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Breeding Ecology and Fitness

Natural selection works not only through mortality but
also through fertility.

(Cavalli-Sforza and Cavalli-Sforza 1995, p. 247)

If you can look into the seeds of time,
And say which grain will grow and which will not. . . .

(Shakespeare, *Macbeth*, 1.3)

Introduction

THERE IS MORE TO FITNESS than surviving dry seasons (fig. 4.1). The genetic fitness of an individual is its ability to survive *and* reproduce (Charlesworth 1980, De Jong 1994). Whether its potential is realized or not is determined by its behavior, physiology, and morphology, as well as by chance. At certain critical times in dry seasons, survival is dependent on beak and body size (chapter 4). It is possible that breeding success is also dependent on beak size and body size in wet seasons. Some birds may be better than others at gaining a territory and a mate, and converting eggs into breeding members of the next generation (Reid et al. 2003, Jensen et al. 2004, Brouwhuis et al. 2010). If so there could be a trade-off between morphological factors influencing survival and those influencing reproduction. For example, some individuals at a disadvantage under stressful conditions of a dry season may survive and then perform particularly well when breeding. Alternatively, survival and reproduction components of fitness may be

uncoupled (Siepielski et al. 2011), such that a particular beak morphology or body size enhances dry season survival but has no influence on reproductive success (Jensen et al. 2004).

Thus finches can be thought of as occupying two niches separated in time, a wet-season and a dry-season niche, just as migrant birds occupy two habitats separated in time. This means that two components of biological success, in addition to chance, have a bearing on life history patterns (box 5.1). The first component is an ability to find foods (seeds) in dry years and dry seasons when food is scarce and there is no breeding, and the second is an ability to find insects and spiders for food and avoid interference at the nest from intruders during breeding. Finches have the same beaks in both niches but the fitness consequences may be different because they use them differently to exploit a different food supply. Their lifetime fitness is determined by how well they perform in both niches.

This chapter introduces the basic features of finch breeding, compares reproduction in years of different rainfall, and discusses the way in which morphology affects reproductive success. Immediate success is raising offspring to independence. Ultimate success is producing offspring that become breeders (recruits). The chapter is not restricted to morphology but considers more broadly the causes of variation among individuals in their reproductive success and their fitness in terms of the recruits they produce. Daphne is unusually suitable for this type of study because the island is small and the small populations of finches are resident and nonmigratory, and banded birds can be recognized as individuals. A few other insular populations have similar advantages (e.g., Gustafsson and Merilä 1994, Komdeur 2003, Smith et al. 2004, Postma and van Noordwijk 2005, Jensen et al. 2004, Schoener et al. 2004, Wheelwright et al. 2007, Calsbeek and Smith 2007, Pelletier et al. 2007), and so do some semi-insular ones (Garant et al. 2005, Price et al. 2008, Wesolowski 2011), though in general it is rarely possible to follow known individuals from birth to reproduction to death, estimate their contributions to the next generation, and identify the important factors determining their success.

Basic Breeding Biology

Rainfall is the driver of productivity in the seasonally arid terrestrial environment (figs. 4.2 and 4.8). Finches are in a state of reproductive readiness when rain arrives sometime in the first two months of a typical year (Grant and Boag 1980, Hau et al. 2004). The first heavy rain

Box 5.1 The Unusual Combination of Large Clutches and Long Lives

Darwin's finches on Daphne, Genovesa (Grant and Grant 1989), and elsewhere in lowland Galápagos habitats deviate from the standard tropical pattern of a slow pace of life (Wikelski et al. 2003) by combining tropical (long life span) and temperate (large clutch size) life histories. It seems an anomalous combination when the standard patterns are long life and small clutches (humid tropics) and short life and large clutches (temperate regions). The explanation lies in opportunities and constraints. Their pace of life is adjustable.

The opportunities for repeated breeding with large clutches arise from strong pulses of food production in some very wet years, coupled with low breeding density following heavy mortality in the preceding dry season. In this respect the finches on Daphne resemble birds in temperate regions (Ashmole 1963, Ricklefs 1980, Grant and Grant 1980b) and in the seasonally arid coastal region of Ecuador (Marchant 1958), in marked contrast to the stable populations under density-dependent competition for food and territories in the relatively unvarying tropical humid environments, as well as on many islands elsewhere in the world (Covas 2012). Significant constraints on reproduction and survival from predators and parasites are present in continental regions generally (Marchant 1960, Martin 2004) but lacking in Galápagos. Snakes and mammals that prey on nestlings in the tropical mainland are absent, and the only conspicuous disease is avipox, which can be debilitating but is rarely fatal for finches (Huber et al. 2010). In the absence of these nest predators, clutches are larger and nestling periods longer than in birds of the coastal region of mainland Ecuador (Marchant 1958, 1959, Grant and Grant 1989). Darwin's finches can live a long time because they do not have to face the hazards of migration, and they do not breed in every year owing to the failure of sufficient rain in some years: in a quarter of the years either no finches bred or just a very few adults did.

Darwin's finches lay smaller clutches in less seasonal habitats. The single species of finch in rain-forested Cocos Island lays clutches of two eggs (Slud 1960, Grant 1986), like unrelated species in similar, rain forest, habitat on the continent. In the absence of nest predators on Cocos Island, food supply and its variation in time is probably the most important factor affecting clutch size. In the mesic habitat of Galápagos highlands finches lay smaller clutches than in the lowlands (Kleindorfer 2007). Their food supply may vary less seasonally than in the lowlands. This has not been studied.



Fig. 5.1 Reproduction. **Upper left:** Nest of *fortis*. **Upper right:** Clutch of 4 *fortis* eggs. **Lower left:** Single egg of each of 4 species, from left to right *magnirostris*, *scandens*, *fortis*, and *fuliginosa*. **Lower right:** Fledgling *fortis*.

stimulates growth of leaves and flowers, and induces singing, chasing, courtship, and pair formation (box 3.1). Nests are built in cactus bushes, rarely in trees (*Bursera*) or on the ground at the base of grasses (*Cloris*) and herbs (*Chamaesyce* and *Sesuvium*). By the end of the second week after the first heavy rain caterpillars appear on the flowers of *Bursera*, *Croton*, and some of the annual plants, and finches begin to lay eggs. Clutches of 2–4 eggs (fig. 5.1) are laid in a typical year, incubated by the female, and hatch 12 days later. Both parents feed the nestlings for 12–14 days, and the fledglings for the next 2–4 weeks, mainly on caterpillars (fig. 2.6). If sufficient rain has fallen, the female starts a second clutch in a new nest within 2 weeks of the fledging of the young from the previous nest, usually with the same male but sometimes with a different one. Occasionally the second clutch is started before the nestlings from the first nest have fledged. This summary captures the essence of all breeding seasons (Boag and Grant 1984b), except for one additional feature. In several years a few *scandens* pairs start to breed in December or January before rain arrives.

