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Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin’s Finch” of Cocos Island, Costa Rica

(foraging ecology/Geospizinae/island populations/morphology/population variation)

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ABSTRACT As a population, Cocos Finches exhibit a broad range of feeding behaviors spanning those of several families of birds on the mainland, while individuals feed as specialists year-round. Although this extreme intraspecific variability occurs as predicted in a tropical oceanic island environment, these specializations challenge contemporary ecological theory in that they are not attributable to individual differences in age, sex, gross morphology, or opportunistic exploitation of patchy resources. Instead, they appear to originate and be maintained behaviorally, possibly via observational learning. This phenomenon adds another direction to the evolutionary radiation of the Darwin’s Finches and underscores the necessity for detailed behavioral and ecological studies at the individual level for understanding animal feeding systems and the causation of phenotypic variation.

Animals within a population that uses a broad array of food types can feed in diverse ways. In extreme cases, individuals can either use all available foods, as generalists, or specialize relative to other individuals. Biologists predict that generalist populations of feeding specialists will occur under conditions of (i) high food predictability (little or no seasonality), (ii) high food availability and variety, (iii) high population density, (iv) low competition between species, and (v) low territoriality (1–5). Additionally, feeding specializations among individuals within a population often correspond with morphological differences among individuals (1, 3, 6–11).

The Darwin’s Finches (Geospizinae), a textbook example of adaptive radiation in which striking beak differences among species correspond with ecological differences among species (11–16), provide strong support as well for the correspondence between ecological and morphological differences among individuals within a population (9–11): Within the Medium Ground Finch (*Geospiza fortis*) population on Isla Daphne Major, for example, larger-billed finches are able to crack and eat harder and larger seeds than smaller-billed finches. Darwin’s Finch populations with the strongest correspondence between diet and morphology tend also to have the greatest morphological variability, due partly to genetic introgression from other populations (10, 11). The Cocos Finch, the only geospizine found outside of the Galápagos Archipelago, has no known opportunity for genetic introgression from another population, and it has correspondingly low morphological variation (11). This low morphological variability is surprising, nonetheless (17), because the foraging behaviors and resources used by this species span those typical of many different families of birds in adjacent mainland habitats, a circumstance generally believed to promote morphological variability (3, 11, 18, 19). Do individual Cocos Finches feed as specialists, and if so, how do they do so despite their lack of morphological specializations? To an-

swer this question, we examined the feeding behavior of individually marked Cocos Finches in relation to traditional sources of feeding variation: morphology, age, sex, and habitat.

ECOLOGICAL CONDITIONS FAVORING INDIVIDUAL SPECIALIZATIONS

If conditions for a generalist population of specialist individuals exist anywhere, a small, isolated tropical island such as Cocos Island—with few species and constantly favorable growing conditions—should be optimal (17). Cocos Island is 46.6 km² in area and is located in the Pacific Ocean about 500 km southwest of Costa Rica (5°32′57″N; 86°59′17″W). In contrast with other low-latitude eastern Pacific islands, it is characterized by heavy year-round rainfall (7–8 m), by a warm seasonally invariant climate (conditions *i* and *ii*; refs. 20 and 21), and by lush homogeneously distributed rainforest of complex physical structure (condition *ii*; ref. 22). The island’s rainforest is a relatively competitor-free environment (numerically and ecologically) for the endemic Cocos Finch (conditions *ii* and *iv*) because only three other resident landbird species (and two lizard species) share the wide range of resources available year-round (condition *ii*; refs. 20 and 23), and because migratory birds are largely restricted to disturbed habitats along the coast (20). Finches are abundant in all habitats at all elevations (condition *iii*; ref. 23). For example, of 550 birds captured within our 3.4-hectare (34,000-m²) study area, at least 89 were regular residents. The population as a whole is extremely generalized ecologically, as one might expect for a species living in such a depauperate avifauna (24). We have observed Cocos Finches to eat diverse arthropods (including crustacea), nectar (at least 29 floral and 3 extrafloral species), fruit (at least 17 species), seeds, small molluscs, and perhaps small lizards. Finches forage with a wide variety of behaviors to acquire these foods (23, 25). The almost invariant finch diets year-round (see below; Fig. 1), the high endemism and low turnover rate of the Cocos avifauna (26), and dietary specialization by the Cocos Flycatcher (20) provide additional evidence for a relatively constant environment with predictable resource availability. We observed only male finches defending territories, and only in the immediate vicinity of their nests during breeding periods with the result that individual feeding home ranges overlapped broadly (condition *v*).

