

EFFECT OF EL NIÑO-SOUTHERN OSCILLATION CONDITIONS ON NESTLING GROWTH RATE IN THE DARK-RUMPED PETREL¹

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Abstract. During a 5-year study of the Dark-rumped Petrel (*Pterodroma phaeopygia*) in the Galápagos Islands we found that chick growth rate was lower and that fledging was later during the El Niño-Southern Oscillation (ENSO) of 1982-1983 than in other years. ENSO chicks attained lower peak mass at a later age than non-ENSO chicks. However, after the pre-fledging mass recession, chicks of all years fledged at similar size and mass. The longer nestling period and slower chick growth of ENSO chicks probably reflect a decrease in the energy available for growth due to lower ocean productivity and reduced food resources during the ENSO. It is likely that the flexible fledging period allows petrels to raise chicks successfully even during periods of food scarcity.

Key words: *Pterodroma phaeopygia*; *El Niño-Southern Oscillation*; *growth*; *Galápagos Islands*.

INTRODUCTION

Because food resources of marine birds are difficult to measure directly, many studies use indirect indices, such as feeding intervals, size of food loads, chick growth rates, and lengths of nestling period, to interpret seabird biology (e.g., Boersma et al. 1980, Gaston and Nettleship 1982). The slow growth rates of pelagic seabirds with one-egg clutches frequently are presumed to reflect characteristics of the food supply (Ashmole and Ashmole 1967). Fluctuations in food resources have, in turn, been linked to altered growth patterns (Pettit et al. 1984).

From 1981-1986, we measured the growth responses of Dark-rumped Petrel chicks (*Pterodroma phaeopygia phaeopygia*), an endangered species in the Galápagos Islands. Data from 1982-1983 were collected during the strongest El Niño-Southern Oscillation (ENSO) on record. During this period the limited ocean productivity of the eastern tropical Pacific Ocean severely reduced food resources and caused major mortality of seabirds (Barber and Chavez 1983, Duffy and Merlen 1986). Although Dark-rumped Petrels continued to nest during the ENSO, we observed

that chick growth was retarded in 1983 (Cruz and Cruz 1985, Valle et al. 1987).

Was this interannual variation in growth a function of environmental change and related food availability? Weather patterns which influence food abundance are known to affect other aspects of reproductive biology and population levels (Anderson et al. 1982). If slow growth, a characteristic of petrels, distributes energy requirements over a longer time, then growth rates may vary considerably with available food resources (Lack 1968). We examine here the differences in growth rates between chicks raised under ENSO conditions and those raised under non-ENSO conditions.

MATERIALS AND METHODS

CLIMATE

The climate of the Galápagos has been described previously (e.g., Wiggins and Porter 1971). Briefly, ocean and atmospheric circulation directly influence two pronounced seasons in the archipelago. During the cool, or *garúa*, season (June-November), the South Equatorial Current (SEC) and southeast tradewinds are well developed. The Cromwell Current, or Equatorial Under Current (EUC), is strongest during this season, flowing beneath and counter to the SEC. As the EUC approaches the Galápagos platform, it is deflected upward and the upwelling brings cool, nutrient-rich waters to the surface. The waters in

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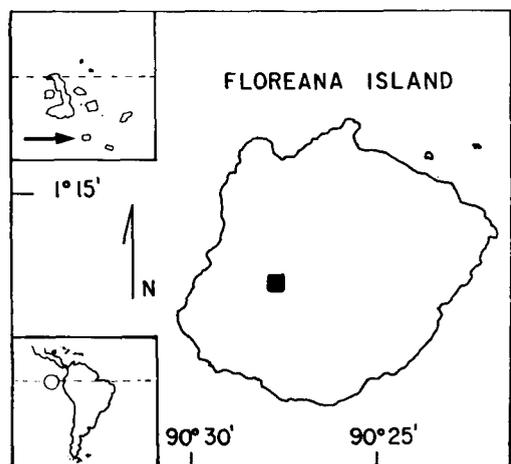


FIGURE 1. Map of Floreana Island with its location in the Galápagos archipelago indicated in the upper left insert. The approximate location of the colony is indicated by a square.

and around the archipelago are, therefore, much more productive than in most tropical oceans (Kogelschatz et al. 1985).

During the warm season (December–May), the SEC and EUC slacken due to weakening south-east tradewinds, and the Northern Equatorial Counter Current shifts southward. Warm tropical waters of reduced salinity and nutrient levels flow out of the Panama Bight and affect the islands. Occasionally, an anomaly known as the El Niño–Southern Oscillation (ENSO) introduces much warmer and nutrient-poor sea water of lower salinity into the archipelago, leading to increases in air temperature and rainfall (Grant 1984) while decreasing ocean productivity (Cane 1983).

STUDY AREA AND FIELD METHODS

We collected data in 1981, and 1983–1986, during a conservation program to control the petrel's predators on Floreana Island (1°13'S, 90°22'W) in the Galápagos National Park (Fig. 1). The colony, with as many as 2,000 nesting pairs (Cruz and Cruz 1987), is located inside a dormant volcano, Cerro Pajas, at 300 m to 640 m above sea level. We checked 43 nests in 1981, 104 nests in 1983, and 100 nests in 1984, 1985, and 1986, from January through September. To minimize disturbance we selected the more easily accessible and least fragile nests. During the incubation period, we assessed nests systematically at least weekly, but more frequent checks were made

in some years. We recorded nest history through fledging, and made morphological measurements through the chick period. The data were analyzed for chicks of known age (to within 3 days) that lived beyond 85 days or were known to have fledged successfully. All birds were weighed with 300 (± 2) g, 500 (± 5) g, or 1,000 (± 10) g Pesola spring scales once a week. Wing length was measured (± 1 mm) from the wrist joint to the tip of the longest primary or feather sheath if primaries had not erupted. We measured the length of the tarsometatarsus (± 0.1 mm) (Pettingill 1970) and the culmen (± 0.1 mm) from the tip of the upper mandible to the edge of the forehead feathers; this measurement is referred to as bill length in the remainder of the paper. Bill height and width were measured at the nostrils (Baldwin et al. 1931). Tail length was measured (± 1 mm) from the tip of the longest rectrix to the point between the middle rectrices where they emerged from the skin.

DATA ANALYSIS

We assessed between-year differences in maximum mass, age of maximum mass, fledging mass and size, and fledging age using one-way analysis of variance (ANOVA). We used 0.05 probability levels except where noted.

Because measurements taken under field conditions are apt to be less than exact, we did not analyze growth rate with the Richards Model, as it may be sensitive to small errors in determination (Brisbin et al. 1986). Instead, we estimated growth rates of each variable using iteration to fit three equations to the data: logistic, Gompertz, and von Bertalanffy. We then analyzed for goodness-of-fit using nonlinear least-squares regression (Ricklefs 1967).

The logistic equation provided the best approximation of the data: $M = A/(1 + be^{-Kt})$, where M is the measured variable, A approaches the maximum measure, b is the proportional gain from the initial measure to the final measure, t is time, and K is a constant, which is proportional to the overall growth rate. We then compared the derived growth constants for interannual differences using the Kruskal-Wallis test. We omitted from analysis the data on body mass for petrel chicks undergoing pre fledging mass recession.

RESULTS

Although mass of individual chicks varied with frequency of feeds and size of food load, average

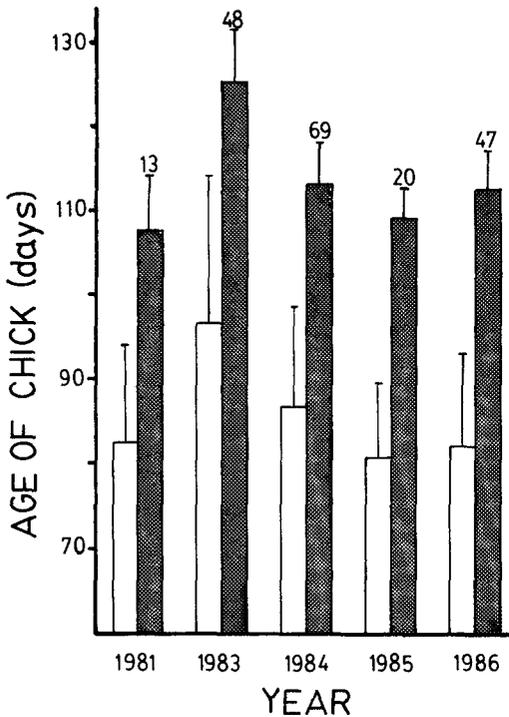


FIGURE 2. Mean age of maximum mass and mean age of fledging in 1981, and 1983–1986 on Floreana Island. Mean age of maximum mass is represented by open columns; SD is indicated with error bars. Mean fledging age is represented by hatched columns; sample sizes were the same for both variables and are indicated above the error bars.

mass tended to increase steadily for the first 3 months of the nestling period and then decreased until fledging. Chicks in non-ENSO years reached a mass equal to that of adult birds about 6 weeks after hatching. They attained their average maximum mass of 585.6 ± 57.33 g ($n = 149$) at approximately 83.0 ± 10.88 days old (Table 1 and Fig. 2). Chicks raised under ENSO conditions reached a mass equal to that of adult birds about 10 weeks after hatching and achieved an average maximum mass of 542.3 ± 69.00 g ($n = 48$) at approximately 96.7 ± 17.30 days. Maximum mass was lower in 1983 (ANOVA $F_{4,177} = 7.95$, $P < 0.01$) and was attained at a later age than in other years (ANOVA $F_{4,177} = 3.55$, $P < 0.025$).

The pre-fledging mass recession was apparent over approximately the last month in the nest. Results of the ANOVA indicated that birds of all years fledged with similar body dimensions. We found no differences between ENSO and non-

TABLE 1. Mean mass and size of Floreana chicks at fledging. Mean maximum mass is included for comparison. Mass is given in grams and size in millimeters.

Year	n	Maximum mass SD	Fledging mass SD	Wing length SD	Tarsus length SD	Bill length SD
1981	13	634.9 58.8	425.1 44.9	292.8 14.5	—	—
1983	48	542.3 69.0	403.2 45.5	291.1 13.7	44.9 1.3	32.3 7.7
1984	69	557.6 53.1	449.3 44.0	299.3 11.0	45.8 1.0	32.7 6.1
1985	20	574.1 50.6	440.2 31.2	293.5 12.9	43.2 1.6	32.8 8.0
1986	47	575.7 66.8	447.9 66.5	291.4 14.1	42.3 0.8	32.5 6.5

ENSO chicks in mass or in the lengths of wing, tarsus, tail, and bill at fledging (Table 1). However, the nestling period was significantly longer in 1983 (ANOVA $F_{4,174} = 70.21$, $P < 0.0001$) than in other years (Fig. 2).

Approximations of mass, wing, and tarsal growth rates for ENSO chicks (K mass = 0.035, K wing = 0.030, and K tarsus = 0.050) were also lower (Kruskal-Wallis $P < 0.0001$) than in other years (mean K for non-ENSO chicks: mass = 0.060 ± 0.0730 , wing = 0.036 ± 0.0041 , tarsus = 0.063 ± 0.0102). However, bill growth showed no consistent trend (Table 2 and Fig. 3).

The 1983 cohort raised during the ENSO attained lower maximum mass at a later age than cohorts from other years. The growth rates for mass, wing length, and length of tarsus (the K value) were also significantly reduced. These chicks fledged with similar body dimensions to chicks in other cohorts, but attained fledging size and mass at later ages than other chicks.

DISCUSSION

Regions of upwelling, such as those that occur around the Galápagos archipelago, are among the most productive parts of the ocean. Here primary productivity is linked with standing stocks of phytoplankton, zooplankton, and nekton, and therefore with the availability of food for higher trophic levels (Bailey 1966). Because plankton-feeding squid are the primary prey of the Dark-rumped Petrel (Simons 1985), a disruption of normal upwelling in the Galápagos region, causing a change in quantity and distribution of phytoplankton, may lead to a reduction in the petrel's food resources.

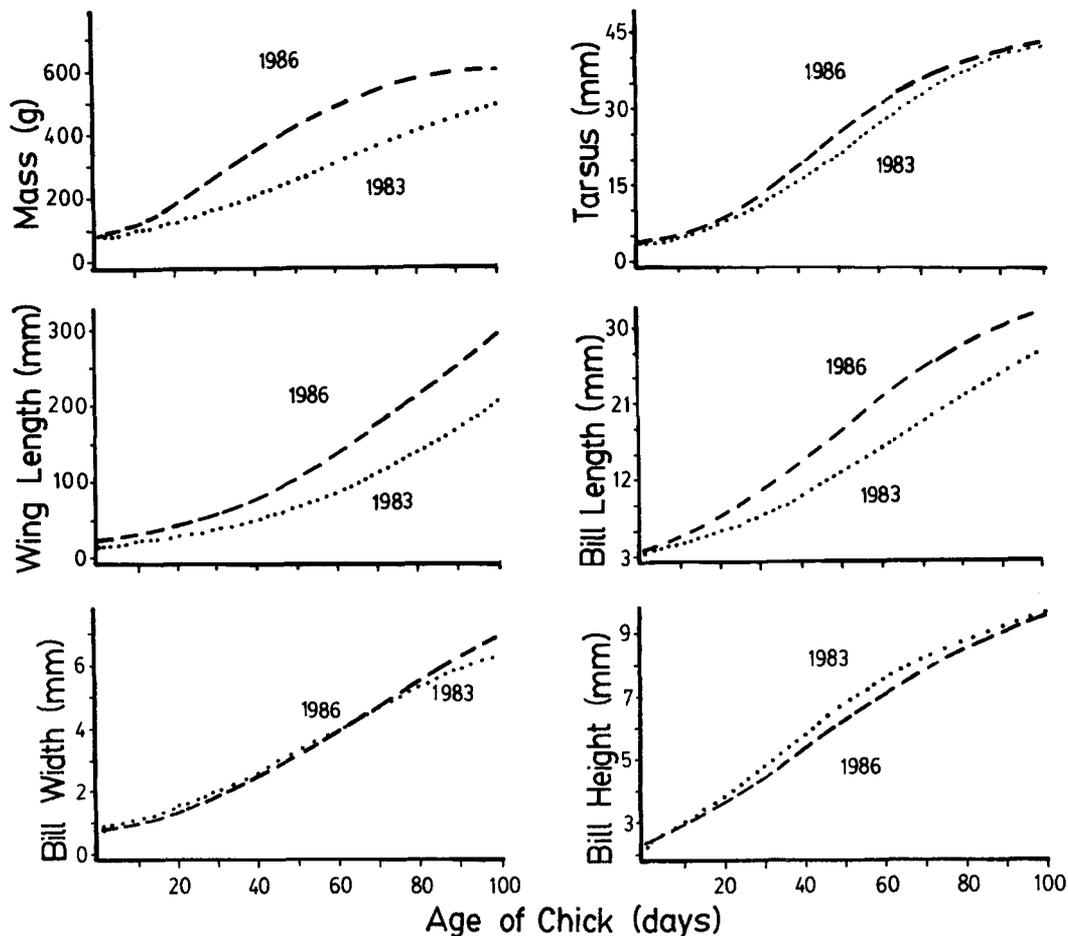


FIGURE 3. Approximated growth of chicks from Floreana during the 1983 ENSO and during 1986, a non-ENSO year. Growth of the wing, tarsus, and bill length, and of mass were significantly lower in 1983.

Although we did not measure food resources directly, other evidence suggests that petrel prey was limited during the ENSO. Marine primary productivity ($C\ mg\ m^{-3}\ day^{-1}$) was up to 20 times lower than normal (Barber and Chavez 1983); upwelling currents were severely curtailed (Kogelschatz et al. 1985); phytoplankton-rich waters were displaced for extended periods (Feldman 1985); and most other seabirds in the region suffered massive reproductive failure due to food shortages (Feldman et al. 1984, Ainley et al. 1988). Our data indicate that petrel nestlings stayed in the nest longer and that growth rate was lower under these conditions. It is likely that the flexible growth rate allows petrels to grow more rapidly when food is abundant and to survive for long periods of slower growth when food is in short supply (Ashmole 1963, Harris 1977).

Ricklefs (1973, 1979, 1983) suggested that the long nestling period and slow growth rate observed in most procellariiforms result from energetic constraints. He proposed that the amount of ingested energy available for growth is limited by the internal allotment of energy or nutrients to thermoregulation. Petrel chicks are thermally independent of their parents shortly after hatching (Simons and Whittow 1984). If certain tissues are needed for mature functions, such as temperature regulation, at an early age, this may constrain continued cellular development and limit growth rate of other body parts. Early maturation of leg and pectoral muscles for thermoregulatory purposes (Ricklefs et al. 1980) may therefore delay the rate of maturation of other tissues, especially flight muscles, resulting in an extended nestling period.

TABLE 2. Logistic analysis of Dark-rumped Petrel growth variables (logistic K) on Floreana Island.

Year	n	K Mass SD	K Wing SD	K Tarsus SD	K Bill length SD	K Bill height SD	K Bill width SD
1981	13	0.053 0.0157	0.036 0.0029	0.057 0.0084	0.028 0.0094	0.056 0.0201	0.055 0.0190
1983	41	0.035 0.0155	0.030 0.0031	0.050 0.0098	0.035 0.0074	0.040 0.0150	0.036 0.0083
1984	61	0.065 0.0157	0.037 0.0070	0.067 0.0150	0.043 0.0085	0.045 0.0154	0.044 0.0138
1985	14	0.060 0.0133	0.037 0.0063	0.070 0.0183	0.040 0.0085	0.042 0.0144	0.034 0.0184
1986	28	0.060 0.0202	0.034 0.0034	0.056 0.0096	0.044 0.0104	0.032 0.0160	0.036 0.0184
χ^2		56.9***	52.5***	57.8***	41.3***	21.6*	18.0**

Note: Kruskal-Wallis test (χ^2 approximation) * = $P < 0.002$, ** = $P < 0.001$, *** = $P < 0.0001$.

Our study indicates that it took longer for chicks to reach the minimal size, or maturation level, necessary to fledge successfully during a period of food stress. We suggest that this resulted from constraints on tissue maturation due to a decline in ingested energy when parents were less able to find food. We would like to have more data on marine productivity, chick feeding intervals, size of food loads, and rate of tissue maturation under different environmental regimes in order to carefully assess this hypothesis.

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