

# RAINFALL ON THE GALÁPAGOS AND THE DEMOGRAPHY OF DARWIN'S FINCHES

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**ABSTRACT.**—Monthly rainfall has been registered at eight sites on four of the Galápagos Islands for a variable number of years. The most extensive, continuous records are from a coastal site on San Cristóbal for the period 1950–67. Analysis of all these data establish the following characteristics: (1) Although rainfall is seasonal, it is very variable, particularly in the wet-season months of January to May. (2) Annual variation is very large. The amount of rainfall tends to alternate in successive years, and a 4-yr periodicity in rainfall is indicated. (3) There is also variation on a longer time scale; the 1950's were 50% wetter than the 1960's. (4) There is more precipitation per year at high elevations than at low elevations, it is distributed more evenly throughout the year, and it varies less among years.

Finch demography, particularly reproductive aspects, is suggested to be influenced by rainfall through the effect of rainfall upon food supply. Several qualitative predictions about reproduction, mortality, and dispersal are made on the basis of the established patterns of variation in rainfall. The meagre data on finch population dynamics are consistent with these predictions, but future research is required to test them adequately. *Received 5 April 1979, accepted 5 November 1979.*

IN the Galápagos Archipelago, one finds the same or similar species of Darwin's finches in habitats ranging from equable highland cloud forest to harsh, unpredictably dry desert (Lack 1947). The occurrence of different species, and of different individuals of the same species, under a wide variety of climatic regimes within a small geographical area allows us to predict and investigate the effects of climate on finch demography. The possibility of looking at several different combinations of finches and climates simultaneously is important, because most studies of climate and avian demography have emphasized the proximate and ultimate factors operating in a single species or under a single climatic regime.

This paper has two purposes. The first is to characterize and quantify patterns of rainfall on the Galápagos Islands. The second is to suggest how such patterns and their variation might determine demographic characteristics of Darwin's finches. Other groups of organisms may be affected by rainfall in a similar manner, so the usefulness of the precipitation analysis extends beyond our present concern with avian demography.

## CLIMATE

For a group of islands straddling the equator, the Galápagos are surprisingly temperate and seasonal. Rain falls occasionally but heavily in the months January–May. The remainder of the year is relatively dry. Seasonality is determined by regular shifts in the positions of water masses. During the dry season, the islands are bathed in the cold water of the Humboldt Current, which originates, in part, as an upwelling off the coast of South America to the southeast (Palmer and Pyle 1966). Warmer water occurs in the intertropical convergence zone. This is located far north of the islands in the dry season and exerts no direct influence on Galápagos climate at that time. But at the end of the year (December–January), the zone moves southwards toward the islands, and it is responsible for the heavy rains in the wet season (Houvenaghel 1974). Usually the zone of warm water extends to within a

couple of degrees north of the islands, but in some years it moves farther south and influences the weather for a longer time. Such years are characterized by unusually heavy rainfall. They are named "El Niño" years, after the warm water current along the western coast of South America with which the rains are associated. They recur irregularly at intervals of 3–14 yr (Palmer and Pyle 1966). The most recent ones were in 1972 and 1975 (Wyrтки et al. 1976, Cowles et al. 1977, Boersma 1978; see Quinn and Burt 1970 and Wyrтки 1975 for discussion of the controlling meteorological factors).

The only published quantitative information on climate in the Galápagos covers the periods 1943–45 on Baltra (S. Seymour) and 1950–59 on San Cristóbal (Alpert 1963). Much more information has been accumulated since then, permitting the first quantitative analysis of rainfall.

#### FINCH POPULATIONS

In contrast to seabirds (Levêque 1964; Snow 1965a, b; Snow and Snow 1967, 1969; Nelson 1968, 1969; Harris 1969a, b, c, d, 1974), land birds on the Galápagos have been virtually ignored from a demographic point of view. Casual observations suggest that the various species of Darwin's finches are very similar in their breeding patterns (e.g. Lack 1947). They breed mainly in the wet season (Lack 1950, Levêque 1964) and lay clutches of up to five eggs, although three seems to be the modal number (Snow 1966a; Downhower 1976, 1978). Reproductive maturity may be delayed (Bowman 1961, Curio and Kramer 1965), and in captivity they live for several years (Orr 1945). Breeding frequency and success, mortality rates and patterns, and population turnover, however, are all unknown. This extraordinary ignorance of *all* species of Darwin's finches has one advantage. It permits us to formulate a theory of finch demography and to make predictions from it almost entirely uncontaminated by prior knowledge (see Lloyd 1960).

As a means of putting our meagre information into a coherent framework and of orienting future research by generating testable predictions, we offer the following explanation for variation in finch demography. It is based in part on an understanding of demographic events on the climatically similar Ecuadorian coastal mainland (Marchant 1959, 1960). Rainfall determines the timing and duration of plant growth and reproduction. Plant responses to rainfall in turn govern arthropod activity and reproduction. Darwin's finches and other land birds feed upon plant products and arthropods. They breed when food resources are abundant and die or disperse when resource levels decline. Finch population characteristics are therefore determined, we suggest, by the quantity, duration, and pattern of occurrence of rainfall, through its effects upon the food of the finches. The main point of interest here is that *variation* in rainfall, in time and space, is responsible for intraspecific and interspecific *variation* in finch demography. Just how this is brought about requires a knowledge of variation in rainfall, which this paper provides.

Rainfall is assigned a primary role in determining food-resource levels, because most of the surface areas of the Galápagos can be classified as arid (Wiggins and Porter 1971). In other parts of the world, breeding of land birds in arid habitats is associated with rainfall (Keast 1959; Marchant 1959, 1960; Serventy 1971; Ward 1971; Davies 1976; Maclean 1976; Nix 1976). In contrast to rainfall, temperatures on the Galápagos are generally not extreme, nor do they vary much diurnally or seasonally, and so are not considered important. Obviously, the success of the theory

