Ecology, 81(9), 2000, pp. 2442–2457
© 2000 by the Ecological Society of America

EFFECTS OF EL NIÑO EVENTS ON DARWIN'S FINCH PRODUCTIVITY

PETER R. GRANT, B. ROSEMARY GRANT, LUKAS F. KELLER, AND KENNETH PETREN

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

Abstract. We studied the effects of heavy and prolonged rainfall associated with four El Niño events on the reproduction of Darwin's finches on the Galápagos island of Daphne Major. Rainfall varied in the El Niño years from 195 mm to 1359 mm, exceeding the maximum in the other years by 40% to 1000%. Two species were studied: *Geospiza fortis,* Medium Ground Finch, and *G. scandens,* Cactus Finch. Almost all eggs, nestlings, and fledglings produced by banded females were recorded in the El Niño years of 1983, 1987, 1991, and 1998. Finch production in these years was compared with production in 10 other years of breeding in the period 1976–1990; there was no breeding in three drought years, 1985, 1988, and 1989.

Breeding differed in the two sets of years in several ways. More broods were produced in El Niño years than in non-El Niño years (maximum 10 clutches per female vs. five clutches), the period of breeding was longer (maximum eight months vs. four), average clutch sizes (range 2–6 eggs) were distinctly larger (four vs. three), and average egg and fledgling production per female was larger by a factor of four. The two species differed in some features of breeding, but differences were minor in comparison with the marked seasonal and annual variation. Finch production varied among El Niño years, being greatest in the year of most rain over the longest period (1983), and least in the next wettest year (1998). The surprisingly low production in 1998 is attributed in part to interactions with other finches, and in part to exceptionally high temperatures. Temperature, although postively correlated with rainfall, had an independent negative effect upon hatching and overall breeding success of *G. fortis.* Breeding by both species in the year of birth (hatch) occurred in two El Niño years with the most extended wet seasons: 1983 and 1987. Young breeders had lower clutch sizes and breeding success than did contemporaneously breeding older birds.

Observations in different El Niño years show that finch population responses to major climatic perturbations such as elevated rainfall vary for two major reasons: the perturbations themselves vary in strength and duration, and responses to them are determined, in part, by preceding conditions. Those preceding conditions, in turn, are determined by whether drought or normal conditions precede the perturbation, and on the interval since the previous El Niño event. Thus, perturbations of natural systems can be fully understood only in a broad temporal context.

Key words: breeding success; Darwin's finches; El Niño; food supply; Galápagos; Geospiza fortis*;* Geospiza scandens.

INTRODUCTION

Environments are heterogeneous in space and time; therefore, population processes such as births and deaths are also likely to be heterogeneous in space and time. Establishing the causal links between the two sets of heterogeneities is best accomplished by controlled experimental perturbations of natural processes. Depending on their scale and complexity, experiments may be limited by low statistical power, excessive costs, or infeasibility. The alternative (or complementary) approach is to quantify ecological processes that are naturally perturbed, preferably with replicated perturbations, and to test causal hypotheses statistically with the resulting data. El Niño events recurring during long-term field studies are highly suitable for this task.

El Niño events are large-scale perturbations of varying strength, occurring in the tropical eastern Pacific, but affecting extratropical regions as well, and recurring at sufficiently short intervals to provide replication in both time and space. They are major departures from normal oceanographic conditions that are coupled to the Southern Oscillation of atmospheric pressure across the Pacific Ocean (Philander 1990, Kerr 1999, Timmermann et al. 1999). They are recognized and classified by anomalously high sea surface temperatures, and are accompanied by heavy and prolonged rain in equatorial areas in the eastern Pacific. At the same time, some areas experience drought, owing to atmospheric teleconnections between them and the areas directly affected by the perturbation. For marine organisms, El Niño events cause widespread mortality and exceptional dispersal outside normal breeding and feeding ranges because of food shortages caused by high sea temperatures and reduced ocean upwellings (Barber and Chavez 1986, Glynn 1988, Wikelski and Trillmich

Manuscript received 12 January 1999; revised 9 August 1999; accepted 16 August 1999.

1997). For terrestrial organisms, their effects vary according to whether a local region is affected by heavy rains or by drought (Wright et al. 1999). The former may foster unusual reproduction (Polis et al. 1997), whereas the latter may cause severe mortality (Hubbell and Foster 1990).

The equatorial Galápagos archipelago lies in the region of El Niño influence that produces heavy rain and unusually high air temperatures. Different components of its biota suffered or prospered in the El Niño event of 1983 (Robinson and del Pino 1985) that began in late 1982 and continued for eight months. It has been described as the most severe event of the century (Cane 1983), possibly of the last 400 years (Glynn 1988). Its effects were experienced throughout the archipelago and, hence, were replicated in space. For example, populations of Darwin's finches on two widely separated islands, Genovesa (Grant and Grant 1987, 1989) and Daphne Major (Gibbs and Grant 1987*a*), responded in the same way to heavy rain and a prolonged wet season (Grant and Grant 1996). Clutch sizes were elevated and finches bred repeatedly. As a result, the breeding season was much longer than usual and population sizes increased during the season by a factor of ~10. On Daphne Major, where almost all birds had been uniquely banded prior to 1983, the extended breeding season permitted recruitment to the breeding population of birds born earlier in that year (Gibbs et al. 1984, Gibbs and Grant 1987*a*).

The specific effects of the El Niño conditions were known by comparing breeding in 1982–1983 with breeding in preceding and succeeding years. Since that study, there have been six years with El Niño events, as classified by oceanographic criteria. The study on Daphne Major (Plate 1) has been continued throughout this period up to the present time. Data obtained in three of the years are sufficiently extensive for comparison with the El Niño event of 1982–1983 and with 10 other years of breeding. The two purposes of this paper are (1) to compare finch production in El Niño and non-El Niño years, and (2) to quantify and interpret variation in production among El Niño years. We examine the possibility that two species with different diets and territory systems show different responses to El Niño conditions.

Methods

Daphne Major is a small island (~34 ha) approximately in the center of the archipelago and ~8 km from the central large island of Santa Cruz (Grant 1999). It has a maximum elevation of 120 m, supports a drought-deciduous vegetation with *Opuntia* cactus, and experiences a hot wet season, typically in the first four months of the year, and a dry cooler season for the remainder of the year. Four finch species breed on the island, mainly the Medium Ground Finch *Geospiza fortis*, a generalist granivore, and the Cactus Finch *G. scandens*, which is a cactus-feeding specialist more

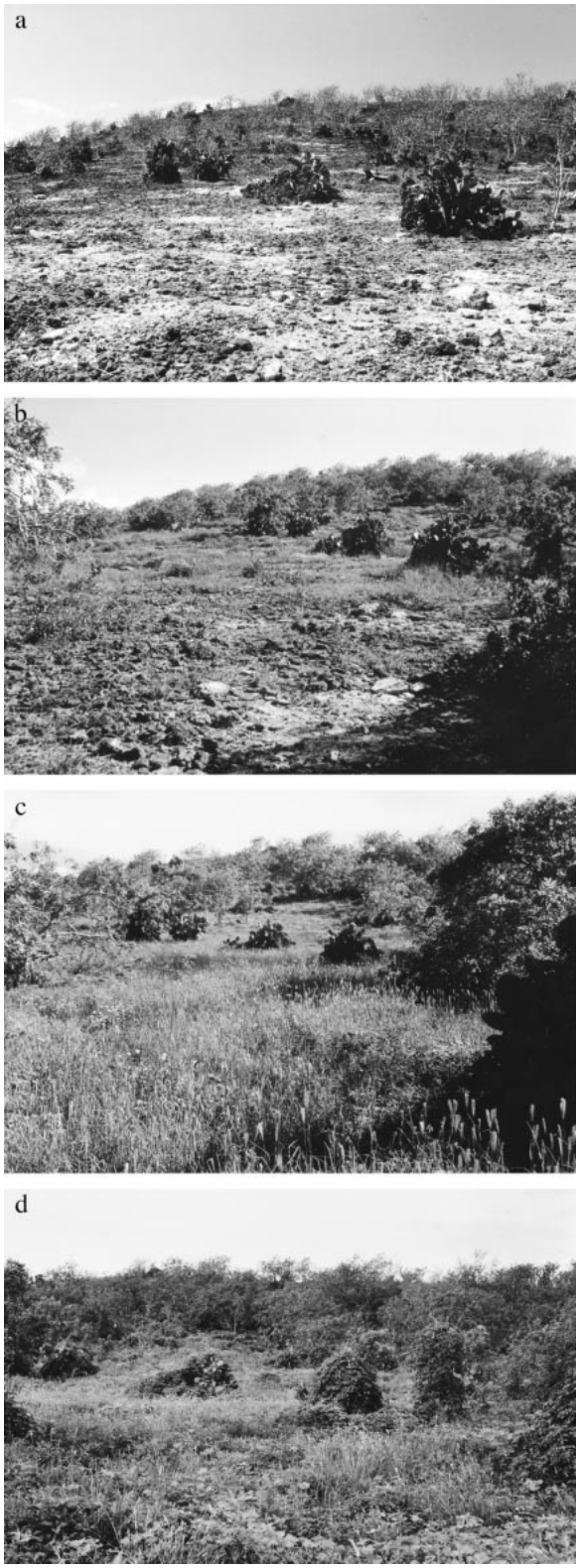

Plate 1. Daphne Major Island under contrasting climatic conditions: (a) typical dry season (1996); (b) typical wet season (1995); (c) El Niño wet season (1997); (d) El Niño wet season (1998).

strongly dependent on its territory for food than is *G. fortis*. In the years 1976–1991 and 1998, numbers of breeding females varied from 60 (1979) to ~250 (1976) for *G. fortis*, and from 18 (1991) to 115 (1983) for *G. scandens*. The other two species, the granivorous Small Ground Finch *G. fuliginosa* and the Large Ground Finch *G. magnirostris*, were either rare throughout (*G. fuliginosa*) or only became breeders during the study (*G. magnirostris*), beginning from just a few pairs in 1983 (Grant and Grant 1995*a*, 1996). These latter two species are considered only briefly at the end of the *Results*.

