

VARIATION IN RESOURCE ABUNDANCE AFFECTS CAPTURE RATES OF BIRDS IN THREE LOWLAND HABITATS IN COSTA RICA

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ABSTRACT.—We examined temporal variation in abundance of understory birds and fruiting plants in young (5–7 yr) and old (25–35 yr) successional habitats and in intact, lowland rain forest at Estacion Biologica La Selva, Costa Rica, between January 1985 and May 1986. Fruit abundance varied seasonally in each habitat but was consistently greatest in the youngest site. Frugivores and nectarivores accounted for four (forest and older successional) or five (younger successional) of the five most frequently captured bird species in each habitat. Capture rates of arboreal frugivores and arboreal frugivore-insectivores were greatest in the youngest site and were not different between older habitats. Temporal variation in capture rates of frugivores resulted from habitat shifts by resident individuals and from arrival and departure of altitudinal and latitudinal migrants. Capture rates of frugivores correlated with fruit abundance in forest and the older successional habitat but not in the youngest site. Capture rates of nectarivores and insectivores varied over time and among habitats, but rates showed no correlation with capture rates of frugivores. The lack of positive correlations in seasonal capture rates among trophic groups and the correlation between frugivores and fruit abundance support the view that temporal and spatial variation in bird abundance in tropical bird communities is at least partially in response to variation in resource abundance. *Received 3 November 1989, accepted 28 July 1990.*

BIRD populations vary in abundance over time and space in both temperate (e.g. Kendeigh 1982, Holmes et al. 1986, many others) and tropical habitats (e.g. Fogden 1972; Karr 1976; Leighton and Leighton 1983; Martin and Karr 1986a; Loiselle 1987a, 1988; Loiselle and Blake 1991; but see Greenberg and Gradwohl 1986). Fluctuations in abundance arise from variation in population processes (Orell and Ojanen 1983, Faaborg et al. 1984, DeSante and Geupel 1987) and from movement of individuals among habitats (Karr and Freemark 1983, Wheelwright 1983, Recher and Holmes 1985, Loiselle et al. 1989, Loiselle and Blake 1991). Such movements may represent random redistribution of individuals (Wiens and Rotenberry 1978, Wiens 1984), but such hypotheses often have been advanced in the absence of data on food abundance. Individual movements may instead reflect responses to changes in microclimatic conditions (Karr and Freemark 1983, Petit 1989) or to temporal and spatial variation in food (e.g. Leighton and Leighton 1983, Wheelwright 1983,

Recher and Holmes 1985, Loiselle and Blake 1991).

Most studies lack concurrent data on fluctuations in both bird population levels and food abundance (but see Wheelwright 1983; Stiles 1985a; Levey 1988a, b; Loiselle and Blake 1991). Consequently, a more direct examination of avian responses to variations in food supply is central to resolving the controversial role of food as an influence in organization of species assemblages (Wiens 1984, Martin 1986). To address this controversy, we used data from concurrent studies on temporal and spatial variation in abundance of tropical frugivores and fruit among three habitats in Costa Rica. We focus mainly on frugivores, but for comparison we examined seasonal rhythms of bird groups (nectarivores, insectivores) that rely on different resources.

Tropical frugivores are particularly appropriate for the study of the influence of resource availability on consumer populations because their diets can be readily determined (e.g. Wheelwright et al. 1984, Loiselle and Blake 1990) and their resources (fruit) accurately measured (Blake et al. 1990). Fruit-eating birds also are a major component of many tropical communi-

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ties (e.g. Stiles 1985b, Loiselle 1988, Karr et al. 1990, Loiselle and Blake 1991), and frugivores disperse seeds from a large proportion of tropical shrubs and trees that produce fruits (e.g. Howe and Smallwood 1982, Stiles 1985b). Thus, it is important both from theoretical and practical standpoints to better understand the interactions between frugivorous birds and fruit-producing plants (Stiles 1985b, c).

STUDY AREA AND METHODS

STUDY AREA

We conducted our research at Estacion Biologica La Selva, located in the lowlands of northeastern Costa Rica, near Puerto Viejo de Sarapiquí, Provincia Heredia (10°25'N, 84°01'W). La Selva encompasses approx. 1,433 ha, of which approx. 67% is primary forest. The station also supports anthropogenic successional habitats in various stages of regrowth. La Selva borders with Parque Nacional Braulio Carrillo (approx. 44,900 ha); continuous forest exists from approx. 40 m to >2,900 m (Pringle et al. 1984).

Rainfall at La Selva averages 3,877 mm/yr (1958–1988, Organization for Tropical Studies unpubl. data). The dry season typically lasts from January or February to April or May, with a second, less pronounced dry season in September and October. Rainfall was low during our study: 2,605 mm fell in 1985, and 753 mm fell from January through May 1986.

We established study plots in young (ca. 5–7 yr) and old (ca. 25–35 yr) successional habitats and in undisturbed primary forest. The young successional plot was located within an approx. 40-ha tract of former pasture bordered by older second growth. Vegetation averaged 5–8 m in height. Scattered large trees (e.g. *Ficus* sp.) also were present. The older successional plot was located within a tract of approx. 20–25 ha bordered by primary forest and younger second growth. Trees averaged 15–20 m over much of the plot. The primary forest plot was within the main block of undisturbed forest of La Selva where canopy height reaches 30–40 m (Hartshorn and Peralta 1988). A more detailed description of the forest at La Selva is in Hartshorn (1983).

METHODS

Birds.—We used mist nets (12-m, 4 shelf, 36-mm mesh) to sample birds in the lower levels of each habitat. Ground-level nets effectively sample most birds in the understory, especially passerines (e.g. Karr 1979, 1981; Karr and Freemark 1983; Levey 1988a, b; Blake 1989; Loiselle and Blake 1991). Mist nets allow simultaneous sampling of different points independent of observer biases (e.g. familiarity with

vocalizations; Karr 1981) and allow direct comparisons among studies (Karr et al. 1990). Mist nets operated at ground level do not provide a sample of the entire avifauna but do provide a quantitative sample of birds that use a defined habitat segment. We recognize that the capture of a bird does not necessarily mean that forest understory is its typical habitat, only that it might have consumed food at that level (see Levey 1988a). As with any sampling technique, mist nets are subject to biases (Lovejoy 1975, Karr 1981, Remsen and Parker 1983, Terborgh 1985c). For example, birds heavier than 100 g, ground- or canopy-dwelling species, and sedentary species may be inadequately represented in captures. Furthermore, capture rates may decline over time as birds “learn” net locations. We opened mist nets for only 2 days every 5–6 weeks at any one location, and recapture rates were high between sample periods. Recapture rates were higher when migrants were excluded. Thus, we feel that any problems associated with “net-shyness” of birds (Terborgh 1985b) were minimized. Levey (1988a, b) and Karr (1990) recently discussed the use of mist nets in studies of tropical birds.

We arranged 30 nets in a grid that covered approx. 4.8 ha in each habitat; nets were ca. 40 m apart. We expanded our forest plot to 54 nets (ca. 9 ha) in September 1985. We operated nets in each area for 4–6 days every 5–6 weeks, starting in January 1985. Each net was operated on only two alternate days each sample. Fifteen nets (18 in forest after September 1985) were opened on any one day, from dawn to approx. 1300, or as close to 7 h/day as possible. Captured birds were banded, weighed, sexed, and aged (if possible). We held all birds (except hummingbirds and raptors) for collection of fecal samples and released birds at the point of capture.

