The Abundance and Seasonality of Forest Canopy Birds on Barro Colorado Island, Panama

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ABSTRACT

The outer canopy of a lowland tropical forest has a less buffered microclimate and more seasonal leaf phenology than the understory. Censuses were conducted from a canopy tower on Barro Colorado Island, Panama, to assess the composition and degree of seasonality of the canopy avifauna. The canopy avifauna shares many species with scrubby second growth; many common canopy species were also found frequently in more open areas. The rarest visitors to the canopy were primarily those from lower strata. Most common species were omnivorous, and restricted insectivores were poorly represented when compared to lower strata. This distribution is correlated with a taxonomic shift from the antbird-woodcreeper-dominated understory to a tanager-dominated canopy avifauna. A majority of common canopy species was significantly seasonal in abundance; the most seasonal resident species tending to be the omnivores. Two sources of overall fluctuation in birds using the outer canopy were an influx of small omnivorous tanagers in the early dry to early wet season, and the presence of temperate-zone migrants, mainly *Dendroica castanea*, from late wet through the dry season.

THE OUTER CANOPY OF A TROPICAL FOREST is a world distinct from the somber understory it shades. The protective shell formed by the foliage of massive trees receives the full brunt of the weather: wind speeds are higher, solar radiation and rainfall are most intense (Allee 1923), and temperatures average 2-5° C warmer than in the understory only 5 m below (Smithsonian Environmental Sciences Program, unpubl.). The biotic environment also differs markedly; large trees cover areas that might have supported many small plants on the forest floor, creating patches of young leaves, flowers, and fruits on a larger scale in the canopy than in the understory below. Furthermore, canopy trees display more pronounced seasonality in leaf loss than understory shrubs in semideciduous tropical forests (Croat 1978, Leigh and Smyth 1979).

As Karr (1976b) argued, birds using different levels of a tropical woodland face radically different seasonal regimes, and the diversity and seasonality of the avifauna of each stratum should differ accordingly. Karr (1976b) showed that in a late scrub community in Panama, the upper strata had a less diverse and more fluctuating bird population than lower strata.

Various authors (Orians 1969, Pearson 1971) have noted the taxonomic affinity of canopy and clearing avifaunas and the dissimilarity between canopy and understory birds. These observations suggest that the influence of differences in phenology, microclimate, or foliage structure of different forest strata may be profound.

Few data are available on the abundance and seasonality of species in the outer canopy. The major problem in analyzing bird use of a tropical forest canopy is the difficulty of observing birds 25-40 m above ground. This difficulty is exacerbated by the similarity of the high sibilant calls of many small tanagers. One solution to this problem is to census birds from a canopy tower or walkway. Lovejoy (1975) censused from such a tower in the Brazilian Amazon but did not separate canopy census results in his published analysis. In this paper I present an analysis of census data taken from a 40 m canopy tower in secondary forest of Barro Colorado Island, Panama (BCI). Censuses were conducted to quantify the seasonal use of a small piece of outer canopy.

STUDY AREA

The canopy tower (fig. 1) is located in the secondary forest (70-100 years old) of the Lutz Watershed of Barro Colorado Island (BCI). For a general description of the history, ecology, and birdlife of BCI see Willis and Eisenmann (1979). The forest on BCI receives an average of 2600 mm of rain annually, distributed in a highly seasonal regime. In most years, a dry season (with less than 10 cm of rain monthly) extends from mid-December to late April, with a wet season during the remainder of the year. During the 1978-1979 study season the dry season began in early December and ended in mid-April. During the dry season a strong northeasterly trade wind blows daily, mainly in the afternoons, and is relatively unbuffered in the forest canopy (Smithsonian ESP unpubl.).

From a biological view, it would be a mistake to define only two seasons on BCI (Foster 1974). Su-

perimposed on the two seasons defined by rainfall are a larger number of phenological seasons defined by plant activities (Leigh and Smythe 1979). For this paper I will consider the following five phenological seasons for the forest canopy:

LATE WET SEASON.—September to mid-December, a period of low leaf production or loss, low fruit or flower availability.

