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BIRD ABUNDANCE AND SEASONALITY IN A COSTA RICAN LOWLAND FOREST CANOPY[1]

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Abstract. I censused forest canopy birds from two emergent trees in lowland wet forest in Costa Rica from April 1985 to May 1986. Composition of the canopy avifauna did not differ overall between census sites. I recorded 89 species and 2,944 individuals during 49 censuses. Forest canopy was dominated by frugivores, especially large-bodied (>100 g) frugivores, and parrots. Furthermore, in contrast to the avifauna of forest canopies in Panama and Peru, I found that the canopy avifauna was primarily composed of forest species, rather than scrub species. Most species occurred in intra- or interspecific flocks. I found that the abundance of small frugivores and small insectivores was seasonally variable. Extent of seasonal variation in fruit crop sizes of *Dipteryx panamensis* may have contributed to the annual variation observed in psittacids. Avifauna of the forest canopy, with few exceptions, was distinct from the understory avifauna; few of the common understory species were recorded in the canopy. Further, in contrast to the canopy avifauna, the understory avifauna was dominated, in terms of species number, by insectivores.

Key words: *Canopy; Costa Rica; frugivores; rain forest; seasonality; tropical.*

INTRODUCTION

Bird species that live in neotropical forest canopies comprise 40 to 50% of forest bird species (Stiles 1983; Blake et al., in press; Karr et al., in press). Canopy trees provide leaf, flower, and fruit resources for birds and other organisms. Despite the clear importance of the canopy to an understanding of tropical forest communities, little work has been completed on birds in this forest zone (but see Pearson 1971, Lovejoy 1974, Greenberg 1981, Munn 1985). Instead, many studies have focussed on birds inhabiting the forest understory (e.g., Munn and Terborgh 1979; Gradwohl and Greenberg 1980; Karr 1980; Karr and Freemark 1983; Levey 1986; Wong 1986; Loiselle and Blake, in press).

Canopy and understory habitats are markedly different in tropical lowland wet forests. The canopy is subject to greater daily variation in light, temperature, wind, and rainfall than is the buffered, dark forest understory (Allee 1926, Fetcher et al. 1985). In Costa Rican wet forest, the site of this study, fruiting and flowering peaks also differ between canopy and understory trees (Frankie et al. 1974). Furthermore, canopy trees show greater seasonality of flowering, fruiting, and leaf loss than understory trees and shrubs (Opler et al. 1980). Canopy habitats have more seasonal populations of insects than do understory habitats (Fogden 1972, Smythe 1982). For these environmental and biotic reasons, birds of the forest canopy are predicted to be more variable seasonally than understory birds (Pearson 1971, Karr 1976).

To test the prediction of greater seasonality in canopy bird assemblages, I censused birds from two emergent canopy trees in lowland wet forest of Costa Rica. This canopy study is the first that reports results from more than one location in a forest canopy. Furthermore, because this Costa Rican forest is less seasonal and wetter than the forest censused in Panama (Greenberg 1981), it provides a good comparison to evaluate the degree of seasonality of birds in the Costa Rican canopy relative to the Panamanian forest canopy. I evaluate seasonality of canopy birds, variability between census trees, and compare those canopy results with ongoing bird studies of the understory avifauna.

METHODS

I conducted canopy censuses in lowland wet forest at Estacion Biologica La Selva (10°25′N, 84°01′W), Costa Rica (for detailed description of this site see Hartshorn 1983). La Selva receives about 4 m of rain annually (Organization for Tropical Studies, unpubl. rainfall data). During the course of this study, rainfall at La Selva was

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TABLE 1. Distribution of canopy censuses by season from Tree 1 and Tree 2. LD, LW, ED, and EW represent late dry (March–April), late wet (September–November), early dry (late December–February), and early wet (May–August) seasons, respectively.

	LD 85	EW 85	LW 85	ED 86	LD 86
Tree 1	3	8	7	7	5
Tree 2	1	2	5	6	5

below normal (total rainfall = 2,847 mm). To facilitate seasonal comparisons of the canopy avifauna, I divided the year into four periods, early and late dry, and early and late wet seasons (Table 1). I selected these periods on the basis of rainfall totals before examining bird census data. Because plant phenology is strongly influenced by rainfall (e.g., Frankie et al. 1974), these divisions also indirectly reflect plant phenological patterns.

I used climbing ropes (Perry 1978) to gain access to the canopies of two emergent trees (*Dipteryx panamensis* and *Hymenolobium pulcherrimum*), each located more than 500 m from the forest edge. I selected the two trees because their height and emergence above most trees of the canopy permitted greater visibility. *Dipteryx* has been the site of previous canopy studies at La Selva (e.g., Perry and Starrett 1980, Fetcher et al. 1985) and is located near a permanent stream (Quebrada El Salto). Major tree species visible from this tree and within the census area (approximately 3.5 ha) included *Dipteryx panamensis, Minquartia guianensis, Lecythis ampla, Socratea durissima, Apeiba membranacea,* and *Pentaclethra macroloba.* Some major vines included *Norantea sessilis, Souroubea* sp., and *Clusia* sp. In contrast, *Hymenolobium* was located along the major ridge that divides the main primary forest block of La Selva ("old" La Selva). Some major trees near this census site included *Virola koschnyi, Pentaclethra macroloba, Miconia multispicata, Socratea durissima,* and *Welfia georgii.* An unindentified vine in the Rubiaceae covered much of the surrounding foliage.

