*5, 6, 13, 14, 20, 28, 46*], R. A. Duncan [*J. Geophys. Res.* **89**, 9980 (1984)], and N. H. Sleep [*J. Geophys. Res.* **95**, 21983 (1990)]. We infer that magmatism ~124 Ma in the White Mountains and Monteregian Hills resulted from the plume head phase of this hot spot. Tracks for Discovery-Bouvet-Meteor are presented by R. A. Duncan; White and McKenzie (*46*) link basalts in the Cape Basin to Bouvet, and we infer that initiation of this plume family resulted in the extended period of kimberlite eruption in southern Africa that began about 128 Ma [see also S. T. Crough, W. J. Morgan, R. B. Hargraves, *Earth Planet. Sci. Lett.* **50**, 260 (1983)]. Data for Eastern Australia are summarized by R. A. Duncan and I. McDougall [in *Intraplate Volcanism in Eastern Australia and New Zealand*, R. W. Johnson, Ed. (Cambridge Univ. Press, Cambridge, 1989), pp. 43–54]; three and possibly four lines of volcanic complexes in eastern Australia and the adjacent Tasman Sea started at 36 Ma, with the earliest volcanism centrally located with respect to an oval-shaped topographic uplift that extends across much of central Queensland and east to the offshore Queensland Plateau. Data in support of a possible Raton plume are given by Suppe *et al.* (*35*) or are mentioned in the text.
40. The simple repeat time (T_R) is calculated from the relationship $T_R = S/NA$, where S is the area of the continents (1.9×10^8 km^2), N is the number of plumes per unit time, and A is the cross-sectional area of the plume head after near-surface spreading. This estimate is used because it is more readily compared with the observed episodicity in the geochronologic record of the continents. An alternate method is to use a probability calculation of the time required for plumes to affect a specified percentage of the surface area; the definition of T_R corresponds to the time for 63% of the surface to be affected.
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43. For plume tails, the volume flux (V) = $B/\rho\alpha\Delta T$, where B = differential mass flux [termed "buoyancy flux" by Sleep (*37*)] = 54.9×10^3 kg/s^{-1} (*37*); heat flux (Q) = $\rho C\Delta T$. The factor of 2 variation in the estimates of Q for plume heads arises from uncertainty in estimates of the amount of entrainment; Q is calculated for source per total ratios of 0.25 and 0.5. $\rho = 3300$ kg/m^{-3}; $\alpha = 3 \times 10^{-5}$ °C^{-1}; $C = 1.25 \times 10^3$ J/kg^{-1}/°C^{-1}. Increasing α as a function of decreasing pressure (*16*) will have the effect of increasing the source per total ratio.
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Hybridization of Bird Species

Peter R. Grant and B. Rosemary Grant

Hybridization, the interbreeding of species, provides favorable conditions for major and rapid evolution to occur. In birds it is widespread. Approximately one in ten species is known to hybridize, and the true global incidence is likely to be much higher. A longitudinal study of Darwin's finch populations on a Galápagos island shows that hybrids exhibit higher fitness than the parental species over several years. Hybrids may be at an occasional disadvantage for ecological rather than genetic reasons in this climatically fluctuating environment. Hybridization presents challenges to the reconstruction of phylogenies, formulation of biological species concepts and definitions, and the practice of biological conservation.

Species of sexually reproducing organisms are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (*1*). Periodically attempts have been made to improve on this definition by dealing inter alia with the awkward fact that for some populations the criterion of demarcation is not absolute (*2–5*). Some populations occasionally interbreed, and then the question becomes one of determining the fates of the offspring (*1, 6*). Therefore, hybridization, which strictly is the interbreeding of species, is of pivotal importance in two respects: in framing ideas about the nature of taxonomic judgments to be made about particular populations (*7*) and more generally for understanding biological processes of evolution including speciation (*1, 2, 8*).

