

# ANNUAL VARIATION IN BIRDS AND PLANTS OF A TROPICAL SECOND-GROWTH WOODLAND<sup>1</sup>

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**Abstract.** We examined effects of successional changes in vegetation on bird species found in a young second-growth woodland in Costa Rica over a four-year period (1985-1988). Significant changes in vegetation structure and plant composition occurred: numbers of small (2-5 cm dbh) trees, woody shrubs, and lianas increased, as did canopy cover; herbaceous shrubs declined in abundance. Total numbers and species of plants producing flowers pollinated by hummingbirds or fruits eaten by birds did not change, but significant changes were noted in fruit production of individual plant species. Overall capture rates of birds in mist nets did not vary significantly among years but significant changes were noted for individual species. Several bird species characteristic of mature forest habitat first appeared in second-growth woodland during latter years of the study; other species, more dependent on early successional habitats, decreased in abundance or disappeared entirely from our study plot. Diets of some fruit-eating birds changed over time, apparently in response to changes in abundance of different fruit species. This study suggests that changes in plant and bird populations may be relatively rapid in tropical second-growth habitats. Such results have important implications for conservation; a range of successional stages may be necessary to support the full complement of bird species that can occur in a given area.

**Key words:** *Annual variation; Costa Rica; diet; frugivores; fruits; habitat selection; second-growth; succession; tropical birds.*

## INTRODUCTION

Disturbed or second-growth habitats in tropical regions are important for many resident bird species, either on a permanent basis or for short-term use of resources (Levey 1988a, 1988b; Blake et al. 1990; Blake and Loiselle 1991; see also Gilbert 1980). Such habitats are important for many migratory bird species as well (Martin 1985; Hutto 1989, 1992; Blake and Loiselle 1991, 1992). Conversion of tropical forests to pastures or other land uses has increased the extent of second-growth habitats in many regions of Central and South America. Despite the increasing occurrence of non-forested habitats in wet tropical regions, few studies have addressed how successional changes in habitat affect plant and animal communities (Uhl and Jordan 1984, Martin and Karr 1986, Saldarriaga 1987, Hutto 1989, Laurance 1991).

Natural disturbances range in size from single treefall gaps to many square kilometers of hurricane damage (e.g., papers in Walker et al. 1991). Responses of plants and animals to such disturbances can be rapid, with the extent of change

dependent on the scale and severity of the disturbance. Anthropogenic disturbances also range over orders of magnitude in area, from small, single-family plots to extensive cattle pastures or monocrops. Short- and long-term effects on native plants and animals also vary. The ability of disturbed habitats to regrow and attain some measure of former complexity and diversity has direct consequences for bird populations.

In cases where land use changes have not resulted in severe environmental degradation, and where seed sources are in relatively close proximity, regrowth of vegetation in tropical habitats can be extremely rapid following disturbance (pers. observ., Uhl and Jordan 1984, Uhl et al. 1990); related, concurrent changes in bird populations are likely to occur in such habitats as well. With the increasing occurrence of disturbed habitats, understanding the consequences of such changes in habitat structure to bird populations becomes increasingly important (Blankespoor 1991), especially because some birds play a key role in ecosystem function (e.g., as seed dispersers and plant pollinators; see Stiles 1985).

Species composition and abundance of birds and fruit-producing shrubs differ among second-growth habitats of different ages and between second-growth and forest habitats (Martin 1985;

<sup>1</sup> Received 17 May 1993. Accepted 1 November 1993.

Martin and Karr 1986; Levey 1988a, 1988b; Hutto 1989; Lynch 1989, 1992; Blake and Loiselle 1991). Two basic approaches can be used to examine successional changes in plants and associated animals. One can either follow changes over time on a given study plot (e.g., Willis 1974) or compare communities in a series of plots of different known ages (e.g., Hutto 1989, Blankespoor 1991). We use the first approach in this study, examining changes in birds and plants over a four-year period (1985–1988) in a young (5–10 year old) anthropogenic second-growth habitat in Costa Rica. We focus on species level responses (changes in activity levels as measured by mist-net captures; changes in diet) to successional changes in habitat. We were particularly interested in determining what factors account for annual changes in bird communities and how quickly these communities either begin to resemble mature forest or are attractive to forest species. To evaluate the influence of changes in resource abundance on bird use of the habitat, we focus on fruit-eating birds and fruit-producing plants. Many resident and migrant birds are attracted to the often abundant supplies of fruit that occur in second-growth habitats (Martin and Karr 1986, Blake and Loiselle 1991). As fruit abundance changes or as plant species composition changes, composition and abundance of fruit-eating birds are also likely to change.

Early successional plant and bird species found in our study site resemble those found in similar habitat throughout the Atlantic forest region of Costa Rica (pers. observ.). Consequently, changes in plant and bird communities observed at our site likely occur in these other habitats as well.

## STUDY AREA

We conducted our research at La Selva Biological Station (Organization for Tropical Studies [OTS]) in the lowlands of northeastern Costa Rica, near Puerto Viejo de Sarapiquí, Provincia Heredia (10°25'N, 84°01'W). La Selva encompasses approximately 1,510 ha, of which about 64% is primary (or slightly disturbed) forest (Clark 1990). The station also supports anthropogenic successional habitats in various stages of regrowth. To the south, La Selva borders Parque Nacional Braulio Carrillo (approximately 44,900 ha); continuous forest exists from approximately 40 m elevation at La Selva to >2,900 m in Braulio Carrillo (Pringle et al. 1984).

Rainfall at La Selva averages 3,877 mm/year

(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 or October. December–April rainfall was below “normal” during three years of this study (i.e., 694 mm in 1985, 743 in 1986, 645 in 1987, and 1,129 in 1988; 30-year ave. rainfall for December–April is 1,185 mm).

