Epilogue

It is now more than forty years that I have paid some attention to the ornithology of this district, without being able to exhaust the subject; new occurrences still arise as long as any inquiries are kept alive.

(Letter XLIX, May 7, 1779: White 1789 [1877], p. 246)

The main difference [between short-term and long-term research] is that with a prolonged study of a natural system, the scientist is not in charge of the schedule.

(Edmondson 1991, p. 235)

Reflections on the Value of Long-Term Studies

LONG-TERM PROCESSES require long-term study. A few such field studies have contributed disproportionately to our knowledge of how natural populations fluctuate in numbers and evolve (e.g., Anderson et al. 1991, Weider et al. 1997, Majerus 1998, Clegg et al. 2002, Beaugrand and Reid 2003, Packer et al. 2005, Baltensweiler et al. 2008, Ozgul et al. 2009, Armitage 2010, Clutton-Brock and Sheldon 2010, Husby et al. 2010, Qvarnström et al. 2010, van der Pol et al. 2010, Hanski 2011, Alberts and Altmann 2012, Lebige et al. 2012, Rijssel and Witte 2013). In the experience of many field biologists the longer the study persists, the greater the insights into the functioning of the study system, and the greater the likelihood of making new discoveries, especially in strongly fluctuating environments (Strayer et al. 1986, Likens

et al. 1989, Edmondson 1991, Cody 1996, Billick and Price 2010). This is an argument for persistence and continuity: persistence to observe, and continuity to interpret, both ecological and evolutionary change. The argument is most cogent for studies of natural and unmanipulated populations whose members are individually identifiable.

In concluding this book we highlight with examples two ways in which benefits are gained from long-term investigations: from enlightenment that comes from the gradual accumulation of data over many years and, in contrast, from rare and unpredictable events.

LONG-TERM DYNAMICS OF A COLOR POLYMORPHISM

In 1978 we discovered a beak color polymorphism in nestlings (fig. 17.1): beaks were either pink or yellow (Grant et al. 1979). The frequency of the yellow morph was distinctly higher among *scandens* than *fortis* nestlings. These observations motivated us to continue recording colors to address questions of inheritance, long-term frequencies, and function, even though they had nothing to do with our primary research program. By continuing, we established that (a) the polymorphism was not a transient one but approximately stable in both *fortis* and *scandens* (fig. 17.2), (b) the frequency of the rarer yellow morph was always higher in *scandens* than in *fortis*, and (c) the morph frequencies of parents and offspring were consistent with a simple model of mendelian inheritance, yellow being recessive to pink (tables A.17.1 and A.17.2). Smaller samples of *magnirostris* showed much less stability in frequencies (fig. A.17.1 and table A.17.3).

A similar polymorphism with similar inheritance is well known in chickens (Bateson 1902, Dunn 1925, Hutt 1949). The responsible gene has been identified (Eriksson et al. 2008) and recently found to be the same gene in Darwin's finches (L. Andersson pers. comm.). Located on chromosome 24 (in chickens), it produces β-carotene deoxygenase 2 (BCO2), an enzyme that cleaves β-carotene into a colorless precursor of vitamin A (Walsh et al. 2011). A *cis*-acting regulatory, tissue-specific mutation inhibits this function in the skin but not in the liver or intestine (Eriksson et al. 2008), and ingested carotenes are deposited in the beak, skin, legs, and fat, where they give the bird a yellow appearance. Birds lacking the mutation appear pink because the blood supply can be seen.

What maintains the polymorphism in its current state, and why is the yellow frequency higher in *scandens* than *fortis*? The answer to the first question appears to be heterozygous advantage (fig. 17.3). The heterozygotes have a clear survival advantage over the yellow homozygotes in *fortis* in our combined data and in three cohorts out of five.

