# Avian Community Response to Lowland Tropical Rainforest Isolation: 40 Years of Change at La Selva Biological Station, Costa Rica

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**Abstract:** *Since 1960, most of the forest surrounding the La Selva Biological Station, an intensively studied tropical research facility in Costa Rica, has been converted to agricultural uses. We used quantitative censuses and analysis of previously published categorical abundances to assess changes in the bird community, and we evaluated potential causes of species-specific changes by assessing their association with habitat, diet, participation in mixed-species flocks, and nest type. Approximately the same percentage of species increased as decreased in abundance from 1960 to 1999 (10–20% of all species, depending on method of assessment). Diet was the single most important trait associated with declining species. At least 50% of the species that declined have insectivorous diets. Use of forest habitat and participation in mixed-species flocks were also significant factors associated with declines, but nest type was unrelated to change in abundance. The species that increased in abundance tended to occur in open habitats and have omnivorous diets. These results reinforce the importance of several population risk factors associated with tropical understory insectivory and mixed-species flocking: patchy spatial distribution, low population density, large home range, and dietary specialization. La Selva's protected area (1611 ha), despite a forested connection on one boundary with a higher elevation national park, is apparently too small to maintain at least one major guild (understory insectivores). This first quantitative assessment of bird community change at La Selva highlights the need to intensify study of the mechanisms and consequences of biological diversity change in tropical forest fragments.*

**Key Words:** bird community, Costa Rica, forest fragmentation, habitat isolation, habitat loss, insectivory, La Selva Biological Station, tropics

Respuesta de la Comunidad Aviar al Aislamiento de Selva Tropical Inundable: 40 Años de Cambios en la Estación Biológica La Selva, Costa Rica

**Resumen:** *Desde 1960, la mayor parte del bosque que rodea a la Estación Biológica La Selva, un centro de investigación en Costa Rica, ha sido convertido a usos agrícolas. Usamos censos cuantitativos y el análisis de categorías de abundancia previamente publicadas para calcular cambios en la comunidad de aves, y evaluamos las potenciales causas de cambios especie-específicos mediante la estimación de su asociación con el hábitat, dieta, participación en parvadas mixtas y tipo de nido. Entre 1960 y 1990, el mismo porcentaje aproximado de especies aumentó y disminuyó en abundancia (10-20% de todas las especies, dependiendo del método de evaluación). La dieta fue el atributo individual más importante asociado con la declinación de especies. Por lo menos 50% de las especies que declinaron tiene dietas insectívoras. El uso del hábitat de bosque y la participación en parvadas mixtas también fueron factores significativos asociados con las declinaciones, pero el tipo de nido no estuvo relacionado con cambios en la abundancia. Las especies que incrementaron su abundancia tendieron a ocurrir en hábitats abiertos y a tener dietas omnívoras. Estos resultados refuerzan la importancia de varios factores de riesgo poblacional asociados con la insectivoría del sotobosque en los*

*trópicos y con las parvadas mixtas: distribución espacial discontinua, baja densidad poblacional, rango de hogar amplio y especialización alimentaria. El área protegida de La Selva (1611 ha), a pesar de una conexión boscosa con un parque nacional de mayor altitud, aparentemente es muy pequeña para mantener a un gremio importante (insectívoros de sotobosque) Esta primera evaluación cuantitativa del cambio en la comunidad de aves en La Selva destaca la necesidad de intensificar el estudio de los mecanismos y consecuencias del cambio en la diversidad biológica en fragmentos de bosque tropical.*

**Palabras Clave:** aislamiento de hábitat, comunidad de aves, Costa Rica, Estación Biológica La Selva, fragmentación de bosques, insectivoría, pérdida de hábitat, trópico