We assigned species to guilds (Appendix) on the basis of observations of foraging behavior and analyses of fecal samples (>3,080 fecal samples; Loiselle and Blake 1990). We supplemented those data in some cases by using various published sources (e.g. Skutch 1954, 1967, 1969; Slud 1964). Most species used a variety of foraging techniques, strata, and food, and placement of a species in a particular guild often was a compromise. We classified species as frugivores if their diet was composed almost entirely of fruit. Frugivore-insectivores were species that commonly fed on both fruit and insects. English and scientific names (Appendix) follow the Check-list (AOU 1983 and supplements).

Fruit.—Fruits were sampled during the same periods that birds were netted. We sampled fruits in two transects (2 × 12.5 m each) located parallel to and 1 m away from the sides of each net (combined sample of 50 m² per net-site). We identified and tagged all plants with fruit displayed below 10 m and counted ripe and unripe fruits on each plant during each sample (i.e. every 5–6 weeks). Although fruits of understory plants vary in size and nutrient content, we

decided to use actual numbers of fruits as our estimate of fruit available to birds. Most understory fruits used by birds are berries of the Melastomataceae or Rubiaceae (Loiselle 1987b, Loiselle and Blake 1990), and it is likely that the large variation in number of fruits available among samples overwhelms any interspecific variation in fruit size or nutrient content. Additional factors, such as digestive efficiency, influence the value of a fruit to a species (see Worthington 1989), but we lack necessary data for most species. Further, digestive efficiency is highly variable—depending on the fruit consumed—within a species and often is not dependent on nutrient or energy content of the fruit (Johnson et al. 1985, Worthington 1989). Thus, we feel that fruit number provides a reasonable estimate of resource availability. We restricted our analyses to those plants known to be visited by birds for their fruit (based on analysis of fecal samples, personal observations of foraging birds; Croat 1978). A more detailed phenological analysis based on all plants is in Loiselle (1987b).

Analyses.—We used one-way analysis of variance (ANOVA; Sokal and Rohlf 1981) followed by a Scheffé multiple comparison among means test (Scheffé test hereafter) to compare fruit abundance among habitats during each sample period. Abundance of fruit during one sample period may be influenced by (correlated with) abundance during the previous sample if fruits remain on a plant or ripen during the intervening period. Thus, samples may not be statistically independent, although they do “represent the actual biology of the systems” (Wiens 1989: 149). Consequently, we used a repeated measures ANOVA (Freund et al. 1986) to compare fruit abundance over time and among habitats. The different sample periods represented repeated measures of each net site within each plot. Tests based on two-way analysis of variance (not a repeated measures design) yielded the same results. We matched sample dates as closely as possible for among-habitat comparisons.

We used number of birds captured per 100 net-hours (one mist net open 1 h = 1 net-hour) as an index of bird abundance during each sample period. To compare capture rates over time among habitats, we combined all captures for a particular sample period to give a single value for each habitat. We then used a Wilcoxon matched-pairs signed-ranks test (Wilcoxon test hereafter) to compare capture rates between habitats.

We examined relationships between bird and fruit abundance through correlation analyses. We used fruit abundance per net-site (averaged over all net sites) and overall capture rate during a given sample period as variables. When an area is netted for the first time, we assume all birds are naive with respect to occurrence and location of nets. Subsequently some learn net locations and avoid capture, or they leave the area. Samples of fruit abundance are not subject to similar behavioral effects and, consequently, we examined

correlations with the first sampling period from each site omitted.

All variables were tested for normality (Wilk-Shapiro test) and equality of variances (Bartlett's test) before statistical analyses and were log-transformed (\ln) when assumptions were violated. Nonparametric tests were used when necessary. Additional statistical tests are identified in the text.

RESULTS

Fruits.—Abundance of ripe and unripe fruit in the understory varied among habitats (Fig. 1; $F = 118.0$ [ripe] and 135.0 [unripe], $P < 0.001$). More fruit was available on the young successional plot than on older plots during each sample period (Fig. 1; Scheffé tests, $P < 0.05$ in all comparisons). In contrast, fruit abundance did not differ between the older successional plot and forest (Fig. 1). Ripe and unripe fruit varied in abundance over time in each habitat (Fig. 1; $F = 6.6$ [ripe] and 21.7 [unripe], $P < 0.001$), and wet-season peaks were significantly greater than dry-season lows. Peak periods of ripe-fruit abundance varied among habitats, while unripe fruit peaked in abundance at all sites during the August through October period (Fig. 1).

We recorded 142 species of bird-dispersed plants bearing fruit, including 55 in the young successional plot, 66 in the older successional plot, and 69 in the forest. The number of species bearing fruit in the understory (i.e. < 10 m) varied among habitats ($F = 135.1$, $P < 0.001$) but was consistently higher in the young than in the older second growth, and higher in the older second growth than in the forest (Fig. 2; Scheffé tests). The number of species bearing fruit varied over time in each habitat ($F = 18.5$, $P < 0.001$). The seasonal pattern in the number of fruiting species generally was similar in all habitats, with lows in the dry season and highs in the wet season (Fig. 2).

We found that the number of fruiting individuals per net site varied among habitats ($F = 304.3$, $P < 0.001$). More individuals were fruiting in the youngest habitat than in either of the older sites (Fig. 2). Fruit-bearing plants were, overall, more abundant in the older successional plot than in forest (Fig. 2), although differences were not significant during each sample (one-way ANOVA, Scheffé tests). The number of individuals bearing fruit varied over time in each habitat ($F = 19.4$, $P < 0.001$). Numbers peaked in the youngest site in the wet season

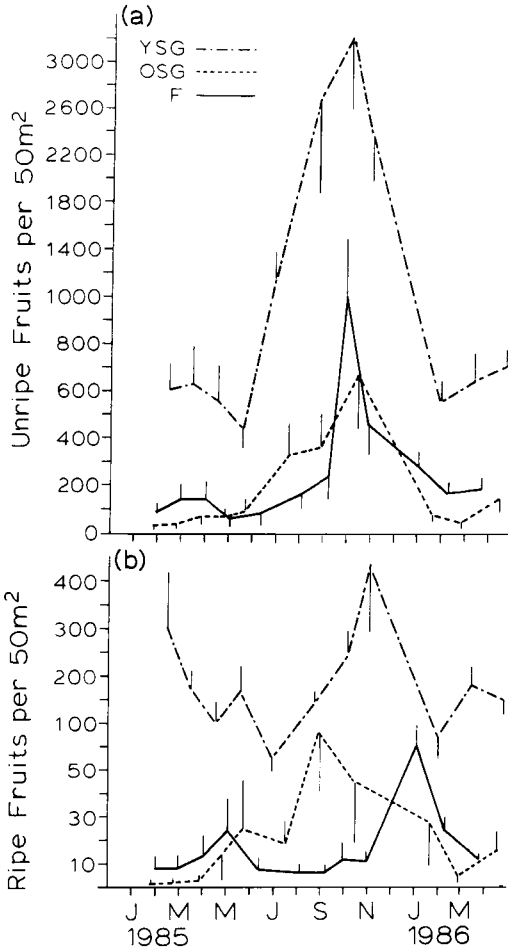


Fig. 1. Seasonal abundance of (a) unripe and (b) ripe understory, bird-dispersed fruits in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva. Values are means; SE are given as vertical lines.

