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FEEDING BEHAVIOR OF FOUR ARBOREAL DARWIN'S FINCHES: ADAPTATIONS TO SPATIAL AND SEASONAL VARIABILITY

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Abstract. In the Galápagos Islands climate and food abundance vary strongly among vegetation zones and between seasons. We studied the foraging behavior of four mainly insectivorous Darwin's finch species on Santa Cruz Island. We compared foraging behavior between (1) the arid zone, where food is scarce, with the humid *Scalesia* zone, where food is abundant; and (2) within each zone between dry and wet seasons. The four species used different feeding substrates in the two vegetation zones and reacted flexibly to the seasonal variation by changing feeding techniques and substrates. Species mainly specialized in resource use and feeding techniques or showed no change in niche breadth when food became more limited in dry conditions. In the arid zone during the dry season, the Large Tree Finch (*Camarhynchus psittacula*) relied on its powerful biting beak to bite open the bark of dry twigs. The Woodpecker Finch (*Cactospiza pallida*) used twigs and cactus spines to access arthropods in tree holes and was the only species that significantly increased the diversity of feeding techniques. The use of tools extends the morphological properties of its beak temporarily without limiting behavioral versatility and flexibility. The Small Tree Finch (*Camarhynchus parvulus*) showed a shift in food types and had a high proportion of plant food in its diet. The Warbler Finch (*Certhidea olivacea*) was not present in our study site in the arid zone.

Key words: Cactospiza pallida, Camarhynchus parvulus, Camarhynchus psittacula, Certhidae olivacea, *Darwin's finches, feeding behavior, Galápagos Islands.*

Comportamiento de Alimentación de Cuatro Pinzones de Darwin: Adaptaciones a la Variabilidad Espacial y Estacional

Resumen. En las Islas Galápagos el clima y la abundancia de comida cambia notablemente entre zonas de vegetación y estaciones. En la Isla Santa Cruz estudiamos la conducta de forrajeo de cuatro especies de Pinzones de Darwin que son mayormente insectívoras. Comparamos la zona árida donde la comida es escasa y de difícil acceso y la zona húmeda de *Scalesia* donde existe abundante comida, y dentro de cada zona entre estación seca y húmeda. Las cuatro especies usaron diferentes substratos para alimentarse en las dos zonas de vegetación y reaccionaron de modo flexible a la variación estacional cambiando las técnicas y substratos de alimentación. En condiciones secas, cuando la comida se volvió limitada, las especies se especializaron principalmente en el uso de recursos y en la conducta de forrajeo, o no cambiaron su amplitud de nicho. En la zona árida durante la estación seca, *Camarhynchus psittacula* contó con su poderoso pico penetrante para picar la corteza de ramas secas. *Cactospiza pallida* usó ramitas y espinas de cactus para capturar artrópodos en los agujeros de los árboles y fue la única especie que incrementó significativamente la diversidad de técnicas para alimentarse. El uso de herramientas amplía temporalmente las propiedades morfológicas de su pico sin limitar la versatilidad y flexibilidad de la conducta. *Camarhynchus parvulus* mostró cambios en los tipos de comida y presentó una alta proporción de alimentos vegetales en su dieta. *Certhidea olivacea* estuvo ausente en nuestra área de investigación en la zona árida.

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INTRODUCTION

Food limitation, both in abundance and in accessibility, strongly influences the evolution of morphological and behavioral traits (Wiens 1989, Martin and Karr 1990). Well-known examples of morphological adaptation to different food types in birds are the varied forms of the beaks of Darwin's ground finches (Bowman 1961, Schluter and Grant 1984, Grant 1986).

Darwin's finches also show remarkable foraging behaviors, such as tool use by the Woodpecker Finch (*Cactospiza pallida*; Eibl-Eibesfeldt 1961), or egg breaking and blood sucking by the Sharp-beaked Ground Finch (*Geospiza difficilis*; Bowman and Billeb 1965). Behavior is more flexible than morphology, especially on a short time scale (Morse 1980). Animals may broaden, narrow, or shift their resource use by changing their behavioral repertoire in response to variation in food supply. In comparison, special morphological structures may be advantageous in exploiting resources that are stable and predictable but hard to access (Ellis et al. 1976, Sherry 1990). Morphological specialization may, however, constrain behavioral flexibility and diversity (Carrascal et al. 1995, Robinson and Wilson 1998).

