# FEEDING HABITS AND MORPHOLOGICAL VARIATION IN COCOS FINCHES

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The Cocos Finch, *Pinaroloxias inornata*, is the only Darwin's finch (Geospizinae) which occurs outside the Galápagos Archipelago. It therefore provides a striking counterpoint to the adaptive radiation of its relatives (Lack 1947, Bowman 1961). Furthermore, unlike those relatives, it lives in the extremely lush (see photographs in Slud 1967), though botanically depauperate, tropical forest habitat (Fournier 1966) of Cocos Island where only three potential avian competitors are resident. It may, therefore, show competitive release (Grant 1972) and provide new insights into the evolution of Darwin's finches. However, despite visits to Cocos Island by several naturalists, little is known of its ecology or behavior.

The Darwin's finches on the Galápagos show a wide range of beak types with an unusually large amount of morphological variation in some populations (Lack 1947, Bowman 1961). Bowman showed that the variable *Geospiza fortis* are more generalized in their diet than the less variable *G. fuliginosa* and suggested a correlation between beak morphology and food diversity. Lack believed that the explanation of the within-population variation lies in some interaction between the degree of specialization in feeding habits and the extent of interspecific competition for food. Unlike Bowman, he stressed the importance of competition. A recent study (Abbott et al. ms) has confirmed that both food diversity and competition have influenced evolution of Darwin's finches in the Galápagos. Lack measured the beaks and wings of a sample of Cocos Finches and found little variation. He therefore characterized the species as "specialized" (Lack 1947:94) on the basis of its pointed beak and presumed insectivorous diet. Although the information available on the feeding habits of the Cocos Finch (Slud 1967) is scanty, the species apparently feeds on nectar, insects and small seeds obtained in a variety of ways.

A generalist species may consist either of behaviorally variable but similar individuals, or of dissimilar individuals, each with different specializations. Individuals of the medium-sized Galápagos ground finch, *Geospiza fortis*, are extremely variable in beak and body size, and different-sized individuals have different feeding habits (Grant 1975, Grant et al. 1975). Such a relationship is absent from the Cocos Finch.

Because so little information is available on the Cocos Finch, it seemed worthwhile to examine its feeding habits quantitatively to try to determine: (1) the range of foraging habits shown by a single Darwin's finch when freed from the constraints (if any) of competitors; (2) whether Cocos Finches are more or less specialized in feeding habits than other Darwin's finches; and (3) if indeed they are generalists, why they do not exhibit increased morphological variation. A three-day visit to Cocos Island from August 13–15, 1973 allowed us to collect some quantitative information on foraging habits of Cocos Finches and to capture and measure a small sample of birds.

## STUDY AREA AND METHODS

Cocos Island (5°33′ N, 86°59′ W) is a forest-covered volcanic island of 46.6 km², lying 500 km to the southwest of Costa Rica, Central America. It is the point of land nearest to the Galápagos Archipelago, which lies an additional 630 km to the southwest. Although no year-round information is available, the island probably has a high annual rainfall with a dry season from December to March like the adjacent Costa Rican mainland. The island rises steeply from the shore and consists largely of a forested plateau of 400–700 m elevation. Because of the rugged nature of the terrain (steep, wet rock), we did not travel far from the coast, but spent all our time in the relatively flat narrow strips of coastal forest and scrub on the north of the island.

Finches were mist-netted at Chatham Bay just above the high tide line and along a stream course below mature rain forest up to 150 m inland. Morphological measures taken were: length of the folded wing held flat and straight on a ruler; culmen length from ante-


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TABLE 1. Measurements taken from a sample of 20 Cocos Finches trapped at Chatham Bay, Cocos Island. Figures in parentheses represent measures made by Lack (1947) on a sample of 124 (beak) and 78 (wing) museum specimens of male Cocos Finches.

| Measurement | Mean | s.d. | CV (%) |
|---|---|---|---|
| Weight (g) | 13.1 | .94 | 7.2 |
| Culmen length (mm) | 10.3 (10.5) | .50 ( .38) | 4.8 (3.6) |
| Beak depth (mm) | 5.6 ( 6.2) | .26 ( .25) | 4.6 (4.0) |
| Gonys width (mm) | 5.5 | .19 | 3.5 |
| Wing length (mm) | 66.1 (68 ) | 1.52 (1.29) | 2.3 (1.9) |
| Tarsus length(mm) | 19.8 | .41 | 2.1 |

rior end of nostril to tip; total beak depth in the plane of the anterior end of the nostrils and at right angles to the commisure; maximum gonys width; length of the tarsometatarsus from the posterior aspect of the tibiotarsus joint to the midpoint of the lowest undivided scute at the distal end; weight to the nearest half gram. Birds were color-banded and released.

