THE FEEDING ECOLOGY OF TANAGERS AND HONEYCREEPERS IN TRINIDAD

BARBARA K. SNOW AND D. W. SNOW

DURING the last 13½ months of our 4½-years' residence in Trinidad (August 1960 to September 1961) we kept systematic records of the feeding behavior of the commoner tanagers and honeycreepers. By this time, besides knowing the bird species well, we had learned to identify most of the trees and shrubs, particularly those in the northern mountain range where we lived.

The correct systematic treatment of the tanagers and honeycreepers is still uncertain. Formerly they were separated as Thraupidae and Coerebidae, but Beecher (1951) argued that the Coerebidae are a heterogeneous group and recommended placing *Coereba* and *Conirostrum* with the Parulidae and the others with the Thraupidae. Whatever their correct systematic arrangement, they form a natural ecological group of small to medium-sized birds of wooded habitats that take a mixed diet of insects and fruit, with some nectar. The tanagers are structurally unspecialized as a group, but the honeycreepers in beak and tongue are to some extent specialized for nectar-eating. As fruit-eaters, both tanagers and honeycreepers typically exploit the smaller, succulent fruits of trees, shrubs, and vines, and are ecologically quite distinct from the larger, specialized fruit-eating birds that exploit the larger and more nutritious fruits of palms, Lauraceae, Burseraceae, and some other tree families (Snow, 1971). They are common and conspicuous birds of the neotropical forests, where many species coexist, frequently with little obvious ecological segregation between them.

The aim of our observations was to determine to what extent and in what ways the different Trinidad species differ in their feeding ecology; for differences are to be expected on theoretical grounds, even though they may not be obvious to casual observation. It is hoped that the results presented here will throw some light on the problems of bird species diversity and competition in the tropics that have been discussed a good deal in recent years, mainly from a theoretical standpoint and on the basis of very general information about the birds concerned and their relation to the habitat.

METHODS

We both spent about 4–5 hours per week searching for feeding birds and recording their activity, by walking slowly along paths and roads in various habitats at times of day when feeding activity was highest. Many records were also obtained when we were engaged on various other ornithological activities, or even when relaxing at

home, as the house was surrounded by neglected citrus trees and secondary forest and overshadowed by two vast trees.

The method of recording was essentially the same as that used in studies of the feeding ecology of birds in temperate woodland (e.g. Hartley, 1953). Each individual bird was accorded only one feeding record while it fed in one tree or bush, but if it then flew to another tree and repeated the same type of feeding behavior, whether insect-searching in the same manner or taking the same fruit, this was registered as a second record. Besides recording the type of foraging or feeding, we estimated the height above the ground. When a bird was searching for insects its area of search was divided into branch or twig (with an estimate of diameter), foliage, flower, fruit, etc. It is undoubtedly easier to obtain records of birds feeding on flowers or fruits than insect-searching, as birds tend to congregate on trees that are flowering or fruiting; so for most of the species the figures are probably biased, but they should be about equally biased. The only species to which this bias may not apply is the Turquoise Tanager (*Tangara mexicana*), which feeds in small flocks both while insect-hunting and while eating fruit.

In addition to the records obtained during the 13½ months of systematic observation, we obtained a number of records earlier, mainly of fruit- and nectar-eating. These are used only in Tables 4 and 7 where they can introduce no bias.

An adequate amount of data for analysis was accumulated for eight species of tanagers and five of honeycreepers (including *Coereba flaveola*); for two other tanagers, *Tachyphonus luctuosus* and *Euphonia trinitatis*, we were able to get only a small number of records. Three tanagers, the forest-dwelling *Habia rubica*, which forages at low levels within the forest and hardly overlaps with the others, and the high-montane *Thraupis cyanocephalus* and *Piranga flava*, are omitted from consideration, as well as the honeycreeper *Conirostrum bicolor*, which is confined to mangroves. Apart from these four, the species dealt with here include all the regularly occurring species of tanagers and honeycreepers in Trinidad.

The weights and measurements quoted, if no reference is given, are from Snow and Snow (1963) or from our unpublished data. The nomenclature follows Meyer de Schauensee (1966), except that by recent rulings of the International Commission on Zoological Nomenclature *Tanagra* has been replaced by *Euphonia* and *Thraupis virens* by *Thraupis episcopus*.

The habitat.—Most of the records were obtained in the Arima Valley in the middle of the Northern Range. This valley, which runs up to a pass over the range at 1,800 feet, contains forest reserves from which a small quantity of selected timber has been felled, and areas of cultivation that include citrus orchards with rough grass, banana gardens, and coffee and cocoa plantations under high shade trees. Records were also obtained from the savanna country at the southern foot of the Northern Range, from other parts of the Northern Range, from the freshwater Nariva Swamp on the eastern side of the island, and flat country under mixed cultivation in east-central Trinidad.

Although the original records were divided into six habitats, so many transitional stages intervene between the various nonforest habitats, especially gardens, plantations, and partly wooded savannas, that the analysis considers only two main habitats: forests, which include records obtained from roads through forests, and others.

The Northern Range is steep and deeply dissected. Hardly any of the forest is on level ground, and much of it is on very steep slopes. The trees are thus steeply tiered, and light can penetrate at many points, giving rise in many places to a flourishing growth of shrubs and other understory plants. Nowhere in the Northern Range of

TABLE 1

MEAN WEIGHTS AND MEASUREMENTS OF TRINIDAD TANAGERS AND HONEYCREEPERS[1]

Species	Weight (g)	Wing	Tail	Tarsus	Culmen	Bill depth
Tangara guttata	18.4	70	50	18	7.8	5.1
Tangara gyrola	20.7	73	47	17	8.0	5.2
Tangara mexicana	20.9	73	50	17	7.8	5.5
Thraupis episcopus	37.1	90	63	20	10.3	7.3
Thraupis palmarum	38.6	94	70	21	10.8	6.3
Ramphocelus carbo	28.5	79	77	22	12.8	9.0
Tachyphonus rufus	36.2	87	76	24	13.8	7.5
Tachyphonus luctuosus	13.5	64	54	16	10.0	5.5
Euphonia violacea	14.7	57	32	16	6.9	5.5
Euphonia trinitatis	(14.0)	54	33	15	5.3	4.2
Cyanerpes caeruleus	12.6	58	27	15	19.9	3.4
Cyanerpes cyaneus	14.2	66	38	14	14.9	3.5
Chlorophanes spiza	18.2	74	49	18	12.2	4.5
Dacnis cayana	14.1	62	41	16	9.9	4.1
Coereba flaveola	10.6	56	35	17	9.9	4.1

[1] All weights and measurements are medians of means for male and female, except for *Euphonia trinitatis*, for which only one weight is available (Junge and Mees, 1958). Other weights and wing-lengths from living specimens (Snow and Snow, 1963); tail and tarsus measurements from freshly dead birds; beak measurements from museum specimens. Culmen length is measured from the anterior end of the nares, beak depth at the level of the anterior end of the nares. Measurements of beak depth in dry skins are on the average about 5–10 per cent less than in fresh specimens.

Trinidad is there anything comparable to the continuous forest canopy found in flat country on the South American mainland. The rainfall and humidity are high, and the trees well-clothed with epiphytes. Vines and other climbers are abundant.

Seasonal changes in the abundance of flowers and fruits in the Arima Valley have been described elsewhere (Snow and Snow, 1964). In general, although most trees and shrubs have well-defined flowering and fruiting seasons, these are well-distributed throughout the year so that a variety of fruit is normally available at any time. Our combined records for all plants (whether fed on by tanagers and honeycreepers or not) show peaks in the numbers of different species in fruit in April–May and November; but if the analysis is confined to those species whose fruits were recorded in the diet of tanagers and honeycreepers, very little seasonal peaking is evident. Somewhat less fruit may be available in the first 3 months of the year than at other times (16, 16, and 17 species recorded in fruit vs. 19–24 species in the other months). Of the flowers at which honeycreepers were recorded feeding, the greatest number of species were available in March–May, with another peak towards the end of the year—a seasonal trend similar to that found for all species of plants for which records were kept. But this probably does not give a true indication of the availability of nectar, as three kinds of flowers (*Erythrina*, *Norantea*, and *Symphonia*) were fed at more than all the others combined, and these all bloom mainly in the period November–March.

Tangara SPECIES

The genus *Tangara* has three representatives in Trinidad, all very similar in dimensions but distinctive enough in plumage. For the insect part of its diet, each proved to be exploiting a feeding niche clearly

TABLE 2
FOOD AND FEEDING HABITATS OF TRINIDAD TANAGERS AND HONEYCREEPERS, MAIN DIVISIONS

	No. records	Per cent in each category: Insect-searching	Fruit	Flowers	Habitat: Forest	Nonforest
Tanagers						
Tangara guttata	96	26	74	—	89	11
Tangara gyrola	564	30	70	—	85	15
Tangara mexicana	433	47	53	—	48	52
Thraupis episcopus	260	37	53	10	30	70
Thraupis palmarum	319	48	43	9	23	77
Ramphocelus carbo	588	50	45	5	28	72
Tachyphonus rufus	238	30	60	10	47	53
Tachyphonus luctuosus	49	71	29	—	71	29
Euphonia violacea	190	3	97	—	45	55
Euphonia trinitatis	12	100	—	—	—	100
Honeycreepers						
Cyanerpes caeruleus	237	40	31	29	73	27
Cyanerpes cyaneus	125	44	44	12	70	30
Chlorophanes spiza	267	15	63	22	74	26
Dacnis cayana	267	49	44	7	58	42
Coereba flaveola[1]	570	8	7	76	56	44

[1] Nine per cent of all records were of feeding on protein corpuscles of *Cecropia*, not included in the table.

distinct from that of its congeners. In certain features of their fruit-eating behavior they also differed from each other.