## Introduction

Conservationists have focused much attention on tropical bird communities because of rapid fragmentation and loss of the region's forest cover, high species richness (Stiles 1985; Terborgh et al. 1990; Bierregaard & Stouffer 1997; Winker 1998), and the vulnerability of tropical forest birds to human disturbance (Levey & Stiles 1994; Canaday 1996; Bierregaard et al. 2001). Insectivorous forest understory species appear to be especially susceptible to fragmentation, edge effects, and related disturbances (Stouffer & Bierregaard 1995*a*; Canaday 1996; Stratford & Stouffer 1999), but little is known as to why. Limited dispersal by forest understory species seems to be a contributing factor (Delevey & Stouffer 2001; Lens et al. 2002; Sekercioglu et al. 2002), but direct evidence for other causes remains scarce. Understanding patterns of decline following fragmentation is important for interpreting ecosystem processes in which birds play key roles, such as pollination, seed dispersal, and herbivory (e.g., as predators of herbivorous insects; Greenberg et al. 2000; Van Bael et al. 2003).

We focused on the lowland, wet-forest avifauna of a single site, La Selva Biological Station, Costa Rica, to take advantage of the comprehensive ecological characterization of its resident birds and extensive avian studies that have taken place since the late 1950s. We examined the relationship between long-term population change and four ecological variables that may influence vulnerability to forest fragmentation: diet, habitat, propensity to join mixed-species flocks, and nest type. Insectivorous birds are particularly sensitive to fragmentation, perhaps because of dietary or foraging substrate specialization (Sherry 1984; Rosenberg 1990; Marra & Remsen 1997). Forest understory birds can decline when their habitat becomes fragmented (Bierregaard & Stouffer 1997; Lens et al. 2002), implying a habitat effect. Mixed-species flocks often roam over large areas, suggesting that component species may be vulnerable to fragmentation (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995*b*; Maldonado-Coelho & Marini 2000). Finally, results of some studies indicate certain nest types are more vulnerable than others to predation (Loiselle & Hoppes 1983; Gibbs 1991; Sieving 1992; Arango-Vélez & Kattan 1997;

Sieving & Karr 1997), which in turn can be affected by fragmentation. Thus, we predicted that species with different nest architecture may respond differently to declines in forest habitat.

The diversity and natural history of the La Selva avifauna have been well documented since Slud's (1960) initial observations, but we know surprisingly little about population trends. Levey and Stiles (1994) observe that several species of forest interior, canopy, and edge have declined and that some nonforest species have increased. Blake and Loiselle (2000) document relative abundances of species both at La Selva and along an elevational transect into the adjacent Braulio Carillo National Park. Although few researchers have focused on population trends, the dramatic land-use transformation surrounding La Selva during the last 40 years suggests that such changes may have taken place. During this time, La Selva has changed from being part of a nearly unbroken forest to forming the tip of a forested peninsula in the middle of pastures, small farms, and plantations (Butterfield 1994). La Selva's only connection to other forested areas is on its southern boundary, where it adjoins Braulio Carrillo National Park. There, the land climbs so abruptly in elevation that lowland forest species may be effectively isolated. La Selva is one the world's most intensively studied tropical sites (Gentry 1990; McDade & Hartshorn 1994), so understanding population changes in resident birds is key to interpreting results of studies on other taxa and forest processes.

We addressed two questions prompted by the land-use changes surrounding the reserve. First, has La Selva suffered the kinds of avian decline that characterize other isolated tropical reserves (e.g., Robinson et al. 2000; Ferraz et al. 2003)? Second, are declining species at La Selva nonrandom with respect to diet, habitat, participation in flocks, and/or nest type? We examined changes in the La Selva avifauna using two independent assessments of abundance: (1) our own quantitative census data on a limited number of small plots initiated in 1976–1978 and repeated in 1996–1997 and (2) published qualitative (categorical) abundances. We also compared these two data sets to assess the validity of our own small-scale quantitative census results, to extend the temporal record, and to extend analysis to the entire La Selva property, including habitats not surveyed intensively.