Traditional approaches to the study of hybridization have included the crossing of lines in the laboratory or greenhouse for genetical analysis, and the estimation of frequencies of phenotypic or genotypic classes in nature, their mating pattern, and their reproductive success. By themselves each is incomplete. In this article, we describe the desired but rarely achieved direct study of hybridization in nature through pedigree analysis. The study populations are birds. We present new information on the consequences of hybridization in populations of Darwin's finches over several generations.

The Broad Patterns

Mayr and Short (*9*) estimated that approximately 10% of 516 nonmarine species of birds regularly hybridize. Meise (*10*) made a broader survey and concluded that 2% of all recent bird species hybridize regularly, and an additional 3% hybridize occasionally. A more definitive estimate can now be made. In the last 2 years the total number of

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species throughout the world has been determined, ordered, and cataloged (*11*) and, separately, a list of the world total number of species known to have hybridized in nature has been compiled (*12*). No other class of organisms of comparable size is known so comprehensively.

As many as 895 species of birds are known to have bred in nature with another species and produced hybrid offspring, out of a world total of 9672 species (Table 1). This amounts to 9.2%, or roughly one out of every ten species.

The incidence of hybridization varies geographically to some extent; it appears to be more frequent in the temperate zone than in the tropics (*10*), despite a larger number of species occurring in the tropics. This may simply reflect geographically unequal knowledge of birds in general. The incidence varies ecologically to some extent, being more frequent among terrestrial birds than among sea birds. Much more pronounced is variation among the orders of birds. Ducks and geese (Anseriformes) show the greatest propensity to hybridize, with an incidence approaching one out of every two species. Others with high incidences include grouse and partridges (Galliformes), woodpeckers (Piciformes), hummingbirds (Trochiliformes), and various hawks and herons (Ciconiiformes). In contrast hybridization has not been recorded in eight of the orders, that is to say, one-third of them. In some cases this is not surprising because there are few species in the order. However, hybridization is known in the smallest order, which has only six species (Coliiformes), and is not known in another (Apodiformes; the swifts) which has more than a hundred species.

These data do not address the question of how often hybridization between any two species occurs. If it is generally rare it will often not be detected, and so the true incidence may be much higher than the recorded incidence of 9.2%. For example, some groups like the tinamous are generally cryptic and rarely studied in detail in nature, whereas the more conspicuous grouse and partridges have received much more attention. Hybridization has not been recorded in the former, whereas more than two dozen kinds of interspecific pairs are known for grouse (*12*). Differential detectability could partly explain why so many cases are known for hummingbirds, ducks, and geese, and so few for a variety of cryptic birds of tropical forests.

Nor do these data address the question of what proportion of potentially hybridizing species actually hybridizes. Obtaining an answer to this would require a mapping of the ranges of the species. Many species do not encounter a congener anywhere in their range: ostriches, emus, and cassowaries are allopatric to all other Struthioniformes, and insular endemics are often remote from their nearest relatives. Moreover, about 15% of species have no congeners, being the sole species of their genus. Thus the incidence of hybridization among potentially hybridizing species is likely to be much higher than the unadjusted global estimate. The comparative study of hybridization to determine the reasons for these patterns of variation (*14*) is a field waiting to be developed.

Consequences of Hybridization

What are the genetic and evolutionary consequences of hybridization? Field studies of bird populations over the last 50 to 100 years have attempted to answer this question. They have established that two populations, previously allopatric or parapatric, may interbreed, though not necessarily at all points of contact (*15, 16*), become sympatric over a large area, or form a zone of hybrids in which the parental taxa are scarce or lacking altogether. The hybrid zone may be broad (*17*) or narrow (*10*), stable over many decades (*10*) or unidirectionally changing (*18, 19*). Mating of birds within the zone has been shown to be random (*20*) or assortative with respect to phenotype (*21, 22*). The fate of hybrids has been difficult to determine, principally because they disperse out of the study areas where they were born, identified, and individually marked. What is known comes largely from indirect sources of evidence. Hybrids may be at a mating disadvantage in comparison with the parental species (*23*), possibly have smaller broods (*24*), or be partially (*22, 25*) or completely (*26, 27*) sterile, but sometimes appear to survive and breed as well as members of the parental species (*21, 22, 25, 28*).