The aim of this study was to clarify how four closely related species of Darwin's finches have adapted to spatial and seasonal food limitations with either morphological adaptations or behavioral versatility. The four species we investigated form a guild of mainly insectivorous tree foragers. They show obvious differences in beak dimensions and form (Bowman 1961). The Large Tree Finch (*Camarhynchus psittacula*) and the Small Tree Finch (*C. parvulus*) both have grasping beaks with curved culmens. The Woodpecker Finch has an elongated probing beak that is suitable for pecking into woody tissue. The probing beak of the Warbler Finch (*Certhidea olivacea*) is finer than that of the other species. The four species live sympatrically on Santa Cruz Island in different vegetation zones distributed along an altitudinal gradient. We selected two vegetation zones that differ greatly with regard to vegetation structure and climate: (1) the arid zone near the coast, a semidesert open-canopy forest; and (2) the evergreen *Scalesia* zone at higher elevations. We investigated and compared foraging behavior of the species in both zones and during the wet and dry season. In the *Scalesia* zone, arthropod prey is abundant in moss, under the bark, and on leaves throughout the year (Tebbich et al. 2002). In the arid zone, arthropods are found almost exclusively under the bark, particularly in the dry season when leaves are absent. (Grant and Grant 1980, Schluter 1982, 1984, Tebbich et al. 2002).

Therefore, food is difficult to access in the arid zone for all four species, and its availability varies strongly between seasons. We aimed to test (1) whether species show flexible behavior between seasons and zones, and if so (2) whether under food-limited conditions they become more or less diverse in substrate use, in feeding techniques or in diet. Optimal foraging theory predicts a broadening of the niche under food limitation, since searching becomes increasingly costly and therefore a wider range of resources should be used (Stephens and Krebs 1986, Gray 1987).

METHODS

STUDY AREA AND CLIMATE

Data were collected on Santa Cruz Island in the Galápagos Archipelago (Ecuador) during three field seasons: December 1995–April 1996, October 1996–April 1997, and January–February 1998. There are two main seasons, a warm and wet period typically from January–May and a dry and cool period for the remainder of the year; however the onset and amount of rainfall are highly variable between years (Grant and Boag 1980). Rainfall measured at sea level during our three study periods for the wet season amounted to 118 mm in 1996, 893 mm in 1997, and 1654 mm in 1998 (an El Niño year). For the dry seasons rainfall was 68 mm in 1996, 761 mm in 1997 (beginning of El Niño year) and 98 mm in 1998. Darwin's finches can experience extreme food limitation during dry years and a superabundance of prey during El Niño periods (Boag and Grant 1984, Grant and Grant 1987).

Rainfall within the archipelago also varies locally and with altitude, creating distinct vegetation zones on the higher islands. The arid zone extends from the coast up to an elevation of 80–120 m. It is the major vegetation zone of the islands and is characterized by a semidesert forest consisting of deciduous trees (mainly palo santo [*Bursera graveolens*], shrubs (e.g., *Croton scouleri*) and cacti (mainly prickly pear [*Opun-*

tia echios var. gigantea] and candelabra [*Jasminocereus thouarsii*]). The *Scalesia* zone is an evergreen, lush cloud forest on the slopes between 300 and 650 m elevation. It is dominated by the treelike *Scalesia pedunculata* (Asteraceae) reaching heights of 15 m. Tree trunks and branches are densely covered with epiphytes, mostly mosses. During the wet season, the *Scalesia* forest frequently receives heavy rains, and during the dry season it is almost continually covered by mist. Therefore conditions are wet throughout the year except in severe droughts.

For intensive foraging observations two sites were selected: in the arid zone we investigated an area of approximately 70 ha (altitude 10–20 m) about 13 km northeast of Puerto Ayora (0°42′S, 90°14′W). In the *Scalesia* zone we worked in an area around Los Gemelos (approximately 110 ha, altitude 580–620 m) 15 km northwest of Puerto Ayora (0°38′S, 90°28′W).