I conducted 49 censuses from 1 April 1985 to 28 April 1986 (Table 1). Censuses began at sunrise (about 06:00). The *Dipteryx* (hereafter referred to as Tree 1) supported a platform 32 m above the ground and I was able to conduct 30 3-hr censuses from this tree. I restricted my census to 2 hr while in the *Hymenolobium* (hereafter referred to as Tree 2) (19 censuses) because no platform was available and I had to conduct the census while hanging from the rope at 30 m. The first census conducted from this tree lasted only 1 hr and was not included in statistical tests comparing results from the two trees.

All birds seen or heard within 100–125 m were recorded in 15-min intervals. The maximum number of individuals per species recorded during any 15-min period was used for analysis of census results (see Loiselle 1987a). I measured distances to nearby canopy trees with a rangefinder during the first few censuses. These distances were then used to estimate distances to birds recorded during these and later censuses. The direction in which a recorded bird was seen or heard was noted to avoid double counting

TABLE 2. Mean number (SE) of individuals and species seen per census during five seasons in 1985–1986 from Tree 1 (1) and Tree 2 (2). Seasons are identified in Table 1. Mean values are given for both entire census period (3 hr) and the first 2 hr only from Tree 1. These latter values are directly comparable to those reported from Tree 2 and were used for statistical tests.

	Late dry 1985		Early wet 1985		Late wet 1985		Early dry 1986	
	1	2[a]	1	2	1	2	1	2
A. Tree 1 (all birds)								
Individuals	82.0	–	48.6	–	62.1	–	63.7	–
	(1.53)	–	(5.00)	–	(3.83)	–	(3.00)	–
Species	26.0	–	22.1	–	29.0	–	33.0	–
	(2.00)	–	(1.71)	–	(1.23)	–	(0.50)	–
B. Tree 1 and Tree 2 (equal census length)								
Individuals	74.7	–	39.8	44.0	51.1	62.6	54.6	58.2
	(3.33)	–	(4.54)	(11.0)	(4.13)	(7.49)	(3.93)	(2.86)
Species	22.7	–	19.0	17.0	24.4	28.4	28.9	31.3
	(0.88)	–	(1.80)	(2.00)	(1.46)	(2.29)	(1.08)	(1.14)

[a] Means not reported because census length was less than 2 hr.

within each 15-min period. Birds flying by or over the canopy were not recorded unless they landed in the census area. Activity declined markedly after 08:00 and few individuals or species were added in the third hour. However, to compare abundances in the two trees, I did not include new individuals or species that were recorded in the third hour from Tree 1.

I divided canopy birds into nine major guilds based on size and diet to evaluate seasonal changes in abundance of birds in relation to their primary resources. These guilds were small- (< 100 g) and large-bodied (> 100 g) frugivores, seed predators (parrots), small- and large-bodied insectivores, nectarivores, frugivore-nectarivore-insectivores, raptors, and scavengers (see Appendix). Both small- and large-bodied frugivores also take insects, and some (e.g., *Ramphastos*) take lizards and frogs (Skutch 1972). My goal was to distinguish birds that regularly eat fruit from birds that rely almost entirely on insects. I did not distinguish fruit dispersers (e.g., *Ramphastos*) from some seed predators (e.g., *Columba*), but I did distinguish parrots as a separate guild because their bill morphology results in little overlap in diet with other fruit and seed eaters (pers. observ.). Most large-bodied insectivores (e.g., *Monasa*) also take small vertebrates (Skutch 1972; Pearson 1975; Sherry 1983; Stiles 1983; pers. observ.). Nectarivores also eat insects and spiders. I did not separate either nectarivores or frugivore-nectarivore-insectivores by body size. Raptors and scavengers accounted for only 1.4% of birds seen, and further division of these guilds seemed unwarranted. I realize that these divisions are broad and that some species could be further separated by finer subdivision. However, broad categories are more appropriate for the sample sizes observed; the frequent absence of species from censuses (Fig. 1) indicates that entire guilds could be absent from some censuses if subdivisions were finer.

TABLE 2. Extended.

Late dry 1986		All	
1	2	1	2
68.4	–	61.9	–
(2.36)	–	(2.49)	–
36.4	–	29.0	–
(0.51)	–	(1.10)	–
60.2	60.2	52.0	58.4
(3.67)	(4.22)	(2.56)	(2.85)
30.8	31.0	24.9	28.8
(1.46)	(1.51)	(1.04)	(1.32)

FIGURE 1. Frequency histogram showing percentage of species with number of individuals per census as indicated.