The breeding of birds in captivity has yielded much more, quantitatively precise

Table 1. The incidence of hybridization among species in the 23 orders of birds. The world list of birds is from Sibley and Monroe (*11*) and the world list of hybridizing species, classified differently in a few cases, is from Panov (*12*), supplemented by new records (*13*).

Order	Species (*n*)	Species hybridizing		Pairs hybridizing (*n*)	Intergeneric pairs of hybridizing species	
		n	%		*n*	%
Struthioniformes	10	0	0.0	0	0	0.0
Tinamiformes	47	0	0.0	0	0	0.0
Craciformes	69	2	2.9	1	0	0.0
Galliformes	214	46	21.5	46	6	13.0
Anseriformes	161	67	41.6	114	35	30.7
Turniciformes	17	0	0.0	0	0	0.0
Piciformes	355	48	13.5	32	0	0.0
Galbuliformes	51	2	3.9	1	0	0.0
Bucerotiformes	56	0	0.0	0	0	0.0
Upupiformes	10	0	0.0	0	0	0.0
Trogoniformes	39	0	0.0	0	0	0.0
Coraciformes	152	8	5.3	4	0	0.0
Coliiformes	6	2	16.7	1	0	0.0
Cuculiformes	143	4	2.8	2	0	0.0
Psittaciformes	358	27	7.5	17	5	29.4
Apodiformes	103	0	0.0	0	0	0.0
Trochiliformes	319	61	19.1	52	36	69.2
Musophagiformes	23	0	0.0	0	0	0.0
Strigiformes	291	2	0.7	1	0	0.0
Columbiformes	313	10	3.2	5	0	0.0
Gruiformes	196	17	8.7	10	3	30.0
Ciconiiformes	1027	139	13.5	92	3	3.3
Passeriformes	5712	460	8.0	320	58	18.2
Total	9672	895	9.2	698	136	19.5

Table 2. Breeding success of hybridizing ground finches (*Geospiza* species), 1983–1991.

Pairs	Clutches (C)	Eggs (E)	Nestlings (N)	Fledglings (F)	N/E	F/C
fortis × *fuliginosa*	31	122	107	92	0.88	2.97
fortis × *scandens*	12	44	31	27	0.70	2.25
fortis × *fortis*	1141	4462	3446	2953	0.77	2.59
fuliginosa × *fuliginosa*	7	28	24	24	0.86	3.43
scandens × *scandens*	559	2071	1550	1264	0.75	2.26