DENSITY ESTIMATES

To estimate breeding density of all four species in both zones point counts were conducted during the wet season in January and February 1997, when Darwin's finches were territorial and singing activity was high. Each count lasted 5 min; 17 points were counted twice in the *Scalesia* zone, and 21 points once in the arid zone. For the points that were counted two times, we calculated a density estimate for each of the two dates and took the higher value. The distance from the point to the location of the birds was estimated to the nearest 10 m. Densities of the four species were estimated using distance sampling (Buckland et al. 1993). This method estimates the number of individuals present that were not counted, using the way the detection declines with distance and assuming that detectability at the point is 100%. The estimated number of undetected birds is added to those counted to calculate the total number present.

FIELD OBSERVATIONS

Finches were located visually or by song. We recorded the type of the first foraging technique, feeding substrate used and, if possible, the prey type obtained. After this observation we switched to a different bird. We collected data from 07:00 to 12:00 and 14:00 to 16:00, six days per week. We regularly alternated visits between the arid and the *Scalesia* zone. We identified 10 different foraging substrates: *fruit, moss* (epiphytic mosses), *leaf* (green leaves attached to trees), *dead leaf* (dead leaves attached to trees), *bark* (on and under the bark of dead trunks and branches), *twig* (under the bark of dead twigs), *seed, bud* (buds of bushes and trees), *tree hole* (excavated cavities and foraging areas of other animals), and *air*. Nine different foraging types were classified: *feed* (eating fruits), *glean* (taking prey from the surface of the substrate), *peck* (forceful and quick vertical downward movement of head and beak onto bark of dead wood), *bite* (biting into petioles of leaves or the bases of curled leaves), *probe* (quickly inserting the beak into moss or curled leaves), *remove* (removing moss with the beak), *chip off* (removing bark of dead wood by inserting either both mandibles or only the lower mandible sideways under the bark and levering the bark forcefully), *tool use* (holding a twig or cactus spine in the beak and inserting it into an opening in the bark or into a tree hole), and *sally* (catching prey in flight). We classified prey items into eight types: *nectar, fruit, insect* (all adult insects), *larvae* (larvae of Hymenoptera and Coleoptera, *caterpillar* (larvae of Lepidoptera), *seed* (seeds on the ground), *spider*, and *other*.

We were able to observe most birds from distances of <10 m without disturbing them, so for Woodpecker Finches, Large Tree Finches, and Small Tree Finches it was often possible to identify the order of their prey items. However, Warbler Finches fed mainly on small insects, so prey identification was often not possible. Overall, there may be an identification bias for large prey types.

STATISTICAL ANALYSES

Point-count data were analyzed using the program DISTANCE (Laake et al. 1993). DISTANCE uses three models to determine the manner in which detection probability varies with distance; each one can be combined with series expansions to adjust the key function to improve the fit of the model to the data. The submodel fitting the data best was determined with AIC (Akaike's Information Criterion), and statistically tested with a goodness-of-fit test. These data were used to estimate population sizes for the data analysis (see below). An $R \times C$ table, an exact test of contingency (Fung and Lee 1989), was used to test for differences in the relative abundance of three species between zones.

TABLE 1. Mean density (number of singing males ha^{-1}) of four Darwin's finch species in two vegetation zones on Santa Cruz Island during the wet season, 1997.

Species	Arid zone		*Scalesia* zone	
	Density	95% CI	Density	95% CI
Small Tree Finch	0.7	0.4–1.1	2.9	2.3–3.8
Woodpecker Finch	0.5	0.2–0.8	1.5	1.0–2.0
Large Tree Finch	0.2	0.0–0.3	0.8	0.6–1.3
Warbler Finch	0		13.5	11.4–16.0

Only the first foraging observation per day of each focal individual was included in the data set (Wagner 1981). Repeated observations of the same individual on different days could not be excluded. To minimize this possibility, observations were distributed over a wide area. Pooling data from different years may also result in an overestimation of degrees of freedom in statistical tests. However, in the *Scalesia* zone, the pooled data set containing first foraging observations did not exceed the total number of birds present in the study area (Tebbich 2000). In the arid zone, the number of first foraging observations exceeded the number of Woodpecker Finches present in the study area. To reduce the problem of overestimating sample size, observations were randomly selected to meet the estimated number of Woodpecker Finches present in the study area.

