

Chapter Title: The Future of Finches on Daphne

Book Title: 40 Years of Evolution

Book Subtitle: Darwin's Finches on Daphne Major Island

Book Author(s): Peter R. Grant and B. Rosemary Grant

Published by: Princeton University Press

Stable URL: <http://www.jstor.com/stable/j.ctt5hhncc.20>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Princeton University Press is collaborating with JSTOR to digitize, preserve and extend access to *40 Years of Evolution*

JSTOR

PART 4

Syntheses





The Future of Finches on Daphne

Scientists cannot predict the future any better than anyone else—even about their own field of research.

(Kendrew, 1966)

Now if I wanted to be one of those ponderous scientific people and “let on” to prove . . . what will occur in the far future by what has occurred in late years, what an opportunity is here!

(Mark Twain 1883, pp. 172–173)

Introduction

OUR GOAL HAS BEEN TO GAIN INSIGHTS into the past by studying the present for long enough to capture significant change (Grant and Grant 1996c, 2011b), to use the information to extrapolate to the broader context of the Darwin’s finch radiation (Grant and Grant 2008a), and to look into the future and ask such questions as what will the Daphne finch community be like at the end of the century? Predictions are hazardous (appendix 10.1), as the cautionary quotations above imply; nonetheless 40 years of experience are a better basis for extrapolation than, say, 4 years.

The present is a guide to both the past and the future. Contemporary study of finches identifies the most important environmental factors that govern their fates. The Daphne study shows that fluctuations in annual rainfall are more important than changes in temperature (Grant

et al. 2000), that droughts have more severe selective effects than abundant rain, and that the effects of any one drought are conditioned by preceding conditions (i.e., how past rainfall has affected the vegetation and food supply of the finches). It shows that two plant species are crucial for the survival of two of the finch species: *scandens* is dependent on *Opuntia* cactus, and *magnirostris* is dependent on *Tribulus*. Members of the Big Bird hybrid lineage are dependent on both. These facts are unlikely to change in the future.

The Past as Context of the Present

Daphne was formed perhaps as recently as 23,000 years ago as a volcanic satellite of Santiago (Geist et al. MS). It became an island about 15,000 years ago when a rapid rise in air temperature caused polar ice melting (Blard et al. 2007, Deschamps et al. 2012), initiating a rise in the level of seawater (box 14.1), and Daphne became separated from an enlarged Santa Cruz Island (fig. 2.4; Grant and Grant 1996b, Geist et al. MS). Continued rise of about 100 m in the next 9,000 years (Grant et al. 2012) reduced the height of the island to half (~ 120 m) and increased its isolation to about 8 km. As the island shrank in size, it may have lost species. In the light of finch communities elsewhere in the archipelago (Grant 1986) the species most likely to have been lost is *Camarhynchus parvulus* (Small Tree Finch).

The history of Daphne and other Galápagos islands has been one of repeated and often rapid climatic change. Conditions were either drier than now or as warm and wet but no wetter (Colinvaux 1972, Restrepo et al. 2012). Periods of one or more centuries in which El Niño events were common alternated with periods when they were apparently scarce or lacking (Anderson 1992, Moy et al. 2002, Riedinger et al. 2002, Rein et al. 2005). About 3,000 years ago an essentially modern climate replaced a drier one. The question we would like to answer is whether observations on Daphne for 40 years are an adequate representation of climatic swings and evolutionary events over centuries and millennia. How frequent are extremes beyond the range of our observations, and what were their effects on vegetation and the finches? Climatic fluctuations are known, whereas evolutionary events must be inferred. We concentrate mainly on rainfall.

The Galápagos coral core data spanning nearly 400 years provide an indirect record of sea-temperature fluctuations and associated rainfall (Dunbar et al. 1994). The record shows that it takes a long time for environmental variation to approach an asymptote (~170 years: Grant

Box 14.1 Mollusks as Markers

Fragments of four or five fossil bivalve mollusks (fig. B.14.1) substantiate the reconstruction of Daphne during the lowering of seawater. The fossils are a mixture of actual shell fragments and impressions in a carbonate rock, together with coral fragments and sea-urchin spines. They were found in sector 19 (fig. A.3.1) in 1991, at an estimated height above seawater of 10–20 m and 20 m upslope from the sea cliff. The mollusks lived in the intertidal, and the valves were washed into calmer waters where the rock was formed. Their age is not known. They have been tentatively identified by Matthew James (pers. comm.) as those of a contemporaneous Galápagos species, *Periglypha multicostata* (Sowerby 1835), which is known to occur as fossils on other Galápagos islands.

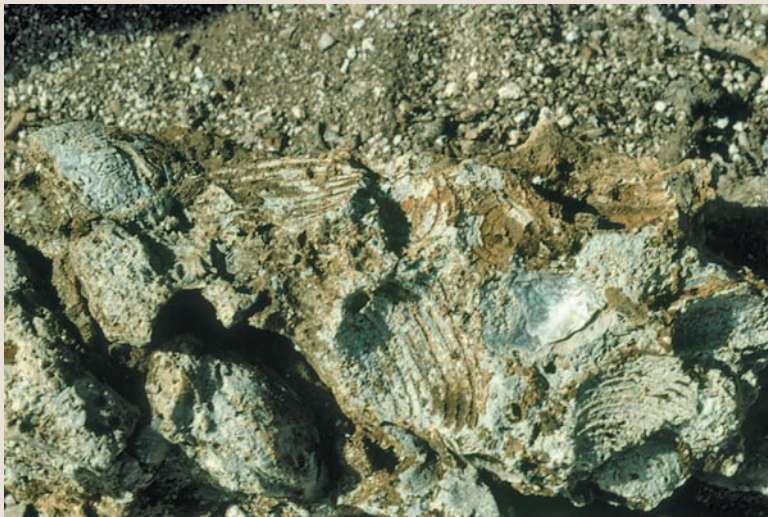


Fig. B.14.1 Fossil bivalve mollusks, tentatively identified as *Periglypha multicostata* (M. James, *in litt.*). It is evidence of submergence of Daphne's peripheral area.

and Grant 1996c). Even though conditions were warmer in some half centuries than others, and more variable in some than others, there is no evidence of a long-term trend or of large-amplitude changes preventing a close approach to an asymptote (fig. 14.1).

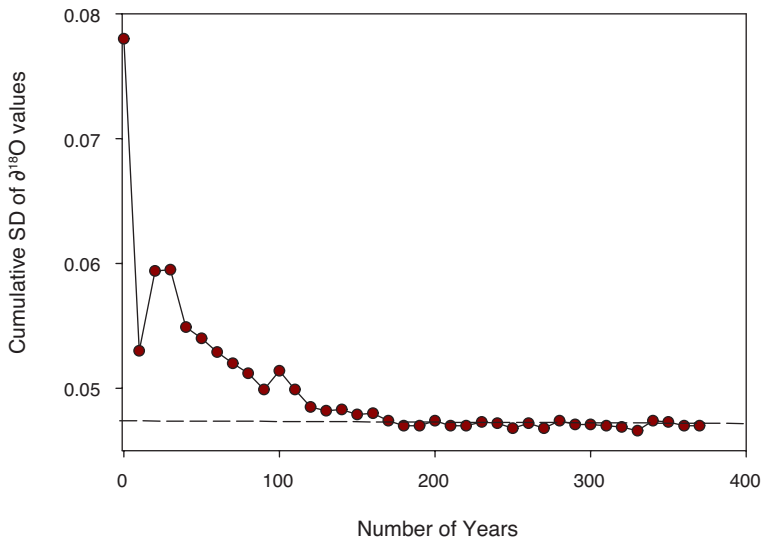


Fig. 14.1 Environmental variation through time. Stable oxygen-isotope ratios provide a measure of sea-surface temperatures in the Galápagos corals *Pavonia clavus* and *P. gigantea*, 1607–1981 (data from Dunbar et al. 1994). Original $\delta^{18}\text{O}$ values have been ln-transformed, and negative signs have been ignored: high values correspond to high sea-surface temperatures. Cumulative standard deviations (SD) from the first five years onward have been expressed as a function of years to show the rate at which an asymptote is approached. It took 170 years to reach approximate constancy: there is no sign of recent upward or downward trends. Variation in isotope values may also reflect variation in rainfall, as they are correlated with rainfall on Santa Cruz ($r = 0.551$) in the years 1965–81 (Grant and Grant 1996c).

What are the extremes in the record? There is no evidence of an El Niño event more severe than the 1982–83 one. Droughts could have strong effects on finch populations if they last for many years. However, short-term reversals between El Niño events of abundant rainfall and La Niña droughts, brought about by the Southern Oscillation of atmospheric pressure differences across the tropical and southern Pacific (Philander 1990), typically prevent severe climatic (drought) conditions from lasting long. In fact there is only one sequence of three successive years (1637–39) of cool sea-surface temperatures and hence low rainfall (Dunbar et al. 1994) in the Galápagos coral core record (Grant and Grant 1996c), and none longer. Ecological and evolutionary effects at this time were possibly more severe than those observed on *Daphne* in 2003–5. With this single exception, we conclude that finches were exposed to the same range of environmental conditions during

the last 40 years as their predecessors experienced over the preceding 400 years.

The likelihood of more extreme conditions and effects increases as we go back further in time. Annual climatic fluctuations are revealed by a variety of proxy measures, including tree rings and pollen, diatoms, and spores from lake, ice, and coral cores (Philander 1990, Michaelsen and Thompson 1992, Flexor 1993, Cobb et al. 2003). These show once-in-a-millennium El Niño events of extraordinary severity occurring about 900 and 1,400 years ago (Michaelsen and Thompson 1992, Restrepo et al. 2012) as well as much earlier (McGlone et al. 1992). They might have had drastic effects upon *Opuntia* cactus and Cactus Finches, in the light of observations on Daphne during the 1982–83 El Niño event and aftermath. Extinction, recolonization, and strong evolutionary change are more likely on this time scale.

MERGE-AND-DIVERGE DYNAMICS

Ecological conditions in the terrestrial Galápagos environment depend on climatic conditions that in turn depend on oceanographic conditions (Grant et al. 2000). These conditions fluctuate on long timescales. Thirty-four years before our study began, cactus bushes were much more sparse on the inner slope of the crater (fig. 1.5) than at any time during our study. This indicates more arid conditions occurred then, and photographs in Beebe (1924) show the same.

Sea-surface temperatures fluctuate at approximately 25-year intervals (Chavez et al. 2003). Our study began at the end of a relatively cool period (Guilderson and Schrag 1998), and the Galápagos are perhaps now beginning to experience the next cool period. If so, a switch from wet to dry conditions, back to the conditions prevailing in the 1970s, may no longer allow hybrids to survive well. If this happens, the current trend of convergence will be reversed and the species will diverge. Thus, over the long term *fortis* and *scandens* on Daphne may alternately converge through hybridization and selection and diverge through selection alone. They may have been doing that for centuries, if not millennia.

The Present as a Guide to the Future

All else being equal, the past 40 years allow a projection into the future by simple extrapolation. However, the origin and flourishing of the hybrid lineage is a reminder of the inherent unpredictability of the bio-

logical system on *Daphne*. Compounding the uncertainty of the future is the prospect of climate change that is being experienced globally (Latif and Spellman 2009). It has given rise to concern about how rising temperatures, more severe droughts, and the increasing frequency of extreme weather events will influence natural communities, and uncertainty as to the consequences (McMichael 2012). Will populations alter reproductive schedules and activity patterns, or shift in latitudinal or altitudinal distribution (Davis et al. 2005, Gardner et al. 2009, Tingley et al. 2009, Colwell and Rangel 2010)? Small populations on islands, and in habitat islands on continents, may be especially vulnerable to the effects of increasing temperatures because they have no escape in space (e.g., Santisteban et al. 2012). Will populations have sufficient time and genetic variation to respond evolutionarily by adapting in physiology, morphology, or in other ways (Lynch and Lande 1993, Gienapp et al. 2008, Gomulkiewicz and Houle 2009, Dillon et al. 2010)? What will be the ecological and evolutionary consequences of altered environments (Parmesan 2006, Lavergne et al. 2009)? Uncertainties are so large that answers have to be full of mights and maybes.

GLOBAL WARMING AND GALÁPAGOS

Climate projections for the rest of the century indicate a moderate rise in temperatures for Galápagos of about 2°C–3°C, a rise of 3°C–5°C for the continent, a 1 m increase in sea level, and, as elsewhere, an increase in climate variability and extreme events (Solomon et al. 2007, Willis and MacDonald 2011). Possible geophysical effects have been registered already. A warming trend in tropical Pacific waters began in the mid-1970s (Guilderson and Schrag 1998, Zhang et al. 1998), associated with a reduced gradient of sea-surface temperatures across the Pacific and a shift in atmospheric convection from the east to central Pacific (Tokinaga et al. 2012). The altered spatial pattern is likely to become much more frequent with global warming (Yeh et al. 2009), and El Niño events may intensify. Thus according to current signs climatic conditions will not return this century to those prevailing before the 1970s.

If the global climate change is already affecting Galápagos climate, we might see a signal in the rainfall data, with a gradual increase in average rainfall and an increase in the variance. No such signal is apparent in figure 14.2. This figure shows no change after the first 10 years in the long-term average rainfall with successive annual additions to the cumulative total. The only possible signals we have experienced were an unusually long El Niño event (1991–93), even longer outside Galápagos waters (Trenberth et al. 1996), and exceptionally high tem-

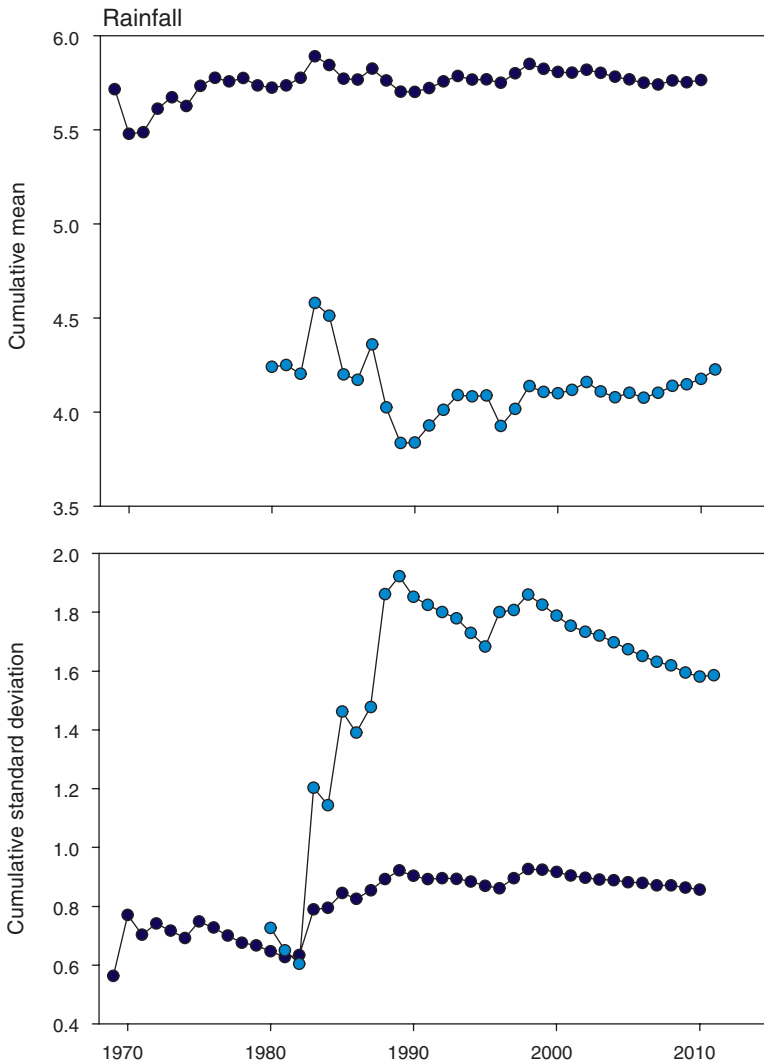


Fig. 14.2 Rainfall (mm) on Daphne (pale blue) and Santa Cruz (dark blue) plotted on a natural log scale as cumulative means (above) and standard deviations (below). The first point on each figure is the average for the first five years. By plotting numbers as a cumulative function of time, we show how they approach a quasi-equilibrium state. The figure shows that rain is lower and more annually variable on Daphne than at the southern coastal location on Santa Cruz; the north shore of Santa Cruz is drier and possibly more variable. Long-term averages are reached in a smaller number of years on Santa Cruz than on Daphne and remain approximately constant, with no obvious tendency to increase or decrease. Annual variation (standard deviation) tends to decline; extreme values have diminishing effects on long-term estimates.

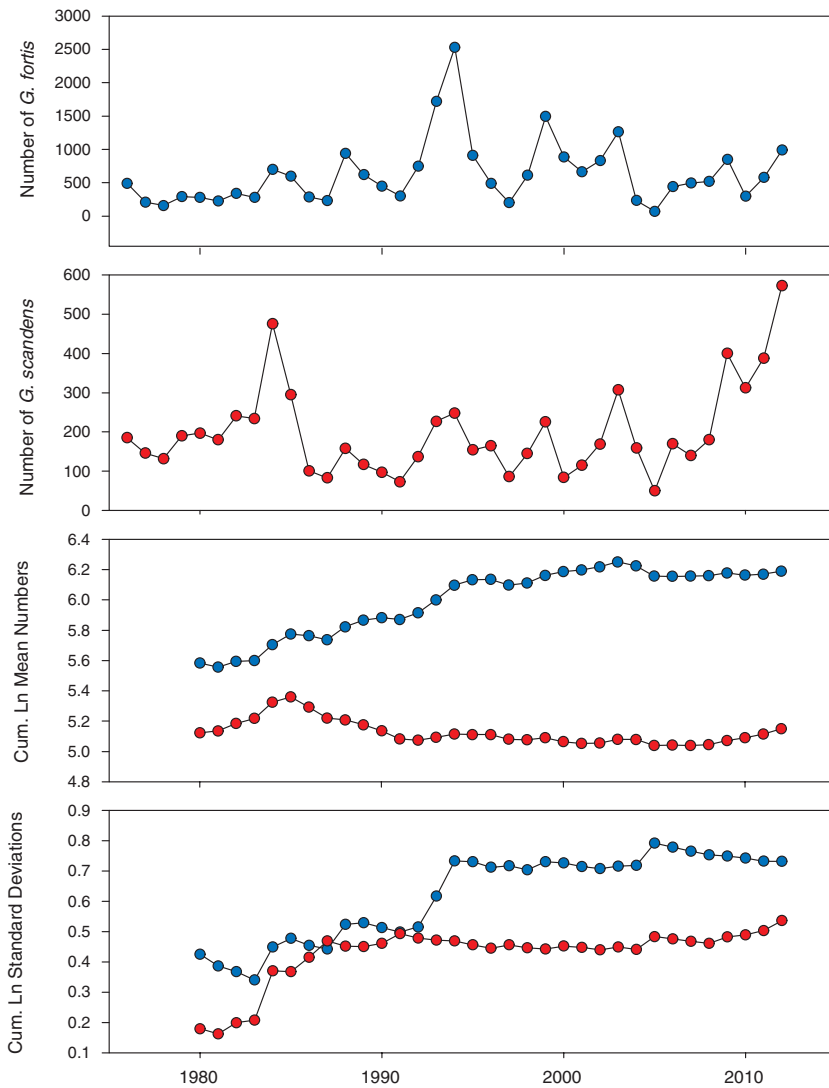


Fig. 14.3 Finch population sizes on Daphne. January 1 estimates are shown in the upper two panels for *fortis* (blue) and *scandens* (red). Annual averages and standard deviations on a natural log scale are plotted as cumulative functions of time in the two panels below, as in figure. 14.2. For both species approximately constant long-term estimates in the cumulative panels were reached in the early 1990s, in other words, after about 15 years. After that, large increases in population sizes as a result of El Niño conditions favorable for breeding had progressively smaller influence on the long-term estimation of averages and standard deviations. *G. fortis* were always more abundant than *scandens*, and fluctuated in numbers much more as a result of occasionally prolific breeding followed by population crashes in droughts.

peratures in the sea and air during the 1997–98 El Niño event, higher even than in the longer and more intense event of 1982–83 (Grant et al. 2000). High temperatures during the 1997–98 El Niño had no conspicuous effect upon the vegetation or the demography of the finches beyond the affected years (fig. 14.3). Long-term average numbers did not increase with successive additions of annual values, with one exception; *scandens* were more abundant in the last year (2012) than in any of the preceding 35 years.

Finch Futures

MEANS AND EXTREMES

Consequences of climate change in Galápagos are difficult to anticipate because there are two aspects to it: average temperature and rainfall and the variance of both. These could have opposite effects on vegetation, arthropods, and finch populations, so the outcome will depend on which one predominates. We focus on rainfall.

An increase in average rainfall will make the climate, vegetation, and finch dynamics on Daphne a little more similar to current conditions on Santa Cruz. Over the long term Daphne has low average rainfall with a high standard deviation, whereas a similar coastal location on the south coast of the much larger Santa Cruz Island has a high average rainfall but low standard deviation (fig. 14.2). Expressed as a coefficient of rainfall variation, Daphne rainfall variance is 60.9% of the mean whereas at the Santa Cruz locality the variance is only 12.6% of the (much higher) mean. The contrast in average rainfall on the two islands and the relative variation implies that population fluctuations are greater on Daphne (they have not been studied on Santa Cruz). Since natural selection occurs under extreme drought conditions causing high mortality on Daphne, it is likely that selection is rarer on Santa Cruz, where finches can move to higher altitudes and encounter different foods in a wetter climatic zone. In 18 of the 37 years in the period 1976–2012 annual rainfall on Daphne was lower than the *minimum* recorded at the coastal site on Santa Cruz in the same period. Therefore selection of the sort observed on Daphne may never have occurred on Santa Cruz during this period. In the future, Daphne may receive more rain, finch population sizes may increase and fluctuate above and below a higher average, and, importantly, selection due to mortality may occur less often.

A different set of consequences follows from the anticipated increase in frequency of extreme climatic events. If intense droughts become

more frequent on Daphne, despite a general tendency for rainfall to increase, finches may be subject to more frequent or intense selection. Annual variation in population density (fig. 14.3) may increase, and so will the risk of extinction (Grant and Grant 1996c). Computer simulations show broad-scale vulnerability of bird populations to the effects of environmental stochasticity (Sæther et al. 2005). In a comparison of 13 species of birds Sæther et al. (2002) found that *Daphne scandens* and *fortis* ranked first and second in environmental stochasticity, and first and third in coefficients of variation in population size over 15 years.

These general considerations apply to all the finch species on Daphne. Some responses to changes in climate are species-specific.

G. FORTIS, SCANDENS, AND FULIGINOSA

Extrapolating beyond measurements, it is reasonable to suppose that populations will prosper in El Niños, suffer in droughts, and their fates will be determined by the relative strengths and durations of these opposing influences. An increase in average rainfall and predominant production of small seeds could foster a continued fusion of the *fortis* and *scandens* populations through introgressive hybridization. On the other hand the current trend of convergence might be reversed if intense droughts increase in frequency and finches become more dependent at those times on *Tribulus* and *Opuntia*. These circumstances would favor greater specialization of *fortis* on *Tribulus* fruits, which would now be more common, and *scandens* on *Opuntia*. *G. scandens* with short beaks as a result of introgressive hybridization would be at a selective disadvantage because they are likely to be relatively inefficient at exploiting *Opuntia* cactus flowers for pollen and nectar. Our reasoning presupposes the continued existence of *Opuntia* on Daphne, and in a warmer and wetter climate this may not be correct.

G. MAGNIROSTRIS

This species is dependent on *Tribulus cistoides*, and to a lesser extent the seeds of *Opuntia echios*. A similar situation exists on the island of Genovesa, where the dry-season diet of *magnirostris* is dominated by a single seed type, *Cordia lutea* (Grant and Grant 1989a). If *Tribulus* or *Cordia* are adversely affected by an altered climate, then *magnirostris* could disappear from one or the other island. Given the near extinction of *magnirostris* in 2005 when the *Tribulus* food supply was nearly exhausted, a small intensification of droughts might administer the coup de grâce for this species on Daphne. Introduction of a disease

specific to *Tribulus* would have the same effect. In 1982 a fungus adversely affected *Tribulus* seed production (Grant and Grant 1993).

HYBRID LINEAGE

It is highly unlikely that we have witnessed the origin of a long-lasting species, but not impossible. The future of the Big Bird lineage will be determined by environmental fluctuations but also by effects of inbreeding, and by ecological and possibly reproductive interactions with other members of the finch community.

According to the relationship between species number and island area among Galápagos islands, Daphne should have two species (fig. 14.4). The establishment of *magnirostris* added a third species to the *fortis-scandens* community. The total becomes four when the lineage

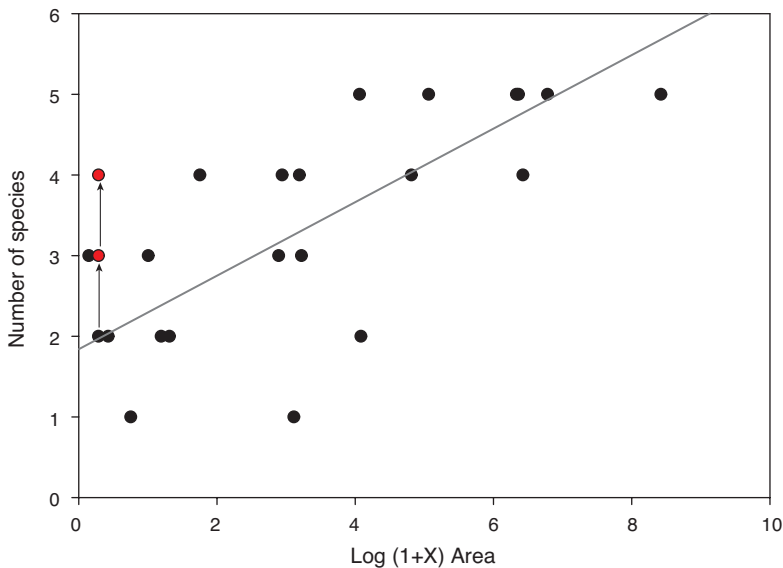


Fig. 14.4 Daphne has more species than predicted from the regression of number of species on the logarithm of area (km^2) for 22 islands. The predicted number is 2. The actual number became 3 with the establishment of *magnirostris* (chapter 6) and is 4 with the inclusion of the hybrid lineage (connected with arrows). For the relationship without Daphne, $r = 0.712$, $p = 0.0002$; with Daphne included as a four-species island, $r = 0.641$, $p = 0.001$. This is a specific example of a global relationship: a short distance from nearest landmass modifies the way area influences the number of species on an island (Kalmar and Currie 2007). From Grant and Grant 1996c.

is counted as one species and five if the occasional *fuliginosa* is included as well (chapter 6). Ignoring *fuliginosa*, the Big Bird lineage has the poorest prospects for long-term persistence because it is much rarer than the other three species. The lineage increased to a maximum of approximately 30 individuals in 2010 (fig. 13.15). Fitnesses may be jeopardized by inbreeding. Effects of inbreeding on fitness and random loss of alleles may increase in time if the population remains small. *G. magnirostris* escaped this fate through repeated immigration (chapter 6), whereas no further immigration is known to have occurred in the hybrid lineage.

The lineage may have an alternative escape through breeding with *fortis*, *scandens*, or even *magnirostris*. In other species it has been found that genes introduced into inbred populations spread rapidly (Saccheri and Brakefield 2002). If members of the lineage breed with any of the other species, the outcome will depend on the direction of gene flow, the rates of introgression of genes, and the fates of those genes. For example, if a female from the lineage breeds with a male *fortis*, the offspring, having imprinted on the father, are likely to breed with *fortis*. In this case genes flow out of the lineage. However if a male from the lineage breeds with a female *fortis*, the offspring, having imprinted on the father's song, are likely to breed with members of the lineage, and genes will flow from *fortis* into the lineage. Repeated introgression of heterospecific alleles, even if infrequent, could nullify the effects of inbreeding in the lineage, restore mean fitness, and allow the population to increase. Since this would also result in the production of small offspring, it might increase the probability of further interspecific breeding in subsequent generations and a gradual fusion of the lineage with *fortis*, an example of reproductive absorption, as happened with line A (chapter 9).

Thus the Big Bird lineage may become extinct, through environmental and demographic stochasticity, deleterious effects of inbreeding, or introgression. On the other hand it may flourish by exploiting a unique, generalized niche. The critical factor determining the future of the lineage may be the rate of interbreeding with other species.

These speculative changes are likely to be dependent on the demographic dynamics of the other species in the community, on their future evolution, and on any change in ecological interactions with those species such as greater competition for food. For example, long-term coexistence of the lineage with the other species could be weakened by an increase in numbers of the principal competitors, the large-beaked members of the *fortis* population. The future of the Daphne community could be monitored every generation (chapter 4), that is, at five-year

intervals, to follow the ecological and evolutionary fates of the new lineage and the other resident species. The community could provide a valuable window into long-term effects of climate change in a natural environment.

INVASIVE PLANT SPECIES AND DISEASE

The future of Daphne finches is uncertain for one final reason: introduced alien organisms, both plants and animals. The introduction of an invasive plant species could alter the dynamics of the plant community and the food supply of the finches. One such plant species, *Cleome viscosa*, has already arrived (fig. 14.5, appendix 1.1). It was introduced to neighboring Baltra, and has explosively spread on this and North Seymour Island. In the last decade we have found *Cleome* on Daphne around seabird nests on the lower plateau and adjacent outer slope (fig. 2.5) and removed them by hand to slow the expected increase in numbers and distribution. Several years of rainfall could make this



Fig. 14.5 Invasive plant. *Cleome viscosa*, a threat to the natural vegetation on Daphne and other islands.

monitoring and removal an impossible task. Some native plant species may be at risk.

Diseases such as avian malaria (*Plasmodium*) could enter the archipelago and devastate finches. A mosquito vector, *Culex quinquefasciatus*, has been present in the archipelago since 1985 (Whiteman et al. 2005). A similar threat is posed by West Nile virus, for which a possible vector (*Aedes taeniorhynchus*) is already present (Bataille et al. 2009a, 2009b).

Finches currently have two persecutors. In some years avipox is contracted by several finches (fig. 5.13), although on Daphne it has not affected survival (Huber et al. 2010). The parasitic fly *Philornis downsi*, known to be in the archipelago in 1964, is much more serious. It is now known from observations (Fessler and Tebbich 2002, Fessler et al. 2006, O'Connor et al. 2010) and experiments (Koop et al. 2011) to cause high nestling mortality of Darwin's finches and other bird species (Fessler and Tebbich 2002, Fessler et al. 2006, Koop et al. 2011). *Philornis* has been recorded intermittently on Daphne but is usually not there, being more prevalent in the moist habitats of high islands. This could change if droughts become scarcer and El Niño events become more frequent.

Genomes for the Future

Darwin set the evolution revolution in motion. The wheels are turning faster every year as a result of genomics. We began the study with no knowledge of how environmental variation caused finch evolution, and no knowledge of its genetic foundation. When we consider how much has been learned in 40 years, it becomes apparent that not only can we not answer all our questions; we cannot anticipate all questions themselves, as some will emerge only from knowledge gained in the future. For the immediate future, however, the crystal ball is clear. Genetic variation, within and among species, will be much better understood now that tools are available for studying whole genomes.

An exciting new era in finch biology began with the sequencing of the *magnirostris* genome in 2011 (Rands et al. 2013) and the *fortis* genome in the following year (Zhang et al. 2012). Genomes of the other species are being sequenced, and knowledge of the genetics of the adaptive radiation will be improved in three ways: in phylogenetic history, in the genetic changes accompanying speciation, and in the genetic basis of adaptive change. The foundation of such studies will be

direct measurement of genetic properties that are the subject of long-term research of microorganism evolution in the laboratory (e.g., Blount et al. 2008) but are currently out of reach of a field study of finches (chapter 9): properties such as mutation, gene duplication, recombination, chromosomal inversions, pleiotropy, linkage, and their various frequencies. Genomic data will reveal what changes in genetic architecture take place during speciation and hint at the causes (Feder et al. 2012, Nosil and Feder 2012). For example, changes may involve selective sweeps, although they are likely to be fewer and more restricted than in genetically incompatible species such as the two species of *Ficedula* flycatchers in Scandinavia (Ellegren et al. 2012). Comparative genomics may also reveal genetic factors that are responsible for, and thus help to explain, the relatively rapid radiation of Darwin's finches and their Caribbean (Burns et al. 2002) and continental (Burns and Naoki 2004) relatives. The next and very large challenge will be to identify the functions of genes to answer questions of what they do and how their expression is controlled and regulated. A particularly promising area of investigation is the genetic basis of beak variation (fig. 12.2), where a start has already been made (Abzhanov et al. 2004, 2006, Mallerino et al. 2011, 2012).

One goal of our future studies is to investigate the genetic changes that take place in a population when it is subject to directional selection on beak size or shape. For a given selection regime how repeatable is the genetic response? Does each selection event result in unique changes in combinations of genes and their regulators stemming from redundancy in genetic networks? Are subsequent changes equally likely, or does one genetic change constrain or potentiate another? Can genetic limitations on phenotypic change be identified? A second goal of future studies is to determine the genetic consequences of hybridization and backcrossing. Hybridization can promote genomic reorganization through the disruption of DNA methylation and mobilization of transposable elements (Michalak 2009). The question we would like to answer is how much evolutionary novelty is generated by restructuring of the genome through introgressive hybridization (Fontdevila 2005)? When genes are exchanged between finch species and new genetic constitutions are thereby constructed, what combinations work well, and why, and what do not? From answers to these questions insight may emerge into the genetic factors that made the Big Bird lineage a success in the first few generations of inbreeding.

Whatever is discovered at genetic level will need to be interpreted in the light of environmental effects on phenotypes (fig. 4.1). This is where the Daphne study can make a contribution to the future.

Summary

The chapter describes the history of Daphne and the Galápagos, and uses information from the long-term study of the finches on Daphne to project into the future. Observations on Daphne for 40 years are an adequate representation of climatic swings and evolutionary events over centuries, as indicated by Galápagos coral core data spanning nearly 400 years that provide an indirect record of sea-temperature fluctuations and associated rainfall. Climate projections for the rest of the century indicate a moderate rise in temperatures for Galápagos of about 2°C–3°C, a 1 m increase in sea level, and, as elsewhere, an increase in climate variability and extreme events. The future of the finches depends on which of two climatic features prevail: an increase in average rainfall or an increase in extremes. If Daphne receives more rain, finch populations may increase in average size but fluctuate less and, importantly, selection due to mortality may occur less often. On the other hand if intense droughts become more frequent, more severe, or last longer, despite a general tendency for rainfall to increase, finches may be subject to more frequent or intense selection. We speculate on the future of the hybridizing species, and the Big Bird lineage, as well as *magnirostris*, in the face of anticipated changes. Unknown factors such as diseases and invasive plant species add to uncertainty about the future: they could have substantial effects upon the finch populations. A new era in understanding finch evolution has just begun with the sequencing of *magnirostris* and *fortis* genomes, and the chapter concludes with some remarks about what is likely to be learned from genomic research in the near future.