They do so by intensively exploiting pollen and nectar from *Opuntia* flowers (figs. 2.17 and 2.19; Grant 1996, Grant and Grant 1981). The longest-lived bird, male *scandens* 18111, hatched in early 1993 before the rains arrived three weeks later, and lived for 17 years.

ANNUAL VARIATION IN REPRODUCTION IN RELATION TO RAIN

Sea temperatures rise in January of a typical year, causing air temperatures to rise, cumulus clouds to develop, and, following the cooling of moisture-laden air, rain to fall (fig. 5.2). The timing and amount of rain and the duration of the wet season vary greatly from year to year under the influence of the El Niño–Southern Oscillation phenomenon. At the extremes are droughts with no breeding (La Niña) and years of abundant rain (El Niño). The extremes of annual rain we have recorded on Daphne are 1 mm in 1988 and 1,359 mm in 1983 (which includes December 1982, when the rains began). In a quarter of the years (10/40) little or no breeding took place, and in 44% of the years almost no offspring survived to the following year. In contrast a wet season with abundant rain can last up to eight months (1982–83), and finches breed at the rate of one brood per month for a potential maximum of eight broods.

The fluctuating climate and somewhat erratic breeding schedules have three main demographic consequences. First, population sizes of breeding finches differ in years of plenty and scarcity by an order of magnitude or more (fig. 5.3). Second, the age structure of populations undergoes substantial change, reflecting the contrasting years of high production and low survival (fig. 5.4). This is more typical of marine fish such as herring and cod, whose population dynamics are dominated by strong cohort effects, than most bird populations that have been studied in detail. Third, the timing of recruitment varies greatly. Entry into the breeding population occurred gradually over five years for members of the 1978 cohorts, abruptly after two years for 1981 cohorts, and after as little as three months at rapidly rising density for 1983 cohorts (Gibbs et al. 1984).

In general the more rain that falls the longer is the breeding season, the more clutches are laid, and the more broods are produced (fig. 5.5). Clutches vary from 2 to 6 eggs and again, in general, the larger the clutch the more fledglings are produced and survive to the next year (Gibbs 1988). Clutches are larger on average in El Niño years than in other years (fig. 5.6), but hatching success and fledging success are not enhanced, in fact they may even be reduced (fig. 5.7), by disturbances caused by prolonged bouts of rain and density-dependent interactions.

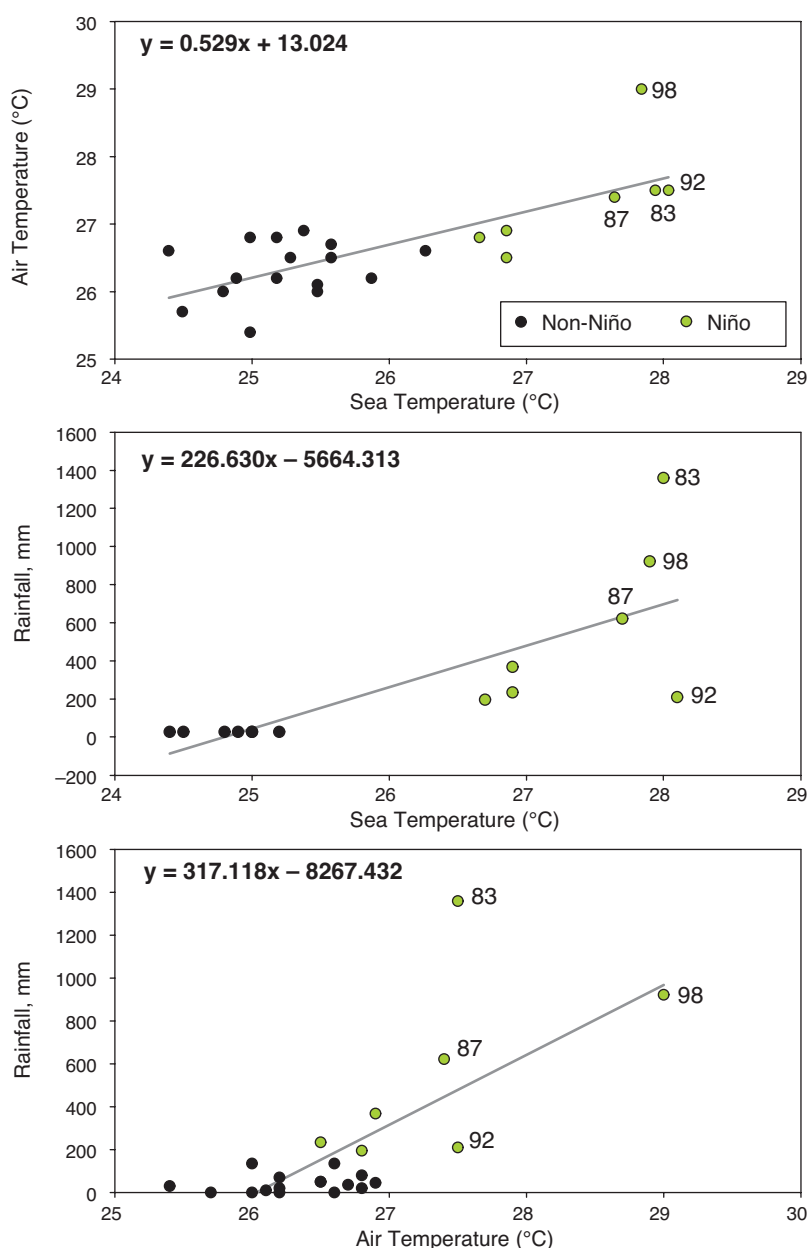


Fig. 5.2 Average daily maximum air temperatures of the warmest two successive months of a year on Santa Cruz Island (1965–98) is a function of the average daily sea temperature of those months at the same location (upper). Annual rainfall on Daphne (1976–98) is a function of the average daily sea temperature (middle) and of the average daily maximum air temperature (lower) recorded on Santa Cruz Island in the warmest two successive months of the year. Seven years of El Niño conditions are shown by green circles. Conditions in four of those years labeled

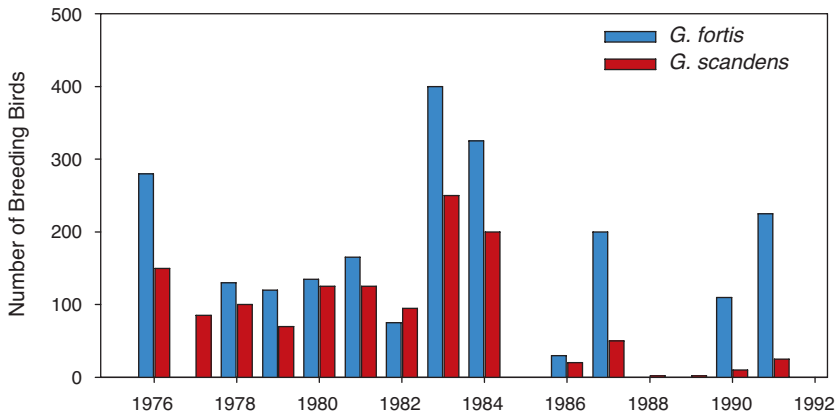


Fig. 5.3 Number of breeding individuals in 1976–91. Not all pairs were studied in 1976, and the numbers of breeders were estimated. There was no breeding in 1985, and only two pairs of *scandens* attempted breeding in 1988 and 1989. Harmonic mean breeding population sizes were 94 *scandens* and 197 *fortis*. Genetically effective population sizes were a quarter to one-half of these values principally as a result of a large variance in the production of recruits per parent (see also Nunney 1993, Engen et al. 2011). From Grant and Grant 1992a.