An annual breeding study of finches on this island was begun in 1976 and has continued to the present. Methods of study have remained basically unchanged. They have been reported in detail in previous publications (Boag and Grant 1984, Millington and Grant 1984, Gibbs and Grant 1987*a*, *b*, Grant and Grant 1992*a*), and will be only summarized here.

Breeding began in November or December 1982 at the start of an El Niño event, but in all other years it started in January, February, or March, following the onset of rain with little or no delay. In the years 1976–1991, almost all nests on the island were found and flagged throughout the breeding season during nest construction, incubation, or, rarely, the nestling phase. From 1992 to 1997, breeding was studied intensively for only 3–6 weeks. Breeding was again studied throughout the breeding season of 1998, except for January, when an estimated 5–10% of pairs attempted to breed. In this year, the study was concentrated on, but not restricted to, nests of banded birds (~12%). Contents of nests were checked regularly, usually at 2–4 d intervals, to determine laying date, clutch size, hatching success, and fledging success. Young were banded and weighed at day 8 after hatching. Their parents were identified by observation. Molecular genetic assessment of parentage in *G. scandens* on this island has shown that all female parents and 92% of male parents are correctly identified by observation (Petren et al. 1999). Preliminary analysis of *G. fortis* data give similar results (L. F. Keller, *unpublished observations*), therefore the production of offspring by identified females is accurately determined by observation.

Finches were banded as adults or nestlings. The percentage of banded birds among the breeders of all species combined had reached 90% by 1980 (N = 265 breeders), and reached 100% in 1992 (N = 336 breeders). After 1992, only a small percentage of nestlings were banded, and by 1998 the percentage of banded birds had fallen to <20%. Numbers of banded adults were determined by a combination of standardized visual censuses in January and February and mapping of territory owners in each year. Numbers of birds without bands were estimated from their percentages in the censuses (Caughley 1977, Gibbs and Grant 1987*a*). Unless otherwise stated, individuals that bred in their year of birth (hatch) were excluded from the analyses. Also excluded were the small number of *G. scandens* pairs, usually <10, that bred at the end of the dry season (Millington and Grant 1984, Grant 1996).

Interbreeding has occurred rarely (<5%), but persistently, between *G. fortis* on the one hand and *G. fuliginosa* and *G. scandens* on the other (Grant 1993). Since 1983, there has been no detectable fitness loss in either survival or reproduction (Grant and Grant 1992*b*). Therefore, backcrosses have been added to the species to which the hybrid backcrossed. F_1 hybrids have been added to the species of their father because paternal song plays a large role in determining the backcrossing pattern (Grant and Grant 1997, 1998).

Seeds form a staple item of nestling diets (Boag and Grant 1984), and arthropods are fed to them in proportion to their availability. Arthropod availability is highest, and for the longest period, in El Niño years (Gibbs and Grant 1987*a*, Grant and Grant 1987, 1989). Arthropod sampling was carried out weekly or once every two weeks in all years except 1976 and 1982 in four ways: in 1977–1978, by sweep-netting for 5 min three times (Boag and Grant 1984); in 1979–1981, by collecting as many caterpillars as possible in 20 min of search devoted to *Bursera graveolens* foliage and another 20 min to *Portulaca howellii* flowers (Millington and Grant 1983); in 1983–1991, by searching all vegetation for 5 min (Gibbs and Grant 1987*a*); and in 1998, by sweep-netting 11 species of plants 10 times each. Following the procedure in Gibbs and Grant (1987*a*), we used standardization factors to adjust all values to numbers of arthropods collected per 5-min period. No attempt was made to discriminate among caterpillars of different sizes.

Rainfall was measured daily in a rain gauge. The gauge was checked occasionally at 1–3 mo intervals outside the breeding season when we were not on the island. Daily air temperature minima and maxima in the shade were also recorded. They were similar to those recorded at a weather station at the Charles Darwin Research Station on Santa Cruz Island, although much less extensive. Mean monthly air temperatures on Daphne and Santa Cruz were positively correlated (r = 0.678, P = 0.0001) across 24 months (January–May) in 1988–1998. We used the average of the daily maxima (at 1200 hours) and minima (at 0600 hours) for the warmest two successive months of a year at the Research Station on Santa Cruz as an air temperature index for each breeding season on Daphne.

Results

Temperature and rainfall

El Niño events result from a weakening of the trade winds and the incursion of anomalously warm water to the archipelago. This causes air temperatures to rise. As a result of the sea–air temperature connection, a linear relationship exists between the average daily air temperature of the warmest two successive months and

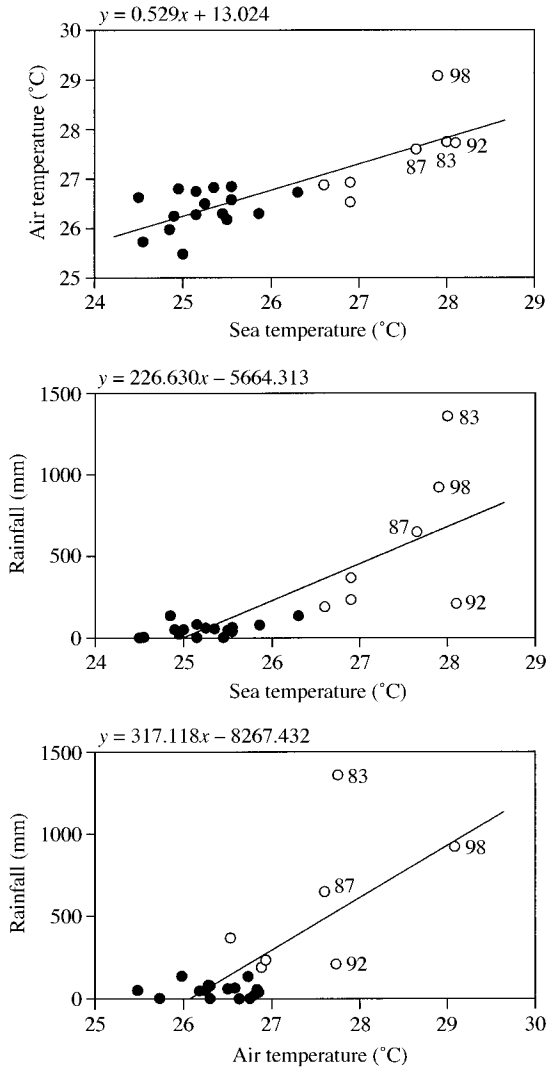

FIG. 1. Average daily maximum air temperature of the warmest two successive months of a year on Santa Cruz Island, Galpagos (1965–1998) is a function of the average daily sea temperature of those months at the same location (upper panel). Annual rainfall on Daphne (1976–1998) is a function of the average daily sea temperature (middle panel) and of average daily maximum air temperatures (lower panel) recorded on Santa Cruz Island in the warmest two successive months of the year. Seven years of El Niño conditions are shown by open circles. Notice that conditions in four of those years (1983, 1987, 1992, 1998, labeled with two digits) were clearly extreme, whereas conditions in three others (1991, 1993, and 1997, unlabeled open circles) were not markedly different from the warmest and wettest of the non-El Niño years (solid circles).

the average daily sea temperature of those months (r^2 = 0.536; Fig. 1). Moisture-laden hot air rises and cools, and rain falls repeatedly and often heavily. Variation in rainfall among all years, El Niño and non-El Niño, is strongly correlated with variation in the highest temperatures of both sea (r^2 = 0.604) and air (r^2 = 0.520; Fig. 1).

Rain in El Niño years is both higher per month, on average, and extends over more months than in a non-El Niño year (Figs. 2 and 3). Note that the amount of annual rainfall varies over approximately one order of magnitude among the four El Niño years (Figs. 2 and 3). As a result of extensive breeding in an El Niño year, finch densities were high in the following year.

Arthropod food

Finches consume caterpillars and other larvae, aphids, spiders, and other arthropods, and feed them to nestlings. Caterpillar numbers varied in relation to annual variation in primary production, which in turn was governed by rainfall (Figs. 4 and 5). Annual variation in mean caterpillar numbers is well predicted by annual variation in rainfall (N = 15 years, r^2 = 0.935, P = 0.0001) and, separately, by average daily temperature in the warmest months (r^2 = 0.555, P = 0.0014). To assess the independent effects on caterpillar numbers of rainfall and temperature, which are intercorrelated (r = 0.767, P = 0.0004), we performed a multiple regression analysis after first transforming rainfall logarithmically to normalize the distribution and reduce the variance. The regression was highly significant ($F_{2,12}$ = 22.273, P = 0.0001, r^2 = 0.788). Partial regression coefficients for rainfall (b = 4.798 ± 1.321, mean ± 1 SE; t = 3.632; P = 0.0034) and temperature (b = 8.529 ± 3.097; t = 2.754; P = 0.0175) were positive and significant.

Caterpillar numbers imperfectly reflect their biomass and, hence, their energy content. In 1979–1981, both numbers (Millington and Grant 1983) and dry biomass (Price 1985) were determined for caterpillars collected on *Bursera* and *Portulaca*. Biomass and numbers were positively correlated in the combined sample (r = 0.669, N = 41, P = 0.0001), as well as in the separate samples from *Portulaca* (r = 0.654, N = 29, P = 0.0001) and *Bursera* (r = 0.680, N = 12, P = 0.015).

Finch production

We analyze finch production in three ways: first by contrasting production in El Niño years with other years (see Fig. 3 legend), then by examining variation among the El Niño years only, and finally by combining the data from all years and seeking statistical explanation of the total variation. We considered each breeding attempt and performance at each stage of breeding to be independent responses of finches to an environment that changes through time.