R × C tables were used to test for differences in feeding techniques, foraging substrates, and prey types used, between wet and dry seasons in each zone and the difference between zones in each season. To measure the amount of specialization, we calculated the Shannon diversity index from the proportions of used substrates, techniques, and food types and the associated variances according to Hutcheson (1970). Then we compared for each parameter (substrate, feeding technique and food) the four diversity indices (*Scalesia* and arid zones × wet and dry seasons) with one-way ANOVAS. We used the *post hoc* comparison of Tukey and Kramer to determine which comparisons were significant. For statistical analysis we used SPSS 7.5.1 for Windows (SPSS Inc. 1996). All tests were two tailed with an alpha level of 0.05.

RESULTS

DENSITY ESTIMATES

Densities of tree finches differed significantly between the arid and *Scalesia* zones (Table 1). Woodpecker Finches, Small Tree Finches, and Large Tree Finches occurred in much higher densities in the *Scalesia* zone than in the arid zone. This difference was significant at $P < 0.05$ since there was no overlap between the 95% confidence intervals. The Warbler Finch was not found in our study area in the arid zone. Relative numbers of the three other species did not differ significantly between arid and *Scalesia* zones ($P = 0.80$, $\chi^2_2 = 0.44$).

RESOURCE USE BETWEEN SEASONS AND VEGETATION ZONES

Small Tree Finch. Small Tree Finches changed substrate (Table 2), feeding technique (Table 3), and diet (Table 4), seasonally in the *Scalesia* zone. During the wet seasons, they gleaned arthropods from the surface of the bark and from leaves, but also bit and probed soft substrates such as moss and dead leaves still attached to the tree. A large part of their diet was vegetable matter (nectar, fruits, leaves, and seeds, comprising 42% of food). In the dry season foraging in dead leaves decreased but probing into moss and the proportion of fruits in their diet increased. In the arid zone they changed feeding techniques and their diet between seasons (Table 5). In the wet season they fed in approximately equal proportions on nectar of flowers, fruits, larvae and seeds. In the dry season feeding on flowers increased. Between zones, Small Tree Finches differed significantly in substrate use and in diet (Table 6).

Large Tree Finch. In the *Scalesia* zone, only feeding techniques differed significantly between seasons (Table 3). In both seasons, Large Tree Finches collected arthropods (adults and larvae) mainly by biting through the bark of twigs or petioles of leaves, but in the wet season they also probed into moss and dead leaves (Table 2). In the arid zone neither feeding substrate nor techniques differed significantly between seasons (Table 5),

TABLE 2. Relative frequency of feeding substrate use by four Darwin's finches on Santa Cruz Island, 1995–1998. Sample size is the number of foraging observations; only one observation was taken from any individual at any one time. *H* is the Shannon diversity index; higher values indicate a greater diversity of substrates was used.

Species Zone	Season	Frequency of use (%)										*H*	*n*
		Fruit	Moss	Leaf	Dead leaf	Bark	Twig	Seed	Bud	Tree hole	Air		
Small Tree Finch													
Scalesia	wet	4	11	13	48	12	0	6	7	0	0	1.58	175
	dry	11	25	15	22	13	0	7	7	0	0	1.83	75
arid	wet	15	11	26	11	15	0	11	11	0	0	1.89	27
	dry	0	13	31	4	13	0	13	26	0	0	1.65	23
Large Tree Finch													
Scalesia	wet	2	6	9	47	2	32	0	2	0	0	1.35	47
	dry	10	0	6	28	6	50	0	0	0	0	1.27	32
arid	wet	0	37	0	0	0	63	0	0	0	0	0.66	8
	dry	0	0	0	0	21	79	0	0	0	0	0.52	14
Woodpecker Finch													
Scalesia	wet	1	57	4	9	29	0	0	0	0	0	1.07	218
	dry	6	74	0	1	19	0	0	0	0	0	0.77	68
arid	wet	4	25	7	0	57	0	0	0	7	0	1.16	21
	dry	1	3	0	0	76	0	0	0	20	0	0.70	21
Warbler Finch													
Scalesia	wet	0	22	32	32	11	1	0	1	0	1	1.41	279
	dry	0	51	37	6	5	0	0	1	0	0	1.07	143

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TABLE 3. Relative use of foraging techniques used by four Darwin's finches on Santa Cruz Island, 1995–1998. Sample size is the number of foraging observations; only one observation was taken from any individual at any one time. *H* is the Shannon diversity index; higher values indicate a greater diversity of substrates was used.