EARLY DRY SEASON.—Mid-December to March, a

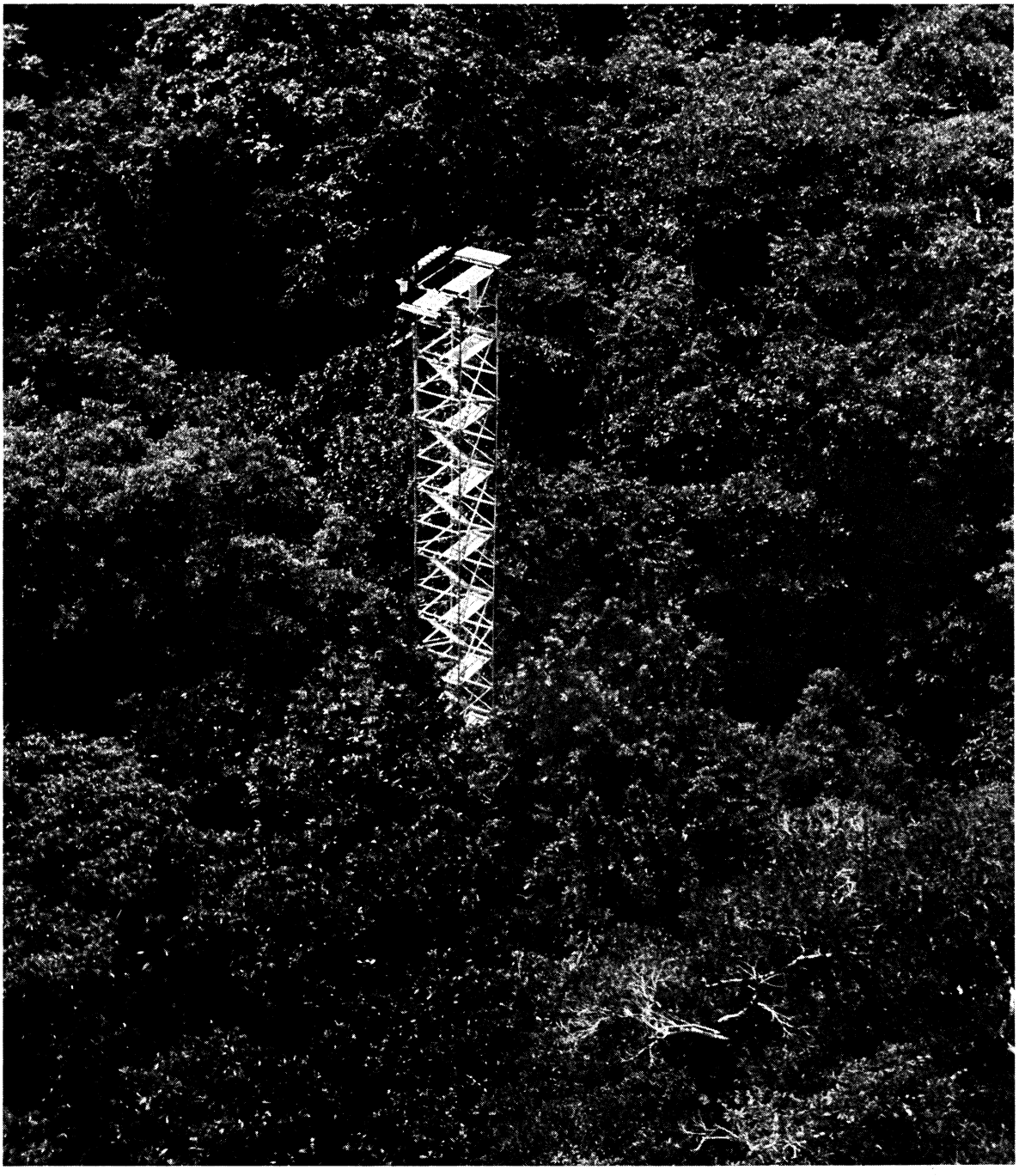

FIGURE 1. Aerial photograph of BCI canopy tower (courtesy of R. Silbergleid).

period of high leaf loss, low leaf production, low fruit availability, and abundant canopy flowers. This season begins a procession of flowering trees that lasts into early July. During this season important flowering trees include: *Virola surinamensis* (Rol.) Warb., Myristicaceae; *Luehea seemannii* Tr. and Planch, Tiliaceae; *Cordia alliodora* (R. and P.) Cham, Boraginaceae; *Tabebuia rosea* (Bertol.) DC., Bignoniaceae; and *Miconia argentea* (SW) DC., Melastomataceae. Many of these flowering trees are not used for nectar, but birds forage in the blossoms for insects (pers. obs., and Leck 1972).

LATE DRY SEASON.—Early March to mid-April, high leaf loss and high leaf production, high fruit availability, and moderate flower availability.

EARLY WET SEASON.—Mid-April to July, a period of heavy leaf production, high fruit availability, moderate flower availability (mainly *Dipteryx panamensis* [Pitt.] Rec. and Mell, Papilonaceae).

MID WET SEASON.—July to early September, a period of low leaf production and low fruit and flower availability. I distinguish this season from late wet season because I censused them in two different years.

Insect abundance is known to be strongly seasonal in the BCI forest (Wolda 1978, Leigh and Smythe 1979). Overall insect biomass, based on ultraviolet light traps, is greatest in the early wet season when new leaf production is maximal. I assume that these results reflect seasonal patterns in abundance of the insects that birds encounter in the canopy foliage during the day.

I censused 2.7 ha of forest canopy in a 75-100 m radius around the tower (depending on visibility). The forest canopy is generally 25-35 m high, sloping up along the sides of the Lutz watershed. A large tree-fall gap disrupted the canopy immediately to the west of the tower; this area of low canopy was not included in the census. While 19 species of canopy tree were visible on the study area, the site was strongly dominated by *Anacardium excelsum* (Bertero and Balb.) Skeels, Anacardiaceae (13 trees, 20% estimated crown cover); and *Ficus yopenensis* Desv., Moraceae (13, 20%). Other trees included: *Pseudobombax septenatum* (Jacq.) Dug., Bombacaceae (5, 8%); *Ceiba pentandra* (L.) Gaertn, Bombacaceae (5, 8%); *Ficus insipida* Willd, Moraceae (4, 8%); *Dipteryx panamensis* (3, 5%); *Virola surinamensis* (3, 5%); *Sterculia apetala* (Jacq.) Karst, Sterculiaceae (3, 5%); *Spondias mombin* L., Anacardiaceae (2, 5%); *Zanthoxylum* sp., Rutaceae (2, 5%); *Terminalia amazonica* (J. F. Gmel) Excell in Pulle, Combretaceae (2, 5%); *Brosimum alicastrum* SW., Moraceae (1, —); *Hyeronima laxiflora* (Tul.) Mull Arg., Euphorbiaceae (1, —); *Platypodium elegans* J. Vogel, Papilionaceae (1. —); *Pterocarpus rorbii* Vahl, Papilionaceae (1, —); *Quararibea asterolepis* Pitt, Bombacaceae (1, —); and *Cordia alliodora* (2, 2%). Common lianas included *Uncaria tomentosa* (Willd.) DC., Rubiaceae; and *Arrabidaea* sp., Bignoniaceae. The abundance of the *Ficus* species, *Pseudobombax* and *Cordia*, characterizes this plot as young forest.