I used ANOVA to evaluate differences in the canopy assemblage between trees and among seasons (Sokal and Rohlf 1981). I used Kruskal-Wallis analysis of variance to test for seasonal differences among guilds when normality of data sets was violated (Shapiro and Wilk 1965, Sokal and Rohlf 1981). All other statistical tests are identified in the text. English and scientific names of all birds seen in the canopy are in the Appendix and follow AOU (1983, 1985, 1987).

RESULTS

GENERAL COMPOSITION

I recorded a total of 89 species, including 82 species from Tree 1 and 72 species from Tree 2 (Appendix). A majority of species (75%) averaged fewer than one individual per census (Fig. 1). Distribution of species among different abundance classes (Fig. 1) did not differ betweeen census sites ($\chi^2 = 2.64$, df = 4, $P > 0.60$). With all censuses combined, however, significantly more species were seen on average from Tree 2 (28.8 species/census) than from Tree 1 (24.9 species/census) (two-tailed t-test, $t = 2.32$, $P < 0.05$, Table 2).

Species composition and abundance patterns were similar between the two trees. Of the 20 most common species in each tree, 16 species

TABLE 3. Twenty most common species recorded in order of their abundance from censuses conducted in Tree 1 and Tree 2. * Indicates that this species was not recorded in the top 20 from the other tree.

Tree 1		Tree 2	
Species	Flock	Species	Flock
Mealy Parrot	Y	Mealy Parrot	Y
White-crowned Parrot	Y	Chestnut-headed Oropendola	Y
Montezuma Oropendola	Y	Scarlet-rumped Cacique	Y
Scarlet-rumped Cacique	Y	Montezuma Oropendola	Y
Keel-billed Toucan	Y	Short-billed Pigeon	N
Olive-backed Euphonia	Y	Brown-hooded Parrot*	Y
Chestnut-mandibled Toucan	Y	Keel-billed Toucan	Y
Chestnut-headed Oropendola	Y	Olive-backed Euphonia	Y
Short-billed Pigeon	N	Chestnut-mandibled Toucan	Y
Collared Aracari	Y	Collared Aracari	Y
Tropical Gnatcatcher	Y	White-crowned Parrot	Y
Masked Tityra*	Y	Red-lored Parrot	Y
Rufous Piha	N[a]	Tropical Gnatcatcher	Y
Red-lored Parrot	Y	Crowned Woodnymph*	N
White-ringed Flycatcher*	Y	Slate-colored Grosbeak*	N
Purple-throated Fruitcrow*	Y	Black-striped Woodcreeper	N[a]
Black-striped Woodcreeper	N[a]	White-fronted Nunbird	Y
White-fronted Nunbird	Y	Slaty-tailed Trogon	N[a]
Slaty-tailed Trogon	N[a]	White-shouldered Tanager*	Y
Shining Honeycreeper*	Y	Rufous Piha	N[a]

[a] Occasionally in mixed-species flocks.

were shared between the two trees (Table 3). These 24 species (from the 20 most common species at both trees) accounted for 76.5% and 77.6% of all individuals recorded from Tree 1 and Tree 2, respectively.

Frugivores (including parrots) clearly dominated this canopy avifauna, with 18 (75%) of the most common species representing those guilds and only four (17%) representing insectivorous species. Nectarivores and frugivore-nectarivore-insectivores each were represented by one species among the 24 most common species. In addition, the canopy assemblage observed from these two trees was dominated by species found primarily in forest habitats. Nineteen (79%) of these 24 common species are primarily forest canopy species (based on Stiles' unpubl. *Checklist of La Selva Birds*; Blake et al., in press). The remaining five species (Chestnut-headed Oropendola, Montezuma Oropendola, Masked Tityra, White-ringed Flycatcher, and Shining Honeycreeper) are more frequently found in forest-edge habitats. In addition, nine of the 10 most abundant forest-canopy birds observed in this study from both census sites forage most often in intra- or interspecific flocks (Table 3).

SEASONALITY IN CANOPY AVIFAUNA

I found that significant variation occurred among seasons in both number of species ($F = 18.9$, $P < 0.001$) and individuals ($F = 3.94$, $P = 0.02$) observed, but not between trees for either species ($P > 0.15$) or individuals ($P = 0.09$) (Table 2); the tree-season interactive effect was not significant in either case ($P > 0.40$) (two-way ANOVA). I observed fewer species from Tree 2 during early wet season 1985 than in other seasons (one-way ANOVA, Student-Newman-Keuls [SNK] multiple range comparisons, $P < 0.05$; Table 2) (Sokal and Rohlf 1981). Similarly, early wet had significantly fewer species than either late wet 1985 or early and late dry season 1986 from Tree 1 (one-way ANOVA, SNK multiple range test, $P < 0.05$) (Table 2).

