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PART 3

Hybridization and Speciation





Long-Term Trends in Hybridization

Hybridization and backcrossing to one or both of the parent types can result in incorporation of alleles from one taxon into the gene pool of the other.

(Harrison 1993, p. 11)

Introgressive hybridization may, then, be a passing stage in the process of species formation. On the other hand, the adaptive value of hybrids may be as high as that of their parent; introgressive hybridization may lead to obliteration of the differences between the incipient species and their fusion into a single variable one, thus undoing the result of the previous divergent development.

(Dobzhansky 1941, p. 350)

Introduction

THE MAIN IMPLICATION of high hybrid fitness and continuing hybridization described in the previous two chapters is that interbreeding species should converge toward an intermediate morphology, and, if unchecked, this convergence would result in complete fusion of the previously reproductively isolated populations (Dobzhansky 1941, Clarke et al. 1998, Grant et al. 2004, Taylor et al. 2006, Grant and Grant 2008b, 2010b, Seehausen et al. 2008, Behm et al. 2010, Webb et al. 2011). It would then represent speciation in reverse, or despeciation of sister species such as *fuliginosa* and *fortis* (Grant et al.

2004). A better metaphor for the situation on Daphne is reproductive (Alerstam et al. 1978, Grant 1986) or genetic (Carney et al. 2000) absorption: *fuliginosa* are absorbed into the *fortis* population by hybridizing and backcrossing solely to *fortis*, with rare recurrent immigration replenishing *fuliginosa* numbers. *G. fortis* and *scandens* are not sister species; nevertheless, regardless of whether this could be regarded as a process of despeciation or not, they serve as a model for understanding the dynamics of recently formed species with incomplete barriers to gene exchange. A similar situation exists on the island of Genovesa with the interbreeding of a different set of three *Geospiza* species, *difficilis*, *conirostris*, and *magnirostris* (Grant and Grant 1989). In both cases the dynamics are entirely natural, in contrast to the several cases of speciation in reverse that have been attributed to human disturbance of the environment such as eutrophication, in fish (Seehausen et al. 2008, Behm et al. 2010, Webb et al. 2011, Vonlanthen et al. 2012) and planktonic *Daphnia* (Keller et al. 2008, Brede et al. 2009).

In this chapter we explore the implications of convergence through hybridization. We ask to what extent did the predicted convergence occur, was it sustained, and what effect did it have on morphological traits and their relationships? The chapter differs from the previous two in encompassing the full 40 years of study, which requires a meshing of heterogeneous data. Up to 1998 we were able to use pedigree information to assign individuals to breeding populations (species), whereas afterward we had to rely on song, morphology, and genetics. We begin by discussing the problem of individual assignments, and our solution, and then consider the effects of hybridization on phenotypic means, variances, and the differences between species over the long term. In the following chapter we discuss changes that take place as a result of selection over 40 years. These occur in dry years of no breeding, and for that reason can be separated from effects of hybridization: the first is associated with mortality, the second with reproduction. The remaining chapters use information on breeding biology, feeding ecology, and morphological evolution to consider how speciation occurs. The present chapter therefore represents an important transition from detail-rich ecology to a broad view of long-term trends.

A Question of Identity

In 1973–76 *fortis* and *scandens* could be readily distinguished by their beak measurements. Distributions of their measurements on two beak axes were discretely separated (fig. 10.1). However, the continuing in-

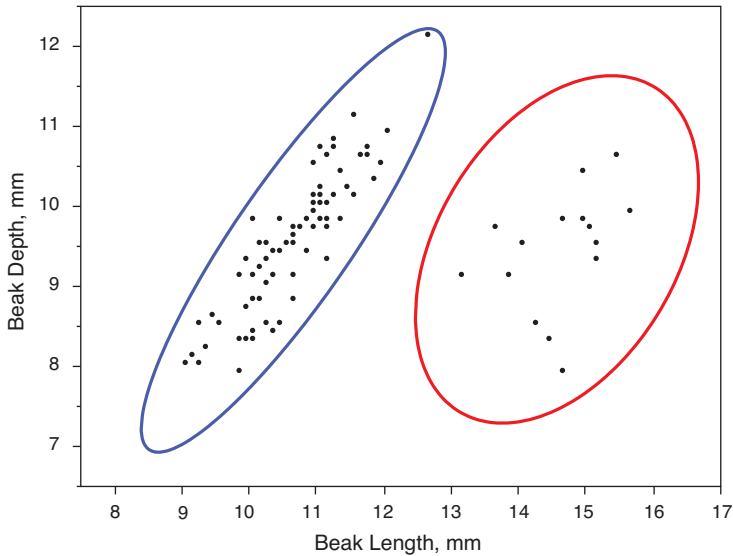


Fig. 10.1 Distributions of *fortis* (blue: $n = 73$) and *scandens* (red: $n = 16$) beak measurements in early 1973, drawn with 99% density ellipses.

progressive hybridization in the first 25 years brought the two species closer together in morphology and genetics, blurring the distinction between them. In the absence of pedigree information, convergence of the species gave rise to a problem in assigning a few individuals to species, especially in the last half dozen years. Our solution was pragmatic (box 10.1).

BLURRING OF GENETIC DISTINCTIONS

Hybridization blurs the genetic distinction between species because F_1 hybrids are neither one species nor another but genetic mixtures of the two. They belong to the population of one parental species or the other according to which one they choose to breed with (box 8.1). In changing the frequencies of alleles in the receiving population they reduce the difference between the populations. Successive backcrossing to one of the parental species and random mortality dilutes the contribution of introgressed genes and results in loss by genetic drift (and selection). In species like the finches that may have been exchanging genes for many generations loss due to drift tends to be counterbalanced by replenishment through introgression (and selection). New combinations of genes will be formed. For example an individual may possess a few

Box 10.1 Assigning Individuals to Species

Morphological criteria were used in the field to classify individuals to species (box 8.1). These criteria became increasingly difficult to apply with complete confidence because the species gradually converged as a result of hybridization. When genetic (microsatellite) data became available after 1987, we used them to identify species and hybrids in three steps. First, an Admixture model in STRUCTURE (Pritchard et al. 2000, 2007) was run to estimate the probability of each individual belonging to *fortis*, *scandens*, or *fuliginosa*. All captured birds were genotyped and therefore included in the analysis. Twenty-four individuals of *fuliginosa* from Santa Cruz were included as a standard for comparison with Daphne birds. Forty-seven Daphne birds (and all Santa Cruz *fuliginosa*) were assigned to one cluster at probabilities of 0.900 or higher. Not all agreed with morphological criteria (box. 8.1), and three were transferred from *fuliginosa* to *fortis* because they were larger than all *fuliginosa* on Santa Cruz Island.

