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PART 2

Developing a Long-Term Perspective





A Potential Competitor Arrives on Daphne

The really surprising fact in this case of the Galapagos Archipelago, and to a lesser extent in some analogous instances, is that the new species formed in the separate islands have not quickly spread to the other islands.

(Darwin 1859, p. 401)

There is a large element of chance in successful island colonizations.

(MacArthur 1972, p. 84)

Introduction

DARWIN ANSWERED THE DILEMMA above in two ways. First, he suggested that deep channels and rapid currents would be strong barriers to the dispersal of sedentary organisms, such as snails and centipedes, although not for mobile animals like birds. Second, he pointed out that potential colonists arriving at an island would have to compete with the local inhabitants. Darwin's second answer remained in the realm of conjecture until an unexpected colonization event occurred in the extraordinary El Niño year of 1982–83. The Large Ground Finch *Geospiza magnirostris* (fig. P.1) established a breeding population on Daphne. We were exceptionally lucky to be in the right place at the right time, because natural colonization is rarely

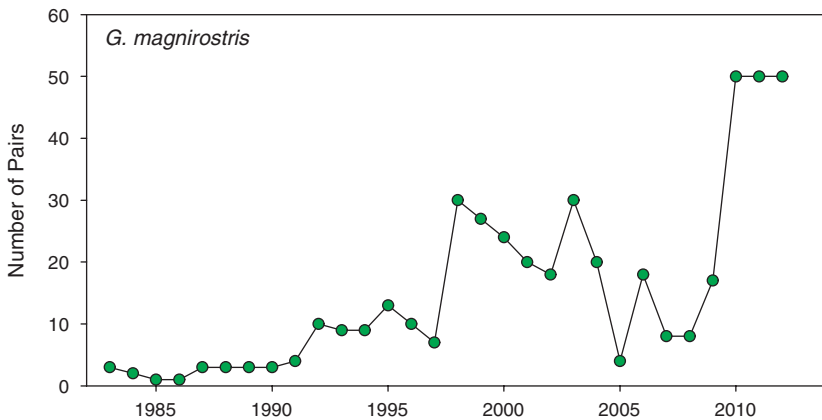


Fig. 6.1 Changes in the size of the breeding population of *magnirostris*.

observed (Sprunt 1953, Bock and Lepthien 1976, Larsson et al. 1988). Instead it is usually reconstructed and interpreted from evidence obtained after the event, often several years after the event (Diamond 1974, Conant 1988, Mathys and Lockwood 2009), or by statistical inference from genetic differences between populations (e.g., Tonniss et al. 2005, Farrington and Petren 2011, Päckert et al. 2013). The *magnirostris* population increased slowly over the first decade and then accelerated, with the result that by 2012 there were 50 pairs breeding on the island (fig. 6.1). This chapter describes the founding of the population and the genetic and morphological changes it underwent in the first three generations (~15 years). The next chapter discusses competition for food with the resident finch species and the influence on the *fortis* trajectory depicted in figure 1.6.

The first few generations after colonization are crucial to the outcome. There is a high risk of failure (extinction) for a variety of reasons associated with the small number of founders involved. First, the habitat may be unsuitable for sustaining a breeding population. Second, inbreeding occurs, with possibly deleterious fitness effects and a loss of genetic variation, and variation may also be lost through random drift. Therefore the population must have sufficient genetic variation to survive a period of inbreeding when it is most vulnerable to extinction through chance demographic and environmental factors (Lande 1993). Despite the likelihood of extinction the population may nonetheless thrive. The external (ecological) environment may be highly favorable because resources are plentiful and enemies are scarce or absent, and

the internal (genetic) environment may be highly favorable because rare alleles may rise in frequency and come together in new, favorable combinations that enhance evolutionary divergence (Mayr 1954, Barton and Charlesworth 1984, Carson and Templeton 1984).

Here we discuss causes and consequences of the colonization, and reflect on how the information illuminates or qualifies theory. The addition of a closely related species to the community is relevant to ideas about speciation (fig. 1.2), so in the following chapters we discuss ecological and evolutionary effects of *magnirostris* on the other species of finches (chapter 7), behavioral interactions with the other species in the breeding season (chapter 8), and long-term morphological and genetic changes in the *magnirostris* population (chapter 11).

Founder Event

At least one pair of *magnirostris* bred on Daphne in 1923 (Beebe 1924). Sometime later the population became extinct (Lack 1945, 1947, Harris 1973); therefore we were surprised to find a male on our first visit in April 1973. In the next 10 years others in immature plumage were occasionally seen and captured in the nonbreeding season. None of these immigrants stayed to breed, and almost all disappeared soon after or at the beginning of the following breeding season, possibly returning to their island of origin. A few *magnirostris* were present when El Niño began in late November 1982, but this time they did not all disappear: five of them, two females and three males, stayed and bred (Gibbs and Grant 1987a, Grant and Grant 1995b). Starting with the first egg laid on December 15 they bred in three combinations and produced a total of 17 fledglings from eight broods. Evidently it took a rare event to nudge a species into joining a community whose changed environment was able to accept it (Grant and Grant 1996c).

CAUSES

What triggered breeding? *G. magnirostris* do not have unique requirements for breeding. There was no obvious reason why they could not have bred on the island before 1982–83, and indeed a male was seen building a nest in 1974 and others were heard singing in 1979–81. It seems certain that the unusually early onset of El Niño was responsible for the founding of the new population, but in what way?