SPECKLED TANAGER (*Tangara guttata*)

This is the smallest of the three *Tangara* species by weight. It has a slightly shorter wing than the other two (Table 1), but its tail and tarsus are both slightly longer than in the other two species. Its plumage is a bright, rather yellowish green with black spots above, and whitish with black spots below. It is more strictly a forest-dweller than the other species studied, and the few feeding records away from the forest were from birds coming to take fruit from shrubs on the borders of cocoa and coffee plantations. It is restricted to the higher parts of the Northern Range; we did not record it below about 1,000 feet and most records were well above this altitude. Even at this height it is not so abundant as the other two *Tangara* species. Occasionally up to five individuals fed together on fruit, but usually they were seen feeding singly or in pairs. A summary of the feeding records for the Speckled Tanager, and for the other species, is given in Tables 2–4.

When insect-searching, Speckled Tanagers confined themselves almost exclusively to the foliage, usually examining the undersides of leaves by

TABLE 3
PER CENT BREAKDOWN OF MAIN INSECT-SEARCHING STATIONS OF TRINIDAD TANAGERS AND HONEYCREEPERS

	No. records	Foliage	Branches and twigs	Flower and seed heads	Ground	Hawking
Tanagers						
Tangara guttata	25	92	8	–	–	–
Tangara gyrola	171	8	90	1	–	2
Tangara mexicana	201	4	91	2	–	2
Thraupis episcopus	96	56	17	11	–	16
Thraupis palmarum	153	89	1	–	–	10
Ramphocelus carbo	290	77	+	2	13	7
Tachyphonus rufus	74	32	3	–	51	14
Tachyphonus luctuosus	35	94	3	–	–	3
Honeycreepers						
Cyanerpes caeruleus	94	17	63	5	–	15
Cyanerpes cyaneus	55	35	36	7	–	22
Chlorophanes spiza	49	14	10	55	–	20
Dacnis cayana	130	69	13	12	–	6
Coereba flaveola	46	63	31	–	2	4

clinging to them upside down and also scanning the leafy tips of twigs by clinging in a vertical position, head downward. At other times they would hop along small branches looking up at the undersides of the leaves above. We were not able to discover what prey were taken.

Although the 14 species of fruits seen to be taken were shared with the other two *Tangara* species, the Speckled Tanager's method of taking fruit is characteristic: all records were of it picking the fruit from a perched position and eating it whole. We never saw it crush fruit to reduce it to a more manageable size or peck pieces out of a large fruit. When picking fruits at the end of slender twigs, it edges its way down the twig, clinging head downward in much the same stance as when hunting insects. Over half the fruits taken were from large shrubs and small trees of the family Melastomaceae; the remainder were from various trees and from shrubs of the genus *Psychotria*. Although Speckled Tanagers frequently come down to below 25 feet to take fruits, all records of insect-searching were above 25 feet except for one record of a bird searching the foliage of a newly-felled tree (Figure 1).

BAY-HEADED TANAGER (*Tangara gyrola*)

This is a bright green bird with a chestnut-brown head. It has a rather shorter tail than the two other *Tangara* species (Table 1). A forest dweller like the Speckled Tanager, unlike the latter it is as plentiful at low altitudes as it is higher up, and as more cultivated land adjoins the low-

TABLE 4

RECORDS OF FRUIT-EATING BY TRINIDAD TANAGERS AND HONEYCREEPERS

		T. guttata	*T. gyrola*	*T. mexicana*	*Th. episcopus*	*Th. palmarum*	*R. carbo*	*T. rufus*	*T. luctuosus*	*E. violacea*	*C. caeruleus*	*C. cyaneus*	*Ch. spiza*	*D. cayana*	*C. flaveola*
Trees and shrubs															
Flacourtiaceae	*Laetia procera*[1]	–	–	8	1	3	5	1	–	–	–	–	–	7	–
Guttiferae	*Clusia* spp.	–	–	–	–	–	–	–	–	–	14	1	3	2	–
Tiliaceae	*Sloanea stipitata*	1	7	–	1	1	2	4	1	–	–	4	–	2	2
Malpighiaceae	*Byrsonima spicata*	–	10	–	–	–	–	–	–	–	–	–	–	1	–
Burseraceae	*Protium heptaphyllum*	–	6	13	9	12	2	9	1	5	–	–	4	4	–
Sapindaceae	*Cupania* sp.	–	–	–	–	–	–	–	–	–	–	8	–	–	1
Aquifoliaceae	*Ilex* sp.	–	3	20	–	–	1	–	–	–	–	–	–	–	–
Myrtaceae	*Calycolpus glaber*	–	–	1	2	2	2	–	–	–	–	–	–	1	1
	Eugenia baileyi	–	–	3	1	3	–	–	–	–	–	–	–	–	–
	Myrcia leptoclada	–	11	–	–	–	–	–	–	1	–	–	–	–	–
	Myrcia sp.	1	–	3	–	–	–	–	–	–	2	–	–	–	–
	Psidium guajava[2]	–	–	3	–	–	4	–	–	–	–	–	–	–	–
Melastomaceae	*Clidemia* spp.	–	2	–	–	–	27	9	–	3	–	–	–	–	–
	Henriettea sp.	–	1	–	–	–	2	2	–	–	–	–	–	–	–
	Miconia spp.	40	127	74	17	35	153	23	5	17	11	20	80	52	12
	(No. of species)	(5)	(7)	(5)	(4)	(5)	(11)	(4)	(2)	(2)	(3)	(4)	(8)	(7)	(4)

[1] Botanical names are those used in "The flora of Trinidad and Tobago," so far as it has been completed, except where changes are needed as a result of recent revisions (N. Y. Sandwith, in litt.).

[2] Introduced species in Trinidad.

[3] Possibly including similar congeneric species.

TABLE 4 (CONTINUED)

		T. gutiata	*T. gyrola*	*T. mexicana*	*Th. episcopus*	*Th. palmarum*	*R. carbo*	*T. rufus*	*T. luctuosus*	*E. violacea*	*C. caeruleus*	*C. cyaneus*	*Ch. spiza*	*D. cayana*	*C. flaveola*
Trees and shrubs															
Araliaceae	*Didymopanax morototoni*	–	13	1	33	49	5	–	–	–	–	–	2	4	1
Rubiaceae	*Chiococca alba*	–	1	15	–	–	–	–	–	1	–	–	3	–	–
	Coussarea paniculata	–	–	–	6	2	5	4	–	1	–	–	–	–	–
	Isertia parviflora	–	–	–	–	–	2	3	–	–	–	–	–	–	–
	Psychotria spp.	1	2	–	–	–	–	–	–	–	–	–	–	–	–
Boraginaceae	*Cordia curassavica*	–	–	7	2	–	18	1	–	–	–	–	–	–	1
	Cordia bicolor[3]	–	5	3	5	5	–	4	–	–	–	–	–	–	5
Verbenaceae	*Aegiphila integrifolia*	–	2	1	–	–	–	–	–	–	–	–	–	–	–
Euphorbiaceae	*Alchornea glandulosa*	9	13	–	1	14	–	–	–	–	11	–	13	16	–
	Hieronyma caribaea	4	14	3	–	–	–	1	–	–	1	–	5	4	1
	Sapium aucuparium	2	1	–	–	–	–	–	–	–	1	3	2	12	8
Ulmaceae	*Trema micrantha*	12	39	11	2	1	1	3	–	29	27	11	34	13	3
Piperaceae	*Piper* sp.	–	–	–	10	–	–	–	–	9	–	–	–	–	–
Moraceae	*Castilloa elastica*[2]	–	–	–	5	–	1	–	–	–	–	–	–	–	–
	Cecropia peltata	3	72	31	26	18	17	18	–	–	–	–	5	3	4
	Ficus citrifolia	–	15	4	–	–	–	2	–	3	–	–	–	–	–
	Ficus clusiifolia	2	48	17	8	11	–	3	–	7	3	5	12	1	8
	Ficus tobagensis	–	4	2	–	–	3	–	–	3	–	–	1	–	–
Vines															
Dilleniaceae	*Davilla aspera*	–	–	–	–	1	5	1	–	–	–	–	–	–	–
	Doliocarpus dentatus	–	–	–	3	3	–	–	–	–	–	5	–	1	–
Lacistemaceae	*Lacistema aggregatum*	–	3	5	1	2	1	–	–	–	–	–	1	2	–

TABLE 4 (CONTINUED)

		T. gutata	*T. gyrola*	*T. mexicana*	*Th. episcopus*	*Th. palmarum*	*R. carbo*	*T. rufus*	*T. luctuosus*	*E. violacea*	*C. caeruleus*	*C. cyaneus*	*Ch. spiza*	*D. cayana*	*C. flaveola*
Marcgraviaceae	*Norantea guianensis*	–	1	–	–	–	–	–	–	–	–	–	–	2	–
Connaraceae	*Rourea surinamensis*	–	–	–	–	–	–	–	–	–	–	–	1	2	1
Compositae	*Wulffia baccata*	–	1	–	–	–	2	–	–	–	4	–	–	2	–
Epiphytes															
Araceae	*Anthurium gracile*	–	–	–	–	–	1	4	–	4	–	–	–	–	–
	Anthurium scandens	–	–	–	–	–	–	3	4	19	–	–	–	–	–
Bromeliaceae	*Aechmaea dichlamydea*	–	–	–	–	–	2	1	–	–	–	–	–	–	–
	Aechmaea mertensii	–	–	–	–	–	2	2	–	–	–	–	–	–	–
	Aechmaea nudicaulis	–	–	–	–	–	–	7	–	38	–	–	–	–	–
	Gravisia aquilega	–	–	–	–	–	14	29	–	–	–	–	–	–	–
	unid. spp.	–	–	–	–	–	2	3	–	–	–	–	–	–	–
Cactaceae	*Rhipsalis* sp.	–	–	2	–	1	–	–	–	32	–	–	–	–	6
Loranthaceae	div. spp.	–	2	10	–	–	–	3	–	29	3	–	6	2	1
Herbs															
Phytolaccaceae	*Phytolacca rivinoides*	–	–	–	–	1	1	1	–	–	–	–	–	–	–
Solanaceae	*Solanum* sp.	–	2	–	–	–	3	–	–	–	–	–	–	–	–