In contrast, I observed more individuals from Tree 1 during late dry season 1985 than in any other season (one-way ANOVA, SNK multiple range comparisons, $P < 0.05$) (Table 2). There was no significant difference in the number of individuals observed from Tree 2 among seasons; however, no comparable censuses were conducted during late dry season 1985 (Table 2). I recorded the fewest individuals during early wet season from both trees (Fig. 2, Table 2).

Absence of temperate migrants during early wet season accounted only minimally for the lower abundance of canopy birds during this season (see Loiselle 1987a) (Fig. 2). Migrants in Costa Rica also include species from higher elevations that descend to La Selva during their

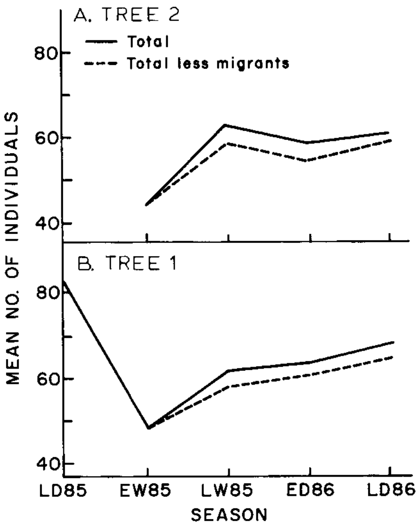

FIGURE 2. Mean number of individuals recorded per census by season from A. Tree 2 and B. Tree 1. Migrants include both temperate and altitudinal migrants. LD85, EW85, and LW85 are late dry, early wet, and late wet season 1985; ED86 and LD86 are early and late dry season 1986.

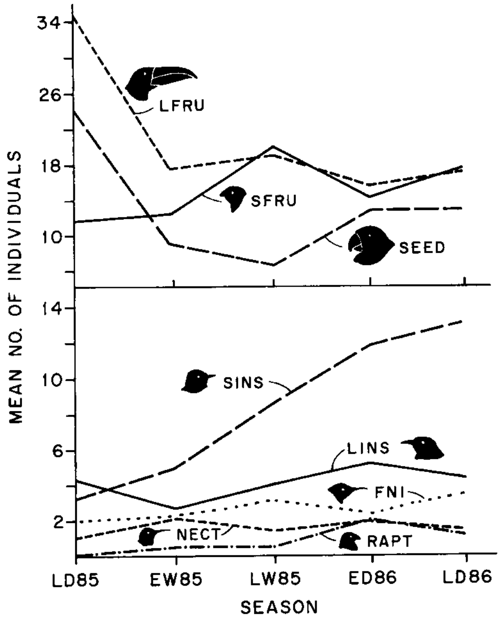

FIGURE 3. Mean number of individuals recorded per census by season for designated guilds from Tree 1. LFRU and SFRU are large- and small-bodied frugivores, SEED are parrots, LINS and SINS are large- and small-bodied insectivores, FNI are frugivore-nectarivore-insectivores, NECT are nectarivores, and RAPT are raptors. Seasons are as in Figure 2.

nonbreeding season (altitudinal migrants) (Loiselle 1987b; Blake et al., in press). Those altitudinal migrants were rare (< 1% of all birds censused) in the canopy and were represented by four species (Yellow-eared Toucanet, Three-wattled Bellbird, Bare-necked Umbrellabird, and Olive-striped Flycatcher). Seasonal changes in canopy-bird abundances are more clearly understood when individual guilds are examined.

Large-bodied frugivores (LFRU), the most abundant guild, showed nearly significant seasonal variation in censuses from Tree 1 (Kruskal-Wallis $H = 7.7$, df $= 4$, $P = 0.10$), but not from Tree 2 (K-W $H = 2.6$, df $= 3$, $P > 0.45$) (Figs. 3, 4). Seasonal variation in Tree 1 was due to a large dry season peak in 1985 and when this season was excluded from analysis, no significant seasonal variation occurred (K-W $H = 0.6$, df $=$ 3, $P > 0.80$).

Abundance of small bodied frugivores (SFRU) peaked during the late wet season in both trees (Figs. 3, 4). Small-bodied insectivores (SINS) also had similar seasonal patterns in both trees with highest abundance recorded during late dry season 1986. These two guilds showed significant seasonal variation in Tree 1 (SFRU: K-W $H =$ 9.8, df $= 4$, $P < 0.05$; SINS: K-W $H = 18.2$, df $= 4$, $P < 0.01$) and approached significance in Tree 2 (SFRU: K-W $H = 6.5$, df $= 3$, $P = 0.09$; SINS: K-W $H = 7.6$, df $= 3$, $P < 0.06$).

