

BIRD ASSEMBLAGES IN SECOND-GROWTH AND OLD-GROWTH FORESTS, COSTA RICA: PERSPECTIVES FROM MIST NETS AND POINT COUNTS

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ABSTRACT.—Second growth has replaced lowland forest in many parts of the Neotropics, providing valuable habitat for many resident and migrant bird species. Given the prevalence of such habitats and the potential benefit for conservation of biodiversity, it is important to understand patterns of diversity in second growth and old growth. Descriptions of species-distribution patterns may depend, however, on method(s) used to sample birds. We used data from mist nets and point counts to (1) describe species diversity and community composition in second-growth (young and old) and old-growth forests at La Selva Biological Station, Costa Rica; and (2) to evaluate perspectives on community composition provided by the two methods. We recorded 249 species from 39 families, including 196 species captured in mist nets (10,019 captures) and 215 recorded during point counts (15,577 observations), which represents ~78% of the terrestrial avifauna known from La Selva (excluding accidentals and birds characteristic of aquatic or aerial habitats). There were 32 threatened species, 22 elevational migrants, and 40 latitudinal migrants. Species richness (based on rarefaction analyses of capture and count data) was greatest in the youngest site. Latitudinal migrants were particularly common in second growth; elevational migrants were present in both young and old forest, but were more important in old-growth forest. Several threatened species common in second growth were not found in old-growth forests. Trophic composition varied less among sites than did species composition. Mist nets and point counts differed in numbers and types of species detected. Counts detected more species than nets in old-growth forest, but not in young second growth. Mist nets detected 62% of the terrestrial avifauna, and point counts detected 68%. Fifty-three species were observed but not captured, and 34 species were captured but not observed. Six families were not represented by mist-net captures. Data from mist nets and point counts both support the conclusion that second-growth vegetation provides habitat for many species. *Received 28 January 2000, accepted 16 September 2000.*

CHANGES IN species diversity and composition along environmental gradients, including elevational and successional, are well known but not necessarily well understood aspects of species-distribution patterns (Rosenzweig 1995). Previously (Blake and Loiselle 2000), we examined changes in diversity and composition of bird assemblages along a tropical forest elevational gradient in Costa Rica (see also Young et al. 1998). Here we take a similar approach to examine changes along a successional gradient from young second-growth to old-growth forest at La Selva Biological Station, Costa Rica.

Second-growth vegetation, which has replaced lowland forest in many parts of the Neotropics, can provide important habitat for bird

species (Terborgh and Weske 1969, Karr 1971, Blake and Loiselle 1991), although suitability of such habitats varies (Borges and Stouffer 1999). Successional habitats may increase connectivity among isolated fragments of forest (Stouffer and Bierregaard 1995a, b), ameliorating some effects of habitat fragmentation, and may be important as foraging sites for some species during certain periods of the year (Martin and Karr 1986, Levey 1988, Blake and Loiselle 1991). Second growth and other disturbed habitats can be especially important to many species of long-distance migrants (e.g. Karr 1976, Martin 1985, Blake and Loiselle 1992a, Petit et al. 1995).

That diversity and composition of tropical bird communities are closely related to habitat is well documented; large changes in diversity can occur over short distances as habitats change (Terborgh et al. 1990, Robinson and Ter-

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borgh 1997). Bird communities of successional habitats (both primary and secondary) typically differ from those of old-growth forest in terms of species richness, composition, and trophic structure (Karr 1971, Blake and Loiselle 1991, Robinson and Terborgh 1997 and references therein). Although old-growth forest typically supports more species of birds, species richness and abundance can be very high in second-growth habitats. A variety of factors (e.g. resource abundance) contributes to that high diversity and abundance.

To understand factors that determine bird distribution and abundance patterns first requires a good description of those patterns. Describing composition of an assemblage of birds in a particular area is not a simple task and depends, to a large extent, on the method(s) employed (Terborgh et al. 1990, Robinson et al. 2000). Mist nets and point counts both have been used to document distribution patterns of birds in many tropical habitats. Mist nets have a longer and perhaps more controversial history in tropical studies (e.g. Terborgh et al. 1990, Remsen and Good 1996, Robinson et al. 2000), but both methods are widely used. Both methods offer benefits and costs (Wallace et al. 1996), and each can provide different perspectives on community structure (Whitman et al. 1997, Blake and Loiselle 2000), leading some to advocate a combination of methods (Gram and Faaborg 1997, Rappole et al. 1998). Comparisons among habitats may be especially influenced by method, although interactions between method and habitat are not well documented.

The major objectives of this paper are two-fold. First, we describe and compare diversity and composition of bird communities in second-growth and old-growth forest at La Selva Biological Station. More specifically, we use the results to determine which species benefit from presence of second-growth forest and which are more likely to be restricted to old-growth forest. We also evaluate possible factors that might affect diversity of species in such habitats. The second major objective is to evaluate differences and similarities in results obtained with mist nets and those obtained with point counts. Both methods are used to describe bird assemblages in tropical habitats, so an understanding of the similarities and differences in results provided by those two methods is im-

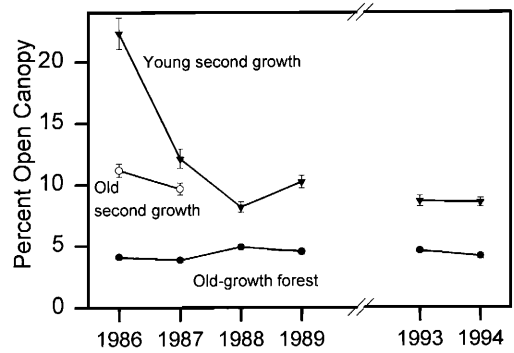


FIG. 1. Spherical densiometer readings of percentage open canopy (4 readings/point, 3 points per mist-net location; 30 net locations in young and old second-growth, 60 locations in old-growth forest). Values are means of the means of the three points per net (with SE).

portant. Further, because observers often differ in abilities (Verner 1985, Bibby et al. 1992), perspectives on community composition can vary with observer. Few studies, however, explicitly consider or evaluate observer variation (Nichols et al. 2000). Thus, we also compare count data by observer.

STUDY AREA

We conducted our research at La Selva Biological Station, located in the lowlands of northeastern Costa Rica (10°25'N, 84°01'W). La Selva encompasses ~1,500 ha, of which ~67% is old-growth forest; it is bordered on the south by Braulio Carrillo National Park (~45,000 ha). The station also supports a variety of anthropogenic successional habitats. Habitats included in this study were young second-growth (YSG; pasture until about 1981), older second-growth (OSG; approximately 25 to 35 years growth at the start of this study in 1985), and old-growth forest (OGF) (see Blake and Loiselle 1991). The three habitats differed substantially in plant species composition and structure, the latter illustrated by differences in amount of open canopy (as recorded with a hand-held spherical densiometer; Fig. 1). Vegetation in YSG averaged 5 to 8 m in height at the start of this study (1985) but changed considerably by 1994 (Loiselle and Blake 1994), with corresponding changes in amount of open canopy (Fig. 1). Trees in the OSG averaged 15 to 20 m in 1985. Old-growth forest sites were

TABLE 1. Summary of birds sampled with mist nets or point counts in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF) at La Selva Biological Station, Costa Rica. Observations (i.e. point count records by sight or sound) are separated by observer (Ob1 and Ob2).

	YSG			OSG		OGF	
	Net	Ob1	Ob2	Net	Net	Ob1	Ob2
Captures or observations	4,526	2,724	4,049	1,463	4,030	4,176	4,628
Species	157	130	155	95	107	115	122
Species (Ob1 + Ob2)			167				132
Species (captures + Ob1 + Ob2)			206				157
Captures/100 mist-net hours	44			26	20		
Observations/count period		136	156			123	129
Mist-net hours (total)	10,177			5,598	20,633		
Total count periods		20	26			34	36

within the main block of undisturbed forest of La Selva where canopy height reaches 30 to 40 m (Hartshorn and Peralta 1988). Canopy cover showed little overall change during the study (Fig. 1) despite the occurrence of treefalls that caused local changes in cover. La Selva receives ~4,000 mm of rain annually. The dry season typically lasts from about late January or early February to March or April, with a second, less-pronounced dry season in September and October (Sanford et al. 1994).

METHODS

Mist nets.—Birds were sampled with mist nets and point counts (see below). Mist-net studies started in La Selva in 1985 and continued until 1994. Most data were collected during December to April (late wet season, dry season, to early wet season), although netting was conducted throughout 1985 (see details in Blake and Loiselle 1991). We used ground-level mist nets (12 × 2.8 m, 36 mm mesh) to sample birds. Nets were located 40 m apart on 5 ha grids in the two second-growth sites (YSG, OSG) and on a 10 ha grid in one OGF site. We also included data from some additional captures in areas immediately adjacent to the YSG plot (i.e. in similar habitat). At the second OGF site, nets were set ~40 m apart along narrow, preexisting trails. Results from the two OGF sites are combined in all analyses. Net locations were random with respect to topography, locations of fruiting plants, treefall gaps, or other factors that might influence capture rates (i.e. we did not select net sites on the basis of a subjective assessment of capture probabilities). Nets were operated from dawn to about 1300 CTZ, but were closed during periods of rain. There were 28 sample periods across 10 years (1985 to 1994) at the main OGF site; 5 sample periods in 2 years (1988 to 1989) at the second OGF site; 14 samples over 3 years (1985 to 1987) at the OSG site; and 25 samples over 10 years (1985 to 1994) at the YSG site (Table 1).