We established a study plot in January 1985 in an area of young second-growth vegetation (approximately 40 ha in size). The study plot was on recent alluvial soil adjacent to Rio Sarapiquí and was bordered by older ( $\approx$ 20–30 year-old) second-growth. On approximately one-third to one-half of the study plot, *Psidium guava* (Myrtaceae) was the dominant tree, creating an open canopy 5–6 m tall. *Psidium* was probably introduced to this area by seeds defecated by horses and/or cattle (G. S. Hartshorn, pers. comm.). Prior to abandonment in 1981 (when the land was purchased by OTS, see Clark 1990), the area was used for pasture; some rapidly growing secondary trees (e.g., *Piper* sp. [Piperaceae], *Miconia* sp. [Melastomataceae], *Vismia* sp. [Guttiferaceae]) were already 3–4 m tall when the study began in 1985. A few tall trees, such as *Ficus* sp. (Moraceae; >20 m tall) and *Nectandra membranacea* (Lauraceae; >8 m tall), were left standing in the plot.

## METHODS

### BIRDS

We used mist nets (12-m, 4 shelf, 36-mm mesh) to sample birds. (See Blake and Loiselle [1991] and Loiselle and Blake [1991] for recent discussions on use of mist nets.) We arranged 30 nets in a grid that covered approximately 5 ha; *Psidium* trees were present on approximately one-third of the study plot. Nets were centered on points located 40 m apart on this grid (i.e., we did not select “good” sites); exact orientation of the nets varied among net-sites in order to minimize disturbance to vegetation when placing nets. We operated nets for four days (=1 sample period) every 5–6 weeks, from late December to April (1985–1988), starting in January 1985. There were three sample periods each year. These sample periods corresponded to a time of year when latitudinal (primarily north temperate) and altitudinal migrant birds were present at the site; relatively few resident birds bred during this time

period (pers. observ.). Each net was operated on only two alternate days each sample. Fifteen nets were opened per day, from sunrise to approximately 13:00 hr, or as close to 7 hr/day as possible. Captured birds were banded, weighed, and sexed and aged (if possible). We held all birds (except hummingbirds and raptors) for collection of fecal samples and then released birds at the point of capture. We determined diets of fruit-eating birds by examining fecal samples for fruit pulp and/or seeds (Loiselle and Blake 1990). We identified >95% of seeds to plant species or genus. Bird names follow American Ornithologists' Union (1983, and supplements).

### PLANTS

Fruits and flowers were sampled during each of 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 m<sup>2</sup>/net-site) (Blake et al. 1990). We identified and tagged all plants with flowers or fruit. Plant names follow an unpublished checklist of La Selva plants (OTS, unpubl. data). We recorded presence of flowers or flower buds and counted ripe and unripe fruits on each plant during each sample (following methods outlined in Loiselle and Blake 1991). Flowers and flower buds were counted starting in 1986. Although fruits vary in size and nutrient content, we decided to use actual numbers of fruits as our estimate of fruit available to birds. Most fruits used by understory birds in this habitat are berries of the Melastomataceae and Rubiaceae and, thus, offer mostly carbohydrate rewards and do not vary greatly in size (Loiselle and Blake 1990, 1991). We restricted our analyses to those plants known to be visited by birds for their fruit or nectar (based on analysis of fecal samples [Loiselle and Blake 1990], personal observations of foraging birds, Croat 1978, Stiles 1980).

Vegetation was sampled on two transects (3 × 12.5 m each) located parallel to each side of each mist net during 1986 and 1989. We measured and recorded the diameter at 1.5 m of all woody stems with a diameter ≥ 2 cm. Lianas ≥ 2 cm thick were counted and measured, as were all woody stems < 2 cm dbh and ≥ 1.5 m tall, non-woody plants (≥ 1.5 m) (e.g., *Renealmia* [Zingiberaceae]; *Heliconia* [Heliconiaceae]), and vines (< 2 cm thick). Canopy cover was measured with a spherical densiometer (Lemmon 1956) at ap-

proximately the same time every year starting in 1986. Four readings, one in each of the cardinal compass points, were taken at each end and at the middle of each net lane (12 readings/net), with the densiometer held at approximately 1.5 m; these 12 readings were then averaged to provide one canopy cover value for each net site per year.

### DATA ANALYSIS

We used non-parametric Wilcoxon matched-pairs test (Sokal and Rohlf 1981) to examine changes in habitat structure between 1986 and 1989 by comparing vegetation characteristics recorded at all net-sites. For analyses of fruit and flower abundance, we summed the number of fruits and numbers of individual fruiting and flowering plants over all 30 net sites during each sample period (three sample periods/year) and determined the number of species with flowers or fruits. We used number of birds captured per net-hour (one net open 1 hr = 1 net-hour) (× 100) as an index of bird activity during each sample period. To compare capture rates over time, we combined all captures from each net site for a particular sample to give a single value for that sample (three sample periods/year); mean capture rate per year was then calculated from these three sample values.

We used one-way analysis of variance (ANOVA) to examine differences in fruit or flower abundance or capture rate of birds among years. Data were tested for normality (Wilk-Shapiro test) and homogeneity of variances (Bartlett's test) (Sokal and Rohlf 1981) and were transformed (natural log) when necessary prior to analysis. If transformed data did not meet assumptions of parametric tests, a non-parametric test (Kruskal-Wallis) was used.

We determined if use of a particular fruit species by frugivorous birds varied among years. To do this, we summed the fecal sample occurrence of seeds from that plant species by year and then used a chi-square goodness of fit test, with the null hypothesis being that frugivores fed on that plant species equally among years (Loiselle and Blake 1990). Frugivorous birds have been shown in aviary trials to make consistent choices among fruit species (e.g., Moermond and Denslow 1985). In field situations, however, we expect that annual changes in fruit abundance and in composition of the frugivorous bird community likely result in annual differences in visitation rates to

and fruit removal from a given plant species. To examine variation in relative use of different fruit species by individual bird species and by all frugivorous birds taken together, we summed the occurrence in the diet of seeds of major plant species by year for a given bird species (or all birds) and used chi-square (contingency table) tests to determine if that bird species changed its proportional use of fruit species among years. We combined diet data over two-year periods (1985 and 1986 vs. 1987 and 1988) for some species because of small sample sizes.