Most observations of foraging were made on the shore, in the scrubland, and in the forest at Chatham Bay. Observation time in each habitat type was roughly proportional to its bird density. A few additional observations were made in similar habitats (but with less dense scrub) at Wafer Bay, 1 km to the southwest. Using 7× binoculars, stop watches and portable tape recorders, we worked independently, timing each foraging bird for a maximum of 300 sec on a single type of continuous foraging activity (e.g., investigating bunches of hanging dead leaves). If, however, a bird engaged in another type of foraging activity, observation of the new activity was continued for 300 sec or until the bird was lost from view. The number of individuals involved in the sample of 103 foraging bouts is not known, but it probably was large, because very few banded birds were resighted after release. We classified birds into two categories: (1) those with black or partly-black plumage or brown plumage and dark beaks; and (2) brown birds with pale beaks. Category 1 includes all adult males and breeding females, and category 2 includes non-breeding females and immature birds, assuming that the Cocos Finch resembles Galápagos finches in plumage characteristics (Curio and Kramer 1965). Observations were made during continuous drizzle, with only occasional dry spells and little sunshine. While this weather may have biased the observations, it is probably typical for the Cocos wet season.

## RESULTS

### MORPHOLOGICAL MEASUREMENTS

A total of 20 finches were captured and measured. Results and comparable figures from Lack (1947) are given in table 1. They show good agreement even though Lack's measures were taken only from black male birds. The largest discrepancy is found in measures of beak depth. Our value is smaller than Lack's, presumably because we measured the beak slightly nearer the tip.

The variability of beak depth ($CV = 4.6$, $N = 20$) is near to that of two similar sized birds from the Central American mainland, the seed-eating fringillid, *Tiaris olivacea* ($CV = 6.0$, $N = 16$, Willson 1969) and the fruit- and insect-eating manakin, *Pipra mentalis* ($CV = 4.8$, $N = 22$, J.N.M.S., unpubl. data). It is also similar to that of the small Galápagos ground finches, *Geospiza difficilis* on Tower Island ($CV = 4.2$, $N = 47$, Bowman 1961) and *G. fuliginosa* at Borrero Bay, Santa Cruz Island ($CV = 4.8$, $N = 65$), but is significantly less ($P < .01$ using the approximate test of Woolf 1968:249) than that of the medium-sized Galápagos ground finch, *G. fortis*, at Borrero Bay ($CV = 7.3$, $N = 72$). The Borrero Bay measurements were made by P. R. Grant (unpubl. data). This small sample of measurements bears out Lack's contention that the Cocos Finch does not show an unusual degree of morphological variation.

### FORAGING HABITS

In only some cases were we able to identify the food taken. This included soft fruit, nectar, small arthropods and grass seeds. Foraging habits were assigned to ten classes. The total time and relative frequency of use of each class are shown in table 2. These classes were noted by Slud (1967), except that he did not identify *Hibiscus tileaceus* (Malvaceae) and *Cecropia pittieri* (Moraceae) as nectar and fruit sources, respectively. We also

TABLE 2. Time spent in various foraging activities by Cocos Finches at Chatham and Wafer Bays, Cocos Island in August 1973.