Unfortunately neither we, nor our assistants, were on the island when the first rains fell at the end of November; assistants arrived in December. One probable factor inducing the immigrants to stay was a rapid response of the vegetation to an unusually large input of rain in the early stages of El Niño. A key component of the vegetation was *Croton scouleri*, a shrub or small tree that responds rapidly to rain by leafing and flowering, and produces an abundance of large and easily accessible, energy-rich seeds (fig. 2.8) that are a major source of food for nestlings and fledglings, as well as adults. A second factor may have been the breeding of *fortis* and *scandens*, which started soon after the first heavy rains fell. We speculate that social stimulation by them combined with a rapidly growing food supply helped to bring the *magnirostris* into breeding condition. Perhaps *magnirostris* needed to build energy reserves before leaving, and as they did so they also developed reproductively. Some emigrated while others stayed and bred. The social stimulation from the song and chasing of resident finches was perhaps enough to tip the hormonal balance of five birds in the direction of staying, and a rapid increase in numbers of *Croton* seeds and arthropods then facilitated their breeding.

In retrospect this was a colonization waiting to happen. It just needed a particularly favorable wet season. Studies of birds in Europe and elsewhere have shown that colonization of a new area has often been preceded by short-term visits of nonbreeding immigrants (O'Connor et al. 1986, Garnett et al. 1992). Sol et al. (2005) surveyed more than six hundred species worldwide and showed that successful colonizers had large brains relative to body size. Perhaps *magnirostris* do also. It is easy to believe by watching them that they have enhanced cognition. For example, when approached by us they are more likely than *fortis* and *scandens* to stand and stare at us before flying away.

First Few Generations

All the original founders disappeared and were replaced by the next generation, a sister and her two brothers. The offspring of one of the brothers did not survive long enough to breed; therefore the population was essentially started by one, presumably unrelated, pair in the F_0 generation, and a single son and daughter in the F_1 generation. The son and daughter, in turn, contributed seven individuals to the next generation (F_2). The small number of founders and the inbreeding that followed conform to the general understanding of the structure of founder

populations, and the likelihood of inbreeding (Crow and Kimura 1970, Charlesworth and Charlesworth 1987).

INBREEDING

We followed the population demographically; established the pedigree by observation, banding, and DNA analysis; and found, as expected theoretically, inbreeding was frequent in the first few generations (fig. 6.2). A high frequency of inbreeding may be due to the high probability of mating with a relative through random mate choice early in the establishment of a small breeding population, or to active mate choice. Using the coefficient of coancestry (ϕ ; Falconer and Mackay 1995) as a measure of the relatedness of breeding pairs, we found no difference between observed and randomly expected average coefficients in the years 1987–92, with one exception: close inbreeding occurred more frequently than expected by chance in 1992. This resulted from closely related birds that formed pairs early in the establishment of the population surviving well and remaining in pairs, even when a few unrelated potential mates became available through immigration. The coefficient of coancestry was 17 times greater in *magnirostris* than in the much larger and long-established *fortis* population (Grant and Grant 1995b).

FITNESS COSTS OF INBREEDING

The population was supplemented by a trickle of immigrants, and at least one of them bred in each year of breeding from 1987 to 1993. This allowed us to compare an inbred group with an outbred group. As expected, inbreeding was found to carry a cost. In the well-sampled 1991 cohort, longevity (maximum = 7 years) varied inversely with inbreeding coefficient (Grant et al. 2001). Inbred birds survived in their first year much less well on average than noninbred birds (fig. 6.3). As far as we could tell, inbreeding depression was restricted to this part of the life history. There was no further inbreeding depression manifested as low clutch size or poor hatching success. Their clutches of 2–5 eggs were typical of the other species. The proportion of eggs that yielded fledglings was lower (50%) than the other species (>60%) but the difference was not statistically significant (Grant and Grant 1995b). Nor was it much lower than on Genovesa, where breeding success of *magnirostris* was estimated to be 60% (Grant and Grant 1989).

The cost of inbreeding was estimated to be 4.5 lethal equivalents (Keller et al. 2002). This is defined as the number of deleterious genes whose cumulative effects equal that of one recessive lethal (Morton et