		Frequency of use (%)										
Species	Season	Feed	Glean	Peck	Bite	Probe	Remove	Chip off	Tool use	Sally	*H*	*n*
Small Tree Finch												
Scalesia	wet	13	22	0	30	32	3	0	0	0	1.43	175
	dry	24	28	0	12	21	15	0	0	0	1.56	75
arid	wet	37	26	0	15	22	0	0	0	0	1.33	27
	dry	52	17	0	9	13	9	0	0	0	1.33	23
Large Tree Finch												
Scalesia	wet	2	13	0	60	17	9	0	0	0	1.16	47
	dry	9	6	0	66	0	19	0	0	0	0.99	32
arid	wet	0	12	0	37	13	38	0	0	0	1.26	8
	dry	0	14	0	57	0	29	0	0	0	0.96	14
Woodpecker Finch												
Scalesia	wet	1	4	10	6	48	12	16	3	0	1.58	218
	dry	6	0	15	0	54	21	3	1	0	1.27	68
arid	wet	5	10	23	0	29	5	23	5	0	1.70	21
	dry	0	0	48	0	5	0	18	29	0	1.17	21
Warbler Finch												
Scalesia	wet	1	72	0	1	23	2	0	0	1	0.79	279
	dry	1	59	0	0	38	2	0	0	0	0.80	143

TABLE 4. Relative use of eight food types by four Darwin's finches on Santa Cruz Island, 1995–1998. Sample size is the number of foraging observations; only one observation was taken from any individual at any one time. *H* is the Shannon diversity index; higher values indicate a greater diversity of substrates was used.

		Frequency of use (%)									
Species	Season	Nectar	Fruit	Insect	Larvae	Seed	Other	Caterpillar	Spider	*H*	*n*
Small Tree Finch											
Scalesia	wet	16	17	1	51	14	0	0	0	1.27	76
	dry	22	40	17	8	13	0	0	0	1.46	40
arid	wet	19	25	0	25	19	0	12	0	1.58	16
	dry	33	0	0	7	20	40	0	0	1.24	15
Large Tree Finch											
Scalesia	wet	0	9	0	55	0	0	36	0	0.92	11
	dry	0	25	0	75	0	0	0	0	0.56	12
arid	wet	0	0	33	67	0	0	0	0	0.64	6
	dry	0	0	29	71	0	0	0	0	0.60	7
Woodpecker Finch											
Scalesia	wet	9	0	26	43	0	0	17	5	1.38	42
	dry	13	38	15	30	0	0	2	2	1.44	47
arid	wet	0	14	28	43	0	0	10	5	1.37	21
	dry	0	0	48	38	0	0	5	9	1.09	21
Warbler Finch											
Scalesia	wet	6	0	7	83	2	0	2	0	0.67	47
	dry	0	6	56	38	0	0	0	0	0.86	16

TABLE 5. Comparison of resource use and diversity between seasons for four Darwin's finch species observed on Santa Cruz Island, 1995–1998. Frequencies of resource use were compared between wet and dry season in the *Scalesia* and arid zones using an R × C test; significant results indicate that the species used different proportions of substrates, techniques, or foods between seasons.[a] The differences between the Shannon diversity indices (*H*) in the wet and the dry season are given. Positive values represent a decrease of diversity in resource use from the wet to the dry season, negative values an increase. Boldface values indicate significantly different diversity index scores between wet and dry seasons, as determined from one-way ANOVAs with Tukey-Kramer *post hoc* tests.