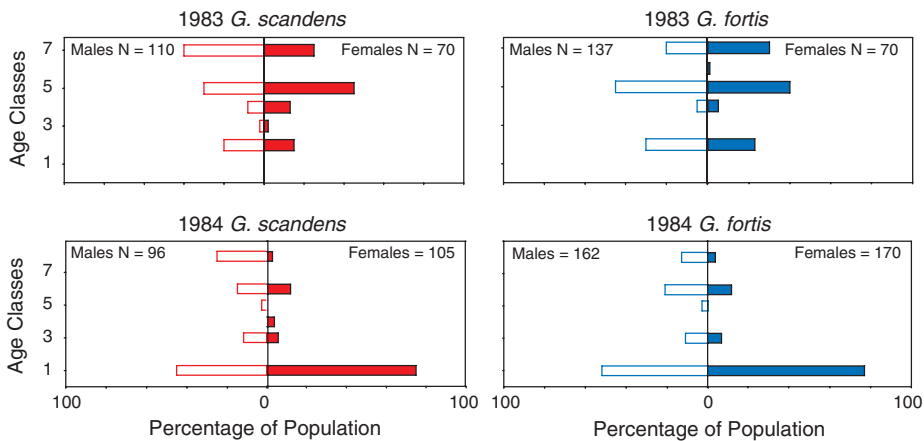


Fig. 5.4 Age structure of *fortis* and *scandens* at the time of breeding in 1983 and 1984. Not included are the individuals that hatched in 1983 and bred later in the same breeding season. From Grant and Grant 1992a.

Fig. 5.2 (continued) with two digits were clearly extreme, whereas conditions in three others (1991, 1993, and 1997, unlabeled green circles) were not markedly different from the warmest and wettest of the non-El Niño years (black circles) except in rainfall (middle). From Grant et al. 2000.

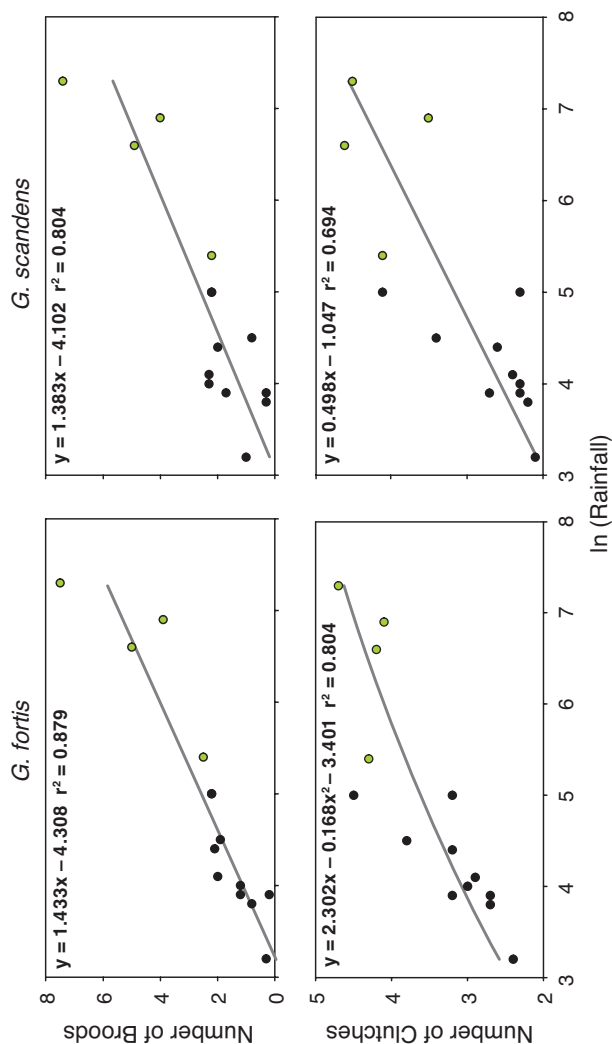


Fig. 5.5 Number of broods per female per year (upper) and the largest average clutch size per female among broods in a year (lower), as functions of rainfall measured in millimeters. Excluded are birds that bred in the year of hatching. All linear relationships, and the squared term in the bottom left relationship, are statistically significant ($p < 0.05$). Green circles identify El Niño years; 1983, 1987, 1991, and 1998. From Grant et al. 2000.

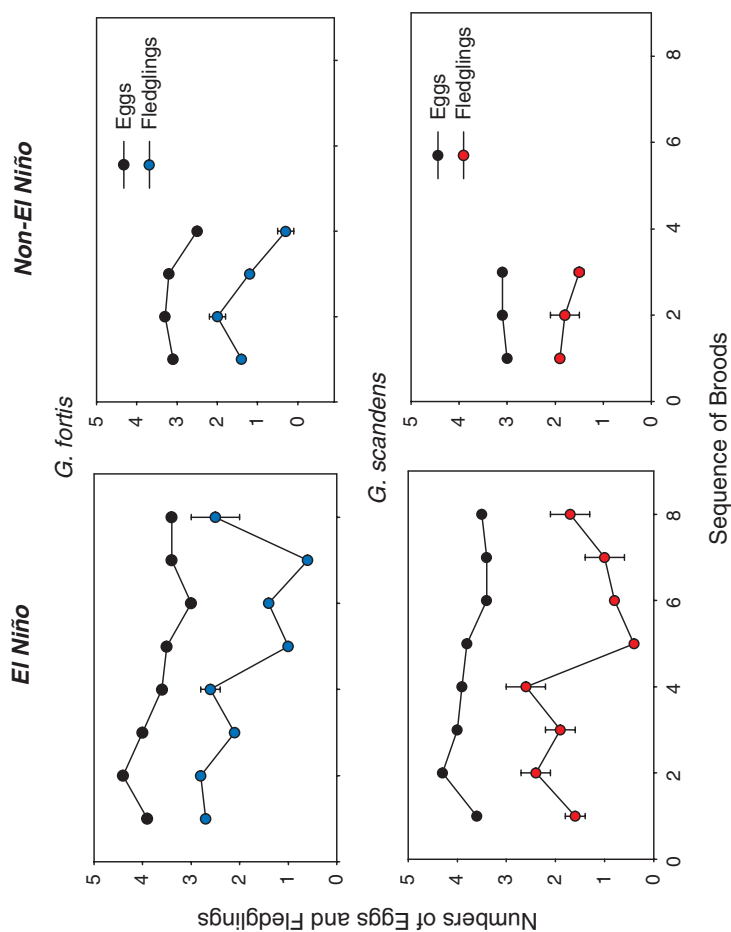


Fig. 5.6 Seasonal variation in mean number of eggs and fledglings produced by identified females in El Niño and non-El Niño years (1976–91, 1998) Brood means for sample sizes of fewer than 10 females have been omitted. Vertical bars indicate 1 s.e. above and below the mean; these are sample-size weighted averages of the means of individual years. Number of broods refers to their sequence. From Grant et al. 2000.