## Methods

### Study Site

La Selva Biological Station, Costa Rica (10°26′N, 83°59′ W), is owned and operated by the Organization for Tropical Studies (OTS) and is composed of 1611 ha of lowland (35–137 m elevation) wet tropical forest on the Caribbean slope of the Cordillera Central. Average annual precipitation is 3962 mm and mean monthly temperature ranges from 24.7° C in January to 27.1° C in August, consistent with a tropical wet-forest life zone (Holdridge 1967; Hartshorn & Hammel 1994; McDade & Hartshorn 1994). About 73% of the La Selva reserve is old-growth lowland rain forest and the remainder contains a variety of habitats, including cleared pasture, secondary forest, and abandoned plantation. The region surrounding La Selva changed from 70% forest cover in 1963 to less than half that by 1983, and much more has been lost since (Butterfield 1994; Read et al. 2001). Old-growth forest at La Selva is dominated by a single tree species, *Penta-clethra macroloba* Willd., which constitutes about 40% of total timber volume (Hartshorn & Hammel 1994). Our censuses were performed entirely on what is known as "original La Selva," which is the 800-ha property initially purchased by OTS in 1968.

### Quantitative Census Data

Censuses were conducted in four sets: (1) nonbreeding season of 1976 (September–October), (2) breeding season of 1978 (May–June; both by T.W.S.), (3) nonbreeding season of 1996 (November–December), and (4) breeding season of 1997 (May–June) (3 and 4 both supervised by B.E.Y.). Each set of censuses was conducted on 20 square plots of 0.25 ha (representing five or, in one set, four habitats). Each plot was marked with colored plastic flagging along the perimeter every 25 m. While an observer walked systematically along the margins and across the interior, every bird seen or heard on the plot was recorded. Each census lasted 2 hours, and each plot was censused once in early morning (roughly 0700–0900 hours) and, on a different day, once in late morning (usually 0900–1100, occasionally as late as noon). All censuses were performed on dry days with little wind when birds were maximally detectable. Two-hour census periods were chosen to increase detectability of cryptic and mobile (flocking) species (Blake & Loiselle 2000). The risk of counting the same bird more than once per 2 hours was minimized by mapping the movement of birds or flocks through the plot so as to make conservative estimates of flock size and abundance per species.

The five different habitats (four replicate plots per habitat) sampled were (1) old-growth alluvial forest along Rio Puerto Viejo, (2) old-growth upland forest at slightly higher elevations, (3) abandoned plantation (*Theobroma cacao* L.), (4) swamp forest, and (5) tree-fall gap. Gap plots contained a major treefall, covering the center of the plot. Gap plots were not censused in 1978 so this breeding-period set covered only 16 plots. To equalize the number of plots between the two sample periods (1970s vs. 1990s), gap censuses from the breeding season of 1997 were omitted from our survey analyses. We located plots in the 1990s as closely as possible to the sites of the 1970s plots, with the exception of the gap plots, which we placed over recent treefall gaps to replicate conditions of the 1970s gap plots.

We examined quantitative surveys in two ways, first with total individuals and second with frequency of occurrence by species across all plots. Abundance for early morning and late morning censuses and breeding and nonbreeding censuses for each plot were pooled within each year to generate one set of abundances for the 1970s and one set for the 1990s. Species frequencies were treated as presence and absence data and thus recorded how many censuses detected a species out of 72 total censuses per time period (2 censuses per plot × 20 non-breeding season plots + 2 × 16 breeding season plots).

### Qualitative Abundance Data

Categorical abundance data were collated from the 40 years spanned by studies by Slud (1960), Stiles (1983), Levey and Stiles (1994), and Zook et al. (1999). Each species was assigned to one of six categories for each source: abundant, common, uncommon, rare, accidental, and no record, in decreasing order of abundance. Species assignments from Slud (1960) were taken from the species' descriptions and directly from tables for the other sources. The "occasional" category was pooled with rare because Slud did not use this category and we were not certain whether occasional was more or less abundant than rare in the other sources. Range categories (e.g., abundant-common) were frequently listed by some of the sources and were treated as halfway between the two categories when determining the number of steps between categories.