Parrots showed significant seasonal variation in abundance from Tree 1 only (K-W $H = 11.4$, df $= 4$, $P < 0.05$), but showed no seasonal variation when the late dry season of 1985 was excluded (K-W $H = 5.2$, df $= 3$, $P > 0.15$). Other guilds contributed less to total canopy avifauna and showed little seasonal variation in either tree. Only raptors, which peaked during early dry season 1986, showed significant seasonal variation at Tree 1 (K-W $H = 14.6$, df $= 4$, $P < 0.01$) (Fig. 4). I did not examine seasonal patterns of scavengers because too few were observed in the census area.

DISCUSSION

COMPARISION WITH OTHER CANOPY AVIFAUNAS

Predominance of frugivores in the canopy of tropical forests is not restricted to Costa Rica. Greenberg (1981) found that the canopy avifauna of Barro Colorado Island, Panama (BCI) was dominated by omnivores (frugivores and nec-

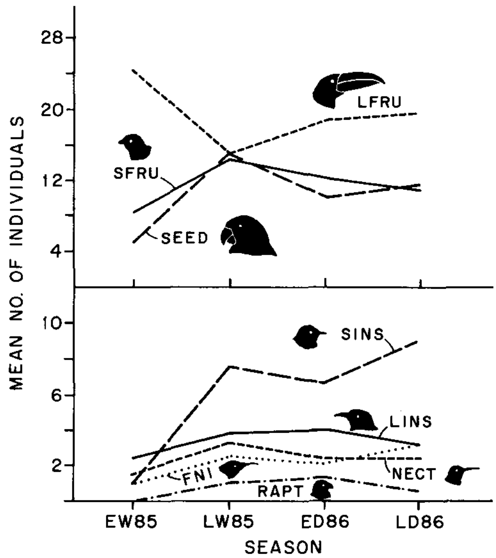

FIGURE 4. Mean number of individuals recorded per census by season for designated guilds from Tree 2. Guild abbreviations are as in Figure 3.

tarivores); he recorded only three insectivorous species among his 20 most common species. Similarly, frugivores dominated the canopy of a Peruvian dry forest (Pearson 1971); 83% of species that spent more than 50% of their foraging time in the upper strata of this forest were frugivores.

Although frugivores dominated the avifauna in both La Selva and BCI, there were considerable differences in the species composition of common birds. Following Greenberg (1981), I excluded parrots, toucans, pigeons, and cracids, and reexamined the 20 most common species from my two census sites. Only five species were among the 20 most common at both BCI and at La Selva (Tropical Gnatcatcher, Shining Honeycreeper, Squirrel Cuckoo, White-ringed Flycatcher, and White-shouldered Tanager). Two of the four most common species at La Selva are not present on BCI (Scarlet-rumped Cacique, Chestnut-headed Oropendola), but are present on the adjacent Panama mainland (Ridgely 1976, Willis and Eisenmann 1979). In contrast, the four most common BCI species (Blue Dacnis, Bay-breasted Warbler, Lesser Greenlet, and Plain-colored Tanager) were recorded from the La Selva canopy, but in low numbers. These species are more common in second growth and forest-edge habitats at La Selva (Stiles, unpubl. *Checklist of La Selva Birds*).

Greenberg (1981) reported that the BCI canopy was dominated by scrub species. Pearson (1975) also reported a predominance of scrub species in the Peruvian canopy (annual rainfall 1,523 mm), but noted that scrub birds only rarely were found in the canopy of wetter forests of Ecuador (2,987 mm rainfall annually) and Bolivia (1,995 mm rainfall annually).

The BCI tower from which Greenberg censused is located in younger and drier forest (70 to 100 years old, 2,600 mm/year) than the La Selva and Ecuador forests and those factors may have accounted for some of the differences observed in canopy composition (see Loiselle 1987a). Furthermore, although approximately the same size as La Selva, BCI (1,500 ha) is an island and has lost an estimated 50 forest species since its isolation (Karr 1982b). La Selva, on the other hand, is connected to foothill and montane forests of Parque Nacional Braulio Carrillo. Willis (1979), in a study of Brazilian woodlots, found that large canopy frugivores were replaced by edge-living omnivores in small woodlots (see also Blake 1983; Blake and Karr 1984; Lovejoy et al. 1986; Levey and Stiles, in press). Thus, the lower number of edge species I observed in the La Selva forest canopy may reflect the fact that this forest has not been completely isolated.

Although I observed seasonality in some guilds and overall in the La Selva canopy, the degree of seasonality was less than that reported for BCI (Greenberg 1981). Higher seasonality at BCI probably was due in large part to the higher abundance of temperate migrants, particularly Bay-breasted Warblers, in the BCI canopy (Loiselle 1987a).