| Foraging activity | Time in seconds | | |
|---|---|---|---|
| | Dark beaks/ black plumage | Pale beaks/ brown plumage | Total[a] |
| Eating *Cecropia pittieri* fruit | 1,295 ( 18.9)[b] | 883 (40.6) | 2,529 ( 21.7) |
| Visiting leaf nectaries of *Hibiscus tiliaceus* | 970 ( 14.1) | 88 ( 4.0) | 1,854 ( 15.9) |
| Gleaning in vine tangles | 1,203 ( 17.5) | 0 ( 0.0) | 1,543 ( 13.5) |
| Gleaning in tree foliage | 852 ( 12.4) | 608 (26.9) | 1,460 ( 12.5) |
| Ground pecking, including turning dead leaves | 150 ( 2.2) | 337 (15.5) | 1,073 ( 9.2) |
| Pecking rock surfaces on shore and stream beds | 464 ( 6.8) | 148 ( 6.8) | 782 ( 6.7) |
| Feeding on surfaces of live branches | 526 ( 7.7) | 42 ( 1.9) | 765 ( 6.5) |
| Stripping bark and investigating dead wood | 606 ( 8.8) | 0 ( 0.0) | 629 ( 5.4) |
| Investigating bunches of hanging dead leaves above ground level | 476 ( 6.9) | 30 ( 1.3) | 553 ( 4.7) |
| Other (Including feeding on fruits, grass seeds and foraging among epiphytic plants) | 326 ( 4.7) | 40 ( 1.8) | 486 ( 4.2) |
| Total | 6,868 (100.0) | 2,176 (99.8) | 11,674 (100.3) |
| Evenness | .86 | .46 | .87 |

[a] Total times included observations of birds whose beaks and plumages were not scored.
[b] Numbers in parentheses are percentages of time spent.

distinguish vine tangles from tree foliage as gleaning sites. No single foraging category predominates, except for the tendency of pale-beaked, brown-plumaged birds to specialize on the readily available *Cecropia* fruits. A useful measure of feeding specialization is the evenness of diversity of foraging habits. This may be expressed by the ratio $N_1/N_0$, where $N_1$ is the exponential of Shannon's entropy and $N_0$ is the total number of classes (Hill 1973). The evenness for birds with dark beaks and/or black plumage (table 2) is considerably higher than for birds with pale beaks and brown plumage. This could occur if the latter group consisted mainly of immature birds which had not developed a full range of feeding skills, or if the sex ratio differed between groups. Our data are insufficient to allow rigorous examination of this question.

Unfortunately, we cannot compare these foraging categories directly with data from other Darwin's finches because the Galápagos environment does not offer several of the foraging possibilities of Cocos Island and because the most similar Galápagos species, the Warbler-finch, *Certhidea olivacea*, has not yet been studied quantitatively. If, however, we combine the categories from table 2 into six classes, i.e., feeding on soft fruit, on the ground, on nectar (or insects at nectar sources), on rock surfaces, foliage gleaning, and all others, we can make comparisons with Galápagos ground finches of the genus *Geospiza*. These birds were observed in a similar way at Academy Bay, Santa Cruz Island in April and May of 1973 by J.N.M.S. and in November 1973 by P. R. Grant and J.N.M.S. Foraging behaviors were classified into the same six groups. Although these classes are heterogeneous, some referring directly to foods and others to substrate type etc., it is possible to compare them because they can all be expressed in terms of the common denomi-

TABLE 3. Percentages of foraging time spent by Cocos Finches and three species of Galápagos finches in six foraging activities.

| Foraging class | *P. inornata* August | *G. fuliginosa* April/May | *G. fuliginosa* November | *G. fortis* April/May | *G. scandens* April/May |
|---|---|---|---|---|---|
| Feeding on soft fruit | 21.7 | 5.6 | 4.4 | 11.3 | 0.2 |
| Feeding on the ground | 9.2 | 47.3 | 46.5 | 60.9 | 32.1 |
| Feeding on nectar | 15.9 | 0.1 | 27.8 | 0.0 | 7.7 |
| Feeding on rock surfaces | 6.7 | 17.1 | 15.8 | 7.7 | 11.3 |
| Foliage gleaning | 30.7 | 28.7 | 3.2 | 5.2 | 21.4 |
| Other | 15.8 | 1.2 | 2.3 | 14.9 | 27.3 |
| Evenness | .89 | .57 | .63 | .54 | .75 |

TABLE 4. Frequency distribution of forage heights of Cocos Finches.