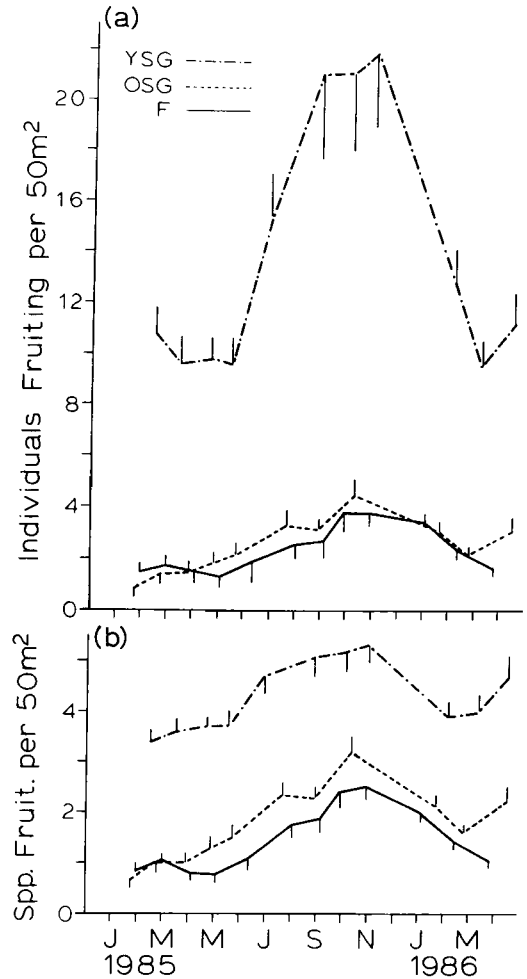


Fig. 2. Seasonal abundance of (a) individuals and (b) species of understory, bird-dispersed fruiting plants and species in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva. Values are means; SE are given as vertical lines.

(Fig. 2), largely because of a sharp increase in number of fruiting *Psychotria pittieri* Standl. (Rubiaceae). Peaks in the number of individuals fruiting were less pronounced in older sites, but still significant (Fig. 2).

Bird species composition.—We captured 4,261 birds representing 2,841 individuals of 162 species (Appendix). Numerically dominant species differed among habitats (Table 1), but Long-tailed Hermit (*Phaethornis superciliosus*) and Ochre-bellied Flycatcher (*Mionectes oleagineus*) were abundant in all habitats. Frugivores and nectarivores accounted for four (in forest and older successional habitats) or five (in younger successional) of the five most frequently cap-

tured species in each habitat (Table 1). Other important guilds included bark and foliage insectivores (Table 2).

Frugivores.—Frugivores (including frugivore-insectivores) accounted for 47% (1,988) of all captures. Frugivore guilds are listed in Table 2. Red-capped (*Pipra mentalis*) and White-collared (*Manacus candei*) manakins accounted for 25% of all frugivore captures; Ochre-bellied Flycatchers accounted for 15%. Temperate migrants (species that breed in North America) accounted for 17% of all frugivore captures; altitudinal migrants (species that breed at higher elevations in Parque Nacional Braulio Carrillo)

TABLE 1. Number of captures (and percentage of total captures) of the five most frequently captured species in each habitat.

Forest		Old second growth		Young second growth	
Species	n (%)	Species	n (%)	Species	n (%)
Wedge-billed Woodcreeper	160 (14.3)	Wedge-billed Woodcreeper	121 (10.7)	White-collared Manakin	169 (8.4)
Red-capped Manakin	143 (12.8)	Long-tailed Hermit	110 (9.7)	Long-tailed Hermit	163 (8.1)
Ochre-bellied Flycatcher	97 (8.7)	Ochre-bellied Flycatcher	89 (7.9)	Bronzy Hermit	151 (7.5)
Long-tailed Hermit	74 (6.6)	Red-capped Manakin	74 (6.5)	Scarlet-rumped Tanager	128 (6.4)
Wood Thrush	57 (5.1)	White-collared Manakin	69 (6.1)	Ochre-bellied Flycatcher	112 (5.6)

accounted for a minimum of 7%. The estimate for altitudinal migrants is conservative because some species (e.g. Red-capped Manakin) counted as residents also were represented by migrant individuals (Loiselle and Blake 1991). Capture rates of all frugivores varied over time within habitats but were consistently higher in young than in old second growth (Wilcoxon test, $P < 0.005$) and higher in old second growth than in forest (Wilcoxon test, $P < 0.05$). Terrestrial frugivores and terrestrial frugivore-insectivores were captured infrequently (Table 2) and accounted for only 11% of all frugivore captures. Consequently, we focus on arboreal frugivores and arboreal frugivore-insectivores.

Capture rates of arboreal frugivores were higher in young second growth than in older second growth (Wilcoxon test, $P < 0.08$) or forest (Wilcoxon test, $P < 0.05$) during most sampling periods, but there was no difference between older habitats ($P > 0.50$) (Fig. 3a). Arboreal frugivores accounted for a greater proportion

of captures in forest (19% of total captures) than in old (14%) or young successional (12%) habitats. Seasonal patterns of capture rates were similar among habitats ($r > 0.68$, $P < 0.05$, all pairwise comparisons). Significance of correlations largely was attributed to arrival and departure of altitudinal migrants (see below), most of whom were arboreal frugivores (e.g. White-ruffed Manakin, *Corapipo leucorroha*).

Capture rates of arboreal frugivore-insectivores were greater in young than in old second growth (Wilcoxon test, $P < 0.007$) or forest ($P < 0.004$) during all sampling periods (Fig. 3b). Capture rates were higher in the older successional habitat than in the forest during most sample periods (Wilcoxon test, $P < 0.07$). Capture rates of arboreal frugivore-insectivores were not correlated among habitats, indicating that seasonal patterns of capture rate differed among habitats.

Much of the variation in capture rates of frugivores was due to changes in capture rates of

TABLE 2. Number of captures (and percentage of total captures) within different trophic groups (+ = <0.5%).

Trophic group	Primary forest	Old second growth	Young second growth
Terrestrial frugivore	14 (1)	13 (1)	47 (2)
Arboreal frugivore	209 (19)	161 (14)	244 (12)
Terrestrial frugivore-insectivore	3 (+)	46 (4)	89 (4)
Arboreal frugivore-insectivore	255 (23)	248 (22)	659 (33)
Terrestrial insectivore	58 (5)	43 (4)	131 (7)
Foliage insectivore (leaf surfaces)	116 (10)	117 (10)	198 (10)
Bark insectivore	173 (16)	142 (13)	50 (2)
Aerial insectivore (flycatcher)	23 (2)	26 (2)	47 (2)
Ant-following insectivore	128 (11)	68 (6)	7 (+)
Nectarivore-insectivore	128 (11)	243 (21)	477 (24)
Granivore (grass seeds)	4 (+)	22 (2)	61 (3)
Carnivore (raptors)	4 (+)	3 (+)	2 (+)
Piscivore	1 (+)	1 (+)	0 (0)

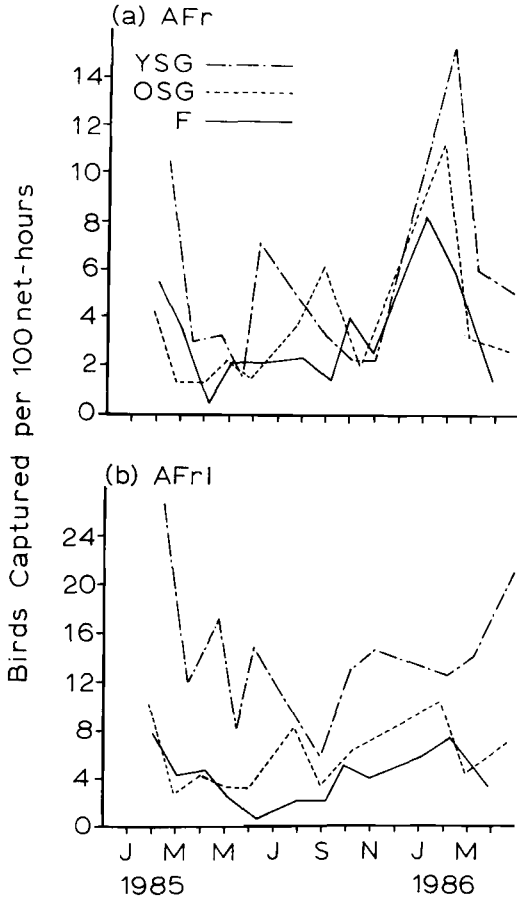


Fig. 3. Capture rates of (a) arboreal frugivores (AFr) and (b) arboreal frugivore-insectivores (AFrI) in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva.

altitudinal and temperate migrants (Fig. 4). Temperate migrants, primarily thrushes (*Turdinae*), were captured most frequently in the youngest habitat; peaks in capture rates corresponded to spring (April to May) and autumn (September to October) passages of migrants through La Selva. Altitudinal migrants, in contrast, were more frequently captured in forest and older second-growth habitats. Capture rates of altitudinal migrants peaked during December to January.