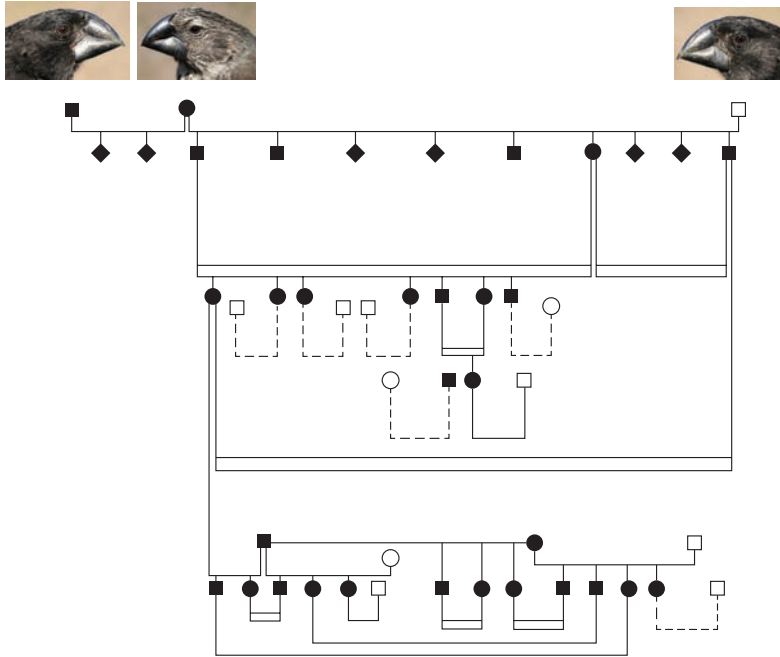


Fig. 6.2 The complete genealogy for *magnirostris* in the years 1983–92. The initial breeders are shown at the top, together with all the fledglings they produced; three of the fledglings became recruits. Below that, only the fledglings that became recruits are shown. Squares, males; circles, females; diamonds, birds of unknown sex. Solid symbols represent banded birds; open symbols, birds without bands. Double horizontal lines indicate breeding pairs of relatives. Broken lines indicate new pairings in 1993 with unknown reproductive outcome. From Grant and Grant 1995b with corrected orientation.

al. 1956), and is measured by the slope of the logistic regression of fitness (0 or 1) on relatedness (f value). For comparison the estimated number for a small population of Song Sparrows (*Melospiza melodia*) in Canada was 2.7 (Keller et al. 2006), whereas larger values have been calculated for island populations of flycatchers (*Ficedula albicollis*) in Sweden (7.5; Kruuk et al. 2002) and Stitchbirds (*Notiomyotis cincta*) in New Zealand (6.9; Brekke et al. 2010).

IMMIGRATION

Immigrants arrived in pulses after the breeding season; most disappeared, but at least one bred in each year of breeding from 1987 to 1993. Immigrants could be identified unambiguously up to March 1992,

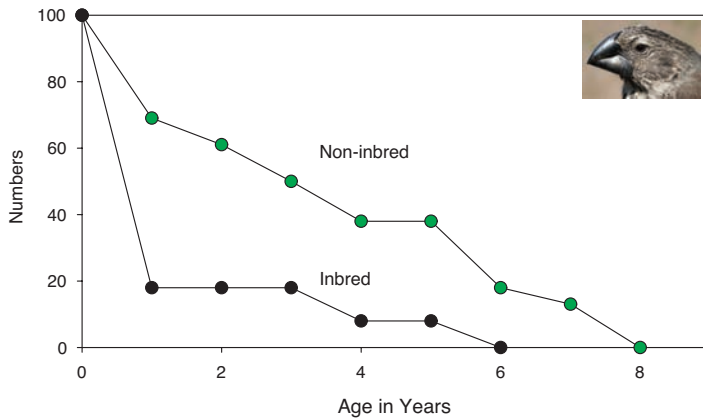


Fig. 6.3 Inbreeding depression in first-year survival but not later. Survival of inbred ($f \geq 0.125$, $n = 17$) and noninbred ($f \leq 0.124$, $n = 14$) members of the 1991 cohort of *magnirostris* are compared. From Grant et al. 2001. Numbers are scaled to an initial 100 of each. Cuckoldry, at 6% in the population ($n_{\text{families}} = 15$, $n_{\text{offspring}} = 86$), is not large enough to be a biasing factor. The severity of inbreeding, as measured by the number of lethal equivalents, is 4.47. For comparison it is close to 0 for *fortis* but 4.27 for *scandens* (Keller et al. 2002).

when continuous and complete monitoring of breeding of all finches on the island ceased, and with a high degree of confidence in the next few years when most breeding was monitored. Captures of immigrants varied annually in the years 1973 to 1995 (fig. 6.4), and were positively correlated with rainfall in the preceding year when presumably they hatched (Grant and Grant 1995b).

By breeding with residents, immigrants had two effects on the population. First, they caused the mean coefficient of inbreeding to decline from 0.25 in 1986, when the brother-sister pair formed, to 0.11 in 1992, 0.03 in 1993, and 0.01 in 1995. Second, as a result, deleterious effects of inbreeding declined.

SELECTION

Up to 2000 there was a trend toward more robust beaks in the *magnirostris* population, but no trend in beak size or body size. Changes in beak shape (table 6.1) are better described as a couple of step-function changes, occurring first after the initial breeding and second from 1991 to 1992. The second transition from relatively pointed beaks to relatively robust beaks was sustained for almost a decade, with all mean values after 1991 being larger than all means up to and

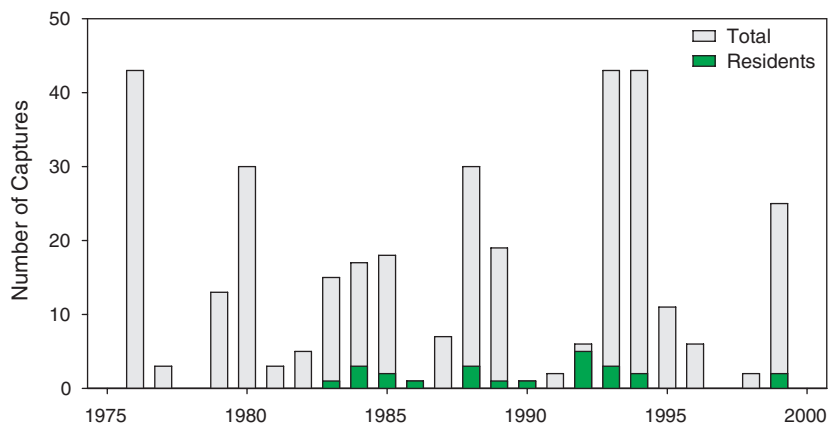


Fig. 6.4 Mist-net captures of *magnirostris* in nonbreeding seasons. Captures were dominated by immigrants after 1983, when breeding began. Netting effort varied among years; standardized captures per unit time are given in Grant and Grant 1995b. From Grant et al. 2001.

