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ADAPTATION TO A NOVEL ENVIRONMENT: FOOD, FORAGING, AND MORPHOLOGY OF THE COCOS ISLAND FLYCATCHER

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ABSTRACT. Cocos Island, Costa Rica, is a small and lushly forested island in the tropical eastern Pacific Ocean between Costa Rica and the Galapagos Archipelago. During two expeditions there, I quantified the stomach contents, available food (i.e., foliage-inhabiting arthropods sampled with sweep nets), foraging behavior, and morphology of the endemic Cocos Island Flycatcher (*Nesotriccus ridgwayi*, Tyrannidae). *Nesotriccus* individuals captured a diversity of arthropods in proportion to their availability ($P \gg 0.1$), using diverse foraging tactics. Stages of the birds' annual cycles differed during the two expeditions, but diet and foraging behavior were remarkably consistent. Fulgoroid Homoptera dominated stomach contents (43–64% of prey individuals), and probably explain why *Nesotriccus* foraged regularly with acrobatic pursuits (11–12% of all feeding tactics) much like a mainland Homoptera specialist, *Terenotriccus erythrurus*. *Nesotriccus* is morphologically and behaviorally distinct from its primarily frugivorous mainland relatives, *Phaeomyias* and *Capsiempis*; its wings and tail are structurally convergent with those of *Terenotriccus*, but its bill is comparatively longer and probably evolved for the capture of non-homopteran insects.

Nesotriccus is a food specialist or generalist depending on one's frame of reference—available food, mainland insectivorous flycatchers, closest mainland relatives, or other resident land birds on the island. The diet and adaptations of *Nesotriccus*, in combination with other evidence, strongly support the hypothesis that insufficient abundance of many resource types precludes persistence in Cocos Island forests by virtually all but the endemic land birds. High endemism of the depauperate land bird fauna on the island appears to have resulted as much from this ecological impoverishment as from a lack of potential immigrants.

RESUMEN. La Isla del Coco es una isla costarricense pequeña y densamente arbolada en el océano Pacífico tropical, entre Costa Rica y el Archipiélago de las Galapagos. Durante dos expediciones a la isla cuantifique los contenidos estomacales, alimento disponible (es decir artrópodos habitantes de los follajes muestreados con redes a mano), comportamiento de forraje y morfología del atrapamoscas endémico (*Nesotriccus ridgwayi*, Tyrannidae) de la Isla del Coco. Individuos de *Nesotriccus* utilizan diversas tácticas de forraje para capturar una diversidad de artrópodos en proporción a disponibilidad ($P \gg 0.1$). Las etapas del ciclo anual de las aves fueron diferentes durante las dos expediciones, pero la dieta y el comportamiento de forraje fueron consistentes de manera remarcable. Los contenidos estomacales estuvieron dominados por Homoptera (Fulgoroidae, 43–64% de los individuos presa) y probablemente eso explique porque *Nesotriccus* forrajea regularmente con cazas acrobáticas (11–12% de todas las tácticas de alimentación) de manera muy similar a la especialista en Homoptera del continente *Terenotriccus erythrurus*. *Nesotriccus* es morfológicamente y por su comportamiento, distinto de sus parientes del continente, primariamente frugívoros, *Phaeomyias* y *Capsiempis*; sus alas y cola son de estructura convergente con aquellas de *Terenotriccus* pero su pico es comparativamente más largo y probablemente ha evolucionado para capturar insectos no-homopteros.

Nesotriccus se alimenta como un especialista o no-especialista, dependiendo del marco de referencia en el que se lo ubique—comida disponible, los atrapamoscas insectívoros del continente, parientes más cercanos del continente u otras aves terrestres residentes en la isla. La dieta y adaptaciones de *Nesotriccus*, en combinación con otra evidencia, apoya fuertemente la hipótesis de que las aves, con excepción de las terrestres endémicas, al no disponer de manera abundante de muchos tipos de recursos se les hace imposible la permanencia en bosques de la Isla del Coco. El alto endemismo de la paupérrima fauna de aves terrestres de la isla, parece haber resultado tanto por su empobrecimiento ecológico como por la falta de inmigrantes potenciales.

Small, remote oceanic islands tend to have few resident species of land birds, and these are often endemic and broad-niched (MacArthur 1972; Lack 1976; Williamson 1981). Island biologists do not currently agree whether the most important cause of this is reduced dispersal or a poverty of ecological resources on such islands (Lack 1976; Abbott 1980; Williamson 1981). The difficulty in resolving this controversy arises from the lack of knowledge of available resources and how island birds use them (Abbott 1980). Many biologists have discussed the morphological characteristics of birds in island populations (e.g., Lack 1947; Van Valen 1965; Grant 1968, 1981; Keast 1968; Grant et al. 1976), but again, a lack of information about available resources and their use has limited interpretation of the data (Abbott 1980). Clearly, the need to study resource availability, resource use, and adaptations of island birds is compelling.

High endemism and low species turnover characterize the land birds of Cocos Island, Costa Rica, and challenge contemporary beliefs about island biogeography (Slud 1976; Abbott 1980). Ecological studies of the biota of this island are virtually nonexistent, probably due in part to its isolation, small size, and humid climate. In this paper I examine the diet, available resources, foraging behavior, and morphology of the Cocos Island Flycatcher (*Nesotriccus ridgwayi*, Tyrannidae), an endemic genus. Specifically, I address six questions: (1) How does *Nesotriccus* feed? (2) What is the nature of the food resource exploited relative to resources available? (3) How seasonal are the behavior and diet of *Nesotriccus*? (4) How has *Nesotriccus* become adapted morphologically to exploit available resources? (5) Is *Nesotriccus* a generalist or specialist? (6) Why is the land bird fauna of Cocos Island depauperate and largely endemic?