The study site was dominated by a few trees that produced fruits or flowers little used by omnivorous birds. While most important food plants were missing from the plot (e.g., *Miconia argentea, Casearia* sp., *Lindackeria laurina* Presl., *Zuelania guidona* (Sw.) Britt and Millsp., Flacourtiaceae), many were present in adjacent areas of the watershed. The important flowering trees on the census plot were (with flowering season): *Anacardium excelsum* (January-April), *Pseudobombax septenatum* (January-February), *Spondias mombin* (May-June), *Dipteryx panamensis* (May-July), *Virola surinamensis* (December-February), *Terminalia amazonica* (August-September), *Cordia alliodora* (February), and the lianas *Uncaria tomentosa* (April-May) and *Arrabidaea* (March). The only trees that produced fruit eaten by birds on the census plot were *Virola surinamensis* (June-August), *Spondias mombin*, and *Ficus yopensensis* (February), which produced large fruit eaten by Toucans, trogons, and large cotingas, and *Hyeronima laxiflora* (December) and *Zanthoxylum* (March), which produced small fruit eaten by a variety of omnivorous birds.

Several features of the study site present problems for generalizations from the census data. The major problem is the small size of the study plot (2.7 ha) which is limited by what is visible from a single tower. A second problem is that BCI is isolated and overall has a depauperate avifauna (Willis 1974, Willis and Eisenmann 1979), but this is a much less serious problem with canopy birds, for BCI has a nearly complete canopy avifauna, missing only a few species that are regular members of the canopy of nearby Pipeline Road (yellow-green Tyrannulet (*Phylloscartes flavovirens*), Syristes (*Syristes sibilator*), white-ringed flycatcher (*Conopias parva*), and scarlet-rumped cacique (*Cacicus uropygialis*); Gale *et al.* 1978). Isolation by a water barrier may discourage local movement, but, nevertheless, a large number of probable immigrations and emigrations to and from the mainland were observed.

METHODS

I conducted 59 censuses during the 10-month period (1 Nov 1978 to 7 Sept 1979). Each census lasted 1.5 to 2 hrs and was conducted between 0615 and 0830 hrs, or between 1600 and 1830 hrs, both periods of peak bird activity for the outer canopy. Censuses of less than two hours ($n = 6$) occurred when dangerous weather conditions (electrical storms) prevailed. A census consisted of recording all birds observed within the census period in the outer foliage of canopy trees and their vines. Only birds actually perched in this vegetation were counted; birds flying over or heard calling from lower strata were not included. The problem of recounting birds was not great because of the low number of individuals observed per species. I kept track of the direction in which birds moved out of the study area to help decide if two sightings should be counted as two individuals; I generally biased my estimates toward the conservative side. Censuses were conducted 5-7 times per month, and were divided nearly equally between mornings and evenings, and spanned most weather conditions, although they were sometimes limited to mornings for periods when the threat of afternoon thunderstorms was great. However, over entire phenological periods, the morning and evening censuses were in close parity, and the avoidance of potentially dangerous weather is probably not a serious bias in the number of birds observed. Thundershowers were short, and my observations indicated that only when rains were heavy was bird activity reduced.

To examine ecological correlates of abundance patterns in birds, I categorized species by dominant foraging behavior based on near daily observation of birds during 18 months in Panamanian lowland forests. Common canopy birds were classified by dominant insectivorous substrate used, as well as the degree to which fruits and flowers are used. The degree of omnivory was quantified by comparing proportions of observations of fruit and flower foraging. Sample sizes are small, since many canopy birds are difficult to observe, and for tanagers and honeycreepers, I consulted Snow and Snow (1971) and my notes from clearing and young second growth to assess the degree of omnivory.

Birds were classified into habitat distribution patterns based on my observations of the habitats used outside of the forest canopy. Categories include: species found commonly in lower forest strata (U); species found commonly in young second growth or large clearings (0); species found commonly only in the canopy (C); species found only as vagrants or transient migrants in central Panama (TM). For all analyses, parrots, toucans, pigeons, cracids, and raptors are not considered. Although common, parrots and toucans were generally present in the outer canopy only while staging to fly to roosts. Raptors are trophically distinct from other birds, yet not common enough to analyze separately. I have followed Ridgely (1976) for nomenclature.

RESULTS

GENERAL COMPOSITION.—86 species of bird were observed in the canopy study area (table 1). As is

TABLE 1. *Abundance, frequency, and general distribution of birds on canopy census.*

Species	Scientific name	Total individuals	Number of censuses	Distribution[a]
Black vulture	*Coragyps atratus*	1	1	—
Gray-headed kite	*Leptodon cayanensis*	1	1	—
Hook-billed kite	*Chondrohierax uncinatus*	5	3	—
Double-toothed kite	*Harpagus bidentatus*	2	2	—
White hawk	*Leucopternis albicollis*	1	1	—
Semiplumbeous hawk	*Leucopternis semiplumbea*	2	1	—
Crane hawk	*Geranospiza caerulescens*	2	2	—
Bat falcon	*Falco rufigularis*	1	1	—
Crested guan	*Penelope purpurascens*	5	4	—
Short-billed pigeon	*Columba nigrirostris*	1	1	—
Orange-chinned parakeet	*Brotogeris jugularis*	79	18	—
Blue-headed parrot	*Pionus menstruus*	2	1	—
Red-lored parrot	*Amazona autumnalis*	44	17	—
Mealy parrot	*Amazona farinosa*	31	12	—
Yellow-billed cuckoo	*Coccyzus americanus*	1	1	TM
Squirrel cuckoo[b]	*Piaya cayana*	31	23	O
White-necked jacobin	*Florisuga mellivora*	18	15	O

TABLE 1. (Continued)

Rufous-crested coquette	*Lophornis delattrei*	1	1	O
Violet-bellied hummingbird[b]	*Damophila julie*	42	26	O
Blue-chested hummingbird	*Amazilia amabilis*	3	3	O
Purple-crowned fairy	*Heliothryx barroti*	8	8	C
Ruby-throated hummingbird[c]	*Archilochus colubris*	1	1	TM
Hummingbird sp.		6	3	
Slaty-tailed trogon	*Trogon massena*	14	9	U
Violaceous trogon	*Trogon violaceus*	8	8	U
Black-chested puffbird	*Notharchus pectoralis*	11	11	O
Pied puffbird	*Notharchus tectus*	1	13	C
Collared araçari	*Pteroglossus torquatus*	48	17	—
Keel-billed toucan	*Ramphastos sulfuratus*	68	34	—
Chestnut-mandibled toucan	*Ramphastos swainsonii*	61	28	—
Lineated woopecker	*Drycocopus lineatus*	1	1	U,O
Black-cheeked woodpecker[b]	*Melanerpes pucheranii*			O
Crimson-crested woodpecker	*Campephilus melanoleucos*	3	3	U,O
Wedge-billed woodcreeper	*Glyphorhynchus spirurus*	1	1	U
Buff-throated woodcreeper	*Xiphorhynchus guttatus*	1	1	U,O
Black-striped woodcreeper	*Xiphorhynchus lachrymosus*	1	1	U
Plain xenops	*Xenops minutus*	3	3	U
Slaty antshrike	*Thamnophilus punctatus*	21	17	U
Checker-throated antwren	*Myrmotherula fulviventris*	4	2	U
White-flanked antwren	*Myrmotherula axillaris*	1	1	U
Dot-winged antwren[b]	*Microrhopias quixensis*	36	15	U
Blue cotinga	*Cotinga natterii*	17	15	C
Rufous mourner	*Rhytipterna holerythra*	2	2	U
Masked tityra	*Tityra semifasciata*	18	17	O
Black-crowned tityra	*Tityra inquisitor*	3	1	O
Purple-throated fruitcrow	*Querula purpurata*	11	5	C
Tropical kingbird	*Tyrannus melancholicus*	1	1	O
Eastern kingbird	*Tyrannus tyrannus*	30[d]	1	TM
Streaked flycatcher	*Myiodynastes maculatus*	2	2	O
Boat-billed flycatcher	*Megarhynchus pitangua*	12	10	O
Social flycatcher	*Myiozetetes similis*	6	3	O
Great-crested flycatcher	*Myiarchus crinitus*	6	6	O
Dusky-capped flycatcher[b]	*Myiarchus tuberculifer*	45	30	O
Eastern wood pewee	*Contopus virens*	6	5	TM
Ruddy-tailed flycatcher	*Terenotriccus erythrurus*	3	3	U
Yellow-margined flycatcher[b]	*Tolmomyias assimilis*	31	26	O,U
Olivaceous flatbill	*Rhynchocyclus olivaceus*	1	1	U
Southern bentbill	*Oncostoma olivaceum*	4	4	U
Forest elaenia	*Myiopagus gaimardii*	3	3	U
Paltry tyrannulet[b]	*Tyranniscus vilissimus*	34	27	O
Yellow-crested tyrannulet	*Tyrannulus elatus*	2	2	O
Brown-capped tyrannulet	*Ornithion brunneicapillum*	14	14	O
Tropical gnatcatcher[b]	*Polioptila plumbea*	38	29	O
Lesser greenlet[b]	*Hylophilus decurtatus*	102	47	U
Bananaquit[b]	*Coereba flaveola*	73	43	O
Green honeycreeper[b]	*Chlorophanes spiza*	48	31	O
Blue dacnis[b]	*Dacnis cayana*	137	46	U,O
Scarlet-thighed dacnis[b]	*Dacnis venustas*	25	13	O
Shining honeycreeper[b]	*Cyanerpes lucidis*	37	18	O
Red-legged honeycreeper[b]	*Cyanerpes cyaneus*	69	29	O
Baltimore oriole	*Icterus galbula*	2	1	TM
Chestnut-headed oropendola	*Zarhynchus wagleri*	8	2	O
Prothonotary warbler	*Protonotaria citrea*	1	1	TM
Tennessee warbler[b]	*Vermivora peregrina*	36	15	O
Chestnut-sided warbler	*Dendroica pensylvanica*	10	10	U,O

TABLE 1. (Continued)

Bay-breasted warbler[b]	*Dendroica castanea*	134	35	U,O
Canada warbler	*Wilsonia canadensis*	1	1	TM
Fulvous-vented euphonia	*Euphonia fulvicrissa*	15	11	O
Plain-colored tanager[b]	*Tangara inornata*	85	26	O
Blue-gray tanager	*Thraupis episcopus*	8	5	O
Palm tanager[b]	*Thraupis palmarum*	22	11	O
Crimson-backed tanager	*Ramphocelus dimidiatus*	1	1	O
Summer tanager	*Piranga rubra*	15	14	O
White-shouldered tanager[b]	*Tachyphonus luctuosus*	65	26	U,O
Sulphur-rumped tanager	*Heterospingus rubifrons*	14	7	O
Slate-colored grosbeak	*Pitylus grossus*	1	1	U

[a]Distributions: O = open areas, second-growth; U = lower strata; C = canopy only; TM = transient migrants or vagrants.
[b]Twenty most common species.
[c]Red-throated ♂ hummingbird with forked tail, most likely this species (no previous Canal Zone record) as it was recorded in February.
[d]Flock of 30 landed briefly during migration—not included in census totals.