TABLE 6.1
The meaning of principal components of morphological variation

	<i>G. fortis</i>	<i>G. scandens</i>	<i>G. magnirostris</i>
PC1-body			
% variance	69.74	70.31	65.33
Weight	0.594	0.604	0.588
Wing length	0.585	0.575	0.584
Tarsus length	0.552	0.552	0.560
PC1-beak			
% variance	86.45	68.29	79.42
Beak length	0.557	0.443	0.550
Beak depth	0.592	0.649	0.596
Beak width	0.584	0.619	0.584
PC2-beak			
% variance	9.57	25.23	13.44
Beak length	0.825	0.887	0.825
Beak depth	-0.313	-0.213	-0.283
Beak width	-0.662	-0.411	-0.488
Sample size (<i>n</i>)	3,868	1,419	632

Note: Each analysis was performed on only one species. Values in the body of the table show the magnitude and sign of the loadings of each trait on the principal components. PC1-body and PC1-beak are positively correlated in *fortis* ($r = 0.743$, $p < 0.0001$), *scandens* ($r = 0.701$, $p < 0.0001$), and *magnirostris* ($r = 0.627$, $p < 0.0001$). Beak shape (PC2-beak) varies independently of body size in *fortis* ($r = 0.000$) and *magnirostris* ($r = 0.067$, $p = 0.0918$) but not in *scandens* ($r = 0.253$, $p < 0.0001$).

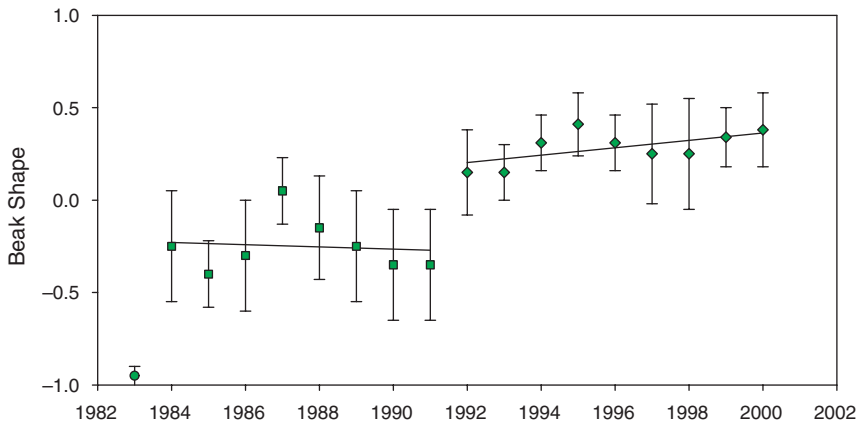


Fig. 6.5 Changes in beak shape, separated into two step-transitions. Beak shape is the second component of a principal components analysis of beak length, depth, and width (table 6.1). Beaks became less pointed and more robust. Lines are least-squares best fits from linear regressions, and are used heuristically to show apparent parallel and flat but displaced morphological trajectories. Annual means and one standard error are shown. After 1983 ($n = 6$), sample sizes varied from 4 (1986) to 29 (1994). From Grant et al. 2001.

including 1991 (fig. 6.5). The pattern is striking, but the interpretation is not straightforward. The transition from 1991 to 1992 could have been the result of chance, selection, or both. It involved the loss of two birds and the addition in 1992 of one immigrant and 10 offspring hatched in 1991.

Genetic Diversity

The founding of a new population is understood better with genetic data. In 1988 we began taking samples of blood for microsatellite DNA analysis, and continued every year thereafter. Ken Petren (1998) developed 16 microsatellite markers for characterizing individuals genetically. Fourteen of the loci were autosomal, and 2 were Z-linked. Some of the birds banded before 1988 were captured and sampled, and the pedigrees of these birds enabled us to reconstruct genetic characteristics of the breeding population before the blood sampling began. None of the original colonists was genotyped, but genetic inferences about them are possible from their offspring. The brother (6501) and sister (6509) of the F_1 generation were each heterozygous

at 10 of the 14 autosomal loci, but different at 6 of them. Either the parents were similarly heterozygous or genetically very different from each other.

LOSSES AND GAINS OF ALLELES

As expected theoretically, the population lost alleles in the first few generations. The brother (6501) and sister (6509) possessed a combined total of 34 alleles at the 14 autosomal loci. Their daughter and son that formed a pair had 27 alleles, and the two offspring of this pair that survived to breed had a total of 22 alleles. Whereas 6501 and 6509 were each heterozygous at 10 loci, their two grandchildren were heterozygous at only 4 and 5 loci respectively. These numbers illustrate the expected pattern of random loss and reduction. The other brother (6505) was not genotyped, nor were his (nonsurviving) offspring.

As the population increased in size, the number of alleles in the population increased, and average heterozygosity, that is, the proportion of loci at which an individual is heterozygous, remained undiminished for many years (fig. 6.6). The standing genetic (allelic) variation doubled in the space of 10 years as a result of input from immigrants. A few individuals contributed disproportionately to the increase. While most immigrants contributed 1 or 2 new alleles to the population, one exceptional male (6102) contributed 11 new autosomal alleles in 1990 and 1991, and two others each contributed 8 new alleles in 1995. Even as late as 1998 one male contributed an additional 6 new alleles (Grant et al. 2001).