Altitudinal movements by several species (e.g. Red-capped Manakin, Ochre-bellied Flycatcher) that are present at La Selva throughout the year contributed substantially to seasonal variation in capture rates of frugivores (Fig. 5). Habitat shifts by residents at La Selva, as indicated

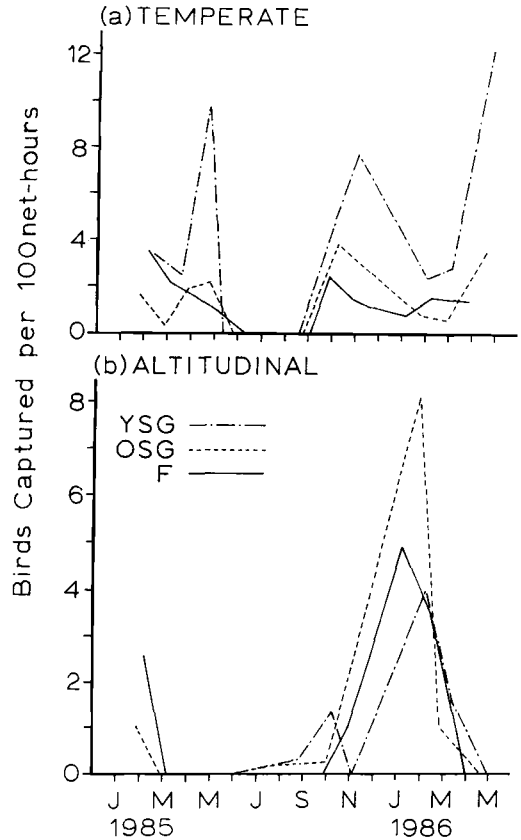


Fig. 4. Capture rates of frugivorous (a) temperate and (b) altitudinal migrants in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva.

by recaptures of individuals between habitats (Table 3), further contributed to temporal and spatial variation in capture rates of frugivores. Capture rates of resident Ochre-bellied Flycatchers, for example, increased in older second-growth habitats at a time when capture rates declined elsewhere. Similarly, Ochre-bellied Flycatchers accounted for 42% of recaptures of frugivores between young and old successional habitats.

Fruit abundance and capture rates of frugivores.— Capture rates of frugivores, particularly in primary forest, generally were greater during periods when fruit was abundant (Figs. 1-3). Capture rates of frugivores in primary forest correlated most strongly with several measures of ripe fruit abundance (Table 4). Capture rates of frugivores in the older successional habitat correlated most strongly with number of spe-

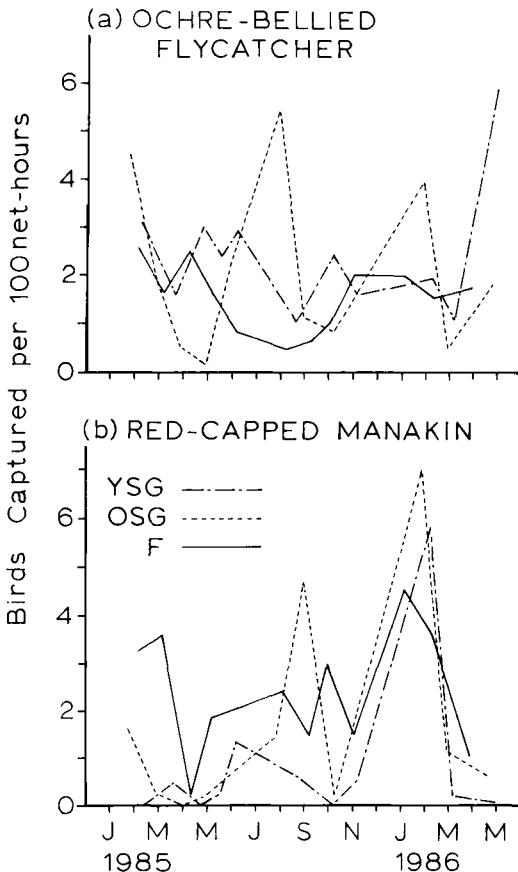


Fig. 5. Capture rates of (a) Ochre-bellied Flycatchers and (b) Red-capped Manakins in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva.

cies and individuals bearing fruit and less strongly with actual fruit abundance. In contrast, capture rates of frugivores in the youngest habitat were negatively correlated with measures of fruit abundance.

Effects of among-habitat differences in fruit abundance on capture rates of frugivores were evident when data from all habitats were used in a correlation analysis ($n = 31$ samples: 11 from forest, 10 from each successional habitat). Capture rates of all frugivores and of arboreal frugivore-insectivores separately were correlated with all measures of fruit abundance ($P < 0.01$, all cases); capture rates of arboreal frugivores were correlated with abundance of ripe fruit ($P < 0.05$), with number of individuals bearing fruit ($P < 0.05$), and with number of species bearing fruit ($P < 0.01$).

TABLE 3. Number of recaptures of marked individuals between habitats.

Trophic group	Habitats		
	YSG-OSG ^a	OSG-forest	YSG-forest
Frugivores			
Species	7	2	2
Individuals	43	2	3
Nectarivores			
Species	6	0	2
Individuals	26	0	3
Insectivores			
Species	5	5	1
Individuals	7	7	2

^a YSG = young second growth; OSG = old second growth.

Nectarivores.—Capture rates of nectarivores were greater throughout the year in the young than in the old second growth (Wilcoxon test, $P < 0.005$), and greater in the old second growth than in forest ($P < 0.005$) (Fig. 6). Capture rates of nectarivores tended to peak in the early dry season (January to February) and early wet season (May to June) in all habitats. Capture rates of nectarivores were correlated positively between second-growth habitats ($r = 0.88$, $P < 0.001$) but not correlated significantly between second-growth habitats and forest. Habitat shifts by nectarivores contributed to variation in capture rates. Hummingbirds accounted for a much greater proportion of recaptures between habitats in our study than expected (Table 3) based on the number of captures of nectarivores, frugivores, and insectivores ($\chi^2 = 13.5$, $P < 0.002$).

Insectivores.—Terrestrial (Fig. 7a) and foliage (Fig. 7b) insectivores were captured more frequently in the young than in the old successional habitat (Wilcoxon tests, $P < 0.05$, both cases) and more frequently in the older successional habitat than in forest (Wilcoxon tests, $P < 0.07$ for terrestrial and $P < 0.05$ for foliage insectivores). Capture rates of terrestrial insectivores were correlated ($P < 0.05$) between successional plots, which indicates a similar seasonal pattern. Ovenbirds (*Seiurus aurocapillus*) and Kentucky Warblers (*Oporornis formosus*) were frequently captured in both habitats (Appendix) and accounted for much of the similarity. Seasonal variation in capture rates of foliage insectivores was less pronounced in the older habitats where temperate migrants were captured less often.