Resource Species	Zone	Sample size (*n* observations)		Freq. of resource use (*P*)	Wet–dry season difference in *H*
		Wet season	Dry season		
Substrates					
Small Tree Finch	*Scalesia*	175	75	<0.001	**–0.25**
	arid	27	23	0.19	**0.25**
Large Tree Finch	*Scalesia*	47	32	0.16	0.08
	arid	8	14	1.00	0.14
Woodpecker Finch	*Scalesia*	218	68	<0.001	**0.30**
	arid	21	21	<0.001	**0.46**
Warbler Finch	*Scalesia*	279	143	0.009	**0.34**
Techniques					
Small Tree Finch	*Scalesia*	175	75	<0.001	**–0.13**
	arid	27	23	0.002	0.00
Large Tree Finch	*Scalesia*	47	32	0.007	0.18
	arid	8	14	0.67	0.30
Woodpecker Finch	*Scalesia*	218	68	0.002	**0.31**
	arid	21	21	0.01	**0.53**
Warbler Finch	*Scalesia*	279	143	0.01	–0.01
Food					
Small Tree Finch	*Scalesia*	76	40	<0.001	**–0.19**
	arid	16	15	0.004	**0.35**
Large Tree Finch[b]	*Scalesia*	11	12	0.09	**0.35**
	arid	6	7		
Woodpecker Finch	*Scalesia*	42	47	<0.001	–0.06
	arid	21	21	0.37	**0.28**
Warbler Finch	*Scalesia*	47	16	<0.001	–0.19

[a] Substrate, technique, and food use frequencies appear in Tables 2, 3, and 4, respectively.
[b] Food types were not compared for the Large Tree Finch in the arid zone because sample sizes were low.

although, sample sizes and therefore statistical power of these comparisons were low. Food types were not compared between seasons in the arid zone because the sample size was too small. Between zones, foraging substrates differed significantly in both seasons (Table 6). Whereas they used various feeding substrates in the Scalesia zone, they specialized almost entirely on bark of dead twigs in the arid zone.

Woodpecker Finch. In the *Scalesia* zone Woodpecker Finches changed substrate, technique, and food between seasons (Table 2–6). During the wet season, Woodpecker Finches searched for prey mainly by probing into moss and by pecking bark. During the dry season, they searched for arthropods mainly in moss. In the arid zone they specialized, like the Large Tree Finch, on bark, but more on the bark of branches and trunks than of twigs. Especially during the dry season, they made use of their large beak to peck off bark. By using twigs or cactus spines as tools to pry arthropods out of tree holes, they were able to exploit an additional substrate which was not used by any of the other species.

Warbler Finch. Warbler Finches were abundant in the *Scalesia* zone but we found none in the arid zone. They typically gleaned foliage, but also probed into moss (Table 2, 3). During the dry season, they increased the use of moss,

TABLE 6. Comparison of resource use and diversity between two vegetation zones for four Darwin's finch species observed on Santa Cruz Island, 1995–1998. Frequencies of substrates used, feeding techniques, and food types were compared between arid and *Scalesia* zones with an R × C test.[a] The differences between the Shannon diversity indices (*H*) in the *Scalesia* and arid zones are given. Positive values represent a decrease of diversity in resource use from the *Scalesia* to the arid zone, negative values an increase. Boldface values indicate significantly different diversity index scores between vegetation zones, as determined from one-way ANOVAs with Tukey-Kramer *post hoc* tests.

Resource Species	Season	Sample size (*n* observations)		Freq. of resource use (*P*)	*Scalesia*–arid zone difference in *H*
		Scalesia zone	Arid zone		
Substrates					
Small Tree Finch	wet	175	17	0.01	**–0.31**
	dry	75	23	0.001	**0.19**
Large Tree Finch	wet	47	8	0.006	**0.69**
	dry	32	14	0.002	**0.75**
Woodpecker Finch	wet	218	21	<0.001	**–0.09**
	dry	68	21	<0.001	**0.07**
Techniques					
Small Tree Finch	wet	175	17	0.15	**0.10**
	dry	75	23	0.21	**0.23**
Large Tree Finch	wet	47	8	1.00	**–0.09**
	dry	32	14	0.54	0.03
Woodpecker Finch	wet	218	21	<0.001	−0.12
	dry	68	21	<0.001	**0.10**
Food					
Small Tree Finch	wet	76	16	0.76	**–0.31**
	dry	40	15	<0.001	**0.23**
Large Tree Finch[b]	wet	11	6		
	dry	12	7		
Woodpecker Finch	wet	42	21	<0.001	0.01
	dry	47	21	0.049	0.35

[a] Substrate, technique, and food frequencies appear in Tables 2, 3, and 4, respectively.
[b] Food types were not compared for the Large Tree Finch because sample sizes were low.

as did the Small Tree Finch and the Woodpecker Finch. A shift in feeding techniques toward more probing accompanied this change.