Point counts.—We also sampled birds with point counts (10 min per count) at the YSG and OGF sites. Six to eight points were established ~200 m apart at each site, centered on the same areas where netting was conducted. Counts were conducted from 1987 to 1994 at the YSG site and one OGF forest site; counts were conducted during 1988 and 1989 at the remaining OGF site. All points were sampled on two to four days during one to three periods per year (December to April) (Table 1). Counts started ~20 min before dawn and continued for no more than 2 h past dawn (Blake 1992). All birds seen or heard were noted. We conducted counts only on days with little or no wind or rain. All counts were conducted by the authors, both of whom are familiar with calls, songs, and plumages of birds in Costa Rica. Both of us conducted counts in both habitats, although number of counts conducted by each of us differed.

Analyses.—Sample effort varied among sites. Thus, we base our comparisons primarily on presence or absence of species or proportions. All captured birds were banded with numbered aluminum bands, but individuals could not be distinguished during counts. Thus, we use total captures (including recaptures) and total observations (which likely include resightings) in all comparisons. Throughout, we treat observers separately, so that our comparisons are based on seven samples: three netting samples (three habitats) and four point count samples (two each from YSG and OGF).

We used Bray-Curtis analyses (variance-regression approach for endpoint selection; Sorensen similarity measure; McCune and Mefford 1997) to graphically compare similarity in community composition among different habitats and between the two methods and observers. Numbers of birds captured or counted per species, family, or trophic group (described below) were relativized (general relativization by row and column totals; Beals 1984) prior to analyses.

Numbers of individuals captured or observed differed among sites, precluding direct comparisons of species numbers. Instead, we calculated rarefaction

curves using a Monte Carlo simulation procedure (EcoSim Version 1.11; Gotelli and Entsminger 1997) that also allows a comparison of number of species expected per site on the basis of the lowest number of individuals recorded among sites being compared; that is, species richness is compared on the basis of the same number of individuals. Simulations were run 1,000 times and mean expected numbers of species at each site were compared based on the 95% CI (i.e. nonoverlapping CIs indicate a significant difference in means).

We assigned species to migratory categories (latitudinal [long-distance] migrant, elevational migrant) on the basis of AOU (1998), Stiles and Skutch (1989), and personal observations. Two species, *Pipra mentalis* and *Mionectes oleagineus* (common English names are in Appendix 1), are represented both by residents (individuals that breed and remain in lowland habitats) and elevational migrants (individuals that breed at higher elevations, but descend to lower elevations during at least part of the nonbreeding season). Because those two species are very common in capture data and because we have no way to determine what proportion are residents or migrants, we treat those two species as a separate migrant category. We further assigned species to trophic groups on the basis of primary foraging substrate and food type; assignments were based on analyses of fecal samples (Loiselle and Blake 1990, Blake and Loiselle 1992b), observations of foraging behavior, and literature accounts (e.g. Stiles and Skutch 1989). We followed Young et al. (1998) in using Parker et al. (1996) to assign conservation (threatened) status to species; all species listed as of medium or higher conservation concern were included. We also included species listed by Collar et al. (1994) as near-threatened or vulnerable in Costa Rica and those listed by Stiles (1985) on the Costa Rican endangered species list.

RESULTS

Species richness and composition.—We recorded 249 species (Table 1, Appendix 1) from 39 families, including 196 species captured in mist nets (10,019 captures) and 215 recorded during point counts (15,577 observations, excluding unidentified birds). There were 32 threatened species, 22 elevational migrants (including *P. mentalis* and *M. oleagineus*), and 40 latitudinal migrants (36 from northern hemisphere, 4 from southern). Overall capture rates and numbers of observations per sample were highest in YSG (Table 1).

Species accumulation curves (based on Monte Carlo simulations) indicated that new species still were being recorded at all sites and by both methods (Fig. 2), but that the rate at which

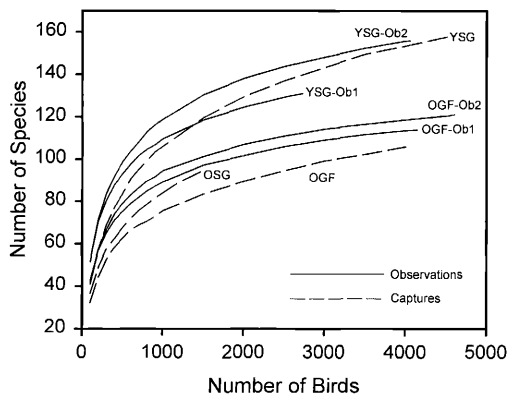


FIG. 2. Species rarefaction curves in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF) based on numbers of captures or numbers of observations. Results for observations are shown separately by observer (Ob1, Ob2).

new species were being added during point counts had decreased in OGF. Species richness was higher in YSG than in older forests on the basis of netting and point counts (Table 2). More species were recorded by observation than by netting in OGF but not in YSG. Accumulation curves generally were similar between observers within a habitat (Fig. 2, Table 2).

Species composition differed among sites and between methods of sampling (Table 3, Fig. 3). Similarities were much higher based on species presence or absence than when based on relativized numbers of records per species (Table 3). In both cases, similarities were highest between observers within a habitat. A Bray-Curtis ordination based on number of records per species (relativized) accounted for 33% of variation on the first axis and 31% on the second (Fig. 3). The netting sample from YSG was, for example, characterized by species such as *Amazilia tzacatl* and *Manacus candei*, whereas observations included more species that typically occur above net levels, such as *Tangara larvata*, *Dendroica pensylvanica*, and *Procnias tricarunculata*. *Thalurania colombica*, *Glyphorhynchus spirurus*, *Phaenostictus mcleannani*, and *Formicarius analis*, among others, were encountered more often in OGF. The ordination reflects preferred habitat and strata of the different species.

Most species (162) were recorded by both methods (nets and counts), but relative importance of individual species frequently varied

TABLE 2. Mean and 95% CI for numbers of species expected in either 1,000 or 2,000 captures or observations, based on 1,000 simulations. Means are considered different if CIs do not overlap.

	1,000		2,000	
	Average	95% CI	Average	95% CI
Netting Data				
Young second-growth	106.5	98.5–114.5	129.1	122.0–136.3
Old second-growth	84.3	79.6–89.0		
Old-growth forest	76.2	69.3–83.2	90.1	83.5–96.7
Observation Data				
YSG Observer 1	109.4	103.9–114.9	124.6	120.7–128.5
YSG Observer 2	119.4	110.8–128.0	138.5	132.4–144.6
OGF Observer 1	89.1	82.6–95.7	101.6	96.1–107.0
OGF Observer 2	94.5	87.9–101.0	107.5	102.1–113.0

with method (Appendix 1). Proportions of individuals per species recorded by nets and counts were poorly correlated within a habitat (Fig. 4A, B); correlations were higher for a given method between habitats (Fig. 4C, D). Not all species or groups of species were equally likely to be recorded by the two methods. Fifty-three species were not captured and 34 species were not recorded during counts. Only 21 species (8.4%) were recorded in all samples (i.e. captured in all three habitats, observed by both observers in both habitats). Species characteristic of count data but which typically were absent from net data tended to be large (>100 g) canopy species such as parrots, toucans, woodpeckers, and several icterids, but also included a variety of small insectivores and frugivores that typically forage above net levels (e.g. *Poliophtila plumbea*, *Euphonia luteicapilla*). In contrast, species typical of mist-net data included smaller species that typically forage at or near ground level (e.g. *Chalybura urochrysis*, *P. mentalis*) as well as species that are not readily detectable by voice (e.g. *Catharus minimus*, *Wilsonia canadensis*).

Just as not all species were recorded by both methods, not all species were recorded by both observers. In YSG, one of us recorded 12 species that the other did not, whereas the reverse was true for 37 species. Differences in the OGF were even less pronounced: 10 species only observed by one, and 17 by the other. Much of that difference is accounted for by the difference in number of samples (20 and 26; Table 1). Further, most of the species recorded by only one observer were rare (i.e. only 1 or 2 individuals recorded during all counts; Appendix 1). Relative proportions of individuals detected per species were similar between observers (Fig. 4E, F).

Differences among species in numbers of individuals recorded during counts or nets were reflected in the relatively low similarity values among samples based on family composition (Table 4, Fig. 5). Trochilidae, Emberizidae, and Furnariidae were more common in netting samples, and the reverse was true for Picidae, Ramphastidae, and Columbidae, among others. The first axis of the ordination reflected those major differences and accounted for 54% of the

TABLE 3. Similarity indices (Sorensen's) based on presence or absence (lower triangle) or relativized numbers (upper triangle) of captures (net) or observations (O1, O2) per species in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF).