### Ecological Characterization of Species

Each species was assigned to one category for each of four ecological variables: habitat, diet, mixed-species flock participation, and nest type. The habitat categories were based on descriptions in Stiles (1983): (1) understory specialists use only forest understory; (2) understory generalists use forest understory and one additional habitat; (3) canopy and edge specialists use only canopy or gaps and edges or both canopy and gaps and edges; (4) forest generalists use canopy or gaps and edges and one or more other habitats (including forest understory); and (5) open habitat species use only young second growth and open or disturbed habitats. We excluded species that use exclusively aquatic or aerial habitats because of either a

paucity of such habitat at the site or difficulties of detection.

The diet categories were based on Stiles and Skutch (1989): (1) vegetarian species eat only plant material such as fruit, seeds, nectar, and leaves; (2) insects and other species regularly eat arthropods plus at least one plant-based material such as nectar or fruit; (3) insectivores eat entirely or essentially only insects, spiders, and other small invertebrates; (4) carnivores eat vertebrates, carrion, or both vertebrates and insects; and (5) omnivores eat more than one category (e.g., insects and two plant materials, or vertebrates, insects, and a plant material).

The flocking-status categories were based on Levey and Stiles (1994): (1) nonflocking, (2) facultative flocking (species that sometimes join mixed-species flocks), and (3) nuclear flocking species (species that form the core of mixed-species flocks).

The nest-type categories were based on information in Stiles and Skutch (1989), Carroll (1994), Young and Zook (1999), Christian and Roberts (2000), Sanchez (2002), Hilty (2003), Remsen (2003), Zimmer and Isler (2003), and Buehler et al. (2004): (1) ground or burrow, (2) cavity (in tree or termitary), (3) open (platform or open cup), and (4) covered (e.g., pouch, pyriform). If a nest was undescribed or ambiguous (e.g., Bronzed Cowbird [*Molothrus aeneus*] parasitizes both open and covered nests) it was not assigned to a category. A spreadsheet with the list of species from La Selva, with their abundance categories, changes in abundance, and ecological characterizations, is available from B.J.S.

### Analysis

We performed a chi-squared test on the census data for each species to determine whether a species had increased, not changed, or decreased from the 1970s to the 1990s (the null hypothesis was that abundance or frequency did not change). If $p < 0.05$ for a chi-squared test, the species was assigned to either a decreasing or an increasing category, depending on the direction of the change in abundance, and to the no-change category otherwise. We did not correct for multiple comparisons (e.g., Bonferroni correction) because we used the test to categorize species, and these categories were subjected to further analyses. Categorical abundance trends were also used to assign each species to one of three categories (increase, decrease, or no change) based on whether there was a net change of more than one qualitative abundance category across all years. For example, a species that changed from abundant to common across all time periods was considered unchanged (a net change of only 1 category, which might be attributable to observer differences), whereas a species that went from abundant to common-uncommon was considered to have decreased (net change of $-1.5$ categories). Change from no record to rare was considered a single change in category.

We used contingency table analyses to determine associations between each ecological variable and population change status (decreasing, no change, or increasing). We did not evaluate interactions among variables (e.g., using logistic regression) because of low cell count frequencies due to many ecological categories.

## Results

### Quantitative Census Data

A total of 130 resident species was observed in quantitative censuses (nonresidents and aquatic/aerial species excluded). Using the census data abundances, 48 of 130 species (36.9%) changed in abundance during the 20-year interval. Of these, 25 (19.2%) increased in abundance and 23 (17.7%) decreased from the 1970s to the 1990s (Table 1). Using the more conservative frequency census data, 27 of 130 of the species (20.8%) changed in abundance, with 13 (10.0%) increasing and 14 (10.8%) decreasing (Table 1). The frequency census data are considered more conservative because each species was counted only once per 2-hour census.