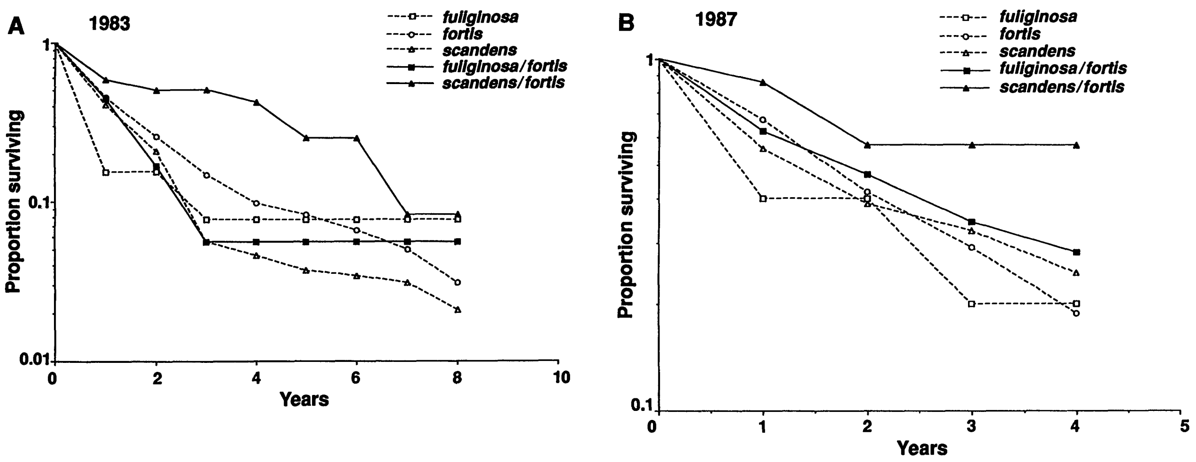

Fig. 1. Survival of three species of ground finches (*Geospiza* spp.) and hybrids born in (**A**) 1983 and (**B**) 1987. Each cohort starts at the fledging stage. Their numbers are as follows, first for 1983 and then for 1987: 13 and 10 *fuliginosa*, 987 and 960 *fortis*, 761 and 163 *scandens*, 18 and 32 *fuliginosa/fortis* hybrids, and 12 and 7 *scandens/fortis* hybrids.

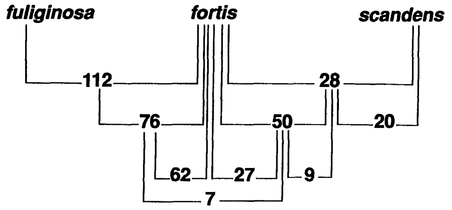

Fig. 2. The total number of fledglings produced from 1976 to 1991 by interspecific and various hybrid pairs. *Geospiza fuliginosa* and *G. scandens* have not been known to interbreed yet they exchange genes through the intermediary *G. fortis*.

information on the fates of hybrids (*18, 27*). At least 1500 different hybrid combinations of birds have been produced in captivity (*10, 29*). Precision is gained at the expense of realism however; what can be achieved in captivity may have little bearing on the incidence and importance of hybridization in nature (*1, 18, 27*).

In our demographic study of hybridizing birds in a natural environment, these difficulties and limitations are avoided or minimized. We used pedigrees to quantify the long-term effects of hybridization across a maximum of five generations.

Hybridization on Daphne Major Island

Daphne Major is a small volcanic island (0.34 km^2) in the center of the Galápagos archipelago, 8 km to the north of the much larger Santa Cruz island (904 km^2) and close to the equator (*8*). Two populations of Darwin's finches are resident on Daphne: *Geospiza fortis*, the medium ground finch (~17 g), and *G. scandens*, the cactus finch (~20 g). They have identical plumages and are similar in body size but differ in beak proportions and associated feeding habits (*8*). A third species, *G. fuliginosa*, the small ground finch (~12 g), occasionally immigrates from Santa Cruz, and a few individuals stay to breed. It is similar in proportions to *G. fortis* but is much smaller.

The banding of finches in 1973 and 1975 with unique combinations of colored plastic and metal leg bands laid the foundation for a long-term breeding study, conducted every year from 1976 to 1991. Over the 16-year period harmonic mean breeding population sizes were 197 *G. fortis*, 94 *G. scandens* (*32*), and 6 *G. fuliginosa*. Breeding occurred only in wet years in this seasonally arid and annually fluctuating climatic environment.

The breeding record shows that hybridization is a rare but recurring event. In 10 out of the 12 years in which *G. fortis* bred, at least one *G. fortis* × *G. fuliginosa* pair was formed, and in half of the breeding years *G. fortis* × *G. scandens* pairs were formed as well. Males and females of each species hybridized at approximately equal frequencies. *Geospiza fuliginosa* never bred with *G. scandens*. Hybridizing birds constituted, on average, 1.9% of breeding *G. fortis* individuals and 0.9% of *G. scandens*. For *G. fuliginosa* the corresponding figure is 70.8%, a high value that reflects the low availability of conspecific mates (*7, 16*). But even this species paired less often with *G. fortis* than would be expected (>99%) on a simple random basis.

A parallel study on Genovesa island gave similar estimates of the frequency of hybridization among the three other species in the genus of Darwin's finches. Although the prevalence of hybridization in Darwin's ground finches may be attributed to their relatively young evolutionary age (*8*), other bird species that are older hybridize at a similar frequency (*25*).