The Cocos Island Flycatcher is the second most abundant of four resident land bird species (Slud 1967; Sherry and T. K. Werner, unpubl. data). A study of *Nesotriccus* is timely because of new information concerning its phylogeny (Lanyon 1984; Sherry, in press), a conspicuous gap in recent discussions of tyrannid genera (Traylor 1977; Fitzpatrick 1980; Traylor and Fitzpatrick 1982), recent ecological studies of mainland tyrannids (Fitzpatrick 1980; Traylor and Fitzpatrick 1982; Sherry 1982, 1983, 1984), and recent studies of how other land birds on Cocos Island exploit available resources (Smith and Sweatman 1976; Werner and Sherry, unpubl. data).

STUDY SITE

Cocos Island, Costa Rica, lies in the tropical eastern Pacific Ocean (5°32′57″N, 86°59′17″W), approximately 630 km northeast of the Galapagos Archipelago and 500 km southwest of Costa Rica. The island is approximately 46.6 km² in area and rises from abrupt cliffs (with heights up to 180 m) around most of its perimeter to a maximum elevation of 573 m on Cerro Iglesias (Hertlein 1963; F. Cortés, pers. comm.). Geologically, Cocos Island, like the Galapagos Islands, arose volcanically during the Pliocene period and probably was never connected with the mainland by a land bridge (Dalrymple and Cox 1968). Typically, the eastward-flowing, equatorial counter-current includes the latitude of Cocos Island, and the warm waters of this current help create a humid climate (up to 8 m of rain annually, C. Hogue, pers. comm.), with the least rainfall between January and March. Air temperatures range between 20°C and 33°C (Hertlein 1963).

Cocos Island is densely forested throughout. It is floristically impoverished with only 155 vascular and 48 nonvascular plant species (Fournier 1966). Life forms are diverse and include epiphytes, palms, ferns, understory shrubs, lianas, vines, and trees. Most behavioral observations were made in three locations with differing vegetation: (1) *Hibiscus tiliaceus* and melastome thickets, ca. 8–10 m high, near the Bahia Wafer beach; (2) interior forest dominated by *Saccoglottis* trees, ca. 20–25 m tall, with an understory including melastomes and rubiaceous shrubs, and with generally little ground cover due to the activity of feral pigs; (3) Mirador cloud forest, ca. 460 m elevation, comprised of an epiphyte-laden canopy dominated by *Saccoglottis* (less than 20 m tall), an understory of tree ferns and occasional *Rooseveltia* palms, and dense ground cover of Piperaceae spp., with occasional ferns.

The island is also faunistically impoverished. At present, 363 arthropod species (Hogue and Miller 1981), two lizards, and 82 bird species (Slud 1967; T. W. Sherry, F. G. Stiles, and T. K. Werner, unpubl. data), but no snakes, lizards, amphibians, or native mammals are known to occur there. Deer, pigs, cats, and rats have established populations (Hogue and Miller 1981), and pigs occur virtually throughout the island (Sherry, unpubl. data). There are only four resident land bird species, of which three are endemic. Cocos Island has never had a permanent settlement and was declared a Costa Rican national park in 1978 (Hogue and Miller 1981).

METHODS

Most observations were made during two brief expeditions to Cocos Island (30 June–6 July, 1978, and 24 February–24 March, 1980); a few observations made during February to April 1984 are also reported. It rained every day during the 1978 expedition, as is typical for that season (Hertlein 1963), and the birds collected were all in a late stage of molt. It was drier during the 1980 expedition with rain about every third day; the birds were either in a late stage of the reproductive cycle, or beginning to molt (Sherry, in press).

DIET AND AVAILABLE FOOD

To facilitate dietary comparisons between *Nesotriccus* and mainland insectivorous flycatchers, the methods used to collect and analyze stomach samples were standardized (see Sherry 1984, for details). I collected actively foraging birds (five males, four females, and two of unknown sex in 1978; four males, 10 females, and one post-fledging male in 1980), mostly before noon, to ensure full stomachs. Birds were collected in *Hibiscus* thickets and interior forest (three widely separated locations) in 1978, and in all habitats but mostly interior forest and cloud forest in 1980. Stomachs were dissected from a bird immediately upon collection and stored in 90% ethanol. All recognizable food remains (arthropods and seeds) were later removed from the contents such that the minimum number of individuals or fruits present could be estimated. For arthropods I reconstructed individuals from body parts so as not to overcount individuals (Sherry 1984). Arthropods were identified to order or family, and species were often identifiable due to the low insect diversity on the island. A reference collection in the Natural History Museum of Los Angeles County (Hogue and Miller 1981) facilitated these identifications.

Because *Nesotriccus* fed extensively on foliage-inhabiting arthropods in 1978 (see below), available arthropods were sampled in 1980 by vigorously beating understory vegetation in 100-sweep units with a 38 cm-diameter beating net (Janzen 1973). Sweeping was conducted during the late morning to correspond as closely as possible with times that birds were collected. Arthropods were killed with cyanide, sorted from plant debris, then identified. Because *Nesotriccus* individuals rarely if ever eat arthropods less than 0.5 mm long (Sherry, unpubl. data), I made no effort to sort smaller arthropods from the debris (see Hespenheide 1979).

I used curves of dietary diversity plotted against sample size (number of stomachs) to determine adequacy of sample size and to estimate dietary diversity of the *Nesotriccus* population in a particular season (Hurtubia 1973; Pielou 1975; Sherry 1984). Although the Shannon-Wiener diversity index (H') is appropriate and frequently used to estimate collection diversity from a sample, the Brillouin diversity measure,

$$H = (1/N)\log_e(N!/(n_{1!} \cdot n_{2!} \ldots n_{t!})),$$

where n_i = number of prey in taxon "i" and $N = \sum_i n_i$, is appropriate for the present application.

Specifically, one uses the Brillouin index to estimate diversity from collections (stomachs, in this case) that are not necessarily random samples of the larger collection (Pielou 1975). The diversity of prey contents in stomach 1 is plotted, then the diversity in stomachs 1 and 2, then in stomachs 1 to 3, and so forth; the curve reaches a plateau if additional stomachs contribute no new information concerning the diversity of the pooled stomach contents.