RESOURCE ABUNDANCE AND SEASONALITY

In general, one might expect that seasonal changes in avian guilds should reflect patterns of resource abundance (Stiles 1980, 1985; Wheelwright 1983; Martin and Karr 1986). Abundance of small frugivores did, in fact, peak during the period of peak fruit abundance (late wet season) at La Selva (Frankie et al. 1974). Abundance of large frugivores, however, did not peak during this period. The influence of a major fruit crop to bird abundance is illustrated by Tree 1 (*D. panamensis*). Parrots often fed heavily on fruits of *Dipteryx* trees, which normally fruit from November to March (Frankie et al. 1974). During late dry season 1985, *Dipteryx* crops were large and many

White-crowned Parrots were foraging in the census tree and in nearby *Dipteryx* trees (Fig. 3). In contrast, the *Dipteryx* crop in the census tree was not as large during dry season 1986 as in 1985 (pers. observ.) and fewer parrots were present.

Abundance of small insectivores also appeared to be related to resource levels; their abundance was highest during periods of leaf flushing (late dry-early wet season), a period of high insect abundance (Fogden 1972; Wolda 1978, 1982) and insect activity (Janzen 1983). Moreover, seasonality of insects is most pronounced for those from the 5–15 mm size class (Smythe 1982), the range taken most frequently by small insectivores (Hespenheide 1971, Karr 1976, Smythe 1982). Large-bodied insectivores, in contrast, did not show any significant seasonal pattern of abundance. Lack of seasonal variation in large insectivores may reflect lower seasonality of their large insect prey or the fact that many large insectivores also often feed on alternative prey, such as small vertebrates. Thus, resource availability likely influences seasonal variability of some birds observed in these censuses.

Nectarivores, because of their small size, often were difficult to observe in the canopy and their abundance likely was underestimated relative to other guilds. Nectarivores were observed more often from Tree 1 during the early wet season (Fig. 3), a period of high flower availability at La Selva (Frankie et al. 1974), but were more common at Tree 2 during late wet season (Fig. 4), a period of low flower availability. Low numbers of observations in both trees (usually less than three individuals per census) may obscure seasonal patterns.

F. G. Stiles (pers. comm.) also has noted considerable variation in daily and weekly abundance of canopy birds that appear tied to resources. For example, when flowering, *Norantea,* a canopy vine, attracted large numbers of temperate migrants (F. G. Stiles, pers. comm.).

ANNUAL VARIATION IN CANOPY AVIFAUNAS

Short-term studies in the tropics provide useful information but must be interpreted cautiously (Wiens 1977; Stiles 1978, 1983; Wolda 1978; Foster 1982; Wheelwright 1986; Levey 1987). My results suggest that identities of the common core of the canopy avifauna observed here likely will remain similar from year to year. However, seasonal patterns in abundance of common species, as well as occurrence of rare species, will vary among years. For example, Great Green Macaws (*Ara ambigua*) were relatively common at La Selva from November 1986 to April 1987 and undoubtedly would have been recorded in canopy censuses conducted during this period. Macaws typically were observed feeding on fruiting *Dipteryx* trees and their irregular occurrence at La Selva may reflect spatial and temporal variation in fruit crops, as well as effects of human-caused disturbance (e.g., logging).

Long-term changes in the La Selva avifauna also are likely to influence the composition of canopy birds. During the past 30 years, more canopy species at La Selva have declined than any other group (Levey and Stiles, in press). Documenting both annual and seasonal fluctuations in forest-canopy birds may increase our understanding of the causes and consequences of long-term changes in this group (Karr 1982a).

COMPARISON WITH UNDERSTORY AVIFAUNA

I sampled forest understory birds at La Selva with mist nets during the same period as I conducted canopy censuses (Loiselle 1987b). Distribution of captures of understory birds (Fig. 5) approximated the result presented for canopy birds (Fig. 1) (Chi-Square test of number of species in each abundance category: $\chi^2 = 5.9$, df = 8, $P > 0.60$). This pattern, many rare species and few common ones, also has been observed in other tropical studies (e.g., Karr et al., in press).

Despite different techniques employed in censusing birds of these two strata, I believe the 20 most common species captured in mist nets (Table 4) adequately represent the common birds of the forest understory. Abundance of large, ground-dwelling birds, such as tinamous, curassows, and quail-doves are underestimated by mist nets, but form a small proportion of the avifauna, based on visual/auditory observations. Unlike the frugivore-dominated canopy, insectivores accounted for the greatest number of species in the forest understory (Table 4) (see also Levey 1986; Blake et al., in press). However, in terms of number of individuals captured, understory frugivores were as abundant as insectivores (Loiselle 1987b). A similar pattern has been noted elsewhere by Stiles (1983, for La Selva), Greenberg (1981, for BCI), and Karr (1976, for Panama mainland). I further found that for understory populations, insectivore capture rates

TABLE 4. Twenty most common species (in decreasing order of mist-net captures) in the forest understory at La Selva (Loiselle 1987b). * indicates that these species also were observed in the forest canopy. N = nectarivore, I = insectivore, F = frugivore.