## RESULTS

### PLANTS

Significant changes in vegetation structure and plant composition occurred over the course of this study. In general, vegetation at this site changed from a nearly impenetrable mass of dense vegetation at understory levels (i.e., <2 m) to a relatively more open understory dominated by shrubs and small trees. This qualitative vegetation change is demonstrated by the decrease in canopy openness (Wilcoxon  $Z = 4.77$ ,  $P < 0.001$ ; Fig. 1) and herbaceous (i.e., non-woody) shrubs (Table 1). In contrast, there was significant recruitment of small (2–5 cm dbh) trees, woody shrubs, and lianas (Table 1). Plant resources directly used by birds (flowers, fruits) showed no significant changes overall among years in overall abundance. For example, number of flowering

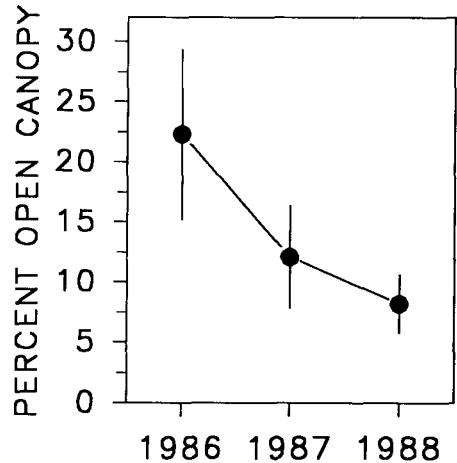


FIGURE 1. Decreases in canopy openness (mean and SE) detected at 1.5 m height in young second-growth from 1986 to 1988; means are based on canopy measures at 30 net sites per year.

plant species (species regularly visited by hummingbirds) remained relatively constant among years (one-way ANOVA,  $F_{3,8} = 0.33$ ,  $P > 0.80$ ). Whereas, the mean number of flowering plants declined markedly from 1985 to 1986, differences among years were not significant (one-way ANOVA,  $F_{3,8} = 1.56$ ,  $P > 0.25$ ) (Table 2). Similarly, neither number of ripe fruits nor number of plants fruiting differed among years ( $F_{3,8} > 0.20$ ,  $P > 0.65$ ) (Table 2).

TABLE 1. Mean number and standard error (SE) of individuals per net-site (75 m<sup>2</sup>) for vegetation parameters measured on transects ( $n = 30$ ) in 1986 and on the same transects in 1989. Results of Wilcoxon tests comparing means (by transects) between years are shown when significant.

Vegetation measure	1986		1989		Wilcoxon test
	Mean	SE	Mean	SE	
Trees (dbh)					
2–3 cm	4.2	0.65	11.3	1.17	$P < 0.001$
4–5 cm	2.1	0.41	3.3	0.47	$P < 0.05$
6–10 cm	4.9	0.64	3.9	0.44	
11–15 cm	2.2	0.33	2.0	0.28	
16–25 cm	0.7	0.20	0.8	0.17	
26–50 cm	0.2	0.11	0.3	0.15	
> 50 cm	0.0	0.00	0.0	0.00	
Lianas (diameter)					
2–3 cm	0.5	0.20	1.9	0.47	$P < 0.01$
4–5 cm	0.1	0.07	0.4	0.18	$P < 0.05$
Woody shrubs and stems	61.2	3.73	85.6	7.19	$P < 0.05$
Vines and tendrils	16.0	3.18	23.5	3.83	
Herbaceous shrubs	16.7	3.87	3.4	1.19	$P < 0.01$
<i>Heliconia</i> , <i>Costus</i>	2.0	1.73	3.4	1.49	

TABLE 2. Mean number of flowering plants or species (per 0.15 ha) and mean number of fruiting individuals or ripe fruits recorded in young second-growth woodland based on three sample periods during each year. SE = standard error of samples during each year.

	1985	1986	1987	1988
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Flowers				
Individuals	46.7 (10.97)	29.0 (7.51)	29.7 (6.89)	24.0 (5.03)
Species	5.0 (0.0)	5.6 (0.88)	5.3 (0.33)	5.0 (0.58)
Fruits <sup>1</sup>				
Individuals	302 (11.1)	337 (27.7)	412 (76.2)	327 (112.8)
Ripe fruits	5,830 (1,773)	4,000 (928)	4,740 (2,442)	5,223 (3,281)
Fruits <sup>2</sup>				
Individuals	251 (20.6)	269 (27.3)	239 (19.9)	195 (11.9)
Ripe fruits	4,767 (2,228)	2,949 (1,364)	690 (330)	1,219 (866)

<sup>1</sup> All species included.

<sup>2</sup> *Psychotria pittieri* not included in totals; see text.

Changes at the plant species level, however, were more pronounced. During the four-year period, 36 species of plants were recorded with ripe fruit from December–April. Of these 36, six species accounted for over 75% of all ripe fruits and plants with fruit. Abundance of three of those six species (*Conostegia subcrustulata*, *Clidemia dentata*, *Piper auritum*) declined significantly (Fig. 2). In contrast, number of fruiting *Psychotria pittieri* plants (the most abundant fruit-producing shrub on the plot) increased significantly from 1985 to 1988 (Fig. 3). A similar increase in fruiting was observed for *Miconia affinis* from 1985 to 1987; fruit production was lower, however, in 1988. *Piper sancti-felicitis* showed no significant trend in fruit production over the four-year period on the study plot (Fig. 3).

#### BIRD ACTIVITY

We captured 2,085 birds of 118 species during this study. Although fewer birds were captured over time, the decline was not significant (Table 3). Capture rate of frugivores generally paralleled capture rate of all birds among years. Captures of nectarivores, on the other hand, declined markedly from 1985 to 1986 but remained fairly constant thereafter (Table 3). Changes in capture rates of nectarivores tended to parallel changes in overall numbers of flowering plants in that mean capture rate and mean number of flowering plants both declined markedly from 1985 to 1986 and remained relatively stable thereafter.