Fig. 17.1 Nestling beak color polymorphism. **Upper left**: *magnirostris* nestling, pink. **Upper right**: *magnirostris* nestling, yellow, from the same nest. **Lower left**: *scandens* fledgling, pink. **Lower right**: *scandens* fledgling, yellow. The yellow morph is also illustrated in figures 13.5 and 13.8.
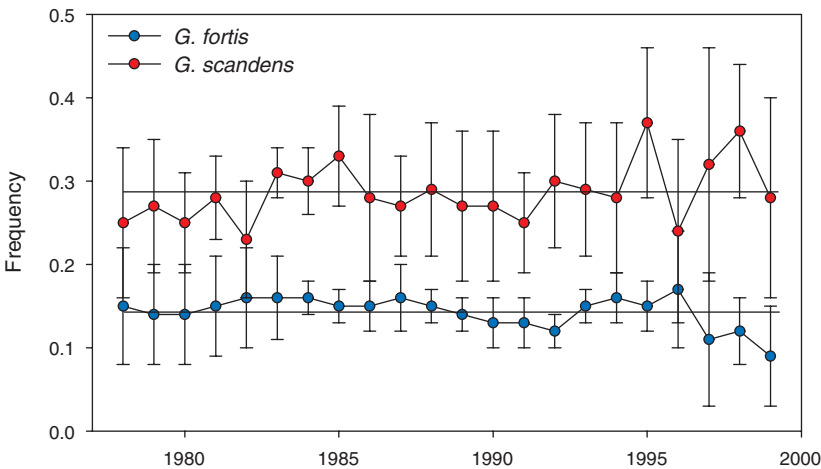

Fig. 17.2 Yellow-morph frequencies exhibit stability in *fortis* and *scandens*. Vertical bars are 95% confidence limits on frequency estimates. Sample sizes are in table A.17.3. After 1999 sample sizes fell below 20 until 2011. In that year the *fortis* frequency was 0.12 ± 0.15 ($n = 34$), and the *scandens* frequency was 0.35 ± 0.22 ($n = 17$). Frequencies of the yellow phenotype in *magnirostris* were much less stable (appendix 17.1), principally as a result of a population bottleneck in the severe drought of 2003–5. Horizontal lines indicate long-term averages.
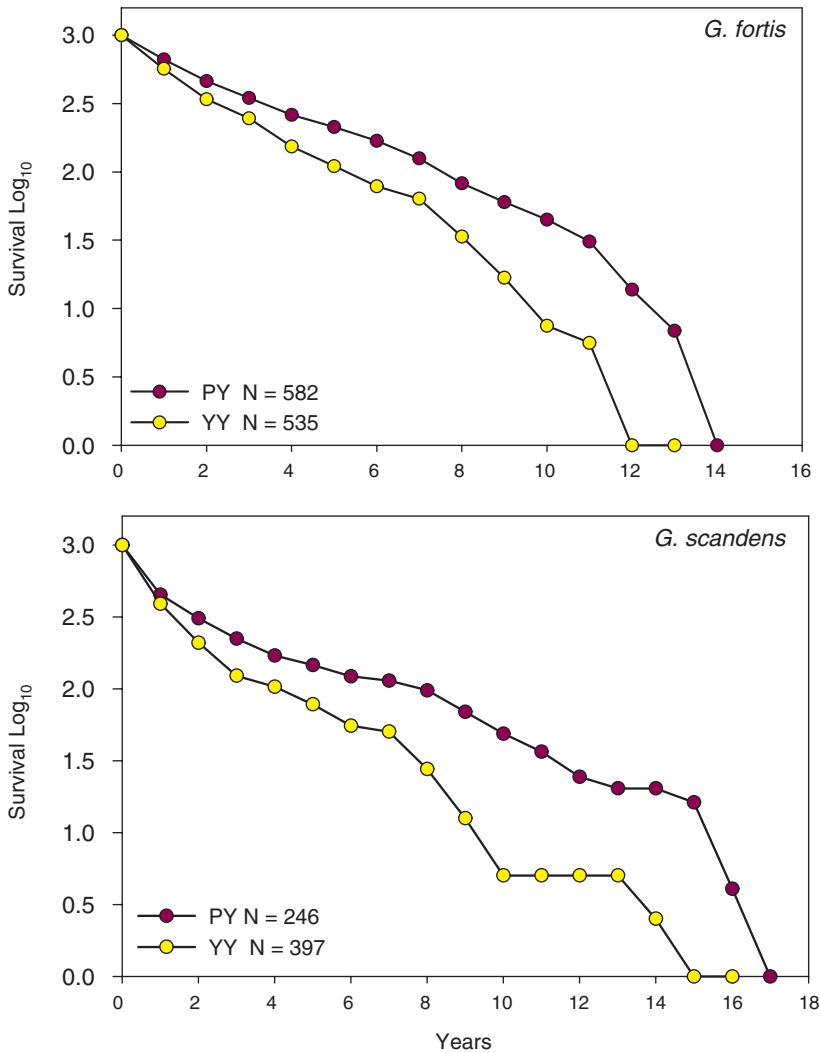
Fig. 17.3 Survival of yellow homozygotes and pink heterozygotes in five cohorts combined. The cohorts hatched in 1981, 1983, 1984, 1987, and 1991. Parents of heterozygotes were identified by having one yellow-morph parent and one pink-morph parent. Offspring with pink-morph fathers and mothers could be either heterozygotes or homozygotes (pink) and therefore are not included. The differences in survival between heterozygotes and yellow homozygotes were significant in both *fortis* ($\chi^2 = 19.517, p = 0.000, n = 582$) and *scandens* ($\chi^2 = 7.695, p = 0.0055, n = 246$) with a proportional hazards model. The survival curves of pink phenotypes of unknown genotype lie between the curves for heterozygotes and yellow homozygotes. This implies a relatively low survival of the pink homozygotes, and hence an advantage to heterozygotes, in comparison with both homozygote classes.