TABLE 4 (CONTINUED)

The following fruits were recorded as taken by only one species; the number of records are given in parentheses.		
Trees		
Annonaceae	*Rollinia exsucca*	*Euphonia violacea* (4)
Hypericaceae	*Vismia* spp.	*Thraupis episcopus* (10)
Sapindaceae	*Matayba guianensis*	*Cyanerpes cyaneus* (4)
Anacardiaceae	*Anacardium occidentale*[2]	*Ramphocelus carbo* (1)
Myrtaceae	*Eugenia malaccensis*[2]	*Tachyphonus luctuosus* (1)
Nyctaginaceae	*Pisonia eggersiana*	*Tachyphonus rufus* (1)
Moraceae	*Artocarpus incisa*[2]	*Thraupis episcopus* (2)
	Ficus religiosa[2]	*Ramphocelus carbo* (2)
Palmaceae	*Roystonea oleracea*	*Thraupis palmarum* (1)
Coniferae	*Podocarpus* sp.	*Euphonia violacea* (1)
Vines		
Marcgraviaceae	*Marcgravia* sp.	*Tangara gyrola* (2)
	Pinzona calineoides	*Thraupis palmarum* (2)
Epiphytes		
Bromeliaceae	*Aechmaea porteoides*	*Tachyphonus rufus* (3)
Araceae	*Epiphyllum hookeri*	*Coereba flaveola* (1)
Herbs		
Rubiaceae	*Geophila herbacea*	*Tachyphonus rufus* (1)

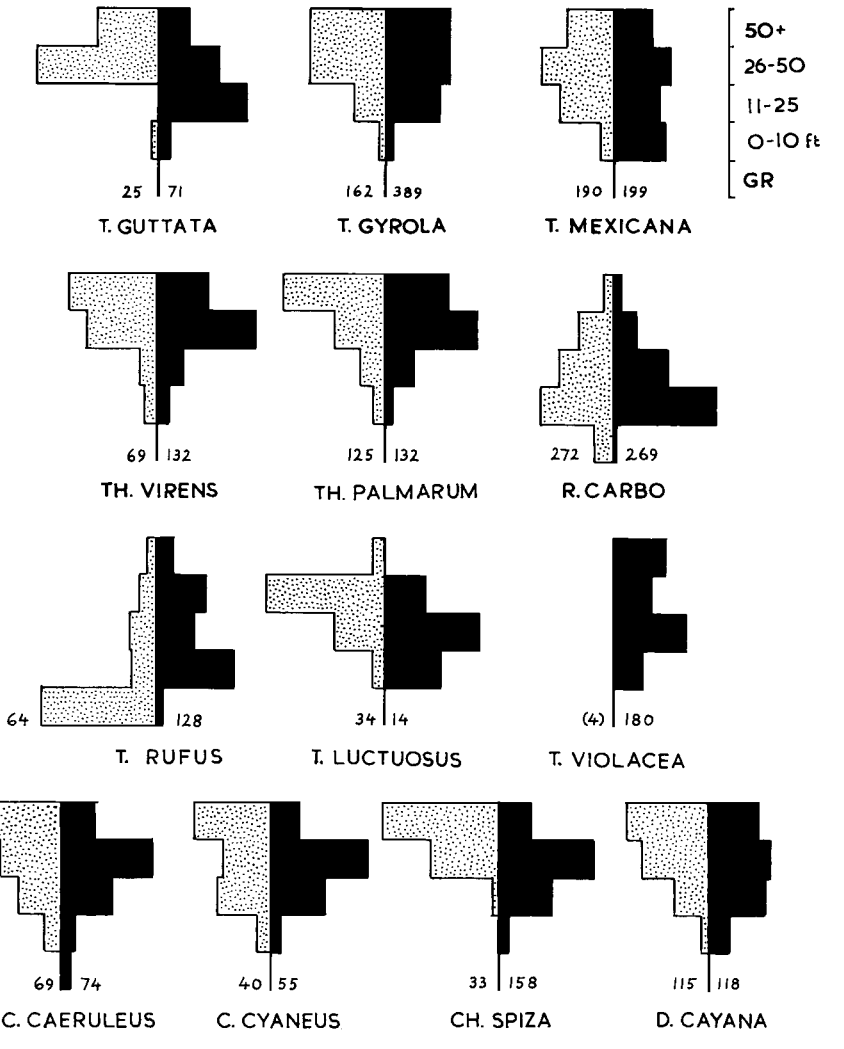

Figure 1. Foraging heights of tanagers and honeycreepers in Trinidad. The histograms show percentages, based on the totals given at the base. Stippled: insect-searching. Black: fruit-eating. Vertical scale at top right-hand corner (GR = ground).

altitude forests, there are more records of it in cultivation. All our records were obtained in the Northern Range, but it also occurs in the much diminished lowland forest. Most of the records, including all the records of insect-searching, were of birds feeding in ones or twos; occasionally more were seen at shrubs or trees with abundant fruit, but Bay-headed Tanagers were never seen moving about in small flocks.

The summary of feeding records (Table 2) shows that Bay-headed and Speckled Tanagers take very similar proportions of fruit to insects. Their methods of insect-searching, however, are very different, as 90 per cent of the Bay-headed Tanager records are of birds examining branches, in nearly all cases the undersides of branches. Typically the bird hops along a branch and every few feet leans down first on one side then on the other to examine the underside. Many records were from trees with a new flush of foliage, and only five records were of birds examining dead twigs and branches. We were seldom able to determine what insects were being taken, but once we saw a Bay-headed Tanager eat a small moth and once a small winged insect, which it placed on a branch to eat.

The main differences between the insect-searching behavior of the Bay-headed Tanager and of the Turquoise Tanager, which follows, were in the diameter of the branches they examined and, to a lesser extent, in the heights at which they foraged. These points are discussed below.

Bay-headed Tanagers were recorded taking a wide variety of fruits (Table 4). The Melastomaceae account for 28 per cent of the records, and *Ficus* spp. and *Cecropia* for a further 31 per cent. Although they come considerably lower to take fruit than when insect-searching, there were only 15 records (3 per cent) of their taking fruit at 10 feet or lower. They swallow nearly all fruits whole; we recorded them pecking pieces out of two kinds of large fruits, but never saw them mandibulate fruit. Occasionally they take fruit on the wing in the manner of manakins (Pipridae), and it may be that the Bay-headed Tanager's slightly shorter tail than its congeners' adapts it to this method of feeding.

Turquoise Tanager (*Tangara mexicana*)

This species is mostly black above with patches of bright blue, and pale yellow below with patches of blue-black. It ranges over a wider variety of habitats than the other two species, from the lowlands up to about 1,800 feet. Just under half of our feeding records were from forest, and the remainder from secondary woodland, orchards, gardens, and partly wooded savanna. Turquoise Tanagers move about and feed in small twittering flocks usually of three to six birds, so that locating and obtaining feeding records for this species is relatively easy.

Nearly all (91 per cent) of the records of insect-searching were of birds examining the underside of twigs and branches. Table 5 shows that most of those examined were fine twigs under ½ inch in diameter, in contrast to those examined by Bay-headed Tanagers, 94 per cent of which had diameters estimated at ½–2 inches. Turquoise Tanagers also frequently examine dead twigs (47 out of 109 twig-searching records of one observer),

TABLE 5
PER CENT OF RECORDS OF INSECT-SEARCHING ON BRANCHES OF DIFFERENT SIZES BY *TANGARA GYROLA* AND *T. MEXICANA*

	T. gyrola	*T. mexicana*
Number of records	145	182
Diameter of branch		
Under ½ inch	6	55
½ inch	30	20
1 inch	32	13
2 inches	23	3
3 inches	6	4
4 inches	3	1
5+ inches and trunk	1	4

which the Bay-headed Tanager rarely does. They forage more readily at lower levels than either of the other two *Tangara* species (Figure 1).

They also show a preference for lower levels in their fruit-eating, as 26 per cent of the records are at heights of 10 feet or below. For this reason, such shrubs as *Chiococca alba* and *Cordia curassavica* are commoner in the diet of the Turquoise than of the Bay-headed Tanager. They normally perch to pick fruit, there being only one record of fruit taken on the wing. The fruits of mistletoes (Loranthaceae) are much more important in their diet than in the other *Tangara* species, and they more readily peck pieces out of large fruits. They were also seen mandibulating fruits to reduce their size or to eliminate the seed before swallowing.