To quantify the heterogeneity of prey taxa in different stomachs (= population dietary heterogeneity, PDH), I calculated G/d.f., where G = the G-statistic for independence (Sokal and Rohlf 1969), and d.f. = degrees of freedom for the particular number of taxa and stomachs examined (see Sherry 1984). To avoid taking logarithms of zero cells I arbitrarily added 0.1 to each frequency value. To compare prey taxa eaten by different species or by one species in two seasons, I calculated Euclidian distances for all pairwise combinations of species or samples taken in different seasons. For this analysis I used $\log_e$ of (1 + % composition) of stomach contents, based on 15 prey taxa (defined by Sherry 1984), and I clustered species (or seasonal samples within species) with a complete-linkage algorithm (Johnson 1967; Holmes et al. 1979). To emphasize frequently eaten taxa I did not standardize prey taxa (to mean = 0, s.d. = 1) across bird species. Comparisons of prey taxa in stomachs with those available were made with the G-statistic (Sokal and Rohlf 1969), using original frequencies.

Original prey taxa eaten by mainland flycatchers clustered into eight statistically significant, biologically meaningful groups (Sherry 1984). *Nesotriccus* stomachs contained six of these: ants, Coleoptera plus Hemiptera, Homoptera plus Arachnida, Orthoptera plus Lepi-

TABLE 1

PERCENT COMPOSITION OF ARTHROPOD REMAINS, AND NUMBER OF FRUIT SEEDS IN STOMACHS
OF *NESOTRICCUS RIDGWAYI*[1]

Arthropod taxon	1978	1980		
		Total	Mirador cloud forest	Forest interior
Orthoptera	12.4 (10)[2]	6.4 (10)	4.5 (2)	6.7 (8)
Heteroptera	—	2.0 (5)	6.7 (2)	1.2 (3)
Homoptera	43.5 (11)	62.3 (15)	51.1 (3)	64.3 (12)
Coleoptera	15.3 (9)	3.7 (5)	—	4.4 (5)
Lepidoptera				
Larvae	1.8 (2)	2.0 (6)	2.2 (1)	2.0 (5)
Adults	1.2 (1)	0.3 (1)	—	0.4 (1)
Diptera	4.1 (5)	5.1 (6)	13.3 (2)	3.6 (4)
Hymenoptera				
Formicidae	13.5 (7)	7.1 (10)	11.1 (3)	6.3 (7)
Other	2.9 (3)	5.7 (7)	2.2 (1)	6.3 (6)
Arachnida	5.3 (5)	5.4 (10)	8.9 (3)	4.8 (7)
Total no. fruit seeds	4 (1)[2]	150 (10)	10 (3)	140 (7)
Total no. arthropods	170	297	45	252
Total no. stomachs	11	15	3	12

[1] From birds collected in 1978 and 1980 on Cocos Island, Costa Rica.
[2] Number of stomachs in which taxon was found given in parentheses.

doptera larvae, parasitoid Hymenoptera plus Diptera, and adult Lepidoptera. I used these groups to calculate cumulative prey-taxon diversity and PDH, primarily for comparisons with mainland flycatchers. I further pooled adult Lepidoptera (the three such specimens were moths) with "parasitoid Hymenoptera plus Diptera" to avoid zero cell frequencies with G-tests.

FORAGING BEHAVIOR AND MORPHOLOGY

I observed *Nesotriccus* forage in *Hibiscus* thickets and interior forest in 1978 and in all three habitats in 1980. Most observations were made before noon both years, but some were made at other times through the day. I recognized six tactic types (Sherry 1982), hawk, snatch, hover, pounce, glean, and pursue. Cocos Island Flycatchers often pursued evasive prey acrobatically after initiating an attack with another tactic. I treated such cases as two behaviors (one of which was "pursue") when tallying tactic types used. I calculated the diversity of foraging tactics used with the Shannon-Wiener information-theory statistic ($H' = -\sum_{i=1}^{6}$ $P_i \log_e P_i$, where p_i = relative frequency of tactic type "i"), and the number of "equally common tactic types" as $e^{H'}$ (MacArthur 1972). To test whether tactics used were identical in 1978 and 1980, I used the G-statistic with original frequencies (Sokal and Rohlf 1969). In addition, I quantified attack distances (cm) and time intervals (sec) between successive attacks (Interattack-intervals, IAIs) to compare species with respect to food accessibility and feeding rate. Distributions of both attack distances (ADs) and IAIs were approximately normalized by a logarithmic transformation (Sherry 1982), and I used the geometric mean (approximately equal to the median) as the statistic to compare such distributions.

RESULTS

DIET

Homoptera dominated the arthropod remains in stomachs of *Nesotriccus ridgwayi*, comprising on average between 43 percent and 64 percent of prey individuals (Table 1). Homoptera was the one taxon found in every stomach examined. Fulgoroidea dominated the Homoptera (95%) and included Nogodinidae (at least two species), Cixiidae (at least one species), Flatidae (at least one species) and Tropiduchidae (one species). The remaining Homoptera were Cercopoidea (mostly one species of Cicadellidae). These same families and species of Homoptera were observed in both the 1978 and 1980 samples of stomachs. After Homoptera, Orthoptera (largely one species of Gryllidae) and Hymenoptera (Formicidae—at least several species)
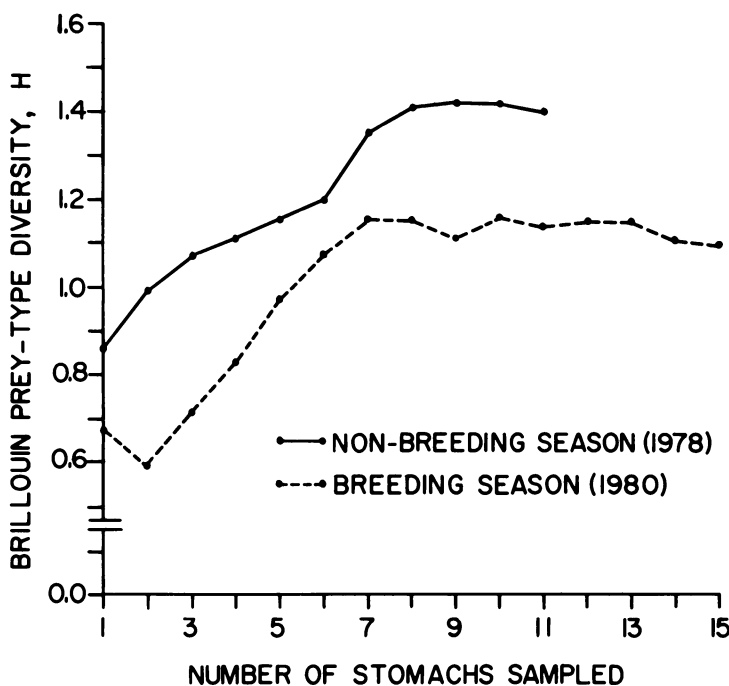
Fig. 1.   Curves of cumulative dietary diversity plotted against sample size (number of stomachs) for breeding-season (1980) and non-breeding-season (1978) samples of *Nesotriccus*.