TABLE 2. *Seasonality and degree of omnivory of 20 common species.*

Species	Seasonality	Comparison[a]	K-W	Omnivory	Supporting data
Violet-bellied hummingbird	Seasonal	ed-ew/mw-lw	12.5, df = 1 p 0.001	high	G. Angher, pers. comm.
Squirrel cuckoo	Aseasonal			never	
Black-cheeked woodpecker	Aseasonal			moderate	uncommon frugivore (no quantified data)
Dot-winged antwren	Seasonal	w/d		never	N = 1100, Fr = 0, Fl = 0
Dusky-capped flycatcher	Aseasonal			moderate	N = 40, Fr = 13%
Yellow-margined flycatcher	Aseasonal			rare	N = 75, Fr = 4%
Paltry tyrannulet	Aseasonal			?	N = 10, Fr = 20%
Tropical gnatcatcher	Aseasonal			never	
Lesser greenlet	Aseasonal			rare	N = 307, Fr = 1%
Bananaquit	Seasonal	lw-ld/ew-mw		high	nectivorous and frugivorous
Shining honeycreeper	Seasonal	ed-mw/lw	13.2, df = 1 p 0.005	high	N = 16, Fr = 44% Fl = 19%
Red-legged honeycreeper	Seasonal	Overall	12, df = 4 p 0.025	high	N = 19, Fr = 58% Fl = 11%
Green honeycreeper	Seasonal	Overall	24, df = 4 p 0.001	high	N = 34, Fr = 50% Fl = 9%
Blue dacnis	Seasonal	w/d	4, df = 1 p 0.05	moderate	N = 112, Fr = 29% Fl = 6%
Scarlet-thighed dacnis	Seasonal	ed-ew/mw-lw	8.4, df = 1 p 0.05	high	N = 7, Fr = 86% Fl = 14%
Tennessee warbler	Seasonal (winter only)			high	nectivorous and frugivorous
Bay-breasted warbler	Seasonal (winter only)	+ lw/ed/ld		moderate	N = 1331, Fr = 23%
Plain-colored tanager	Seasonal	ed-ew/mw-lw	8.6, df = 1 p 0.05	high	N = 37, Fr = 40%
White-shouldered tanager	Aseasonal			moderate	N = 264, Fr = 11%
Palm tanager	?			high	highly frugivorous

[a]symbols: l = late, e = early, d = dry, and w = wet.

typical of any small plot in a tropical forest, this number accumulated slowly through time; the mean number of species (excluding toucans, etc.) per census was only 17. Many species were rare visitors; less than 10 individuals were observed for 38 species (averaging less than one per month). On the other hand, a number of species was truly common. I consider the 20 most common species (total numbers seen) to be the core species of the canopy avifauna in further analysis (see table 2). The single most

abundant species was blue dacnis with an average of 2.5 ind./census. But bay-breasted warbler, a temperate-zone migrant, was nearly as abundant (2.4/census), even though present for only 5.5 of the 10 months.

SEASONAL CHANGES IN CENSUS TOTALS.—Variation in total number of individuals per census has a strong seasonal component (Kruskall-Wallis $X^2 = 13$, d.f. $= 4$, $p < 0.05$) with the highest counts in late wet to late dry seasons (see fig. 2). Much of the fluctuation is a result of the influx of migrants, mainly bay-breasted warbler, during the winter months (late wet-late dry season). When only tropical residents are plotted (fig. 2), the census totals are relatively constant except for a strong peak in the late dry season (K-W 10.6, d.f. $= 4$, $p < 0.05$).

SEASONAL VARIATION IN SPECIES' ABUNDANCES.—Seasonal variation in abundance characterizes many canopy species. The 20 most common species were analyzed for such seasonal patterns of occurrence, and over half (11) showed statistically significant variation (tables 2 and 3). The primary pattern of tropical resident species is a dry-early wet season peak. Six species display a strong population peak during this period (fig. 3). In the case of the red-legged honeycreeper and scarlet-thighed dacnis the peak is concentrated into one or two seasons; shining honeycreeper has a broader peak with only a late wet-season depression. A secondary pattern is a general wet-season peak, found in two species of residents (blue dacnis and dot-winged antwren). Bananaquit had a unique pattern of seasonality with high populations in late wet to late dry seasons. Palm tanagers showed some seasonality, occurring commonly in June, but were overall too infrequent (20 occurrences) to reject a null hypothesis of aseasonality.

While the two common temperate-zone migrants (tennessee and bay-breasted warblers) displayed the expected seasonality, disappearing in temperate summer, bay-breasted warbler also showed a significant decline through the winter (fig. 3).