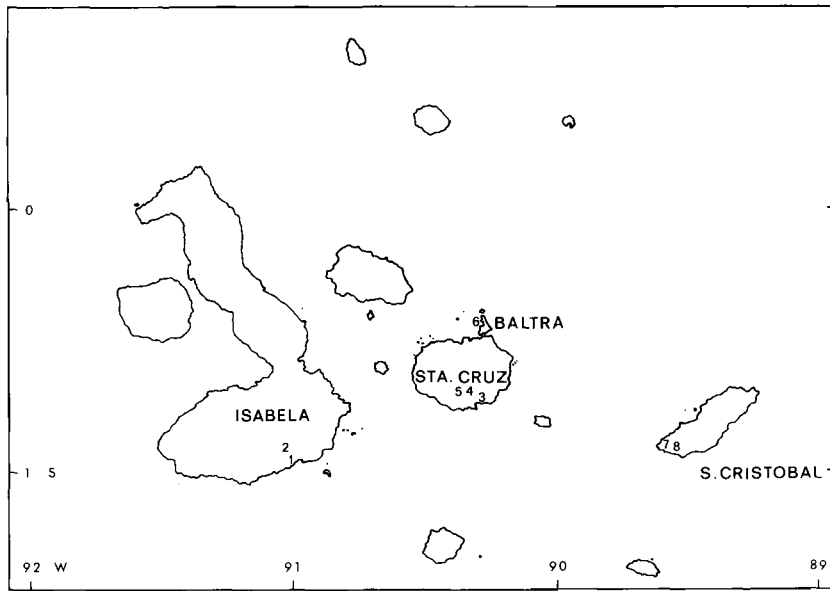


Fig. 1. Map of the Galápagos showing the weather stations: 1 = Villamil, 2 = Santo Tomás, 3 = Estación Biológica Charles Darwin, 4 = Bella Vista, 5 = Zona de Reserva, 6 = Aeropuerto, 7 = Puerto Bacquerizo, 8 = El Progreso. See also Table 1.

we present here in accounting for finch demography depends upon the extent to which other factors, such as temperature, cloud cover, and phenological differences among food species, impinge upon the rain  $\rightarrow$  food  $\rightarrow$  finch relationship (e.g. Davies 1977). Our approach is evolutionary, and we do not discuss the precise combination of proximate factors that may induce breeding in these equatorial species (e.g. see Ward 1969).

We will first establish the patterns of rainfall and then use them to make qualitative predictions about finch demography. We emphasize that, in the interest of objectivity, we present the predictions here before having assembled any quantitative data to test them.

#### DATA AND METHODS

Records of monthly precipitation have been obtained for different numbers of years at eight sites on four islands (Fig. 1). The records of rainfall from 1960 onward have been taken from the files of the

TABLE 1. Annual rainfall characteristics at eight sites on four Galápagos islands.

Island	Locality	Altitude (m)	Years (n)	Mean (mm) $\pm$ SE	Coefficient of variation
Santa Cruz	EBCD <sup>a</sup>	6	1965-75 (11)	406.23 $\pm$ 80.46	65.69
Isabela	Villamil	6	1965-75 (11)	350.78 $\pm$ 72.45	68.50
San Cristóbal	Pto. Bacquerizo	6	1950-70 (21)	383.46 $\pm$ 75.46	90.18
Baltra	Aeropuerto	6	1964-71, 1973 (9)	85.79 $\pm$ 23.25	81.32
Santa Cruz	Bella Vista	194	1965-67, 1969 (4)	1,248.48 $\pm$ 162.26	25.99
	Zona de Reserva	200	1968-70, 1972 (4)	1,132.15 $\pm$ 316.34	55.88
Isabela	Sto. Tomás	360	1970, 1972-74 (4)	1,099.43 $\pm$ 226.70	41.24
San Cristóbal	El Progreso	250	1965-71 (7)	1,182.90 $\pm$ 205.45	45.94

<sup>a</sup> EBCD is an abbreviation of the Estación Biológica Charles Darwin.

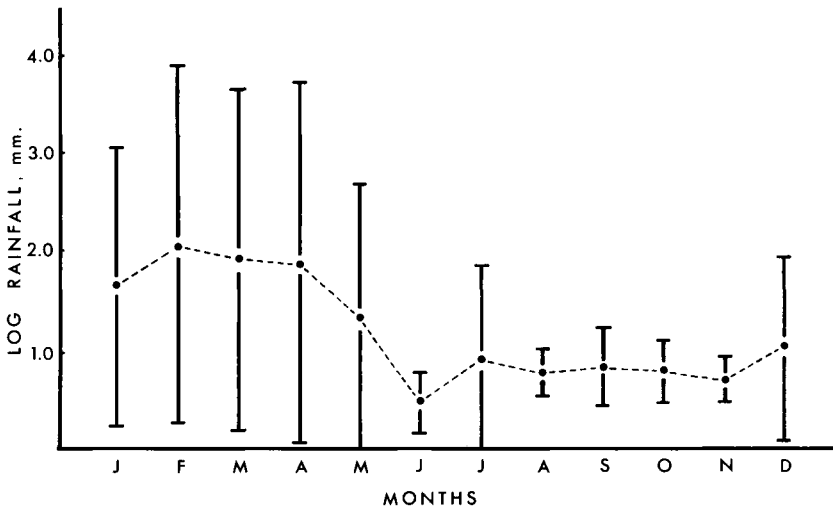


Fig. 2. Mean monthly rainfall, with 95% confidence limits, at Puerto Bacquerizo, Isla San Cristóbal, for the period 1950-67.

Estación Biológica Charles Darwin (Charles Darwin Research Station) on Santa Cruz; they are also published in *Anuario Meteorológico*, S.N.M.H., Quito, Ecuador. Data for the period before 1960 have been taken from Alpert (1963). Details of precipitation at the eight sites are given in Table 1.

## RESULTS

*The seasonal pattern.*—The basic pattern of seasonal variation in precipitation is shown in Figs. 2 and 3. Relatively large amounts of rain may fall in the first 5 months of the year. Any one of these months may be the wettest of the year, although there is a tendency for February to have this distinction (Table 2). At coastal sites, such as Pto. Bacquerizo, the monthly precipitation during the rest of the year is trivial. Wet and dry seasons, of variable length, are recognized on this basis. Because rainfall patterns are correlated with changes in sea and air temperatures, our terminology parallels that of Harris (1974) and others, who have called the wet and dry seasons hot and cool, respectively.

Even though rain falls heavily in the months January-May, it does so on relatively

TABLE 2. Number of extremely wet and extremely dry months on three islands: Santa Cruz (Bahía Academia, 1965-75), Isabela (Villamil, 1965-75), and San Cristóbal (Puerto Bacquerizo, 1950-70).