TABLE 4. Correlation coefficients between capture rates of frugivores and measures of fruit abundance in primary forest ($n = 11$), old second growth ($n = 10$), and young second growth ($n = 10$) habitats. * = $P < 0.05$; ** = $P < 0.01$.

Habitat	Fruits		Individuals		Species	
	No. ripe	No. unripe	No. with ripe fruits	No. with any fruits	No. with ripe fruits	No. with any fruits
Forest						
All frugivores	0.76**	0.34	0.57 ^a	0.40	0.68*	0.31
Arboreal frugivores	0.73**	0.29	0.49	0.49	0.62*	0.41
Arbor. frug.-insectivores	0.62*	0.34	0.54 ^a	0.25	0.60*	0.15
Old second growth						
All frugivores	0.47	0.35	0.65*	0.66*	0.63*	0.64*
Arboreal frugivores	0.56 ^a	0.21	0.53	0.52	0.46	0.52
Arbor. frug.-insectivores	0.37	0.41	0.65*	0.71*	0.67*	0.68*
Young second growth						
All frugivores	-0.49	-0.42	-0.32	-0.34	-0.64*	-0.20
Arboreal frugivores	-0.65*	-0.31	-0.33	-0.16	-0.75*	-0.14
Arbor. frug.-insectivores	-0.08	-0.27	0.23	-0.30	-0.38	-0.08

^a $P < 0.10$.

Capture rates of aerial-salliers (flycatchers) were not consistently greatest in any habitat. Noticeable peaks in capture rate in the youngest site (Fig. 7c) corresponded to periods when *Empidonax* flycatchers were present. Capture rates of aerial-salliers were not correlated between sites.

Fewer bark insectivores were captured in the youngest habitat than in the older areas (Wilcoxon tests, $P < 0.005$), but there was no consistent difference between old second growth and primary forest (Fig. 7d). Capture rates tended to be greatest in the dry season, particularly in older habitats, but were not correlated between any two habitats.

Capture rates of ant-following insectivores varied with the presence of army ants (e.g. *Eciton burchelli*). Army ants were seen frequently in forest and old successional sites, where capture rates of ant-following insectivores were consistently greater than in the young successional site (Wilcoxon tests, $P < 0.05$; Fig. 7e). Army ants were seen rarely in the young second growth, and only one ant-following species (Bare-crowned Antbird, *Gymnocichla nudiceps*) was captured more than once in that habitat (Appendix).

With one exception, capture rates of different insectivore groups were not significantly correlated between groups within habitats, which indicates that seasonal patterns of abundance differed among groups. Capture rates of terrestrial insectivores and foliage insectivores were

positively correlated ($r = 0.66$, $P < 0.05$) in the young second-growth site. Similarly, capture rates of insectivores generally were not correlated with capture rates of frugivores or nectarivores. Bark insectivores were positively correlated with capture rates of nectarivores in the

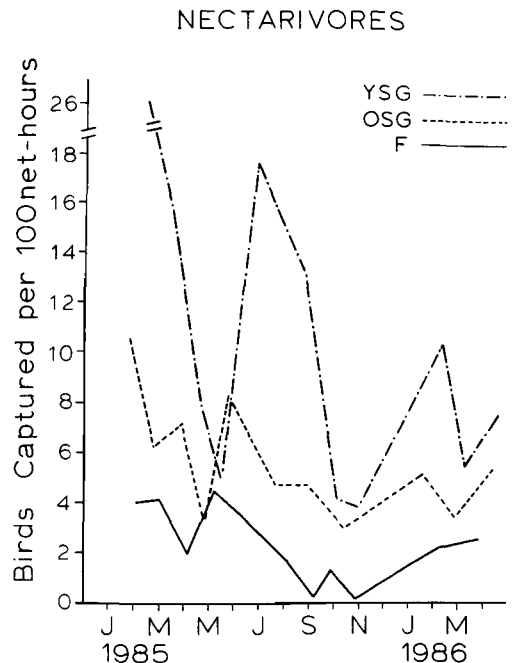


Fig. 6. Capture rates of nectarivores in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva.

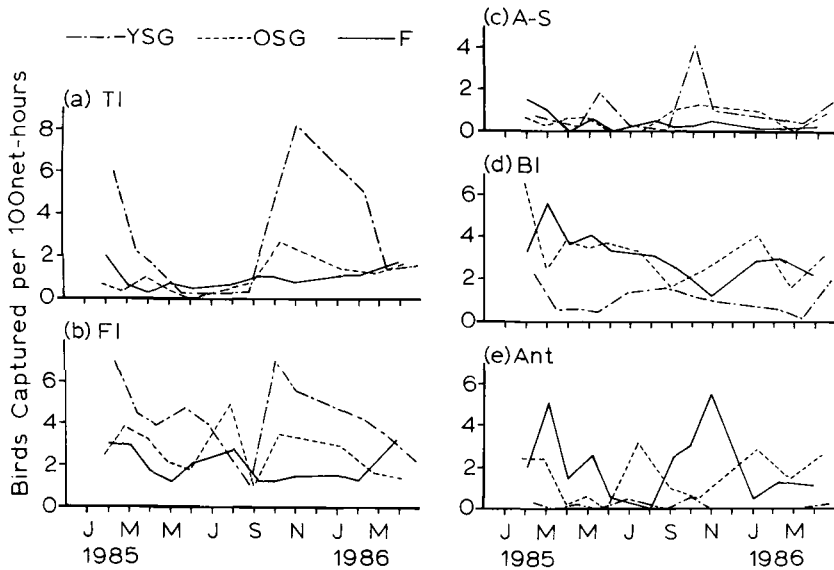


Fig. 7. Capture rates of (a) terrestrial insectivores (TI), (b) foliage insectivores (FI), (c) aerial-salliers (A-S), (d) bark insectivores (BI), and (e) ant-following insectivores (Ant) in young second growth (YSG), old second growth (OSG), and forest (F) at La Selva.

old second growth ($r = 0.75$, $P < 0.01$) and in primary forest ($r = 0.72$, $P < 0.01$) and with capture rate of arboreal frugivore-insectivores in the old second-growth site ($r = 0.64$, $P < 0.05$). Ant-following insectivores also were correlated with arboreal frugivore-insectivores in the old second growth ($r = 0.63$, $P < 0.05$). The biological significance of these correlations was not immediately apparent. Furthermore, the number of significant correlations (5 of 75 pairwise comparisons) was not significantly greater than expected by chance.

DISCUSSION

Fruit as a variable resource for tropical birds.—Several authors have commented on the often patchy and erratic nature of fruit as a food supply for tropical birds (e.g. Fogden 1972, Karr 1976, Fleming 1979, Herrera 1985, Levey 1988b). Fruiting phenology often is well defined, even in aseasonal, wet tropical climates (Frankie et al. 1974, Hilty 1980), although fruiting seasons may show marked variation between years (Fogden 1972, Foster 1982, Wheelwright 1986). Fruit production at La Selva generally peaks in the mid-to-late rainy season and reaches a low during the late dry season (Frankie et al. 1974, Opler et al. 1980, Denslow et al. 1986, Loiselle 1987b). Rainfall was below normal during our

study (1985 was the driest year on record at La Selva), but seasonal patterns of fruit production were similar to those reported by previous studies.