Thraupis SPECIES

The two *Thraupis* species dealt with here (and *T. cyanocephala*, which is omitted) are the largest tanagers in Trinidad. The Palm Tanager (*T. palmarum*) is slightly bigger than the Blue-gray Tanager (*T. episcopus*), but their proportions are extremely similar except that the Palm Tanager has a distinctly finer beak (Table 1). They are not forest birds but nest and feed in gardens, orchards, and savanna country. They feed occasionally just inside the forest, mostly where roads run through forest reserves, which accounts for the forest habitat records (Table 2). Both species feed occasionally on the nectar of such large flowering trees as the immortelle (*Erythrina micropteryx*), widely introduced as a shade tree, and the native *Erythrina glauca* and *Tabebuia serratifolia*, a habit not recorded in the *Tangara* species. Although the proportions of feeding on fruit, flowers, and insects recorded for the Blue-gray and Palm Tanagers are rather similar, the two species exploit quite different niches in their insect-foraging and show a fairly wide divergence in their fruit-eating.

BLUE-GRAY TANAGER (*Thraupis episcopus*)

The Blue-gray Tanager, pale grayish-blue with brighter blue wings and tail, is common at all altitudes in a variety of nonforest habitats. Like the Palm Tanager, it comes down to feed near the ground much more rarely than do the *Tangara* species, only 6 per cent of all records being below 10 feet and 18 per cent below 25 feet.

When insect-searching, the Blue-gray Tanager typically seeks prey that escape by moving rather than relying on being well-hidden. Its usual method is to hop fairly swiftly along a branch among foliage, examining the undersides of leaves and branches above it and the uppersides of leaves on its own level, and darting forward or fluttering up to snatch its prey. In the same manner it sometimes searches for insects among the flowers of trees, and it also hawks for insects. Occasionally it leans down to search the underside of a thicker branch in the manner of a Bay-headed Tanager, and has been seen to find a caterpillar or chrysalis by this means.

Blue-gray Tanagers take a variety of fruits, always eating them while perched. They frequently take pieces out of larger fruits in situ, e.g. the introduced breadfruit tree (*Artocarpus incisa*) and the rubber *Castilloa elastica*, and the native *Coussarea paniculata*. They take two kinds of fruits that are not generally taken by any of the other tanagers, *Vismia* (two species) whose ½-inch long berries they sometimes bill before swallowing, and the fruits of *Piper* spp. which otherwise were seen to be taken only by *Euphonia violacea*. The latter have a catkinlike fruit 2 or more inches long, which the Blue-gray Tanager deals with in a special way: it plucks one, flies with it to another perch, and there lays it across a branch and eats pieces out of it.

PALM TANAGER (*Thraupis palmarum*)

This is a rather uniform olive-green bird with darker wings. Like the Blue-gray Tanager, which it resembles closely in size and structure, it is generally common in all sorts of nonforest habitats. It normally feeds singly or in pairs, and like the Blue-gray Tanager prefers to feed well above the ground, only 19 per cent of the 257 feeding records being from less than 25 feet.

The Palm Tanager's method of insect-searching is quite specialized. It forages almost exclusively among leaves, usually very large leaves, and to do this it clings vertically head downward, or upside down, to the petiole of the leaf or the leaf itself. When examining the leaf of a coconut palm, the Palm Tanager starts on the upper surface of a leaflet and then works towards the tip, its weight causing the leaflet to hang down with the bird hanging vertically to it. It examines bamboo leaves in the

same way (an introduced plant in Trinidad, growing to well over 50 feet), but normally examines the undersides of the large palmate or semipalmate leaves of native trees such as *Cecropia peltata*, *Pachira insignis*, and *Didymopanax morototoni*, and other kinds of foliage as well while hanging or clinging to them upside down. Of all our records of foliage-searching, 66 per cent were from trees with particularly large leaves. Usually it was not possible to see what prey was being taken, but caterpillars were certainly eaten occasionally.

Palm leaves are particularly hard and slippery and must be difficult to cling to, and the Palm Tanager was the only species ever seen foraging on them. An examination of live birds and freshly dead specimens showed that the Palm Tanager's claws are noticeably sharper than those of the other tanagers. Its tail averages 7 mm longer than the Blue-gray Tanager's, a rather greater difference than would be expected from its slightly greater size. Possibly this is advantageous for clinging head downward and upside down, as the Speckled Tanager has the longest tail of the three *Tangara* species and also forages in a head-downward or upside-down position.

The Palm Tanager was seen to take 24 different kinds of fruit, the proportion of fruit records being lower than for the Blue-gray Tanager (43 per cent as against 53 per cent), a difference that is probably significant as it lacks the specialized fruit-eating behavior of the Blue-gray Tanager. It can take rather larger fruits than the latter, swallowing *Coussarea* fruits whole instead of pecking pieces out of them, and taking the fruits of the cabbage palm (*Roystonea oleracea*) which are about ½ inch long. Berries of the Melastomaceae are not a particularly important item in its diet, a characteristic in which it resembles the Blue-gray Tanager and differs from the other tanagers.

Ramphocelus AND *Tachyphonus*

Ramphocelus and *Tachyphonus* show some general similarities of ecological preference and of appearance, and are probably closely related. One of the three Trinidad species, *T. luctuosus*, is much less common than the other two and the few records of its feeding are dealt with at the end. The other two, *R. carbo* and *T. rufus*, are both common birds, both frequently feed at low levels and even on the ground, and both lack the green, blue, and yellow colors of the more aboreal tanagers already considered.

SILVER-BEAKED TANAGER (*Ramphocelus carbo*)

The male Silver-beak is very dark, almost blackish crimson, except for the throat and breast which are deep crimson; the female is generally

duller with the crimson replaced by reddish brown. The base of the lower mandible is enlarged and, in the male, of a conspicuous silver gray. They are common birds, frequently forage in pairs or family groups, and are often noisy, so that we were able to get a large number of feeding records.

Silver-beaks feed both on insects and fruit at a much lower level than the *Tangara* and *Thraupis* species, 48 per cent of our records of insect-searching and 55 per cent of our fruit-eating records being at 10 feet or lower and only a small fraction of the total being above 50 feet. They frequent cultivation, young stages of secondary forest, and savanna country, only rarely entering forest for fruit and nectar, although they are common along roadsides running through forested areas.

On the ground Silver-beaks feed on the short grass of roadsides as well as among the rough grass and weeds of cultivated areas and plantations. Above ground their foraging for insects is nearly all among foliage (Table 3), either the thick herbaceous growth on the edge of roads and clearings or the thick low canopy of second-growth trees and shrubs. When searching, they hop about on top of the foliage, moving fairly rapidly and sometimes darting forwards. Beetles, other winged insects, and caterpillars are among the prey taken and, judging from the quick and cursory method of searching, the usual prey are insects that rely on movement to escape capture rather than on crypsis. Silver-beaks were recorded taking nectar from three species of trees and two of vines, often at higher levels than when feeding on fruit and insects. They were the only tanagers seen feeding at the flowers of the vine *Dioclea guianensis*, which they exploited by breaking into the base of the flowers, presumably to get at the nectar.

Silver-beaks were recorded feeding on many different kinds of fruits, but berries of the Melastomaceae were by far the most important, accounting for 64 per cent of the 286 records of fruit-eating. The berries of *Clidemia* spp., small shrubs usually less than 5 feet high, were particularly favored. Fruits of the larger Melastomaceae eaten abundantly by the Silver-beak are also much eaten by the *Tangara* and *Thraupis* species, but the Silver-beak usually feeds at a lower level and often in more open and exposed places, so that the actual overlap is not great. Most fruit is eaten whole, but occasionally the Silver-beak will peck pieces out of a large fruit or crush a fruit to reduce its size.

We have 20 records of Silver-beaks taking the fruits of four species of epiphytic bromeliads. The fruits of these bromeliads are very tough-skinned, with a spine at the tip, and both the Silver-beak and the White-lined Tanager (*Tachyphonus rufus*), for which they are also an important food, mandibulate them, swallowing the pulp and small seeds and dropping the skin with its spine.

WHITE-LINED TANAGER (*Tachyphonus rufus*)

The White-lined Tanager is sexually dimorphic, the male being entirely black except for a white shoulder patch and the female a uniform rufous brown. It is common and widespread, but not so abundant as the Silver-beak. We recorded it foraging in forest almost as much as in cultivated areas, and had some records from savanna, though not from such open habitats as the Silver-beak. It is the most terrestrial of the tanagers here considered, half of our insect-searching records being of birds feeding on the ground. It sometimes feeds at army ant swarms, perching about a foot above the ground and pouncing down to the ground to take the insects flushed by the ants. At times it uses the same technique, perching on a slight elevation, when feeding on the ground without the assistance of army ants, or it may stand in an upright thrushlike stance or hover briefly about 6 inches above the ground before darting forward or pouncing down on some insect. We saw birds feeding in this way taking grasshoppers and smaller insects that were not identified. When insect-searching in trees, it hops rapidly along the finer branches, looking around and above it, and sometimes darting up or forward to take prey from a leaf or twig. We never saw it examining leaves, twigs, or branches closely.

The White-lined Tanager takes a fairly wide variety of fruits (Table 4), showing a distinct preference for fruits of epiphytes. Nearly a third of the fruits recorded were taken from five bromeliad species. It often hovers to take these fruits, then flies to a nearby perch to eat them in the manner described for the Silver-beak. We also saw it chew and drop the inedible parts of three other kinds of fruit, *Coussarea paniculata*, *Cordia bicolor*, and *Protium heptaphyllum*; it swallowed other fruits whole. The Melastomaceae constitute only 23 per cent of the records of fruit-eating, a marked difference from the Silver-beak, for which they made up 64 per cent.

In its nectar-feeding, the White-lined Tanager is fairly similar to the Silver-beak. It was recorded sucking honey in situ from the flowers of three trees, *Erythrina glauca*, *E. micropteryx*, and *Symphonia globulifera*, and from the vine *Norantea* by picking the flower and crunching its base so as to squeeze the honey out.