METHODS AND RESULTS

To document the foraging behavior of individual finches during our 10-month study, we recorded the number and types of foraging attempts made by uniquely color-marked individuals in a gridded 3.4-hectare *Hibiscus tiliaceus*

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Abbreviation: ECB, equally common behavior.

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(Malvaceae) thicket near Wafer Bay. Our observations spanned two cycles of nonbreeding (Dec. 1983 and Apr.–July 1984) followed by breeding activity (Feb.–Mar. and Aug.–Sept. 1984). A foraging attempt was regarded as a discreet action by a bird to obtain food in a particular place regardless of its duration or success. Data are presented in this paper for the 89 marked birds for which we had 3 or more “bird-days” (20 or more foraging observations per day = 1 bird-day). All birds for which we had observed fewer than 3 bird-days were excluded from analyses, since their restricted foraging diversity (Kruskal–Wallis tests, $P < 0.05$) could have been an artifact of small sample size.

We categorized the 26,770 foraging attempts, made by the 89 finches (19 females, 29 males and 41 juveniles of both sexes) that met our sample size criterion, into nine behaviors: gleaning from branches, probing in branches, gleaning from leaves, extracting leaf-miner larvae (Lepidoptera), probing in dead-leaf clusters (these five tactics all involve arthropod prey), probing extra-floral nectaries for nectar, probing flowers for nectar, gleaning from the ground (for seeds and insects), and “other” (which comprised less than 2% of observations).

Individuals Are Specialized. Individual finches consistently used one or a few of these nine behaviors over the course of our study, and different individuals used different behaviors. Four birds with different foraging behaviors illustrate the range in degree of specialization (see Fig. 1): An adult female depended 87.0% on insects gleaned from leaves, and used this behavior more than any other on all 13 days that she was observed (Dec. 1983–Sept. 1984; Fig. 1A); 81.1% of an adult male’s foraging behaviors were gleaning branches for insects over the 17 days he was observed (Dec. 1983–Aug. 1984; Fig. 1B); another adult male probed and gleaned dead-leaf clusters for crickets and cockroaches for 58.3% of his behaviors over the 30 days of observation (Feb.–Sept. 1984; Fig. 1C); and a juvenile (sex unknown) gleaned insects from leaves 19.1% and took extrafloral nectar 41.9% over the 16 days of observation (Feb.–Sept. 1984; Fig. 1D).

We calculated Shannon–Weaver diversity indices to compare the breadth of foraging behaviors used by individual birds with those of the population as a whole (all 89 finches). We then transformed each of these values by expressing it as a power of e (the base of natural logarithms) to give units of “equally common behaviors” (ECBs) for ease of interpretation (27). The ECB value for the Cocos Finch population (7.39) was greater than that of any individual (range 1.07–5.75; Fig. 2).

We tested this pattern statistically, using a Monte Carlo procedure. Accordingly, we compared the set of foraging behaviors used by each individual finch to a random set, chosen according to the null hypothesis that the total repertoire of each individual was the same as that of the other 88 individuals in our sample population. We pooled bird-days by individual, with n representing the total number of foraging behaviors observed for a given individual finch. We then randomly drew 99 sets of n behaviors (with n matched to the observed sample size) for each of the 89 finches from the total pool of all behaviors used by the other 88 finches, and we sampled with replacement. We then calculated the Brillouin diversity index for each set of random and observed birds. [Unlike many other indices, this index can be used with zero cells to measure the diversity of a collection of behaviors rather than to estimate from samples the diversity of a larger population: $H = (1/N) \log_e (N!/(n_1!n_2!\dots n_9!))$, in which n_i is the frequency of behavior i , and $N = \sum n_i$ (ref. 28).] The null hypothesis was rejected if the Brillouin diversity calculated for actual behaviors of an individual was lower than 99% of the randomly generated diversity values for that individual.