Production of fruits by understory shrubs and treelets typically is greater and more seasonal in young habitats at La Selva than in forest (Opler et al. 1980, Levey 1988b, this study). Periods of ripe-fruit abundance also showed substantial among-habitat variation at La Selva (Levey 1988b, this study). The greater overall abundance of fruits and fruiting plants in second-growth habitats (Martin 1985, Levey 1988b, this study) means that there is a greater probability of fruit being available at any location within such habitats. Thus, fruit may be a reliable resource at some temporal and spatial scales but, at the same time, may exhibit considerable variation in abundance and distribution patterns at different scales of resolution.

Temporal and spatial variation in frugivore abundance.—Large seasonal fluctuations in frugivore abundance occur in many tropical regions (e.g. Leighton and Leighton 1983; Martin and Karr 1986a; Wong 1986; Loiselle 1987b, 1988; Levey 1988b). Temporal fluctuations in capture rates at La Selva are influenced by arrival and departure of temperate migrants (Fig. 4), many of which are at least partly frugivorous while in the tropics (Morton 1971, Greenberg 1981, Mar-

tin 1985, Loiselle and Blake 1990) and by altitudinal migrants (Loiselle and Blake 1991).

Approximately 75 species of birds in Costa Rica are known or suspected to make seasonal, altitudinal movements (Stiles 1985c); some 25 species regularly reach La Selva (Blake et al. 1990, Levey and Stiles in press). Most altitudinal migrants present at La Selva from approximately October to April are frugivores (Stiles 1985c, Blake et al. 1990, Loiselle and Blake 1991). Movements by those species (e.g. White-ruffed Manakin, Olive-striped Flycatcher [*Mionectes olivaceus*]) into and out of lowland habitats contribute substantially to observed variation in capture rates at La Selva. Unlike temperate migrants, altitudinal migrants were captured more frequently in older forest than in young second growth, and they were more common in mid-“winter” (December and January) than were temperate migrants (see Fig. 4; also Blake et al. 1990). Stiles (1985c) noted that approximately 86% of altitudinal migrants in Costa Rica are forest-dependent.

Individuals of some species that are resident at La Selva throughout the year (e.g. Red-capped Manakin, Ochre-bellied Flycatcher) also move up and down the elevational gradient. These movements contribute substantially to seasonal variation in capture rates of frugivores. Evidence for altitudinal movements by Red-capped Manakins and Ochre-bellied Flycatchers comes, indirectly, from changes in capture rates that parallel changes in captures of species that do not breed at La Selva (e.g. White-ruffed Manakin; cf. Figs. 4b and 5) and, directly, from recaptures of marked individuals between La Selva and sites at higher elevations (e.g. 250, 500 m) in Parque Nacional Braulio Carrillo (Blake et al. 1990). Habitat shifts by residents at La Selva further contribute to temporal and spatial variation in capture rates of frugivores. As with altitudinal movements, evidence for habitat shifts comes indirectly from complementary changes in capture rates in different habitats and directly from recaptures of marked individuals between habitats.

Fruit and frugivore abundance.—We examined temporal changes in abundance (capture rates) of frugivores to determine if such changes were influenced by spatial and temporal variation in fruit abundance or simply a reflection of movements of individuals unrelated to fruit abundance. Although data are largely correlative, results of several studies support the former

hypothesis (Skutch 1967; Fogden 1972; Morton 1971, 1977; Karr 1982; Leighton and Leighton 1983; Martin and Karr 1986a).

Birds choose among different kinds of fruits (e.g. Moermond and Denslow 1985 and references therein; Loiselle and Blake 1990) and can select among different habitats or habitat patches on the basis of fruit abundance (Martin 1985, Blake and Hoppes 1986, Martin and Karr 1986b, Levey 1988a). Further, relative frugivore abundance typically matches relative fruit abundance in different habitats at La Selva (Stiles in Herrera 1985, Levey 1988a, this study: Table 4) and elsewhere (e.g. Martin 1985). During this study, peak fruit production, particularly in the younger habitats, occurred during September to November when many frugivorous (temperate) migrants were present. Ripe fruit was most abundant in the forest during December and January, when altitudinal migrants, particularly the highly frugivorous White-ruffed Manakin, were common.

The timing of altitudinal movements of frugivores was associated with changes in fruit abundance along the La Selva–Braulio Carrillo forest transect (Loiselle and Blake 1991). Further, the proportion of altitudinal migrants that are frugivorous is greater than expected, based on relative proportions of frugivores in highland source faunas (Slud 1964, Stiles 1985c, Loiselle 1987b). This supports the view that movements by those species are tied to resource abundance (see also Wheelwright 1983).

The degree to which frugivore abundance is directly related to fruit abundance may vary among habitats. Significant correlations between capture rates and several measures of fruit abundance were demonstrated within older habitats but not in the youngest habitat (see also Levey 1988b). Young successional habitats can be a profitable area in which to forage for fruits because of greater fruit density, local diversity, and temporal reliability, despite large seasonal fluctuations in abundance of fruit (Martin 1985, Levey 1988b). Orange-billed Sparrows (*Arremon aurantirostris*), for example, were more frugivorous (i.e. greater percentage of diet made up of fruit) in young than in older second growth where fruit was less available (Loiselle and Blake 1990). Similarly, birds that forage in young successional habitats may be more selective in their choice of fruits. This selectivity indicates that different species of frugivores may respond to abundance of different subsets of fruiting spe-

cies rather than to overall fruit abundance (Loiselle and Blake 1990).

The lack of positive correlation between fruit and frugivore abundance in younger areas may be due to the great abundance of fruit in such habitats. Fruit abundance in young habitats may never be low enough to influence capture rates of resident frugivores. In fact, capture rates in younger areas may be influenced by fruit levels in other habitats. During periods of fruit shortage in forest habitats, individuals of some species may move into younger habitats to forage to take advantage of the abundant food supply (cf. Terborgh 1985a). Such observations support the view that birds track resources among habitats (e.g. Terborgh and Winter 1980, Wheelwright 1983). During our study, for example, capture rates of Red-capped Manakins simultaneously decreased in the forest when fruit supplies were low and increased in second-growth sites where more ripe fruit was available (see also Levey 1988b). A similar pattern was shown by Ochre-bellied Flycatchers (see above, and Figs. 1a and 5a).

Our data are based on captures of birds in mist nets set at ground level and do not represent the complete bird community (Karr 1981, 1990; Terborgh 1985c; Blake et al. 1990). Many frugivores in primary forest are large birds that occur primarily in the canopy (e.g. parrots, guans, cotingids). These species rarely descend to ground level and are not represented in net captures. Comparisons among habitats that are based on mist nets thus ignore this component of the community. Capture rates of many species that typically forage at net level (e.g. manakins, several wrens and flycatchers, Wood Thrush, Long-tailed Hermit, Kentucky Warbler, Ovenbird, others) did differ among habitats, indicating that differences in capture rates were not simply a function of canopy height.

We sampled fruit in the understory as well, and excluded canopy fruits in our samples (Blake et al. 1990). Although variation in capture rates of understory frugivores may reflect responses to variation in abundance of canopy fruits, we do not believe that was important here. Use of canopy fruits did not vary seasonally in diets of birds captured in forests (Loiselle and Blake 1990), which indicates that birds did not move into the canopy at any one time of the year more than another. Also, understory frugivores were not recorded during a concurrent study of canopy birds (Loiselle 1987a, 1988).

Comparisons with nectarivores and insectivores.— If observed changes in capture rates were unrelated to resource abundance but were instead related to some abiotic factor (e.g. rainfall) or to sampling effects (e.g. birds learning locations of mist nets), then we expect some similarity in temporal patterns of capture rates among trophic groups. We found no evidence to support this suggestion. The capture rates of frugivores were not correlated with those of other trophic groups.