Although the White-lined Tanager resembles the Silver-beak in feeding generally at a much lower level than the *Tangara* and *Thraupis* species, it collects much less of its insect food from the 1 to 10-foot level than does the Silver-beak as it seldom exploits thick herbaceous vegetation. Our records of fruit-eating at this level are biased by a collection of bromeliads on low racks beneath a large tree in our garden, at which we obtained many of our records of White-lined Tanagers feeding (as bromeliads

continue to flourish on fallen trees and boughs in the wild, the situation was not altogether artificial).

WHITE-SHOULDERED TANAGER (*Tachyphonus luctuosus*)

Our feeding records for this species are meagre, as it is far less plentiful than its larger congener. The male's plumage is similar to that of *T. rufus*, with a larger shoulder patch; the female is greenish above and pale yellow below. Its weight is only one third that of *T. rufus*. It is more of a forest dweller than *T. rufus*, being found in forest, forest-edge, and secondary growth.

Our records for the White-shouldered Tanager show a higher percentage of insect-searching than for any other tanager except *Euphonia trinitatis*, for which we had even fewer records. It searches entirely in foliage, often rather thick foliage, where it flits swiftly about looking around, picking insects from leaves, and making fluttering sallies after insects it disturbs. A green stick-insect was the only insect definitely seen to be taken. This method of insect-hunting is similar to that used by *T. rufus* when foraging in trees, but the two species feed at different heights: 68 per cent of the White-shouldered Tanager's, but only 14 per cent of the White-lined Tanager's insect-searching was above 25 feet. As the two species also prefer different habitats, they must have little overlap in their feeding niches.

Euphonia SPECIES

Three species of *Euphonia* are recorded for Trinidad, but one, *E. musica*, is apparently of irregular occurrence and we obtained no records. One of the other two, the Violaceous Euphonia (*E. violacea*), is abundant while the Trinidad Euphonia (*E. trinitatis*) is widely distributed but not nearly so numerous. These two tanagers show only minor differences in plumage: both are sexually dimorphic, the males dark purplish blue above with a yellow patch on the forehead or crown, and yellow below. The Trinidad Euphonia is distinguished by a bluish-black throat. Both females are green above and greenish-yellow below. The Trinidad Euphonia is slightly smaller than the Violaceous, and has a distinctly finer bill (Table 1).

In their feeding ecology the two species appear to be completely different. The Violaceous Euphonia is an almost exclusively frugivorous bird, 97 per cent of our feeding records being fruit (Table 2). Epiphytes, which flourish on all the trees in Trinidad, accounted for 62 per cent of the fruit records. Some epiphytic fruits, such as *Aechmaea nudicaulis* (the only bromeliad recorded in its diet), the Violaceous Euphonia shares extensively with other tanagers (e.g. *Tachyphonus rufus*), but others such

as the mistletoes (29 records) and the epiphytic cactus *Rhipsalis* (32 records) are shared in only a small degree with *Tangara mexicana*. The Violaceous Euphonia also takes many more aroid fruits (*Anthurium* spp.) than any of the other tanagers.

To take many of the epiphytic fruits it clings head downward or upside down, and it often hovers briefly to pick the fruits of *Rhipsalis* which are attached to hanging stringlike stems. It chews the fruits of *Rhipsalis* and *Aechmaea nudicaulis*, swallowing the pulp and seeds, which adhere together, and dropping the tough skin. It pecks pieces out of fruits that are too big to swallow, or sometimes crushes them to reduce their size. Like the Blue-gray Tanager, but no other tanagers, the Violaceous Euphonia takes the fruit of *Piper*, which it usually eats in situ, getting the catkinlike fruit in its beak and nibbling along it. To feed on *Piper* and some other shrubs it comes down below 10 feet, but many of the epiphytes on which it feeds grow high up near the crowns of tall trees; thus it feeds almost equally at all levels, 85 of our records of fruit-eating being above and 95 below 20 feet.

For the much less plentiful Trinidad Euphonia we unfortunately obtained only 12 feeding records, all of insect-searching. Ten were of birds examining the undersides of fine twigs, less than ¼-inch in diameter, by perching across the twig and leaning down first on one side then on the other. Nearly all the records were high up, between 50 and 100 feet in large trees of gardens or cultivation with shade trees. It also sings and nests and apparently spends most if its time at these heights. Mees (Junge and Mees, 1958) also notes that the Trinidad Euphonia keeps to the tops of high trees, and mentions that these are often infested with mistletoes, but he apparently did not see the bird feeding on the berries. As many *Euphonia* species are known to be specialized mistletoe berry-eaters and their digestive systems are adapted to this diet, the Trinidad Euphonia may at times eat them (indeed, Forbes (1880) includes *E. trinitatis* among the species with a specialized digestive tract); but the fact remains that we never saw them doing so, and the markedly fine beak also suggests some degree of adaptation to a different diet.

DIFFERENCES IN FEEDING ECOLOGY BETWEEN TANAGERS

Within each genus, the records show little overlap in the feeding niches of the different species. The segregation is partly by habitat, but mostly by the niches exploited within the habitat. Details have been given in the preceding sections. In general considerably more overlap exists in the fruits eaten by closely related species than in the insect fractions of their diets, though even in the fruits some striking differences are evident between species, e.g. the tendency for *Thraupis episcopus* to take com-

pound fruits the other tanagers rarely or never eat, and the tendency of *Tachyphonus rufus* to take bromeliad fruits that only *Ramphocelus carbo* eats in any quantity and the other species very rarely or not at all.

The two numerically most important genera, *Tangara* and *Thraupis*, exhibit some other general differences. Compared with *Tangara*, *Thraupis* species inhabit mainly nonforest habitats, include nectar in their diet, take smaller proportions of fruit, feed generally higher, seldom coming down low even for fruit, and hawk for insects more frequently. Other differences in insect-searching are interspecific rather than generic.

In comparing the two *Tachyphonus* and the two *Euphonia* species, although the numbers of records for the mainly or entirely insectivorous members of each genus are unsatisfactorily low, manifestly the species dependent on an insect diet are far less plentiful than the frugivorous or partly frugivorous species. This is amply corroborated in other families in Trinidad, where the largely frugivorous manakins (Pipridae), of which there are two species, greatly outnumber insectivorous birds of equivalent size in the same forest habitat, such as the wren *Thryothorus rutilus* and such small flycatchers as *Myiornis ecaudatus* and *Platyrinchus mystaceus*, and the small antbirds *Dysithamnus mentalis* and *Myrmotherula axillaris*. In the course of a 3½-year mist-netting program, both in the forest and in forest edge and cultivated habitats, the following numbers of different individuals of more or less specialized frugivores and insectivores were caught:

Frugivores:		Insectivores:	
Pipra erythrocephala	471	*Thryothorus rutilus*	19
Manacus manacus	246	*Myrmotherula axillaris*	5
Euphonia violacea	51	*Platyrinchus mystaceus*	4
		Dysithamnus mentalis	3

In contrast to the high number of individuals of frugivorous birds, the number of species mainly or entirely dependent on fruit is small. Thus Trinidad supports four mainly or entirely frugivorous passerines, the two manakins, *Euphonia violacea* and *Procnias averano* (Snow, 1970), whereas the mainly or entirely insectivorous families Tyrannidae, Formicariidae, and Furnariidae contain 51 species.

The number of insect species in any wooded habitat in Trinidad must enormously exceed the number of kinds of fruits eaten by birds. Moreover fruits are conspicuous and the number of ways they can be plucked efficiently is very limited, affording little opportunity for specialized feeding adaptations. The reverse is true of insect-feeding; insects conceal themselves and are otherwise adapted to escape predation in many different ways, and often in different ways at different stages of their life cycles.

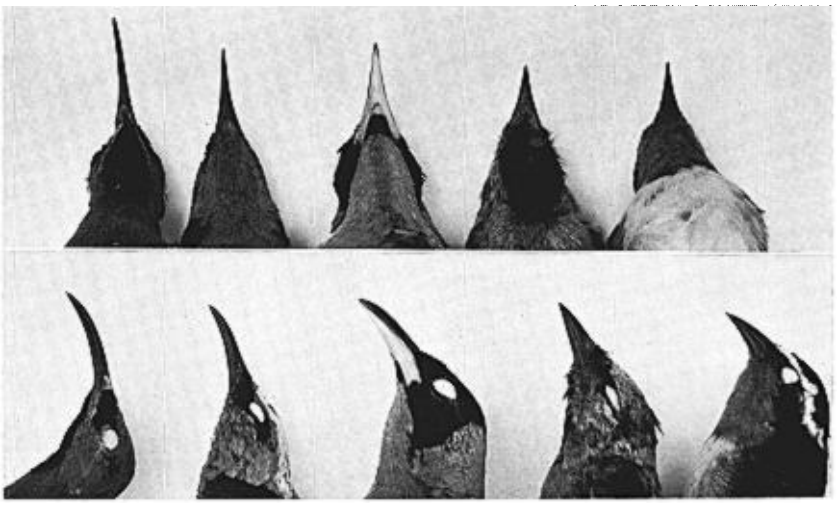

Figure 2. Beaks of Trinidad honeycreepers, from left to right: *Cyanerpes caeruleus*, *C. cyaneus*, *Chlorophanes spiza*, *Dacnis cayana*, *Coereba flaveola*.

Consequently a predator on insects has much greater scope for specialization than does a fruit-eater.

These general considerations seem adequate to account for the fact that fruit-eating birds in Trinidad are more numerous in individuals but less numerous in species than insectivorous birds (see Snow, 1971, for a fuller discussion of the evolutionary consequences of fruit-eating). There seems little doubt that they also account for the fact that in a family of birds of mixed diet, such as the tanagers, the techniques of insect-hunting and the parts of the vegetation searched for insects seem to constitute the crucial distinctions between species, so far as feeding ecology is concerned.

FEEDING ECOLOGY OF HONEYCREEPERS

Trinidad has four resident true honeycreepers and the Bananaquit (*Coereba flaveola*), which may be more closely related to the wood warblers (Parulidae) (one other species, the Bicolored Conebill (*Conirostrum bicolor*), occurs only in mangrove swamps and is not included in this survey). The very considerable differences in beak size and shape between these five species are shown in Figure 2.

PURPLE HONEYCREEPER (*Cyanerpes caeruleus*) AND RED-LEGGED HONEYCREEPER (*C. cyaneus*)

The male Purple Honeycreeper (*C. caeruleus*) is purple with black wings and tail and bright yellow legs; the male Red-legged Honeycreeper

(*C. cyaneus*) is dark blue with a turquoise crown, black wings and tail, and bright red legs. The females of both species are mainly green, darker above and paler with dark streaks below. Both species have long slender decurved beaks.

The Purple Honeycreeper is the smallest of the four true honeycreepers (Table 1) and has the longest, slenderest, and most decurved beak. The beak is probably adapted not only to eating nectar, of which the Purple Honeycreeper takes more than the three other species (Table 2), but also to its particular method of insect-hunting: 63 per cent of the records of insect-searching were of birds examining the undersides of fine twigs ½ to ⅛ inch in diameter, perching across the twigs and leaning over. Sometimes at least the prey is tiny spiders, and if one of them attempts to escape by descending on a thread the bird flutters after it. The small twigs examined in this way are often dead ones on an otherwise healthy tree. The long beak is also used for probing inside leaf buds and dead seed capsules.

The Purple Honeycreeper takes a smaller percentage of fruit than the other honeycreepers, and its narrow bill probably prevents it from including many of the fruits the other species eat. Of the Melastomaceae, only three *Miconia* species with rather small fruits were recorded in its diet; these *Miconia* fruits are probably near the upper size limit for Purple Honeycreepers. The fig *Ficus clusiifolia* it has to squeeze and crush before swallowing. Purple Honeycreepers occasionally use their beaks for piercing and then sucking fruits; we saw them treat tangerines and oranges in this way on several occasions, and a juicy native fruit, *Myrcia* sp. The long bill may also be advantageous in eating the edible portions of the fruits of the strangling climber *Clusia rosea*, a 3-inch woody capsule that splits open into many segments partly exposing the arillate seeds within. Purple Honeycreepers probe into these capsules, even coming to the ground to eat fallen fruit. The three other honeycreepers were less often seen taking *Clusia* fruit, though in Costa Rica Skutch (1962) records that they do so regularly.

The Red-legged Honeycreeper (*C. cyaneus*) is the least common of the Trinidad honeycreepers. Mees (Junge and Mees, 1958), who collected in Trinidad in 1953–54, found it uncommon and only saw it three times, whereas Léotaud (1866) and Belcher and Smooker (1937) reported it as common. We found that it seemed to disappear locally and reappear after a few weeks, but with no apparent regularity. Probably the species carries out local or even longer irregular movements.

Only 12 per cent of our Red-legged Honeycreeper records are of nectar feeding, compared with 44 per cent fruit-eating (Table 2), in contrast to the Purple Honeycreeper in which both stand at about 30 per cent. Red-

legged Honeycreepers were seen taking fruits of four species of *Miconia*, which appeared to be well within its size range. They are particularly fond of fleshy arils: thus 35 per cent of the fruit records are from three trees and one vine with arillate fruits, *Sloanea stipitata*, *Cupania* sp., *Matayba guianensis*, and *Doliocarpus dentatus*, none of which were seen to be taken by other honeycreepers or tanagers.

We found no difference in the Red-legged and Purple Honeycreepers' method of examining twigs; both examine the undersides of fine twigs less than ½-inch in diameter. But this made up a considerably smaller percentage of the Red-legged than of the Purple Honeycreeper's insect-hunting records, 36 per cent as compared to 63 per cent (Table 3), as the Red-legged Honeycreeper forages as much among foliage as on twigs. It usually examines the uppersides of leaves and was often seen pecking off food items that were too small to identify. Probably because of its rather long pointed wing, combined with a relatively short tarsus, the Red-legged Honeycreeper is adept at hovering, and it hovers frequently when foraging among leaves and also to take insects coming to flowers. Altogether 40 per cent of its recorded insect-hunting (including hawking for insects) was on the wing.

The heights at which Red-legged and Purple Honeycreepers feed are very similar (Figure 1). Both feed rather higher when insect-searching than when taking fruit. The proportions of feeding records from forest and nonforest habitats are also similar in both.

GREEN HONEYCREEPER (*Chlorophanes spiza*) AND BLUE DACNIS (*Dacnis cayana*)

The Green Honeycreeper (*C. spiza*) and the Blue Dacnis (*D. cayana*) both have relatively shorter and wider beaks than the *Cyanerpes* species (Table 1, Figure 2), and their beaks are nearly straight. They have a general similarity of plumage and proportions, and are considered together. The Green Honeycreeper is the largest of the Trinidad honeycreepers. The male is bright, slightly bluish green with black cheeks and crown; the female is duller green above and yellowish green below. The male Blue Dacnis is bright turquoise blue with a black throat, tail, and patch on the back; the wings are black with turquoise edgings. The female is green with black wings edged with green. The Blue Dacnis is about 22 per cent smaller than the Green Honeycreeper by weight, being about the same size as the Red-legged Honeycreeper from which it differs in having a relatively longer tarsus and tail and a shorter wing and beak.

Fruit forms a major part of the Green Honeycreeper's diet. Probably all of the Trinidad *Miconia* species are of suitable size for it to take (we recorded it feeding on eight species), although some of the shrub

species may be too low to be attractive to it. It takes nearly all fruit from a perched position and eats it whole, but we watched it pulling off pieces from fruits of *Protium heptaphyllum*, which are almost certainly too big (about ⅝-inch long) for it to swallow. We also saw it chew and drop the rather large fruits of *Ficus tobagensis*, which are about ¾-inch in diameter.

Although a rather small proportion of feeding records (15 per cent) were of insect-hunting (Table 2), the Green Honeycreeper has a specialized technique of insect-catching not seen in the other species. More than half of the insect-searching records were at flowers, mainly tree flowers with long stamens that attract insects. Green Honeycreepers perch among such flowers and dart about catching small insects that come to them, usually snapping them up in flight. For this their beaks are well-adapted, being wide at the gape (Figure 2). Green Honeycreepers occasionally take nectar from the same kinds of flowering trees, e.g. *Eugenia jambos*, *Calliandra guildingii*, *Inga* spp., and *Zanthoxylum* spp., trees ignored by the other nectar-eating birds except for the Bananaquit and the smallest hummingbirds. Probably they provide too little nectar to be attractive to the larger nectar-eaters, but are exploited by Green Honeycreepers because they come to the flowers for another purpose.

Like the *Cyanerpes* species, the Green Honeycreeper is largely a forest dweller, at times moving out into secondary forest and cultivation with trees. It takes fruit at similar heights to the other honeycreepers, but searches for insects at a rather higher level (Figure 1), owing to the fact that it forages near the flowering heads of forest trees.

The Blue Dacnis takes less nectar than any of the other honeycreepers; records of its feeding on fruit and insects are almost equal (Table 2). Nearly all its insect searching is among foliage, where it flits rapidly about examining both sides of the leaves, occasionally hanging to examine the underside of leaves or stretching up to examine and take something from the underside of a leaf above it. It was never seen to examine the undersides of twigs and branches in the manner of the Red-legged and Purple Honeycreepers. A characteristic searching posture is to duck its head below the twig it is perched on to examine the leaves just below it. It also examines and probes the leafy bases of bromeliads, and often probes into flower buds or seeding flower heads. We saw it take small green caterpillars and aphids. Its insect-hunting is often at a lower level than the Green Honeycreeper's, 22 per cent being below 25 feet as compared to 3 per cent in the latter.

The Blue Dacnis takes a wide variety of fruit; 26 species were recorded in its diet, 65 per cent of the records being from the families Euphorbiaceae (three tree species) and Melastomaceae (seven species). It takes its fruit

TABLE 6
RECORDS OF NECTAR-EATING BY *COEREBA FLAVEOLA*

More than 20 records	Trees	*Symphonia globulifera, Clathrotropis brachypetala, Erithrina micropteryx,*[1] *Cordia bicolor,*[2] *Tabebuia serratifolia*
11–20 records	Trees	*Vismia* spp., *Calliandra guildingii, Inga ingoides, Inga venosa, Warszewiczia coccinea, Isertia parviflora, Tabernaemontana* sp., *Cocos nucifera*
	Vines	*Bignonia unguis-cati*
1–10 records[3]	Trees	*Mangifera indica,*[1] *Spondias monbin,*[1] *Erythrina glauca, Lonchocarpus sericeus, Brownea latifolia, Pithecellobium jupunba, Pentaclethra macroloba, Inga* sp., *Samanea saman,*[1] *Dipteryx odorata,*[1] *Licania biglandulosa, Terminalia obovata, Cordia alliodora, Vitex divaricata, Tectona grandis,*[1] *Ocotea oblonga, Alchornea glandulosa, Hieronyma caribaea, Cecropia peltata*
	Shrubs	*Hibiscus rosa-sinensis*[1]
	Vines	*Norantea guianensis, Dioclea* sp., *Gurania spinulosa, Mandevilla hirsuta*
	Epiphytes	*Aechmaea nudicaulis*
	Herbs	*Justicia* sp., *Manihot utilissima,*[1] *Heliconia bihai, Heliconia hirsuta*

[1] Introduced species in Trinidad.
[2] Possibly including similar congeneric species.
[3] Seven unidentified species are omitted.

form a perched position or sometimes when clinging upside down. It was seen pecking pieces out of two kinds of fruit in situ; the others were swallowed whole. It feeds more often in nonforest habitats than the other honeycreepers, and is sometimes found in savanna country as well as in secondary forest and cultivation.

BANANAQUIT (*Coereba flaveola*)

The Bananaquit (*Coereba flaveola*) is black above with a yellow rump and upper tail coverts, and yellow below with a pale gray throat. It has a broad white eyestreak and white tips to the lateral tail feathers. It is lighter in weight and shorter in wing than the four honeycreepers, but it has the longest tarsus except for the much larger Green Honeycreeper (Table 1). Its bill is slightly decurved, very pointed, and about the same length as that of the Blue Dacnis (Figure 2).

The Bananaquit is probably the most abundant and successful bird in Trinidad. An idea of its abundance in relation to the four honeycreepers is provided by the number of different individuals caught during 3½ years of mist-netting, mostly in the same forest-edge area. Nets were never set

specially to catch honeycreepers or Bananaquits, and as they all feed at a variety of heights the numbers caught are probably a fair indication of relative abundance: Bananaquit, 234; Green Honeycreeper, 21; Red-legged Honeycreeper, 14; Blue Dacnis, 11; and Purple Honeycreeper, 10.

As well as being the most abundant of all the species considered here in a variety of wooded habitats, the Bananaquit occupies almost every type of nonforest habitat, such as town gardens, swamps, and even coconut plantations along the coast that attract very few other birds, besides all cultivated habitats with any tree growth. Its versatility is well-known, and especially its habit of taking sugar from the table in Tobago (Gross, 1958). It appears to be equally at home feeding at any level above the ground, and was even seen on a footpath turning over leaves.

The Bananaquit is primarily a nectar-feeder (Table 2). It has clearly specialized as a perching nectar-eater and as such no other bird in Trinidad can compete with it. The four true honeycreepers, as already seen, take only a small proportion of nectar, and that mostly from a few species of trees with large flowers. Our records show the Bananaquit feeding at 50 different flower species (Table 6), and no doubt further watching would easily add to the list. Of these, 32 were large trees (5 introduced), 7 were small trees or shrubs (2 introduced), 7 were vines, and 4 were herbaceous plants. Of the 432 nectar-feeding records, 27 per cent were from the two large trees, *Erythrina micropteryx* and *Symphonia globulifera*, which provide such a large proportion of the honeycreeper nectar-feeding records. The vine *Norantea*, a significant source of nectar for the Purple, Red-legged, and Green Honeycreepers, was only recorded twice for the Bananaquit, and not at all for the Blue Dacnis, which suggests that their bills are too short for probing into this flower's long corolla.

Most of the trees on which the Bananaquit, but not the other honeycreepers, feeds have very small flowers, often in clusters. Probably such flowers are only a worthwhile source of nectar for the Bananaquit because of its very small size (average 10.6 g compared with 12.6–18.2 g for the other four honeycreepers) and its extremely swift feeding movements. Besides flitting or hopping swiftly from one group of flowers to the next, its head movements are very quick and in a few seconds it can probe into 10 or more flowers in a cluster, if they are close together in umbels or cymes. From observations on the feeding of different hummingbirds in Trinidad a correlation was apparent between the size of flower, the amount of nectar produced (as measured by the time that a hummingbird spent at a flower), and the size of the hummingbird feeding at it (Snow and Snow, MS). Thus the bigger hummingbirds feed mostly at the bigger

flowers, and only the small hummingbirds feed at the very small-flowered trees exploited by the Bananaquit. Even so the number of plant species recorded for the Bananaquit is greater than for any of the hummingbird species. Whereas a hummingbird has to collect sufficient nectar to compensate for the energy used up in hovering in front of the flower, the Bananaquit is perched, makes only head movements, and often hops from one cluster of flowers to the next. Presumably therefore it is economic for it to feed at flowers that would not be economic for a hummingbird.

The Bananaquit thrusts its beak into most flowers in the usual way, from the front, but it obtains nectar from at least three native plants with long corollas (*Tabernaemontana* spp., *Tabebuia serratifolia*, and *Mandevilla hirsuta*) by piercing the corolla at the base, and it tackles some introduced flowers in the same way. Probably the relatively short, sharp, and slightly curved beak of the Bananaquit is adapted for rapid probing from a perched position into a number of flowers clustered together, a feeding method for which the longer curved beaks of *Cyanerpes* are not suited.

When insect-searching, Bananaquits mostly examine leaves and occasionally twigs, often clinging upside down to examine their undersides. But such records amounted to only 8 per cent of the total. An equally important source of protein appears to be the protein corpuscles (Mullerian bodies) at the base of the petioles of *Cecropia peltata*, a fast-growing tree of secondary forest (Table 2). Protein corpuscles are tiny white granules provided by the tree for the ants that live symbiotically within its trunk and branches, and are rapidly renewed by the tree when they have been eaten. Apart from a single record for the Blue Dacnis, no other honeycreeper or tanager was recorded feeding on them, but Skutch (1954) records that in Costa Rica *Tangara gyrola* does so.

Although Bananaquits were seen taking 15 kinds of fruit, these amounted only to 7 per cent of the total feeding records. They usually pierced and sucked the fruits of *Cordia bicolor* and *Ficus clusiifolia*. They chewed two of the *Miconia* species to extract the juice and then dropped the skins, a method no other birds were seen to use for these fruits. *Rhipsalis* was also chewed, but was treated in this way by other species too. They took other fruits whole from a perched position.

SEASONAL DIFFERENCES IN FOOD OF HONEYCREEPERS

Because they feed largely at the flowers of a few trees that flower seasonally, the proportion of the main foods taken by honeycreepers varies seasonally. As no differences were apparent between the species in this respect, all the feeding records have been combined in Table 7. (The Tanagers showed a similar seasonal change in the amount of nectar-

TABLE 7
SEASONAL VARIATION IN MAIN FOODS TAKEN BY HONEYCREEPERS

Months	No. records	Per cent composition		
		Nectar	Fruit	Insects
January–March	161	48	12	39
April–June	167	5	57	38
July–September	277	1	54	45
October–December	293	25	49	26

feeding, but as it always formed a small percentage of the total it had less effect on the other percentages.)

The proportion of insect-foraging remains most similar throughout the year, being lowest in the period October–December. At this time both nectar and fruit are plentiful, as some of the abundant large-flowered trees begin to bloom in November and many fruits ripen after the short dry season in September (Snow and Snow, 1964). The proportion of nectar taken varies most during the year, owing to the fact that 80 per cent of the nectar (according to our records) is taken from only three species, the introduced but now widespread tree *Erythrina micropteryx*, the native tree *Symphonia globulifera*, and the vine *Norantea guianensis*. These all flower mainly in the last 3 and first 3 months of the year, the latter being the main dry season. Fewest fruits ripen during the dry season, and the honeycreepers take the lowest proportion of fruits then. For the rest of the year, from April to December, fruit-eating remains at a high level, accounting for at least half the feeding records.

The seasonal variation in nectar-feeding by the honeycreepers is in contrast to the stable seasonal pattern for the Bananaquit (Table 8), for which nectar-feeding provided about 75 per cent of the records throughout the year. The Bananaquit exploits far more different kinds of flowers than the honeycreepers, including many small ones, and many of them are in flower at all seasons. In general the trees with large flowers bloom

TABLE 8
SEASONAL VARIATION IN MAIN FOODS TAKEN BY *COEREBA FLAVEOLA*

Months	No. records	Per cent composition			
		Nectar	Fruit	Insects	Protein corpuscles
January–March	68	73 (13)[1]	0	13	14
April–June	168	75 (22)	10	8	8
July–September	149	76 (16)	5	9	10
October–December	171	77 (18)	9	6	8

[1] Figures in parentheses show the number of flower species.

during the dry season and those with small flowers during the wet season (Snow and Snow, 1964).

DIFFERENCES IN FEEDING ECOLOGY BETWEEN HONEYCREEPERS

The most significant difference between the feeding ecologies of the two *Cyanerpes* species is probably in their insect-searching, in which they show only a small overlap. There are also some differences in the fruits they take. The Green Honeycreeper and Blue Dacnis have methods of insect-hunting that are even more distinct from each other's, and certainly constitute the main ecological difference between the two species so far as food is concerned. In addition, nectar forms an insignificant part of the diet of the Blue Dacnis compared with the Green Honeycreeper. The fruits eaten by the two species overlap widely.

The *Cyanerpes* species are more restricted in the variety of fruit taken than the other two species. Thus the Purple and Red-legged Honeycreepers were each recorded taking 12 species of fruits, compared with 22 and 26 species for the Green Honeycreeper and Blue Dacnis. This difference is probably directly correlated with the longer narrower beaks of the *Cyanerpes* species (Figure 2), to which may also be attributed their preference for arillate fruits from which they can peck off small pieces of soft aril instead of swallowing the whole fruit.