Fitness Consequences of Hybridization

The fitness of an organism is its contribution of offspring to the next generation (*35*). Hybrids are generally expected to have lower fitness than the offspring of conspecific pairs because they are constituted from two genetic stocks that may be incompatible to a greater or lesser extent (*1*). Alternatively hybrids may have higher fitness through benefits associated with enhanced heterozygosity, or experience neither a fitness advantage or disadvantage.

The Daphne data allow a partitioning of hybrid fitness into components of survival and reproduction to assess these possibilities. They can then be compared with component values for the nonhybridizing members of the respective species to obtain an index of relative fitness for each component, evaluated with respect to a specified base-line population as is the practice in the assessment of effects of inbreeding (*35*). We chose the birds breeding in 1983 as the base population because almost all birds had been banded by then (~92%) and because parents of most of them were known. Moreover, virtually every nest on the island was found in that year and in all subsequent years, the parents were identified, and the fates of all of the offspring were determined. The smallness of the island has allowed a complete documentation of every individual.

In the period 1983 to 1991 finches bred in 6 of the 9 years. Those that hybridized were at no obvious disadvantage. They bred as many times as conspecific pairs and produced clutches of similar size. The mean clutch size of *G. fortis* × *G. fuliginosa* pairs (3.9 eggs) was statistically indistinguishable (ANOVA, $P > 0.1$) from mean clutch sizes of *G. fortis* pairs (3.9) and *G. fuliginosa* pairs (4.0). *Geospiza scandens* produced smaller clutches when paired conspecifically (3.7) or with *G. fortis* (3.7).

Indices of breeding success (Table 2) do not indicate a loss of fitness at hatching or fledging stages. Mixed pairs of *G. fortis* and *G. fuliginosa* had higher hatching success than *G. fortis* breeding conspecifically (χ^2 (2) = 6.89, $P < 0.01$), and intermediate breeding (fledging) success between the high value for *G. fuliginosa* and the low value for *G. fortis*. Hatching and breeding success were a little lower for *G. scandens* when paired conspecifically or with *G. for-*

tis. The only sign of hybrid inferiority is a slightly lower hatching success of G. *fortis* × G. *scandens* pairs, which is not significantly different from that of either G. *fortis* or G. *scandens* pairs (χ^2 tests, $P > 0.1$).

Survival of hybrids and conspecifics over 8 years is shown in Fig. 1A. Both types of hybrids born in 1983 survived better than their G. *fortis* and G. *scandens* contemporaries, and one type (G. *fortis* × G. *scandens*) survived better than G. *fuliginosa* as well. Annual survival of G. *fortis* × G. *scandens* hybrids was higher than the survival of each of the parental species in 6 of the 8 years. The next cohorts of similar size for comparison were born in 1987. Hybrid survival over the following 4 years was higher than any conspecific survival (Fig. 1B). For both the 1983 and 1987 cohorts the G. *fortis* × G. *scandens* hybrids survived best. Thus for the survival component of fitness, hybrids outperformed the parental species.

Hybrids, as well as surviving well, breed well; they are fertile as well as viable. They have backcrossed to G. *fortis* and G. *scandens*, but not to the relatively rare G. *fuliginosa*, and the backcrosses have survived to breed with G. *fortis* (Fig. 2). Judged against the standard of G. *fortis*, they have relatively high breeding fitness (Table 3). Hybrids and backcrosses with G. *scandens* genes have lower hatching success than those with G. *fuliginosa* genes. Nevertheless, in terms of their ability to produce fledglings, they all do about as well as G. *fortis* and G. *scandens* or better, and in some cases distinctly better.

Table 3. Relative fitness of Darwin's finches and hybrids. The average hatching success per egg or fledging success per clutch for a particular group of pairs ($\overline{W}_i$) is expressed as a proportion of the success of *G. fortis* pairs ($\overline{W}_F$) breeding in the same years. Pairs are conspecific, interspecific (hybridizing), or backcrosses.