All 89 birds were significantly more specialized than random ($P < 0.01$). These results are possible only with a

generalist species composed of specialist individuals, and thus we rejected the null hypothesis of no individual specializations. Of the 89 individuals, 62 concentrated at least 50% of their foraging attempts on one behavior alone. Furthermore, seasonal foraging variability was minimal: Four representative individuals, whose ECB values range from 1.67 to 4.5, illustrate the temporal consistency of the specializations (Fig. 1) across two breeding and nonbreeding seasons.

Feeding Differences Are Unrelated to Morphological Differences. To evaluate whether or not the little morphological variation within the Cocos Finch population could explain why individuals exploit different resources, we compared individual finch morphology and foraging behavior. Using canonical correlation analysis (29), we compared eight standard, log-transformed, morphological measurements (total mass; beak length, width, depth, and pointedness as defined by the bill depth measured at 4 mm posterior from the tip; wing length; and tarsus and toe length) for each finch for which we had all measurements ($N = 53$) with frequency of use of the eight foraging behaviors (excluding the “other” category). We found no significant relationship between any linear combination of finch morphological characteristics and foraging behaviors (Bartlett’s λ test, $\chi^2 = 71.98$, $P = 0.23$ for 64 degrees of freedom). In a more conservative test, we grouped birds by their dominant foraging behavior and compared morphology between groups with a MANOVA procedure (BMDP4V) (43). To maximize the chance of a significant positive result, this analysis included only those birds whose dominant behavior comprised at least 50% of their foraging behavior and for whom we had measured all eight morphological characters ($N = 39$). Morphology of birds classed as branch gleaners, branch probers, leaf gleaners, leaf-miner extractors, and dead-leaf gleaners and probers did not differ significantly ($P = 0.13$; $F = 1.35$ with 32, 101.17 degrees of freedom). The behavioral classes of extra-floral nectar, flower probing, ground gleaning, and other could not be used in this analysis due to cell sizes less than or equal to 1.

Feeding Differences Are Unrelated to Sex and Age Differences. Feeding differences are correlated with differences in sex, age, or both in a variety of animals (6–8, 19) but not in the Cocos Finch. We assessed the relative importance of individual versus sex or age differences in feeding behavior by partitioning finch feeding variation into its within-class component and between-class component (1, 2, 19). When each individual was regarded as a separate class, the between-class component of foraging niche breadth (in this case, between 89 individual classes) comprised 49.4% of the total breadth for the population of 89 finches. A between-class component of foraging niche breadth of this magnitude far exceeds the maximum value of 33% reported for other vertebrates (1, 19). We then repartitioned foraging observations two ways, first by sex (pooled males versus pooled females, juveniles excluded), then by age (juveniles versus adults). In both cases, the between-class component (2.0% and 3.9%, respectively) was a small fraction of the total foraging variability. Juveniles and adults of both sexes specialized on the same resources. We conclude that neither sex nor age of a Cocos Finch explains the observed foraging variability.

Feeding Differences Are Unrelated to Differences in Foraging Time and Place. If resources were temporally or spatially patchy among birds’ home ranges, foraging specializations could result simply from individuals encountering and using different resources (30–32). However, the consistency and persistence of Cocos Finch specializations over many months (e.g., Fig. 1) and the wide overlap of finch home ranges within our 3.4-hectare study site eliminate this hypothesis. Further, we used radiotelemetry to track eight birds intensively for several days. All eight consistently and