The Bananaquit has obviously specialized as a nectar-feeder able to exploit as many kinds of flowers as possible. Its rapid feeding movements have already been mentioned, and its small size, which makes it profitable to collect nectar from a perched position from flowers that are too small for a hummingbird to find economic. Its short rounded wind adapts it for quick flitting from flower head to flower head but not for hovering. It was in fact never seen to hover, and we had only two records of hawking, for both of which a longer and more pointed wing is more suitable. Furthermore it has a relatively longer tarsus than the honeycreepers and is extremely good at clinging, as was often brough home to us whenever we removed Bananaquits from mist nets. The long tarsus and strong grip are no doubt effective for perching and clinging to all kinds of surfaces, and in making the frequent rapid adjustments of body position necessary when extracting nectar from flower clusters.

In discussing the feeding ecology of the tanagers we showed that frugivorous species tend to be more numerous in individuals than insectivorous species in the same habitat, and argued that this depends on the very different availabilities of these two kinds of food. The data for the honeycreepers tend to show the same, though it is not easy to be sure of the relative abundance of all the species. Certainly the Green Honeycreeper is the most abundant, and of the four species it feeds most on

fruit and least on insects (Table 2). The other three feed to much the same extent on insects, and they differ little in abundance except that the Red-legged Honeycreeper is erratic in its occurrence, as already mentioned.

As a source of bird food nectar is comparable to fruit. It is a conspicuous source of food, and the less specialized flowers (like the smaller fruits) provide what may be regarded as a single source of plentiful food. It will thus be expected that specialized nectar-eaters that can take nectar from unspecialized flowers (unspecialized in the sense of not being adapted for pollination by particular kinds of birds, as are the long-corollaed hummingbird flowers) will be few in number of species but numerous in individuals. In fact the Bananaquit is the only species in Trinidad that successfully exploits many of the small unspecialized flowers, and it is far more abundant than any of the honeycreepers, which feed about as much on insects as on nectar and take nectar mainly from a few kinds of large flowers. The relationship between the Bananaquit and the honeycreepers is in this respect very similar to that between the manakins and the tanagers, discussed in a previous section.

Comparison with Other Areas

It is obviously of prime interest, in a comparative study of the feeding ecology of a widespread and numerous group of birds such as the tanagers and honeycreepers, to know whether interspecific differences in feeding behavior found in one area apply more widely to the species all over their ranges. Are the differences the result of local adjustments between closely related species through competition for the resources of that area, or are they more general specific characters? The question is especially relevant in the present case because Trinidad is an island with a relatively impoverished fauna compared with the adjacent mainland, so that it might be expected that the Trinidad populations of a species would have wider ecological niches than the conspecific mainland populations.

At this stage it is hardly possible to do more than raise these questions as a matter for future investigation. It is clear from numerous general statements in the literature that the main ecological characteristics of the genera and some of the species dealt with here—their niches in a very broad sense—are similar in many other areas and probably all over their ranges. Thus *Tangara* species are generally tree-living, forest-inhabiting tanagers that spend a good deal of their time high up in the canopy, *Tachyphonus rufus* is a tanager of forest-edge or even savanna country that feeds much nearer or even on the ground, *Ramphocelus* species frequent low bushy growth more than most other tanagers, and so on. But the finer differences in food preferences and in the manner of foraging have so far not received much attention.

A more detailed comparison, but still rather a limited one, can be made between Trinidad and Central America, where Skutch (1954, 1962) has published information on the feeding habits of tanagers and honeycreepers, mainly in Costa Rica. Skutch's data are descriptive rather than quantitative, so that it is not possible to compare the amount of feeding on different foods or in different ways; but they indicate that Central American populations show many of the same specific characteristics of feeding ecology as the Trinidad populations, with few, if any, important differences. Skutch's descriptions of the insect-foraging behavior of the different honeycreepers agree especially closely with what we found in Trinidad. He also notes the honeycreepers' fondness for arillate fruits. Skutch's account of the main feeding methods and foods of the Bananaquit also agrees very closely with what we observed. His accounts of the feeding behavior of three tanagers that also occur in Trinidad suggest a broad similarity with what we found, but it is not clear whether the differences in fruit preference we found among the tanagers apply to Central America.

The genus *Euphonia*, of which a number of species, very similar in size and structure, may occur together on the mainland, but only two in Trinidad, would repay more detailed study. As already noted, the indications from the literature are that all members of the genus are specialists on mistletoe fruits on the mainland, including species that closely resemble *E. trinitatis* (*E. luteicapilla*, *E. chlorotica*, and *E. laniirostris*); but *E. trinitatis*, according to our records, feeds mainly, or even exclusively, by foraging for insects.

We have tried to show that interspecific differences in wing and tail length, beak size and shape, and tarsus length are in many cases correlated with differences in feeding ecology. Closer investigation would probably show that this is a general rule, and that other subtler structural differences are involved, which we have not detected. It is thus to be expected that species that are structurally uniform all over their ranges will have similar feeding ecologies, and that subspecific differences involving size and proportions will be reflected in minor differences in feeding ecology. A study of museum skins may indicate what differences in feeding ecology are to be expected between sympatric species before any field work is undertaken.

MacArthur (1969, and earlier papers) has argued, from statistical analysis of bird species diversity and forest structure, that the number of bird species occurring in any given forest habitat depends on the physical complexity of the forest rather than on its floristic diversity. The results reported here contradict MacArthur's thesis, insofar as many of the observed specific differences in fruit-eating and nectar-eating depend on

the floristic diversity of the habitat. Knowledge of the insect fauna and of the feeding habits of insectivorous birds in tropical forests is so incomplete that it is not possible to examine the relations between birds and their insect prey quantitatively. As many insects are plant-specific, insect diversity must surely be correlated with floristic diversity, which should mean that the greater the floristic diversity, the more numerous will be the potential niches for insectivorous birds. The structural diversity of forest must also be correlated with floristic diversity; indeed at the finer structural level at which a feeding bird operates, floristic and structural diversity are almost synonymous. We feel, therefore, that in bypassing floristic diversity, MacArthur's correlations, though statistically sound, do not reflect the underlying ecological reality.

ACKNOWLEDGMENTS

We are indebted especially to the late N. Y. Sandwith, also to N. W. Simmonds and J. J. Wurdack for plant identifications, and to the New York Zoological Society for supporting our work, which was carried out while one of us (D.W.S.) was Resident Naturalist at the Society's tropical field station in Trinidad; and we acknowledge with gratitude a grant (G 4385) from the National Science Foundation.

SUMMARY

The feeding ecologies of 14 species of tanagers and honeycreepers are analyzed from records made over a 13½-month period in the Northern Range of Trinidad. Nearly all the species concerned have a mixed diet mainly of insects and fruit; nectar is a more or less important element in the diet of several species. Closely related species show little or no overlap in their methods of procuring the insect fraction of their diets; each species has a characteristic method of foraging for insects, which is reflected in its body proportions. On the other hand, despite some marked specific preferences for certain kinds of fruit, there is considerable overlap between species in the fruit fraction of their diets. It thus seems that the crucial differences between species, so far as feeding ecology is concerned, lie in their insect-searching techniques.

Within both the tanagers and the honeycreepers a correlation exists between numerical abundance and the amount of fruit-eating: the more frugivorous species tend to be the more abundant. A comparison between the tanagers and honeycreepers, taken as a group, and the more specialized insectivorous and frugivorous birds of similar size, living in the same habitats, shows a similar correlation. It is argued that on theoretical grounds fruit, as a main food supply, can be expected to support a larger number of individuals of a few species, and insects a smaller number of individuals belonging to a large number of species.

The most specialized nectar-feeder among the species dealt with, the

Bananaquit (*Coereba flaveola*) provides a parallel with the specialized fruit-eaters, combining a high number of individuals with the successful exploitation of many fundamentally similar food sources (flowers).

Skutch's data for Central America suggest that many of the differences in feeding ecology found in Trinidad are typical of the species generally over their ranges.

The results of this work are briefly discussed in relation to the hypothesis of MacArthur that bird species diversity depends on structural diversity of the habitat rather than on floristic diversity.

LITERATURE CITED

BEECHER, W. J. 1951. Convergence in the Coerebidae. Wilson Bull., 63: 274–287.

BELCHER, C., AND G. D. SMOOKER. 1937. Birds of the colony of Trinidad and Tobago, part 6. Ibis, 1, 14th Ser.: 504–550.

FORBES, W. A. 1880. On the structure of the stomach in certain genera of tanagers. Proc. Zool. Soc. London, 1880: 143–147.

GROSS, A. O. 1958. Life history of the Bananaquit on Tobago Island. Wilson Bull., 70: 257–279.

HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol., 22: 261–288.

JUNGE, G. C. A., AND G. F. MEES. 1958. The avifauna of Trinidad and Tobago. Zool. Verhand. (Leiden), No. 37.

LÉOTAUD, A. 1866. Oiseaux de l'Ile de la Trinidad. Port-of-Spain, Chronicle Publishing Office.

MACARTHUR, R. H. 1969. Patterns of communities in the tropics. Biol. J. Linnean Soc., 1: 19–30.

MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Narberth, Pennsylvania, Livingston Publ. Co.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna, No. 31.

SKUTCH, A. F. 1962. Life histories of honeycreepers. Condor, 64: 92–116.

SNOW, B. K. 1970. A field study of the Bearded Bellbird in Trinidad. Ibis, 112: 299–329.

SNOW, D. W. 1971. Evolutionary aspects of fruit-eating in birds. Ibis, in press.

SNOW, D. W., AND B. K. SNOW. 1963. Weights and wing-lengths of some Trinidad birds. Zoologica, 48: 1–12.

SNOW, D. W., AND B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica, 49: 1–35.

The Old Forge, Wingrave, Aylesbury, Buckinghamshire, England. Accepted 25 February 1970.