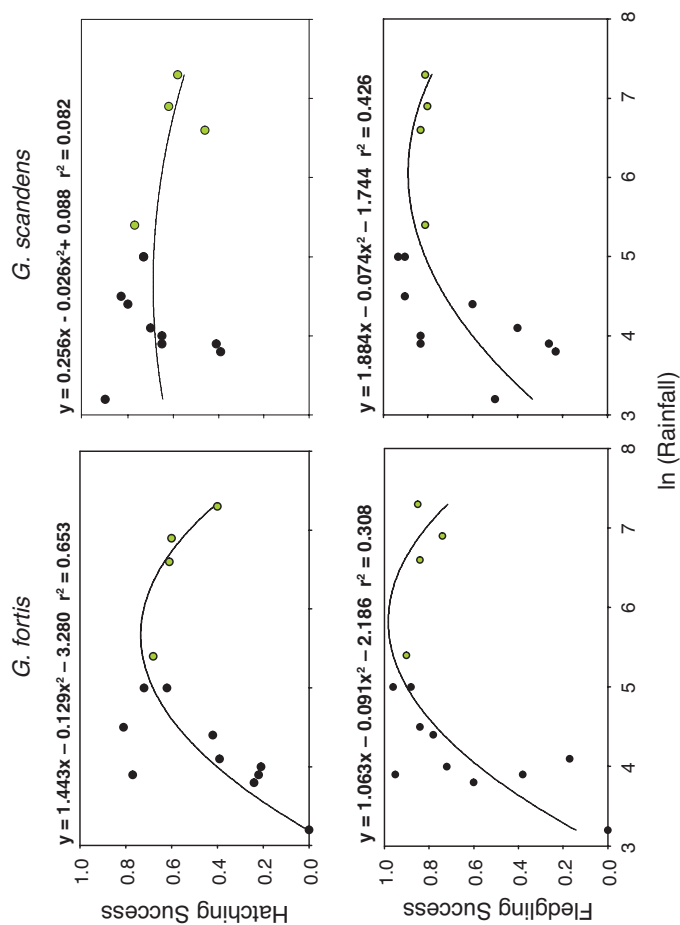


Fig. 5.7 Annual variation in hatching and fledging success in relation to rainfall (with years of El Niño conditions shown by green circles as in fig. 5.5). Both linear and squared terms are significant in the *fortis* relationship between hatching success and rainfall. Of the remainder the only significant (linear) relationship is *scandens* fledging success in relation to rainfall; nevertheless curvilinear lines of best fit are shown. Neither hatching success nor fledging success is enhanced in years of extensive rain. From Grant et al. 2000.

Despite this possible reduction, the increased number of broods means that the greatest potential reproductive fitness is to be gained in years of El Niño conditions (fig. 5.8). These occur at intervals of approximately four to seven years, as do droughts.

It follows that the fittest individuals are those that can survive the droughts and then take advantage of breeding repeatedly in El Niños. An extreme example is provided by the longest-lived female *fortis*, 5960. She hatched in the El Niño of 1983 and died after another in 1998, having experienced four others, 1987 and 1991–93, and several droughts. Starting in 1984 she produced a minimum of 23 clutches of 72 eggs with 8 mates, yielding a minimum of 45 nestlings, 33 fledglings, and 5 recruits. These large numbers are minima because we were not present on the island for all of her breeding. Extremes like this are valuable because they reveal what is possible (table 5.1); see box 5.1 for a brief discussion of the unusual combination of prolific reproduction and long lives. Extreme successes are put in perspective by the numerous failures. As is general with bird populations (Newton 1989), most fledglings do not survive their first year, and many breeders fail to fledge any young (Grant and Grant 1992a, 1996c).

Predicting Reproductive Success

The longer a bird lives, the more opportunities it has to breed and thereby gain high fitness. On this simple basis we used multiple regression analysis to predict the number of fledglings an individual produces in its lifetime and the number of recruits it contributes to the next generation, which vary considerably (fig. 5.9). The variables employed to do this and the procedures are explained in the legend of figure 5.10.

THE COHORTS OF 1975

We begin with the cohorts produced in 1975. The advantage of focusing on a cohort is that all members are the same age and experience the same environment. This eliminates some uncontrolled variables that could complicate interpretation of the predictions. Members of the 1975 cohorts bred for the first time in 1976 and then suffered heavy mortality, and as a result our *fortis* samples are small (20 males and 21 females) and *scandens* samples are too small for analysis. Nonetheless, despite this restriction, we found strong predictors of fitness (fig. 5.10). Longevity predicts number of clutches, number of clutches predicts

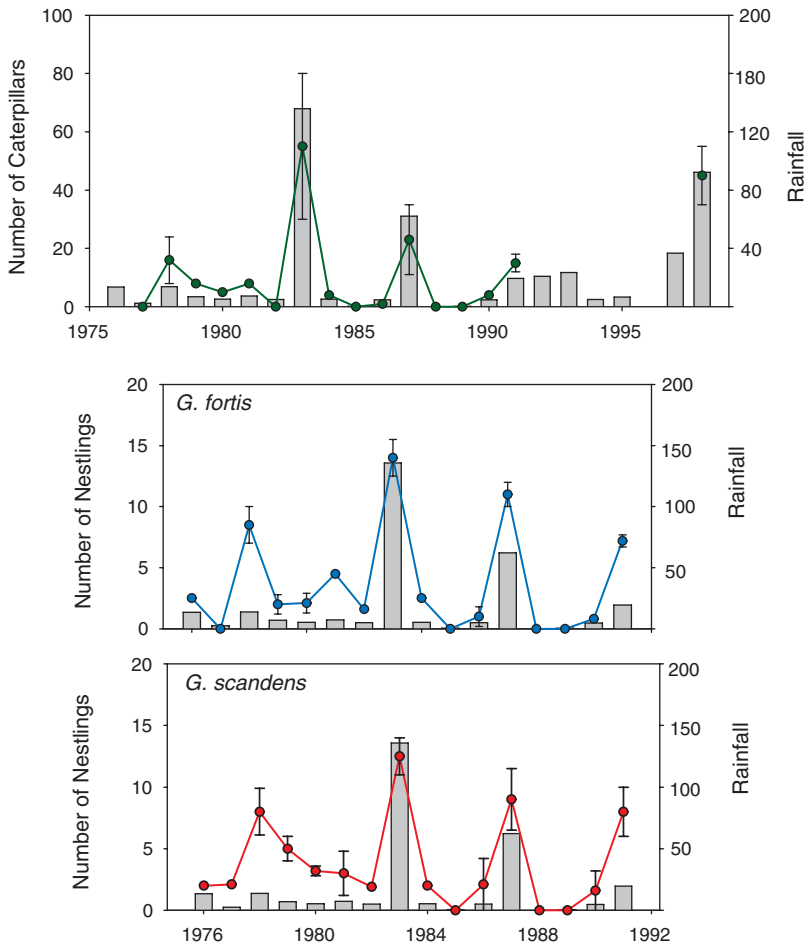


Fig. 5.8 Upper: Annual variation in caterpillar numbers (mean \pm s.e. of weekly or biweekly samples) in relation to rainfall shown by histogram bars (from Grant et al. 2000). El Niño years were 1983, 1987, 1991–93, and 1997–98. **Middle and lower:** Annual variation in the mean number of nestlings per female in relation to rainfall. Vertical bars are 95% confidence intervals on the estimates of the means. Only those females breeding in the first month of the breeding season after the first rains are included. Others, usually young, began breeding later in some years, and in a few years there was no breeding at all. Pre-rains breeding by a few *scandens* females have been ignored. For each species mean number of nestlings is highly correlated with rainfall, and so is the mean number of clutches per female (from Grant and Grant 1996b).

TABLE 5.1
Maximum lifetime values of reproductive traits of females

	<i>G. fortis</i>	<i>G. scandens</i>
Eggs	97	99
Clutches (total)	29	27
Clutches (successful)	15	17
Nestlings	49	60
Fledglings	39	46
Recruits	15	10
Life span	16	17
Number of mates	8	11

Note: Successful clutches are those that yielded at least one fledgling. The total biomass of eggs, each about 2 g (Grant 1982), is approximately 10 times the body weight of the mothers, which is far greater than the ~1.4 theoretically expected from metabolic life history theory (Charnov et al. 2007). Note that high numbers of mates imply high genetic diversity of offspring.

number of fledglings, and number of fledglings predicts number of recruits. There is strong statistical support at each step in the linear flow of causality. Morphological traits have little influence on any of the predictions of reproductive fitness, in contrast to their importance in dry season survival (chapter 4), partly as a result of a restriction of the analysis to those that bred successfully at least once by excluding all the failures.

One relationship deserves comment. Beak size of males was negatively correlated with number of fledglings produced over their lifetime after removal of the substantial statistical effects of numbers of clutches on fledglings. This is a small support ($p = 0.025$) for the idea of a trade-off between reproduction and survival; large males survived better than small males (chapter 4), but small males were relatively successful in producing fledglings, though not recruits.

FOUR LATER COHORTS

The same, strong, links in the linear chain of causality were shown by the larger cohorts produced in 1978, 1981, 1983, and 1987 (Grant and Grant 2000b, 2011a). These results are summarized in figure 5.11, where the numbers of statistically significant relationships out of a total of 15 groups are shown above the arrows: 4 cohorts, 2 species, 2 sexes, minus one group with an insufficient sample size. The trends

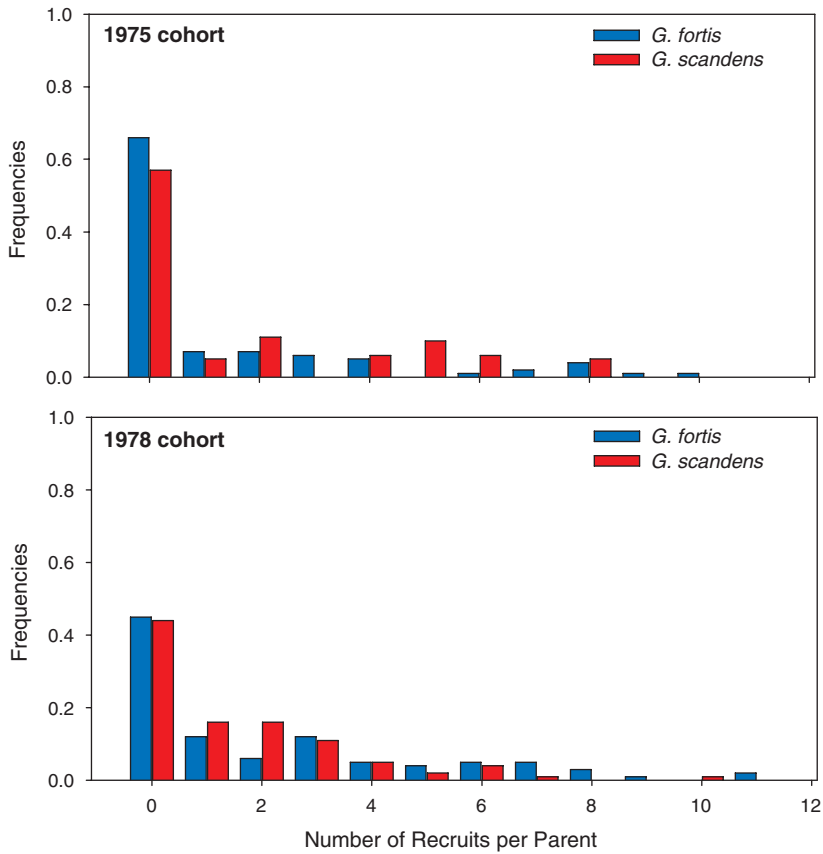


Fig. 5.9 Variation in lifetime recruitment of offspring produced by members of two cohorts of *fortis* and *scandens*. Based on Grant and Grant 1992a.

strongly apply to females, to the males paired with them, to both *fortis* and *scandens*, and to all cohorts despite marked differences in environmental conditions experienced in their starting years (Grant and Grant 2011a). Other factors predict fitness in some years, but to a minor extent.

THE CONTRIBUTION OF MORPHOLOGY TO FITNESS

Morphological variables are rarely significant predictors of longevity or fitness beyond what is expected from occasional size-selective mortality in dry seasons. To make this point, we summarize the results of

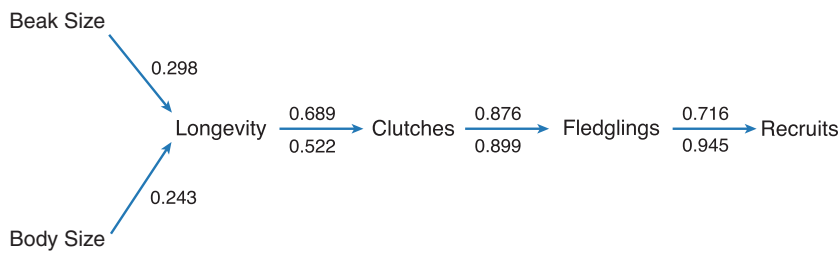


Fig. 5.10 A causal flow diagram for the 1975 cohorts of male and female *fortis*, showing how lifetime production of recruits is determined by lifetime production of clutches and fledglings and ultimately by lifespan (longevity). Body size and two beak variables (size and shape) were used to predict each of the independent variables to the right, and additionally longevity was used to predict clutches, fledglings and recruits, clutches were used to predict fledglings, and fledglings were used to predict recruits. A step-down procedure was used to eliminate variables that were not significant (Grant and Grant 2011a). R^2 values of the single best predictor are shown above the arrow lines for males and below them for females. They give the proportion of variation statistically explained by the predictor variables. Two minor indirect predictors have been omitted. Statistical significance of each of the predictions of longevity is $p < 0.05$. All other predictions are significant at $p < 0.0001$. Sample sizes are 20 males and 21 females.

conducting a total of 68 multiple regression analyses of all five cohorts. Body size or the beak traits were significant predictors of longevity, reproduction, or recruits in only 18 (26.5%). In 14 of the 18 their signs, positive or negative, were consistent with the direction of dry-season selective mortalities (e.g., fig. 11.1) and therefore explicable solely by differential mortality. Moreover, with one exception all morphological variables were minor predictors in analyses of lifetime production of clutches, fledglings, and recruits. Regression slopes were relatively low, and so were R^2 values. Significance levels ranged from 0.038 to 0.003 and generally exceeded 0.01 (12 of the 18), whereas those of the major predictors were usually less than 0.0001. Finally, when cohorts experienced no selection, as was the case for the 1987 cohort of *fortis* (beak shape) and *scandens* (beak size and shape), morphological variables did not predict longevity or any of the reproductive fitness measures.

The ultimate measure of fitness is lifetime number of recruits. In three of the regressions morphological variables added significantly to the prediction of recruits by number of fledglings, but two of the partial regression coefficients were marginally significant ($p \sim 0.04$) and therefore of doubtful reliability. Simple regression analyses predicting number of recruits give the same result: three significant predictions, one

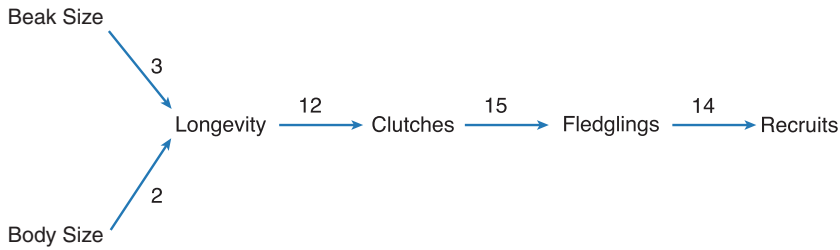


Fig. 5.11 A causal flow diagram, similar to figure 5.10, for the 1978, 1981, 1983, and 1987 cohorts of both *fortis* and *scandens*: four cohorts, two species, two sexes. Males and females of each species of the four cohorts were analyzed separately by the same procedure described in figure 5.10. In total 15 analyses were performed for each variable in the chain; the sample size of female *scandens* in the 1981 cohort was insufficient for analysis. The numbers of partial regression coefficients out of the total that were significant at $p < 0.05$ are shown above the arrows. For the prediction of clutches, fledglings, and recruits along the chain there are 45 partial regression coefficients, and 35 of them are significant at $p < 0.0001$. In contrast none of the other coefficients are significant at this level. The maximum number is five for the prediction of fledglings by longevity $p = 0.0334\text{--}0.0001$). These and other secondary predictors of lesser explanatory value have been omitted for simplicity. Sample sizes are approximately the same as in Grant and Grant 2011a. Paternity was checked in the 1987 cohort with microsatellite markers (chapter 3). Taking extra-pair paternity into account does not change the predictions of fitness and fledglings for either species of this cohort; therefore analyses of other cohorts are not likely to be distorted by ignoring extra-pair paternity (appendix 5.1). The probability of a *fortis* male gaining paternity from extra-pair mating is close to 0 until age 5–6 yr, and gains exceed losses on average only when males reach age 7 or 8 yr (Grant and Grant 2011a). This is an additional advantage of a long life span.

body size, the others beak size, and in all three instances the significance level is between 0.05 and 0.01.

We conclude that morphology makes little difference to whether a finch breeds successfully or not. It may affect mating success to a small extent in some years, as happened in the four years following the 1977 drought, when the *fortis* sex ratio was strongly male-biased (Price 1984a, 1984b, Price and Grant 1984), but the effects of morphology on breeding success are minor. From the cohort analyses there is little evidence of a trade-off between wet-season and dry-season performance of birds with a particular beak morphology or body size. Kingsolver and Diamond (2011) concluded from a large meta-analysis that trade-offs among fitness components are generally rare.

THE CONTRIBUTION OF OFFSPRING TO PARENTAL FITNESS

The close association between recruits and fledglings (figs. 5.10 and 5.11) means that the number of recruits per parent can be considered a random sample of the offspring they produce. Given this, there is little additional scope for recruitment to be influenced by the particular properties of recruited offspring. We compared offspring that became recruits with those that did not and found few, and inconsistent, differences in morphology between them (Grant and Grant 2000b). Female recruits from the 1981 cohort of *fortis* were larger than those that failed to become recruits, whereas male recruits from the 1983 cohort of *fortis* were smaller than the failures. Female recruits from the 1978 cohort of *scandens* hatched earlier than the failures, whereas female recruits from the 1981 cohort of *fortis* hatched later than the failures. Inconsistencies are explained by the fact that different cohorts experience different conditions, the most important being the conditions in the first year of life, when mortality is highest.

LONGEVITY

The longer a bird lives the more offspring it produces. In the preceding statistical relationships longevity has a positive influence on number of fledglings of five groups out of the fifteen, and on recruits of two more, over and above its influence on number of clutches (fig. 5.9): any bias due to unrecorded extrapair paternity (appendix 5.1) should be small (fig. 5.11). Longevity could influence reproductive output in various ways. For example, long-lived birds may gain an advantage when old and experienced in producing healthy and vigorous offspring by breeding early in a season and feeding them a rich supply of insect food (Grant and Grant 2000b).