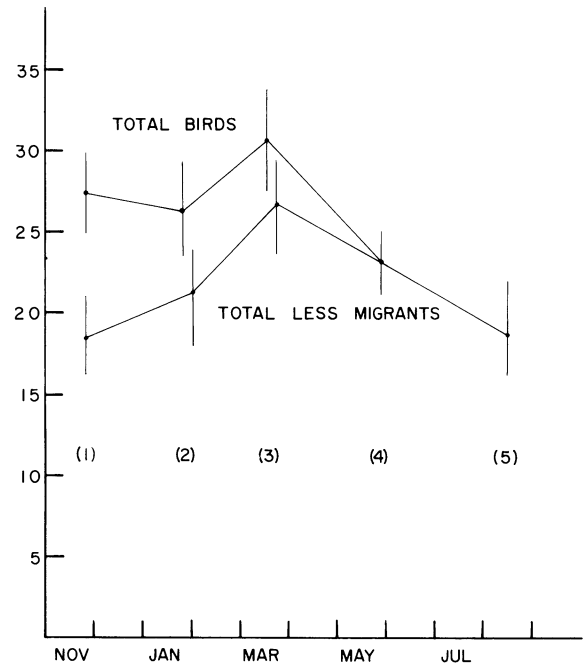

FIGURE 2. Mean ± standard error of total number of bird and total species less migrants during the study period (toucans, parrots, cracids, pigeons, and raptors not included in this or other figures). Seasons are I = late wet, 2 = early dry, 3 = late dry, 4 = early wet, and 5 = mid wet.

DISCUSSION

THE GENERAL DISTRIBUTION OF CANOPY BIRDS.—As noted by Orians (1969) and Pearson (1971) for Costa Rican and Peruvian forests, but not for sites in Ecuador and Bolivia (Pearson 1975), a plurality of

TABLE 3. *Seasonal abundance in some common canopy species. Each entry represents average number of individuals per census (and standard error).*

	late wet	early dry	late dry	early wet	mid wet
Violet-bellied hummingbird	0.1(0.1)	0.7(0.3)	1.2(0.4)	0.8(0.2)	0.4(0.2)
Dot-winged antwren	0.8(0.2)	0.2(0.2)	0.2(0.2)	0.6(0.3)	1.2(0.5)
Bananaquit	1.4(0.2)	1.8(0.3)	1.4(0.2)	1.4(0.1)	0.4(0.1)
Shining honeycreeper	0.1(0.1)	0.9(0.4)	0.8(0.4)	0.6(0.3)	1.0(0.2)
Red-legged honeycreeper	0.8(0.3)	1.7(0.4)	3.5(0.7)	1.0(0.3)	0.1(0.1)
Green honeycreeper	0.2(0.1)	1.4(0.3)	1.4(0.3)	0.9(0.2)	0.3(0.1)
Blue dacnis	3.0(0.6)	2.3(0.8)	1.9(0.5)	2.2(0.5)	2.8(0.6)
Scarlet-thighed dacnis	0	0.3(0.2)	0.6(0.3)	0.8(0.3)	0.1(0.1)
Bay-breasted warbler	4.8(0.4)	3.7(0.5)	2.6(0.4)	0	0
Plain-colored tanager	0.8(0.4)	1.5(0.5)	2.0(0.8)	2.5(0.6)	1.3(0.7)

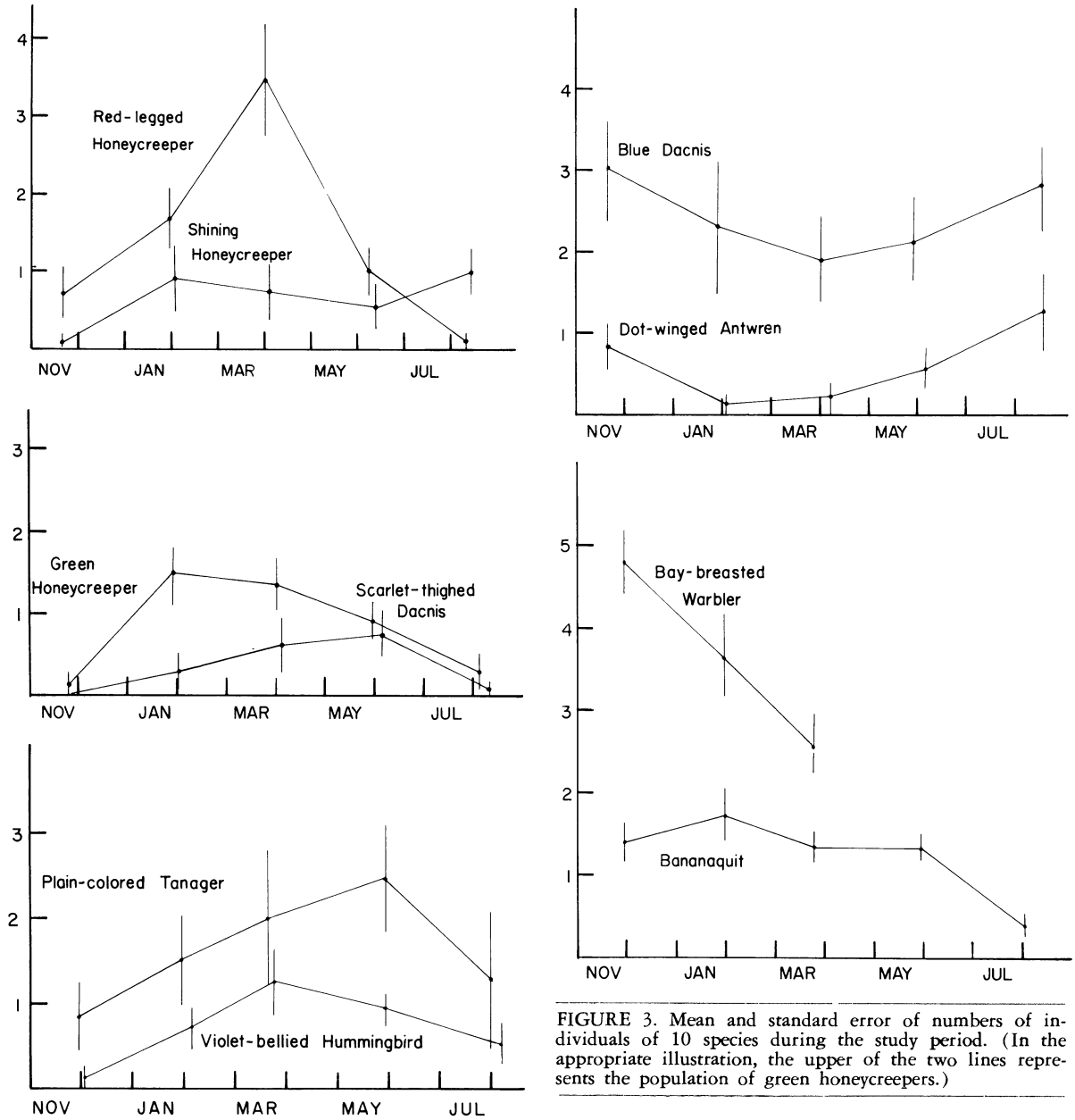

FIGURE 3. Mean and standard error of numbers of individuals of 10 species during the study period. (In the appropriate illustration, the upper of the two lines represents the population of green honeycreepers.)

species on the canopy census was common in second-growth areas. However, almost as many species (17 versus 30) were common in the forest understory; only four species were found commonly only in the canopy. The dominance of birds found also in second growth is more apparent when the relative abundance of birds of different distribution types is examined. When the census results are used to rank canopy species by abundance (i.e., first through tenth most common species, etc.), the high proportion of "second-growth" species among the most common birds becomes obvious (see table 4). For example, second-growth birds make up 70 percent of the 20 most common species. On the other hand, lower-strata birds comprise most of the rarest species (44% of the 27 rarest species). Transient migrants and vagrants are among the rarest species because they are only present for short periods of time.

There are limits to the overall similarities of the clearing and canopy avifaunas. The forest canopy has a rich supply of vagrant forest understory species. These same species probably never wander any sub-

TABLE 4. *General distribution and abundance rankings of canopy birds.*[a]

Abundance	Rank class	O	U	O/U	C	TM
1-10	(38-137 ind.)	6	1	3	0	0
11-20	(22-38 ind.)	8	1	1	0	0
21-30	(14-22 ind.)	5	2	0	2	0
31-40	(6-13 ind.)	5	1	1	2	1
41-50	(2-5 ind. including ties)	2	7	1	0	1
51-60	(1 ind. including ties)	4	5	3	0	5
Total		30	17	9	4	7

[a]O = open areas, second growth; U = lower strata; C = canopy only; TM = transient migrants or vagrants.

stantial distance into large, cleared areas. Many birds of young second growth, such as saltators, wrens, and some tanagers, were never observed in the BCI canopy and probably do not occur in other canopies.

FORAGING BEHAVIOR OF COMMON CANOPY BIRDS.—Omnivory, here defined as the use of both arthropod and plant material (e.g., fruit and nectar) as food, predominates among the common birds of the outer canopy (see table 2). Of the 20 most common species, 15 are at least occasionally frugivorous and seven are nectarivorous. Only three species (dot-winged antwren, squirrel cuckoo, and tropical gnatcatcher) are totally insectivorous. This situation is in contrast to lower strata where many common species, including antbirds, woodcreepers and some tyrannids, are complete insectivores. Twelve of the 20 most common species on transects in the BCI forest (table 5) were restricted insectivores; these censuses are biased toward understory and mid-level species. In part, this gradient of restricted insectivory to omnivory is correlated with a taxonomic shift from a lower stratum dominated by the antbirds, woodcreepers, and ovenbirds (10/20 on transects) to a canopy dominated by the tanagers and honeycreepers (8/20). Such a taxonomic shift is characteristic of movements from tropics to subtropics and forest to edge (Willis 1966).

FORAGING ECOLOGY AND SEASONAL ABUNDANCE.—With one exception (and excluding temperate-zone migrants) the most highly omnivorous species are those that display seasonal variation in abundance (table 2); these include the "honeycreepers," plain-colored tanager and violet-bellied hummingbird. The proportion of frugivory and nectivory for the six seasonal species ranges from 30 to 90 percent (with one value of 0%) and for seven aseasonal species it ranges from zero to 13 percent (Willcoxon test $p < 0.01$). The exception is the dot-winged antwren which is a seasonally common, restricted insectivore. The tanagers that display seasonality in abundance in the BCI canopy are seasonal in their abundance on BCI in general, including clearings and understory. Dot-winged antwrens maintain a fairly constant population in the BCI forest and are seasonal in the canopy by virtue of foraging forays from lower strata.

TABLE 5. *Twenty common understory transect birds from censuses during winters 1977-1979.*

Species	Family	Specialized insectivore[a]
Wedge-billed woodcreeper	Dendrocolaptidae	SI
Black-striped woodcreeper	"	SI
Slaty antshrike	Formicariidae	SI
Spot-crowned antvireo	"	SI
Checker-throated antwren	"	SI
White-flanked antwren	"	SI
Dot-winged antwren	"	SI
Chestnut-backed antwren	"	SI
Spotted antwren	"	SI
Red-capped manakin	Pipridae	O
Yellow-margined flycatcher	Tyrannidae	O
Ruddy-tailed flycatcher	"	SI
Southern bentbill	"	SI
Lesser greenlet	Vireonidae	O
Bananaquit	Coeribidae	O
Blue dacnis	"	O
Chestnut-sided warbler	Parulidae	O
Bay-breasted warbler	"	O
White-shouldered tanager	Thraupidae	O

[a]SI refers to restricted insectivore (i.e., no frugivory or nectivory observed). O refers to species where some frugivory or nectivory was observed, no matter how rare.