Overall, fewer bird species were captured in 1988 than in earlier years (Table 3). We exam-

ined annual variation in capture rates for 19 species that were relatively common on the plot and that were active foragers at mist-net levels. These species were selected because we felt that variation in capture rates among years reflected real differences in their activity on the plot. Capture rates of seven species changed significantly over time (Table 3)—more species than expected by chance alone (i.e., only one of 19 species expected to change due to chance alone). Capture rates of six species declined, whereas that of *Phaethornis longuemareus* increased; these trends were consistent with knowledge of species' preferred habitats. For example, all six species that showed significant declines are species characteristic of young-second growth and edge in Costa Rican wet forests and are rarely found in forest interior (Stiles and Skutch 1989, Blake et al. 1990). Mean capture rates of several additional species showed declining or increasing trends over the four-year period, but capture rates were often highly variable within years (Table 3). Capture rates of eight species showed no annual change or no consistent trend.

Only three new species (i.e., species not captured in any previous sample) were represented in mist-net captures in 1988; 10 new species were represented in 1987, and 10 in 1986 (Table 4). In several instances, these "new" species (e.g., *Legatus*, *Polioptila*, *Dendroica*) were birds that occur primarily in forest canopy and that rarely descend to mist-net levels. Several species, though, are birds found primarily in understory of undisturbed wet forests and their presence in

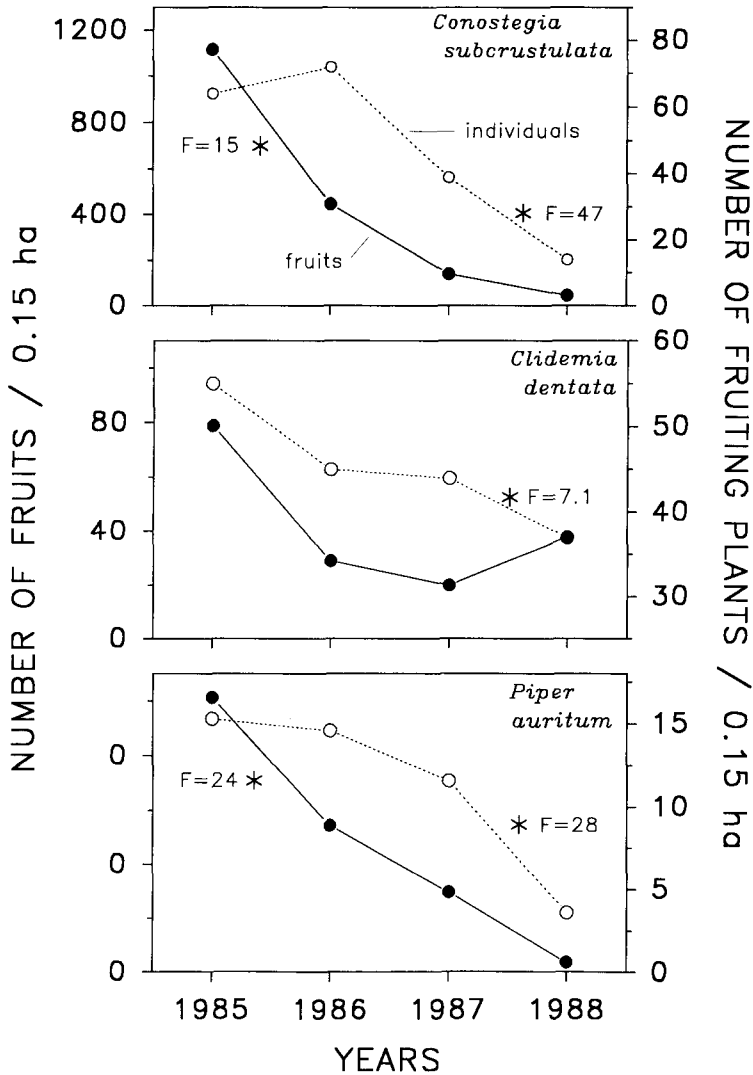


FIGURE 2. Mean number of individual fruiting plants or ripe fruits recorded during each year for three common plant species. We used total rather than ripe fruits for *Piper auritum* because fruits do not always change color upon maturity and the height of plants made it impossible to test fruit ripeness by touch. Significant differences in mean number of individuals or ripe fruits among years (ANOVA) are indicated.

second-growth during the latter years of this study might indicate the increasing suitability of this habitat for these birds (see Table 4).

#### DIETS OF FRUIT-EATING BIRDS

We examined annual variation in the diets of fruit-eating birds, restricting our analyses to the six common plants that accounted for over 75% of all fruits produced (see above). In general changes in use of a given fruit species paralleled

annual changes in the abundance of that fruit species. Specifically, consumption of *Conostegia subcrustulata* and *Piper auritum* fruits declined with time, whereas the reverse was true for *Miconia affinis* and *Psychotria pittieri* (Fig. 4). Moreover, fruit-eating birds as a whole (i.e., all frugivorous species combined) changed their relative intake of these six fruit species among years (4 year  $\times$  6 plant species contingency table,  $\chi^2 = 104.2$ ,  $P < 0.0001$ ).

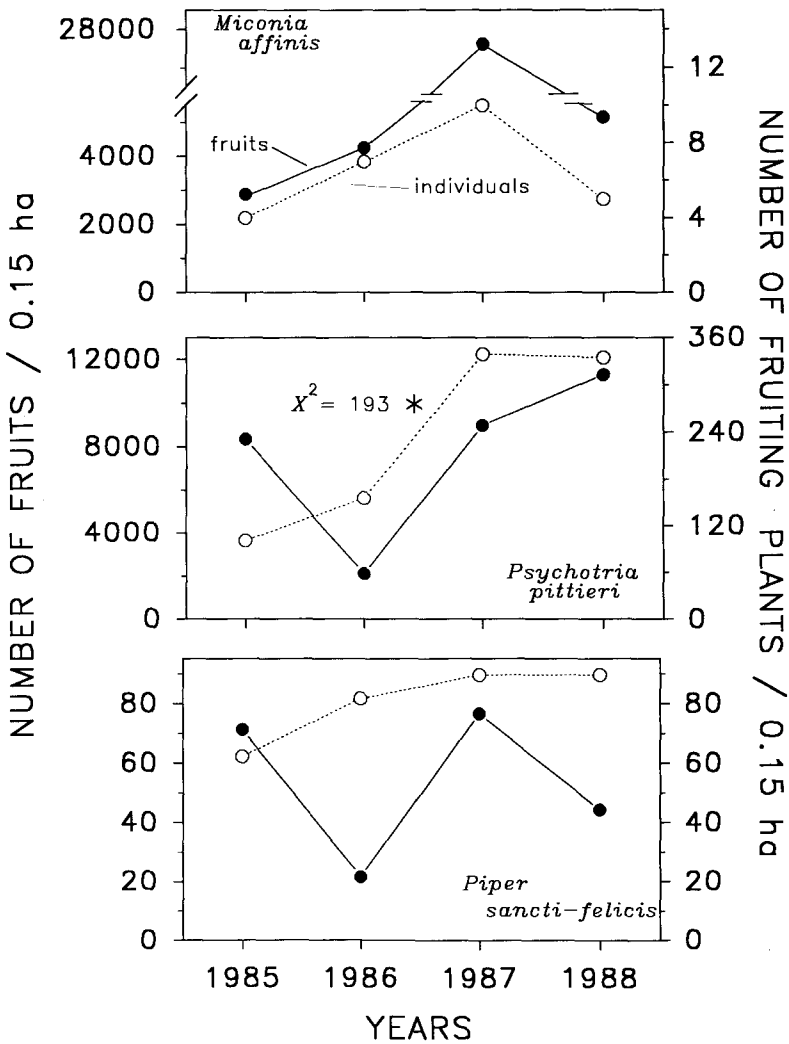


FIGURE 3. Number of fruits and individual fruiting plants for three common plant species in young second-growth. Significant differences in mean number of individuals or fruits among years (Kruskal-Wallis test) are indicated. We used maximum number of fruits recorded during any one year rather than mean number of fruits because of aseasonal fruit production between samples within years to *Psychotria pittieri* and *Miconia affinis*.

Whether or not individual bird species showed significant differences among years in the relative use of these six major fruit species appeared to be related to the persistence of these birds on the plot during the duration of this study. Two of the six most common fruit-eating birds, *Manacus candei* and *Pipra mentalis*, showed significant ( $\chi^2 = 22, P < 0.01$  for *Manacus*) or nearly significant ( $\chi^2 = 9.3, P < 0.06$  for *Pipra*) differences among years in consumption of common fruits (Fig. 5). Both *Pipra* and, in particular, *Manacus* included relatively more *Psychotria pittieri* and

*Miconia affinis* fruits, and relatively fewer *Conostegia subcrustulata* fruits in their diets in later years. Capture rates for both of these bird species were relatively constant among years (Table 3), suggesting that these birds adjusted to changes in fruit abundance by altering their diet. In contrast, *Habia fuscicauda* showed no variation in capture rates or relative use of fruit among years (Table 3, Fig. 5). Nonetheless, *Habia* included relatively fewer fruits of the two fruiting plants that were declining in abundance and included relatively more of the two fruiting plant species

TABLE 3. Mean (and SE) capture rates of common species, total individuals, frugivores, nectarivores, and mean number of species captured in young second-growth woodland. Results of analysis of variance ( $F$ ) or Kruskal-Wallis ( $\chi^2$ ) tests are shown.

Species	1985	1986	1987	1988	$F$ or $\chi^2$	$P$
<b>Species tending to increase</b>						
<i>Phaethornis longuemareus</i>	0.1 ± 0.08	0.2 ± 0.08	0.1 ± 0.08	0.5 ± 0.14	$\chi^2 = 5.8$	<0.05
<i>Hylocichla ustulata</i>	0.6 ± 0.33	1.1 ± 0.40	1.4 ± 1.04	2.1 ± 1.18		NS
<b>Species tending to decrease</b>						
<i>Glaucis aenea</i>	6.9 ± 1.70	2.4 ± 0.44	0.7 ± 0.43	1.0 ± 0.54	$F = 10.2$	<0.005
<i>Seiurus aurocapillus</i> <sup>2</sup>	2.1 ± 0.79	1.6 ± 0.64	1.6 ± 0.17	0.8 ± 0.31	$F = 6.4$	<0.05
<i>Catharus ustulatus</i>	2.6 ± 2.53	3.2 ± 2.94	1.7 ± 1.70	0.1 ± 0.08		NS
<i>Dumetella carolinensis</i> <sup>1</sup>	1.4 ± 0.35	1.1 ± 0.21	1.0 ± 0.41	0.3 ± 0.15	$F = 5.1$	<0.05
<i>Ramphocelus passerinii</i>	5.2 ± 3.36	2.2 ± 0.50	1.1 ± 0.54	0.2 ± 0.08	$F = 4.2$	<0.05
<i>Salpator maximus</i>	3.0 ± 0.60	1.6 ± 0.21	1.0 ± 0.40	0.3 ± 0.08	$F = 8.7$	<0.01
<i>Arremonops conirostris</i> <sup>1</sup>	2.5 ± 1.02	0.9 ± 0.16	0.5 ± 0.25	0.0 ± 0.0	$\chi^2 = 5.2$	<0.05
<b>Species showing little change</b>						
<i>Phaethornis superciliosus</i>	5.7 ± 1.88	2.8 ± 0.56	4.2 ± 0.63	3.6 ± 0.34		NS
<i>Amazilia tzacatl</i>	1.5 ± 0.76	0.7 ± 0.28	1.0 ± 0.36	0.8 ± 0.06		NS
<i>Chalybura urochrysa</i>	0.4 ± 0.43	0.2 ± 0.24	0.5 ± 0.13	0.7 ± 0.42		NS
<i>Glyphorynchus spirurus</i> <sup>1</sup>	0.5 ± 0.02	0.2 ± 0.14	0.9 ± 0.30	0.5 ± 0.13	$\chi^2 = 3.1$	<0.10
<i>Mionectes oleagineus</i>	2.6 ± 0.49	3.0 ± 1.45	4.0 ± 1.23	2.0 ± 0.65		NS
<i>Pipra mentalis</i>	0.2 ± 0.15	2.0 ± 1.90	2.6 ± 1.01	1.7 ± 1.24	NS	NS
<i>Manacus candei</i>	4.6 ± 2.22	4.9 ± 0.49	4.7 ± 0.28	3.8 ± 0.62		NS
<i>Oporornis formosus</i>	1.2 ± 0.67	1.0 ± 0.61	0.7 ± 0.01	1.2 ± 0.59		NS
<i>Habia fuscicauda</i>	1.2 ± 0.43	0.5 ± 0.003	1.0 ± 0.28	0.9 ± 0.31		NS
<i>Arremon aurantirostris</i> <sup>1</sup>	0.5 ± 0.38	0.4 ± 0.22	0.7 ± 0.27	0.7 ± 0.23		NS
<b>Results of all birds</b>						
Total individuals	60.4 ± 17.9	43.9 ± 5.1	39.0 ± 3.3	30.2 ± 5.4		NS
Frugivores	28.6 ± 5.8	27.1 ± 2.1	22.7 ± 2.3	15.2 ± 3.4		NS
Nectarivores	16.7 ± 4.3	7.9 ± 1.1	7.9 ± 0.6	6.9 ± 0.4	$F = 3.4$	<0.08
Mean number of species	45.3 ± 3.3	43.7 ± 0.3	43.7 ± 1.0	35.0 ± 1.6	$F = 4.7$	<0.05

<sup>1</sup> Comparing 1985-1986 vs. 1987-1988.<sup>2</sup> Comparing 1985-1987 vs. 1988.



TABLE 4. Year that new species were first captured in young second-growth woodland.

First captured in 1986	First captured in 1987	First captured in 1988
<i>Geotrygon montana</i> <sup>1</sup>	<i>Micrastur mirandollei</i> <sup>1</sup>	<i>Dendrocincla fuliginosa</i> <sup>1</sup>
<i>Phaenostictus mcleannani</i> <sup>1</sup>	<i>Torgon rufus</i> <sup>1</sup>	<i>Formicarius analis</i> <sup>1</sup>
<i>Hylopezus fulviventris</i> <sup>2</sup>	<i>Xenops minutus</i>	<i>Polioptila plumbea</i> <sup>1,5</sup>
<i>Empidonax flaviventris</i> <sup>2,3</sup>	<i>Cymbilaimus lineatus</i>	
<i>Legatus leucophaeus</i> <sup>3,5</sup>	<i>Mionectes olivaceus</i> <sup>1,4</sup>	
<i>Corapipo leucorrhoa</i> <sup>1,4</sup>	<i>Aphanotriccus capitalis</i>	
<i>Thryothorus thoracicus</i>	<i>Phaeothlypis fulvicauda</i>	
<i>Myadestes melanops</i> <sup>1,4</sup>	<i>Chlorophanes spiza</i> <sup>5</sup>	
<i>Dendroica magnolia</i>	<i>Tachyphonus rufus</i> <sup>5</sup>	
<i>Tangara icterocephala</i> <sup>4</sup>	<i>Piranga olivacea</i> <sup>3,5</sup>	

<sup>1</sup> Found primarily in primary forest.

<sup>2</sup> Found primarily in older second-growth.

<sup>3</sup> Latitudinal migrant.

<sup>4</sup> Altitudinal migrant.

<sup>5</sup> Primarily found in canopy.

that were increasing in abundance over the years (compare Figs. 2, 3, and 5).

Three species that declined in abundance (capture rates) over time (i.e., *Ramphocelus passerinii*, *Saltator maximus*, and *Dumetella carolinensis*; Table 3), did not differ in fruit use among years ( $P > 0.30$  in all cases). At least for *Ramphocelus* and *Saltator*, fruits generally included in their diet were from plant species that also declined in abundance over the same time period (Figs. 2, 5). These data suggest that these bird species may be less flexible in dietary preference, and may have left the area due to changes in abundance of favored food resources (e.g., *Piper auritum*, *Conostegia subcrustulata*). Changes in vegetation structure (Table 1) or insect resource abundance, however, may also have influenced habitat selection by these birds and the importance of these factors for this study is unknown.

## DISCUSSION

The Atlantic lowlands of Costa Rica have been disturbed by humans for many hundreds of years (Boucher et al. 1983). Charcoal found in the soils of La Selva suggest a long history of human occupation at this site as well (R. Sanford, pers. comm.). In addition, large-scale natural disturbances (e.g., hurricanes, earthquakes), likely resulted in relatively frequent, but spatially dispersed forest openings in the region (Yih et al. 1991). Prior to major human-induced changes in the landscape, many of the common bird species captured in young second-growth at La Selva (e.g., *Glaucidis aenea*, *Ramphocelus passerinii*, *Arremonops conirostris*, *Saltator maximus*) likely were restricted to such natural disturbances. As

vegetation in disturbed habitats regrew, second-growth birds would have had to move in search of new habitats. Even today, birds and other animals of second-growth habitats probably need to move in search of spatially and temporally variable disturbed habitats. As a consequence of these movements, and as results from our study indicate, second-growth bird and plant communities can be quite dynamic over relatively short time periods (Loiselle and Blake 1992).

We have observed two basic responses of birds to changes in fruit resources in this second-growth habitat, and in our other studies of fruit-frugivore systems in Costa Rica. In conjunction with seasonal declines in fruit resources, some obligate frugivores move to new habitats or forest elevations where fruit resources are more abundant (Blake and Loiselle 1991, Loiselle and Blake 1991; also Wheelwright 1983). Such movements are temporary (few days to several months), with species later returning to breeding habitats. That birds often return to breeding habitats when fruit abundance still is relatively low (F. G. Stiles and L. Rosselli, pers. comm.) indicates that factors other than fruit availability likely influence such movements. A second response to changes in fruit abundance is a concomitant switch in resource use. This can either be a switch in relative use of resource types (e.g., fruits to insects) or a switch in relative use of fruit species (e.g., as in *Manacus*, this study). Which strategy is employed by frugivores likely depends on the importance of fruit in the diet (i.e., obligate vs. opportunistic fruit-feeder), the seasonal availability of fruit in the preferred (breeding) habitat (i.e., fruit production that is adequate year-round

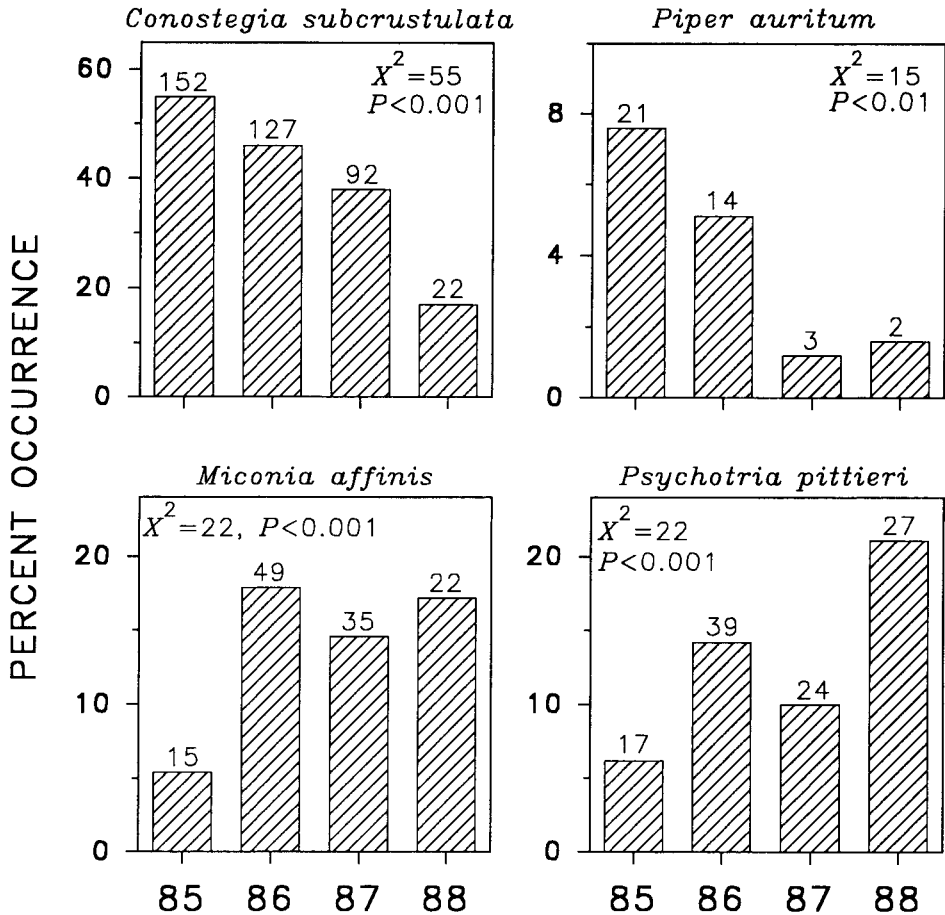


FIGURE 4. Percent occurrence of four common plant species in diets of fruit-eating birds over four years in young second-growth woodland. The numbers above bars indicate the number of fecal samples where seeds of this plant species were encountered. Results of Chi-square tests that examined differences among years in number of fecal samples containing these fruits are shown (see Methods).

for maintenance or that drops below some threshold), and the presence or absence of specialized breeding systems (see below).

Bird species typically found only in early second-growth habitats (e.g., *Ramphocelus passerinii*) may have left the site both as a consequence of resource changes (declines in fruit abundance) and as a result of habitat changes (denser vegetation, less open canopy). In contrast, species typically found in second-growth habitats of various ages (e.g., *Manacus*), may be less sensitive to short-term habitat changes and more likely to persist in such areas over longer periods.

Four of the eight common bird species that showed little change in activity among years have lek breeding systems. *Mionectes oleagineus* and *Pipra mentalis*, however, are generally birds of

mature forest, and most individuals captured during this study were transients from lowland mature or foothill forest. By contrast, active *Manacus candei* and *Phaethornis superciliosus* leks were located near our second-growth plot, in similar habitat. Such leks are traditional and persist over many years (Snow 1962, Stiles and Wolf 1979, pers. observ.). Consequently, species with specialized breeding systems may be more likely to remain in second-growth habitats over time, despite changes in vegetation structure and resource abundance. It should be remembered, however, that the abundance of *Heliconia* and *Costus*, two important plant genera for *Phaethornis* hummingbirds, did not change during this study (Table 1).

This second-growth woodland was approxi-

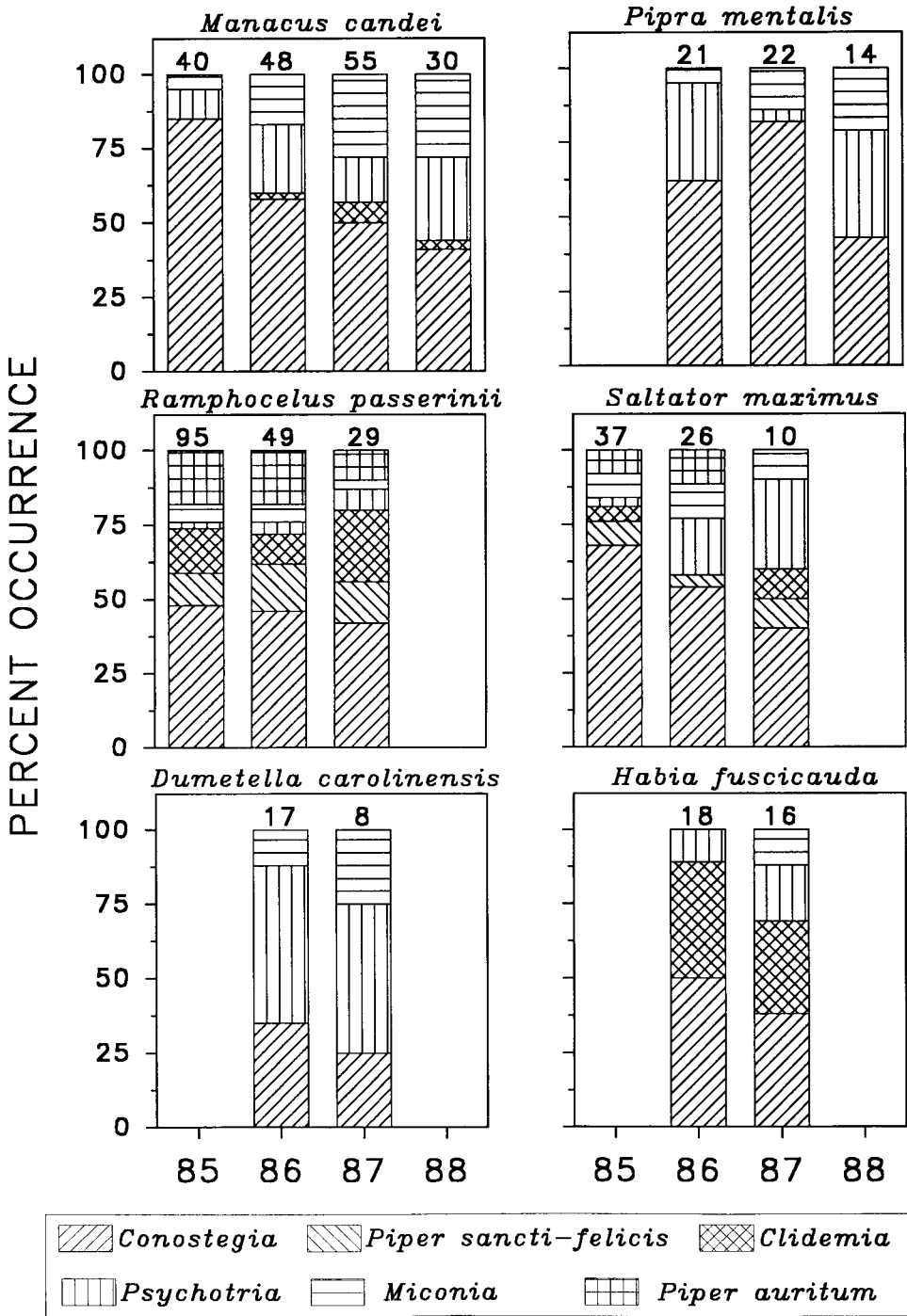


FIGURE 5. Percent occurrence of fruiting plants in the diets of common fruit-eating birds over a four year period in young second-growth woodland. Only common plants that regularly occurred in the diets of these birds are shown in the figure. For *Habia fuscicauda* and *Dumetella carolinensis*, data were combined for two-year periods (1985 and 1986 combined and shown in 1986 column; 1987 and 1988 combined and shown in 1987 column) to alleviate sample size problems.

mately 10 years old by the end of this study, and we saw evidence that birds typical of mature forest understory were colonizing the habitat (Table 4). For example, we believe that some species (e.g., *Trogon rufus*, *Dendrocicla fuliginosa*, *Formicarius analis*, and *Xenops minutus*), more commonly found in older forest, colonized the plot during this study. We do not know for certain, however, if these species were able to successfully breed in this habitat. At least *Trogon rufus* and *Formicarius analis* appeared to set up territories as regular singing behavior was recorded during censuses in later years. Nonetheless, the rapid change in the vegetation, together with the relatively early colonization by some forest understory species suggests that rapidly regenerating second-growth is an important alternative habitat for some forest species. Preservation of some species may be enhanced by the presence of such habitats. It is important to recognize, however, that the majority of forest species have not been found on this plot, indicating that second-growth habitats, while beneficial for some species, will not substitute for mature forest.

Naturally disturbed and human-disturbed habitats are prevalent in this region of Central America and, especially in regenerating forests, support many plant and animal species that do not occur inside mature forest. Thus, they contribute to the region's biodiversity (Brown and Brown 1992). Moreover, such regenerating habitats often provide important resources (fruit, nectar) for birds (and other animals) during periods of food shortage in more mature forests (Stiles 1983, Terborgh 1983, Levey 1988a, Blake et al. 1990, Blake and Loiselle 1991; also Gilbert 1980). Maintenance of a mosaic of habitat types in a particular region or reserve may require substantial and active management intervention. As protected forests become more isolated and restricted in Central America, and to the extent that surrounding land use becomes more intense and resembles natural ecosystems to a lesser degree, the management of natural forests for biodiversity may entail the creation of some disturbed areas (cf. Gilbert 1980). Dependent on the size of the protected forest patch, disturbed areas can be allowed to mature naturally while other areas are disturbed, thus providing a temporal and spatial mosaic of habitat patches. Alternatively, managed areas may need to be disturbed periodically (perhaps on a 15–20 year

cycle), providing a spatial mosaic of patches within the forest that is relatively constant over time.

#### ACKNOWLEDGMENTS

We thank J. Hunt, R. Hutto, R. Marquis, and E. Wiener for many helpful discussions and comments on this manuscript. We greatly appreciate the help and support of David and Deborah Clark and Ronald Suarez for facilitating our research at Estación Biológica La Selva and the numerous researchers and staff who have made work at this tropical site so enjoyable over the years. We thank the Organization for Tropical Studies, the Department of Zoology-University of Wisconsin (Guyer Fellowship), the National Geographic Society, and the Douroucouli Foundation for their financial support.

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