| Foraging height (m) | Frequency of observations |
|---|---|
| 0 | 24 |
| 0.1– 4.0 | 32 |
| 4.1– 8.0 | 25 |
| 8.1–12.0 | 9 |
| 12.1–16.0 | 2 |
| >16.1 | 2 |
| $\bar{x} = 4.27 \pm 0.49$ (s.e.) | n = 94 |

nator of foraging time. We emphasize, however, that the comparison is crude. Evenness coefficients of diversity in foraging habits were calculated for each set of data and are presented in table 3. All species are fairly generalized in their foraging habits according to this classification, but the Cocos Finch is much more of a generalist than *Geospiza fortis* or *G. fuliginosa*, but similar to *G. scandens*. *G. fortis* and *G. fuliginosa* both spend a large proportion of their time foraging on the ground, which is the basis of the difference.

Table 4 shows the frequency distribution of foraging heights of the Cocos Finches. Eighty-six per cent of all foraging bouts occurred at or below 8 m, although the observations probably were biased in this direction by poor visibility of individuals foraging high in the canopy.

## DISCUSSION

The data in tables 2 and 3 indicate that the Cocos Finch is a generalist in foraging habits and is more generalized than some of its Galápagos relatives. This finding is consistent with the hypothesis that competitive release has allowed Cocos Finches to exploit a wide variety of foods and feeding techniques. However, because of the large differences in feeding opportunities between Cocos and the Galápagos, it provides only relatively weak support for Lack's (1947) position that competition has been an important determinant of the evolution of Darwin's finches.

An alternative comparison may be made between the Cocos Finch and birds that inhabit the structurally similar, but considerably more diverse, forests on the Central American mainland. Karr (1971) noted that many tropical American species are food generalists but he gave no detailed data which can be compared with the Cocos Finch. At least some Central American forest birds may, however, be very specialized foragers; for example, the Checker-throated Antwren (*Myrmotherula fulviventris*) spends over 90% of its foraging time investigating hanging bunches of dead leaves (Wiley 1971, Smith and Sweatman, unpubl. data), compared with 4.7% for the Cocos Finch. In order to make useful comparisons between Cocos, Galápagos and the Central American mainland, we need more detailed information collected under closely comparable conditions.

The picture emerging from these two approaches is that the Cocos Finch is generalized in its foraging habits. We were unable to determine whether individuals are generalists in addition to the population, as a whole, because we did not observe the foraging of banded individuals. Van Valen (1965) put forward an influential hypothesis that competitive release may lead to increased morphological variation. This does not seem to be the case in the Cocos Finch, which is less variable in beak morphology than the more specialized *Geospiza fortis*, despite the latter's larger number of competitors. Following Grant (1967, 1971), Willson (1969) and Pulliam (1973), we must seek another explanation of differences in morphological variation between species. Grant et al. (ms) have suggested that primary causes of increased morphological variation in the beaks of Darwin's finches may be (a) spatial heterogeneity in habitat use with different phenotypes occupying different types of habitat "patches," and (b) temporal heterogeneity in the supply of different foods, leading to different optimum phenotypes at different times of the year and in different years. Thus, the Cocos Finch may be relatively invariate in its beak structure because its 13 g body weight, and pointed and fairly slender beak represent an ideal, generalized phenotype for the temporally and spatially homogenous Cocos environment. Whether the climate on Cocos really is more stable and the habitat less patchy remains to be established. In addition, we need detailed comparative studies of the Cocos Finch and its Galápagos relatives. Perhaps the methods employed in this brief study could be developed and combined with a closer functional analysis of feeding specializations to gain a better understanding of the evolution of Darwin's finches.

## SUMMARY

Twenty Cocos Finches were captured, measured and released. The foraging habits of a sample of these birds were classified and com-

pared with those of some Darwin's finches from the Galápagos. As predicted from the relative absence of competitors, the Cocos Finch is generalized in its foraging habits, but structural differences in the habitat and differences in the nature of available foods complicate comparisons with both the Galápagos and the Central American mainland. Unlike some Galápagos finches, the Cocos Finch shows little morphological variation in beak characters. This may be due to the different spectrum of available foods on Cocos or may be a consequence of higher temporal and spatial heterogeneity in the Galápagos environment.

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