The heterozygotes also have the same advantage in *scandens* in our combined data and in two of the cohorts, but in one cohort the yellow homozygotes survived better than the heterozygotes.

The answer to the second question is not yet known, but there are two reasons for believing the higher frequency of the yellow morph in *scandens* is associated with exploitation of the carotene-rich pollen of *Opuntia* cactus (Grant and Grant 1981, Grant 1996). First, a fitness advantage to the yellow morph was experienced by the cohort of *scandens* produced in a year (1991) when cactus flowers were abundant during the nestling and fledgling phases. Cactus flowers were generally rare in 1981–87 when offspring of the other four cohorts were being fed by parents. Nevertheless first-year survival of the yellow morphs in the five cohorts was positively correlated with flower abundance ($r = 0.945$, $p = 0.005$), in contrast to a lack of correlation among the heterozygotes ($r = -0.100$, $p = 0.950$). The second reason is an association between yellow-morph frequency and cactus feeding in other populations of *Geospiza* species. On Wolf *difficilis* are uniquely monomorphic for the yellow morph (Grant et al. 1979) and are known to be dependent on cactus flowers during the breeding season. Likewise *conirostris* on Genovesa are strongly dependent on cactus flowers and have a high frequency of the yellow morph (Grant and Grant 1980b, 1989). All other finch populations that have been studied so far have lower frequencies of the yellow morph and are less dependent on cactus pollen.

The association with cactus feeding raises the question of why depositing carotenoids in tissues would be beneficial. Carotenoids have a signaling function in the context of courtship or territorial defense when deposited in feathers (McGraw et al. 2005, Hill 2007) or in the beaks of adults (Navarro et al. 2010, Walsh et al. 2011). However, there is no signaling value to the particular color of nestling beaks; parents do not feed the different-color morphs preferentially, according to our observations (Grant et al. 1979). Moreover the color can no longer be seen easily after the first week of life when melanin becomes deposited in the dermis of beaks and masks the underlying color.

A physiological value is more probable. Carotenoids function as a protective mechanism against oxidative damage by eliminating free-radical scavengers (Surai 2002, Hill and Johnson 2012) and by being the source of vitamin A. However, carotenoids and vitamin A are toxic in high concentrations (Russel 1999, Blomhoff 2001), leading, among other things, to impairment of skeletal muscles (Huggins et al. 2010). When Darwin's finches are feeding almost exclusively on *Opuntia* pollen, the high concentration of ingested carotenoids might be toxic and difficult for the liver to break down and excrete fast enough, or toxic

when stored as vitamin A in high concentration in the duodenum (Olson 1984, Tajima et al. 2001). An ability to sequester carotenoids in the beak and other peripheral tissues and release them gradually later could be advantageous. Yellow-morph chickens become bleached when nutritionally stressed, implying storage, release, and utilization of the carotenoids (P. B. Siegel pers. comm.).

The toxic avoidance hypothesis could be tested in other species. Although the polymorphism appears to be rare in bird species (Grant et al. 1979), pairs of related species can be found with either pink or yellow beaks or legs (e.g., European thrushes, *Turdus ericetorum* and *T. merula*, and gulls, *Larus argentatus* and *L. fuscus*).

This example of a genetic polymorphism followed through time illustrates the value of studying long enough to answer basic questions. It enabled us to establish the stability of the polymorphism and the association with cactus flowering. The long term was also needed to both detect and quantify a perturbing factor: introgressive hybridization between species with different morph frequencies. The effect is small (table A.17.4), however, because hybrids and backcrosses are a minority of the breeding populations.