THE SOURCE OF IMMIGRANTS

Where did the immigrants come from? At the outset the large neighboring island of Santa Cruz, at a distance of 8 km, seemed the most likely source, but we also knew that the founders were unusually variable in beak morphology (Grant and Grant 1995b), which was a hint that they may have come from more than one island. Two of the five founders were captured and measured. The beak depth of one was 18.6 mm, and that of the other was 15.0 mm. Their measurements did not differ from those of four others that did not stay to breed; nevertheless the larger of the two measured founders was exceptional, possessing the second-largest beak among the total sample of 243 individuals measured up to 1993.

We used genetic information to answer the question of origin by comparing genotypes of birds on Daphne with genotypes of samples

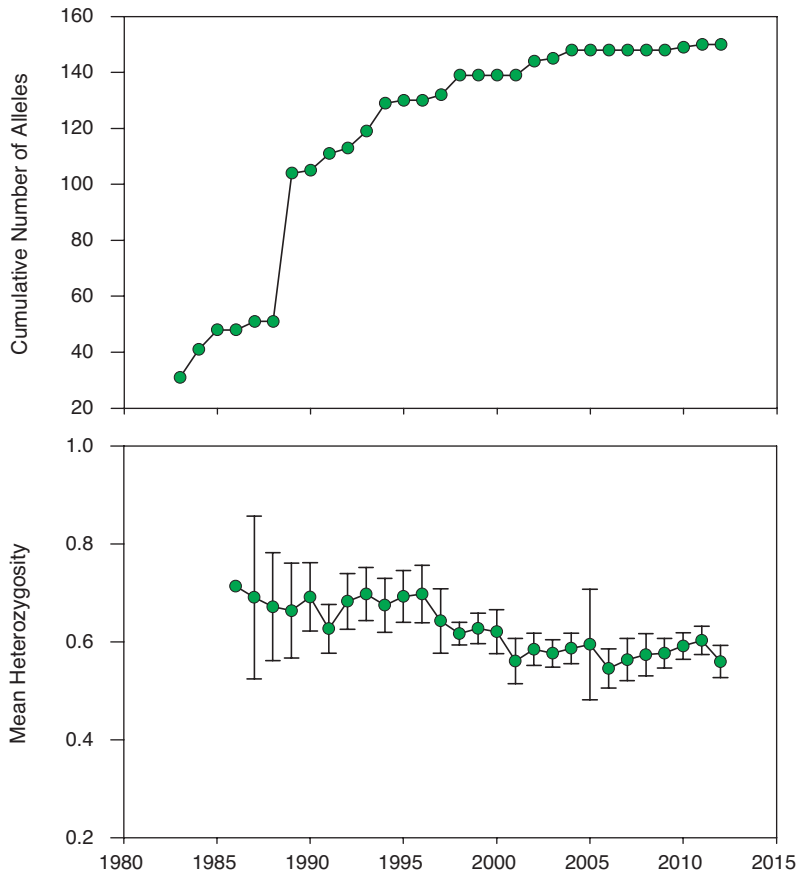


Fig. 6.6 Cumulative numbers of alleles (above) and average observed heterozygosity (below) through time ($n = 588$ individuals). The cumulative numbers increased toward an apparent plateau; 95% of the total 150 alleles had been recorded by 2002. The first point in the allele figure is the number estimated for the five founders from the minimum number known for the two parents of the second generation (Grant et al. 2001). The introduction of new alleles from immigrants far exceeded subsequent losses and the loss of two of the original alleles. As a result of these dynamics the number of alleles in the breeding population had approximately doubled seven years after the population was founded. For the lower figure an index of heterozygosity was calculated for each individual as the proportion of 14 autosomal loci that were heterozygous. Means with 95% confidence limits are shown. There are no bars on the first point, because the two birds then had an identical heterozygosity index. Mean heterozygosity remained stable until about 1996, after which it declined to a lower level in the next five years.

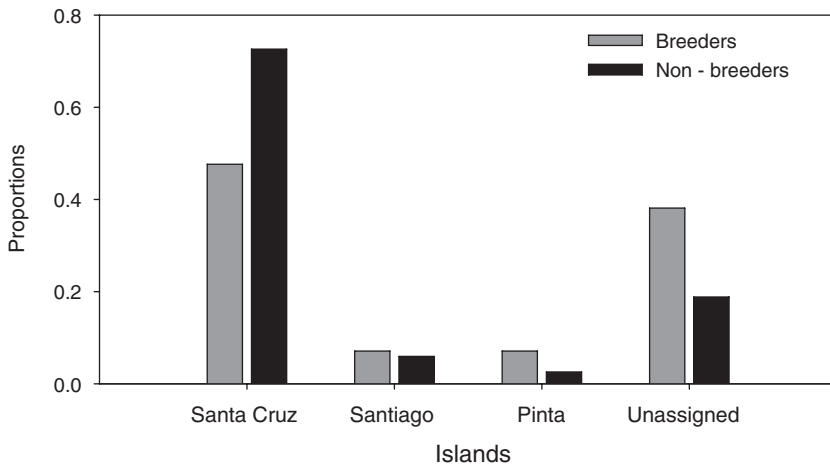


Fig. 6.7 Proportions of immigrants from different islands, as determined by using microsatellite DNA markers. Up to 1998, 117 birds without bands were captured on Daphne. We used a Bayesian modeling approach to assign them to potential source populations (Pritchard et al. 2000), and the following samples to genetically characterize the source populations: Santa Cruz (12), Santiago (10), Rábida (5), Isabela (6), Marchena (10), Pinta (7), Genovesa (32), and Fernandina (9). Three islands were identified as sources of birds on Daphne by the majority rule: Santa Cruz (85), Santiago (7), and Pinta (3). Twenty-two could not be assigned to any island. Of the 22 birds that bred on Daphne, 18 were from Santa Cruz, 1 was from Santiago, and 3 were unassigned. The analysis was repeated with 159 birds captured in the years 1998–2008 with almost identical results (Grant and Grant 2010b), and with 127 additional birds captured in 2009–12, again with almost identical results (two came from Marchena, and one bred). These results indicate continuing, heterogeneous immigration. It is striking that none were assigned to the genetically well-characterized Genovesa population.