Peak capture rates of hummingbirds at the youngest site occurred during the dry season, when flower production typically peaks (Frankie et al. 1974, Opler et al. 1980, Loiselle 1987b). A similar pattern was noted by Martin and Karr (1986a). Stiles (1980, 1985a, c) noted that marked seasonal fluctuations in abundances of hummingbirds often are related to seasonal shifts in flower abundance that promote interhabitat and altitudinal movements (see also Feinsinger 1980). The habitat shifts by hummingbirds we recorded (evidenced by captures between habitats) also may have been in response to resource availability. Long-tailed Hermits accounted for most of the captures between habitats and are known to move long distances while foraging (Stiles and Wolf 1979).

Capture rates of insectivores at La Selva varied independently of frugivores and nectarivores. Similarly, there was little agreement among insectivore groups in temporal patterns of captures. Temporal patterns of abundance vary among groups of insects (Smythe 1982, Wolda 1982) and among different parts of the habitat (Fogden 1972, Smythe 1974). Thus, birds that depend on different types of insects (Sherry 1984) may display different seasonal patterns of abundance. Lack of similarity in temporal patterns of capture rates suggests responses to different factors, perhaps related to the different resource bases that the groups depend on. In sum, much evidence exists to strongly implicate fluctuations in resource abundance as a factor influencing fluctuations in bird abundances.

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APPENDIX. Number of captures from each study site at La Selva. Migratory status (Mig) and Guild are indicated. Migratory status: T = temperate (North America); I = intratropical (breed south of Costa Rica); or A = altitudinal (parentheses indicate partial altitudinal migrant [see text]). Guild: BI, FI, TI, Ant = bark, foliage, terrestrial, and ant-following insectivores; AS = aerial-salliers; AFR and TFR = arboreal and terrestrial frugivore-insectivores; NI = nectarivore-insectivore; Gran. = grass seed eater; Carn. = carnivore; Fish = piscivore. Species represented by only 1 or 2 captures are listed only.

Species	Mig	Guild	Young second growth	Old second growth	Forest
<i>Crypturellus soui</i> , Little Tinamou		TFR	10		
<i>Leucopternis semiplumbea</i> , Semiplumbeous Hawk		Carn.		2	1
<i>Micrastur ruficollis</i> , Barred Forest-Falcon		Carn.		1	2
<i>Claravis pretiosa</i> , Blue Ground-Dove		TFR	14		
<i>Leptotila cassini</i> , Gray-chested Dove		TFR	29	12	
<i>Geotrygon veraguensis</i> , Olive-backed Quail-Dove		TFR			7
<i>G. montana</i> , Ruddy Quail-Dove		TFR	2	1	6
<i>Crotophaga sulcirostris</i> , Groove-billed Ani		TI	4		
<i>Nyctidromus albicollis</i> , Common Parakee		AS	2	2	
<i>Glaucis aenea</i> , Bronzy Hermit		NI	151	43	1
<i>Threnetes ruckeri</i> , Band-tailed Barbthroat		NI	52	22	3
<i>Phaethornis superciliosus</i> , Long-tailed Hermit		NI	163	110	74
<i>P. longuemareus</i> , Little Hermit		NI	4	7	3
<i>Eutoxeres aquila</i> , White-tipped Sicklebill	A	NI	1	3	1
<i>Florisuga mellivora</i> , White-necked Jacobin	A	NI	3	8	6
<i>Klais guimeti</i> , Violet-headed Hummingbird		NI		2	1
<i>Thalurania colombica</i> , Crowned Woodnymph	(A)	NI	21	18	15
<i>Amazilia amabilis</i> , Blue-chested Hummingbird		NI		4	2
<i>A. tzacatl</i> , Rufous-tailed Hummingbird		NI	56	11	1
<i>Microchera albocoronata</i> , Snowcap	A	NI		4	
<i>Chalybura urochrysis</i> , Bronze-tailed Plumeleteer		NI	24	10	21
<i>Trogon rufus</i> , Black-throated Trogon		AFr		8	4
<i>Baryphthengus ruficapillus</i> , Rufous Motmot		AFr	2		8
<i>Electron platyrhynchum</i> , Broad-billed Motmot		AFr	4		3
<i>Malacoptila panamensis</i> , White-whiskered Puffbird		FI			5
<i>Galbula ruficauda</i> , Rufous-tailed Jacamar		AS	5	1	
<i>Pteroglossus torquatus</i> , Collared Aracari		AFr	6	1	4
<i>Ramphastos sulfuratus</i> , Keel-billed Toucan		AFr	2	1	
<i>Celeus castaneus</i> , Chestnut-colored Woodpecker		BI	3		
<i>Synallaxis brachyura</i> , Slaty Spinetail		FI	11	1	
<i>Hyloctistes subulatus</i> , Striped Woodhaunter		FI		1	4
<i>Automolus ochrolaemus</i> , Buff-throated Foliage-gleaner		FI	17	32	1
<i>Xenops minutus</i> , Plain Xenops		BI		17	1
<i>Sclerurus guatemalensis</i> , Scaly-throated Leaf-tosser		TI			12
<i>Dendrocincla fuliginosa</i> , Plain-brown Woodcreeper		Ant		16	25
<i>Glyphorhynchus spirurus</i> , Wedge-billed Woodcreeper		BI	20	121	160
<i>Dendrocolaptes certhia</i> , Barred Woodcreeper		Ant	1	1	5
<i>Xiphorhynchus guttatus</i> , Buff-throated Woodcreeper		BI	22	3	
<i>X. erythropygius</i> , Spotted Woodcreeper		BI			11
<i>Taraba major</i> , Great Antshrike		FI	7		
<i>Thamnophilus punctatus</i> , Slaty Antshrike		FI	1	8	9
<i>Myrmotherula fulviventris</i> , Checker-throated Antwren		FI		1	4
<i>M. axillaris</i> , White-flanked Antwren		FI		3	7
<i>Cercomacra tyrannina</i> , Dusky Antbird		FI	10	1	
<i>Gymnocichla nudiceps</i> , Bare-crowned Antbird		Ant	5		
<i>Myrmeciza exsul</i> , Chestnut-backed Antbird		FI		9	5
<i>Hylophylax naevioides</i> , Spotted Antbird		Ant		2	25
<i>Gymnopithys leucaspis</i> , Bicolored Antbird		Ant		28	43
<i>Phaenostictus mcleannani</i> , Ocellated Antbird		Ant	1	21	30
<i>Formicarius analis</i> , Black-faced Antthrush		TI		3	15
<i>Mionectes olivaceus</i> , Olive-striped Flycatcher	A	AFr		20	9
<i>M. oleagineus</i> , Ochre-bellied Flycatcher	(A)	AFr	112	89	97
<i>Leptopogon amaurocephalus</i> , Sepia-capped Flycatcher		FI	12		
<i>Capsiempis flaveola</i> , Yellow Tyrannulet		FI	7		

APPENDIX. Continued.