were about equally important, taking into consideration percentages and frequency of occurrence; Arachnida (spiders) and Coleoptera (largely a zygopine curculionid and a species of Cerambycidae) were next in overall importance (Table 1; Sherry, unpubl. data). Fruit, represented by seeds, was moderately important in the 1980 sample of stomachs and present in only one stomach from the 1978 sample (Table 1). The large numbers of seeds in the 1980 forest-interior sample resulted from one stomach with 122 seeds, probably because far fewer many-seeded fruits were eaten. I never observed *Nesotriccus* eat fruit, but one individual netted near Bahia Wafer in February 1984 regurgitated one *Clusia rosea* seed. Fruit was a minor part of the contents of most, if not all, the stomachs examined.

Individual stomachs of *Nesotriccus* tended to contain just a sample of the arthropod types eaten by a particular population (Fig. 1), but a plateau in the curve of cumulative diet diversity against sample size was evident with both 1978 and 1980 data in samples of eight stomachs or more. The 1978 plateau indicates slightly greater diet breadth than the 1980 sample. Both plateau values of population diet diversity, 1.1 and 1.4 (Fig. 1), are well within the range (0 to >1.5) for mainland insectivorous flycatchers (Sherry 1984). Population dietary heterogeneity (PDH), which quantifies for a collection of stomachs how independent each stomach is from every other with respect to prey taxa, was slightly higher in the more diverse 1978 collection of stomachs (1.68) than the 1980 collection (1.56). Both values, however, fall within the range for mainland flycatchers and would place *Nesotriccus* in the second highest quartile of values observed in 16 mainland species (Sherry 1984). Canopy-inhabiting mainland tyrannids had PDHs most comparable to *Nesotriccus*, which is primarily a canopy forager (Sherry, unpubl. data). I conclude that *Nesotriccus* had a diet neither more nor less diverse (but see below) and neither more nor less heterogeneous than average mainland flycatchers that also feed primarily on arthropods.

I tested the null hypothesis that *Nesotriccus* ate the same arthropod taxa in the wet (1978) as in the dry (1980) season, as indicated by the stomach contents, and rejected this hypothesis (Table 1; $G = 28.0$, 5 d.f., $P < 0.001$). The 1980 collection of stomachs contained relatively more Homoptera, and fewer Orthoptera, Coleoptera, and Formicidae than did the 1978 collection (Table 1).
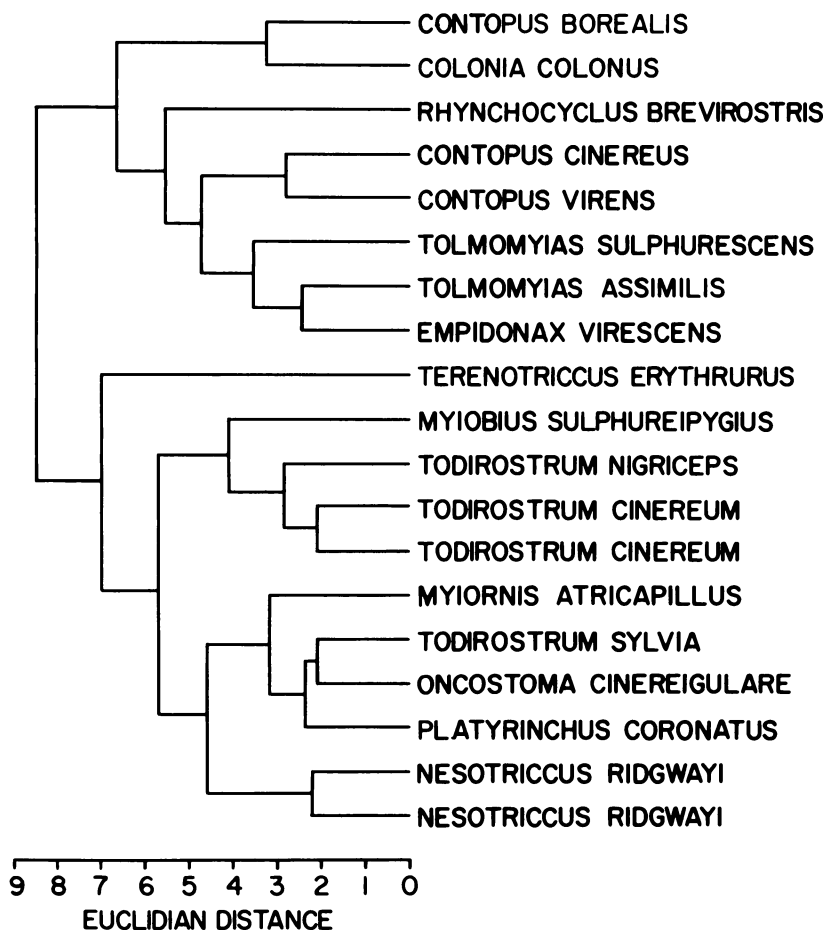
FIG. 2.   Clustering of tyrannid species based on the pooled arthropod taxa in stomachs. For *Nesotriccus ridgwayi* and *Todirostrum cinereum* both non-breeding and breeding-season samples of stomach contents were available; for all other species just non-breeding samples were available (Sherry 1984).