El Niño vs. non-El Niño years

Productivity.—Annual production of eggs and fledglings per identified (banded) female was much higher in El Niño years than in non-El Niño years (Table 1). On average, females of both *G. fortis* and *G. scandens* laid about 4–5 times as many eggs in El Niño years as in non-El Niño years. The species differed to a small extent: *G. scandens* females produced slightly more

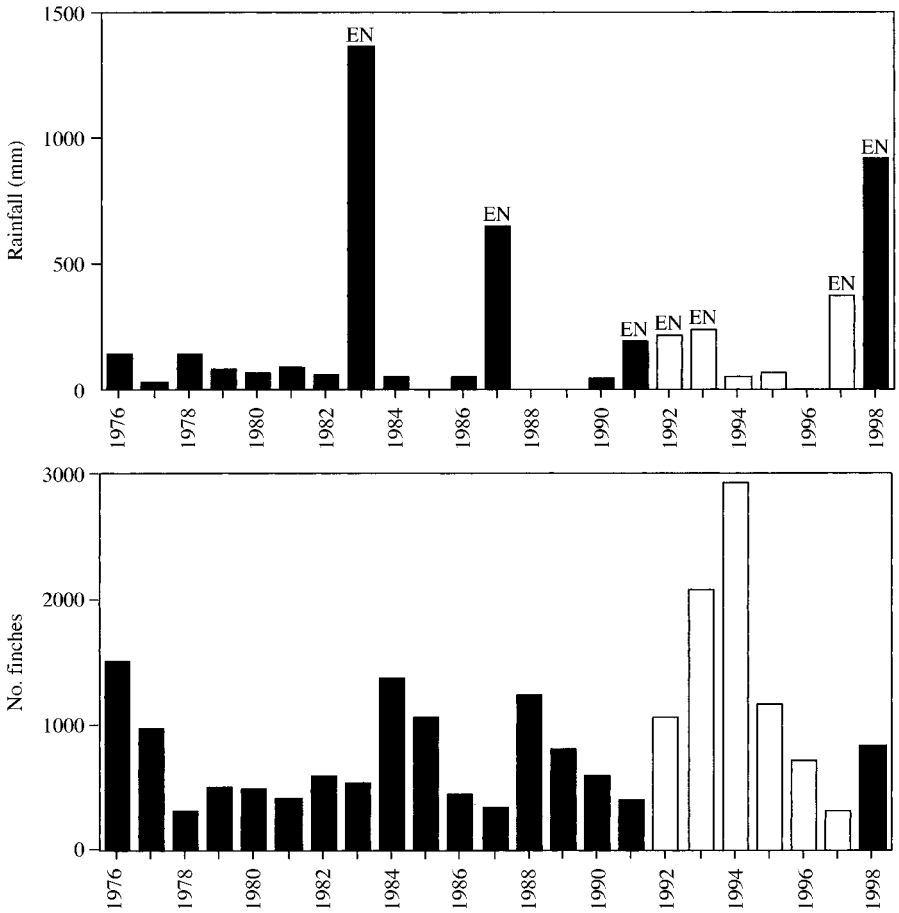

FIG. 2. Annual variation in rainfall and January numbers of all four finch species combined. Years of El Niño events are indicated by ''EN,'' and years of incomplete study of breeding are indicated by open bars. The 1983 event began in November 1982 (see Fig. 3), and rainfall for November and December of 1982 has been added to the total for 1983. Note the large increases in finch numbers following an El Niño year, especially in 1994 after three consecutive El Niño years.

eggs, on average, than did *G. fortis* females in El Niño years, but fewer than *G. fortis* in non-El Niño years. In a two-factor ANOVA of species and year type, there was a significant difference between the species ($F_{1, 1319} = 7.892$, $P = 0.005$) and a more strongly significant interaction between species and the year factor ($F_{1, 1319} = 9.610$, $P = 0.002$).

Differences in fledgling production between El Niño and non-El Niño years parallel those in egg production, with a fourfold difference between the two groups of years for each species. In a two-factor ANOVA, the effect of year type was significant ($P < 0.0001$), whereas the effect of species and the species × year interaction were not significant ($P > 0.1$).

Production was high in El Niño years because favorable conditions for breeding persisted for many months, as a result of rain falling either in many months or in a few months (e.g., 1991), but heavily (Fig. 3). A second factor is the enlarged clutch sizes when breeding conditions are best. These two variables are considered separately in the following section.

Duration of breeding.—Repeated breeding by successful breeders occurs at intervals of ~30 d; the egg phase of breeding lasts for <16 d and the nestling phase lasts for <14 d (Boag and Grant 1984, Gibbs and Grant 1987*a*). We refer to all clutches begun in a 30-d period as a brood, the first brood beginning with the first egg laid after the onset of rain. In the El Niño years, 4–8 broods were produced, whereas in the non-El Niño years, the number varied from one to four. This comparison excludes the drought years of 1985, 1988, and 1989, when no reproduction occurred.

The number of broods per year is a function of the number of months of rain in the eight years, 1982–1991 and 1998, for which we have monthly records ($r = 0.948$, $N = 8$, $P < 0.0003$). For these eight years, the annual total rainfall is tightly correlated with the number of months of rainfall >15 mm ($r = 0.985$, $N = 8$, $P < 0.0001$); 15 mm is needed for caterpillar production. As a result, the number of broods is strongly correlated with total rainfall ($r = 0.939$, $N = 8$, $P < 0.0005$). Relationships between the average number

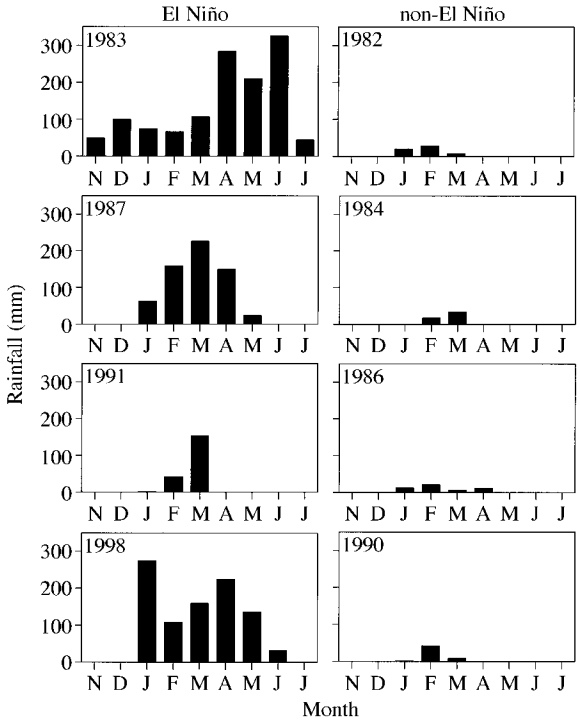

FIG. 3. Monthly variation in rainfall in four El Niño years and four non-El Niño years when rainfall was sufficient for breeding to occur. Note that rainfall was insufficient for breeding in 1985, 1988, and 1989, and breeding data were incomplete in the years 1992–1997.

of broods per female and rainfall in the full data set of 14 years for the two species are shown in Fig. 6 (upper panel). Analysis of the number of clutches per female gives similar results, whether all clutches are considered or only those producing at least one nestling, thereby eliminating repeat clutches following complete hatching failure.

Mean clutch sizes.—Clutch sizes, varying from two to six eggs, were distinctly higher in El Niño years than in non-El Niño years (Fig. 6, lower panel). The only years in which clutches of six eggs were produced were the El Niño years of 1983 (both species), 1987, and 1991 (*G. fortis*). The modal clutch was four in each of the El Niño years and three in all non-El Niño years, with three exceptions: for *G. scandens* it was three in 1998, and for both species it was four in the non-El Niño years of 1978 and 1981. Fig. 7 shows the magnitude of the differences between clutch sizes in El Niño and non-El Niño years, their persistence across broods, and the fact that the elevated clutch sizes in El Niño years remained larger than the maximum in non-El Niño years until the fifth or sixth broods.

Differences between mean clutch sizes in El Niño years and non-El Niño years are demonstrated by the results of a three-factor ANOVA, the factors being species (*G. fortis* vs. *G. scandens*), years (El Niño vs. non-El Niño), and broods (1–3 only, always matched for species). All main effects were significant, with years having the strongest effect and species the weakest (Table 2). The only significant interaction was between years and broods; variation among broods differs between El Niño and non-El Niño years. The absence of significant interactions between species and the other two factors indicates a consistent difference between the species that is not dependent upon years or broods.

Breeding success.—On average, about half of the eggs yielded fledglings (Table 3). Success in breeding per nesting attempt (brood) can be decomposed into two components; the fractional conversion of eggs to nestlings (hatching success) and of nestlings to fledglings (fledging success) (Table 3). The species differed in these two measures of success much more in non-El Niño years than in El Niño years; *G. fortis* had lower hatching success but higher fledging success than *G. scandens* in non-El Niño years (Table 3). Success in the two groups of years was statistically assessed with

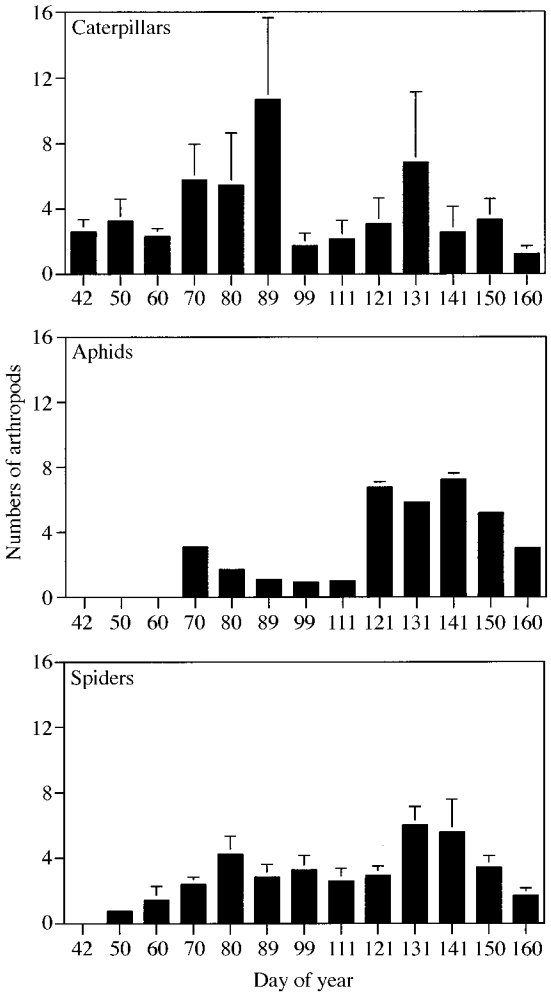

FIG. 4. Arthropod numbers during the breeding season of 1998, shown as mean + 1 SE of 10 sweep net samples from each of 11 plant species.