In a second STRUCTURE analysis without *fuliginosa* all birds were predefined as *fortis* and *scandens*, and the program assigned each individual to one species or the other by the majority rule ($p \geq 0.500$). Third, to identify hybrids the Admixture model was run with all individuals of all three species ($n = 3,125$). Each individual was entered as one of the three predefined species, and one- or two-generations-back options were chosen to allow hybrid identification. Results of these runs were lists of birds with probabilities of assignment to *fortis*, *scandens*, *fuliginosa*, and categories with mixed ancestry in parental or grandparental generations. Generally these last two are F_1 and B_1 , that is, backcross generation 1. Individuals were considered to have mixed ancestry when support for the species designation fell below $p = 0.9$. Hybrids among the mixed ancestry categories were operationally defined by the majority rule. The totals were 236 *fortis* with *fuliginosa* ancestry in the parental generation, 44 *fortis* with *scandens* ancestry, and 83 *scandens* with *fortis* ancestry. Three immigrants and the unusual birds described in chapter 13 were excluded from these analyses.

alleles of another species inherited from a great grandparent that hybridized. By breeding with another individual of similar genetic constitution it may, through chance Mendelian segregation of alleles, produce an offspring with strong genetic features of that other species, and be assigned to that species by assignment tests.

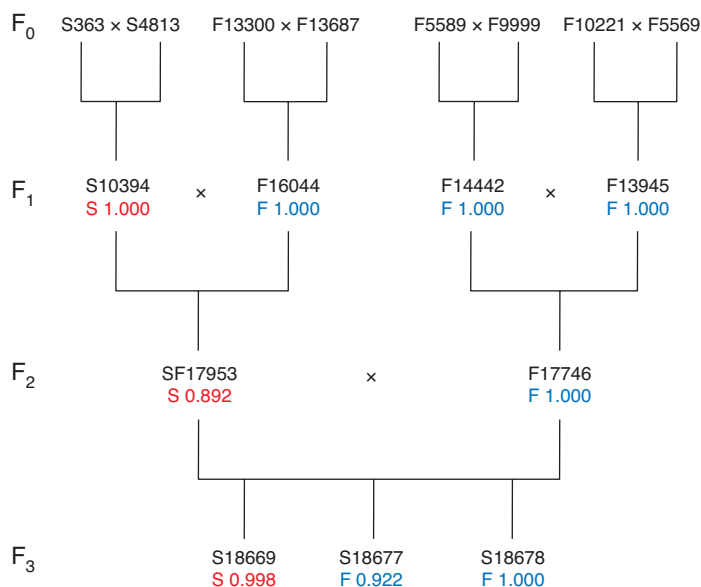


Fig. 10.2 Genetic results of hybridization: heterogeneity among sibs of the F₃ generation. Parentage of all F₂ and F₃ generation hybrids was confirmed genetically. Genetic assignments were made by the program STRUCTURE, with an Admixture model. Only *fortis* and *scandens* (not *fuliginosa*) were entered (box 10.1). Probabilities of belonging to *fortis* (F) or *scandens* (S) populations are shown in color. Figure 8.8 shows the songs of 10394 and the father of his mate.

Two examples from the pedigrees illustrate this effect of latent alleles that come together in chance combinations. In the first example, genetically assigned hybrid offspring (box 10.1) are formed from the genomes of parents that are both assigned genetically to one species with a probability of greater than 0.98. There are five *fortis* × *fuliginosa* hybrids in the pedigree with such *fortis* parents (paternity confirmed genetically). The second example illustrates the possibility of two species being produced from the breeding of two hybrids. A *fortis* × *fuliginosa* backcross to *fortis* (B₁), female 15779, bred with a male on a territory adjacent to her natal territory. The male was cuckolded by her F₁ hybrid father (10376). Assignment probabilities to *fortis* of daughter and father were 0.873 and 0.878 respectively, yet the assignment probabilities of the two offspring, 17637 and 17638, were 0.924 and 0.020, leading to the conclusion that the first is a *fortis* and the second is a *fuliginosa* (see also fig. 10.2)! The example illustrated in figure 10.2 shows that such genetic anomalies are produced also by *fortis* breeding with *scandens*.

These findings have two implications, one methodological, the other biological. The first is that genetic characterization of individuals does not always reflect the population- or species-based pedigree. A few errors of assignment may be made whether one uses genetic criteria (box 10.2) or morphological criteria (box 10.1). The biological consequence is the potential fusing of two populations into one and the loss of their separate identity.

BLURRING OF MORPHOLOGICAL DISTINCTIONS

The size and proportions of the beaks of *fortis* and *scandens* at the start of the study provide a point of reference for the changes that took place afterward. In 1973 it was possible to draw a line of demarcation down the middle of the gap between the distributions of the two species. This is illustrated with 1975 data in figure 10.3 because the samples sizes are larger than in 1973 and the frequency distributions re-

Box 10.2 Genetic Hybrids

Darwin's finches have 38 pairs of chromosomes (Jo 1983). An individual receives a random sample of one of each of the 38 chromosomes from each parent. By chance an offspring may receive more alleles indicative of the species of one parent than of the other. Our 16 microsatellite markers—14 autosomal and 2 sex-linked—are on 15 at most of the 38. Thus the chances of a moderate parent-of-origin bias in the genetic constitution of some individuals are quite high against a background of small differences between populations in the frequency of most alleles and a scarcity of fixed differences. The average difference in allele frequencies between *fortis* and *fuliginosa* is only a third of the difference between *fortis* and *scandens* frequencies.

Concordance between genetic and pedigree assignments is 66% for *fortis* with *scandens* ancestry ($n = 53$ offspring) and 69% for *fortis* with *fuliginosa* ancestry ($n = 52$ offspring). The low values are to be expected with closely related species (Vähä and Primmer 2006). Broader sampling of markers on more chromosomes would reduce the discrepancies, but given the available genetic markers, we must recognize that genetically identified hybrids are not necessarily pedigree hybrids (F_1 and B_1). For this reason we refer to them as genetic hybrids.

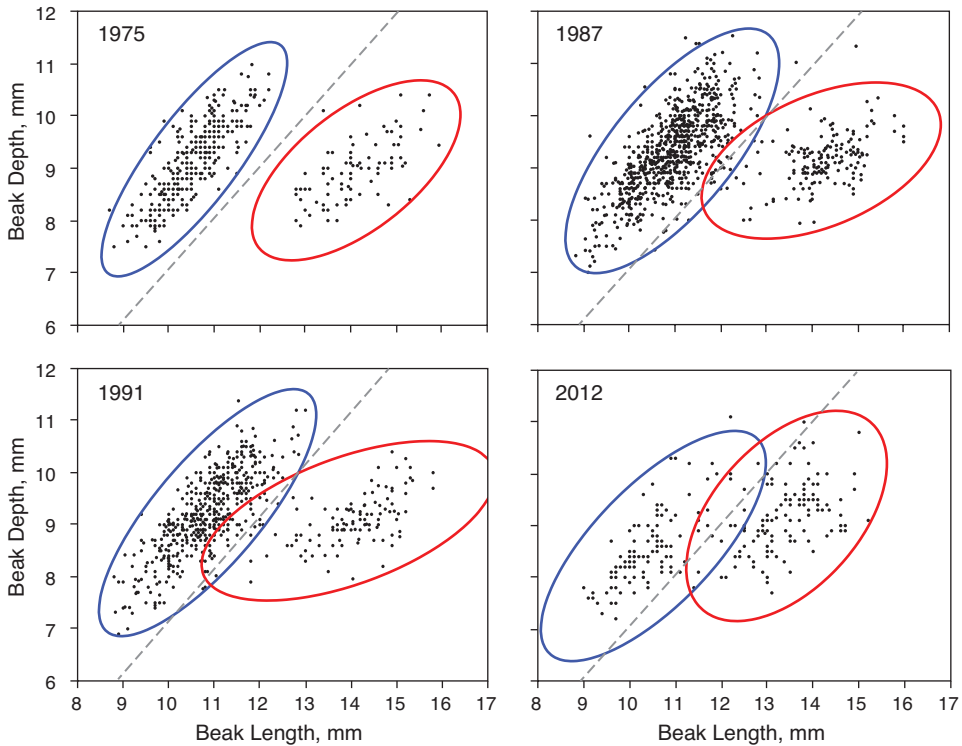


Fig. 10.3 A line of demarcation is drawn by eye midway between the beak distributions of *fortis* (left: $n = 316$) and *scandens* (right: $n = 87$) in 1975. Ellipses are 99% densities as in figure 10.1. The first sample in 1973 (illustrated in fig. 10.1) shows the same pattern, but sample sizes are much smaller. The other three plots show the progress of the species toward overlapping the line of demarcation as well as each other. Note the change in orientation of the *scandens* ellipses.

mained the same over the three years (fig. 10.1). The ellipse enclosing the predicted 99% of the *fortis* measurements crossed the line of demarcation for the first time in 1978, and by 1987 the ellipses of both species had crossed the line and overlapped each other. Overlap then increased, with the result that by the end of the study the original line of demarcation ran right through the middle of the overlap zone (fig. 10.3): each species had invaded the morphological space of the other. *G. fortis* and *fuliginosa* were not clearly separable right from the beginning (box 8.1), and they also penetrated further into each other's morphological space through introgressive hybridization (fig. 9.6).

Morphological Convergence

G. fortis and *scandens* became more similar to each other in all dimensions. Convergence was strongest and most regular in beak shape (fig. 10.4). Both species changed in beak dimensions, to approximately the same degree but in different ways. The average beak depth of *fortis* was 9% smaller at the end of the study (2012) than at the beginning (1973), whereas beak length had decreased by only 2% on average. The opposite was true of *scandens*; average beak length was 8% smaller at the end, but beak depth was only 1% smaller. Episodic selection and random sampling effects contribute to some of the year-to-year changes but do not produce the systematic trend illustrated in figure 10.4. Instead, the explanation for the regular increase in similarity—an hypothesis based on observed hybridization (chapters 8 and 9)—is that it was caused by the gradually accumulating effects of introgressive hybridization.

Differences between the species are most pronounced on a beak-shape axis (PC2-beak: length/depth or width). By the end of the study

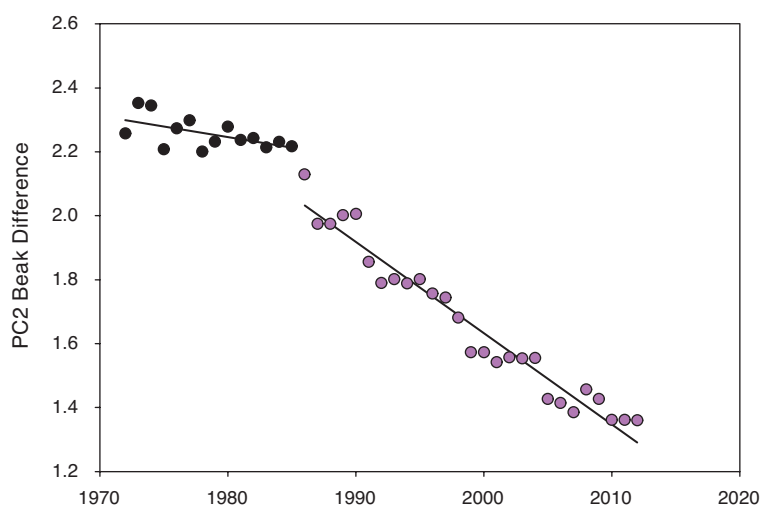


Fig. 10.4 Convergence of *fortis* and *scandens* in beak shape (PC2-beak) from 1986 onward. This is attributable to hybridization in 1983 and 1984 with subsequent backcrossing. To emphasize the contrast before (black dots) and after (purple dots) hybridization, two ordinary least-squares regression lines are fitted. This is done for heuristic and not statistical purposes since sequential points are not independent. By simple extrapolation, the species will be identical morphologically in the year 2057.

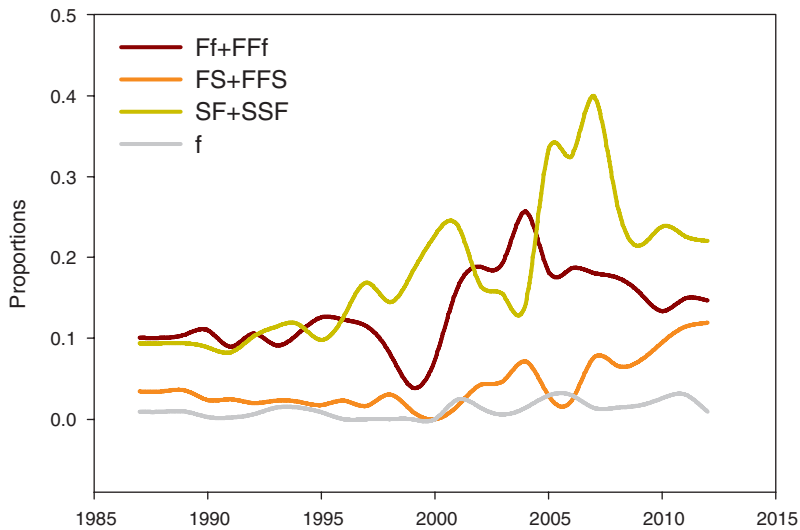


Fig. 10.5 The frequency of *fuliginosa* (f) and three categories of hybrids (F_1 and backcrosses combined). Frequencies of *fuliginosa* (f), *fortis* \times *fuliginosa* (Ff + FFf), and *fortis* \times *scandens* (FS + FFS) hybrids are expressed as proportions of the population of *fortis* in which they bred. Frequencies of *scandens* \times *fortis* (SF + SSF) hybrids are expressed as proportions of the population of *scandens* in which they bred. Cubic splines are fitted to the data. Sample sizes are in table 10.1.

the difference between the species was only 57% of the difference at the beginning. If the documented convergence continues at the same rate, the two species will become identical in 43 more years, in the year 2057. This extrapolation assumes all else is equal, including an unchanging environment, which seems highly unlikely. The dangers of such extrapolation are well known (appendix 10.1).

Frequencies of Hybrids

The hypothesis that convergence was caused by introgressive hybridization assumes that hybrids were present in most if not all years of breeding. This is indeed so (fig. 10.5). Genetically identified hybrids were present among newly captured birds in every year from 1987 onward, and in some of the preceding years back to 1978. Average frequencies of hybrids (F_1 and backcrosses combined) over a period of 26 years are 0.111 for Ff (*fortis* \times *fuliginosa*) and 0.038 for FS (*for-*

tis × *scandens*) in the *fortis* breeding population and 0.154 for SF (*scandens* × *fortis*) in the *scandens* breeding population. Overall 14.9% of *fortis* and 15.4% of *scandens* had mixed ancestry as detected by our assays.

Three features stand out from the temporal pattern of hybrid frequencies. First, hybrids increased in frequency from about the year 2000 onward. Second, F_1 hybrids formed by *fortis* breeding with *scandens* backcrossed to *scandens* more frequently than to *fortis* in every year, to judge from the relative frequencies. This stands in contrast to the observed higher frequency in the opposite direction at the beginning of the study (chapters 8 and 9). Third, the frequency of *fuliginosa* × *fortis* hybrids was consistently intermediate between the frequencies of the two classes of *fortis* × *scandens* hybrids. All three features match what we know from pedigrees from 1987 to 1998.

New, genetically identified *fuliginosa* appeared in the samples in most years. They were either immigrants or hybrids with a strong complement of *fuliginosa* genes (box 10.2). The maximum was 10, in 1993, but most of them never bred. They were always rare, and never exceeded 3.1% of the *fortis* population.

Morphological Variation

The hypothesis of introgressive hybridization without selective penalty predicts an increase in morphological variation with continuing hybridization (chapter 9). In the post-pedigree period of the study an increase in frequency of hybrids in the samples (fig. 10.5), and the inferred increase in frequency of hybridization in the last decade, lead us to expect an increase in morphological variation. We use coefficients of variation ($100 \times \text{s.d.}/\text{mean}$) to assess this because average size of several traits changed across years, especially in the latter half of the study (chapter 7).

In agreement with the prediction, variation in the composite measure of beak shape (PC2-beak) increased systematically in both *fortis* and *scandens* (fig. 10.6), and at about the same rate. *G. fortis* started and finished about twice as variable as *scandens*. The difference between species in magnitude of the variation (different intercepts) is explicable in terms of two sources of introgression into the *fortis* population, from *scandens* (larger) and *fuliginosa* (smaller), but only one into the *scandens* population, from *fortis* (chapters 8 and 9). Another likely factor is greater introgression into the *fortis* population (from *fuliginosa*) than into the *scandens* population early in the study (chapter 8).

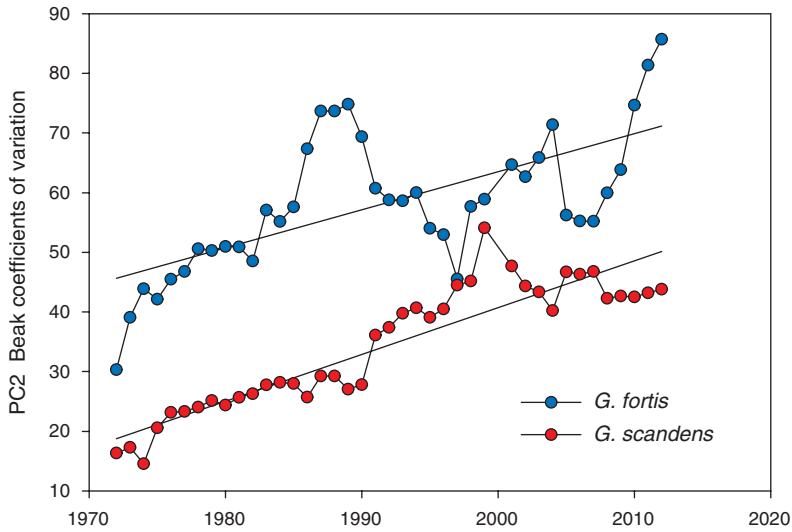


Fig. 10.6 Increases in variation in beak shape (PC2-beak) in *fortis* (blue) and *scandens* (red) across years. Ordinary least-squares regression lines of best fit are shown for heuristic and not statistical purposes.

Similarity in the rate of increase of variation in the two species (equal slopes) is expected from the approximately equal frequencies of birds with mixed ancestry during the study (p. 192), combined with minor genetic contributions from conspecific immigrants (fig. 9.5). Annual variation in individual beak dimensions fluctuated, in both species, but combined to produce the trend in shape. Noteworthy in figure 10.6 is a strong increasing trend in *fortis* variation after 2007 to the point where variation in the last three years exceeded all preceding values. The terminal increase corresponds with an increase in genetic input from *scandens* (fig. 10.5).

Annual values of variation fluctuate around the trend lines of best fit, more strongly for *fortis* than for *scandens*. Stochasticity contributes to the fluctuations because the numbers of hybridizing birds are always low. In addition hybridization varies in time. According to the pedigrees introgression occurred earlier in *fortis* than in *scandens*. Figure 10.6 shows two periods of substantial increase in *fortis* variation in the early part of the study, the first in the 1970s before pedigree data had been obtained, and the next in the 1980s when backcrossing to *fortis* was observed to be higher than in *scandens*. Two small increases in *scandens* variation occurred at times of known hybridization, 1991 and 1998.

With hybridization followed by backcrossing and introgression causing an increase in variation, there should be a positive association between the coefficient of variation and the number of hybrids and backcrosses in the samples from 1987 to 2012. The two are strongly correlated in *scandens* ($r = 0.643$, $p = 0.0004$, $n = 26$), whereas the *fortis* correlation is on the borderline of significance ($r = 0.385$, $p = 0.0520$, $n = 26$).

A third test employs the technique of hybrid removal. In chapter 9 we compared samples with and without hybrids and known backcrosses to quantify the effects of hybrids on genetic and phenotypic variation. This was done in the early part of the study with pedigree data, when *fortis* hybridized more with *fuliginosa* than with *scandens*. By adding hybrids to samples that lacked them, we found evidence for an increase in both phenotypic and genetic variation in proportion to the magnitude of the difference between the traits of interbreeding species. Here we repeat the procedure with phenotypic data from 1987 onward, when hybrids could be identified genetically, but this time by removing hybrids from the total samples.

The manipulation of removing hybrids from the analyses had three notable effects on the trends in coefficients of variation of beak shape (fig. 10.7). First, *scandens* variation was reduced across the 26-year period. This agrees with expectation. Second, despite the large effect, variation still increased over the period, albeit at a lower level. Third, *fortis* variation was scarcely affected. The second and third consequences do not contradict the hybridization hypothesis, but they do show that the trends are not produced solely by recent, identifiable hybridization. After 1993 genotyped individuals rarely amounted to more than 50% of each breeding population, so we suspect that the samples of genotyped birds, after the known hybrids had been removed, contained alleles from unidentified hybrids.