Contingency tables for the census data show that diet was a statistically significant factor associated with population decline in both the abundance ($\chi^2 = 30.25$, df $= 8$, $p < 0.001$) and frequency ($\chi^2 = 23.47$, df $= 8$, $p = 0.003$) analysis (Table 1). According to the abundance census data, 12 of the 23 species (52.2%) that declined were insectivores. The frequency data showed an even stronger trend, with 9 of 14 (64.3%) declining species in the insectivorous diet category. No insectivore increased in abundance in the analyses of the censuses. higher than expected numbers of both vegetarian and omnivorous species increased, however, in both abundance and frequency census tables (Table 1). Flocking was a statistically significant factor in the frequency census data ($\chi^2 = 9.79$, df $= 4$, $p = 0.044$) and nearly significant in the abundance census data ($\chi^2 = 7.82$, df $= 4$, $p = 0.098$), with nuclear species declining more than expected. Neither habitat nor nest type category was associated significantly with population trend detected using the quantitative censuses.

### Qualitative Abundance Data

A total of 236 species (nearly the entire set of known residents at La Selva) was analyzed using published categorical abundance. Most of the species in this analysis that were not detected in the censuses were either rare or nonforest birds (i.e., occupying habitats not included in the censuses). Based on these 236 species, 49 (20.8%) changed in abundance from 1960 to 1999. Of these, 24 (10.2%) increased and 25 (10.6%) decreased (Table 3).

**Table 1. Number of bird species increasing, decreasing, and remaining stable (sorted by habitat, diet, flocking behavior, and nest type) at La Selva Biological Reserve, Costa Rica, based on quantitative and qualitative estimates of abundance.***