Species	Guild
*Wedge-billed Woodcreeper *Glyphorynchus spirurus*	I
*Red-capped Manakin *Pipra mentalis*	F
Ochre-bellied Flycatcher *Mionectes oleagineus*	F/I
*Long-tailed Hermit *Phaethornis superciliosus*	N
Wood Thrush *Hylocichla mustelina*	I/F
White-ruffed Manakin *Corapipo leucorrhoa*	F
Bicolored Antbird *Gymnopithys leucaspis*	I
White-breasted Wood-Wren *Henicorhina leucosticta*	I
Ocellated Antbird *Phaenostictus mcleannani*	I
Spotted Antbird *Hylophylax naevioides*	I
Plain-brown Woodcreeper *Dendrocincla fuliginosa*	I
Bronze-tailed Plumeleteer *Chalybura urochrysia*	N
Olive Tanager *Chlorothraupis carmioli*	F/I
Swainson's Thrush *Catharus ustulatus*	F/I
Ruddy-tailed Flycatcher *Terenotriccus erythrurus*	I
*[a]Tawny-crested Tanager *Tachyphonus delatrii*	F/I
[a]Song Wren *Cyphorhinus phaeocephalus*	I
[b]Black-faced Antthrush *Formicarius analis*	I
*[b]Crowned Woodnymph *Thalurania colombica*	N
Tawny-crowned Greenlet *Hylophilus ochraceiceps*	I

[a,b] Represent species with equal number of captures.

as a whole displayed less seasonality than either understory frugivores or nectarivores (Loiselle 1987b), a pattern that also was apparent in the canopy censuses and elsewhere (Karr 1976, Martin and Karr 1986). Unfortunately, because of the different sampling techniques, I am not able to directly compare the degree of seasonal variation of guilds between canopy and understory habitats.

Five common understory birds were observed in the canopy (Table 4), but I saw only two of

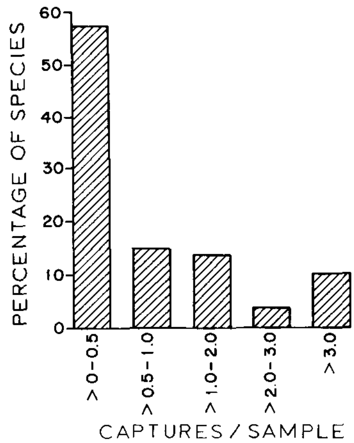

FIGURE 5. Frequency histogram showing percentage of species with number of individuals captured in forest understory per sample as indicated (from Loiselle 1987b).

these species (Crowned Woodnymph and Tawny-crested Tanager) regularly. Stiles (1980) noted that male and female Crowned Woodnymphs differed in vertical foraging preferences with males occurring more often in the canopy than females. Both Stiles (1983) and Pearson (1971, 1977) observed that canopy birds foraged over a greater vertical range compared to understory birds.

CONCLUSIONS

Frugivores (> 100 g) and parrots dominated the canopy at La Selva. I observed significant seasonal variation among some guilds and the canopy assemblage as a whole, but seasonality of this assemblage appeared less than that observed in Panama by Greenberg (1981). Results from a single-year study of La Selva canopy birds conducted from only two sites should be interpreted cautiously. More long-term studies on canopy assemblages with simultaneous monitoring of resources are needed.

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APPENDIX. Number of individuals recorded over all dates from censuses conducted in *Dipteryx* (Tree 1) and *Hymenolobium* (Tree 2) during 1985–1986. Guilds are described in the text. English and scientific names follow American Ornithologists' Union (1983, 1985).