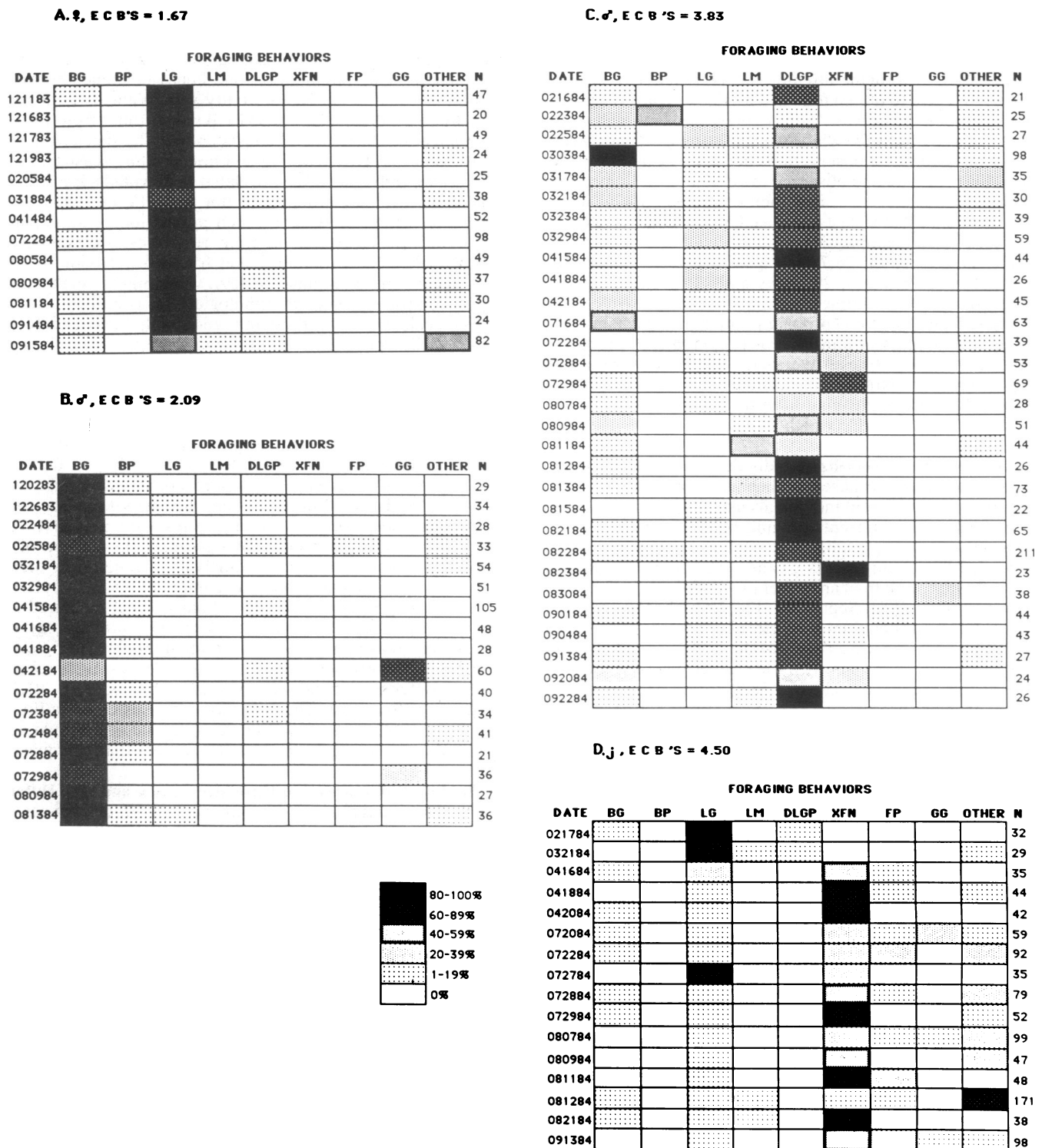


FIG. 1. Foraging behaviors of four representative Cocos Finches with broadly overlapping home ranges. Letters A-D denote individual birds; j denotes juvenile. Observation date (month, day, year) and sample size (number of observed foraging attempts) for each row are in the left and right columns, respectively. Behaviors (columns) are BG, branch glean; BP, branch probe; LG, leaf glean; LM, glean leaf-miner; DLGP, dead leaf glean or probe; XFN, extra-floral nectar; FP, flower probe; GG, ground glean. The shading inside each box gives percentage use of each behavior for that date (see key). The equally common behavior (ECB) index (27), in our application, expresses foraging behavior diversity in terms of number of behavioral classes, specifically that number among which observations are equally common, with the same diversity value (H') as the observed value; this ECB value increases with both the number of behavioral categories used and the degree to which those categories are used equally. If all individuals used identical foraging behaviors, then the relative frequencies of all nine behavioral categories would be identical among birds and the diversity values (ECBs) for all finches would be equal to the population value.