Species	Mig	Guild	Young second growth	Old second growth	Forest
<i>Oncostoma cinereigulare</i> , Northern Bentbill		FI	1	13	
<i>Rhynchocyclus brevirostris</i> , Eye-ringed Flatbill		FI			6
<i>Tolmomyias assimilis</i> , Yellow-margined Flycatcher		FI	10		1
<i>Platyrinchus coronatus</i> , Golden-crowned Spadebill		FI			10
<i>Onychorhynchus mexicanus</i> , Royal Flycatcher		AS	5	4	4
<i>Terenotriccus erythrus</i> , Ruddy-tailed Flycatcher		AS		7	17
<i>Empidonax virescens</i> , Acadian Flycatcher	T	AS	12	10	2
<i>Empidonax</i> sp.†	T	AS	20	1	
<i>Attila spadiceus</i> , Bright-rumped Attila		FI	9		2
<i>Rhytipterna holerythra</i> , Rufous Mourner		FI	1	3	3
<i>Myiarchus crinitus</i> , Great Crested Flycatcher	T	AFrI	9		
<i>Pitangus sulphuratus</i> , Great Kiskadee		AFrI	3		
<i>Megarynchus pitangua</i> , Boat-billed Flycatcher		AFrI	3		
<i>Myiozetetes granadensis</i> , Gray-capped Flycatcher		AFrI	10		
<i>Legatus leucophaeus</i> , Piratic Flycatcher	I	AFr	3		
<i>Tyrannus tyrannus</i> , Eastern Kingbird	T	AFr	9		
<i>Tityra semifasciata</i> , Masked Tityra		AFr	2		2
<i>Piprites griseiceps</i> , Gray-headed Manakin		FI		3	
<i>Manacus candei</i> , White-collared Manakin		AFr	169	69	5
<i>Corapipo leucorrhoea</i> , White-ruffed Manakin	A	AFr	9	16	55
<i>Pipra mentalis</i> , Red-capped Manakin	(A)	AFr	38	74	143
<i>Thryothorus atrogularis</i> , Black-throated Wren		FI	10		
<i>T. nigricapillus</i> , Bay Wren		FI	6	14	
<i>Henicorhina leucosticta</i> , White-breasted Wood-Wren		FI	19	13	36
<i>Microcerculus philomela</i> , Nightingale Wren		TI		14	8
<i>Cyphorhinus phaeocephalus</i> , Song Wren		TI			16
<i>Microbates cinereiventris</i> , Tawny-faced Gnatwren		FI	1	1	7
<i>Ramphocaenus melanurus</i> , Long-billed Gnatwren		FI	5	2	
<i>Catharus minimus</i> , Gray-cheeked Thrush	T	AFrI	16	3	3
<i>C. ustulatus</i> , Swainson's Thrush	T	AFrI	86	32	18
<i>Hyllocichla mustelina</i> , Wood Thrush	T	AFrI	31	20	57
<i>Turdus obsoletus</i> , Pale-vented Robin	A	AFrI	19	8	13
<i>T. grayi</i> , Clay-colored Robin		AFrI	16		
<i>Dumetella carolinensis</i> , Gray Catbird	T	AFrI	32		
<i>Hylophilus ochraceiceps</i> , Tawny-crowned Greenlet		FI		1	14
<i>Vermivora pinus</i> , Blue-winged Warbler	T	FI	3		
<i>Dendroica pensylvanica</i> , Chestnut-sided Warbler	T	FI	23	5	
<i>D. castanea</i> , Bay-breasted Warbler	T	AFr	2		1
<i>Helminthos vermivorus</i> , Worm-eating Warbler	T	FI	10	1	
<i>Seiurus aurocapillus</i> , Ovenbird	T	TI	73	7	
<i>S. noveboracensis</i> , Northern Waterthrush	T	TI	4	1	
<i>S. motacilla</i> , Louisiana Waterthrush	T	TI	1		3
<i>Oporornis formosus</i> , Kentucky Warbler	T	TI	45	17	3
<i>O. philadelphia</i> , Mourning Warbler	T	FI	9		
<i>Geothlypis semiflava</i> , Olive-crowned Yellowthroat		FI	6		
<i>Wilsonia citrina</i> , Hooded Warbler	T	FI	4		
<i>W. canadensis</i> , Canada Warbler	T	FI	2	2	1
<i>Phaeothlypis fulvicauda</i> , Buff-rumped Warbler		TI	3	1	1
<i>Tangara larvata</i> , Golden-masked Tanager		AFr	6		
<i>Euphonia gouldi</i> , Olive-backed Euphonia		AFr	4		3
<i>Thraupis episcopus</i> , Blue-gray Tanager		AFrI	5		
<i>Chlorothraupis carmioli</i> , Olive Tanager		AFrI			19
<i>Tachyphonus luctuosus</i> , White-shouldered Tanager		FI	3	2	
<i>T. delatrii</i> , Tawny-crested Tanager		AFrI			16
<i>Habia fuscicauda</i> , Red-throated Ant-Tanager		AFrI	30	10	
<i>Piranga rubra</i> , Summer Tanager	T	AFrI	2	3	
<i>Ramphocelus sanguinolentus</i> , Crimson-collared Tanager		AFrI	10		
<i>R. passerinii</i> , Scarlet-rumped Tanager		AFrI	128	3	1
<i>Mitrospingus cassinii</i> , Dusky-faced Tanager		AFrI	10	15	

APPENDIX. Continued.

Species	Mig	Guild	Young second growth	Old second growth	Forest
<i>Saltator maximus</i> , Buff-throated Saltator		AFrI	90		
<i>Caryothraustes polioaster</i> , Black-faced Grosbeak		AFrI	4	2	
<i>Cyanocopsa cyanooides</i> , Blue-black Grosbeak		AFrI	12	28	2
<i>Arremon aurantirostris</i> , Orange-billed Sparrow		TFrI	19	44	1
<i>Arremonops conirostris</i> , Black-striped Sparrow		TFrI	60	2	1
<i>Sporophila aurita</i> , Variable Seedeater		Gran.	53	17	3
<i>Oryzoborus funereus</i> , Thick-billed Seed-Finch		Gran.	6	5	1
<i>Amblycercus holosericeus</i> , Yellow-billed Caci que		FI	6		
<i>Cacicus uropygialis</i> , Scarlet-rumped Caci que		AFrI		3	
Total mist net hours			4,515	4,370	5,928
Total captures (all species)			2,012	1,133	1,116
Total species (all species)			123	88	80

Species represented by 1 or 2 captures in young second growth (Y), old second growth (O), or forest (F): *Tinamus major* (F); *Accipiter superciliosus* (Y); *Micrastur mirandollei* (F); *Penelope purpurascens* (F); *Crax rubra* (F); *Columba nigrirostris* (O); *Columbina talpacoti* (Y); *Aratinga nana* (Y); *Piaya cayana* (Y); *Hylocharis eliciae*† (O); *Chloroceryle aenea* (O & F); *Ramphastos swainsonii* (Y); *Veniliornis fumigatus* (O); *Piculus leucolaemus* (Y); *Dryocopus lineatus* (Y); *Campephilus guatemalensis* (F); *Lepidocolaptes souleyetii* (Y); *Thamnophilus doliatus* (Y); *Dysithamnus striaticeps* (F); *Microrhopias quixensis* (O); *Hylopezus fulviventris* (Y); *Todirostrum sylvia* (Y); *Contopus virens* (Y); *Empidonax flaviventris* (Y & O); *Myiodynastes luteiventris* (Y); *Pachyramphus cinnamomeus* (Y); *P. polychopterus* (Y & O); *Thryothorus thoracicus* (Y); *Myadestes melanops* (Y); *Catharus fuscescens* (O); *Vireo olivaceus* (Y & O); *V. flavoviridis* (Y); *Hylophilus decurtatus* (Y); *Vermivora chrysoptera* (Y); *Dendroica magnolia* (Y); *D. fusca* (Y); *Mniotilta varia* (Y); *Coereba flaveola* (Y); *Tangara icterocephala* (Y); *Saltator atriceps* (Y); *Pheucticus ludovicianus* (Y); *Volatina jacarina* (Y); *Icterus galbula* (Y).

† Primarily *Empidonax traillii*.

‡ Probable altitudinal migrant.