Species	Number of individuals Tree 1	Tree 2
Scavengers		
King Vulture *Sarcoramphus papa*	2	0
Raptors		
Double-toothed Kite *Harpagus bidentatus*	8	0
Tiny Hawk *Accipiter superciliosus*	0	1
Semiplumbeous Hawk *Leucopternis semiplumbea*	9	9
Laughing Falcon *Herpetotheres cachinnans*	6	4
Slaty-backed Forest-Falcon *Micrastur mirandollei*	0	2
Collared Forest-Falcon *M. semitorquatus*	1	0
Seed eaters (parrots)		
Crimson-fronted Parakeet *Aratinga finschi*	2	0
Olive-throated Parakeet *A. nana*	2	0
Aratinga sp.[a]	1	0
Orange-chinned Parakeet *Brotogeris jugularis*	23	5
Brown-hooded Parrot *Pionopsitta haematotis*	26	47
White-crowned Parrot *Pionus senilis*	106	37
Red-lored Parrot *Amazona autumnalis*	44	29
Mealy Parrot *A. farinosa*	131	90
Nectarivores		
Long-tailed Hermit *Phaethornis superciliosus*	2	1
White-necked Jacobin *Florisuga mellivora*	4	3
Crowned Woodnymph *Thalurania colombica*	35	24
Purple-crowned Fairy *Heliothryx barroti*	0	8
Hummingbird species	4	11
Large frugivores		
Crested Guan *Penelope purpurascens*	5	7
Short-billed Pigeon *Columba nigrirostris*	74	48
Slaty-tailed Trogon *Trogon massena*	38	23
Lattice-tailed Trogon *T. clathratus*	1	1
Collared Aracari *Pteroglossus torquatus*	69	42
Yellow-eared Toucanet *Selenidera spectabilis*	0	8
Keel-billed Toucan *Ramphastos sulfuratus*	82	44
Chestnut-mandibled Toucan *R. swainsonii*	77	43
Purple-throated Fruitcrow *Querula purpurata*	42	15
Bare-necked Umbrellabird *Cephalopterus glabricollis*	5	1
Three-wattled Bellbird *Procnias tricarunculata*	4	6
Chestnut-headed Oropendola *Psarocolius wagleri*	74	65
Montezuma Oropendola *P. montezuma*	101	58
Small frugivores		
Olive-striped Flycatcher *Mionectes olivaceus*	2	0
Boat-billed Flycatcher *Megarynchus pitangua*	7	1
Gray-capped Flycatcher *Myiozetetes granadensis*	18	0
Masked Tityra *Tityra semifasciata*	48	13
Black-crowned Tityra *T. inquisitor*	6	2
Rufous Piha *Lipaugus unirufus*	44	19
Snowy Cotinga *Carpodectes nitidus*	26	15
Red-capped Manakin *Pipra mentalis*	0	1
Yellow-throated Vireo *Vireo flavifrons*	1	0
Red-eyed Vireo *V. olivaceus*	6	6
Bay-breasted Warbler *Dendroica castanea*	2	5
Plain-colored Tanager *Tangara inornata*	2	0
Golden-masked Tanager *T. larvata*	4	3
Yellow-crowned Euphonia *Euphonia luteicapilla*	14	3
Olive-backed Euphonia *E. gouldi*	80	44
White-vented Euphonia *E. minuta*	13	3
White-shouldered Tanager *Tachyphonus luctuosus*	14	19
Tawny-crested Tanager *T. delatrii*	12	1
Summer Tanager *Piranga rubra*	1	2

APPENDIX. Continued.

APPENDIX. Continued.

Species	Number of individuals	
	Tree 1	Tree 2
Slate-colored Grosbeak		
Pitylus grossus	32	23
Black-faced Grosbeak		
Caryothraustes poliogaster	4	2
Scarlet-rumped Cacique		
Cacicus uropygialis	93	59
Large insectivores		
Squirrel Cuckoo		
Piaya cayana	27	14
White-necked Puffbird		
Bucco macrorhynchus	6	2
White-fronted Nunbird		
Monasa morphoeus	39	23
Chestnut-colored Woodpecker		
Celeus castaneus	13	10
Lineated Woodpecker		
Dryocopus lineatus	1	1
Pale-billed Woodpecker		
Campephilus quatemalensis	32	14
Small insectivores		
Black-cheeked Woodpecker		
Melanerpes pucherani	3	2
Smoky-brown Woodpecker		
Veniliornis fumigatus	2	0
Rufous-winged Woodpecker		
Piculus leucolaemus	0	1
Cinnamon Woodpecker		
Celeus loricatus	9	2
Woodpecker sp.[a]	1	4
Striped Woodhaunter		
Hyloctistes subulatus	1	0
Wedge-billed Woodcreeper		
Glyphorhynchus spirurus	1	0
Barred Woodcreeper		
Dendrocolaptes certhia	1	0
Black-striped Woodcreeper		
Xiphorhynchus lachrymosus	39	23
Paltry Tyrannulet		
Zimmerius vilissimus	1	4

APPENDIX. Continued.

Species	Number of individuals	
	Tree 1	Tree 2
Black-capped Pygmy-Tyrant		
Myiornis atricapillus	16	5
Yellow-margined Flycatcher		
Tolmomyias assimilis	21	14
Contopus sp.	2	2
Empidonax sp.	1	4
Rufous Mourner		
Rhytipterna holerythra	13	13
Great Crested Flycatcher		
Myiarchus crinitus	2	0
White-ringed Flycatcher		
Coryphotriccus albovittatus	42	1
Cinnamon Becard		
Pachyramphus cinnamomeus	1	0
Tropical Gnatcatcher		
Polioptila plumbea	52	26
Lesser Greenlet		
Hylophilus decurtatus	12	11
Green Shrike-Vireo		
Vireolanius pulchellus	8	0
Chestnut-sided Warbler		
Dendroica pensylvanica	24	12
Blackburnian Warbler		
D. fusca	2	1
Dendroica sp.	0	1
Canada Warbler		
Wilsonia canadensis	1	0
Frugivore-nectarivore-insectivores		
Tennessee Warbler		
Vermivora peregrina	11	4
Blue Dacnis		
Dacnis cayana	12	11
Green Honeycreeper		
Chlorophanes spiza	14	7
Shining Honeycreeper		
Cyanerpes lucidus	38	18
Northern Oriole		
Icterus galbula	2	4

[a] Not counted as a separate species.