ALLOMETRY

As described in chapter 9, beak dimensions of adults are correlated positively with each other in all three species, but they vary in how they are correlated as well as in the strength of the correlations: their allometric relations differ. In a sample of measurements of adult *fortis*, beak depth and length increase at roughly the same rate as birds get larger, and the same applies to *fuliginosa*. The dimensions are approximately isometric. In contrast, *scandens* beak length increases at a faster rate than beak depth; the two dimensions scale with size allometrically. When two species with different allometries hybridize, their

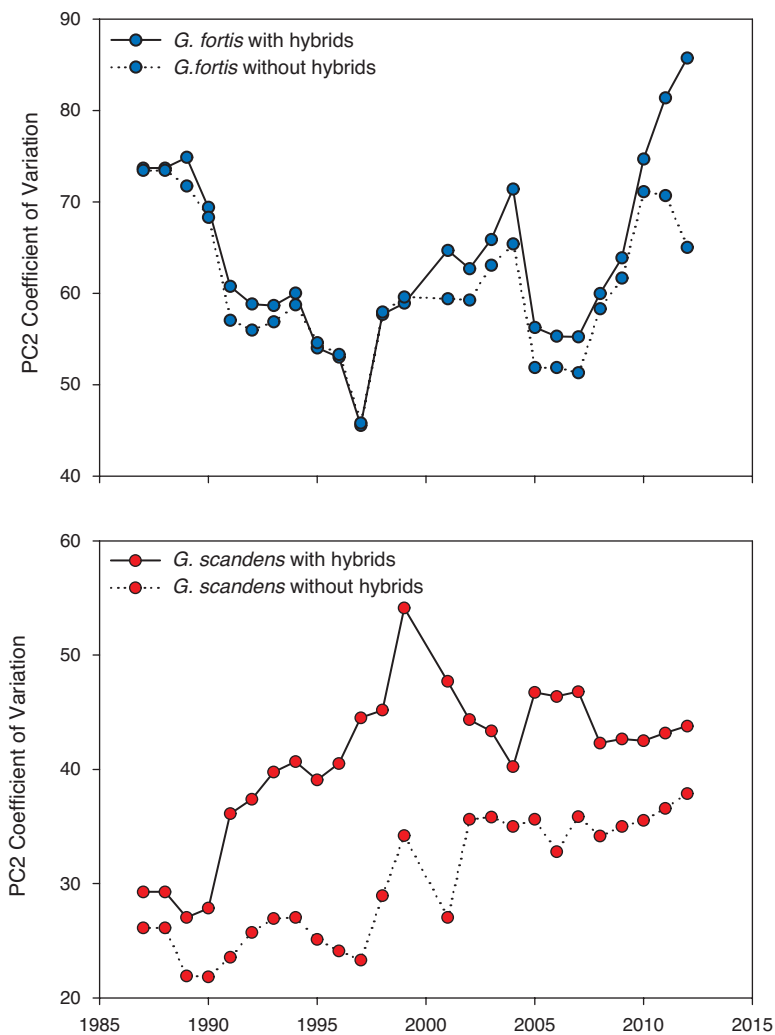


Fig. 10.7 The effects of hybrids and backcrosses on coefficients of variation of beak shape are much stronger in *scandens* (below) than *fortis* (above). This is shown by the difference between samples with hybrids (solid line) and without hybrids (broken line). Adapted from figure 10.6 for the period when hybrid frequencies (including backcrosses) were quantified (fig. 10.5). Introgressive hybridization also creates a small degree of skewness in the *scandens* frequency distributions as shown by the same removal procedure. Grant and Grant 2002a.

allometries change. Interbreeding of *fortis* and *fuliginosa* should have little effect on the relationship of beak length and depth, because the two species lie approximately on the same line of allometry. Interbreeding of *fortis* and *scandens*, on the other hand, leads to an allometric change because the slopes of their lines of allometry are different and because one is displaced (transposed) relative to the other on the beak-length axis. This is a strong prediction, but the direction of change is not easy to predict, because it depends on the particular individuals that interbreed.

The predicted change is observed in figure 10.3. While the orientation of the *fortis* distribution of measurements on two beak size axes remained approximately constant, the *scandens* distribution changed in two ways: initially the slope became shallower; then it became steeper. The first change is interpretable in terms of pedigree data in 1991, when the first extensive backcrossing occurred from *scandens* \times *fortis* hybrids to *scandens*. The second shift occurred when we had no pedigree data, and therefore we do not know how it occurred. It resulted in the generation of individuals in previously unoccupied morphological space. Notice in figure 10.3, for example, that in 1991 there were no *scandens* with beak lengths of 13–14 mm that had beak depths greater than 9.5 mm, but in 2012 there were plenty. The most likely explanation is a change in mating patterns of hybridizing birds, from a disproportionate pairing of small birds (chapter 9) to a pairing of large birds.

Allometric slopes changed unidirectionally in *fortis* and bidirectionally in *scandens* (fig. 10.8). The *fortis* change is consistent with a small genetic influence of *scandens*. However, removal of the F_1 hybrids and backcrosses from both *fuliginosa* and *scandens* (not shown in the figure) had almost no effect upon the trend. The biphasic shift in *scandens* allometry is consistent with an altered pattern of hybridization explained in the previous paragraph. Removal of hybrids from the *scandens* sample has the same effect as in figure 10.7, dampening but not eliminating the trend. Remarkably the allometric slopes of the two species, so different in the 1970s, were identical in 2012.

Genetic Convergence

Considering the whole period for which microsatellite data were available, both species underwent genetic changes. The microsatellite loci are presumed to be selectively neutral, and therefore serve as markers for random drift. Gradual, long-term, and unidirectional increases in allele frequencies could be caused by genetic drift or close linkage with

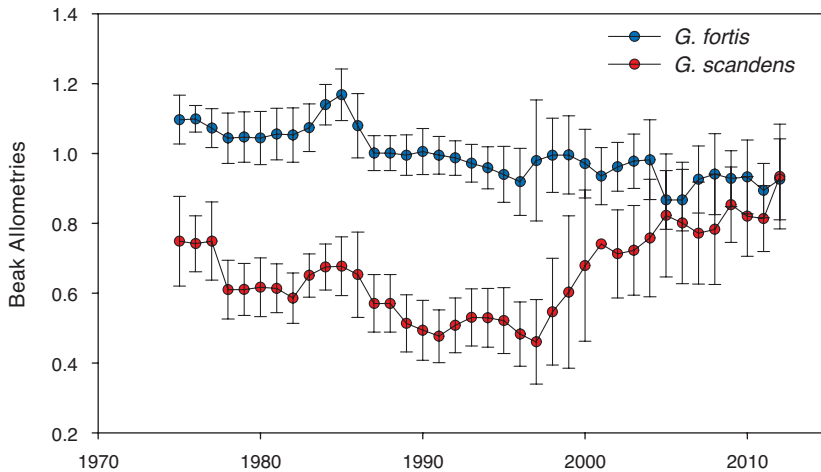


Fig. 10.8 Reduced major-axis slope coefficients for beak depth regressed on beak length in each year from 1975 onward. Samples of *scandens* (red) in 1973 and 1974 were too small for reliable analysis. *G. fortis* estimates are in blue. Coefficients are shown with 95% confidence limits.

selected genes, but also by continuing introgression. The best candidates for introgressed alleles start out as common in one population and initially rare or absent in the other population, and gradually rise in frequency in the latter. Temporal dynamics of two are illustrated in figure 10.9.