| Data type and ecological variable | Bird population status | | | |
|---|---|---|---|---|
| | decrease | no change | increase | total |
| **Census abundance** | | | | |
| habitat | | | | |
|   understory specialist | 4 (1.95) | 6 (6.94) | 1 (2.12) | 11 |
|   understory generalist | 5 (5.84) | 22 (20.82) | 6 (6.35) | 33 |
|   canopy/edge specialist | 1 (1.24) | 6 (4.42) | 0 (1.35) | 7 |
|   forest generalist | 13 (12.21) | 41 (43.52) | 15 (13.27) | 69 |
|   open habitats | 0 (1.77) | 7 (6.31) | 3 (1.92) | 10 |
|   total | 23 | 82 | 25 | 130 |
| diet | | | | |
|   vegetarian | 0 (2.48) | 7 (8.83) | 7 (2.69) | 14 |
|   arthropods and other | 4 (7.61) | 30 (27.12) | 9 (8.27) | 43 |
|   insectivore | 12 (5.48) | 19 (19.55) | 0 (5.96) | 31 |
|   carnivore (and other) | 3 (3.01) | 13 (10.72) | 1 (3.27) | 17 |
|   omnivore | 4 (4.42) | 13 (15.77) | 8 (4.81) | 25 |
|   total | 23 | 82 | 25 | 130 |
| flocking behavior | | | | |
|   nonflocking | 8 (12.38) | 45 (44.15) | 17 (13.46) | 70 |
|   facultative | 9 (7.78) | 29 (27.75) | 6 (8.46) | 44 |
|   nuclear | 6 (2.83) | 8 (10.09) | 2 (3.08) | 16 |
|   total | 23 | 82 | 25 | 130 |
| nest | | | | |
|   ground and burrow | 2 (1.55) | 6 (5.70) | 1 (1.76) | 9 |
|   cavity | 3 (5.67) | 24 (20.88) | 6 (6.45) | 33 |
|   platform and cup | 8 (9.80) | 34 (36.07) | 15 (11.13) | 57 |
|   covered and pouch | 9 (4.98) | 17 (18.35) | 3 (5.66) | 29 |
|   total | 22 | 81 | 25 | 128* |
| **Census frequency** | | | | |
| habitat | | | | |
|   understory specialist | 3 (1.18) | 7 (8.72) | 1 (1.10) | 11 |
|   understory generalist | 4 (3.55) | 26 (26.15) | 3 (3.30) | 33 |
|   canopy/edge specialist | 0 (0.75) | 7 (5.55) | 0 (0.70) | 7 |
|   forest generalist | 7 (7.43) | 54 (54.67) | 8 (6.90) | 69 |
|   open habitats | 0 (1.08) | 9 (7.92) | 1 (1.00) | 10 |
|   total | 14 | 103 | 13 | 130 |
| diet | | | | |
|   vegetarian | 0 (1.51) | 10 (11.09) | 4 (1.40) | 14 |
|   arthropods and other | 2 (4.63) | 37 (34.07) | 4 (4.30) | 43 |
|   insectivore | 9 (3.34) | 22 (24.56) | 0 (3.10) | 31 |
|   carnivore (and other) | 2 (1.83) | 14 (13.47) | 1 (1.70) | 17 |
|   omnivore | 1 (2.69) | 20 (19.81) | 4 (2.50) | 25 |
|   total | 14 | 103 | 13 | 130 |
| flocking behavior | | | | |
|   nonflocking | 4 (7.54) | 57 (55.46) | 9 (7.00) | 70 |
|   facultative | 5 (4.74) | 36 (34.86) | 3 (4.40) | 44 |
|   nuclear | 5 (1.72) | 10 (12.68) | 1 (1.60) | 16 |
|   total | 14 | 103 | 13 | 130 |
| nest | | | | |
|   ground and burrow | 2 (0.91) | 6 (7.17) | 1 (0.91) | 9 |
|   cavity | 2 (3.35) | 28 (26.30) | 3 (3.35) | 33 |
|   platform and cup | 4 (5.79) | 44 (45.42) | 9 (5.79) | 57 |
|   covered and pouch | 5 (2.95) | 24 (23.11) | 0 (2.95) | 29 |
|   total | 13 | 102 | 13 | 128 |
| **Qualitative estimate** | | | | |
| habitat | | | | |
|   understory specialist | 7 (1.91) | 10 (14.26) | 1 (1.83) | 18 |
|   understory generalist | 7 (4.98) | 38 (37.24) | 2 (4.78) | 47 |
|   canopy/edge specialist | 1 (1.59) | 13 (11.89) | 1 (1.53) | 15 |
|   forest generalist | 9 (10.91) | 93 (81.61) | 1 (10.47) | 103 |
|   open habitats | 1 (5.61) | 33 (42.00) | 19 (5.39) | 53 |
|   total | 25 | 187 | 24 | 236 |

*continued*

**Table 1. (continued)**

| Data type and ecological variable | Bird population status | | | |
|---|---|---|---|---|
| | decrease | no change | increase | total |
| diet | | | | |
|   vegetarian | 0 (2.54) | 19 (19.02) | 5 (2.44) | 24 |
|   arthropods and other | 5 (6.89) | 56 (51.50) | 4 (6.61) | 65 |
|   insectivore | 14 (6.14) | 33 (45.96) | 11 (5.90) | 58 |
|   carnivore (and other) | 5 (4.87) | 40 (36.45) | 1 (4.68) | 46 |
|   omnivore | 1 (4.56) | 39 (34.07) | 3 (4.37) | 43 |
|   total | 25 | 187 | 24 | 236 |
| flocking behavior | | | | |
|   nonflocking | 11 (16.10) | 120 (120.44) | 21 (15.46) | 152 |
|   facultative | 8 (6.57) | 51 (49.13) | 3 (6.31) | 62 |
|   nuclear | 6 (2.33) | 16 (17.43) | 0 (2.24) | 22 |
|   total | 25 | 187 | 24 | 236 |
| nest | | | | |
|   ground and burrow | 4 (1.79) | 13 (13.50) | 0 (1.71) | 17 |
|   cavity | 3 (5.37) | 44 (40.49) | 4 (5.14) | 51 |
|   platform and cup | 12 (12.21) | 89 (92.09) | 15 (11.70) | 116 |
|   covered and pouch | 5 (4.63) | 35 (34.93) | 4 (4.44) | 44 |
|   total | 24 | 181 | 23 | 228 |