Pairs	Hatching ($\overline{W}_{i1}/\overline{W}_{F1}$)	Fledging ($\overline{W}_{i2}/\overline{W}_{F2}$)
fortis × *fortis*	1.00	1.00
fortis × *fuliginosa*	1.14	0.98
fortis × *scandens*	0.91	1.07
fortis × *fortis/fuliginosa*	1.07	1.02
fortis × *fortis/scandens*	0.98	1.20
fortis × *fort/fort/ful*	1.05	1.52
fortis × *fort/fort/scan*	0.93	0.98
scandens × *fortis/scandens*	0.88	1.22
scandens × *scandens*	0.99	1.01
fuliginosa × *fuliginosa*	1.10	1.45

Genetic incompatibilities between other hybridizing species sometimes appear in the F_1 generation, or with the production of recombinants in the F_2 generation. In the first case they are usually manifested as partial or complete sterility in the heterogametic sex (females); this is known as Haldane's rule (*35, 36*) and has been found in captive (*29, 36*) and wild birds (*25*). There is no evidence for it in Darwin's finches. For example, female G. *fortis* × G. *fuliginosa* hybrids have produced a total of 17 clutches when paired with G. *fortis* males, and experienced a 79% hatching success, whereas 19 clutches from the reciprocal pairs over the same period yielded the same average clutch size but a lower (54%), not higher, hatching success. Nor is there evidence for hybrid breakdown in the F_2 generation. Four clutches produced by two F_1 pairs had high hatching (0.86) and fledging (0.86) success (Table 3).

Survival and breeding components of fitness, treated separately so far, are now combined to provide an overall measure of fitness (Table 4). The 1987 cohorts are used for this purpose because backcrosses are represented, as well as F_1 hybrids and the three species. Fitness over the first 4 years is the product of survival, recruitment to the breeding population, and production of fledglings in the breeding seasons of 1990 and 1991. A value of 1.0 for a class of finches indicates numerical replacement; the starting number of fledglings born in 1987 has been replaced by an equal number of fledglings born in 1990 and 1991. The fitness values for both types of hybrids and two types of backcrosses exceed 1.0, whereas G. *fuliginosa*, G. *fortis*, and G. *scandens* all have fitness values less than 1.0. The fitness differentials arise largely from the higher survival of hybrids and backcrosses (not shown in Fig. 1) than parental species because recruitment and breeding were more equal among the various groups. Future breeding by a decreasing number of G. *fortis* and G. *scandens* is likely to bring their fitness values up to or above 1.0, because they have the potential to live and breed for 15 years (*32*), but the difference between their fitnesses and the fitnesses of hybrids and backcrosses is likely to remain.

Table 4. Fitnesses of the 1987 cohorts of Darwin's finches over 4 years: three species, two types of hybrids, and two types of backcrosses to *G. fortis*. Fitness is the product of three components, expressed as proportions (survival and recruitment) or numbers (breeding success).

Species	Initial cohort (*n*)	Survival	Recruitment	Breeding (fledglings/ breeder)	Product
fuliginosa	10	0.200	0.500	3.0	0.300
fortis	960	0.188	0.763	5.9	0.844
scandens	163	0.245	0.488	6.5	0.780
fortis/fuliginosa	32	0.281	0.677	7.0	1.330
fortis/scandens	7	0.571	0.750	6.7	2.868
fortis/fortis/fuliginosa	34	0.256	0.917	7.1	1.669
fortis/fortis/scandens	43	0.353	0.636	5.1	1.148

Thus of the three possible outcomes of hybridization—higher, lower, or unaltered fitness—higher fitness is the one manifested by the 1987 cohorts of Darwin's finches on Daphne Major Island. Earlier cohorts provide supporting evidence of their superiority.

The Causes of Hybrid Superiority

Hybrids may be superior because they have phenotypes that are capable of dealing with the exigencies of the environment better than parental species phenotypes. For example, finch hybrids may be better at exploiting a part of the food supply than the parental species as a result of their generally intermediate beak sizes. As discussed below, this advantage may not persist for long. Alternatively, elevated heterozygosity levels could give them their advantage, particularly if hybridization was preceded by a period of inbreeding in the two parental species. During a severe drought on Daphne in 1977, finch mortality was heavy and population sizes became temporarily small. Inbreeding depression might have been expected in subsequent generations, but there was little evidence for it in G. *fortis* up to 1987 (*37*). *Geospiza scandens* remains to be investigated in this regard.