repeatedly used the same dominant behavior throughout their home ranges and throughout the day (unpublished data). Finally, to control explicitly for any effects of resource

patchiness, we observed all individual finches that we could distinguish (using either color bands or plumage) feeding at the same time and place, in each of six *Hibiscus tiliaceus*

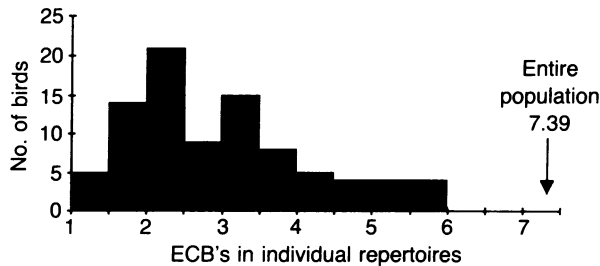


FIG. 2. Frequency distribution of number of ECBs for 89 individual Cocos Finches and the ECB value for pooled behaviors of all 89 individuals.

shrubs during 1-hr observation periods between 0800 and 1000. Within each of the six shrubs, individual finches consistently used significantly different foraging behaviors and ignored resources used concurrently by other finches ($P < 0.005$, G test; Fig. 3).

DISCUSSION

Comparisons with Other Species. Several studies of other animal species (33–38) report individual feeding specializations that do not appear to be constrained by the animals' age, sex, or morphology. "Majoring" and "minoring" of bumblebees, which often involve complex behaviors that must be learned initially and practiced to attain proficiency (34), appear to be analogous to the specializations we observed in the Cocos Finch. The Cocos Finch is a particularly dramatic example of this phenomenon, however, because of the (i)

broad range of resources used, (ii) persistence of the specializations throughout the year, (iii) concurrent use by different specialists of the same patch of habitat (shrub), and (iv) demonstrable independence of behavior from morphology, sex, and age. The occurrence of such specializations in at least four classes of animals (gastropods, insects, fish, and birds) necessitates more detailed behavioral studies at the individual level for a better understanding both of their prevalence in nature and of their proximate and ultimate causes.

Origin of Feeding Specialization in Cocos Finches. Feeding behavior specializations could be genetic in origin (39). An intriguing possibility is that a genetic basis exists for behavioral plasticity or the potential to learn complex (and novel) behavioral tasks, and not necessarily for each of many behaviors with which individuals harvest different resources. Specializations could also be physiologically constrained (reviewed in ref. 40) or learned—either by trial and error (34, 35, 38) or by observation of other animals (33). The potential to learn feeding behaviors from other animals (i.e., culturally) is widespread (41). Two sets of anecdotal observations suggest that Cocos Finch specializations arise in part via observational learning: (i) Throughout the year we repeatedly ($n > 20$) observed a juvenile finch follow an adult within 1–2 m and alternately watch the adult, then imitate its feeding behavior, often in precisely the location vacated by the adult. [We also observed juvenile finches approach and imitate feeding behaviors of Yellow Warblers (*Dendroica petechia*), a Prothonotary Warbler (*Protonotaria citrea*), and sandpipers (*Calidris* spp.).] (ii) Juveniles (up to several months after fledging) almost invariably foraged in groups (2–30 individ-