from populations on other islands. Multiple sources were confirmed: immigrants ($n = 117$) came from not one but three islands (fig. 6.7). The majority came from Santa Cruz (72.6%), as suspected. The others came from Santiago, Pinta, and possibly other islands or other locations within the large islands of Isabela and Santa Cruz because a significant minority (18.8%) could not be assigned to a single island (Grant and Grant 2010b). One bird from Santiago and one from Marchena bred on Daphne, and the remaining breeding birds all originated from Santa Cruz. This heterogeneity demonstrates much more inter-island movement of *magnirostris* than had been suspected.

NONRANDOM COLONIZATION

It is generally assumed in models of gene flow that colonization is random with respect to genotype and phenotype (Rannala 1996, Slatkin 1996, Johnson et al. 2000). However, there are genetic and phenotypic indications of nonrandom colonization of *magnirostris*. For those immigrants genotyped at 12–14 autosomal loci, the mean heterozygosity of the 22 breeders (0.707 ± 0.125 s.d.) was nearly 10% higher than the mean heterozygosity of 91 nonbreeders (0.639 ± 0.114). With regard to morphology, the immigrants that bred (26 measured) were larger in beak size than 174 contemporary immigrants that did not breed on Daphne (Grant and Grant 1995b). The morphological difference may reflect an underlying genetic difference because beak size is a heritable trait (Grant and Grant 1994; also chapter 3). These differences demonstrate that colonization was selective and not random.

Song

Song is a nongenetic, culturally transmitted trait (Bowman 1983, Grant and Grant 1996d). Only males sing, and they learn their single song type as juveniles, usually from their fathers when dependent on parents for food. A species often sings different songs on different islands (Bowman 1983, Grant et al. 2000b); therefore song is a cultural signature of an immigrant's island of origin. Three *magnirostris* song types have been recorded on Daphne (fig. 6.8). Song A has been recorded only on Santa Cruz, type B has been recorded on Santa Cruz, Santiago, Pinta, and, rarely, Genovesa, and type C has not been recorded anywhere except on Daphne. Thus at least one source of the founders was Santa Cruz, as shown by both song and genetic data. Furthermore, song may influence the decision of immigrants to stay on Daphne and join a breeding population. The evidence for this is that immigrants came from three of the islands where song type B has been recorded (fig. 6.7).

The initial immigrant breeders brought two song types to the island in 1982: A and B (fig. 6.8), rendered onomatopoeically as *pee-oo* and *chi-urrrrrr* respectively. The frequency of the three types subsequently changed radically (fig. 6.9). Type B was not present when the third, type C (*zee-urr*), was first heard in 1986. The first breeder (6102) with type C song bred in 1990. Remarkably, from that year on type C rapidly became the majority type, and in some years the only song type, largely owing to 6102's reproductive success. There is no evidence to suggest

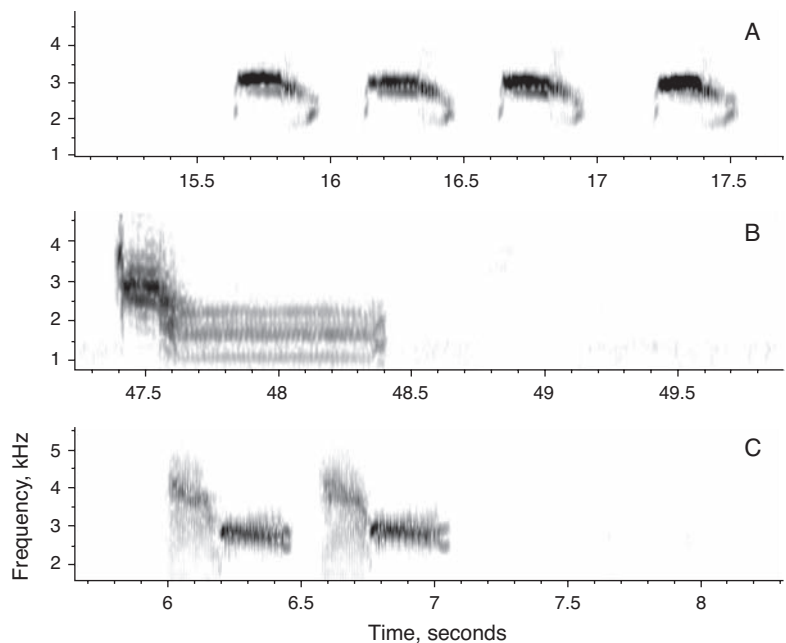


Fig. 6.8 Sonograms of the three types of song sung by *magnirostris* males on Daphne. Note the difference between B and C in which part has maximum amplitude (blackness). From Grant and Grant 1995b.

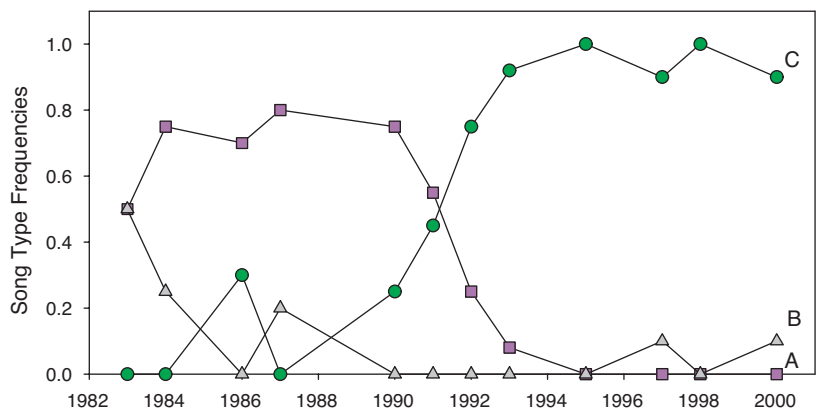


Fig. 6.9 Changes in the frequencies of the three song types. The song type of one of the three original colonists is not known. Up to 1998 all but one of 49 sons of known paternal song type sang the type of their (social) father, be it A or C. In dry years there was no singing or breeding. From Grant et al. 2001.

that song type C increased in frequency so dramatically because it was an intrinsically more effective territorial and mating signal than the others. Rather it was brought into the population by a robust and large male, who carried 12 new alleles at the 16 loci assayed, at a time when the population was experiencing inbreeding depression. His lineage had better fledging and recruitment success than the others. Changes in song type frequencies appear to be a consequence of his reproduction, aided by small population size and chance events. By 1995 types A and B were extinct, although type B reappeared several times, presumably as a result of recurrent immigration, yet remained rare.

Colonization Success

What determines colonization success? A broad study of more than 2,700 avian introductions found that living long was a stronger influence than reproducing fast (Sol et al. 2012). Although ours is only a single study, several additional lessons can be learned from our experience with *magnirostris* about the role of chance and deterministic factors (ecological and genetic) in the founding of a new population. We believe they apply to similar environments elsewhere.

At the outset the odds were against colonization success, for three reasons. First, the expected population size is low, in fact so low there is no detectable peak in the finch density distribution that is determined by food supply and depicted as an adaptive landscape in figure 2.16. Second, if the density distribution remains unchanged, the *magnirostris* should be especially vulnerable to extinction because the strongly fluctuating climate periodically reduces both food supply and finch numbers to low levels (chapters 4 and 5). Third, ignoring the very rare *fuliginosa*, Daphne was already occupied by as many species (two) as are predicted from the relationship between species number and island area (Grant and Grant 1996c).

Nevertheless, in spite of the odds against success, four factors aided colonization: a favorable environment, genetic diversity of the colonists, recurrent immigration, and competitive dominance. First, the abundant rain and vegetation response that lasted for eight months in 1982–83 allowed a breeding population to become established and produce many young. Subsequent El Niños gave additional boosts to population growth. Second, the population started genetically diverse at microsatellite loci and possibly fitness-related loci as well. The brother and sister that constituted the F_1 generation were highly heterozygous, implying genetic diversity in the founder parents. Third, immigration

was recurrent, and by introducing new alleles immigrants helped the population to emerge from a demographic and genetic bottleneck at the end of the first decade. This had the important effect of decreasing the chances of inbreeding through random pairing, and helped to end the period of time when the population sustained a genetic load through close inbreeding. Repeated addition of immigrants to the breeding population was possible because the habitat was suitable and the breeding population remained small for several years.

The original pair (F_0 generation) and most of their offspring died before 1985, which shows how precarious population establishment can be. However their son (6501) and daughter (6509) survived for 10 and 11 years. To illustrate how unusual this is, only one bird in our total sample of 398 *magnirostris* banded before the year 2000 lived for 12 years! The 6501 \times 6509 pair also produced more fledglings (27) than any other pair, and seven out of the eight that survived for at least one year became breeders. It appears anomalous that these highly inbred birds ($f = 0.25$) experienced the highest success. However, they were unusually heterozygous, and they had a demographic advantage in entering the population at extremely low density. Their diets, typical of the species, were dominated by the large and hard seeds of *Tribulus*, *Opuntia*, and *Cacabus* (fig. 6.10). Although the diet of *magnirostris* overlaps the diets of *fortis* and *scandens* (fig. 6.11), *magnirostris* has two advantages over these species: being larger they are socially dominant at individual food sources, and having larger beaks they can crack the large seeds faster (Grant 1981b). Moreover *magnirostris* are presumably able to dissipate heat with relatively little water loss as a result of having large beaks (Greenberg et al. 2012). So in addition to genetic factors that contributed to their robustness, these two individuals started long lives under favorable environmental circumstances.

Another lesson is that with recurrent immigration important events with long-term consequences may occur a few generations after the founding of a population (see also chapters 7 and 11). For example, a single immigrant male, 6102, had a disproportionate effect on the genetic (microsatellite) and song characteristics of the population from 1991 onward, a little more than eight years after a breeding population was founded. Genetic intervention and augmentation by this robust male helped the population to emerge from a genetic bottleneck and to increase substantially in number of breeders (fig. 6.1). Genetic rescue has been observed elsewhere. An example occurred coincidentally in the same year in Sweden, when a single immigrant wolf (*Canis lupus*) rescued a severely bottlenecked population in Scandinavia, with almost identical results. It introduced 10 new microsatellite alleles, elevated heterozygosity, and eliminated inbreeding depression (Vilà et al.



Fig. 6.10 Large Ground Finches feeding. **Upper left:** *Croton scouleri* fruits. **Upper right:** Red aril of *Bursera graveolens* (on Genovesa) removed before the fruit is cracked (G. B. Estes). **Lower left:** *Tribulus cistoides* mericarp (K. T. Grant). **Lower right:** *Tribulus cistoides* mericarp cracked with beak braced against a rock.

2003; Adams et al. 2011 give a similar example). Short-term genetic rescue was documented in a study of Song Sparrows *Melospiza melodia* on Mandarte Island in Canada (Marr et al. 2002).

The fourth factor, competitive dominance, forms the subject of the next chapter.

Summary

G. magnirostris became a member of the community of finches breeding on Daphne when, in 1982–83, two female and three male immigrants stayed to breed. They produced 17 fledglings, among which only a sister and two brothers survived and bred. This illustrates the precarious nature of colonization at the earliest stages. We used observations of pairs, diets, morphological measurements, and microsatellite DNA

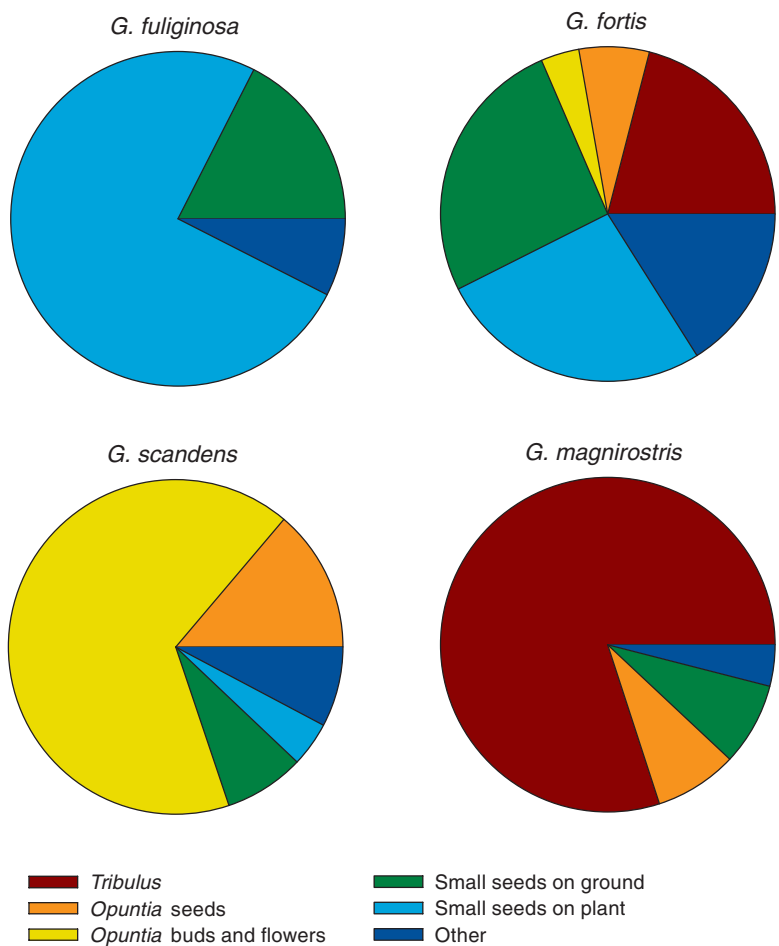


Fig. 6.11 Dry-season diets of the four *Geospiza* species on Daphne. Feeding observations were made on large samples of birds in January to March 1985 and 1986 spanning a drought: 164 *fortis*, 116 *scandens*, 40 *fuliginosa*, and 15 *magnirostris*. The food eaten by an identified bird was recorded only once, when it was first seen feeding. Dietary categories are *Tribulus* seeds, *Opuntia* seeds, *Opuntia* flowers or buds, small seeds on plants, small seeds on the ground, and others, including insects and nectar from *Bursera* and *Portulaca* flowers. All *fuliginosa* and some *magnirostris* were immigrants. Feeding is illustrated in figures 2.19, 2.20, B.2.2, and 6.10.

markers to interpret the initial colonization and subsequent population development. Some expectations from theory were confirmed. The environment was favorable, founders were genetically variable, inbreeding occurred at a high frequency as a result of random mating when numbers remained low, inbreeding depression in survival was strong, and some microsatellite alleles were lost. Unexpectedly colonization was not random with respect to genotype, as often assumed by theory: individuals that immigrated and bred differed from those that disappeared. Immigration occurred repeatedly, from more than one island, with the result that introgression of alleles from later colonists increased genetic variation and alleviated the effects of inbreeding depression. One exceptional individual had a disproportionate effect on the genetic and song characteristics of the population when, eight years after the breeding population was founded, he introduced 11 new autosomal alleles and a new song type, which rapidly became the most abundant type. The arrival of this particularly robust individual at a time when the population was showing signs of inbreeding depression illustrates the role of chance in colonization. Thus the characteristics and fate of the population were molded by an interplay of stochastic and deterministic processes (fig. 4.1) that affected genotype, phenotype, and a culturally inherited trait, song. The interplay governed which particular individuals stayed to breed and, as modulated by the environment, their subsequent success.