*Expected values in parentheses. Fewer species were analyzed for nest type because of unknown or ambiguous nests.

These same qualitative abundance data showed that population status change was significantly associated with habitat ($\chi^2 = 68.79$, df $= 8$, $p < 0.001$), diet ($\chi^2 = 32.44$, df $= 8$, $p < 0.001$), and flocking status ($\chi^2 = 13.85$, df $= 4$, $p = 0.008$), whereas nest type was not significant. Among habitats, more understory species declined than expected, whereas open habitat species increased. Nineteen of 24 species that increased (79.2%) were classified as open habitat species. For diet, 14 of 25 species that decreased (56%) were insectivorous. Insectivorous species, however, also increased more than expected. According to the analysis of flocking behavior, both nuclear and facultative flocking species decreased more than expected, whereas nonflocking species increased more than expected (Table 1).

### Comparison of Quantitative and Qualitative Abundance Change

The frequency census data and the qualitative data were generally consistent, identifying similar proportions of species (roughly 10%) both increasing and decreasing, whereas slightly higher percentages were found with the less conservative quantitative abundance data. Inspection of the contingency tables comparing trends using quantitative census versus qualitative literature data (Table 2) showed that the majority of species fell on the diagonal (i.e., increases by one method correspond with increases by the other, and vice versa). The agreement between the two methods gives us confidence that both methods are measuring essentially the same phenomena. In no case were opposing trends found in censuses versus literature assessments (e.g., a species decreasing using one method and increasing in the other). Fewer than half

the species that decreased in the censuses declined in the literature assessments, however, and there was little overlap between the methods when detecting birds that increased.

## Discussion

### Changes in the La Selva Bird Community

Two independent data sets show that avian community structure has changed at La Selva during the past 40 years, concurrent with almost complete deforestation in the lowlands surrounding the site. The strongest ecological factor associated with changes in abundance in both quantitative and literature surveys was diet: insectivores

**Table 2. Comparison of the three bird abundance data sets (quantitative abundance, quantitative frequency, and qualitative abundance) spanning nearly 40 years at La Selva Biological Reserve, Costa Rica.**

| Quantitative estimate | Qualitative estimate | | | |
|---|---|---|---|---|
| | decrease | no change | increase | total |
| Abundance | | | | |
|   decrease | 10 | 13 | 0 | 23 |
|   no change | 7 | 71 | 4 | 82 |
|   increase | 0 | 23 | 2 | 25 |
|   total | 17 | 107 | 6 | 130 |
| Frequency | | | | |
|   decrease | 9 | 5 | 0 | 14 |
|   no change | 8 | 90 | 5 | 103 |
|   increase | 0 | 12 | 1 | 13 |
|   total | 17 | 107 | 6 | 130 |

declined more than members of any other guild. Both the analysis of census frequencies and the literature data showed that participation in mixed-species flocks was a significant factor, with nuclear flock species declining more than others. Habitat was significantly associated with abundance change in the literature surveys, such that understory species declined more than others. Declines in forest understory birds, especially insectivores and participants in mixed-species flocks, were consistent with effects of tropical forest fragmentation elsewhere, including the Amazon Basin (Stouffer & Bierregaard 1995*a*, 1995*b*; Stratford & Stouffer 1999) and Barro Colorado Island, Panama (Willis 1974; Sieving & Karr 1997; Robinson 1999).