Relatively high fitness of hybrids in other situations has been attributed to novel combinations of environmental factors often associated with disturbed habitats (*18, 30, 31*). Whatever the causes are of high fitness of Darwin's finch hybrids, extrinsic or intrinsic, this is not one of them. Their environment is not novel, nor has it ever been disturbed either naturally or artificially. Therein lies a major part of the significance of our findings.

The Nature of Species

The discovery of superior hybrid fitness over several years suggests that the three study populations of Darwin's finches are fusing into a single panmictic population, and calls into question their designation as species.

Over the long term, fusion is unlikely. The Galápagos climate fluctuates markedly, and so does the quantity and composition of the food supply (*8, 38*). Within the G.

fortis population different phenotypes survive best under different conditions. Large individuals are favored by natural selection under dry conditions whereas small individuals are favored in the aftermath of very wet conditions (*38*). Hybrids and backcrosses, being generally intermediate between parental species in morphology, will be periodically at a disadvantage. In the future, when conditions return to those that favored large size before the 1982–83 El Niño event (*38*), the hybrids, especially those between G. *fortis* and G. *fuliginosa*, are expected to be at a disadvantage. At the current rate of interbreeding, fusion will occur slowly (*39*) until those conditions return. Thus over the long term there should be a selection-hybridization balance, and the interbreeding populations will remain distinct phenotypically and genetically.

Elsewhere in the archipelago G. *fortis* coexists with G. *fuliginosa* on 15 islands and with G. *scandens* on 14 of them (*8*). Coexisting species are morphologically distinct and apparently do not interbreed, although none of the species has been studied on these islands in as much detail as on Daphne, and hybridization, if it occurs rarely, will have escaped detection. This situation of hybridization in one location and a lack of it in other areas occupied sympatrically by the same taxa is not unique. It occurs in other birds (*15, 16*), as well as in salamanders (*40*) and snakes (*41*).

Hybridization and fluctuations in relative fitness of hybrids illustrate the challenges to our concepts of species that arise from moderately rare but significant events in the real world.

Conclusion

Hybridization is evolutionarily important because it produces novel combinations of genes, as well as new alleles (*4, 42*), thereby creating favorable genetic conditions for rapid and major evolutionary change to occur (*43*). The most dramatic outcome is the formation of new polyploid species. As many as 40% of plant species may have arisen in this way (*44*). Although hybridization is rarer in animals generally, it is widespread in some taxa such as birds, as reviewed in this article, other vertebrates, and certain groups of insects (*45*). The stability of hybrid zones in birds and other taxa shows that it is not ephemeral, and the high fitness of Darwin's finch hybrids shows that it is not inconsequential. Animal species may be more like plants than is generally realized, many possessing genetic systems open to invasion, especially early in their existence as quasi-independent lineages.

The widespread exchange of genes through hybridization and the resulting patterns of reticulate evolution at gene level pose two types of problems for the evolutionary biologist: the elucidation of evolutionary histories through the comparison of molecules in the surviving taxa (*46*) and the recognition and delimitation of species (*2, 5, 6*). Hybridization poses a problem of an entirely different nature in the area of biological conservation. O'Brien and Mayr (*47*) have drawn attention to the fact that hybridizing species fall outside the limits of protection afforded by the U.S. Endangered Species Act of 1973. Underlying the so-called hybrid policy (*47*) is the notion that a species loses its strict identity when hybridizing, or at least it has the potential of doing so. Recognition of the widespread occurrence of hybridization and backcrossing in nature, even though seldom common, casts the notion in a different light. If rarity increases the chances of interbreeding with a related species, presumably because conspecific mates are scarce, then the species most in need of protection, by virtue of their rarity, are the ones most likely to lose it under current practice, by hybridizing. Both the conservation (*48*) and evolutionary (*31, 45*) implications of hybridization are profound.

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