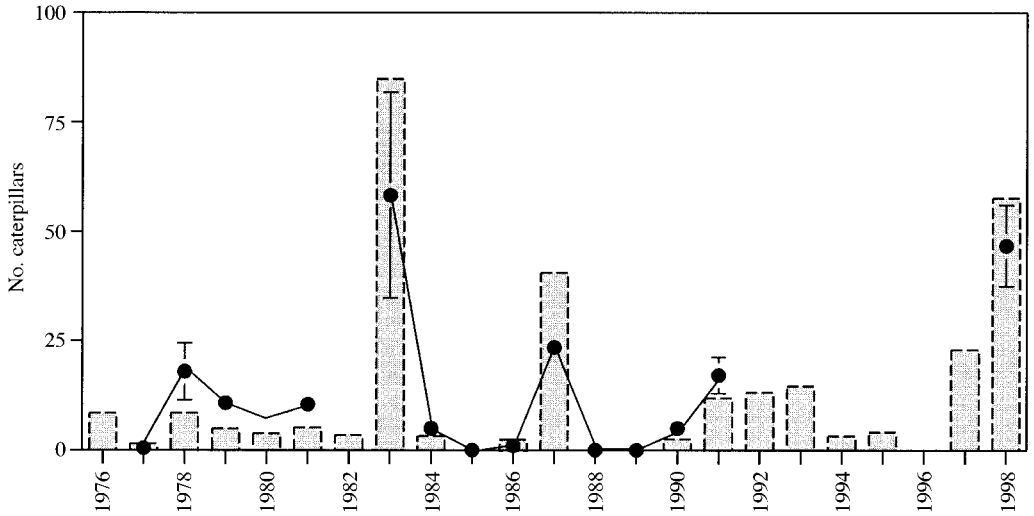

FIG. 5. Annual variation in caterpillar numbers, shown as mean + 1 SE of a variable number of weekly or biweekly samples against a histogram background of annual variation in rainfall.

arcsine square-root transformed fractions in two-factor ANOVA that excluded birds breeding in the year of birth (Table 4). These show pronounced differences at hatching between years and species. A highly significant interaction indicates that the difference between the species depended on year type. A small difference at fledging occurred between species, but not between years, and was opposite in direction to the difference in hatching success. Thus, the interspecific differences tended to cancel, with the result that the species did not differ in overall breeding success. Breeding success did not vary significantly among years either, but there was a significant interaction between species and years, with *G. fortis* having higher success in El Niño years than in non-El Niño years, and the opposite applying to *G. scandens.*

Hatching and fledging success were not at their highest values in any El Niño year for either species (Fig. 8). Their lowest values occur in the driest years. Fledgling production was not a simple function of how many eggs are laid (Fig. 7).

TABLE 1. Annual production of eggs and fledglings per female for two species of Darwin's finches in El Niño and non-El Niño years.

Species	El Niño			Non-El Niño		
	Mean	1 SD	*N*	Mean	1 SD	*N*
Eggs						
G. fortis	16.06	8.198	304	4.26	2.342	568
G. scandens	18.00	8.885	115	3.36	2.237	336
Fledglings						
G. fortis	8.70	4.610	304	2.07	2.178	568
G. scandens	8.79	4.688	115	2.21	1.807	336

Note: Females that bred in their year of hatching (1983 and 1987) are not included.

Variation among El Niño years

Despite the consistent differences between El Niño and non-El Niño years in finch production, there was significant variation among El Niño years in six features (see Table 5, Fig. 9). Differences between species are indicated in Table 5.

Mean egg and fledgling production.—First, in each species, mean egg production of females differed significantly among El Niño years (one-factor ANOVA, $P < 0.0001$ in each case), from high values of >20 eggs in 1983 to low values of <10 eggs in 1998. Second, in each species, fledgling production varied among years (one-factor ANOVA, $P < 0.0001$ in each case). The species differed in both forms of production in 1983 (Table 5).

Mean clutch size.—Mean clutch sizes were highest in 1983, the wettest year, and lowest in 1998, the next wettest year (Table 5).

Mean clutch size of *G. scandens* varied among El Niño years (one-factor ANOVA, $F_{3,117} = 4.772$, $P < 0.0036$), being significantly higher in 1983 than in 1998 (SNK test, $P < 0.05$), whereas mean clutch size of *G. fortis* did not vary significantly among years ($F_{3,309} = 1.892$, $P = 0.1309$).

Mean number of clutches per female.—Mean number of clutches per female varied significantly among El Niño years (one-factor ANOVA, $P = 0.0001$ in each case). The highest mean numbers in *G. fortis* (6.6 clutches) and *G. scandens* (5.7 clutches) were produced in 1983. These are two to three times higher than the lowest mean number in *G. fortis* (2.1 clutches) and *G. scandens* (2.6 clutches) in 1998. Apart from 1983, *G. scandens* had the larger number of clutches in each year. Differences between the species were significant, in opposite directions, in 1983 and 1987 (Table 5).

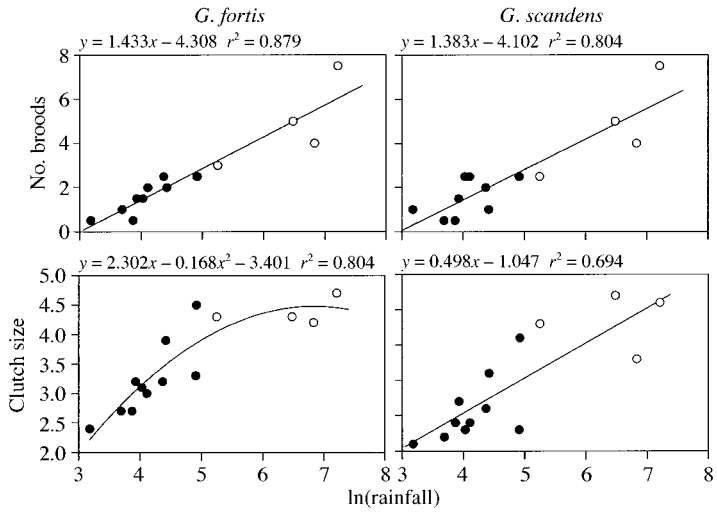

FIG. 6. The upper panels show the total number of broods per female per year, and the lower panels show the largest average clutch size per female among broods in a year as a function of the natural log of annual rainfall (measured in millimeters). These exclude data for years with no breeding and the breeding of birds in their year of birth (hatch). Statistics for the number of broods are: $F_{1,12} = 86.813$, $P = 0.0001$ for *G. fortis;* $F_{1,12} = 49.221$, $P = 0.0001$ for *G. scandens.* For average clutch size, $F_{2,11} = 24.478$, $P = 0.0001$ for *G. fortis;* $F_{1,12} = 27.16$, $P = 0.0001$ for *G. scandens.* Both partial regression coefficients are statistically significant in the equation for clutch size of *G. fortis*; $P = 0.0143$ ($t = 2.904$) for the unsquared term, and $P = 0.0455$ ($t = 2.254$) for the squared term. Squared terms are not significant (t tests, $P > 0.1$) in equations for the other three relationships. Years of El Niño conditions are shown by open circles.

Breeding success.—Breeding success (percentage of eggs that yielded fledglings) varied among years, from high mean values in 1991 of 60.5% (*G. fortis*) and 61.2% (*G. scandens*) to low values of 47.5% (*G. fortis*) in 1983 and 42.5% (*G. scandens*) in 1987. Breeding success of *G. scandens* was also low in 1983 in comparison to 1991 and 1998. Fig. 9 shows that the low success in 1983 resulted from a decline in hatching success as the breeding season progressed. Heavy rains may have played a role in reducing hatching success, as indicated by significant negative correlations between monthly hatching success and monthly rainfall for both *G. fortis* ($r = -0.907$, $N = 8$, $P = 0.0019$) and *G. scandens* ($r = -0.858$, $N = 8$, $P = 0.0064$) in 1983. In other years, with shorter breeding seasons and lower monthly rainfall, a seasonal decline in hatching success did (1998) or did not (1987, 1991) occur (see Figs. 3 and 9).

For the first half of the 1983 season, the hatching success of *G. fortis* (60.3%) was almost as high as for the comparable first four broods in 1987 (63.0%) and 1991 (68.7%). For *G. scandens* (62.8%), it was higher than in 1987 (45.4%) but lower than in 1991 (78.1%). The decline in the second half of the 1983 breeding season was manifested by all birds, and was not the result of poorer breeders breeding only or disproportionately in the second half (cf. Curio 1983, Nol and Smith 1987, Sæther 1990, Korpimäki and Wiehn 1998, Ratcliffe et al. 1998).