All species altered at least some of their feeding substrates, foraging techniques, and prey items between wet and dry seasons in each zone (Table 5), and between arid and *Scalesia* zones in each season, respectively (Table 6). Among the three species that occurred in both zones the Woodpecker Finch was the most flexible. It showed significant differences in 10 out of 12 comparisons, followed by the Small Tree Finch (8 out of 12) and the Large Tree Finch (3 out of 10).

DIVERSITY OF RESOURCE USE

In all four species the diversity of resource use and feeding techniques differed significantly ($P < 0.05$ for all comparisons; except for feeding techniques in the Warbler Finch) between zones and seasons (Small Tree Finch, substrate: $F_{3, 296} = 260.9$, technique: $F_{3, 269} = 206.6$, food: $F_{3, 143} = 78.1$; Large Tree Finch, substrate: $F_{3,97} = 159.5$, technique: $F_{3,97} = 15.3$; Woodpecker Finch, substrate: $F_{3, 376} = 473.5$, technique: $F_{3, 376} = 147.8$, food: $F_{3,297} = 256.7$; Warbler Finch, substrate: $F_{1, 420} = 5079$, technique: $F_{1, 420} = 1.0$, $P = 0.3$, food: $F_{1,61} = 14.2$).

From wet to dry season, finches specialized (9 of 20 comparisons) or showed no significant change (8 of 20 comparisons; Table 5) but significantly increased in diversity only in three comparisons, in the measured parameters. Similarly, between zones, tree finches tended to specialize in the arid zone (eight out of 17 comparisons) or showed no significant change (eight of 17 comparisons, Table 6) but significantly di-

versified only in four comparisons. The diversity of feeding techniques increased only in the Woodpecker Finch in the arid zone.

DISCUSSION

As with the well-studied ground finches, the four species studied showed both morphological and behavioral adaptations to food limitation under dry conditions. But they did so to varying extents. Over the long term, there have been pronounced morphological adaptation of the beaks to different food types and to different feeding substrates. On the short time scale of variation in season and zone, the finches have reacted with behavioral flexibility. Small Tree Finches and Warbler Finches reacted to variation between seasons by using different feeding techniques. Large Tree Finches changed feeding techniques between seasons only in the *Scalesia* zone and the Woodpecker Finch only in the arid zone. Between zones all species differed in substrate use but only the Woodpecker Finch changed feeding technique and diet as well. As indicated by the significant changes between wet and dry conditions, the Woodpecker Finch seemed to be the most flexible and the Large Tree Finch the least flexible among the three species that occurred in both zones. However, sample sizes for the Large Tree Finch were small and therefore the latter result has to be interpreted with caution.

We believe that the lower density of all species in the arid zone was the result of food limitation. In the humid *Scalesia* zone insects are abundant in moss under the bark and on leaves, during both seasons. In the arid zone insect abundance is significantly lower even in the wet season (Tebbich et al. 2002). However, since the relative abundance of the four tree-finch species was similar, there is no indication that one species is better adapted to foraging in the arid zone than in the *Scalesia* zone. The Warbler Finch may be an exception; it was not present in our study site in the arid zone in either season. According to Lack (1945) the Warbler Finch inhabits only the humid zones of Santa Cruz Island, but Bowman (1961) noted that this species may occur in the arid zone in exceptionally wet years. With its small beak it is unable to penetrate bark. This may prove an insurmountable limit to food in the arid zone. However, a species closely related to the Warbler Finch, *Certhidea fusca,* and with a beak morphology very similar to that finch, lives in the arid zone on the outer islands of the Galápagos archipelago (Petren et al. 1999, Grant and Grant 2002). So it is not likely the morphology of the beak alone restricts the Warbler Finch to higher elevations or wetter climates.