Dietarily, *Nesotriccus* clustered with a group of small-bodied "euscarthmine" flycatchers on the mainland (Fig. 2; Sherry 1982). Even though the 1978 and 1980 collections of *Nesotriccus* prey were significantly different, they clustered together when compared with mainland flycatchers (Fig. 2). This dendrogram (Fig. 2) contains one other species (*Todirostrum cinereum*) for which breeding and non-breeding season collections of stomachs were available, and again the taxa were not different enough to obscure a predator-specific identity with respect to arthropod taxa in stomachs. This result did not depend on the clustering algorithm used since primary clusters based on similarity matrices invariably combine samples that are each other's nearest neighbor, as were the *Todirostrum* and *Nesotriccus* collections from different seasons.

The final dietary character examined was the number of items per stomach. In 1978, the mean ($\pm$ 1 s.d.) was 15.45 ± 4.78 items per stomach (N = 11 stomachs), whereas in 1980 it was 19.8 ± 7.29 items (N = 15 stomachs). This difference was not statistically significant ($t = 1.72$, 24 d.f., $P > 0.05$).

PREY SELECTION

To understand prey selection, it is important to know what resources are available (e.g., Smith 1982). A total of 403 arthropods were collected with 200 sweeps of a beating net at

TABLE 2
PERCENT COMPOSITION BY TAXON OF UNDERSTORY, LEAF-INHABITING ARTHROPODS IN TWO HABITATS ON COCOS ISLAND[1]

Arthropod taxon	Mirador cloud forest	Interior forest	Interior forest
Orthoptera	3.2	1.1	2.4
Heteroptera	1.2	0.9	2.0
Homoptera	52.6	6.4	14.1
Coleoptera	3.0	1.1	2.4
Lepidoptera			
Larvae	0.3	0.2	0.5
Adults	3.0	0.9	2.0
Diptera	17.9	18.5	40.9
Hymenoptera			
Formicidae	7.9	64.9	22.5[2]
Other	3.2	1.1	2.4
Arachnida	7.7	4.9	10.8
Total no. arthropods	403	1001	453
Total no. sweeps	200	400	(400)

[1] Data from March 1980.
[2] Ants <2 mm long excluded from the analysis.

the Mirador, and 1001 arthropods were collected with 400 sweeps in interior forest (Table 2). I excluded mites (all of which were less than 1 mm) from all analyses because they were never eaten by *Nesotriccus* (Table 1). Clearly, Homoptera dominated the Mirador sweeps, whereas ants and Diptera dominated forest-interior sweeps (Table 2). This difference was consistent, moreover, within local sets of 100-sweeps. Homoptera dominated both sets of 100 sweeps in Mirador cloud forest whereas ants and Diptera were the two most important taxa in all four 100-sweep samples of forest interior. I therefore examined the relationship between diets and available prey separately for Mirador and forest-interior samples.

Three *Nesotriccus* were collected in 1980 at the Mirador in the vicinity where arthropods were sweep-sampled. I could not reject the null hypothesis that these Mirador flycatchers ate arthropods (Table 1) in proportion to their availability as quantified by the two-hundred sweeps (Table 2; $G = 3.25$, 4 d.f., $P \gg 0.1$). I executed the test again with different groupings of prey, and in no case could I approach rejection of the null hypothesis.

Twelve flycatchers were collected in forest-interior habitat, four of these along Rio Genio in the vicinity of the forest-interior sweep-sample locations and eight in very similar forest in the island interior along ridges above Bahia Chatham. These flycatcher stomachs contained different arthropods (Table 1) from the sweep samples (Table 2; $G = 467.36$, 4 d.f., $P \ll 0.01$). A large number of small ants (<2 mm) in the forest-interior sweeps (Table 2), most of which were in one 100-sweep sample, provided the most obvious explanation for the discrepancy. I excluded ants less than 2 mm long from the forest-interior sweep sample and still observed a significant difference between arthropod taxa in stomachs (Table 1) and those "available" (Table 2, $G = 185.97$, 4 d.f., $P \ll 0.01$).

Two hypotheses may explain why prey taxa were selected in proportion to those available on the Mirador but not in the forest interior. First, flycatcher behavior (selectivity) may not be the same in the two habitats, or second, the sweeps of vegetation may not have sampled what was available to the birds in the forest-interior habitat. Two lines of evidence suggesting that behavior did not differ are (a) that the birds were at a comparable stage of breeding (pers. observ.), thus equalizing demand for food throughout the island, and more importantly, (b) that prey in Mirador and forest-interior stomachs were statistically indistinguishable in size (Sherry, unpubl. data) as well as proportions of taxa represented (Table 1; $G = 2.69$, 4 d.f., $P \gg 0.1$). Because *Nesotriccus* concentrates its foraging in the canopy, and only occasionally pursues an arthropod to the ground (pers. observ.), it forages farther from where I sampled available arthropods in the taller, forest-interior habitat, than in Mirador cloud forest habitat. I tentatively conclude that the Mirador sweeps were more representative of the arthropods

TABLE 3

PERCENT COMPOSITION OF FORAGING TACTICS USED BY *NESOTRICCUS*[1]

| | Foraging tactic | | | | | | | |
Year	Hawk	Snatch	Hover	Pounce	Glean	Pursue	(N)[2]	H'[3]
1978	15.5	43.1	6.5	8.1	15.5	11.3	123	1.57
1980	20.7	40.0	5.9	11.9	9.6	11.9	135	1.59

[1] Data taken in 1978 and 1980, on Cocos Island, Costa Rica.
[2] N = Sample size.
[3] H' = Shannon-Wiener diversity index (see text).

available to *Nesotriccus* within canopy throughout the island, and that *Nesotriccus* ate arthropods in proportions remarkably similar to those in which they were available.

FORAGING BEHAVIOR

I could not reject the null hypothesis that frequencies of foraging tactics were identical in 1978 and 1980 (G = 9.04, 5 d.f., P > 0.1). Cocos Island Flycatchers used more snatches to capture prey than any other foraging tactic (Table 3). Most of these were "upward-strikes" rather than "downward-strikes" (for definitions, see Fitzpatrick 1980), 43 versus 11. *Nesotriccus* also employed a variety of other foraging tactics frequently (Table 3) in contrast to many mainland genera of tyrannids that are stereotyped upward-strikers (Fitzpatrick 1980; Sherry 1982). The information-theory indices of diversity (H') were 1.57 and 1.59 for the 1978 and 1980 samples of foraging tactics, respectively (Table 3). These values are 88–89 percent of the maximum possible value (H'$_{max}$ = log$_e$6 = 1.79, for six foraging categories). Mainland insectivorous flycatchers, categorized for the same foraging tactics, gave an approximately normal distribution of H' values ($\bar{X}$ = 0.70, s^2 = 0.124, n = 16 species; Fig. 3). The null hypothesis that *Nesotriccus* foraging tactics were not more diverse than those of ecologically similar mainland species was rejected (t = 2.4, 15 d.f., P < 0.025, one-tailed). This was a conservative result insofar as the mainland diversity values were inflated because I arbitrarily added 0.001 to each frequency value. The number of "equally-common foraging tactics" for *Nesotriccus* was $e^{1.57}$ = 4.81 compared with $e^{0.7}$ = 2.01 for an average mainland flycatcher. I conclude that *Nesotriccus* as a population used a more diverse array of foraging tactics (by a factor of greater than two) than mainland insectivorous flycatchers, and this resulted from both the equitability and total number of tactics used by *Nesotriccus*.

I compared inter-attack-intervals (in seconds) in the two seasons. Mean natural logarithm of IAIs ± 1 s.d. were 2.46 ± 0.915 (N = 56) and 2.37 ± 0.7798 (N = 73) in 1978 and 1980, respectively (t = 0.59, P ≫ 0.1). I also compared attack distances (originally in cm). Mean natural logarithm of ADs ± 1 s.d. were 3.89 ± 0.789 (N = 83) and 3.69 ± 0.729 (N = 82), respectively (t = 1.69, P > 0.05). I conclude that foraging behavior of non-breeding *Nesotriccus* in 1978 was statistically indistinguishable from that of the late-breeding-stage population in 1980 in all respects measured.

DISCUSSION

DIET OF *NESOTRICCUS*

The most conspicuous characteristic of *Nesotriccus* stomach contents is the numerical dominance and consistent representation of Homoptera (Table 1). The high relative abundance of Homoptera where *Nesotriccus* feeds provides the simplest explanation. I cannot reject this hypothesis for the 1980 observations of stomach contents and available arthropods in Mirador cloud forest, and additional data suggest that this hypothesis may have applied in other habitats as well. A relative abundance of Homoptera throughout the island, if a general phenomenon, is consistent with the "disharmoniousness" of the Cocos Island entomofauna (Hogue and Miller 1981) and that of many islands (Williamson 1981). For example, grasshoppers, mantids, treehoppers, many beetle and fly families, most butterfly families, and bees have never been recorded on Cocos Island (Hogue and Miller 1981). A disproportionate representation of Homoptera was also observed on several Caribbean islands (Janzen 1973), although the explanation for this phenomenon, if a general one, remains obscure.

The breadth of prey types eaten is another characteristic of *Nesotriccus* stomach contents. Although the diversity of prey taxa (Fig. 1) was no more or less than that of mainland
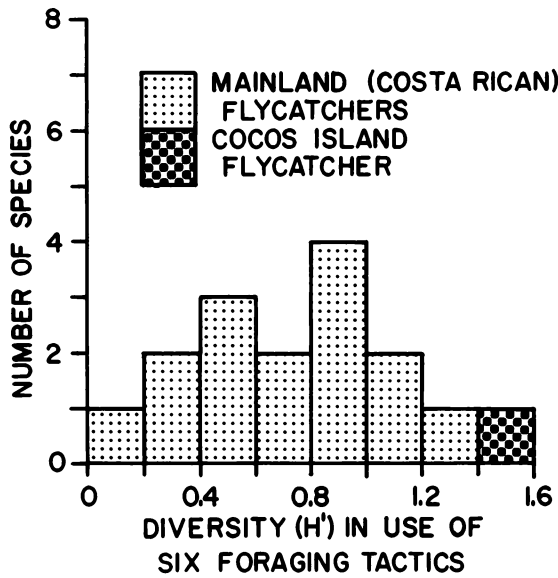
FIG. 3. Frequency distribution of diversity values (H') for the use 17 flycatcher species (*N. ridgewayi* and 16 species from mainland Costa Rica, Sherry 1982) made of six possible foraging tactics.

insectivorous flycatchers, the range of prey *types,* from the perspective of the skills required to detect or catch or handle prey, was greater for *Nesotriccus.* This assertion follows from two kinds of evidence. First, the prey taxa of *Nesotriccus* (Table 1) broadly spanned those of at least four mainland guilds (Sherry 1982): Homoptera plus Arachnida eaten by pursuing species of flycatcher, Orthoptera plus Lepidoptera larvae eaten by searching species, Coleoptera plus Hemiptera plus Formicidae eaten by several canopy or open-country species, and Diptera plus parasitoid Hymenoptera eaten by *Todirostrum* flycatchers. On the mainland, different flycatchers tended to eat one group of arthropod taxa to the exclusion of others depending on where and how the bird hunted, detected, or captured prey (Sherry 1984). Secondly, the diversity of foraging tactics *Nesotriccus* used was significantly greater than that of mainland species (Fig. 3). Furthermore, a factor-analysis of eight behavioral and nine morphological characters of insectivorous Neotropical flycatchers (including *Nesotriccus*) demonstrated that the latter broadly overlaps at least two mainland guilds insofar as it had close to the extreme scores on two multivariate axes ("pursuer" and "pouncer-gleaner," Sherry 1982).

SEASONAL VARIATION IN DIET AND BEHAVIOR

Although arthropod abundance was not quantified in 1978, I noted (field record, 1 July), "how *very few* insects I saw on the vegetation compared with what I would have seen in the lowland rainforest in Costa Rica proper." In 1980, by contrast, arthropods were abundant and easily captured especially in non-forested habitat. Considerations of foraging optimality (reviewed by Pyke et al. 1977) predict that *Nesotriccus* should have been relatively selective when food was abundant in 1980. The 1980 stomach samples indeed contained significantly different arthropod taxa from the 1978 samples and were more dominated by Homoptera. Correspondingly, the cumulative population diversity (Fig. 1) and PDH were lower in 1980 than 1978. Number of items per stomach was greater in 1980, and IAIs and ADs were both shorter (although none of these differences was significant), suggesting higher feeding rates on more accessible food. Availability of fruit (Table 1) may have contributed to overall food abundance. At present, however, I cannot exclude the alternative hypothesis that Homoptera were disproportionately abundant in 1980, compared with 1978, and eaten in proportion to their abundance.

Similarities of stomach contents and foraging behaviors in 1978 and 1980 were more striking than differences. This was so even though rainfall regimes on the island and stage of the *Nesotriccus* annual cycle differed considerably. The two sets of stomach contents were more similar to each other than either was to that of any other tropical flycatcher for which I had

data (Fig. 2). The same observation applies to the stomachs of *Todirostrum cinereum*. Clearly, diets of these tropical flycatchers change seasonally, but not enough to obscure a species-specific dietary identity. Several ecologists have suggested that vertebrates are opportunistic, that available food fluctuates dramatically and unpredictably, and that species-specific segregation of diets with respect to prey types is minimal (Wiens 1977; Wiens and Rotenberry 1979; Bell 1980; Fenton and Thomas 1980; Rotenberry 1980; Fenton 1982; Rosenberg et al. 1982). This view does not apply to *Nesotriccus* and the insectivorous tropical flycatchers inhabiting the humid Caribbean lowlands of Costa Rica (Sherry 1984). These flycatchers illustrate considerable dietary specialization and/or homogeneity, and appropriate morphological adaptations (Sherry 1982), perhaps because resources in such environments do not fluctuate as dramatically as in seasonal tropical and higher-latitude environments. I infer that Homoptera and other diverse arthropod types (and correspondingly broad foraging tactics) are fundamental to *Nesotriccus* ecology. Subsequent discussion of morphological adaptation, specialization, and island colonization is based on this premise.

ADAPTATIONS OF *NESOTRICCUS*

The consistently broad range of prey types eaten by *Nesotriccus* prompts the question of the configuration of morphological characteristics "optimal" for a species performing in one environment the ecological role of many species, each adapted and specialized for a different role, in another environment. Specifically, if pursuing flycatchers have a different morphology from aerial-hawking species on the mainland (Sherry 1982), what can we predict about *Nesotriccus* which both pursues and aerially hawks? Fitzpatrick (1978) suggested that generalist flycatchers tend to have intermediate morphological characters.

Nesotriccus appears, instead, to have evolved in such a way that different morphological complexes (e.g., wings vs bill) are each appropriate to a different behavior or component of the diet and, thus, less well adapted to other components. Wing aspect-ratio (pointedness), and "effective" wing and tail area (i.e., effect of body mass removed statistically) of *Nesotriccus* are appropriate for acrobatic flight and are virtually indistinguishable from those of *Terenotriccus erythrurus*, a mainland Central and South American tyrannid (Sherry 1982, 1983). Both species pursue evasive prey acrobatically within vegetation, and *Terenotriccus* is a specialist on fulgoroid Homoptera (Sherry 1984). *Nesotriccus*, however, has a relatively long bill quite unlike that of *Terenotriccus*, and its "effective" bill size (length, width, and depth) is most similar to mainland euscarthmine flycatchers (Sherry 1982). The diet and foraging behavior of *Nesotriccus* broadly overlap those of euscarthmine species (Table 1; Sherry 1982, 1984), and I suggest that the bill of *Nesotriccus* has become adapted accordingly. Elongation of the bill of *Nesotriccus*, relative to its closest living relatives (see below), supports the above hypothesis, but wing and tail data are not presently available for similar comparisons.

Palate and syrinx morphology, nest and egg characteristics, song, and plumage strongly suggest that *Capsiempis flaveola* and especially *Phaeomyias murina* are the closest relatives of *Nesotriccus* (Lanyon 1984; Sherry, in press) and probably much like its ancestor. Both *Phaeomyias* and *Capsiempis* belong to a group of elaeniine Tyrannidae that are generalized frugivores/insectivores that mostly upward hover-glean (*Phaeomyias*) or perch-glean (*Capsiempis*, Fitzpatrick 1980). *Phaeomyias* relies heavily on mistletoe (Loranthaceae) fruits in canopy vegetation throughout much of the year (Fitzpatrick 1980, pers. comm.). If the *Nesotriccus* ancestor was at all like *Phaeomyias* or *Capsiempis*, then *Nesotriccus* has changed considerably since reaching the island. The ancestor would necessarily have switched from frugivory to insectivory and added several foraging tactics (aerial hawk, pounce, and acrobatic pursuit) to its repertoire. Morphologically, *Phaeomyias* and *Capsiempis* have short bills like other frugivorous Tyrannidae (Fitzpatrick 1978, pers. comm.; Traylor and Fitzpatrick 1982). The bill length of *Nesotriccus* is more than twice that of *Phaeomyias* (exposed culmen = 13.8 and 6.2 mm, respectively), and should be effective in catching active and agile arthropods such as Diptera (Sherry 1982) or Orthoptera (Greenberg 1981), but longer bills may also be effective for larger prey (Grant 1968; Hespenheide 1973, 1975). *Nesotriccus*, thus, has many morphological and behavioral characteristics expected for its diet, and this flycatcher has presumably changed considerably in these respects from its putative ancestor.