Four long-term trends are evident. First, introgressive hybridization between *fortis* and *scandens* is episodic on a scale of decades. This is indicated by initial scarcity of *fortis* alleles in the *scandens* population (fig. 10.9), and lack of morphological convergence prior to the mid-1980s (fig. 10.4). As suggested on page 192, *fortis* and *scandens* may not have been exchanging genes much if at all before the study began and in the first few years. Consistent with this suggestion, *scandens* experienced inbreeding depression that was counteracted by interbreeding with *fortis* (fig. 8.15), whereas no such effect was detected in *fortis*, probably because *fortis* and *fuliginosa* had been hybridizing.

Second, *fortis* and *scandens* species became increasingly different in genetic constitution from their respective populations in 1982 (fig. 10.10 upper). At the same time each became more similar to the starting (1982) genetic constitution of the other (fig. 10.10 lower). These trends reflect bidirectional gene flow, and they are stronger in *scandens* than in *fortis* because change in *fortis* with respect to *scandens* was dampened by genetic input from *fuliginosa*.

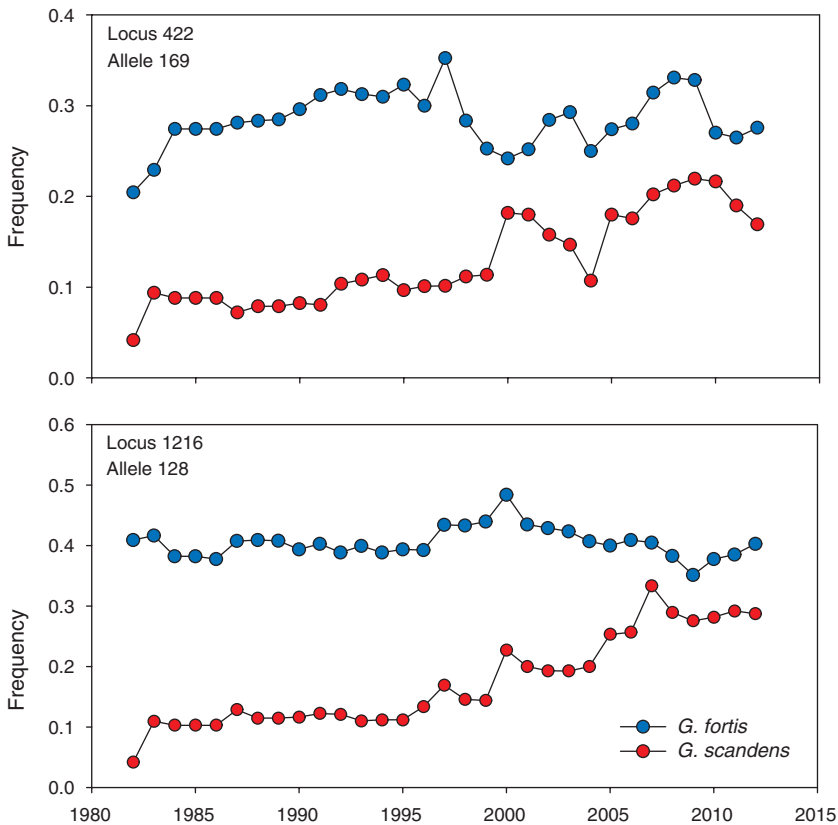


Fig. 10.9 Two candidates for introgressed alleles from *fortis* to *scandens*. In 1982 they were present in *fortis* but almost absent in *scandens* (single individuals only).

Third, the species converged genetically (fig. 10.11). This happened most rapidly between 1998 and 2007. The trend was slightly reversed in the last five years, but we are more impressed by the overall congruence between genetic and morphological convergence over the 30 years (fig. 10.11 lower).

Fourth, average multilocus heterozygosity remained stable in both *fortis* and *scandens* (fig. 10.12), even in the face of gene exchange, though with a possible slight increase after 2004 (fig. 10.5). Stability of the hybridizing species contrasts with a decline in heterozygosity in the nonhybridizing *magnirostris* at a time when immigration rate declined and inbreeding may have increased (chapter 11; also Markert et al. 2004). Hybrids are more heterozygous than their parental species

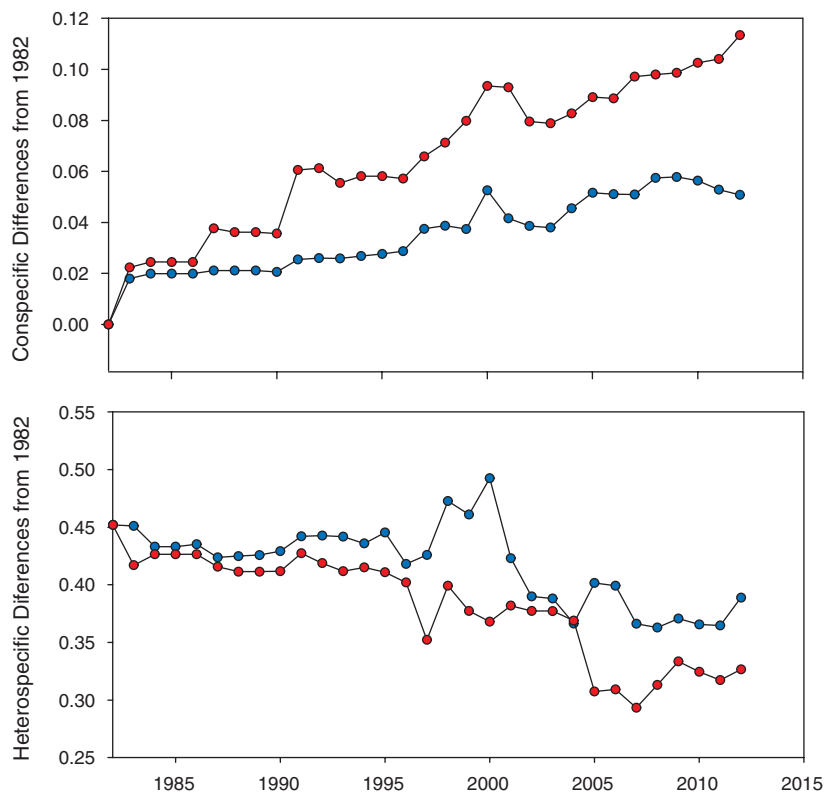


Fig. 10.10 **Upper:** *G. fortis* and *scandens* became increasingly different in genetic constitution from their own respective populations in 1982, as measured by Nei's genetic distance (D) with 14 microsatellite loci based on the frequency of shared alleles. The two species changed at different rates. **Lower:** The two species' genetic constitutions became increasingly similar to each other's in 1982.

(table 10.1). Being relatively uncommon, removing them from the total samples results in only a slight reduction in average heterozygosity (fig. 10.12).

Two Species or One?

Are *fortis* and *scandens* now one species? The answer to when two species become one has to be arbitrary under the biological species concept (de Queiroz 1998, Harrison 1998, Helbig et al. 2002) because

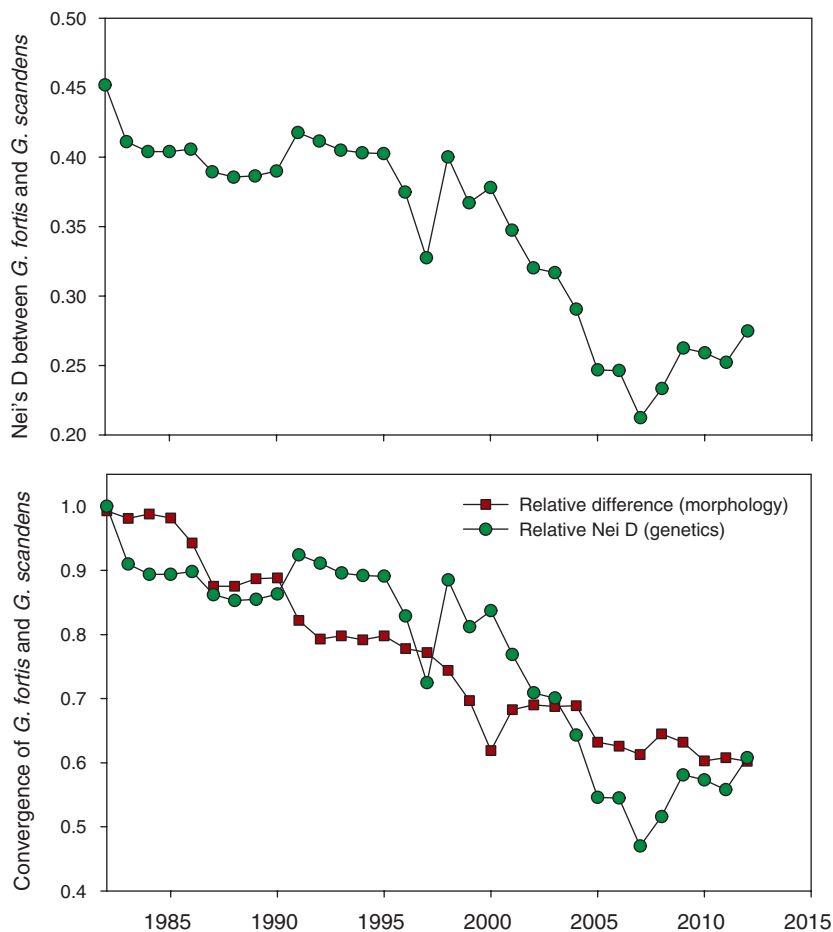


Fig. 10.11 Genetic and morphological convergence. **Upper:** Genetic convergence. Genetic distances (D) between *fortis* and *scandens* are calculated for each pair of annual samples of allele frequencies. **Lower:** Morphological convergence from figure 10.4 has been superimposed on the genetic convergence in the upper figure after standardizing both by giving a value of 1.0 to the difference between the species in each trait in 1982. Extrapolations to the x-axis give the expected year when the species will be identical, assuming unchanging rates of convergence. This is 2057 for morphological convergence and 2049 for genetic convergence.

despeciation, like speciation, is a gradual and continuous process and is not a categorical switch from one state to another. We consider them still to be two species because they constitute two populations separated almost completely by song. But clearly they are heading in the direction of one species, on *Daphne*.

TABLE 10.1

Differences in mean heterozygosities at 14 autosomal microsatellite loci between the three species and three classes of hybrids (F_1 and backcrosses combined)

Group	Sample size (<i>n</i>)	Mean \pm SD
<i>fortis</i> (<i>F</i>)	1,891	0.661 \pm 0.127
<i>fuliginosa</i> (<i>f</i>)	47	0.696 \pm 0.152
<i>scandens</i> (<i>s</i>)	821	0.658 \pm 0.127
<i>Ff</i> + <i>FFf</i>	255	0.745 \pm 0.107
<i>FS</i> + <i>FFS</i>	86	0.737 \pm 0.128
<i>SF</i> + <i>SSF</i>	149	0.717 \pm 0.121

Note: In each case the breeding population to which each group of hybrids belongs is indicated by the first initial. SD = standard deviation.

Plumage and Behavior

In this and the preceding chapters we have focused on morphological effects of introgressive hybridization. There are other possible effects that deserve a brief mention. The first, behavior, is conjectural, whereas the second, plumage, is quantitative and more substantive.

In the first two decades only *fortis* approached us while we occupied caves for meals or for banding. This changed, gradually, and by the end of the study *scandens* were just as likely as *fortis* to approach or even hop onto our boots or shoulders. The change in *scandens* behavior could be due to copying *fortis*, to inherited factors through introgressive hybridization from about 1991 onward, or both. *G. magnirostris* never showed the same behavior on Daphne, which is curious because on Genovesa they were regular camp birds (Grant and Grant 1989). The inheritance of tameness is an unexplored topic with these birds.

Male ground finches acquire increasing amounts of black in their plumage with successive molts (Grant 1990). *G. scandens* acquire fully black plumage faster than *fortis*. The difference may be due to inherited factors that display dominance, because backcrosses to either *fortis* or to *scandens* acquire fully black plumage as fast as *scandens* and faster than *fortis* (appendix 10.2).

Discussion

Some changes take place slowly. Two decades of measurement were needed for us to be confident that population variation in beak shape