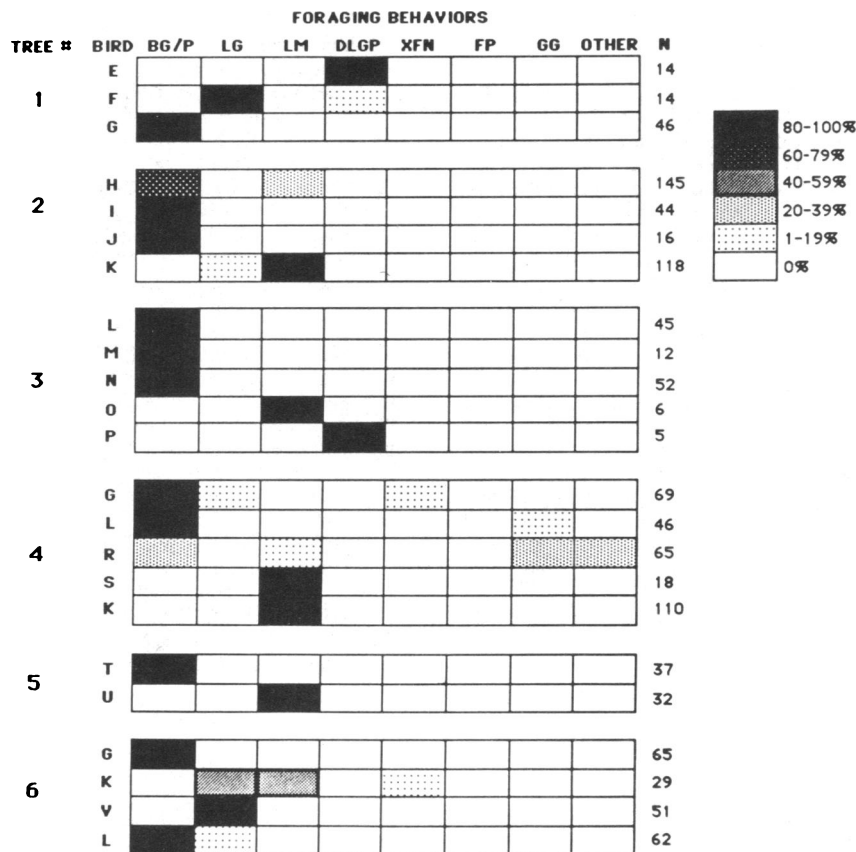


FIG. 3. Heterogeneous behavior of different finch individuals foraging concurrently in *Hibiscus tiliaceus* shrubs. Columns represent the foraging behavior of each of 17 finches; each row represents a different finch (rows E–V; letters in this figure do not indicate the same individuals as in Fig. 1). See Fig. 1 for key to abbreviations of foraging behaviors. Finches were foraging in six *Hibiscus* shrubs (blocks 1–6) of similar size (6–8 m high), structure, and location. Sample sizes (number of observed foraging attempts) are to the right of each row.

uals), within which they could easily watch and imitate other individuals.

We do not know the ultimate cause of the Cocos Finch behavioral specializations, but foraging efficiency may be particularly important in environments such as Cocos Island with periods of prolonged and heavy rainfall and high abundance of conspecifics. Juveniles of other Darwin's finch species can take up to a year to attain the foraging efficiency of adults (11), and Cocos Finches could attain foraging proficiency more rapidly with a restricted than broad behavioral repertoire. Strong intraspecific competition may also favor specialization as a way to increase foraging efficiency (reviewed in ref. 40).

CONCLUSION

In conclusion, our results show that Cocos Finches exploit diverse resources with behavioral means—i.e., with intraspecific behavioral specializations that persist year-round, independently of morphological differentiation. Behavioral specializations and their possible cultural transmission in this species seem to function in lieu of morphological specialization and, as Morse (42) has noted for tool use and other novel behaviors, may be disproportionately represented on islands. Because such ecological characteristics of animals are not sufficiently explained by morphological variation, ecologists must better integrate such behavioral variability into resource-use models. We suggest that the foraging specializations of individual Cocos Finches could provide a powerful within-population model for niche differentiation by species within larger faunas. This analogy would be particularly valid if intraspecific competition is prerequisite to intrapopulation specializations in the same way that interspecific competition is thought to be an integral component of species divergence in the course of adaptive radiation (11).

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