The decline was sharpest from brood 4 to brood 5. Roughly half of the females produced clutches at both times. Total nest failures increased from 21% to 50% for the 33 *G. fortis* females that bred at both times, and their hatching success decreased (arcsine square-root transformed data, paired $t_{32} = 3.63$, $P = 0.001$). Nest failures and hatching success of *G. scandens* varied in the same way (paired $t_{30} = 3.463$, $P = 0.0016$). In neither species was the decline in hatching success

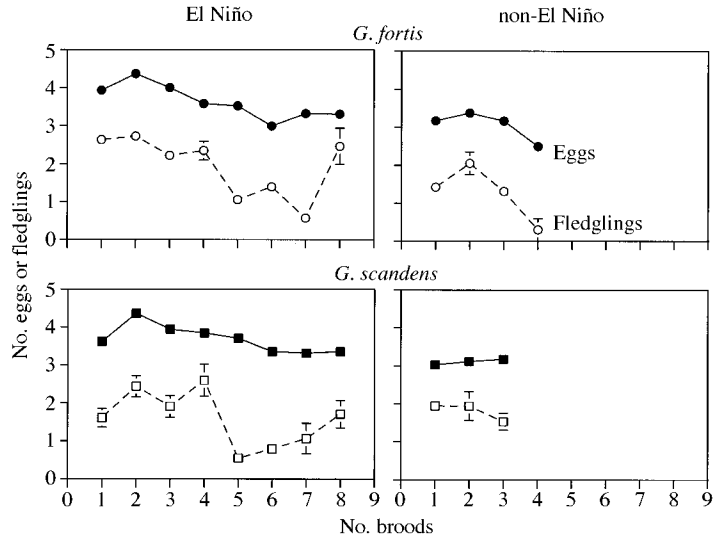

FIG. 7. Seasonal variation in mean number of eggs and fledglings produced by identified females in El Niño years and non-El Niño years. Brood means for sample sizes of <10 females have been omitted. Vertical error bars indicate ±1 standard error of the mean; these are sample-size weighted averages of the means for individual years.

TABLE 2. Results of a three-factor ANOVA of mean clutch size variation in two species of Darwin's finches.

Source of variation	df	SS	MS	*F*	*P*
Species	1	4.472	4.472	7.135	0.0076
Years	1	362.202	362.202	577.863	0.0001
Broods	2	41.695	20.847	33.260	0.0001
Species × years	1	0.394	0.394	0.629	0.4278
Species × broods	2	0.808	0.404	0.645	0.5248
Years × broods	2	16.181	8.090	12.907	0.0001
Species × years × broods	2	0.666	0.333	0.531	0.5881
Residual	2 505	1 570.122	0.627		

Notes: The factors are species (*G. fortis* or *G. scandens*), years (El Niño or non-El Niño), and broods (1, 2, or 3).

caused solely by complete nest failures, as partial hatching of clutches also declined (*G. fortis:* paired $t_{16} = 2.452$, $P = 0.0261$; *G. scandens:* paired $t_9 = 4.375$, $P = 0.0018$).

Breeding in year of birth.—Some birds that fledged in the El Niño years of 1983 and 1987 bred in the same year. They contributed to broods 4–8 in 1983, and mainly to brood 4 in 1987. The two remarkable features about this early breeding, apart from the fact of early breeding itself, are the large numbers of birds involved and the moderately high success. In 1983, 105 *G. fortis* and 39 *G. scandens* female young-of-the-year bred. Their production was generally lower than that of adults breeding at the same time (Table 6). Two-factor ANOVA for each species displayed significant brood effects on variation in egg, nestling, and fledgling production ($P < 0.025$–0.0001), but few differences between young and older birds (Table 6). In 1987, nine *G. fortis* and two *G. scandens* females bred in their year of birth (hatch). Production of eggs, nestlings, and fledglings by young *G. fortis* females was lower than that of adults breeding at the same time (one-factor ANOVA, $P < 0.0001$ in each case).

TABLE 3. Success of breeding by female finches in El Niño and non-El Niño years.

Species	Mean	1 SD	*N*
Hatching success: eggs → nestlings			
El Niño years			
G. fortis	0.63	0.239	304
G. scandens	0.60	0.224	115
Non-El Niño years			
G. fortis	0.58	0.410	570
G. scandens	0.73	0.342	358
Fledging success: nestlings → fledglings			
El Niño years			
G. fortis	0.87	0.171	290
G. scandens	0.83	0.187	111
Non-El Niño years			
G. fortis	0.80	0.349	419
G. scandens	0.74	0.360	321
Breeding success: eggs → fledglings			
El Niño years			
G. fortis	0.56	0.242	304
G. scandens	0.50	0.219	115
Non-El Niño years			
G. fortis	0.47	0.414	570
G. scandens	0.56	0.387	358

Statistical explanation of breeding variation in El Niño and non-El Niño years combined

The number of broods per female per year was strongly associated with the number of caterpillars in the years (excluding droughts) when caterpillars were sampled (*G. fortis*: $r = 0.915$, $P = 0.0001$; *G. scandens*: $r = 0.902$, $P = 0.0001$). The number of caterpillars was also correlated with the maximum average clutch sizes per female per year, which is usually the average clutch size at the time of the second brood (see Fig. 6); (*G. fortis*: $r = 0.774$, $P = 0.0031$; *G. scandens*: $r = 0.725$, $P = 0.0077$). Annual variation in other, less well sampled, components of nestling diest (e.g., spiders and aphids; Fig. 4) is consistent with these relationships. The number of caterpillars is positively and strongly correlated with annual rainfall ($r^2 = 0.935$, $P = 0.0001$); because we have rainfall data in more years than we have caterpillar data, we used rainfall, together with air temperature and density, in multiple regression analyses of yearly variation in breeding output and success.

There are three main results. First, rainfall had a strong positive effect, and temperature had a weaker negative effect, on the number of broods and maximum clutch sizes in both species (Table 7). Second, total finch density had an additional negative effect on maximum clutch size in *G. scandens.* The magnitude of the total r^2 values for both species is noteworthy. Third, measures of success were less well predicted by these environmental variables, and none was statistically related to finch density (all $P > 0.2$). Rainfall was a predictor of hatching, fledging, and overall breeding success in *G. fortis,* but only of fledging success in *G. scandens.* Temperature, although positively correlated with rainfall ($r = 0.736$, $N = 14$, $P = 0.0027$), had an independent negative effect on hatching and breeding success in *G. fortis.*

Geospiza fuliginosa *and* G. magnirostris

Two species were not included in the analyses just discussed because their breeding numbers were generally low. The maximum number of *Geospiza fuligi-*

TABLE 4. Results of two-factor ANOVA of three measures of success in the breeding of females of *Geospiza fortis* and *G. scandens*.

Source	df	SS	MS	*F*	*P*
Hatching success: eggs → nestlings					
Species	1	2.282	2.282	8.370	0.0039
Years	1	2.192	2.192	8.041	0.0046
Species × years	1	4.496	4.496	16.492	0.0001
Residual	1343	366.162	0.273		
Fledging success: nestlings → fledglings					
Species	1	1.231	1.231	5.412	0.0202
Years	1	0.798	0.798	3.509	0.0613
Species × years	1	0.001	0.001	0.002	0.9631
Residual	1149	261.357	0.227		
Breeding success: eggs → fledglings					
Species	1	0.290	0.290	0.993	0.3192
Years	1	0.036	0.036	0.123	0.7257
Species × years	1	2.522	2.522	8.636	0.0034
Residual	1343	392.214	0.292		

Notes: Individual values were arcsine square-root transformed prior to analysis. The factors are species (*G. fortis* and *G. scandens*) and years (El Niño and non-El Niño).

nosa pairs was seven in 1976. The number of breeding pairs of *G. magnirostris* exceeded 10 only after 1991 ($N = 27$ pairs in 1998). Their breeding characteristics in 1998 were almost identical to those of *G. fortis* and *G. scandens.* They bred the same number of times (four), showed the same initial increase followed by a decrease in mean clutch size, and had the same maximum mean clutch size (4.2 ± 0.18 eggs, mean ± 1 SE, $N = 11$) at the same time (brood 2) as *G. fortis* (4.2 ± 0.12 eggs, $N = 25$). Breeding success (0.59) was lower than that of *G. fortis* (0.68), and was similar to that of *G. scandens* (0.60).

DISCUSSION

El Niño events are amplifications of normal seasonal processes in the eastern tropical Pacific region. They are not discrete phenomena (Philander 1990), and as shown in the rainfall data of this study (Fig. 1), the effects of the weakest El Niño events are not much different from those of the strongest of the normal wet seasons (e.g., Fig. 6). On the other hand, the strongest El Niño events are much more intense (Fig. 1) and longer lasting than normal wet seasons. Thus, production of terrestrial organisms is expected to be greater in El Niño than in non-El Niño years, on average, and also to vary substantially among years experiencing El Niño events. Our results conform to both expectations. Finches, responding to the onset of rainfall with little delay in each case, bred four to eight times in El Niño years, instead of the usual one (or none) to four times. Females laid four times as many eggs, on average, and fledged four times as many young. They responded to increases in rain with increases in clutch sizes. The least productive El Niño year differed little from the most productive normal year. These results both replicate and give perspective to the extraordinary production in the extraordinarily wet year of 1983 (Robinson and del Pino 1985, Gibbs and Grant 1987*a*).

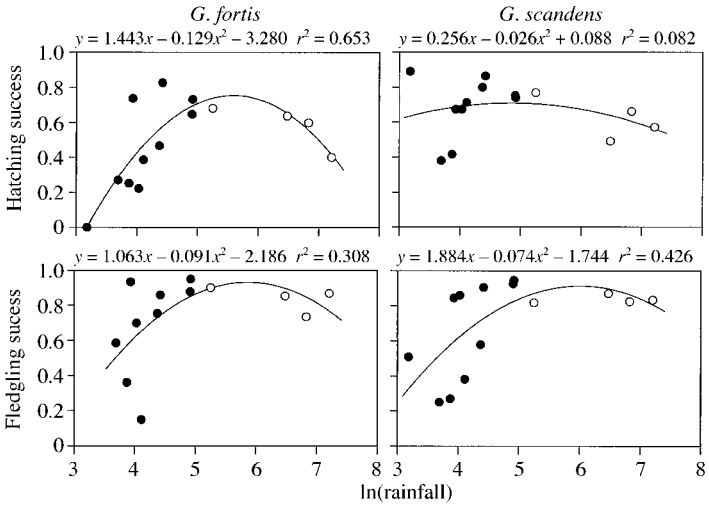

FIG. 8. Annual variation in hatching and fledging success in relation to the natural log of rainfall (measured in millimeters). For hatching success, $F_{2,11} = 10.368$, $P = 0.0029$ for *G. fortis;* $F_{2,11} = 0.490$, $P = 0.6254$ for *G. scandens.* For fledging success, $F_{2,10} = 2.229$, $P = 0.1583$ for *G. fortis;* $F_{2,11} = 4.078$, $P = 0.0473$ for *G. scandens.* Both partial regression coefficients are statistically significant in only the equation for *G. fortis* hatching success; $P = 0.0016$ ($t = 4.144$) for the unsquared term, and $P = 0.0023$ ($t = 3.935$) for the squared term. All statistical tests were performed on arcsine square-root transformed data. Regardless of statistical significance, lines of best fit are shown for all relationships. Years of El Niño conditions are shown by open circles.