RARE EVENTS AND THEIR CONSEQUENCES

A second value of long-term studies is the detection of rare but strong events, coupled with an understanding of the long-lasting consequences for the environment, for the organisms that exploit it, and for the relationship between the two (Grant and Grant 2010d). Short-term studies are more likely to miss such events and fail to interpret, or misinterpret, the consequences. The best example is the critical El Niño event of 1982–83. If we had stopped before that year, after the tenth field season, we could have concluded, incorrectly, that droughts invariably select for large body and beak size, hybrids do not breed, and the island cannot support another species. If we had started after 1983, we would have missed the colonization by *magnirostris* and the *fortis × scandens* hybrid that gave rise to the hybrid lineage. Our appreciation of the ecological and evolutionary importance of annual environmental variation and hybridization would have been greatly diminished (Grant and Grant 1996c).

We are intrigued by the idea that a chance conjunction of rare events may be especially potent evolutionarily. For example, extinction of dinosaurs and many other organisms at the same time may have been caused by a combination of two rare phenomena, the impact of an asteroid or comet and extreme volcanism, and not by one of them alone (Keller 2012, Renne et al. 2013). Similarly, the current success of the

hybrid lineage can be traced to two improbable and unrelated events in the 1980s. First, a *fortis-scandens* hybrid immigrated in 1981, and second, this was followed by the establishment of a breeding population of *magnirostris* at the end of 1982. Almost certainly an important factor in the success of both was the unusually favorable ecological conditions caused by the exceptionally prolonged, once-in-400-years El Niño event in 1982–83. There was no connection between the two colonization events. Twenty years later a connection was made when *magnirostris* determined the fate of the hybrid lineage by competitively eliminating most of the large members of the *fortis* population in the drought of 2003–5. Without the 1983 El Niño event and the population of *magnirostris* that it fostered, members of the hybrid lineage may not have survived beyond 2004. Rare events need not be exactly coincident to have profound and long-lasting effects, and the consequences may emerge after a long delay, as these examples illustrate. So although the environment determines the direction of evolution, there is an element of chance in what constitutes the environment at any one time; hence evolution is partly stochastic.

CHANGES IN PERSPECTIVE

With regard to the larger picture, results of studying finches on a single island for 40 years have changed our perspective on the broad context of adaptive radiation to a more dynamic, less unidirectional one. The results suggest a high degree of change and instability in the properties of populations and communities: species are repeatedly gained by fission and divergence, and lost by fusion and extinction (Grant and Grant 1996c, 2008a). The archipelago exhibits a similar instability through volcanism and changing sea-level and climates. Thus the radiation of finches is best viewed as the joint product of inherent (biological) and environmental dynamism, not marching inexorably to its current and fixed state in a constant and permanent environment, with ecological niches being sequentially filled along the way, but oscillating about a long-term trend of increasing diversity. The radiation cannot be fully understood without an appreciation of environmental change over short and long spans of time. Radiations of cichlid fishes in the African Great Lakes are other examples of recent and rapid radiations (Kocher 2004, Seehausen 2006, Santos and Salzburger 2012) (and much more prolific), and they appear to exhibit a similar dynamism. As in the finches, hybridization is believed to have been important early in the radiations (Seehausen 2004, Albertson and Kocher 2005) in an environment of profound tectonic and topographical change (Schwarzer et al. 2012).

Fig. 17.4 Finis. **Upper**: Field laboratory, kitchen, and cave for cool reflection (ch. 15, epigraph). **Lower**: Boots.

Long-term studies should build toward greater understanding and revelation and not simply repeat what has gone on before. We never reached an identifiable point of diminishing returns, or experienced a sense of completion. By the end of the study (fig. 17.4) the environment had changed (fig. 1.5), and the composition of the Daphne community of finches and the characteristics of the individual populations had been transformed (fig. 15.1). Change was continuing. In the last

year (2012) *scandens* were more numerous, *fortis* beaks were more variable, *scandens* beaks were more blunt, and *fortis* and *scandens* were more similar morphologically than at any other time in the study. Questions remain, to be answered in the future even as more arise. Therefore one conclusion we draw after 40 years is the same as the conclusion we reached after 20 years: long-term studies of ecology and evolution should be pursued in an open-ended way because for many of them there is no logical end point (Grant and Grant 1996c, 2010d). Daphne finches have much more to teach us.