	YSG-net	YSG-O1	YSG-O2	OSG-net	OGF-net	OGF-O1	OGF-O2
YSG-net	—	0.24	0.25	0.31	0.21	0.08	0.07
YSG-O1	0.67	—	0.57	0.13	0.08	0.22	0.20
YSG-O2	0.72	0.83	—	0.14	0.09	0.21	0.18
OSG-net	0.60	0.50	0.51	—	0.34	0.12	0.10
OGF-net	0.55	0.47	0.48	0.70	—	0.22	0.22
OGF-O1	0.42	0.56	0.55	0.47	0.65	—	0.66
OGF-O2	0.41	0.54	0.53	0.46	0.66	0.89	—

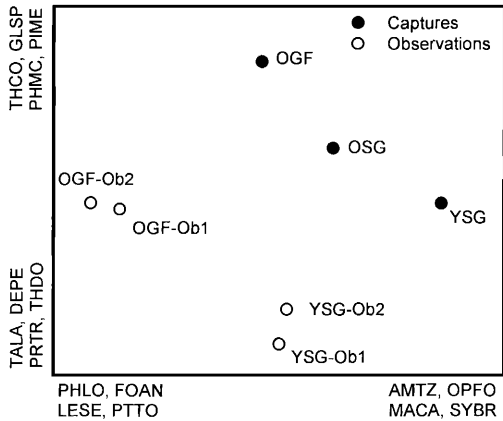


FIG. 3. Bray-Curtis ordination of samples based on relativized numbers of captures or observations in different species (see Fig. 2 for sample codes). Eight species most strongly correlated (positively, negatively) with each of the first two axes are indicated: AMTZ = *A. tzacatl*; DEPE = *D. pensylvanica*; FOAN = *F. analis*; GLSP = *G. spirurus*; LESE = *Leucopternis semiplunbea*; MACA = *Ma. candei*; OPFO = *O. formosus*; PHLO = *Phaet. longuemareus*; PHMC = *Phaen. mcleannani*; PIME = *P. mentalis*; PRTR = *Pr. tricarunculata*; PTTO = *Pteroglossus torquatus*; SYBR = *Synallaxis brachyura*; TALA = *Ta. larvata*; THCO = *T. colombica*; and THDO = *Thamnophilus doliatus*.

variation among samples. In contrast, the second axis accounted for only 14% of variation and primarily separated observation samples by habitat.

Migrants.—Migrants accounted for 15 to 30% of species and from 6 to 44% of captures or observations (counting *P. mentalis* and *M. oleagineus* as migrants) (Table 5). Latitudinal migrants were dominated by Parulidae (17 species) and Tyrannidae (8 species); elevational migrants were primarily Trochilidae (6 species), Tyrannidae (3 species), Pipridae (3 species), and Turdidae (3 species). Relative distribution of numbers of species among the four migrant categories was not influenced by method, observer, or habitat, with one exception. Distribution of species among the four categories differed between YSG and OGF for observer 2 ($\chi^2 = 8.8$, $df = 3$, $P < 0.05$), primarily due to differences in number of species of latitudinal migrants recorded in the two habitats (Table 5).

In contrast to numbers of species, relative distribution of numbers of captures or observations among the different migrant categories

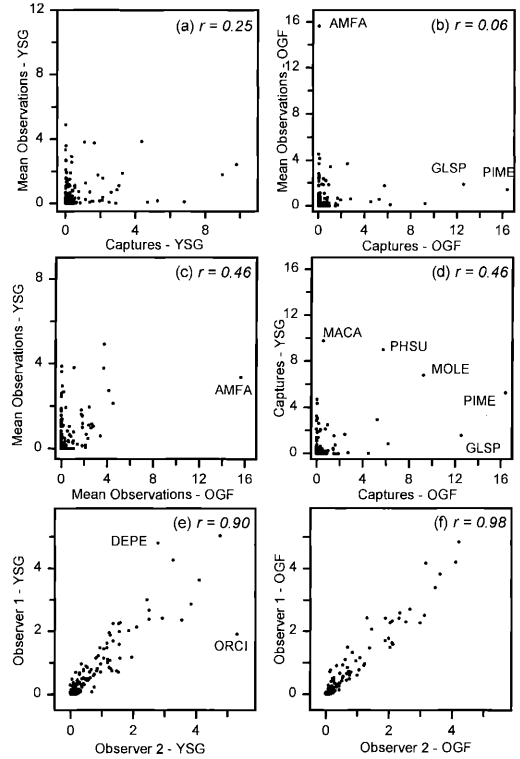


FIG. 4. Percentages accounted for by different species in different samples or between different methods: (A) means of the two observers plotted against captures in young second-growth; (B) means of the two observers plotted against captures in old-growth forest; (C) means of the two observers in young second-growth plotted against means from old-growth forest; (D) captures in young second-growth plotted against captures in old-growth forest; (E) observers plotted against each other for young second-growth; (F) observers plotted against each other in old-growth forest (the point for *Amazona farinosa* is omitted from the panel but was included in calculation of the correlation coefficient). In each comparison, all species not detected by either method or either observer are excluded (i.e. no 0, 0 values are included in the figures or in calculation of correlation coefficients). Species indicated are: AMFA—*Amazona farinosa*; DEPE—*D. pensylvanica*; GLSP—*G. spirurus*; MACA—*Ma. candei*; MOLE—*M. oleagineus*; ORCI—*Ortalis cinereiceps*; PHSU—*Phaethornis superciliosus*; PIME—*P. mentalis*.

was influenced by habitat and method ($\chi^2 > 100$, $P < 0.0001$ in most cases); captures and observations gave different perspectives on the relative importance of the different migrant groups. Observers did not differ in relative numbers of observations among the four mi-

TABLE 4. Similarity indices (Sorensen's) based on relativized numbers of captures (net) or observations (O1, O2) per family (lower triangle) or guild (upper triangle) in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF).

	YSG-net	YSG-O1	YSG-O2	OSG-net	OGF-net	OGF-O1	OGF-O2
YSG-net	—	0.60	0.60	0.77	0.58	0.52	0.53
YSG-O1	0.38	—	0.87	0.55	0.46	0.59	0.56
YSG-O2	0.37	0.68	—	0.57	0.50	0.71	0.69
OSG-net	0.63	0.33	0.31	—	0.76	0.55	0.54
OGF-net	0.42	0.35	0.35	0.57	—	0.55	0.53
OGF-O1	0.26	0.50	0.59	0.23	0.34	—	0.91
OGF-O2	0.27	0.49	0.50	0.23	0.32	0.81	—

grant categories in OGF ($\chi^2 = 4.8$, $df = 3$, $P > 0.15$), but did in YSG ($\chi^2 = 11.0$, $df = 3$, $P < 0.05$), primarily due to differences in detections of latitudinal migrants.

Threatened species.—Thirty-two threatened species were recorded, accounting for 7 to 18% of species in a given sample (Table 6). Although percentages were higher in OGF than in younger sites and higher for observations than for captures, there were no significant differences based on numbers of species. Similarly, observers did not differ in number of threatened species recorded during counts. In contrast, relatively more threatened individuals were captured in OGF than in the two second-growth sites ($\chi^2 = 54.3$, $df = 2$, $P < 0.0001$). Further, more threatened birds were observed in YSG than were captured ($\chi^2 = 43.7$, $df = 2$, $P < 0.001$); differences between captures and observations were less pronounced in OGF ($\chi^2 =$

5.9, $df = 2$, $P < 0.06$). The slight difference was, in fact, due to differences between observers ($\chi^2 = 5.65$, $df = 1$, $P < 0.05$) rather than to method.

Trophic groups.—Trophic composition varied both by habitat and by method (Table 7, Fig. 6). Foliage insectivores and arboreal frugivore-insectivores accounted for >20% of species in each sample except for the mist-net sample from OGF (18%). Nectarivore-insectivore species (primarily Trochilidae) were more characteristic of netting samples, whereas bark insectivores, arboreal frugivores, and carnivores were more important in OGF observations. The first axis of the ordination accounted for 52% of variation in species-distribution patterns among trophic groups; the second axis (29%) largely separated YSG observations from other samples.

Relative importance of different trophic groups changed when comparisons were based on numbers of captures or observations rather than species. Foliage insectivores were less important, particularly in netting samples, whereas arboreal frugivores increased in importance. Proportions of individuals per guild were correlated among netting samples ($r > 0.73$) and among count samples ($r > 0.60$) but not between netting and counts. Correlations were highest between observers within a habitat (YSG $r = 0.955$; OGF $r = 0.993$). The first axis of the ordinations accounted for 40% of the variation and largely separated netting and observation samples, particularly OGF. Netting samples had more nectarivore-insectivores, granivores, and flycatching insectivores, with fewer hawks and arboreal frugivores. The second axis (37%) indicated that frugivores and frugivore-insectivores were more common in younger habitats whereas bark insectivores, flycatchers, and army-ant followers were more typical of old-growth. Despite changes in rel-

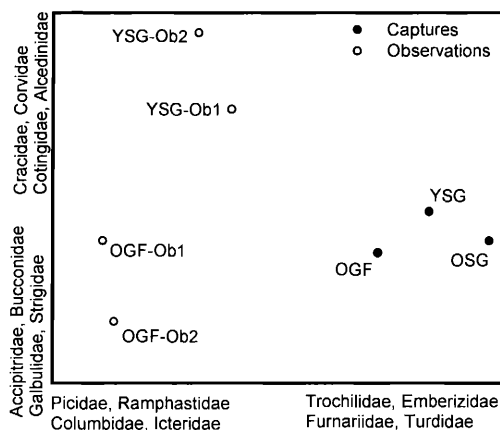


FIG. 5. Bray-Curtis ordination of samples based on relativized numbers of captures or observations from different families (see Fig. 2 for sample codes). Families most strongly correlated with the first two axes are indicated.

TABLE 5. Number and percentage of species and records (captures or point counts) for different migratory categories. Partial elevational migrants are *P. mentalis* and *M. oleagineus*.

	Residents		Latitudinal		Elevational		Partial elevational	
	No.	%	No.	%	No.	%	No.	%
Species								
Young second-growth	107	68.2	35	22.3	13	8.3	2	1.3
Old second-growth	69	72.6	16	16.8	8	8.4	2	2.1
Old-growth forest	84	78.5	12	11.2	9	8.4	2	1.9
YSG Observer 1	103	79.2	18	13.8	7	5.4	2	1.5
YSG Observer 2	122	78.7	24	15.5	7	4.5	2	1.3
OGF Observer 1	97	84.3	7	6.1	9	7.8	2	1.7
OGF Observer 2	101	82.8	7	5.7	12	9.8	2	1.6
Mist-net captures or point-count records								
Young second-growth	2,990	66.1	762	16.8	229	5.1	545	12.0
Old second-growth	985	67.3	144	9.8	91	6.2	243	16.6
Old-growth forest	2,254	55.9	283	7.0	460	11.4	1,033	25.6
YSG Observer 1	2,379	87.3	228	8.4	109	4.0	8	0.3
YSG Observer 2	3,581	88.4	262	6.5	196	4.8	10	0.2
OGF Observer 1	3,883	93.0	103	2.5	118	2.8	72	1.7
OGF Observer 2	4,339	93.8	84	1.8	132	2.8	73	1.6

ative positions of samples in the two ordinations (species and individuals), the distance matrices were more similar than expected by chance (Mantel test, $r = 0.768$, $P = 0.005$ based on 1,000 simulations). Similarity values were, overall, higher based on guilds than when based on species or family composition. Observers were, once again, very similar (i.e. close together in the ordinations).

DISCUSSION

SPECIES RICHNESS AND COMPOSITION

Capture and observation data both document the high diversity of birds in secondary and old-growth forest at La Selva Biological Station. More than 400 species of birds have been recorded at least once at La Selva (Blake et al. 1990), with ~365 recorded more than 5 times (excluding accidentals). Thus, the 249 species recorded by counts and netting consti-

tute ~69% of the species regularly found at La Selva—78% if species characteristic of aquatic systems or that are primarily aerial (e.g. swifts, swallows) also are excluded. Point counts alone included ~68% of the 317 terrestrial species and mist nets captured 62%. Second-growth and old-growth forests differed both in species richness and composition. More species were detected in second growth than in older forests by both methods. Within netting samples, for example, there was a clear gradient from young second-growth to older second-growth to old-growth forest in species diversity and in similarity of the avifauna. The youngest and oldest sites shared 116 species out of a combined total of 246 (i.e. excluding the three species only recorded in old second-growth), indicating considerable turnover in species composition over relatively short distances (~1 km from YSG to OSG and 3.5 km from YSG to OGF sites). Turnover was less with respect to trophic composition, suggesting that different species may ful-

TABLE 6. Percentage of total species or birds captured (netting) or recorded during point counts (counts) accounted for by species classified as threatened (see text for classification) in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF). Ob1 and Ob2 indicate different observers.

	Netting			Counts—YSG		Counts—OGF	
	YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2
Species	7.0	7.4	10.3	9.2	10.3	15.7	18.0
Captures or observations	5.8	4.9	9.4	9.3	9.2	8.3	9.8

TABLE 7. Percentage of species or records in different foraging guilds based on mist-net captures and point count samples in young second-growth (YSG), old second-growth (OSG), and lowland old-growth forest (OGF) at La Selva Biological Station, Costa Rica. Ob1 and Ob2 refer to different observers.

Feeding guild	Netting data			Counts—YSG		Counts—OGF	
	YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2
Species per guild							
Terrestrial frugivore	3.2	2.1	3.7	1.5	1.3	2.6	1.6
Arboreal frugivore	8.9	6.3	8.4	16.8	12.8	17.4	18.0
Terrestrial frugivore–insectivore	1.9	2.1	2.8	4.6	3.8	3.5	3.3
Arboreal frugivore–insectivore	25.9	22.1	17.8	30.5	30.1	22.6	22.1
Terrestrial insectivore	5.1	7.4	7.5	3.1	3.2	5.2	4.1
Foliage insectivore	27.8	23.2	25.2	23.7	23.7	24.3	23.0
Bark insectivore	5.1	4.2	6.5	3.8	4.5	7.0	8.2
Flycatching insectivore	4.4	8.4	4.7	3.1	4.5	2.6	3.3
Army-ant followers	2.5	5.3	4.7	0.8	1.9	4.3	4.9
Nectarivore–insectivore	8.9	13.7	11.2	6.9	7.1	6.1	5.7
Nectarivore–frugivore	0.6		1.9		0.6	0.9	1.6
Granivore	2.5	2.1	1.9	0.8	0.6		
Carnivore	2.5	2.1	2.8	3.8	3.8	3.5	4.1
Piscivore	0.6	1.1	0.9	0.8	1.3		
Captures or observations per guild							
Terrestrial frugivore	1.9	1.0	0.8	1.9	1.4	0.9	1.1
Arboreal frugivore	17.3	16.6	24.7	17.8	22.6	33.9	34.6
Terrestrial frugivore–insectivore	3.6	4.0	0.3	7.2	6.2	2.5	3.2
Arboreal frugivore–insectivore	30.7	22.3	22.4	36.5	36.7	25.2	26.0
Terrestrial insectivore	6.1	4.2	3.8	3.7	3.4	3.0	3.2
Foliage insectivore	10.4	10.7	9.2	22.7	19.0	19.3	16.9
Bark insectivore	2.8	12.3	13.9	2.1	2.6	6.9	5.9
Flycatching insectivore	1.6	2.0	2.3	0.4	0.8	0.7	1.2
Army-ant followers	1.2	5.6	10.8	0.3	0.3	1.5	1.4
Nectarivore–insectivore	21.8	19.3	10.8	6.8	6.0	4.8	4.8
Nectarivore–frugivore					0.2	0.4	0.5
Granivore	2.5	1.7	0.7	0.2	0.2		
Carnivore	0.2	0.3	0.3	0.4	0.6	0.8	1.0
Piscivore		0.1		0.1	0.1		

fill similar ecological roles in the different habitats.

Second growth versus old growth.—The presence of second-growth vegetation clearly contributes to the overall diversity of the avifauna at the station (and in the lowlands of Costa Rica in general). By the same token, the high diversity in second growth is due in large measure to the proximity of old-growth forest, the primary habitat (and certainly the source habitat) for many species found in second growth. Second-growth vegetation that develops as a consequence of human activities differs greatly in structure and plant species composition (Corlett 1994). Land-use history (e.g. pasture, crops, tree plantation) can influence the type of vegetation that regenerates (Stouffer and Bierregaard 1995a) and, as a consequence, secondary successional habitats can provide a complex mosaic of microhabitats that can attract and

sustain many species and individuals. Successional habitats that result from natural disturbances such as river meanders (i.e. primary successional habitats) also can be important for many birds (Remsen and Parker 1983, Robinson and Terborgh 1997). As is true for secondary successional gradients, major changes in bird assemblages occur along primary successional gradients, with many species restricted to early or late stages (see Robinson and Terborgh 1997). Proximity of both early and late stages likely is a major factor in the high overall diversity of birds in many lowland Amazonian forests.

Old-growth forest at La Selva Biological Station and elsewhere in the Caribbean lowlands of Costa Rica often has second-growth vegetation in close proximity, allowing some birds to move back and forth among such habitats (Blake and Loiselle 1991). Certainly, the high

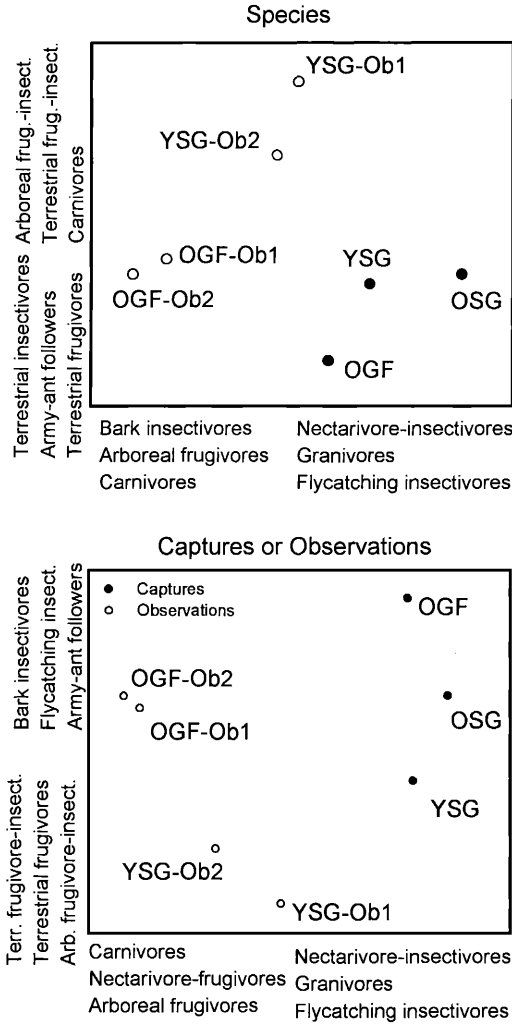


FIG. 6. Bray-Curtis ordination of samples based on relativized numbers of species (upper panel) or captures or observations (lower panel) from different trophic groups (see Fig. 2 for sample codes). Trophic groups most strongly correlated with the first two axes are indicated.

diversity of the young second-growth site would not be possible without the nearby old growth. Proximity of both old and younger habitats may have other consequences as well. Movement by birds from older forests into regenerating pastures may contribute to the regeneration process (Guevara et al. 1986, Da Silva et al. 1996). Dispersal of seeds from second growth into older forests also can occur, allowing second-growth species to invade forests (Janzen 1986). We have, for example, docu-

mented (through recaptures of marked individuals) movements between young and old forests by seed dispersers (e.g. *P. mentalis*, *M. oleagineus*) and pollinators (e.g. *Eutoxeres aquila*, *Phaethornis superciliosus*). Similarly, Graham (1996) found that a juvenile *P. mentalis* made regular trips of at least 1 km from old-growth forest to a fruiting tree outside the forest at La Selva.

Old-growth tropical forest is one of the most diverse natural habitats. The number of bird species found in lowland Neotropical forests can be high (e.g. point diversities of >160 species in Manu National Park, Peru; Terborgh et al. 1990; >150 species on our 10 ha plot in old-growth forest in La Selva). Yet, birds also can be very diverse and abundant in various types of secondary forests (Robinson and Terborgh 1997). Species richness often is positively associated with productivity, at least over some scales (Rosenzweig 1995). The open canopy and consequent high light levels reaching the understory of some types of second-growth vegetation can lead to high rates of fruit, flower, and foliage production. Flowers and fruits were more abundant and more spatially predictable within the understory (i.e. <10 m) of our young second-growth site than within the older sites (Blake and Loiselle 1991), contributing to the diversity and abundance of frugivores and nectarivores captured and seen in the young site.

Species richness may further be influenced by species turnover, which can lead to the accumulation of many species over time. During the 10 years of this study, vegetation structure and composition within the young second-growth site changed considerably (Fig. 1; Loiselle and Blake 1994) and, as a consequence, some bird species that were common on the study plot at the beginning of the study (e.g. *Glaucis aenea*, *Ramphocelus passerini*) had disappeared from the site by the time this study was completed. Conversely, other species, more typical of older sites (e.g. *Trogon rufus*, *F. analis*) moved into the younger site. Thus, the high species total of the young second-growth site (206 species) at least partially reflects the accumulation of species over the length of this study rather than the occurrence of so many species at one time. Nonetheless, we have recorded >120 species in the younger site within a single sampling period (captures, counts,

general observations). Turnover accounts for less of the species total in the older site, where habitat did not change as much over time.

A third factor influencing species totals is presence of transients. Various migrants, for example, may be present in the area for short periods of time but nonetheless contribute to the species totals. Latitudinal migrants often are more common in younger habitats (both primary and secondary successional) than in older forests (Petit et al. 1995, Robinson and Terborgh 1997). Other nonmigrant species may move into second-growth habitats temporarily (e.g. on hourly, daily, or seasonal basis) to take advantage of fruit or other resources, but may not remain to breed. Hummingbirds, for example, frequently move among habitats at La Selva, tracking phenologies of flowers (Stiles 1980; see also Stouffer and Bierregaard 1995b).

Transients may contribute to species totals in both young and old habitats. *Ma. candei* and *Sporophila americana*, for example, are typically found in second growth or pastures, but occasionally occur in old-growth forest, either in large treefall gaps or simply as transients in the understory. Many species found in the youngest site are species that typically breed in older forests within La Selva (e.g. *T. massena*, *Myrmeciza exsul*, *F. analis*, *Rhynchocyclus brevirostris*) or at higher elevations in Braulio Carrillo National Park (i.e. elevational migrants; e.g. *P. pipra*, *Corapipo altera*, *Pr. tricarunculata*). Presence of those and similar species in second-growth habitats likely will occur only when older forests are close enough to provide a source pool of individuals. Finally, the high species richness in the youngest site relative to the oldest site may be a consequence of sampling effects, which will be discussed later in the comparison of methods.

Migrants and threatened species.—Migrants contribute to the diversity and dynamics of bird communities at La Selva (Blake et al. 1990, Levey and Stiles 1994). Latitudinal migrants have been recorded at La Selva in virtually all months except June and July, whereas elevational migrants can be recorded throughout the year, depending on species. Although generalizations ignore species-specific differences, as a group latitudinal migrants tend to be more characteristic of second growth and elevational migrants of old-growth forest, but both types of migrants use both types of habitat. Neotrop-

ical migrants often are common in second growth (Petit et al. 1995), suggesting that such areas are suitable nonbreeding habitats (*but see* van Horne 1983). In fact, survival rates for migrants may not differ between young successional and mature forest (Conway et al. 1995), but such patterns may vary with region. Survival rates of *Hylocichla mustelina*, for example, did not differ between young and old forest in Belize (Conway et al. 1995), but did in Veracruz, Mexico (Rappole et al. 1989). Similarly, although capture rates did not differ between habitats in Belize for *Seiurus aurocapillus* or *Oporornis formosus*, they did in Costa Rica (Appendix 1).

Habitat preferences vary among elevational migrants as well. Some species of elevational migrants largely are restricted to old-growth forest interiors (e.g. *Cephalopterus glabricollis*, *Myadestes melanops*), whereas others frequently occur in well-developed second growth (*C. altera*), pastures with scattered trees (*Pr. tricarunculata*), or edges (*Pheucticus tibialis*) (J. Blake pers. observ.). Further, use of second growth by elevational migrants may vary among years (Loiselle and Blake 1992).

We found threatened species using both young and old forests. Although more threatened species were found in older forests (e.g. *Crax rubra*, *Neomorphus geoffroyi*, *Ce. glabricollis*), several species (e.g. *Ch. urochrysis*, *Pr. tricarunculata*, *Saltator atriceps*) were common in second growth. *Aphanotriccus capitalis* and *Gymnocichla nudiceps*, for example, can most regularly be found at La Selva in or near our youngest site. Neither species occurs in old-growth forest and their continued presence at La Selva will depend on availability of younger, regenerating vegetation.

Trophic composition.—Trophic composition differed between young and old sites, reflecting differences in availability of resources or foraging sites (Blake and Loiselle 1991). Nectarivores were more common in younger sites (based on both captures and observations), likely because of the abundance of flowers in the understory. An increase in disturbance and light levels in small fragments of forest in Brazil (Stouffer and Bierregaard 1995b) was the apparent cause of increased captures of hummingbirds in those fragments. Similarly, the decrease in captures of hummingbirds in our youngest site over time (Loiselle and Blake

1994) likely reflected a decrease in availability of flowers as the habitat changed and light levels decreased.

Frugivores and frugivore–insectivores were important components of all habitats, with the former somewhat more important in older sites and the latter in the youngest site. The reliance of many plant species on birds for dispersal of their seeds (Gentry 1982, Loiselle and Blake 1999) indicates the important role that many frugivores likely play in the regeneration of second growth and forests. As with hummingbirds, declines in abundance of some frugivores (e.g. *R. passerini*, *S. maximus*) in the youngest site reflected changes in the habitat and declines in abundance of some types of fruit.

Insectivores accounted for most species, as is true in most forests (Karr et al. 1990), but there were substantial differences among habitats in the importance of different groups. Increases in numbers of flocking species, ant-followers, and ground-feeding insectivores contributed to higher species totals in older forests along a primary successional gradient in Peru (Robinson and Terborgh 1997). Similarly, species that follow army ants (e.g. *Eciton burchelli*) were more diverse and more abundant in this study in older second-growth and old-growth forest than in the younger site. Army-ant swarms were observed in the youngest site on a fairly regular basis but typically with few attendant birds. In contrast, swarms within forest often were accompanied by a variety of species and many individuals, with *Ph. mcleannani* the most common. Army-ant followers, unlike hummingbirds, decreased in abundance and disappeared from small fragments surrounded by pasture (Stouffer and Bierregaard 1995a), but recolonized the fragments after the surrounding pasture matrix had regenerated into second growth. *G. nudiceps* was the only regularly encountered ant follower from the Thamnophilidae in our youngest site; *Phaen. mcleannani*, *Hypophylax naevioides*, and *Gymnophithys leucaspis* were rarely or never captured or observed in the youngest site, but were regularly encountered in older sites. Other typical ant-followers (e.g. *Dendrocincla fuliginosa*, *Dendrocolaptes sanctithomae*) also were rarely encountered in the youngest site. Bark insectivores also were more diverse and common in the older sites, presumably because of the greater density, diversity, and size range of trees.

MIST NETS AND POINT COUNTS

Species richness and composition.—Data from mist-net captures and from point counts may, in some cases, provide comparable descriptions of certain aspects of community composition (Blake and Loiselle 2000), but results also differ in ways that affect our understanding of community structure. Further, neither method is likely to provide an unbiased estimate of abundance or diversity (Dawson et al. 1995). In this study, both methods indicated higher species totals in the young site than in the old site, but more species were recorded by counts than by captures in both areas. The difference between methods was considerably greater, however, in old-growth forest, where 24% more species were observed than captured compared to 6% in young second-growth.

Previous comparisons of mist-net and point-count data have typically, but not always, reported higher species totals based on counts, with results often dependent on the habitat or type of bird (i.e. migrant or resident) being considered. Nets may be more effective than point counts in second growth (Rappole et al. 1998), but typically record fewer species of most groups in mature forest (Whitman et al. 1997). Studies that focus on migrants (e.g. Gram and Faaborg 1997, Rappole et al. 1998) often report higher detection frequencies with nets, particularly in second growth. Because many migrants tend to be small, relatively quiet while on nonbreeding grounds, and common in second growth or disturbed habitats, their high representation in net captures is not surprising.

Differences between capture and count data reflect species-specific differences in behavior (e.g. singing, foraging). Few species are both commonly captured and commonly observed (Fig. 4A, B), although exceptions to this pattern do occur. Both *Phaet. superciliosus* and *Ma. candei* were, for example, commonly captured and commonly observed in the youngest site. Although correlations between captures and observations were low in both habitats, the correlation was higher in the youngest site than in the old-growth site (Fig. 4A, B). In the older site, two species that each accounted for at least 12% of captures (*G. spirurus*, *P. mentalis*) accounted for less than 2 to 3% each of observations; *Amazona farinosa* accounted for almost 16% of observations in old growth but was never captured.

Most families were represented by both capture and count data, but notable differences occurred in the number of species per family. Psittacidae were the most extreme, with only one individual of one species (*Aratinga nana*) captured, but many individuals of eight species observed. Similarly, although four species of Cotingidae were observed, none were captured. Members of both those families are large, canopy species that rarely descend to net level and, even at net level, they would rarely be expected to be captured in nets of 36 mm mesh. In contrast, more species of Parulidae were captured (18 species) than observed (11 species). Other families were equally represented (in terms of species) by netting and observations (e.g. Furnariidae, Dendrocolaptidae, Thamnophilidae, Tyrannidae, Thraupidae). Similarities in numbers of species do not, however, indicate similarity in number of individuals captured or observed; many species of tyrannids were captured only rarely and many parulids were rarely observed. As a consequence, similarity values among sites and samples were much higher when based on species presence or absence than when based on relativized numbers of captures or observations. Thus, both methods may record similar species and numbers of species, but still provide quite different perspectives on community composition.

As a consequence of species differences, the two methods also provide different perspectives on the importance of different migrant categories or trophic groups. Latitudinal and elevational migrants both account for higher percentages of captures than of observations (see also Wallace et al. 1996). Further, the difference in relative importance of elevational migrants in young and old-growth forest was more pronounced based on netting data than based on observation data. Substantial differences also existed between netting and count data in relative importance of trophic groups. For example, foliage insectivores accounted for comparable percentages of species in all samples, but account for much higher percentages of observations than of captures. Nectarivores, in contrast, were much more important in captures than in observations although comparable numbers of species were recorded by both methods. Some of those differences may reflect speed of movement and ease of identification.

Hummingbirds are small, have relatively weak songs, move rapidly through the understory, and often occur high in the canopy, all factors that can make them difficult to identify. Whitman et al. (1997) found that nets and counts also provided similar estimates of relative proportions of species in different migrant and trophic categories although counts typically included more species.

Probability of capture or observation.—A variety of other factors influence the probability that species or individuals will be captured or observed, or both. Behavior can be a major influence on likelihood of detection by either method (Karr 1981, Bibby et al. 1992, Remsen and Good 1996). Size has long been known to affect probability of capture (Karr 1981) and also can affect observation data, particularly in tall forest where identification of small, nonvocalizing individuals in the canopy may be difficult.

Vegetation height clearly affects likelihood of capture, with consequences for estimates of diversity (Remsen and Good 1996, Robinson and Terborgh 1997). A similar consideration applies to count data; species and individuals high in the canopy may be missed by observers at ground level. In fact, detections of ground-dwelling species by observers in the canopy may be more likely than the reverse, given the differences in quality of songs produced by many species of those two different strata (Waide and Narins 1988). Loisele (1987, 1988) conducted canopy censuses from two emergent trees in old-growth forest at La Selva and detected 17 species that were not recorded by our ground-based point counts. Although the canopy censuses were not within the specific areas included in this study, many of those 17 species probably occurred in our old-growth sites, but simply were not detected. Some of those species included migrants that are not likely to vocalize and will thus frequently be overlooked (e.g. *Vireo flavifrons*, *Vermivora peregrina*, *W. canadensis*) or are species that are rare at La Selva (e.g. *Accipiter superciliosus*, *Ta. inornata*).

Observer variation.—Comparisons of mist-net and point-count data also must consider effects of observer variation. Observers differ in ability to detect and identify birds (Nichols et al. 2000) leading to errors of commission (misidentification by sight or sound, errors in estimation of numbers, errors in estimating distance) and omission (lack of ability to hear certain fre-

quencies, ignoring certain songs). Except in obvious cases, misidentifications are difficult to assess or detect, unless recordings have been made of all vocalizations (Parker 1991). Errors of omission are difficult to assess without simultaneous comparisons among observers (Nichols et al. 2000). In our case, we differed little either in the species that we recorded or in the proportion of records accounted for by each species. If observers differ in abilities and if observers conduct counts in different habitats or areas, then results may not be comparable.

SUMMARY

Both second-growth and old-growth forest contribute to the diversity and abundance of bird species in the lowlands of Costa Rica. Species richness is high in second-growth habitats due in part to the proximity of old-growth forest that likely serves as the source habitat for many species found in second growth. Importance of second-growth habitats may vary seasonally (e.g. as latitudinal and elevational migrants move into and out of such habitats). Second-growth habitats often have an abundant supply of resources, such as fruit and flowers, that may be important food sources for some species during certain periods of the year. Individuals from old-growth forest may move into second growth on an hourly, daily, or seasonal basis to feed on fruit, nectar, or other resources. Second growth also may be important for threatened species or species for whom old-growth forest is not suitable. Consequently, maintenance of the full complement of species in the region likely depends on the presence of a mosaic of habitats, including both young and old habitats. It is important to emphasize, however, that old-growth forest not only is more threatened as a habitat, but also is critical for the long-term survival of the majority of species. High diversity would not be maintained without old growth, but would be maintained (although at a lower level) without second growth.

Mist nets and point counts both provide descriptions of community composition, but those descriptions, although similar in some broad aspects, differ in the details. Ground-level nets obviously do not sample canopy birds and counts frequently overlook secretive or nonvocalizing species. Similarly, the two meth-

ods differ in likelihood of detecting different groups of species; latitudinal migrants frequently are better sampled by nets, particularly in second-growth habitats. Trophic groups also may be differentially represented by the two methods. Evaluations of the differential effectiveness of nets and counts should include consideration of observer effects. Learning the many different songs and calls that separate the hundreds of species found in tropical habitats requires a substantial investment of time. Further, even with training, observers may differ in their likelihood to detect or notice certain species. Thus, just as nets and counts may provide different perspectives on community composition, observers too may provide different perspectives.

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APPENDIX 1. Percentage of totals for species captured in mist nets or recorded during point counts in young second-growth (YSG), old second-growth (OSG), and old-growth forest (OGF) at La Selva Biological Station, Costa Rica. Ob1 (J.G.B.) and Ob2 (B.A.L.) indicate different observers. Status indicates whether species are migrants (L = latitudinal; E = elevational) or threatened (T) (see text for descriptions). Taxonomic sequence follows AOU (1998).

Species	Status	Netting			Count—YSG			Count—OGF	
		YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2	
Great Tinamou (<i>Tinamus major</i>)				0.05	0.95	0.96	2.27	2.98	
Little Tinamou (<i>Crypturellus soui</i>)		0.33			2.68	2.49			
Slaty-breasted Tinamou (<i>Crypturellus boucardi</i>)	T				0.88	0.74	0.02	0.06	
Turkey Vulture (<i>Cathartes aura</i>)		0.02			0.04		0.02	0.02	
Gray-headed Kite (<i>Leptodon cayanensis</i>)	L	0.09				0.02			
Double-toothed Kite (<i>Harpagus bidentatus</i>)									
Plumbeous Kite (<i>Ictinia plumbea</i>)									
Tiny Hawk (<i>Accipiter superciliosus</i>)									
Semiplumbeous Hawk (<i>Leucopternis semiplumbea</i>)	T		0.21	0.15	0.18	0.12	0.43	0.52	
Black Hawk-Eagle (<i>Spizaetus tyrannus</i>)	T					0.02			
Barred Forest-Falcon (<i>Micrastur ruficollis</i>)		0.02	0.07	0.17		0.10	0.12	0.17	
Slaty-backed Forest-Falcon (<i>Micrastur mirandollei</i>)		0.02		0.02	0.15	0.22	0.22	0.26	
Collared Forest-Falcon (<i>Micrastur semitorquatus</i>)						0.07		0.04	
Laughing Falcon (<i>Herpethotheres cachinnans</i>)					0.04				
Gray-headed Chachalaca (<i>Ortalis cinericeps</i>)	T	0.02		0.02	1.91	5.31	0.17	0.24	
Crested Guan (<i>Penelope purpurascens</i>)	T			0.02	0.07	0.32	0.77	1.06	
Great Curassow (<i>Crax rubra</i>)	T						0.24	0.19	
Black-eared Wood-Quail (<i>Odontophorus melanotis</i>)						0.02	0.02		
White-throated Crane (<i>Laterallus albigularis</i>)									
Gray-necked Wood-Rail (<i>Aramides cajaneae</i>)					0.04	0.10			
Pale-vented Pigeon (<i>Columba cayennensis</i>)									
Scaled Pigeon (<i>Columba speciosa</i>)									
Red-billed Pigeon (<i>Columba flavirostris</i>)					0.11	0.22	0.02	0.17	
Short-billed Pigeon (<i>Columba nigrirostris</i>)	T		0.07		2.13	2.10	4.84	4.21	
Ruddy Ground-Dove (<i>Columbina talpacoti</i>)		0.04							
Blue Ground-Dove (<i>Claravis pretiosa</i>)		0.33				0.37			
Gray-chested Dove (<i>Leptotila cassini</i>)		1.15	0.89		1.43	1.06			
Olive-backed Quail-Dove (<i>Geotrygon veraguensis</i>)	T	0.02		0.37			0.14	0.09	
Violaceous Quail-Dove (<i>Geotrygon violacea</i>)		0.31	0.07	0.02			0.02		
Ruddy Quail-Dove (<i>Geotrygon montana</i>)				0.42					
Crimson-fronted Parakeet (<i>Aratinga finschi</i>)	E				0.26	0.05	0.72	0.13	
Olive-throated Parakeet (<i>Aratinga nana</i>)		0.02				0.07		0.02	
Great Green Macaw (<i>Ara ambigua</i>)	T, E								
Orange-chinned Parakeet (<i>Brotogeris jugularis</i>)					0.62	0.77	2.42	1.88	
Brown-hooded Parrot (<i>Pionopsitta haematotis</i>)	T				0.11	0.20	1.48	2.03	
White-crowned Parrot (<i>Pionus senilis</i>)	T				1.95	1.23	0.91	0.35	
Red-lore Parrot (<i>Amazona autumnalis</i>)	T				0.33	0.42			

APPENDIX 1. Continued.

Species	Status	Netting			Count—YSG			Count—OGF	
		YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2	
Yellow-eared Toucanet (<i>Selenidera spectabilis</i>)	E, T						0.05	0.19	
Keel-billed Toucan (<i>Ramphastos sulfuratus</i>)		0.04	0.07		2.02	1.85	2.59	2.33	
Chestnut-mandibled Toucan (<i>Ramphastos swainsonii</i>)	T	0.02			0.73	1.33	2.51	3.11	
Black-cheeked Woodpecker (<i>Meelanerpes pucherani</i>)					0.84	1.23	0.10	0.11	
Smoky-brown Woodpecker (<i>Veniliornis fumigatus</i>)			0.07						
Rufous-winged Woodpecker (<i>Piculus simplex</i>)	T	0.02				0.02	0.02	0.04	
Cinnamon Woodpecker (<i>Celex loritatus</i>)							0.07	0.04	
Chestnut-colored Woodpecker (<i>Celex castaneus</i>)		0.07				0.12	0.36	0.43	
Lineated Woodpecker (<i>Dryocopus lineatus</i>)		0.02			0.15	0.25	0.17	0.15	
Pale-billed Woodpecker (<i>Campephilus guatemalensis</i>)				0.02	0.99	1.19	2.30	2.53	
Slaty Spinetail (<i>Synallaxis brachyura</i>)		0.31	0.07		0.07	0.10			
Striped Woodhaunter (<i>Hylocichla subulatus</i>)			0.07				0.07	0.15	
Buff-throated Foliage-gleaner (<i>Automolus ochrolaemus</i>)		1.15	2.67	0.05	0.33	0.12	0.05	0.11	
Plain Xenops (<i>Xenops minutus</i>)		0.15	1.30	0.45	0.04			0.06	
Scaly-throated Leaf-tosser (<i>Sclerurus guatemalensis</i>)	T			0.92			0.02	0.02	
Plain-brown Woodcreeper (<i>Deconychura fuliginosa</i>)		0.44	1.57	1.46				0.02	
Long-tailed Woodcreeper (<i>Deconychura longicauda</i>)				0.02				0.02	
Wedge-billed Woodcreeper (<i>Glyphorhynchus spirurus</i>)		1.57	10.73	12.56	0.04	0.20	2.42	1.30	
Northern Barred Woodcreeper (<i>Dendrocolaptes sanctithomae</i>)		0.38	0.14	0.47		0.12	0.36	0.28	
Cocoa Woodcreeper (<i>Xiphorhynchus susurrans</i>)		0.75	0.21	0.05	0.77	0.67	1.15	1.08	
Black-striped Woodcreeper (<i>Xiphorhynchus lachrymosus</i>)				0.12			0.12	0.15	
Spotted Woodcreeper (<i>Xiphorhynchus erythropygius</i>)		0.15		0.72					
Streak-headed Woodcreeper (<i>Lepidocolaptes soulleyetii</i>)					0.44	0.10			
Fasciated Antshrike (<i>Cymbilaimus lineatus</i>)		0.04			0.59	0.74			
Great Antshrike (<i>Taraba major</i>)		0.24			0.07	0.07			
Barred Antshrike (<i>Thamnophilus doliatius</i>)		0.02	0.82				0.65	0.67	
Western Slaty-Antshrike (<i>Thamnophilus atrinucha</i>)		0.02		0.52			0.07	0.11	
Streak-crowned Antwren (<i>Dysithamnus striaticeps</i>)	T			0.32			0.05		
Checker-throated Antwren (<i>Myrmotherula fulviventris</i>)			0.07	0.84			0.19	0.09	
White-flanked Antwren (<i>Myrmotherula axillaris</i>)			0.21	0.45					
Dot-winged Antwren (<i>Micropus quixensis</i>)			0.07		0.04	0.10			
Dusky Antbird (<i>Cercomacra tyrannina</i>)		0.38	0.07		0.51	0.42			
Bare-crowned Antbird (<i>Gymnocichla nudiceps</i>)	T	0.38	0.07		0.29	0.17			
Chestnut-backed Antbird (<i>Myrmeciza exsul</i>)		0.20	0.82	0.62	0.70	0.62	2.32	2.10	
Spotted Antbird (<i>Hylophylax naevioides</i>)			0.14	1.51		0.02	0.24	0.17	

APPENDIX 1. Continued.

Species	Status	Netting			Count—YSG			Count—OGF		
		YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2	Ob1	Ob2
Bicolored Antbird (<i>Gymnophaps leucaspis</i>)			1.98	4.54			0.31	0.37		
Ocellated Antbird (<i>Phaenostictus mcleannani</i>)		0.04	1.78	2.78			0.57	0.56		
Black-faced Anthrush (<i>Formicarius analis</i>)		0.22	0.34	0.87	1.69	1.36	1.58	2.12		
Streak-chested Antpitta (<i>Hylopezus perspicillatus</i>)				0.05			0.77	0.15		
Thicket Antpitta (<i>Hylopezus atres</i>)		0.02			1.14	1.58				
Brown-capped Tyrannulet (<i>Ornithion brunneicapillum</i>)				0.02				0.02		
Yellow Tyrannulet (<i>Capsiempis flaveola</i>)		0.24			0.48	0.05				
Olive-striped Flycatcher (<i>Mionectes olivaceus</i>)	E	0.35	1.64	1.49				0.02		
Ochre-bellied Flycatcher (<i>Mionectes oleagineus</i>)	E	6.78	9.02	9.23	0.11	0.07	0.26	0.19		
Sepia-capped Flycatcher (<i>Leptopogon amaurocephalus</i>)		0.60				0.02				
Paltry Tyrannulet (<i>Zimmerius vilissimus</i>)	E	0.02		0.02	0.73	0.42	1.10	0.63		
Black-capped Pygmy-Tyrant (<i>Myiornis atricapillus</i>)				0.02			0.48	0.76		
Northern Bentbill (<i>Oncostoma cinereigulare</i>)		0.38	1.03		0.70	0.96				
Slate-headed Tody-Flycatcher (<i>Poecilatriccus sylvia</i>)		0.09				0.02				
Common Tody-Flycatcher (<i>Todirostrum cinereum</i>)					0.04	0.05				
Eye-ringed Flatbill (<i>Rhynchocycclus brevirostris</i>)			0.07	0.52			0.14	0.43		
Yellow-olive Flycatcher (<i>Tolmomyias sulphureus</i>)					0.04	0.02				
Yellow-margined Flycatcher (<i>Tolmomyias assimilis</i>)		0.27		0.07	0.04	0.27	0.50	0.22		
Golden-crowned Spadebill (<i>Platyrinchus coronatus</i>)				0.74			0.24	0.35		
Royal Flycatcher (<i>Onychorhynchus coronatus</i>)		0.27	0.27	0.20		0.02				
Ruddy-tailed Flycatcher (<i>Terenotriccus erythrorus</i>)			0.48	1.69			0.10	0.09		
Tawny-chested Flycatcher (<i>Aphanostriccus capitatus</i>)	T	0.33								
Eastern Wood-Pewee (<i>Contopus virens</i>)	L	0.04			0.04					
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	L	0.13	0.07	0.05	0.04	0.05		0.09		
Acadian Flycatcher (<i>Empidonax virens</i>)	L	0.44	0.82	0.30		0.17	0.05	0.04		
Willow Flycatcher (<i>Empidonax traillii</i>)	L	0.53	0.07		0.29	0.35				
Long-tailed Tyrant (<i>Colonia coloma</i>)					0.07	0.15				
Bright-rumped Attila (<i>Attila spadiceus</i>)		0.53		0.27	1.14	0.82	1.77	1.99		
Rufous Mourner (<i>Rhytipterna holerythra</i>)		0.04	0.21	0.10	0.37	0.22	1.05	0.95		
Dusky-capped Flycatcher (<i>Myiarchus tuberculifer</i>)					0.07					
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	L	0.22			0.15	0.52	0.34	0.32		
Great Kiskadee (<i>Pitangus sulphuratus</i>)		0.07			0.15	0.12				
Boat-billed Flycatcher (<i>Megarynchus pitangua</i>)		0.07			1.47	1.16	0.02	0.06		
Social Flycatcher (<i>Myiozetetes similis</i>)		0.04			1.17	1.95				
Gray-capped Flycatcher (<i>Myiozetetes granadensis</i>)		0.33			2.35	3.53	0.10	0.06		
White-ringed Flycatcher (<i>Conopias albocinctata</i>)		0.02			0.70	0.17				

APPENDIX 1. Continued.

Species	Status	Netting			Count—YSG			Count—OGF	
		YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2	
Tropical Gnatcatcher (<i>Poliophtila plumbea</i>)		0.02			0.29	0.44	1.48	0.69	
Black-faced Solitaire (<i>Myadestes melanops</i>)	E	0.51		0.32					
Veery (<i>Catharus fuscescens</i>)	L		0.07						
Gray-cheeked Thrush (<i>Catharus minimus</i>)	L	0.35	0.21	0.10					
Swainson's Thrush (<i>Catharus ustulatus</i>)	L	2.50	2.94	0.94		0.15			
Wood Thrush (<i>Hylocichla mustelina</i>)	L, T	2.94	1.64	5.26	0.81	0.86	0.67	0.45	
Pale-vented Robin (<i>Turdus obsoletus</i>)	E	2.12	0.55	0.77	0.07	0.69			
Clay-colored Robin (<i>Turdus grayi</i>)		0.40			0.37	0.10			
White-throated Robin (<i>Turdus assimilis</i>)	E	0.07							
Gray Catbird (<i>Dumetella carolinensis</i>)	L	1.39			0.04	0.10			
Blue-winged Warbler (<i>Vermivora pinus</i>)	L	0.07							
Golden-winged Warbler (<i>Vermivora chrysoptera</i>)	L, T	0.11							
Tennessee Warbler (<i>Vermivora peregrina</i>)	L					0.05			
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	L	1.08	0.48	0.02	4.81	0.02	1.32	0.84	
Magnolia Warbler (<i>Dendroica magnaolia</i>)	L	0.02			0.04	2.79			
Blackburnian Warbler (<i>Dendroica fusca</i>)	L	0.02				0.02			
Bay-breasted Warbler (<i>Dendroica castanea</i>)	L	0.04		0.02			0.02		
Cerulean Warbler (<i>Dendroica cerulea</i>)	L, T	0.02			0.04	0.02	0.02		
Black-and-white Warbler (<i>Mniotilta varia</i>)	L	0.04							
Worm-eating Warbler (<i>Heimitheros vermicorvus</i>)	L, T	0.35	0.41	0.02		0.02			
Ovenbird (<i>Seiurus aurocapillus</i>)	L	2.87	0.68						
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	L	0.11	0.07						
Louisiana Waterthrush (<i>Seiurus motacilla</i>)	L	0.02		0.07					
Kentucky Warbler (<i>Oporornis formosus</i>)	L	2.61	1.85	0.17	0.88	0.49			
Mourning Warbler (<i>Oporornis philadelphia</i>)	L	0.27				0.05			
Olive-crowned Warbler (<i>Geothlypis semiflaca</i>)	L	0.22		0.02		0.02			
Hooded Warbler (<i>Wilsonia citrina</i>)	L	0.09							
Canada Warbler (<i>Wilsonia canadensis</i>)	L	0.04	0.14	0.02		0.02			
Buff-rumped Warbler (<i>Phaeothlypis fulvicauda</i>)		0.15	0.07	0.05	0.07	0.02	0.02	0.02	
Bannaquit (<i>Coereba flaveola</i>)		0.07			0.04	0.07	0.07		
Dusky-faced Tanager (<i>Mitrospingus cassinii</i>)		0.49	1.09		0.26	0.17			
Olive Tanager (<i>Chlorothraupis carmioli</i>)		0.09	0.14	1.94	0.22	0.10	0.53	0.54	
White-shouldered Tanager (<i>Tachyphonus luctuosus</i>)				0.07			0.10	0.28	
Tawny-crested Tanager (<i>Tachyphonus aclatrii</i>)				0.82			0.12	0.30	
White-lined Tanager (<i>Tachyphonus rufus</i>)		0.02							

APPENDIX 1. Continued.

Species	Status	Netting			Count—YSG			Count—OGF		
		YSG	OSG	OGF	Ob1	Ob2	Ob1	Ob2	Ob1	Ob2
Red-throated Ant-Tanager (<i>Habia fuscicauda</i>)		2.12	1.03		1.87	1.26				
Summer Tanager (<i>Piranga rubra</i>)	L	0.04	0.27	0.02	0.04	0.05				0.02
Scarlet Tanager (<i>Piranga olivacea</i>)	L	0.02	0.07		0.11	0.10				
Crimson-collared Tanager (<i>Ramphocelus sanguinolentus</i>)		0.31			0.04	0.07				
Passerini's Tanager (<i>Ramphocelus passerinii</i>)		4.35	0.21	0.05	3.63	4.10				
Blue-gray Tanager (<i>Thraupis episcopus</i>)		0.27				0.07				
Palm Tanager (<i>Thraupis palmarum</i>)						0.05				
Yellow-crowned Euphonia (<i>Euphonia luteicapilla</i>)		0.24	0.14	1.02	0.29	0.10	0.29	0.35	0.29	0.35
Olive-backed Euphonia (<i>Euphonia gouldi</i>)					0.51	0.64			3.40	3.46
White-vented Euphonia (<i>Euphonia minuta</i>)		0.02			0.22	0.37			0.26	0.43
Silver-throated Tanager (<i>Tangara icterocephala</i>)	E	0.24			1.14	1.06			0.05	0.02
Golden-hooded Tanager (<i>Tangara larcata</i>)				0.07	0.07	0.02			0.29	0.09
Blue Dacnis (<i>Dacnis cayana</i>)		0.02		0.02		0.02			0.12	0.26
Green Honeycreeper (<i>Chlorophanes spiza</i>)				0.02		0.22			0.36	0.45
Shining Honeycreeper (<i>Cyanerpes lucidus</i>)		0.04								
Blue-black Grassquit (<i>Volatinia jacarina</i>)		2.10	1.37	0.35	0.18	0.17				
Variable Seedeater (<i>Sporophila americana</i>)		0.02								
White-collared Seedeater (<i>Sporophila torqueola</i>)		0.29	0.34	0.37						
Thick-billed Seed-Finch (<i>Oryzoborus funereus</i>)		1.39	3.90	0.15	0.84	0.54			0.05	0.02
Orange-billed Sparrow (<i>Arremon aurantirostris</i>)		1.83	0.14	0.07	1.98	1.56				
Black-striped Sparrow (<i>Arremonops conirostris</i>)		3.25	0.07		2.24	1.53				
Buff-throated Saltator (<i>Saltator maximus</i>)		0.09			1.47	0.94				
Black-headed Saltator (<i>Saltator atriceps</i>)	T				0.95	0.35			0.69	0.80
Slate-colored Grosbeak (<i>Saltator grossus</i>)		0.13	0.14		0.15	0.27				
Black-faced Grosbeak (<i>Caryothraustes polioptaster</i>)	L	0.02		0.35	0.11	0.02			0.05	0.04
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)		0.62	1.98			0.10				
Blue-black Grosbeak (<i>Cyanocompsa cyanoides</i>)		0.04				0.07				
Black-cowled Oriole (<i>Icterus dominicensis</i>)		0.02				0.25				
Baltimore Oriole (<i>Icterus galbula</i>)	L	0.20			0.15	0.47				
Yellow-billed Cuckoo (<i>Amblycercus holosericeus</i>)					0.48	0.47			4.19	4.11
Scarlet-rumped Cuckoo (<i>Cacicus uropygialis</i>)					3.01	2.42			0.91	1.21
Chestnut-headed Oropendola (<i>Psaracolius wagleri</i>)			0.21	0.05	0.29	0.22			3.81	3.61
Montezuma Oropendola (<i>Psaracolius montezuma</i>)					5.03	4.77				