TABLE 5. Variation in breeding among four El Niño years for *Geospiza fortis* and *G. scandens*. Means (± 1 SD) are shown for identified (banded) females.

Reproductive measure	1983			1987
	G. fortis	*G. scandens*	*t* test	*G. fortis*
Number of females	66	64		105
Number of eggs	26.6 ± 6.55	21.9 ± 8.07	****	16.8 ± 6.18
Number of nestlings	14.3 ± 4.73	12.4 ± 5.34	*	11.0 ± 4.83
Number of fledglings	12.5 ± 4.58	10.3 ± 4.58	**	9.4 ± 4.50
Number of clutches	6.8 ± 1.70	5.6 ± 2.02	****	4.4 ± 1.65
Clutch size	3.97 ± 0.457	3.90 ± 0.543		3.79 ± 0.709
Proportion of eggs hatched	0.54 ± 0.157	0.57 ± 0.203		0.64 ± 0.229
Proportion of nestlings fledged	0.87 ± 0.128	0.83 ± 0.133		0.85 ± 0.166
Proportion of eggs fledged	0.47 ± 0.156	0.48 ± 0.188		0.55 ± 0.236

Notes: Significant interspecific differences by *t* tests are indicated with asterisks: $*P < 0.05$; $**P < 0.01$; $****P < 0.0001$. There were no significant interspecific differences in 1991 or 1994.

El Niño events lift the usual constraints on the length of the breeding season, and may be likened to the experimental manipulation of food supply through a regime of supplemental watering, while leaving other potentially influential factors either unaffected (photoperiod) or affected in a minor way (temperature). This quasi-experimental approach enables us to reject two ideas that might seem reasonable in the absence of El Niño events: (1) that there is an inherently fixed maximum length of the breeding season, perhaps set by an annual program of molting, for example (Hahn et al. 1997), and (2) that finches require at least a year to mature and become proficient breeders. Instead, the length of the breeding season appears to be governed by a food supply that is replenished for as long as the rain continues, or even longer (e.g., 1991), and finches are capable of breeding at an age of three months (Gibbs et al. 1984, Gibbs and Grant 1987*a*). Early breeding is noteworthy because many temperate zone birds exhibit a ''juvenile refractoriness'' that prevents them from breeding for about a year (under natural conditions) (Nicholls et al. 1988), although crossbills (McCabe and McCabe 1933) and Zebra Finches (Zann 1996), which are opportunistic breeders, are not so constrained and can breed at a very early age.

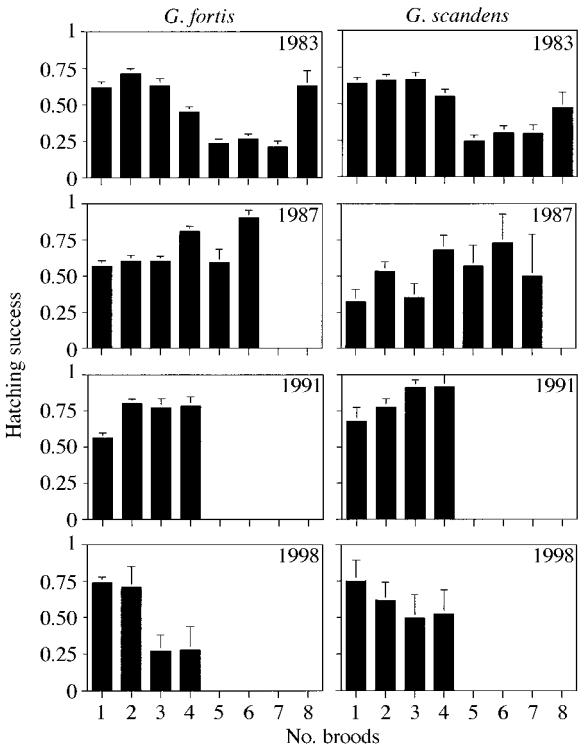

FIG. 9. Seasonal variation in hatching success (mean + 1 SE) in four El Niño years. Females breeding in their year of birth (hatch) are not included.

The link between rain and finch production is food supply: seeds and fruits, nectar and pollen, and various arthropods (but particularly caterpillars, spiders, and aphids) all increase with more rain (Grant and Boag 1980, Boag and Grant 1984, Price 1985, Gibbs and Grant 1987*a*, Grant and Grant 1989). Among the 12 years when caterpillars were sampled, the pattern of annual variation was clear, in spite of differences in methods of sampling. Their abundance was positively correlated with the number of broods produced and the maximum mean clutch sizes of both species. Other components of nestling diets were sampled in only a few years, yet their annual variation is consistent with that of the relationships for caterpillars (Gibbs and Grant 1987*a*). Therefore, enhanced finch production can be interpreted as being primarily the result of enhanced food production. Marked temporal variation in passerine bird production as a result of fluctuations in food supply is a characteristic of seasonally arid habitats in both tropical (Marchant 1960, Grant and Grant 1980) and temperate regions (Maclean 1976, Rotenberry and Wiens 1991, Morin 1992, Zann et al. 1996, Lloyd 1999).

Elsewhere, it has been experimentally demonstrated that food supply influences reproduction through the timing of breeding, clutch sizes, and the number of breeding attempts (Smith et al. 1980, Martin 1987, Arcese and Smith 1988, Daan et al. 1989, 1990, Perrins and McCleery 1989, Sanz and Moreno 1995, Nager et

TABLE 5. Extended.

1987		1991		1998	
G. scandens	*t* test	*G. fortis*	*G. scandens*	*G. fortis*	*G. scandens*
17		121	17	14	17
19.8 ± 8.5		10.3 ± 3.47	11.4 ± 3.30	7.7 ± 3.81	8.2 ± 3.26
10.2 ± 5.85		7.2 ± 3.16	8.7 ± 3.40	4.4 ± 2.24	5.5 ± 2.94
8.7 ± 5.06		6.5 ± 2.99	7.3 ± 3.16	3.4 ± 2.56	4.5 ± 2.67
5.5 ± 2.12	*	2.7 ± 0.91	3.1 ± 0.78	2.1 ± 1.07	2.6 ± 1.06
3.46 ± 0.644		3.80 ± 0.697	0.65 ± 0.563	3.79 ± 0.702	3.30 ± 0.684
0.49 ± 0.222	*	0.67 ± 0.280	0.77 ± 0.182	0.60 ± 0.266	0.66 ± 0.249
0.87 ± 0.121		0.90 ± 0.163	0.82 ± 0.257	0.74 ± 0.330	0.82 ± 0.305
0.42 ± 0.199	*	0.61 ± 0.276	0.61 ± 0.233	0.46 ± 0.278	0.56 ± 0.291

al. 1997, Verhulst et al. 1997, Korpimäki and Wiehn 1998). All of these studies were conducted in the temperate zone, where timing is crucial (Perrins and McCleery 1989, Rowe et al. 1994, Wiggins et al. 1994, Young 1994, Winkler and Allen 1996, Visser et al. 1998). Birds that do not breed as soon as food conditions permit (Perrins 1970) may experience appreciable fitness loss (Nager and van Noordwijk 1995, van Noordwijk et al. 1995, Nilsson and Svensson 1996, Wiggins et al. 1998). The experimental approach is not available to us with Darwin's finches. Nevertheless, high annual variation in rainfall, as a proxy measure of total food supply, allows an assessment of this factor through long-term monitoring and statistical comparisons.

Although the food factor is the most important determinant of a lengthened breeding season and large clutch sizes in El Niño years, it is not sufficient to explain annual variation in finch production. This is clearly evident in the anomalously low production in both species in 1998, a year with very high rainfall. Two other factors have been identified as important in this study, especially in El Niño years. The first is temperature. In multiple regression analyses, the average daily temperature in the warmest two months had an independent negative effect on the number of broods and clutch sizes of both species, and on the breeding success of *Geospiza fortis*. In all cases, these statistical effects were minor in comparison with major positive effects of rainfall. Thus, the strong tendency for production to increase with total amount of rainfall (and food supply) is offset to a small degree by the high temperatures that accompany high rainfall, perhaps as a result of increased energetic costs of breeding.

The second factor is density-dependent interactions with other finches. Finches compete for food and mates, engage in territorial disputes, visit each others' nests, and kill or remove eggs and chicks (B. R. Grant and P. R. Grant, *unpublished observations*); there are no other nest predators on the island. These interactions are both intraspecific and interspecific. As overall density increases, interactions are expected to become more prevalent and possibly more intense. Interactions have been repeatedly observed but not quantified, nor have the increases in density within seasons been estimated. Negative effects of density on clutch size have been demonstrated in the temperate zone (Dhondt et al. 1992, Kempenaers and Dhondt 1992, Both 1998*a*; see also Both 1998*b*).

The evidence for effects of density-dependent inter-

TABLE 6. Breeding of females in their year of birth, 1983, contrasted with breeding of older adults. Means (± 1 SD) are shown for identified (banded) females.

Brood no.	Young females				Old females			
	No. eggs	No. nestlings	No. fledglings	*N*	No. eggs	No. nestlings	No. fledglings	*N*
G. fortis								
4	3.8 ± 0.67**	1.4 ± 1.33*	0.5 ± 0.82*	34	4.2 ± 0.63**	2.2 ± 1.53*	1.9 ± 1.51*	56
5	3.7 ± 0.75*	0.8 ± 1.17	0.3 ± 0.70	53	4.1 ± 0.93*	1.1 ± 1.22	0.6 ± 1.05	57
6	3.1 ± 0.71*	0.8 ± 1.10	0.5 ± 0.94	58	3.4 ± 0.74*	1.1 ± 1.26	0.9 ± 1.12	53
7	3.1 ± 0.61	0.8 ± 1.23	0.5 ± 1.00	40	3.3 ± 0.74	0.6 ± 1.16	0.5 ± 1.06	38
8	3.0 ± 0.53	2.4 ± 3.16	1.4 ± 1.68	8	3.4 ± 0.63	2.6 ± 1.51	2.6 ± 1.51	14
G. scandens								
4	3.7 ± 0.82*	1.8 ± 1.72	1.3 ± 1.75	6	4.2 ± 0.57*	2.3 ± 1.50	1.8 ± 1.46	52
5	3.9 ± 0.72	1.1 ± 1.33	0.2 ± 0.72	20	3.7 ± 0.97	1.0 ± 1.31	0.6 ± 0.97	41
6	3.1 ± 0.77	0.8 ± 1.26	0.6 ± 1.05	22	3.4 ± 0.70	1.1 ± 1.31	0.8 ± 1.21	47
7	3.2 ± 0.83	0.7 ± 1.12	0.6 ± 1.13	9	3.3 ± 0.64	1.1 ± 1.29	1.1 ± 2.27	32
8	2.7 ± 0.58	1.0 ± 1.73	1.0 ± 1.73	3	3.3 ± 0.48	2.6 ± 2.85	1.6 ± 1.41	16

Notes: Asterisks indicate significant differences, using SNK post hoc tests, between young and old females: * $P < 0.05$, ** $P < 0.01$.

TABLE 7. Summary of multiple regression analyses of numbers of broods, maximum average clutch size, and three measures of success (arcsine square-root transformed) in 14 years.

Variable	Coefficient	1 SE	t	P	Contribution to total r^2†
Number of broods					
G. fortis ($F_{2,11}$ = 15.83****)					
Intercept	23.077				
ln(rainfall)	1.177	0.213	5.530	0.0002	0.651
temperature	−1.002	0.298	3.368	0.0063	0.091
					0.742
G. scandens ($F_{2,11}$ = 8.74**)					
Intercept	15.812				
ln(rainfall)	0.790	0.193	4.096	0.0018	0.535
temperature	−0.660	0.270	2.445	0.0325	0.079
					0.614
Clutch size					
G. fortis ($F_{3,10}$ = 21.77****)					
Intercept	10.933				
ln(rainfall)	0.714	0.106	6.719	0.0001	0.693
temperature	−0.395	0.146	2.698	0.0024	0.131
density	−0.001	0.001	1.482	0.1692	0.043
					0.867
G. scandens ($F_{3,10}$ = 22.90****)					
Intercept	10.559				
ln(rainfall)	0.663	0.101	6.550	0.0001	0.660
temperature	−0.371	0.140	2.657	0.0240	0.125
density	−0.001	0.000	2.428	0.0356	0.089
					0.873
Hatching success					
G. fortis ($F_{2,11}$ = 6.05*)					
Intercept	7.355				
ln(rainfall)	0.258	0.075	3.457	0.0054	0.456
temperature	−0.292	0.104	2.802	0.0172	0.068
					0.524
G. scandens ($F_{2,11}$ = 0.275)					
Intercept	1.595				
ln(rainfall)	−0.018	0.060	0.297	0.7719	0.027
temperature	−0.020	0.083	0.242	0.8135	0.021
					0.048
Fledging success					
G. fortis ($F_{2,10}$ = 3.171)					
Intercept	6.479				
ln(rainfall)	0.237	0.094	2.518	0.0305	0.383
temperature	−0.246	0.122	2.017	0.0713	0.006
					0.388
G. scandens ($F_{2,11}$ = 3.561)					
Intercept	4.628				
ln(rainfall)	0.206	0.079	2.613	0.0241	0.342
temperature	−0.172	0.110	1.555	0.1482	0.051
					0.393
Overall breeding success					
G. fortis ($F_{2,11}$ = 8.73**)					
Intercept	7.908				
ln(rainfall)	0.303	0.073	4.174	0.0016	0.581
temperature	−0.325	0.102	3.203	0.0084	0.032
					0.614
G. scandens ($F_{2,11}$ = 1.01)					
Intercept	3.207				
ln(rainfall)	0.099	0.070	1.422	0.1829	0.144
temperature	−0.108	0.098	1.110	0.2907	0.012
					0.156

Notes: Temperature refers to the average air temperature of the warmest two months, and density refers to total number of finches on 1 January. Density makes no significant contribution to any of the analyses (all $P > 0.2$), except clutch size.

† For each species and reproductive parameter, the contribution of individual variables is summed.

*$P < 0.05$; **$P < 0.01$; ****$P < 0.0001$.

actions in our study is indirect. First, a small negative effect of finch numbers on *G. scandens* maximum clutch sizes was revealed in multiple regression analysis. Second, finch numbers doubled from one year to the next only as the result of prolific breeding in El Niño years, with a single exception at the highest density: breeding in 1993 did not result in a doubling of numbers by the beginning of 1994 (Fig. 2). Third, seasonal declines in clutch sizes and breeding success are not matched by a seasonal decline in food supply, and must be accounted for by other factors. A pulse of food in April 1983 (and two pulses in 1998; Fig. 4) did not result in an increase in clutch size, fledging success, or subsequent survival, perhaps as a consequence of interactions at high density as well as prolonged rainfall at this time (Gibbs and Grant 1987*a*). Other indications of negative effects of density are lower survival of finches hatched in the second half of 1983 (Gibbs and Grant 1987*a*), and inferior growth of finches hatched in the second half of 1987 (Grant and Grant 1995*b*) compared with those hatched in the first half of the two years. Multiple regression analyses may underestimate the negative effects of interactions associated with density if the interactions increase with density nonlinearly, occur only above a threshhold density, and vary with food supply partly independently of density. Analyses are further limited by our lack of quantitative estimates of densities as they changed during breeding seasons.

We suggest that food, temperature, and density factors interact, both seasonally and annually, in the following way. Initial clutch sizes are set by food intake rates that match food availability, and that are higher in El Niño years than in non-El Niño years. After the first brood has become independent and the second brood is being reared, the energetic costs of reproduction increase: the energetic benefits gained from a readily available and plentiful food supply are reduced by rising energetic costs of nest and territory defense as overall density, of adults and fledglings combined, increases. High air temperatures may contribute to these increasing costs of reproduction and ensuing fatigue. For example, the relatively short breeding season and anomalously low production in 1998, despite the second greatest quantity of rain recorded in 23 years and a sustained, large production of caterpillars and other arthropods, may have been caused by high energetic costs as a result of exceptionally high air temperatures (Fig. 1) and high density (Fig. 2). There is experimental support from temperate-zone studies for the postulated positive effect of food and negative effect of density on clutch sizes (e.g., Arcese and Smith 1988, Arcese et al. 1992).

Rainfall, in addition to enhancing finch production through its effects upon food supply, could occasionally have a negative effect. There are indications of such an effect in the seasonal decline in breeding success of both species in 1983. Observations on both Daphne (Gibbs and Grant 1987*a*) and Genovesa (Grant and Grant 1989) suggest that prolonged and uninterrupted rain prevents females from simultaneously foraging and brooding eggs or nestlings, and this causes nest abandonment or starvation of nestlings. Foraging success may be lower at such times as a result of lower arthropod mobility and detectability (Rotenberry and Wiens 1991).

Our suggestions regarding the effects of food, density, rainfall, and temperature on the breeding of finches apply to both *G. fortis and G. scandens.* Both species responded strongly and similarly to favorable conditions for breeding in El Niño years by producing larger clutches and breeding for a longer period. Nevertheless, there are indications of unequal outcomes of those responses, with *G. scandens* experiencing less success in hatching eggs than *G. fortis.* It is possible that *G. scandens,* the more strongly territorial species and more dependent for food from within the territory (Boag and Grant 1984), experienced more energetic stress than did *G. fortis* in El Niño years. A statistically significant negative relationship between density and clutch size in *G. scandens* suggests that it is more susceptible than *G. fortis* to density influences on reproduction through territorial interactions.

These results from a study of variation in El Niño and non-El Niño years are not specific to the one island of Daphne, nor are they specific to finches. El Niño events affect all islands in the Galápagos archipelago (Robinson and del Pino 1985, Grant and Grant 1996, Wikelski and Trillmich 1997), although to different degrees and to an unstudied extent in the highlands. Therefore, the breeding responses registered on Daphne are likely to be typical of finch responses elsewhere in the archipelago at low elevations. A parallel study on Genovesa (Grant and Grant 1989) provides a check on the generality of the Daphne results. Finch species on Genovesa responded to favorable conditions in 1983 and 1987 in a way similar to that of the congeneric species on Daphne, by breeding longer and producing larger clutches, except when densities were high (Grant and Grant 1989). The two studies combined, including the rare species *G. fuliginosa* and *G. magnirostris* on Daphne, encompass all six species in the ground finch genus *Geospiza.* The results can be further generalized to other arid regions of the world where a seasonal food supply is governed by annually variable rainfall that occurs erratically in relation to the seasonal progression of photoperiod and temperature (Maclean 1976, Rotenberry and Wiens 1991, Morin 1992, Zann et al. 1996, Lloyd 1999).

We conclude by noting that effects of El Niño events on finch populations vary for two main reasons; the climatic perturbations vary in strength and duration, and responses to them are determined, in part, by preceding conditions. Those preceding conditions, in turn, are determined by whether drought or normal conditions precede the perturbation, on the interval since the

previous El Niño event, and on how these patterns in time have affected finch densities and the vegetation on which the finches depend for food. For example, finch populations responded very differently to the similar rainfall in 1983 and 1998, in large part because the starting densities and vegetation were markedly different; the first of these events followed a dry year and the second followed an El Niño year. Our general conclusion is that individual perturbations of natural systems can be fully understood only in a broad, temporal context.

Acknowledgments

Fieldwork was conducted with permission and support from the Galápagos National Parks Service and the Charles Darwin Research Station, Galápagos. Funding has been received from NSERC (Canada) and NSF, most recently BSR-9615383. We thank the Charles Darwin Research Station for supplying temperature data, the numerous assistants who have given help in the field, E. Monson and C. Edwards for help in the 1998 season, G. Estes for reading the rain gauge when we were not on the island, and T. Hahn, S. Robinson, and two referees for comments on the manuscript.

Literature Cited

Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology **57**:119–136.

Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular Song Sparrow population. Ecology **73**:805–822.

Barber, R. T., and F. P. Chavez. 1986. Ocean variability in relation to living resources during the 1982–83 El Niño. Nature **319**:279–285.

Boag, P. T., and P. R. Grant. 1984. Darwin's finches on Isla Daphne Major, Galápagos: breeding and feeding ecology in a climatically variable environment. Ecological Monographs **54**:463–489.

Both, C. 1998*a*. Experimental evidence for density dependence of reproduction in great tits. Journal of Animal Ecology **67**:667–674.

Both, C. 1998*b*. Density dependence of clutch size in great tits: habitat heterogeneity or individual adjustment. Journal of Animal Ecology **67**:659–666.

Cane, M. A. 1983. Oceanographic events during El Niño. Science **222**:1189–1195.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York, New York, USA.

Curio, E. 1983. Why do young birds reproduce less well? Ibis **125**:400–404.

Daan, S., C. Dijkstra, R. H. Drent, and T. Meijer. 1989. Food supply and the annual timing of avian reproduction. Proceedings of the International Ornithological Congress **XIX**: 392–407.

Daan, S., C. Dijkstra, and J. M. Tinbergen. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. Behaviour **114**:83–116.

Dhondt, A. A., B. Kempenaers, and F. Adriaensen. 1992. Density-dependent clutch size caused by habitat heterogeneity. Journal of Animal Ecology **61**:643–648.

Gibbs, H. L., and P. R. Grant. 1987*a*. Ecological consequences of an exceptionally strong El Niño event on Darwin's finches. Ecology **68**:1735–1746.

Gibbs, H. L., and P. R. Grant 1987*b*. Adult survivorship in Darwin's ground finch (*Geospiza*) populations in a variable environment. Journal of Animal Ecology **56**:797–813.

Gibbs, H. L., P. R. Grant, and J. Weiland. 1984. Breeding of Darwin's finches at an unusually early age in an El Niño year. Auk **101**:872–874.

Glynn, P. 1988. El Niño–Southern Oscillation 1982–1983: nearshore population, community, and ecosystem responses. Annual Review of Ecology and Systematics **19**:309–345.

Grant, B. R. 1996. Pollen digestion by Darwin's finches and its importance for early breeding. Ecology **77**:489–499.

Grant, B. R., and P. R. Grant. 1989. Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos. University of Chicago Press, Chicago, Illinois, USA.

Grant, B. R., and P. R. Grant. 1998. Hybridization and speciation in Darwin's finches. The role of sexual imprinting on a culturally inherited trait. Pages 404–422 *in* D. J. Howard and S. H. Berlocher, editors. Endless forms: species and speciation. Oxford University Press, New York, New York, USA.

Grant, P. R. 1993. Hybridization of Darwin's finches on Isla Daphne Major, Galápagos. Philosophical Transactions of the Royal Society of London B **340**:127–139.

Grant, P. R. 1999. Ecology and evolution of Darwin's finches. Second edition. Princeton University Press, Princeton, New Jersey, USA.

Grant, P. R., and P. T. Boag. 1980. Rainfall in the Galápagos and the demography of Darwin's finches. Auk **97**:227–244.

Grant, P. R., and B. R. Grant. 1980. The breeding and feeding characteristics of Darwin's finches on Isla Genovesa, Galápagos. Ecological Monographs **50**:381–410.

Grant, P. R., and B. R. Grant. 1987. The extraordinary El Niño event of 1982–83: effects on Darwin's finches on Isla Genovesa, Galápagos. Oikos **45**:55–66.

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

Grant, P. R., and B. R. Grant. 1992*b*. Hybridization of bird species. Science **256**:193–197.

Grant, P. R., and B. R. Grant. 1995*a*. The founding of a new population of Darwin's finches. Evolution **49**:229–240.

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

Grant, P. R., and B. R. Grant. 1996. Finch communities in a climatically fluctuating environment. Pages 343–390 *in* M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, New York, New York, USA.

Grant, P. R., and B. R. Grant. 1997. Mating patterns of Darwin's finch hybrids determined by song and morphology. Biological Journal of the Linnean Society **60**:317–343.

Hahn, T. P., T. Boswell, J. C. Wingfield, and G. F. Ball. 1997. Temporal flexibility in avian reproduction: patterns and mechanisms. Pages 39–80 *in* V. Nolan, E. D. Ketterson, and C. F. Thompson, editors. Current Ornithology. Volume 12. Plenum, New York, New York, USA.

Hubbell, S. P., and R. B. Foster. 1990. Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado Island. Pages 522–541 *in* A. Gentry, editor. Four neotropical forests. Yale University Press, New Haven, Connecticut, USA.

Kempenaers, B., and A. A. Dhondt. 1992. Experimental test of a hypothesis explaining density-dependent clutch-size in tits *Parus* spp. Ibis **134**:192–194.

Kerr, R. A. 1999. Big El Niños ride the back of slower climate change. Science **283**:1108–1109.

Korpimäki, E., and J. Wiehn. 1998. Clutch size of kestrels:

seasonal decline and experimental evidence for food limitation under fluctuating food conditions. Oikos **83**:259–272.

Lloyd, P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. Ibis **141**: 637–643.

Maclean, G. L. 1976. Arid-zone ornithology in Africa and South America. Proceedings of the International Ornithological Congress **XVI**:468–480.

Marchant, S. 1960. The breeding of some S. W. Ecuadorean birds. Ibis **102**:349–381, 584–599.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics **18**:453–487.

McCabe, T. T., and F. B. McCabe. 1933. Notes on the anatomy and breeding habits of crossbills. Condor **35**:136–147.

Millington, S. J., and P. R. Grant. 1983. Feeding ecology and territoriality of the Cactus Finch *Geospiza scandens* on Isla Daphne Major, Galápagos. Oecologia **58**:76–83.

Millington, S. J., and P. R. Grant. 1984. The breeding ecology of the Cactus Finch (*Geospiza scandens*) on Isla Daphne Major, Galápagos. Ardea **72**:177–188.

Morin, M. P. 1992. The breeding biology of an endangered Hawaiian honeycreeper, the Laysan Finch. Condor **94**:646–667.

Nager, R. G., C. Rügger, and A. J. van Noordwijk. 1997. Nutrient or energy limitation on egg formation: a feeding experiment in great tits. Journal of Animal Ecology **66**: 495–507.

Nager, R. G., and A. J. van Noordwijk. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. American Naturalist **146**:454–474.

Nicholls, T. J., A. R. Goldsmith, and A. Dawson. 1988. Photorefractoriness in birds and comparison with mammals. Physiological Reviews **68**:133–176.

Nilsson, J.-Å., and E. Svensson. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London B **263**:711–714.

Nol, E., and J. N. M. Smith. 1987. Effects of age and breeding experience on the seasonal reproductive success of Song Sparrows. Journal of Animal Ecology **56**:301–313.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis **112**:242–255.

Perrins, C. M., and R. H. McCleery. 1989. Laying date and clutch size in the Great Tit. Wilson Bulletin **101**:236–253.

Petren, K., B. R. Grant, and P. R. Grant. 1999. Low extrapair paternity in the Cactus Finch *Geospiza scandens.* Auk **116**: 252–256.

Philander, S. G. H. 1990. El Niño, La Niña and the Southern Oscillation. Academic Press, San Diego, California, USA.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Piñero. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology **78**: 1884–1897.

Price, T. D. 1985. Reproductive responses to varying food supply in a population of Darwin's finches: clutch size, growth rates and hatching synchrony. Oecologia **66**:411–416.

Ratcliffe, N., R. W. Furness, and N. I. Klomp. 1998. Influences of breeding experience on the reproductive performance of Great Skuas *Catharacta skua.* Journal of Avian Biology **29**:293–298.

Robinson, G., and E. M. del Pino, editors. 1985. El Niño in Galápagos: the 1982–83 event. Charles Darwin Foundation, Quito, Ecuador.

Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology **72**:1325–1335.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist **143**:698–722.

Sæther, B. E. 1990. Age-specific variation in reproductive performance in birds. Current Ornithology **7**:251–283.

Sanz, J. J., and J. Moreno. 1995. Experimentally induced clutch size enlargements affect reproductive success in the Pied Flycatcher. Oecologia **103**:358–364.

Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island song sparrow population. Oecologia **47**:164–170.

Timmermann, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature **398**:694–697.

van Noordwijk, A. J., R. H. McCleery, and C. M. Perrins. 1995. Selection for the timing of Great Tit breeding in relation to caterpillar growth and temperature. Journal of Animal Ecology **64**:451–458.

Verhulst, S., J. M. Tinbergen, and S. Daan. 1997. Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts? Functional Ecology **11**:714–722.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society of London B **265**:1867–1870.

Wiggins, D. A., T. Pärt, and L. Gustafsson. 1994. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. Oikos **70**:359–364.

Wiggins, D. A., T. Pärt, and L. Gustafsson. 1998. Timing of breeding and reproductive costs in Collared Flycatchers. Auk **116**:1063–1067.

Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution **51**:922–936.

Winkler, D. W., and P. E. Allen. 1996. The seasonal decline in Tree Swallow clutch size: physiological constraint or strategic adjustment? Ecology **77**:922–932.

Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology **80**:1632–1647.

Young, B. E. 1994. Geographic and seasonal patterns of clutch-size variations in House Wrens. Auk **111**:545–555.

Zann, R. A. 1996. The Zebra Finch: a synthesis of field and laboratory studies. Oxford University Press, Oxford, UK.

Zann, R. A., S. R. Morton, K. R. Jones, and N. T. Burley. 1996. The timing of breeding by Zebra Finches in relation to rainfall in central Australia. Emu **95**:208–222.