SEASONAL VARIATION IN ABUNDANCE OF OMNIVORES AND INSECTIVORES.—In figure 4, census totals for each season were subdivided into predominantly insectivorous (including species such as greenlet and yellow-margined flycatcher with less than 5 percent omnivory) and omnivorous species. While both groups showed statistically significant seasonal variation, the more common omnivores show a strong

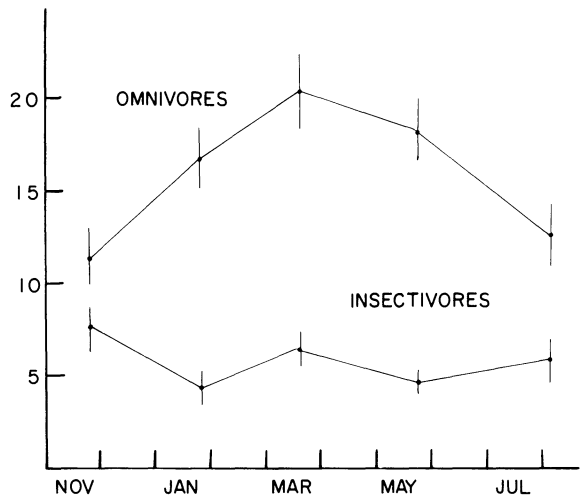

FIGURE 4. Mean and standard error of numbers of species of omnivores and insectivores during the study period. (See text for criteria for each group.)

peak corresponding with the late dry-season peak for all resident birds (fig. 2). Variation in omnivores accounts for the overall seasonality in the census numbers. Insectivores show small peaks in the late wet and late dry seasons.

Six of the eight seasonally variable resident species are most common within the period from early dry to mid-wet season. Leck (1972) and Karr (1977) noted a group of nectarivore-frugivores that occurs in central Panamanian forests and forest clearings in the dry season. Both authors hypothesize that these species are local migrants from drier habitats. In addition George Angher and I have observed the nectivorous species feeding on the *Heliconia latispatha* Benth. (Musaceae) and *Tichospermum mexicanum* (DC.) Bell. (Tiliaceae) in clearings during the period when they are absent from forests. These species undertake some sort of local movement into the forest canopy when mass flowering trees are common. The occurrence of several of these nectivorous-frugivorous species in the canopy well into the wet season is understandable for two reasons: 1) *Dipteryx* extends the mass flowering of canopy trees well into the wet season (early July); and 2), most of these species are either nectivorous-frugivorous (shining and green honeycreeper) or primarily frugivorous (scarlet-thighed dacnis, plain-colored tanager). A number of small bird-sized fruit-producing trees are producing fruit at the onset of the rainy season (including several species of *Miconia*).

The seasonal patterns of some common canopy species defy such simple analysis. Blue dacnis and bananaquit display different seasonal patterns from other honeycreepers. Bananaquit was constantly common from late wet season through dry season but gradually disappeared in the early to mid-wet season. Blue dacnis was least common in the dry to early wet season when other tanagers had their peaks. Blue dacnis was generally abundant in the late wet season, probably the nadir for small fruit and flower availability (Foster 1974, Leigh and Smythe 1979). During the dry season, blue dacnis disappeared from understory antwren flocks completely and was scarce at fruiting trees.

NUMERICAL DOMINANCE OF BAY-BREASTED WARBLERS.—Bay-breasted warbler was the most abundant and frequent species on canopy censuses while it was present in Panama from 1 November to 15 April. Every time birds were observed from the canopy tower, bay-breasted warblers were present with generally from 3-7 warblers on a census. They were the first birds to be active in the canopy at dawn and after rain stopped.

The strong numerical dominance of bay-breasted warbler in the forest canopy is probably not unique to Barro Colorado Island or to one winter. During 1977-1978 and 1978-1979 I observed bay-breasted warblers as common in canopy flocks along the Rio Limbo and Rio Frijoles in the Pipeline Road forest. I censused 10 canopy flocks in the virgin lowland forests at the base of Cerro Pirre, Darien, and found that bay-breasted warblers comprised 25 percent of all individuals in these flocks; in several flocks the nucleus appeared to be a group of 15-20 birds. If anything, numbers on the BCI census were low, because BCI is near the northwest edge of the bay-breasted warbler's winter range. The suggestion by Karr (1976a) that migrants are rare in midwinter in Panama lowland forests should be reevaluated in light of the abundance of bay-breasted warblers in the outer canopy.

No obvious shift in the number of resident tropical birds was observed in response to the influx of bay-breasted warblers and other migrants. Early and mid-wet season numbers of resident birds are essentially the same as late wet- and early dry-season numbers, despite a large influx of migrants during this period. The strong late dry-season peak in residents occurs at a time when migrants are still present in good numbers (fig. 2). The similarity of mid- and late wet-season numbers is probably the most telling since these seasons are probably the most similar in food availability. It appears that in the

late wet season the outer canopy supports an influx of migrants, with no decrease in residents; yet the last wet season is a time when insects, fruit, and flowers may be the most scarce.

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