## Potential Mechanisms of Population Decline at La Selva

The data support our hypothesis that understory insectivores are especially vulnerable to habitat fragmentation, but the mechanisms need further investigation. The life-history traits of several of the declining species are virtually unknown and could influence their ability to persist in fragments (Sieving 1992; Sieving & Karr 1997). Data from Terborgh et al. (1990) and Robinson et al. (2000) show that many tropical understory insectivores occur at population densities as low as 2–3 pairs/100 ha. Based on insectivore species densities from lowland forests at Cocha Cashu, Peru (Terborgh et al. 1990), and Pipeline Road, Soberania National Park, Panama (Robinson et al. 2000), and the amount of acceptable habitat at La Selva in the 1970s, we estimated population sizes of several insectivores to be unsustainably small if La Selva is as isolated from other lowland sites as we suspect (C. Leumas, T.W.S., and B.J.S., unpublished data). Small populations are vulnerable to extirpation because of demographic stochasticity, inbreeding, genetic drift, and other problems (Pimm et al. 1988; Westemeier et al. 1998), and the less dense the initial population, the smaller the post-fragmentation population will be. Vulnerability to fragmentation is compounded by the reluctance of many of these forest-interior species to cross nonforest matrix (Stouffer & Bierregaard 1995*b*; Stratford & Stouffer 1999; Develey & Stouffer 2001; Sekercioglu et al. 2002), which would reduce gene flow.

Given the association of insectivorous diet with abundance decline in our analysis, problems associated with insectivory and dietary specialization, such as patchy distribution of resources (Karr 1982), large home range (Terborgh et al. 1990), and reluctance to disperse (Develey & Stouffer 2001), may be strongly associated with vulnerability to fragmentation in the tropics. Demographic factors in tropical birds such as slow physiological rate (Wikelski et al. 2003), long life span, low clutch size (Martin 1996, 2004), and high nest predation (Skutch 1949), particularly if associated with understory habitat or insec-

tivory, may also be associated with vulnerability to extirpation in a fragmented tropical landscape.

Several of the species that declined are either facultative or nuclear members of mixed-species flocks. The large area requirements of these flocks may prohibit them from persisting in fragments (Stouffer & Bierregaard 1995*b*). Once nuclear species are gone, facultative species that may depend heavily on mixed-species flocks for foraging opportunities or security against predators may also be adversely affected. Some of the most abundant species in the 1970s La Selva censuses were antwrens (*Myrmotherula fulviventris, M. axillaris,* and *Microrhopias quixensis*). All three are nuclear species in mixed-species flocks, and all declined to zero in the 1990s censuses. The Sulfur-rumped Flycatcher (*Myiobius sulphureipygius*) was a regular, if not obligate follower of antwren flocks at La Selva, at least during the nonbreeding season (Slud 1960; Stiles & Skutch 1989; T.W.S. unpublished data), and it frequently forages by picking off insects that other flock members flush (Sherry 1984). As expected if flock followers like *M. sulphureipygius* are vulnerable to flock disintegration, this species declined to zero in the censuses, although this was not classified as a significant decrease because of its rarity in the 1970s. Another facultative flocking species, the Green Shrike-Vireo (*Vireolanius pulchellus*), frequently follows tanager flocks (Stiles & Skutch 1989), and may have declined because of the loss of the nuclear tanager species *Chlorothraupis carmioli* and *Tachyphonus delatrii*. The White-fronted Nunbird (*Monasa morphoeus*) also flocks with larger canopy-foraging species, which may help explain its decline.

Although we detected no association of nest type with abundance change at La Selva, a variety of interpretations are possible. Nest predation may have been more intense but affected all nest types equally, yielding little or no pattern in our analysis. Also, we may not have detected an effect of nest type because there is nearly as much variability in nest predation risk within types as between (e.g., hanging nests most likely differ in depredation risk depending on whether the nest is built next to stinging Hymenoptera; