THE ROYAL SOCIETY

Non-random fitness variation in two populations of Darwin's finches

Peter R. Grant* **and B. Rosemary Grant**

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, USA

Darwinian fitness of an individual is measured by the number of recruits it contributes to the next generation. We studied variation in fitness among members of three cohorts of two species of Darwin's finches living on the Galápagos island of Daphne Major: the medium ground finch (*Geospiza fortis*) and cactus finch (*Geospiza scandens*). Individuals of both species live for up to 16 years. Variation in fitness was neither random nor heritable. Non-randomness arises as a result of a few individuals living for an exceptionally long time and breeding many times. For each cohort, the number of recruits per breeder is strongly predicted by the number of fledglings per breeder. In turn, the number of fledglings is strongly predicted by longevity of the breeder. These results suggest that the most important determinant of fitness is the ability of an individual to survive to breed in many years. Morphological traits affect this ability. Although morphological traits are heritable they do not change unidirectionally because they are selected in opposite directions, and in different combinations, under fluctuating environmental conditions. Non-random fitness variation in fluctuating populations implies much smaller genetically effective sizes than breeding population sizes.

Keywords: Galápagos; Darwin's finches; longevity; fledglings; recruits; heritability

1. INTRODUCTION

Fitnesses of members of a population vary enormously, for reasons that have remained elusive (Clutton-Brock 1988). Long-term studies of bird populations have quantitatively demonstrated the variation in nature most extensively. A consensus of findings from 23 studies was summarized ten years ago by Newton (1989) as follows: (i) a large fraction of fledglings die before they can breed, (ii) not all the individuals which survive to attempt breeding subsequently produce offspring, (iii) successful individuals vary greatly in productivity, (iv) breeding life span is the most important determinant of fledgling production, (v) number of fledglings is an important determinant of number of recruits, and so is breeding life span but to a lesser extent, and (vi) much of the variation in fitness, as indexed by lifetime production of offspring, is apparently due to chance. This last conclusion followed from a general failure to find correlations between fitness and other properties of the breeders such as body size and social factors, and failure to find heritable variation in fitness, rather than from explicit testing and failure to reject a null hypothesis that variation in fitness among parents can be ascribed to chance (but see McCleery & Perrins 1988; Dhondt 1989; Fitzpatrick & Woolfenden 1989).

Assessing the roles of chance and deterministic factors has been hampered by incomplete information on recruitment, because many offspring disperse beyond the borders of study areas (Lambrechts *et al.* 1999). As a result, all but one of the studies surveyed by Newton had to use local recruitment or the surrogate of offspring (fledgling) production as a measure of fitness. This problem has not been rectified by more recent work (e.g. Perrins *et al.* 1991; Lebreton & North 1993; Lambrechts *et al.* 1999). It can be eliminated on small and well-isolated islands where populations are discretely defined by geography, and immigration and emigration are low or effectively nil (Hochachka *et al.* 1989; Grant & Grant 1992, 1996). In this paper we report the results of a 24-year study of fitness variation in two species of Darwin's finches, *Geospiza fortis* (medium ground finch) and *Geospiza scandens* (cactus finch), on the small ($0.34\,\mathrm{km}^2$) Galápagos island of Daphne Major (Grant & Grant 1996). The nearest island is 8 km distant. The goals of the study were to use different cohorts of individually marked birds to (i) test for non-randomness in the frequency distribution of recruits among parents, (ii) attempt a statistical explanation of the variation in terms of life-history and morphological variables of the parents, (iii) test the hypothesis that recruitment success is partly determined by variation in properties of the offspring themselves, and (iv) test the hypothesis that variation in fitness of the parents, and in the major contributors to their fitness of survival and reproduction, is heritable.

2. MATERIAL AND METHODS

(a) *Study methods*

In the years 1976–1978 most nests were found and nestlings were banded. In the years 1979–1991 and 1998 an attempt was made to find every nest on the island throughout each breeding season and to band all the nestlings (Grant & Grant 1992; Grant *et al.* 2000). From 1992 to 1997 we spent approximately the first half of each breeding season on the island. There was no breeding in 1996 and 1999. Thus no more than half of the nestlings were banded and half of the number of fledglings determined in six of the last nine years.

Most birds were banded as eight-day nestlings, others were captured in mist-nets, beginning in 1973. Captured birds were measured (see §2(b)) and given a unique combination of three coloured plastic and one numbered metal band prior to their release. Parentage was determined by observation of banded adults attending nests. Microsatellite DNA analyses show no

---

*Author for correspondence (prgrant@princeton.edu).

Received 13 September 1999 *Accepted* 20 October 1999

evidence of misidentified maternity, but a low level of misidentified paternity (*ca.* 8% in *G. scandens* (Petren *et al.* 1999), and approximately double that in *G. fortis* (L. F. Keller, unpublished data)). Survival was determined every year by extensive and repeated surveys over the whole island, and by observing and identifying territorial males and their mates. Recruitment to the breeding population, as recognized by the laying of at least one egg by the individual or its mate, is likely to have been determined accurately. A very small number of recruits may have been missed in the years 1992–1997 if they bred only in the second half of a single breeding season.

Longevities of all members of the 1978–1987 cohorts were determined with the following exceptions; one 1983 *G. fortis* female, two 1987 *G. fortis* males and one 1987 *G. scandens* male were alive in 1999. Maximum longevity was 16 years for *G. fortis* (both sexes) and *G. scandens* males, and 11 years for *G. scandens* females. Effects of incomplete breeding data on analyses of the cohorts of 1978 and their offspring are likely to be minor. We may have missed one nest of each of the last three surviving members of the 1978 cohort of *G. fortis* in 1992, and one nest of the last survivor in 1993. Breeding of the offspring of the 1978 cohort after 1991 was underestimated. However, the number of recruits hatched in these years was small, and a minor fraction of the total recruits produced during the lifetimes of the offspring of the 1978 cohorts: five out of 382 (1.3%) *G. fortis* and three out of 43 (7.0%) *G. scandens*. Underestimation of the breeding of the 1981 and 1983 cohorts and their offspring was greater.

(b) *Analyses and measurements*

Fitness is measured by the number of offspring per parent that survive to breed, i.e. they become recruits to the breeding population (generation 2) and hence become potential contributors to generation 3. This ignores the temporal pattern of recruitment, which influences fitness for short-lived species undergoing systematic changes in breeding density (Stearns 1992).

Fitness is governed by the survival and reproduction of parents and the survival to breeding of their offspring. If same-sex members of a breeding population have equal abilities to survive, reproduce and produce recruits, and they and their offspring are subjected to random hazards, the expected variation in fitness of the breeders is a Poisson distribution. This null hypothesis was tested using the χ^2-test with data on fitness (lifetime number of recruits), survival (longevity) and reproduction (lifetime number of fledglings) from the largest and most complete cohorts: 1978, 1981 and 1983. Negative binomial distributions were also fitted to the data and tested by χ^2. The negative binomial is equivalent to a particular mixture of Poisson distributions with different means (Cavalli-Sforza & Bodmer 1971), and is appropriate with our data because entry of recruits into the breeding population is usually staggered. Coefficients were estimated by maximum likelihood with the Nlin procedure in SAS (SAS Institute, Inc.).

For the same three cohorts multiple regression analysis was used to predict fitness, survival and reproduction in terms of a few morphological and life-history variables suspected of being important for fitness. All independent variables were transformed to natural logs ($\log_e x$) prior to analysis. $\text{Log}_e x + 0.5$ was used for age at first breeding for the 1983 cohort because some birds bred (and some of those died) in their year of hatching, and $\log_e x + 1$ was used for number of fledglings for all cohorts and longevity of the 1983 cohort. Longevity was predicted by hatching date (days $1 \ldots n$ for each member of a cohort), age at first breeding in years, beak shape (length–depth) and structural body size as indexed by the first component from principal components analyses of morphological variation. Correlation matrices were used in separate principal components analyses for each sex of each species. The measured traits were mass (g), wing length, tarsus length, beak length, beak depth and beak width (all in millimetres), as described in Grant & Grant (1994). Predicted lifetime number of fledglings was estimated by all these variables together with longevity, then lifetime number of recruits was predicted by all these and lifetime number of fledglings.

Table 1. *Numbers of fledglings banded, and the numbers of those that eventually bred, in 11 sets of cohorts*

(In the remaining years there was no breeding, or little breeding yielding no recruitment.)

	G. fortis		*G. scandens*	
year	banded	bred (%)	banded	bred (%)
1976	376	1 (<0.1)	93	0 (0)
1978	222	89 (40.0)	164	43 (26.2)
1979	82	13 (15.8)	110	15 (13.6)
1980	37	0 (0)	134	2 (1.5)
1981	276	50 (18.2)	231	29 (12.6)
1983	1018	310 (30.5)	785	154 (19.6)
1984	427	45 (10.5)	208	4 (1.9)
1986	8	2 (25.0)	11	0 (0)
1987	1043	183 (17.6)	164	27 (16.5)
1990	33	6 (18.2)	4	0 (0)
1991	782	245 (31.3)	138	32 (23.2)

Logistic regression was used to test for associations between recruitment success and offspring morphology (principal component scores) and their dates of hatching; offspring that became recruits were scored as 1 and those that did not were scored as 0. For these analyses hatching dates were combined for all years after standardizing by dividing deviations from the annual mean by the standard deviation for that year. Significance of coefficients was tested by χ^2-tests.

Heritability hypotheses were tested by simple regressions with data from the 1978 cohort members and their offspring that survived to breed. The traits were longevity, and mean numbers of fledglings and recruits. Members of the 1978 cohort of *G. fortis* (table 1) produced a total of 888 fledglings in their lifetime (1979–1993), of which 244 (27.5%) bred (1981–1998). Members of the *G. scandens* cohort produced 469 fledglings (1979–1991), of which 89 (19.0%) bred (1981–1998). Analyses of heritable variation are necessarily restricted to those individuals that survived to breed. All statistical tests were two-tailed.

3. RESULTS

(a) *Variation in fitness*

Breeding, and the survival of offspring to breed (recruitment), vary greatly among years (table 1) as a result of annual fluctuations in rainfall and food supply in this seasonally arid environment (Grant & Grant 1996; Grant *et al.* 2000). 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

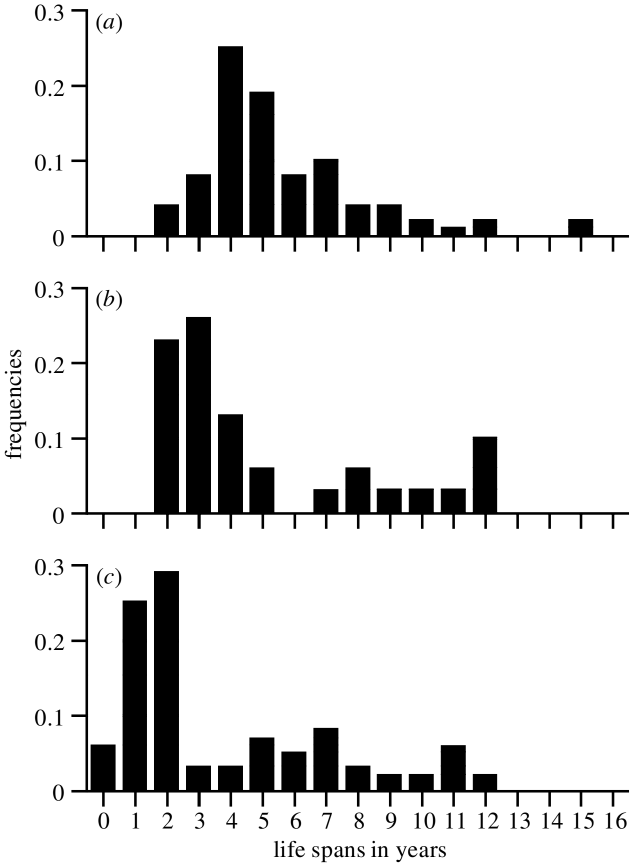

Figure 1. Annual variation in the distribution of life spans of *G. fortis* males, after the breeding of the first member of a cohort. (*a*) 1978, $n=48$; (*b*) 1981, $n=32$; (*c*) 1983, $n=112$.

as three months at rapidly rising density for 1983 cohorts (maximum four years). Recruitment was proportionally higher in *G. fortis*, the more abundant species, than in *G. scandens*. It never exceeded 40% for either species.

Frequency distributions of longevity (figure 1), fledglings and recruits among parents is non-random in most cases. Variances are greater than expected (table 2); some parents have exceptionally high recruitment success. For members of the 1981 and 1983 cohorts the variance is proportionally greater when allowance is made for incomplete recruit data after 1991 by doubling the known number of recruits they produced during this time. However, this adjustment has little effect on the statistics, and is not included in the table. With few exceptions, the Poisson distribution does not provide a good fit to any of the data. The negative binomial does not fit the distribution of longevities or fledglings produced by the 1978 and 1983 cohorts, even though entry into their respective breeding populations was more staggered than it was for the 1981 cohorts. The negative binomial best fits the distributions of recruits among breeders, but not for all cohorts.

Non-randomness increases through the life span of cohorts (figure 2). This temporal pattern arises as a consequence of relatively few individuals living long enough (figure 1) to take advantage of very favourable conditions for breeding. Standardized variances increased in 1987 and 1991, both productive El Niño years (>four broods), but, with one exception (*G. fortis* males), did not increase in 1984, a relatively unproductive year (one or two broods) (figure 2).

Table 2. *Standardized variances (variance–mean) of fitness (recruits per breeder) and two contributors to fitness, fledglings per breeder and breeder longevity*

	G. fortis		*G. scandens*	
	males	females	males	females
1978 cohort				
numbers	48	41	20	23
recruits	3.46^{***}	3.54^{***b}	1.21	2.45^{***a}
fledglings	37.89^{***b}	12.17^{***c}	5.90^{***c}	8.26^{***c}
longevity	1.23^{**c}	1.63^{**a}	1.10^{a}	0.93
1981 cohort				
numbers	32	19	12	8
recruits	3.05^{***}	3.05^{***}	3.90^{***}	3.67
fledglings	11.58^{***}	5.68^{***}	6.72^{***}	5.25^{***}
longevity	2.60^{***c}	1.78^{*c}	2.82^{***c}	0.54^{a}
1983 cohort				
numbers	113	194	52	103
recruits	2.38^{***}	2.59^{***}	2.49^{***}	3.09^{***a}
fledglings	8.44^{***c}	9.46^{***c}	5.43^{***a}	7.34^{***c}
longevity	3.01^{***c}	3.24^{***c}	4.01^{***c}	1.83^{***c}

$^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$, statistically significant departures from Poisson expectation by χ^2-tests.
$^{a}p<0.05$, $^{b}p<0.01$, $^{c}p<0.001$, departures from negative binomial expectation by χ^2-tests.

(b) *Predictions of fitness from properties of the parents*

There are two major results from multiple linear regression analyses (table 3). First, the strongest predictor of fitness is reproductive output; the more fledglings an individual produces in its lifetime the larger is its contribution of recruits to the next generation of breeders. Second, the strongest predictor of reproductive output is longevity; the longer an individual lives the more fledglings it produces.

Longevity is less well predicted than recruitment and fledgling production. Separate analyses of the shorter-lived and the longer-lived members of a cohort show that variation in longevity among the shorter-lived group is sometimes predictable, whereas variation among the longer-lived groups is not (all $F<1.7$, $p>0.2$; most $p>0.6$). For these analyses the data were split into two halves either side of the median age for the cohort. Despite the reduced power of these tests as a result of smaller sample sizes (8–55), and the reduced range of variation (zero to two years), longevity was predicted in the short-lived *G. fortis* 1983 males by age at first breeding ($b'=0.499$, $t_{32}=2.797$, $p=0.0091$), and in the short-lived (zero to two years) *G. scandens* 1983 females also by age at first breeding ($b'=0.409$, $t_{43}=2.219$, $p=0.0322$). Thus deterministic factors may come into play prominently early in life, while for those who survive beyond the cohort's median age it may be more a matter of chance who survives thereafter for a short time and who survives for a long time.

In the analyses of complete data (table 3) all of the independent variables made some contribution to predicting longevity, fledglings or recruits of some cohorts. A feature of these predictions is inconsistency in sign and among years. For example, early hatching is

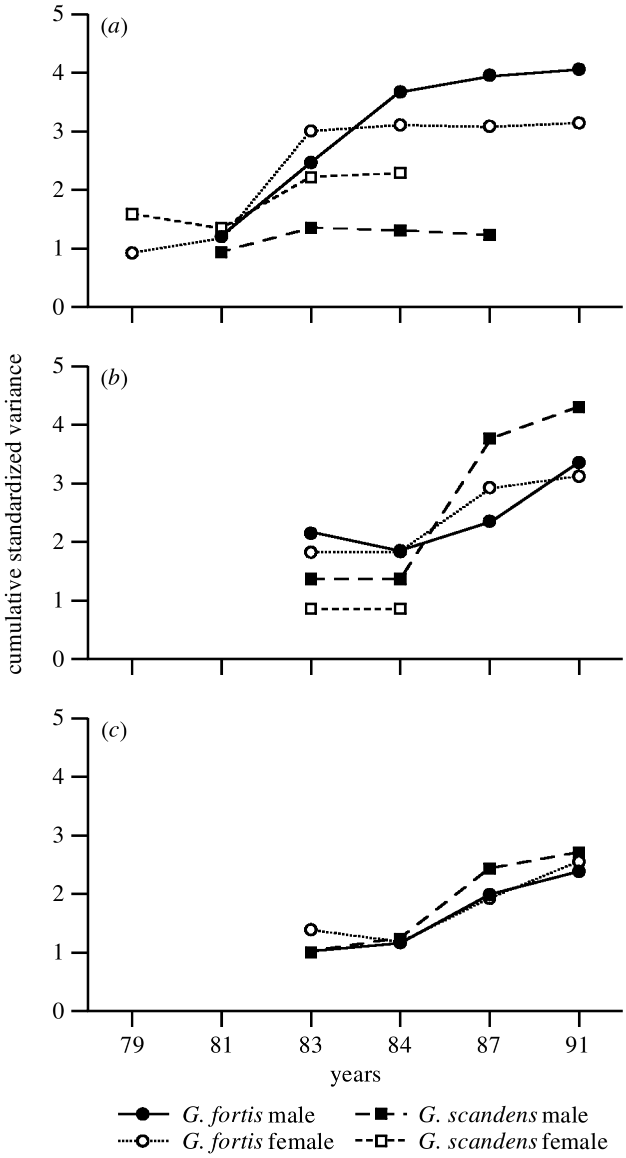

Figure 2. Changes in the standardized variances (variance–mean) of recruits per parent over the lifetimes of three sets of cohorts. (*a*) 1978, (*b*) 1981 and (*c*) 1983.

associated with long life in *G. fortis* and *G. scandens*, whereas late hatching is associated with high recruit production by female *G. fortis* and high fledgling production by female *G. scandens*. Data for male and female parental groups are not entirely independent since some recruits had both male and female parents from the same cohort. As a result the regressions for male and female parents might be expected to be similar, with those for males being weaker as a result of some misassigned paternity of offspring, especially in *G. fortis*. Regressions do tend to be similar, but female regressions are not consistently stronger than male regressions, nor are the coefficients consistently larger (table 3).

Results for the 1978 cohorts are illustrated with path diagrams (figure 3). The diagrams are based on the methods of path analysis of causal pathways, hypothesized *a priori*, between longevity, fledglings and fitness (generalizations (iv) and (v) in §1). They are not restricted to those pathways, and for comprehensive illustration the diagrams include other pathways identified by the regression analyses. The indirect pathway from longevity to recruits via fledgling production is consistently stronger than the direct pathway. Other pathways are inconsistent between species and sexes.

(c) *Properties of the offspring and recruitment success*

Offspring that became recruits differed occasionally from those that did not in small and inconsistent ways. For offspring of 1978 cohorts *G. scandens* recruits were larger (males) and hatched earlier (females) than non-recruits of the same sex (logistic regressions: male body size $= 0.855 \pm 0.443$ (s.e.), $p = 0.0533$, $r^2 = 0.114$, $n = 50$; female hatch date coefficient $= -1.634 \pm 0.778$, $p = 0.0357$, $r^2 = 0.134$, $n = 38$). For offspring of 1981 cohorts *G. fortis* female recruits were larger and hatched later than non-recruits (body size $= 1.024 \pm 0.451$, $p = 0.0233$; hatch date coefficient $= 1.421 \pm 0.737$, $p = 0.0537$, $r^2 = 0.137$, $n = 61$). For offspring of 1983 cohorts *G. fortis* male recruits were smaller than non-recruits (body size $= -0.332 \pm 0.162$, $p = 0.0409$, $r^2 = 0.022$, $n = 225$). None of the other coefficients was significantly different from zero (all $p > 0.1$).

(d) *Heritability of fitness, reproduction and longevity*

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). Regression analyses were performed to predict either (i) all generation 3 recruits, or (ii) just those produced by the largest single cohorts (1981 or 1983) of generation 2. Sample sizes of 1978 cohort parents were 36 *G. fortis* males and 26 females (14 pairs), and 15 *G. scandens* males and 17 females. None of the regressions of mid-offspring values on single parent or mid-parent values is significant (all $p > 0.15$) from either type of analysis. The hypothesis of heritable variation in fitness has no support. Variation in lifetime production of fledglings and longevity are also not detectably heritable by the same methods and with the same samples (all $p > 0.24$).

(e) *Predictability of fitness between generations*

Absence of detectable heritable variation does not mean the absence of predictability of fitness between parents and offspring. The number of recruits produced by members of the 1978 cohorts does predict the total (as opposed to mean) number of recruits that they contribute to the next generation (generation 3); for *G. fortis* males $b = 1.559 \pm 0.263$, $t_{34} = 5.925$, $p = 0.0001$, and females $b = 1.708 \pm 0.417$, $t_{24} = 4.091$, $p = 0.0004$, and for *G. scandens* females $b = 0.806 \pm 0.260$, $t_{15} = 3.106$, $p = 0.0072$, but for males $b = 0.057 \pm 0.575$, $t_{13} = 0.100$, $p = 0.920$. In general more recruits beget more recruits.

Similarly the total (as opposed to mean) number of generation 3 fledglings is predicted from the number of fledglings (generation 2) produced by their *G. fortis* parents (generation 1) (males $b = 1.511 \pm 0.401$, $t_{34} = 3.766$, $p = 0.0006$; females $b = 1.292 \pm 0.535$, $t_{24} = 2.400$, $p = 0.0249$), although not by their *G. scandens* parents (both $p > 0.7$).

Breeding success (fledglings produced) of a parent in generation 1 predicts the number of recruits in generation 3

Table 3. *Standardized partial regression coefficients from regression analyses predicting longevity, fledglings or recruits produced by members of three sets of cohorts*

(1, 2 and 3 are generations 1, 2 and 3. Values in parentheses indicate coefficients after fledglings or longevity have been deleted because of high intercorrelations. All but three individuals of the 1981 cohorts bred for the first time in 1983, therefore age at first breeding was not included in these analyses. Body size is PC1. Beak shape is length–depth. Two sample sizes are shown, the first for longevity and fledglings, and the second for recruits. Results for the 1981 and 1983 cohorts are scarcely affected when recruit numbers are adjusted by doubling the known number of recruits produced after 1991 (see § 3(a)). — indicates lack of significance ($p > 0.1$). The sample size of the *G. scandens* 1981 cohort of females (eight) is too small for analysis.)

	G. fortis		*G. scandens*	
	males	females	males	females
1978 cohort				
1: longevity				
hatch date	-0.423^{**}	—	—	—
beak shape	0.402^{**}	—	—	—
2: fledglings				
longevity	0.693^{****}	0.868^{****}	—	0.444^{*}
age at 1st breeding	—	—	-0.763^{*}	—
body size	—	-0.212^{*}	—	—
beak shape	—	—	—	-0.614^{***}
3: recruits				
fledglings	(0.452^{*})	(0.621^{****})	—	—
hatch date	—	0.386^{*}	—	—
samples	41, 36	36, 26	18, 13	19, 14
1981 cohort				
1: longevity	—	—	—	—
2: fledglings				
longevity	0.744^{****}	0.691^{****}	0.818^{****}	—
beak shape	—	—	-0.486^{*}	—
3: recruits				
fledglings	0.758^{****}	1.043^{****}	(0.773^{****})	—
longevity	(0.547^{***})	(0.483^{*})	(0.682^{***})	—
samples	29, 25	14, 13	15, 13	—
1983 cohort				
1: longevity	—	—	—	—
hatch date	—	—	—	-0.343^{*}
age at 1st breeding	—	—	0.339^{*}	0.430^{***}
body size		—	0.402^{**}	—
beak shape	0.296^{*}	—	—	—
2: fledglings				
longevity	0.836^{****}	0.818^{****}	0.706^{****}	0.941^{****}
age at 1st breeding	—	—	-0.424^{*}	-0.218^{*}
3: recruits				
fledglings	(0.627^{****})	0.651^{****}	0.717^{***}	0.847^{****}
longevity	(0.577^{****})	(0.603^{****})	(0.420^{*})	(0.536^{****})
body size	—	0.160^{*}	—	—
samples	76, 64	108, 97	37, 25	55, 39

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.005$ and $^{****}p < 0.001$.

for *G. fortis* males ($b = 0.321 \pm 0.103$, $t_{34} = 3.132$, $p = 0.0036$), possibly for females ($b = 0.256 \pm 0.152$, $t_{24} = 1.688$, $p = 0.1044$), but not for *G. scandens* males ($b = -0.028 \pm 0.120$, $t_{13} = 0.234$, $p = 0.8186$) or females ($b = -0.045 \pm 0.104$, $t_{15} = 0.431$, $p = 0.6725$).

4. DISCUSSION

Results of this study are consistent with the first five generalizations given in § 1. They strengthen them by being based on two long-lived, tropical, passerine bird species whose recruitment has been determined completely or almost completely. The results throw new light on the sixth generalization concerning the enigmatic role of chance in producing variation in fitness. The main result here is that variation in fitness is neither detectably heritable nor entirely random. The variation has environmental causes and, despite the lack of heritability, evolutionary (genetic) consequences.

As appears to be the case in other bird species (Grant & Grant 1992; Barrowclough & Rockwell 1993), nonrandomness arises through some individuals being able to live long enough to reproduce many times. Long life (maximum 16 years, both species) is translated into large production of fledglings (maximum 46, from a *G. fortis* male), which is translated into high recruitment (maximum 16, from a *G. fortis* female; see also figure 3). Variation in recruitment departs strongly from random

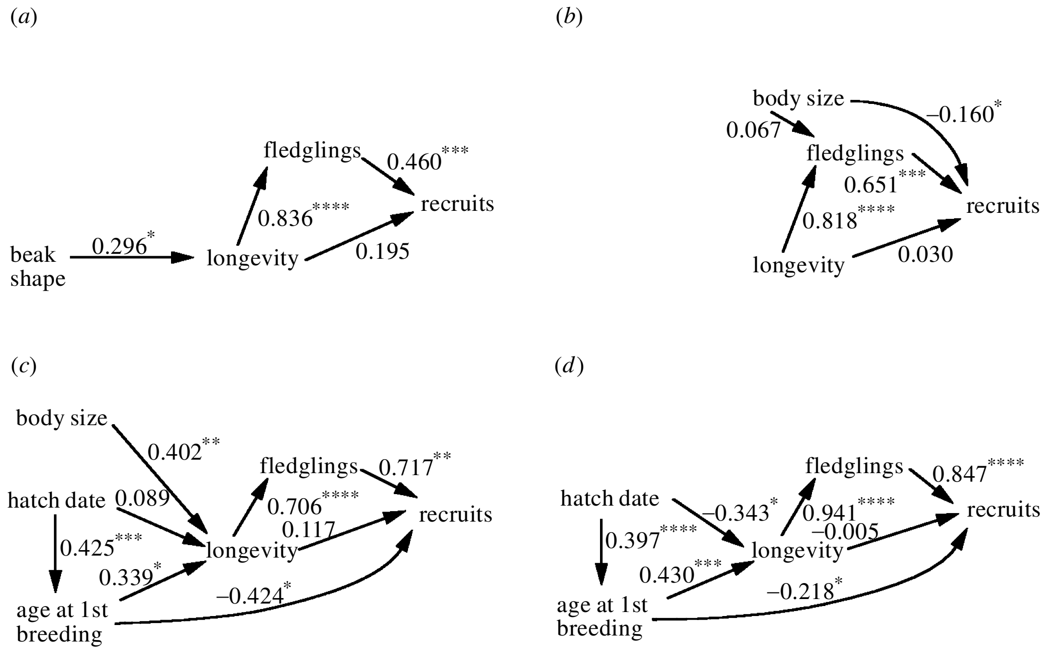

Figure 3. Path diagrams to represent the causal relationships between measured variables and fitness (recruits) for the 1983 cohorts. Where age at first breeding significantly predicts longevity the pathways from hatching date to both of them have been added. Pathways for unmeasured variables and correlations between causal factors have been omitted. Path coefficients are the standardized partial regression coefficients recalculated after deletion of non-significant morphological and life-history variables; they differ to a minor extent from the coefficients in table 3. Significance of the coefficients is indicated by $^{****}p<0.001$, $^{***}p<0.005$, $^{**}p<0.01$, $^{*}p<0.05$. (*a*) *G. fortis* males; (*b*) *G. fortis* females; (*c*) *G. scandens* males; (*d*) *G. scandens* females.

expectations according to a Poisson model, but conforms to negative binomial expectations in most cases. This can be interpreted as reflecting variation in the reproductive abilities and circumstances of breeders, and variation in the abilities and circumstances experienced by their offspring prior to reaching breeding age. Both deterministic and stochastic factors contribute to a shift, from fledgling production to recruitment, in the distribution of fitness among parents over their lifetimes towards that expected from a negative binomial, in other words towards the expectation from a mixture of Poisson distributions with different means.

The key question is: What governs longevity of the breeders? Combining the present results with long-term ecological studies on the same island (Grant & Grant 1996; Grant *et al.* 2000), we suggest the answer is that both life-history and morphological traits influence longevity in ways that vary depending upon fluctuations in environmental conditions. The particular factors and directions of selective influence change because the environment fluctuates from droughts and low food supply to an abundance of rain and enhanced food supply at approximately four-year intervals, or once per finch generation on average (Grant & Grant 1992). These influences are manifested against a background of largely random environmental effects, and while biologically important they generally stand out rather weakly in statistical analyses.

Among life-history traits the importance of hatching date is shown by the results of multiple regression analyses. Long life was associated with early hatching in *G. fortis* (1978, males) and *G. scandens* (1983, females). This suggests that entering a population at relatively low density early in the season when food supply is generally at its highest level confers an advantage, environmental in origin, upon both species in some years. They may gain good condition thereby, in terms of maturation of tissues and storage of energy, and if circumstances are favourable they may be able to breed at an early age as a result (1983).

The importance of morphological traits is shown by statistical associations between long life and large body size in *G. scandens* (1983, males) and beak shape in *G. fortis* (1978 and 1983, males). All cohorts, but especially the 1983 ones, experienced a decline and change in composition in their food supply in 1984–1986. Mortality was heavy, particularly among *G. scandens* whose cactus supply was depleted. Large size was an advantage to male *G. scandens* at this time, as their success is dependent upon gaining a territory which they occupy and defend year round, and large size confers an advantage in territorial disputes. *G. fortis* males, in contrast, are territorial only in the breeding season. *G. fortis* in general, and not just the 1983 cohort, were subject to directional selection in favour of size-independent long and shallow beaks when the food supply changed in composition and declined in abundance (Gibbs & Grant 1987; Grant & Grant 1995, 1996).

In addition to the above example, the importance of environmental fluctuations is shown by a general lack of consistency among cohorts of the same species and sex groups in the effects of morphological and life-history traits on fitness, longevity and the production of fledglings. There are two interrelated reasons for this inconsistency.

First, environmental conditions differ between pre- and post-recruitment phases of the life cycle. The fates of males and females of the 1983 cohort of *G. scandens* illustrate the point. Those that became recruits early in their life, in their year of hatching or in the following one, produced a relatively large number of offspring but, possibly as a consequence, lived for a short time. The environment deteriorated in 1984–1986. Despite living long the survivors which had not bred previously produced relatively few offspring. Second, different cohorts experienced different conditions at one or both phases: one cohort's pre-recruitment phase is its predecessor's post-recruitment phase. For example the 1984–1986 period of strong mortality occurred after all recruitment of members of the 1978 and 1981 cohorts had taken place but before recruitment of the 1983 cohorts was complete.

Thus components of fitness at different life-history stages of the same and different cohorts may covary, positively or negatively (Price & Grant 1984; Price & Schluter 1991; Schluter & Smith 1986), or be entirely independent, depending on the specific details of inter-annual variation in environmental conditions.

These conclusions are not restricted to Darwin's finches and their particular tropical environment. Passerine bird populations in the temperate zone experience significant annual variation in environmental conditions, even though less extreme than in the Galápagos archipelago. Temperatures and food supply vary in both non-breeding seasons and at the beginning of breeding. This causes marked variation in survival and local recruitment, mediated by variation in food supply, the timing of breeding and local density (Hochachka *et al.* 1989; Van Noordwijk *et al.* 1995; Visser *et al.* 1998; Both *et al.* 1999; Visser & Verboven 1999). Such details illustrate the general importance ascribed to environmental variation in determining low (or zero) heritabilities of life-history traits and fitness itself (Charlesworth 1987; Price & Schluter 1991).

Non-random fitness variation caused by fluctuating environmental pressures has two interesting evolutionary implications. First, although morphological traits contribute to fitness and are heritable (Grant & Grant 1999) they do not change unidirectionally because they are selected in opposite directions, and in different combinations, under fluctuating environmental conditions (Gibbs & Grant 1987). This implies that a net directional evolutionary trend is more likely to come about as a result of a directional change in the environment (Grant 1999), such as might be produced by global warming for example, than as a result of current oscillations.

Second, non-random fitness variation with standardized variances substantially greater than 1.0 imply that genetically effective population sizes are much smaller than sizes of the breeding populations. This appears to be generally true for plant and animal populations, especially for those whose sizes fluctuate (Frankham 1995). Estimates for bird populations may average about 25% of breeding numbers (Grant & Grant 1992), with minima as low as 10% (Rockwell & Barrowclough 1995; Collias & Collias 1996), or even less (Freeman-Gallant 1996). We note that the process of narrowing the genetic variation in one generation may be continued in the following generation by the tendency for lineages to have high success in successive generations. Genetic and non-genetic maternal effects upon offspring condition which are still present when the offspring breed (Merilä 1996; Potti 1999) may contribute to the trans-generation continuity.

We thank the Charles Darwin Research Station (Galápagos) and the Galápagos National Parks Service for logistical support, the National Science Foundation (USA) and National Science and Engineering Research Council (Canada) for financial support, many field assistants, and L. F. Keller for estimation of coefficients for the negative binomial distributions.

REFERENCES

Barrowclough, G. F. & Rockwell, R. F. 1993 Variance of lifetime reproductive success: estimation based on demographic data. *Am. Nat.* **141**, 281–295.

Both, C., Visser, M. E. & Verboven, N. 1999 Density-dependent recruitment rates in great tits: the importance of being heavier. *Proc. R. Soc. Lond.* B **266**, 465–469.

Cavalli-Sforza, L. L. & Bodmer, W. F. 1971 *The genetics of human populations.* San Francisco, CA: W. H. Freeman & Co.

Charlesworth, B. 1987 The heritability of fitness. In *Sexual selection: testing the alternatives* (ed. J. Bradbury & M. Andersson), pp. 21–40. New York: Wiley.

Clutton-Brock, T. H. (ed.) 1988 *Reproductive success. Studies of individual variation in contrasting breeding systems.* University of Chicago Press.

Collias, N. E. & Collias, E. C. 1996 Social organization of a red junglefowl, *Gallus gallus*, population related to evolution theory. *Anim. Behav.* **51**, 1337–1354.

Dhondt, A. A. 1989 Blue tit. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 15–33. London: Academic Press.

Fitzpatrick, J. W. & Woolfenden, G. E. 1989 Florida scrub jay. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 201–218. London: Academic Press.

Frankham, R. 1995 Effective population size/adult population size ratios in wildlife: a review. *Genet. Res. Camb.* **66**, 95–107.

Freeman-Gallant, C. R. 1996 Microgeographic patterns of genetic and morphological variation in savannah sparrows (*Passerella sandwichensis*). *Evolution* **50**, 1631–1637.

Gibbs, H. L. & Grant, P. R. 1987 Oscillating selection on Darwin's finches. *Nature* **327**, 511–513.

Grant, P. R. 1999 *Ecology and evolution of Darwin's finches*, 2nd edn. Princeton University Press.

Grant, P. R. & Grant, B. R. 1992 Demography and the genetically effective sizes of two populations of Darwin's finches. *Ecology* **73**, 766–784.

Grant, P. R. & Grant, B. R. 1994 Phenotypic and genetic effects of hybridization in Darwin's finches. *Evolution* **48**, 297–316.

Grant, P. R. & Grant, B. R. 1995 Predicting microevolutionary responses to directional natural selection on heritable variation. *Evolution* **49**, 241–251.

Grant, P. R. & Grant, B. R. 1996 Finch communities in a climatically fluctuating environment. In *Long-term studies of vertebrate communities* (ed. M. L. Cody & J. A. Smallwood), pp. 343–390. New York: Academic Press.

Grant, P. R. & Grant, B. R. 1999 Quantitative genetic variation in populations of Darwin's finches. In *Adaptive genetic variation in the wild* (ed. T. A. Mousseau, B. Sinervo & J. A. Endler), pp. 3–40. New York: Oxford University Press.

Grant, P. R., Grant, B. R., Keller, L. F. & Petren, K. 2000 Effects of El Niño events on Darwin's finches. *Ecology* **81**. (In the press.)

Hochachka, W. M., Smith, J. N. M. & Arcese, P. 1989 Song sparrow. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 135–152. London: Academic Press.

Lambrechts, M. M., Blondel, J., Caizergues, A., Dias, P. C., Pradel, R. & Thomas, D. W. 1999 Will estimates of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify processes underlying adaptation? *Oikos* **86**, 147–151.

Lebreton, J.-D. & North, P. M. (eds) 1993 *Marked individuals in the study of bird populations.* Basel, Switzerland: Birkhäuser.

McCleery, R. H. & Perrins, C. M. 1988 Lifetime reproductive success of the great tit, *Parus major*. In *Reproductive success. Studies of individual variation in contrasting breeding systems* (ed. T. H. Clutton-Brock), pp. 136–153. University of Chicago Press.

Merilä, J. 1996 Genetic variation in offspring condition: an experiment. *Funct. Ecol.* **10**, 465–474.

Newton, I. (ed.) 1989 *Lifetime reproduction in birds.* London: Academic Press.

Perrins, C. M., Lebreton, J.-D. & Hirons, G. J. M. 1991 *Bird population studies. Relevance to conservation and management.* Oxford University Press.

Petren, K., Grant, B. R. & Grant, P. R. 1999 Extrapair paternity in the cactus finch *Geospiza scandens*. *Auk* **116**, 252–256.

Potti, J. 1999 Maternal effects and the pervasive impact of nestling history on egg size in a passerine bird. *Evolution* **53**, 279–285.

Price, T. D. & Grant, P. R. 1984 Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* **38**, 483–495.

Price, T. & Schluter, D. 1991 On the low heritability of life history traits. *Evolution* **45**, 853–862.

Rockwell, R. F. & Barrowclough, G. F. 1995 Effective population size and lifetime reproductive success. *Biol. Conserv.* **9**, 1225–1233.

Schluter, D. & Smith, J. N. M. 1986 Natural selection on beak and body size in the song sparrow. *Evolution* **40**, 221–231.

Stearns, S. C. 1992 *The evolution of life histories.* Oxford University Press.

Van Noordwijk, A. J., McCleery, R. H. & Perrins, C. M. 1995 Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J. Anim. Ecol.* **64**, 451–458.

Visser, M. E. & Verboven, N. 1999 Long-term fitness effects of fledgling date in great tits. *Oikos* **85**, 445–450.

Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond.* B **265**, 1867–1870.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.