IS *NESOTRICCUS* A GENERALIST OR SPECIALIST?

One may make ecological inferences about *Nesotriccus* from its diet and feeding behavior, and evolutionary inferences from its ancestry and from heritable traits such as morphology. *Nesotriccus* is an ecological generalist compared with mainland insectivorous flycatchers in

TABLE 4

CLOSEST RELATIVE, HABITAT AND ABUNDANCE, AND DIET OF THE FOUR RESIDENT LAND BIRD
SPECIES OF COCOS ISLAND, COSTA RICA

Species	Closest relative	Habitat and abundance[1]	Diet[2]
Dendroica petechia aureola	D. petechia aureola[3]	Edge vegetation near beach, common	Small insects
Coccyzus ferrugineus	C. minor	Edge vegetation near beach, regular; rarer inland	Large arthropods (and small lizards?)
Nesotriccus ridgwayi	Phaeomyias (or Capsiempis)	All habitats, common	Diverse small Arthropods, some fruit
Pinaroloxias inornata	Geospizinae	All habitats, common–abundant	Arthropods (including crustaceans), fruit, nectar, seeds, small lizards (?)

[1] Based on Slud (1967) and Sherry and Werner (unpubl. data).
[2] Based on Slud (1967), Smith and Sweatman (1976), the present study, and Werner and Sherry (unpubl. data).
[3] Population inhabiting the Galapagos Archipelago.

that it catches diverse arthropod types with diverse feeding behaviors. The close match between diet and available foliage-inhabiting arthropods also classifies *Nesotriccus* as a generalist by the definition of some ecologists (e.g., Smith 1982). Evolutionarily, however, this flycatcher appears to have acquired specialized aerodynamic capabilities and a bill specialized to capture active and/or large-sized prey. Relative to *Phaeomyias, Nesotriccus* has ceased to rely on fruit and has become specialized largely on insects. It would be of considerable interest if *Nesotriccus* is more "specialized" than *Phaeomyias* since animals are expected to broaden their diets when they colonize competitor-poor environments. *Nesotriccus* is certainly both an evolutionary and ecological specialist in comparison with *Pinaroloxias inornata* (Geospizinae), the endemic genus of Darwin's Finch with which *Nesotriccus* shares all Cocos Island habitats (Table 4).

Nesotriccus seems to be both an ecological generalist and an evolutionary specialist. The foregoing discussion suggests moreover that generalization and specialization are meaningful concepts only in a comparative sense, and the conclusions depend on the reference used for comparison.

WHY IS THE RESIDENT LAND BIRD FAUNA OF COCOS ISLAND DEPAUPERATE AND LARGELY ENDEMIC?

Three lines of evidence suggest that Cocos Island is ecologically impoverished from the perspective of land birds (see Lack 1976; Abbott 1980), and that few immigrants are adapted to survive in the forest which covers much of the island. (1) Many arthropod taxa that birds encounter on the mainland are poorly represented or absent from the island, and few taxa, except perhaps Homoptera, compensate in population density for missing taxa. The ability of *Nesotriccus* to live and breed in Cocos Island forest (Slud 1967; Sherry and Werner, unpubl. data) probably reflects its adaptation for exploitation of particular arthropods for which it was not previously adapted. *Nesotriccus* also eats fruit, but the virtual absence of fruit in the 1978 stomach samples suggests that fruit was rare at that time. That fruit might be seasonally rare on a floristically impoverished island such as Cocos is not unexpected and further emphasizes the predicament of any frugivore that successfully disperses to the island (cf. Faaburg and Terborgh 1980).

(2) Evidence from the four resident land birds on Cocos Island suggests that evolutionary modification of the species was necessary before they could expand into forest habitat. Specifically, these species illustrate a trend in which greater endemism, from none to a level of subfamily, and greater morphological divergence from closest living relatives correspond with broader habitat use and diet, and with greater abundance in forest (Table 4). Scarcity of appropriate food is a more likely explanation than predation for the avoidance of forest by

certain Cocos species (Table 4) because at present the forest contains no snakes, raptors, or other obvious avian predators. Whether or not the residents depress resources enough to affect each other or other land birds is unknown.

(3) The distribution and ecology of migratory birds also suggest that interior forest provides poor foraging opportunities. Migratory land birds, many of which inhabit forested habitats elsewhere, occur overwhelmingly in edge habitats on Cocos Island, generally near shore (Slud 1967; F. G. Stiles, pers. comm.; Sherry, unpubl. data). The exception is the American Redstart (*Setophaga ruticilla,* Parulinae). One female that I collected on 29 February, 1980 in subcanopy on a forested ridge between Bahia Wafer and Bahia Chatham had been eating fulgoroid Homoptera (10 of 11 identifiable items in the stomach). A yearling male observed on 14 April, 1984 foraged much as *Nesotriccus* does in interior forest between Bahia Wafer and the Mirador. Redstarts eat Homoptera elsewhere and are convergent morphologically and behaviorally with tyrannid flycatchers that specialize on Homoptera (Robinson and Holmes 1982; Sherry 1982, 1983, unpubl. data).

Potential colonists have arrived on Cocos Island, both independently and with man's assistance (T. W. Sherry, T. K. Werner, and F. G. Stiles, unpubl. data), even though no new species have definitely established breeding populations since the avifauna was described late in the last century (Slud 1976). Thus, lack of immigrants cannot alone explain why Cocos Island has a depauperate and endemic avifauna. This conclusion does not mean that dispersal barriers have not also contributed to the small number of resident land birds on isolated oceanic islands (Williamson 1981), especially if birds tend to disperse better than the organisms upon which they rely for food.

ACKNOWLEDGMENTS

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