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Frequency of wettest months												
Santa Cruz	3	3	3	2	0	0	0	0	0	0	0	0
Isabela	3	4	2	2	0	0	0	0	0	0	0	0
San Cristóbal												
1950-59	0	6	3	0	1	0	0	0	0	0	0	0
1960-70	5	2	1	1	0	0	0	0	0	0	0	0
Total	5	8	5	1	1	0	0	0	0	0	0	0
Frequency of completely dry months												
Santa Cruz	0	1	2	3	1	0	0	0	0	0	0	0
Isabela	0	1	1	3	4	1	0	0	0	0	0	0
San Cristóbal	1	0	1	6	2	1	1	0	0	0	0	0

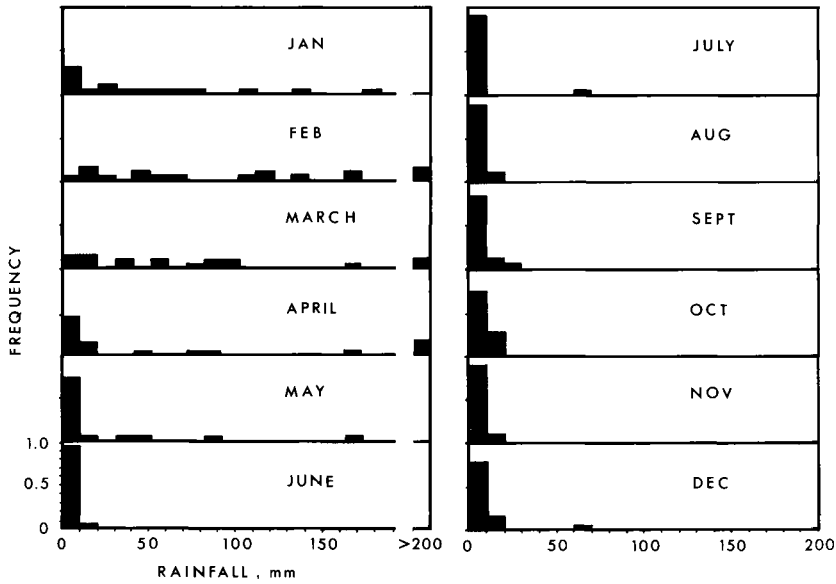


Fig. 3. Frequency of occurrence of monthly rainfall in 10-mm classes at Puerto Bacquerizo, Isla San Cristóbal, for the period 1950-67.

few days. Conversely, precipitation is more frequent in the dry season than in the wet season: in the dry season, precipitation occurs in the form of fog-drip (*garúa*) as well as rain. The most extensive records of daily precipitation are from EBCD, 1965-75. These show that the months February-June have fewer days of precipitation, on average, than the rest of the year. April is the lowest with  $5.8 \pm 1.7$  days ( $\bar{x} \pm SE$ ). September has the most days of rain ( $16.3 \pm 1.7$ ). Altogether, precipitation occurs on 10-40% of the days in the wet season and on 25-60% of the days in the dry season. Wet-season precipitation is apt to be concentrated into short periods of time. The maximum recorded in 24 h at EBCD was 148 mm in 1976; it is likely that this fell in much less than 24 h.

*Variation in the seasonal pattern.*—Variation in monthly rainfall is much greater in the wet season than in the dry season (Figs. 2, 3). High variation in July and December (Fig. 2) disrupts a clear dichotomy. It is caused by single exceptional values for these months (Fig. 3). In general we can say that precipitation is large and variable in the wet season, small and relatively unvarying in the dry season.

Large variation in the wet-season months is produced by the occasional very heavy rain (Fig. 3) and by the occasional complete absence of rain (Table 2). Complete absence of rain is characteristic of, but not restricted to, the wet-season months. April and May are most often completely dry. In the cumulative 105 wet-season months during the period 1950-70 at Pto. Bacquerizo, no rain fell in 20 of them (19.0%). On average, then, 1 month out of the 5 that constitute the wet season was completely dry. One month out of 5 was also very wet, as more than 100 mm per month fell 23 times (20.9%) in the same 21-yr period. The absolute maximum for this period was 486.9 mm in February 1953.

The distribution of rainfall within the wet season is not constant from year to year (see below). In the 1950's the wettest month was generally February, but in the

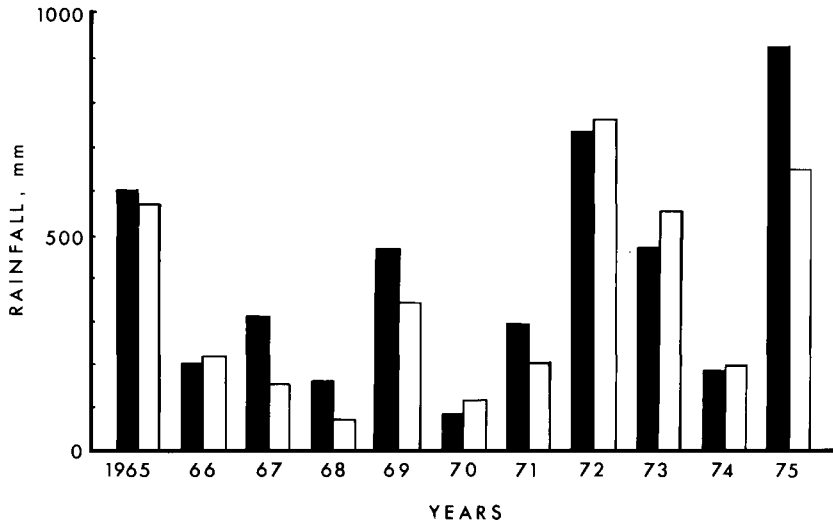


Fig. 4. Annual rainfall at Estación Biológica Charles Darwin, Isla Santa Cruz (solid bars), and Villamil, Isla Isabela (open bars).

1960's it was usually January (Table 2). Rain fell proportionately earlier, within the January–May period, in the 1960's than in the 1950's ( $\chi^2_4 = 9.98$ ,  $P > 0.05$ ).

*Altitudinal variation in seasonal patterns.*—Seasonal patterns and their variations have been established on the basis of rainfall records at coastal stations. There are limited data from other sites at coastal and higher elevations (Table 1). Sites at higher elevations have more precipitation per year, but the total varies relatively less from year to year than at coastal sites (Table 1). The seasonal contrast between wet and dry periods is present but less pronounced at the higher elevations. This is illustrated by calculations of the evenness of rainfall, using the statistic  $J$  derived from information theory. Thus precipitation was distributed more evenly among the 12 months of the year at the high-elevation stations of El Progreso ( $J$  values 0.81–0.90; geometric mean,  $G = 0.85$ ) than at the coastal station of EBCD ( $J$  values 0.67–0.85;  $G = 0.76$ ) in the period 1965–71. In consequence, high-elevation precipitation is significantly less variable than low-elevation precipitation (ANOVA on total data, log-transformed,  $F_{1,166} = 63.34$ ,  $P < 0.001$ ).

*Geographical differences in annual variation.*—Eight sites on four central and southern islands exhibit positive correlations of annual rainfall in all pairwise combinations (Table 3, Fig. 4). Only five correlation coefficients are statistically significant; others are large but the degrees of freedom are few (e.g. Pto. Bacquerizo with EBCD,  $r = 0.987$ ,  $df = 1$ ,  $P > 0.05$ ). Thus, annual variations in climate are similar in this part of the archipelago.

Similarity in mean annual rainfall between two sites, as measured by Whittaker's (1960) index, is not a simple correlate of geographical distance between sites; for the total sample  $r_s = 0.210$ ,  $n = 21$ ,  $P > 0.1$ ; for just the four coastal sites  $r_s = -0.286$ ,  $n = 6$ ,  $P > 0.1$ . But sites with similar exposure on different islands have similar patterns of rainfall. For example, EBCD and Villamil are on the south coasts of Santa Cruz and Isabela, respectively, both are exposed to the rain-bearing winds from the southeast, and they have similar rainfall (Fig. 4, Tables 1 and 3). In

TABLE 3. Correlations of annual rainfall at eight sites. Values of  $r$  are given above the diagonal and degrees of freedom are given below. Probabilities are shown by \* ( $<0.05$ ), \*\* ( $<0.01$ ), \*\*\* ( $<0.005$ ), and \*\*\*\* ( $<0.001$ ).

	SANTA CRUZ			ISABELA		SAN CRISTÓBAL		BALTRA
	EBCD	Bella Vista	Zona de Reserva	Villamil	Sto. Tomás	Pto. Bacquerizo	El Progreso	Aeropuerto
EBCD		0.927	0.950*	0.902****	0.964*	0.987	0.708	0.756*
Bella Vista	2		—	0.716	—	0.966	0.889	0.637
Zona de Reserva	2	—		0.840	—	—	0.990	0.975
Villamil	9	2	2		0.931	0.727	0.570	0.818*
Sto. Tomás	2	—	—	2		—	—	—
Pto. Bacquerizo	1	1	—	1	—		0.789	0.294
El Progreso	5	2	1	5	—	1		0.819
Aeropuerto	6	2	1	6	—	2	5	

contrast, Baltra is to some extent in the rain shadow of Santa Cruz, being close to the north shore of that island (Fig. 1). The annual rainfall of Baltra is much lower than at any other site (Table 1), and correlations with rainfall at other sites are among the weakest (Table 3). Less than 1 mm of rain was recorded in both 1967 and 1970. Such dryness may be characteristic of the small low islands in the archipelago and of the northwest slopes of large islands. For example, the altitudinal extent of arid-zone vegetation on Santa Cruz reflects a rainshadow effect; the upper limit is at an altitude of 40 m on the south side and of 430 m on the north side (Itow 1975).

*Predictability of rainfall: months.*—Predictability of rainfall is the degree to which future rainfall can be “anticipated” from a knowledge of past rainfall. We use the data from the 1950–67 record at Pto. Bacquerizo to assess this by correlation analysis and then apply Colwell’s (1974) alternative method of analysis.

The frequency distributions of most monthly rainfall totals were approximately symmetrical; therefore we used untransformed data in correlation analyses. Out of the 66 pairwise correlations possible between monthly rainfalls within a calendar year, only eight are statistically significant. The significance levels of all but one, however, allow confident rejection of the possibility of spurious correlation. All significant correlations have a positive sign. Three involve successive months: November and December at the end of the dry season ( $r = 0.625$ ,  $P < 0.005$ ), April and May at the end of the wet season ( $r = 0.863$ ,  $P < 0.001$ ), and the strongest association, between June and July ( $r = 0.916$ ,  $P < 0.001$ ). One to 8 months separate correlated members of other pairs: January with May ( $r = 0.560$ ,  $P < 0.05$ ), February with April ( $r = 0.769$ ,  $P < 0.001$ ), February with May ( $r = 0.693$ ,  $P < 0.001$ ), and March with the following November ( $r = 0.716$ ,  $P < 0.001$ ) and December ( $r = 0.619$ ,  $P < 0.005$ ).

This last pair of correlations is a surprise. In contrast to this result, November and December rainfalls are not correlated (separately) with any of the monthly rainfalls in the *following* wet season. In fact, eight of the 10 correlation coefficients have a negative sign. Such a high frequency of negative coefficients has no counterpart in any comparable subset of within-year correlations, among which the overall frequency of negative coefficients was only 15 out of 66. This suggests a tendency for rainfall conditions to alternate in successive years. This possibility will be considered in the next section.

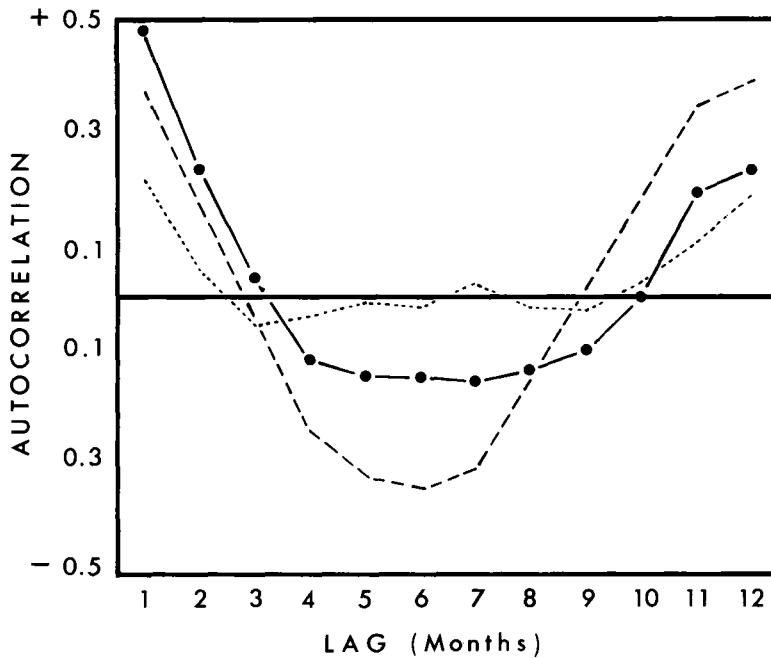


Fig. 5. Autocorrelelogram of monthly rainfall at Puerto Bacquerizo, Isla San Cristóbal, for the period 1950–1967. For comparison, autocorrelations are shown for North American shrubsteppe (dotted line) and tall-grass prairie (broken line) habitats, adapted from Wiens (1974).

Correlations between successive months in the wet season are stronger than those in the dry season. In addition to the significant April–May correlation, statistical significance is approached by the correlations between January and February ( $r = 0.419$ ,  $P \cong 0.09$ ), February and March ( $r = 0.437$ ,  $P \cong 0.07$ ), and March and April ( $r = 0.462$ ,  $P \cong 0.06$ ). Periods of the wet season larger than 1 month are also correlated. Thus rainfall in the period November–February, inclusive, is significantly correlated ( $r = 0.721$ ,  $P < 0.001$ ) with succeeding rainfall (in the months with at least 20 mm).

Predictability without regard to position within the year can be evaluated by autocorrelation analysis. In this analysis correlation coefficients are computed for precipitation between all months that are 1–12 months apart. There is a relatively high correlation between the rainfall in successive months (Fig. 5). As the lag between months increases, the correlation values fall rapidly to just below zero and remain there until the lag spans roughly a year, when they rise above zero. The sequence of values close to zero, spanning most of the autocorrelation spectrum, reflects unpredictability in the rainfall. The asymmetry of the curve in Fig. 5 about a plane running through a lag of 6 months reflects the fact that annual predictability is substantially less than contiguous-monthly predictability.

For comparison, two curves from contrasting North American habitats are also shown in Fig. 5. Sharp and regular seasonality is present in many temperate grasslands. This is manifested as strong negative correlations between months that are 6 months apart and strong positive correlations for months that are 1 or 12 months apart. Less regularly seasonal habitats, like shrubsteppe and other semi-desert hab-



TABLE 4. Rainfall predictability on a scale of 0 to 1. See text for details.

	Wet season only	Dry season only	Total year
Constancy	0.053	0.265	0.058
Contingency	0.128	0.104	0.350
Overall predictability	0.181	0.369	0.408

itats, have shallow curves. Pto. Bacquerizo has characteristics intermediate between these two extremes, and it has one unusual feature. The predictability of next-month rainfall is twice as great as next-year rainfall, whereas in temperate zone habitats these predictabilities are closer to unity (e.g. see data in Wiens 1974).

Colwell (1974) has devised a measure of predictability from information theory that may be used to quantify the year-to-year regularity in monthly precipitation totals. This measure comprises two elements, which he calls constancy and contingency. Constancy is a measure of the degree to which uniformity of rainfall among months of the year contributes to predictability. In the present context contingency is a measure of the repeatability from year to year of seasonal variation in rainfall; the pattern may be homogeneous (uniform) or heterogeneous (seasonal).

Calculations from Pto. Bacquerizo data in log frequency classes give a constancy value for annual rainfall pattern of 0.06, a contingency of 0.35, and hence an overall predictability of 0.41, on a scale from 0 to 1 (Table 4). The low constancy shows seasonality to be strongly expressed, while the moderate contingency shows that the seasonality is repeated from year to year, but not with a high degree of precision. In comparison with four other sites in North and South America considered by Colwell (see also Inger and Colwell 1977), the Galápagos have particularly unpredictable rainfall because it is particularly inconstant; amount of precipitation varies enormously among months of the year.

The table also gives values for these properties within seasons. Wet season precipitation is seen to be less predictable than dry season precipitation, due largely to nonuniform distribution of rain within the wet season (constancy). Note also that annual repeatability of rainfall pattern (contingency) is much lower within each season than it is for the year as a whole.

*Predictability of rainfall: years.*—Extensive data are required to identify pattern in the annual variation of rainfall at a site. The most extensive data are from Pto. Bacquerizo, where they are complete for 1950–67. Data are missing for the periods April–May 1968, June–August 1969, and September–December 1970. Missing data have been estimated by regressing values for the months in question on rainfall in the preceding same number of months to give a data set for 21 successive yr (Fig. 6).

The range of variation is very large, 64.0–1,421.9 mm, as is the coefficient of variation (Table 1; see also Fig. 4). Comparable North American habitats show appreciably less annual variation in rainfall (Wiens 1974). There is a tendency for relatively dry and relatively wet years to alternate, as was suggested by an earlier analysis.

Predictability was evaluated by autocorrelation (Fig. 7), as was monthly variation. This shows a regularity that is not obvious by inspection of Fig. 6. Years with an even or with an odd lag have correlations of different sign. Even-lag years show consistent positive correlations, whereas odd-lag years show consistent negative cor-

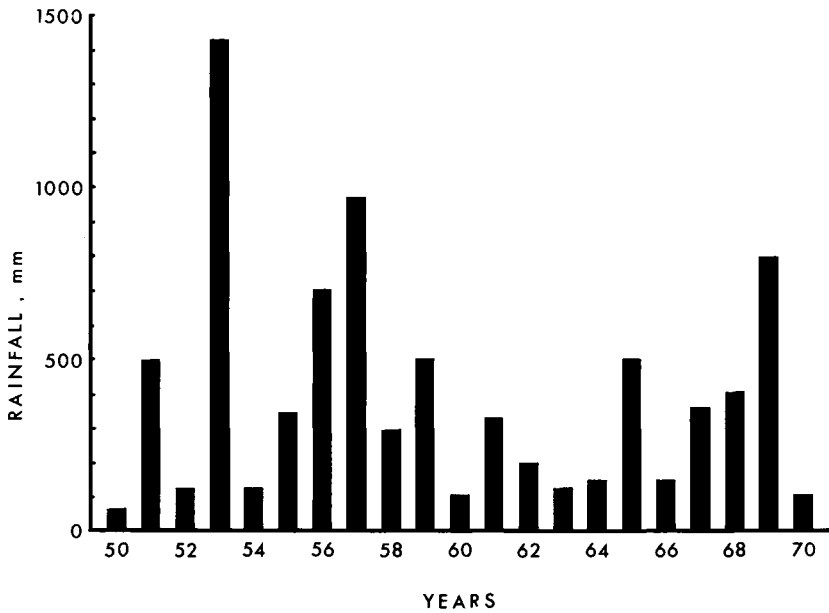


Fig. 6. Annual rainfall at Puerto Bacquerizo, Isla San Cristóbal. See text for details of the estimation of annual totals for the years 1968–70.

relations. Moreover, years separated by a lag of 4 or multiples thereof have the highest correlations, suggesting a 4-yr periodicity in rainfall. The highest correlations are for years with 12- and 16-yr lags, but these may be partly artifactual consequences of small sample size and relatively strong dependence upon years (1968–70) when rainfall was estimated for some months. The data are insufficient for spectral analysis, the technique generally used for identifying dominant periodicities.

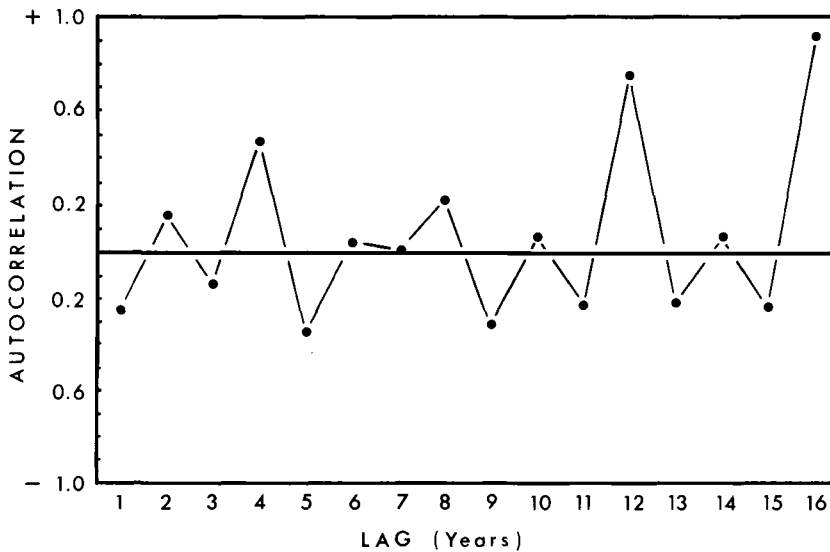


Fig. 7. Autocorrelogram of annual rainfall at Puerto Bacquerizo, Isla San Cristóbal, for the period 1950–70.

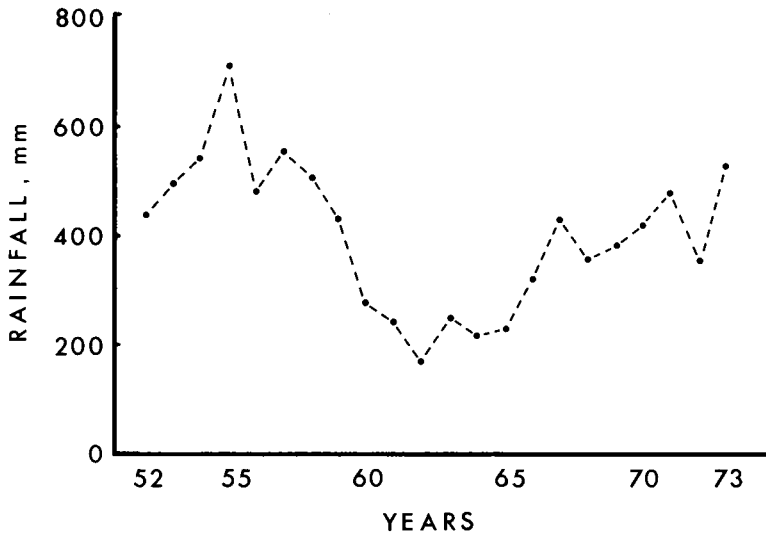


Fig. 8. Five-year moving average of rainfall at Puerto Bacquerizo, Isla San Cristóbal (1950–70), and Estación Biológica Charles Darwin, Isla Santa Cruz (1971–75).

The more limited samples from EBCD and Villamil exhibit different patterns of recurrent variation but agree between themselves in reaching highest positive correlations (0.29, 0.43) when the lag is 3 yr, and highest negative correlations ( $-0.75$ ,  $-0.79$ ) when the lag is 5 yr. These, however, are based on small samples.

A difference between decades is apparent in Fig. 6 (see also Table 2). The average annual rainfall in the 1950's (495.4 mm) was 50% greater than in the 1960's (302.0 mm). Five-year moving averages of rainfall (Fig. 8) exhibit a pronounced decline from the 1950's to the 1960's, followed by a probable increase in the 1970's to the level reached 20 yr earlier. The extrapolation into the 1970's is achieved by using EBCD rainfall in place of the missing data from Pto. Bacquerizo. The justification for this is the similar mean annual rainfall at the two sites (Table 1) and the strong correlation in annual variation in the few years when records were kept at both sites.

In summary, there is some regularity and hence predictability in the annual variation of rainfall. Rainfall in the next year can be predicted with much less precision than can rainfall 4 yr ahead, although wet and dry years tend to alternate. Perhaps by coincidence, the driest years were spaced exactly 10 yr apart (Fig. 6).

#### PREDICTIONS AND DISCUSSION

The principal facts emerging from the analysis of rainfall are:

(1) Although rainfall is seasonal, it is very variable, particularly in the wet-season months of January–May. During a single wet season, some months may be completely dry and others may receive abundant rain.

(2) Annual variation is very large, and wet and dry years are very different. Amount of rainfall tends to alternate in successive years, and a 4-yr periodicity in rainfall is indicated.

TABLE 5. Summary of predictions from the hypothesis that finch demography is largely governed by the effects of rainfall on plant and arthropod reproduction. Some observations have been made that are relevant to those marked with an asterisk (see text).

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- 1.\* Reproductive responses to the first heavy rainfall in the wet season are rapid.
  - 2.\* Timing of breeding varies to a small extent among feeding specialists in relation to different plant phenologies.
  - 3.\* Breeding is more restricted in the wet season at low than at high elevations.
  4. Breeding is patchy in space and time at low elevations, less so or not at all at high elevations.
  5. High-elevation birds tend to differ from low elevation birds in being more *K*-selected.
  6. Adult mortality is higher in the dry than in the wet season.
  7. Population sizes are lowest in completely dry years and highest in the second of two successive wet years.
  - 8.\* Dispersal is most prevalent in the dry season of a wet year.
  - 9.\* Finch faunal composition changes among years. Lowland populations of ground finches show this to the greatest degree.
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(3) Superimposed upon this annual variation is variation among decades. The 1950's were much wetter than the 1960's.

(4) There is more precipitation per year at high elevations than at low elevations, and it is distributed more evenly throughout the year and varies less among years.

(5) Annual variations in climate are similar among islands, but in any one year different islands, and different parts of single large islands, receive different quantities of rain.

From a finch's point of view there is considerable uncertainty as to when, in the wet season, rain will fall, how much will fall, and over what period of time. This uncertainty should be reflected in demography. For the purpose of prediction, it is assumed that rainfall is a faithful, if indirect, measure of finch food production. There is no empirical support from the Galápagos for this assumption. We do not know whether 100 mm of rain has the same effect upon the vegetation if it falls all on 1 day or on 2 days a month apart. We are also ignorant of the relationship between the quantity of rain per rainfall and the threshold of reproductive responses of the finches. Observations by Marchant (1959, 1960) at Ancón (lat. 2°S) on the coastal mainland of Ecuador throw light on these two points (climates of Ancón and Galápagos are extremely similar; see data in Svenson 1946 and Marchant 1959, 1960). Plant growth and bird reproduction at Ancón were apparently stimulated by as little as half an inch of rain ( $\cong 13$  mm) in one shower, although both were sustained only when the soil did not dry out before the next shower. Therefore, the daily and weekly pattern of occurrence of rainfall can be important, as can factors such as cloud cover, which influences the rate of water loss from soil and plants. These have to be ignored because of insufficient data for analysis; they are assumed to be relatively unimportant. Instead, the following predictions are framed in terms of monthly and annual variation. Patterns of variation in rainfall on these time scales are strong enough to permit qualitative predictions about finch populations, even though some of the links in the causal chain are unknown and some important detail is lacking. The main predictions are summarized in Table 5.

*Reproduction and mortality.*—Unpredictability of rainfall in the wet season, with regard to both time of occurrence and duration (i.e. period spanned by first and last rainfall), should select for quick reproductive response to the first heavy fall, as happens in other arid regions (e.g. Marshall and Serventy 1958, Ruwet 1964, Lack 1968, Ward 1971, Maclean 1976). Reproductive responses apparently are quick.

Snow (1966a) recorded nest-construction and egg-laying by *Geospiza fortis* and *G. fuliginosa* on Santa Cruz in only 9–15 days after a heavy rain in November 1963; there had been scarcely any overt reproductive activity before the rain. The uncertainty in rainfall selects for immediate breeding, because good feeding conditions may last only a short time. The length of time that conditions are suitable for breeding is itself uncertain, a consequence of which is that breeding attempts will sometimes fail when no further rain falls after the initial rain, because food production is not sustained long enough. Again this appears to be true, to judge from anecdotal accounts (e.g. Beebe 1924). Marchant (1959) observed the same at Ancón.

Differences in this pattern of response should occur in finch species whose diets contain components having different phenologies. Thus, although the finches in general exploit caterpillars and arthropods on the green vegetation following the rains, *G. scandens* feeds largely on *Opuntia* flowers (Smith et al. 1978), and *Platyspiza crassirostris* feeds largely on buds (Bowman 1961). *Opuntia* starts flowering in November, and buds are available earlier than defoliating caterpillars, so these two finch species should start breeding earlier than the others. In support of these predictions, *G. scandens* were territorial on Santa Fe in the second week of January 1974, before the rains began, while *G. fortis* and *G. fuliginosa* were not (pers. obs.); the data were not quantified, however. *Platyspiza crassirostris* were observed breeding earlier than other species on Santa Cruz by Sammalisto (1966), but again this was not quantified. A predication for future testing is that *G. conirostris* breeds early on Genovesa, because, like *G. scandens*, it exploits *Opuntia* flowers (Abbott et al. 1977). In contrast, on Española, where *Opuntia* is relatively rare, *G. conirostris* breeds slightly later than *G. fuliginosa* (Downhower 1976). It is possible that an early abundance of food is responsible for the apparent early breeding of *Camarhynchus pallidus* on San Cristóbal noted by Lack (1950). Among species other than Darwin's finches, breeding patterns appear to be associated with food phenologies in at least two other species of Galápagos land birds (Snow 1966b, de Vries 1975).

Because seasonality is more pronounced at low than at high elevations, breeding should be more restricted to the wet season at low than at high elevations. Observations on Santa Cruz reported by Snow (1966a) conform to this expectation. The breeding season should be shorter, on average, at the low elevations, but its length should have a larger variance. The earlier onset of breeding at high elevations (Lack 1947, 1950; Bowman 1961) agrees with this, but information is lacking on the cessation of breeding. In very wet years, such as 1972, breeding may occur in all months of the year on Santa Cruz (P. Kramer pers. comm.), but the distribution of breeding activity throughout the year at high and at low elevations is not known, and continuous breeding may only occur at high elevations. Likewise, in the wet year of 1969 on Santa Fe, *G. fuliginosa* and *G. scandens* bred in every month from April to October (de Vries 1976, pers. comm.).

In these ways the difference between breeding seasons at low and high elevations parallels the difference between temperate and tropical regions. High-elevation birds should show a tendency towards characteristics of tropical birds, relative to the low elevation birds. These "K-selected" characteristics include small clutches, slow growth rates, long nestling periods, low feeding rates of nestlings, high nestling mortality, high expectation of further life at fledging, delayed maturity, and low population turnover. The predicted differences between high and low elevation breeding characteristics are probably small and hence difficult to detect without large samples of observations. Interestingly, the predictions are exactly opposite to

predicted trends in the humid tropics, where relatively more temperate conditions prevail at high altitudes.

This last set of predictions must be qualified with a cautionary remark. Some of the tropical characteristics, for example low feeding rates of nestlings and hence slow growth rates, are responses to selection pressures from nest predators. These pressures are assumed to be stronger in the tropics than in temperate regions (Skutch 1966, Ricklefs 1976). But on the Galápagos, nest predators (mockingbirds, snakes, etc.) may be no more plentiful and harmful at high elevations than at low elevations, so the appropriate difference in selection regimes attributable to nest predation may not exist. It is known that nest predation by mockingbirds can be a severe hazard to finches on low-lying Española (Downhower 1978).

At low elevations, and on low small islands such as Baltra, breeding will not be attempted in years when the rains fail to materialize. In years of relatively little rain, spatial patchiness in rainfall at low elevations should result in a corresponding spatial patchiness in breeding activity. Thus variation in breeding activity has a spatial as well as a temporal component, pronounced at low elevations and weak or lacking at high elevations. This is not meant to imply that breeding is an all-or-nothing phenomenon dependent upon when and where rain falls. Rather, the amount of breeding is likely to be variable owing to the operation of extrinsic factors (e.g. rainfall) and intrinsic factors (e.g. age-dependent responses). The number of pairs of a species breeding should be an increasing function of the amount of rainfall over a certain range from the threshold amount, which stimulates one or a few pairs to breed, up to a maximum set by population size, nest-site limitation, and density-dependent interaction. A possible consequence is that the degree of synchronization of breeding decreases with an increase in the amount of rainfall and with an increase in the spread of rainfall over time.

Adult mortality rates should be higher in the dry season than in the wet season, and populations should reach their lowest levels in the dry season of years when the rains fail, because this is when food resources should be lowest. Average population sizes will be larger in some decades than in others.

Population maxima will be reached at the end of the breeding season in the second of two successive wet years (e.g. 1957, 1973). It will be possible to test this prediction by comparing population sizes on Daphne Major in 1973 (Grant et al. 1975) with those in subsequent years.

Population sizes may change by a factor of five or six through the course of a single breeding season if a very wet year follows a dry year, as happened in 1952–53 (Fig. 6). Three broods can be produced by a pair in one breeding season of 5 months, as 7–8 weeks are required for the first brood, and 6 weeks are required for successive broods (pers. obs. on Daphne Major). If one assumes an average of 3 young per brood (because the modal clutch size is 3), three broods yield 9 offspring. Unless maturity is delayed, there should be few if any nonbreeders in years of plenty that follow a year of scarcity, so an original pair can give rise to an additional nine individuals. This may be a little high, as it ignores possible density effects upon survival, but, on the other hand, the breeding season may last for longer than 5 months (see de Vries 1976), so more than three broods may be produced. Furthermore, we cannot dismiss the possibility that young birds may breed in their first year.

Before leaving the subjects of reproduction and mortality, we should mention two additional expectations. These are not derived from the theory as outlined here but

from observations made elsewhere. Lloyd (1960) demonstrated a tendency for several species of arid zone Ecuadorian birds to produce smaller clutches in a climatically poor year than in average or better years. There may be feedback between plant growth and clutch size, and Darwin's finches may be expected to show the same phenomenon, again more at low altitudes than at high ones. Second, Maclean (1976) made the interesting suggestion that the threshold of bird-breeding response to rainfall is higher in South Africa (20 mm) than in Ecuador (13 mm), because subsequent rainfall is more uncertain in South Africa. Apparently the higher threshold is a necessary, safer guarantee of sufficient conditions for successful reproduction. If there is spatial variation in the Galápagos in the uncertainty of future rainfall within the wet season, there might be parallel variation in threshold responses. Unfortunately, Galápagos rainfall data are insufficient to pursue this, and moreover we do not yet know what is a sufficient amount of rainfall for finch reproduction to be successful. Possibly it varies among years in relation to the amount of rain that fell in the previous year and its persistent effects upon the vegetation.

*Dispersal.*—Dispersal should occur between breeding seasons, and it should be particularly prevalent in the dry season of a wet year (and in the second of two successive wet years), because this is when food supply is declining and populations are at their largest. It is consistent with this prediction that the unusual distribution records of finches obtained by the California Academy of Sciences expedition in 1905–06 (Harris 1973) were from a very dry period (Svenson 1946) following a year (1904) that had abundant (“El Niño”) rain on the west coast of South America and possibly in the Galápagos too (Alpert 1963). It is possible that the adaptive radiation of the finches proceeded faster during relatively dry periods, such as occurred more than 10,000 yr ago (Colinvaux 1972), when interisland dispersal may have occurred less often than now.

*Faunal composition.*—Different rainfall conditions should favor different combinations of plant and arthropod species. As a consequence, finch species, adapted to exploiting different combinations of plant and arthropod species (Abbott et al. 1977, Bowman 1961, Lack 1947), should change in numerical proportions as their food supply changes. If annuals are the plants most affected by variation in rainfall, numerical proportions should change more among the ground finches, which feed upon them, than among the tree finches, which do not. Lowland populations should show these proportional changes more than highland ones.

A specific example of faunal change is provided by *Geospiza scandens* and *G. fortis* on Daphne Major, although the connection with rainfall is speculative. To judge from the number of specimens of these two species in museum collections (4 and 42, respectively; Lack 1945) and observations by Beebe (1924), *G. scandens* was relatively rarer in the 1920's and 1930's than now when it is approximately 25–40% as numerous as *G. fortis* (Grant et al. 1975 and unpubl. data). Photographs taken by W. Beebe in 1923 (Beebe 1924) and by L. S. V. Venables in 1939 (unpubl.), when matched with modern ones, show a relative sparseness in cactus growth. *Geospiza scandens* is dependent upon *Opuntia* flowers and fruits for a large part of the year, so it is tempting to suggest that *Opuntia* production and reproduction is favored more by current rainfall regimes than by regimes 50 yr ago. Alternatively, or additionally, *G. fortis* may be faring less well now than 40–50 yr ago, perhaps because it is generally drier now, and annual production of small seeds is generally lower. Future observations may clarify the causes of such changes.

## CONCLUSION

We conclude by emphasizing the need for quantitative data to test the predictions we have made. The hypothesized relationships between climate and demography are now specific to the Galápagos. They should also hold in water-limited regions in other parts of the world such as North America (e.g. deserts, tundra etc.). Therefore, there is scope for testing the predictions in regions more accessible to ornithologists, where the monitoring of climate has been more comprehensive and more rigorous than on the Galápagos (e.g. see Wiens 1974).

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