Another possibility is that long-lived birds gain a reproductive advantage in acquiring different mates in successive breeding seasons while being socially monogamous at any one time. There is statistical evidence for this in the production of fledglings by females of the 1983 cohorts of *fortis* and *scandens*: those females with most mates in their lifetime produced the most fledglings (Grant and Grant 2011a). The causes of this relationship could lie in the social environment, such as behavioral compatibility of particular combinations of parents, or it could be genetic, such as compatibility or diversity of the genetic contributions of the parents to their offspring (e.g., see fig. 4.1). However, in only one case is there evidence of a positive influence of lifetime



Fig. 5.12 Predators of finches. **Upper left:** Short-eared Owl, *Asio flammeus*. **Upper right:** Galápagos Hawk, *Buteo galapagoensis*. **Lower left:** Great Blue Heron, *Ardea herodias*. **Lower right:** Great Egret, *Casmerodius albus*. Owls breed on other islands and visit Daphne for long periods. Analysis of pellets shows they sometimes feed on other islands and roost on Daphne (appendix 5.2). They also die there. A pair of hawks bred on the island in the 1920s (Beebe 1924). Individual hawks, herons, and egrets are rare visitors. All four predators feed on finches but not on nestlings.

number of mates on lifetime production of recruits, and that is from the 1983 cohort of *scandens* females (Grant and Grant 2011a). All these statistical indications of influences from partial regression coefficients are relatively weak and account for little additional variation in fledgling or recruit production after controlling for the number of clutches.

The question left unanswered by these analyses is what governs longevity? The short answer is dry-season survival, which is sometimes dependent on morphology, and random environmental effects. It may be largely a matter of chance which birds survive a long time and which die young. Those that survive long enough to breed may be more or less



Fig. 5.13 Debility and mortality. **Upper left:** Avipox on leg of immigrant *fuliginosa*. **Upper right:** Banded finch in owl pellet. **Lower left:** Egg and killed nestling in *mag-nirostris* nest (two other nestlings were killed, one with its head bitten off). **Lower right:** Two dead *fortis* with claws apparently entangled. The lower two figures illustrate the fact that finches are each others' own enemies in the breeding season.

equally equipped to continue living a long time, while subject to the random vicissitudes of territory quality, mate quality, susceptibility to predation by short-eared owls and egrets (fig. 5.12 and appendix 5.2), and other mortality factors (fig. 5.13), as well as accidents. Alternatively there may be genetic factors influencing survival, and also behavioral, ecological, and physiological factors that we have failed to detect. Whatever the causes, the consequence of a long life is high reproductive fitness.

These remarks apply to variation in longevity among members of the same cohort. There are differences among cohorts in average longevity caused by enduring effects of different environmental conditions (food supply, population density) experienced by finches early in life (fig. 5.14), as has been observed in other species elsewhere (e.g., Reid et al. 2003).

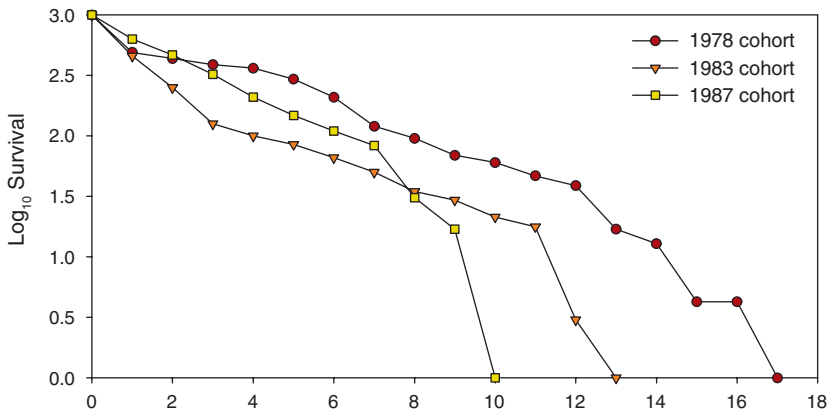


Fig. 5.14 Differences in survivorship among cohorts of *fortis* males. Numbers have been standardized to 1,000 alive in year of hatching prior to log-transformation. Actual numbers are 223, 1,019, and 955 for cohorts produced in 1978, 1983, and 1987 respectively. Differences in survivorship reflect differences in population density and food supply. Survival was greater in the cohort produced in a non-El Niño year (1978) than in the two El Niño years owing to low density in early life following the drought of 1977. *G. scandens* survival varies among cohorts in a similar way.

INBREEDING

Inbreeding makes a small contribution to variation in longevity. Inbreeding is associated with reduced fitness in both species, especially in the rare instances when close relatives breed with each other. We estimated a reduction of 21% in first year survival of a *scandens* offspring with an inbreeding coefficient (f) of 0.25, and 45% reduction in annual probability of survival of adults with $f = 0.25$ (Keller et al. 2002). The magnitude of inbreeding depression in both juveniles and adults is most severe in dry years of low food supply and high number of competitors. For example, under conditions of low rainfall the survival of a juvenile *scandens* with $f = 0.25$ was reduced by 65% compared with a noninbred juvenile, but under wetter conditions there was no difference. Thus inbreeding depression was revealed only under stressful conditions. In adults inbreeding depression was five times more severe in years of low food availability and high population density. Very few inbred *scandens* succeeded in breeding, and none produced grand-offspring. *G. fortis* experienced inbreeding depression only as a reduced probability of recruitment (Keller et al. 2002, Markert et al. 2004). Despite the adverse effects of inbreeding there is no statistical evidence of inbreeding avoidance (Gibbs and Grant 1989), nor is in-

breeding minimized by differential dispersal of the sexes from birth to breeding territory (Krakower 1996). The same, a lack of inbreeding avoidance, was found in small insular populations of Song Sparrows, *Melospiza melodia* (Keller and Arcese 1998), and House Sparrows, *Passer domesticus* (Billing et al. 2012).

Variation in Fitness

The fitness of an individual is governed by its ability to survive and reproduce, and by the ability of its offspring to survive to breed. Fitness varies substantially among breeders (fig. 5.9). If same-sex members of a breeding population have equal abilities to survive, reproduce, and produce recruits, and they and their offspring are subject to random hazards, the expected variation in fitness of the breeders is a Poisson distribution, characterized by a variance that is equal to the mean. However, the variance is greater than the mean in both *fortis* and *scandens*; moreover the variance increases in relation to the mean during the life span of cohorts as a consequence of a few individuals living long enough to take advantage of exceptionally favorable conditions for breeding in El Niño years (fig. 5.15). The increase in fitness with age demonstrates both deterministic and stochastic factors: the increase is governed deterministically, but who survives is partly stochastic.

Evolutionary consequences of fitness variation depend on whether it is heritable or not (Charlesworth 1987). If it is heritable, the lifetime number of recruits (generation 2) produced by 1978 males or females (parental generation 1) should predict the mean lifetime number of *their* recruits (generation 3). We used regression analysis to explore this possibility and found no evidence of heritable variation in clutch size (Gibbs 1988), number of fledglings, number of recruits, or longevity (Grant and Grant 2000b). The lack of heritable variation in fitness was also discovered at about the same time in red deer (Kruuk et al. 2000), although Merilä and Sheldon (2000) found significant but low heritability for male flycatcher life span and female recruitment success. Lack of heritable variation in fitness is expected in varying environments (Charlesworth 1987).