Optimal foraging theory predicts a broadening of the niche under food limitation (Stephens and Krebs 1986, Gray 1987). With respect to substrate and diet, our finding contrasts with this expectation. When we found significant change in response to presumed food limitation in dry conditions, we mainly found specialization in resource use and feeding techniques. Such specialization is not unique to these finches: it has been shown that Darwin's ground finches can also respond to dry conditions with specialization (Schluter 1982). One possibility is that this specialization is a response to interspecific competition, where species specialize on resources they exploit most effectively (Svardson 1949, MacArthur et al. 1972). We found no evidence to support the hypothesis that specialization is a response to elevated levels of interspecific competition at times of food limitation, for we observed almost no aggressive interactions between the studied species in the feeding context. However, this hypothesis cannot be excluded completely, as present foraging patterns may be a result of competition in the past (Wiens 1989).

There are alternative hypotheses which would explain why animals do not generalize under food limitation. Behavioral limitation may prevent these finches from foraging optimally (Shimp 1969, Bitterman 1975, Schluter 1982). In addition, there are environmental conditions in which increasing the niche breadth is not optimal. One of these conditions is when search time between patches does not decline as search time within patches decreases (MacArthur and Pianka 1966). Rapaport (1971) suggested that the profitability of prey items should more strongly determine diet choice when food abundance decreases. Optimal foraging theory predicts niche broadening only if the absolute abundance of food decreases while the relative abundance of food types remains the same. In the light of these considerations, one probable and parsimonious explanation is that the lower diversity of resource use by these finches reflects a reduced availability in the range both of feeding substrates and of food. In the arid zone, arthropods are mainly under the bark and in tree

holes, especially in the dry season, and therefore they are hard to access. The three species reacted to this reduced accessibility of arthropods differently. One species relied more on the morphological adaptation of its beak; the other two species altered their behavior. With its small beak the Small Tree Finch was not effective in accessing food under bark; therefore it appeared to respond by feeding on plant food.

The Woodpecker Finch and the Large Tree Finch are both specialized to feed under bark, but differ in the diversity and flexibility of feeding techniques. While the Large Tree Finch relied on its powerful beak and used one technique (bite) almost exclusively in both zones, the Woodpecker Finch used a wide variety of techniques, and used different techniques in the two zones. In the closely related Cocos Finch (*Pinarolaxias inornata*) a high diversity of feeding techniques is the result of individual specialization (Werner and Sherry 1987). This was not the case in our study species. Analysis of continuous focal animal observations showed that individuals did not specialize in different feeding techniques (Tebbich 2000).

The morphological specialization of the Large Tree Finch went along with low behavioral versatility. The curved culmen is suitable neither for pecking (Bowman 1961) nor for probing deeply into substrate. The Woodpecker Finch used a behavioral adaptation, tool use, to temporarily extend the morphological properties of its beak without limiting behavioral versatility. It seemed to circumvent the trade-off between morphological specialization and behavioral flexibility. Using tools is costly, since obtaining prey with tools is more time consuming than using conventional feeding techniques (Tebbich et al. 2002). In contrast to morphological adaptation these costs are not permanent; the Woodpecker Finch needs only to pay them when necessary. Apart from tool use other extraordinary behaviors have evolved among Darwin's finches. The Sharp-beaked Ground Finch (*Geospiza difficilis*) pecks at the developing feathers of sea birds, draws blood, and drinks it (Bowman and Billeb 1965). They also crack eggs by pushing them against rocks with their feet (Grant 1986). Two other ground finches, the Small Ground Finch (*Geospiza fuliginosa*) and the Large Cactus Finch (*Geospiza conirostris*) use a similar technique to dislodge stones and look underneath them for food (DeBenedictis 1966). The role of these special feeding techniques in the foraging ecology of these ground finches still needs to be investigated.

In summary, along with long-term morphological adaptation the investigated Darwin's finches also show behavioral flexibility in response to short-term changes. Special feeding techniques such as tool use may be a way to solve the trade-off between morphological specialization and behavioral flexibility.

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