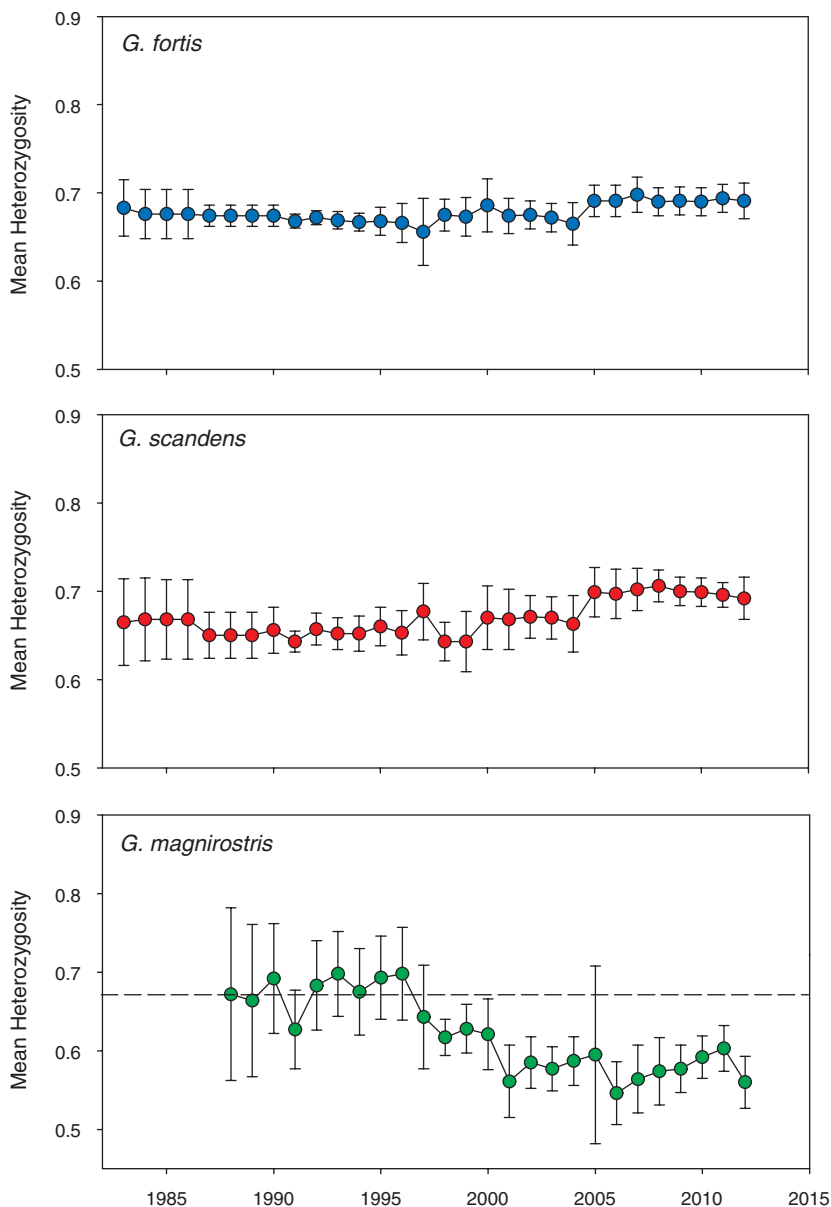


Fig. 10.12 Average observed multilocus heterozygosity (with 95% confidence intervals) at 14 autosomal microsatellite loci in three species. Stability of *fortis* and *scandens* values, with possible increases in the last few years, is emphasized here by the contrast with a strong decrease in heterozygosities in the nonhybridizing population of *magnirostris* from 1996 to 2001. The long-term average for *fortis* and *scandens* is shown on the lower figure as a broken horizontal line. Removal of

was increasing (fig. 10.6). However, changes over the last 15 years were not simply an unaltered extension of changes in the first 25 years. Some trends changed direction (figs. 10.7 and 10.8), while others became more pronounced (fig. 10.6). Frequencies of hybrids increased (fig. 10.5), indicating an increased frequency of hybridization and relatively high survival of hybrids (chapter 8), and new hybrid morphologies were produced (fig. 10.3), suggesting changed mating patterns. We conclude that introgression caused striking convergence of *fortis* and *scandens* over the 40-year period.

Despite support for the hypothesis, differences in variation between the species were not fully accounted for by our estimates of introgression. The *fortis* trends were affected to a minor extent by removal of the F_1 hybrids and backcrosses from samples, and although the *scandens* trends were reduced, they were nevertheless seen after removal of hybrids from the analyses. Thus short-term effects of known hybridization are not sufficient to explain the trends of increasing variation. We encountered the same in analyses restricted to data from the pedigrees (chapter 9). There and here we suggest the most likely explanation is a cumulative (storage) effect of past hybridization, particularly in *fortis*. Consistent with this suggestion, *fortis* \times *fuliginosa* hybrid offspring determined genetically are sometimes formed from the genomes of parents that are both assigned genetically to *fortis* with a probability of greater than 0.98 (p. 187). This surprising outcome is probably attributable to the random segregation of alleles and the combination by chance of heterospecific alleles in high frequency.

Simple diffusion models applied to beak dimensions or allele frequencies show that a pair of hybridizing species may fuse into one panmictic population at a rate that depends upon the hybridization frequency (Boag and Grant 1984a, Clarke et al. 1998). At constant rates of hybridization the approach to identity, which is inherently frequency-dependent, is rapid at first and declines with increasing similarity. We found an approximately linear trend with time. This may simply reflect the rapid initial phase of progress toward identity. Alternatively, introgression rates may not be constant but increase with increasing similarity. There is evidence for this in the higher frequency of hybrids in samples of measurements after 2000 (fig. 10.5), although the genetic convergence trend was reversed in the last few years (fig. 10.11).

In the first half of the study heritable variation underlying beak and body size traits of both species appeared to be roughly stable (chapters

Fig. 10.12 (continued) hybrids from *fortis* and *scandens* samples reduces average heterozygosities by only about 0.01, and therefore they are not shown. Sample sizes are 2,133 *fortis*, 1,024 *scandens*, and 588 *magnirostris*.

3 and 9), in agreement with the introgression-selection balance model in figure 9.1. This appears to have changed in the second half of the study, in the light of a doubling of phenotypic variation in both species from beginning to the end (fig. 10.6) and an unmeasured increase in additive genetic variance from introgression. The chief implication is that selection, which opposes increases in variation (fig. 9.1), must be relatively weak, and differences between species in variation must be more a function of differences in genetic input than output. Consistent with this reasoning, we could find no hybrid disadvantage in the last 30 years (chapter 8; also next chapter).

Summary

In this chapter we explore the implications of convergence through hybridization. It differs from the previous two chapters in encompassing the full 40 years of study, and represents a transition from chapters that are rich in ecological detail to ones with a broad view of long-term trends. Hybridization led to morphological convergence through introgression and the blurring of both morphological and genetic distinctions between *fortis* and *scandens*. The difference between species in beak shape gradually decreased to a value of 57% of the starting difference, due principally to decreases in beak depth of *fortis* and beak length of *scandens*. Hybridization increased in the last decade, as inferred from an increase in the frequency of genetically identified F_1 hybrids and backcrosses in samples. Beak shape variation increased from start to finish, at the same rate in the two species but more smoothly and evenly in *scandens* than in *fortis*. The increases resulted in an approximate doubling of variation in 40 years in both species. Removal of the known genetic hybrids from the samples had a strong effect on *scandens* samples, reducing the level of variation in all years, but not eliminating the trend. Removal of the known hybrids from the *fortis* sample had scarcely any effect on the trend. Beak shape allometries changed, due principally to bidirectional change in *scandens*: initially toward lower slopes of beak depth in relation to beak length, followed by a strong shift in the opposite direction. Most but not all of these observations are consistent with an hypothesis of immediate, short-term effects of introgressive hybridization on morphological and genetic variation. In addition there may be a cumulative (storage) effect of past introgression, particularly in *fortis*.