However, there is a subtle but important distinction to be made between average and total lifetime number of recruits to the grandparental generation 3 in the finches. The number of recruits (generation 2) produced by members of the 1978 cohorts (generation 1) does predict the total number of recruits that they contribute to the next generation (generation 3) in simple regressions (Grant and Grant

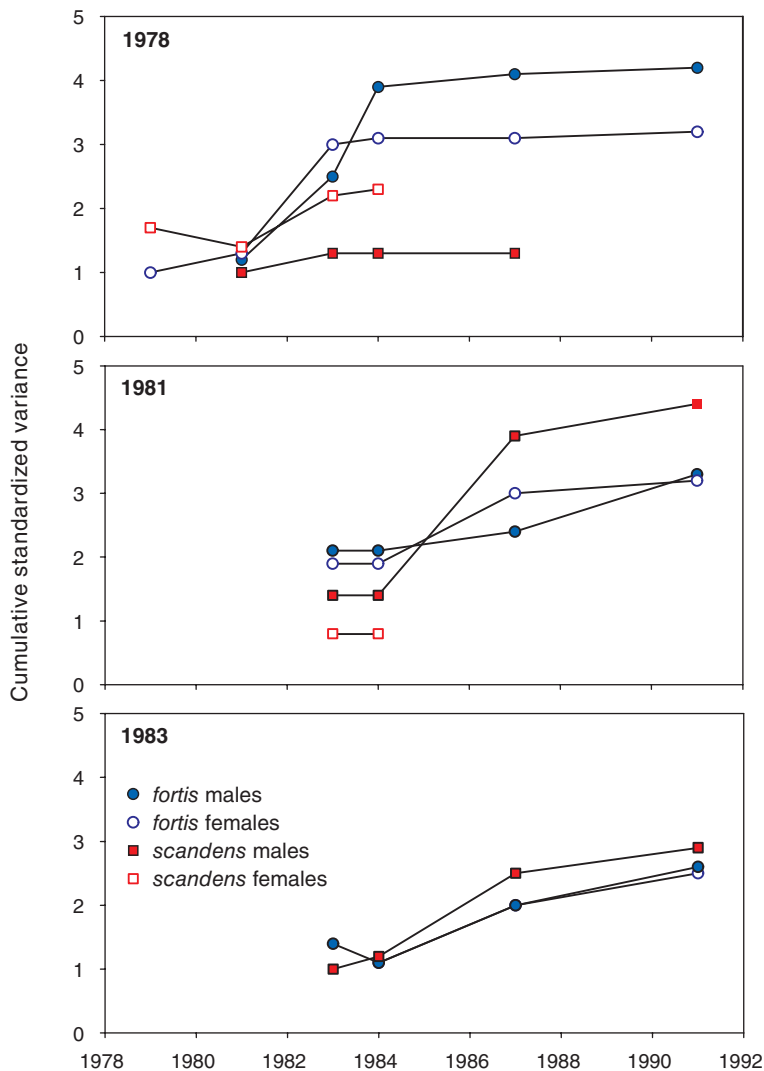


Fig. 5.15 Increase in nonrandom recruit production per parent (males and females averaged) over the lifetimes of three sets of cohorts: 1978, 1981, and 1983. The standardized variance (variance/mean) of recruits per parent is expected theoretically to remain at 1.0 in an idealized randomly breeding population, but instead increases systematically with the age of the breeders as a result of some gaining disproportionate recruitment success (adapted from Grant and Grant 2000b). Cohorts vary in recruit productions according to an unpredictable temporal pattern in the environmental fluctuations: at what ages they experience times of plenty and times of scarcity. For example, on average a female *fortis* hatched in 1983 had to live for 6 yr and produce 10 fledglings to replace herself (genetically) with 2 recruits, whereas a female of the 1978 cohort achieved replacement in 2.5 yr with 5 fledglings.

2000b): *fortis* males ($p = 0.0001$), females ($p = 0.0004$), *scandens* females ($p = 0.0072$) but not males ($p > 0.1$). Thus absence of detectable heritable variation does not mean the absence of predictability of fitness between parents and offspring. In general more recruits beget more recruits, with the result that some lineages proliferate and others do not.

Discussion

The principal contributors to lifetime fitness variation are morphology-dependent survival in the dry-season niche and morphology-independent reproduction in the wet-season niche. The lack of seasonal coupling means there are no specific demographic consequences of morphological evolution such as higher or lower reproductive rates, unlike some other species elsewhere (Ozgul et al. 2009, Schoener 2011, Miner et al. 2012): the feedback from ecological to evolutionary change is unidirectional and not bidirectional except in long-term coevolution of beaks and seeds or the woody tissues that contain them (Grant and Grant 1982, Benkman 1999).

Morphological and reproductive traits are sensitive to environmental change in fundamentally different ways. Morphology is almost fixed after growth has ceased in the first year (Boag 1984) and is highly heritable (chapter 3), whereas clutch size is phenotypically plastic, adjusted by females to the prevailing feeding conditions, and its heritability is close to zero (Gibbs 1988). Finches are at the mercy of the environment in the sense that being large, for example, may be selectively favored in one drought and disfavored in another (chapter 4): a finch may or may not be lucky to have the appropriate beak and body size for the circumstances it encounters. In contrast finches do control their reproduction, and adjust their reproductive effort and output in response to food supply and population density. Their behavioral flexibility extends to skill in rearing the offspring, to a degree dependent on age and experience, by among other things choosing defensible and cryptic nest sites and regulating interference from other finches there (Grant and Grant 1996c). This is easier when populations are low and food is abundant. In these respects both the general and the social environments influence fitness (fig. 4.1).

The contrast between morphology and reproductive traits has left its mark on the finch radiation. Species have diversified in morphology yet have largely retained uniformity and flexibility in breeding characteristics.

Summary

The chapter considers the causes of variation among individuals in reproductive success and overall fitness in terms of the number of recruits they produce in their lifetime. Reproduction is dependent on the amount of rain and the duration of the wet season, which vary enormously from year to year under the influence of the El Niño–Southern Oscillation phenomenon. Living a long life is key to an individual's fitness because the longer a bird lives the more opportunities it has to breed. Longevity is determined by an ability to survive droughts, which is sometimes dependent on morphology (*fortis*), but beyond that it may be largely a matter of chance which birds survive a long time and which die young. Those that survive long enough to breed may be more or less equally equipped to continue living a long time, while subject to random environmental effects such as interactions with aggressive neighbors, susceptibility to predation, and accidents. Longevity predicts total number of clutches, number of clutches predicts number of fledglings, and number of fledglings predicts number of recruits.

Morphological variables are rarely significant predictors of longevity or fitness over and above what is expected from occasional size-selective mortality in dry seasons. There is little evidence of a trade-off between wet-season and dry-season performance of birds with a particular morphology. When measured as lifetime production of recruits, fitness varies from 0 to 15 offspring per breeder. Variation in fitness is not heritable. A few individuals live for an exceptionally long time, up to 17 years, and breed many times. The variation in fitness has environmental causes and evolutionary (genetic) consequences, despite the lack of heritability, because in general more recruits beget more recruits, with the result that some lineages proliferate and others do not.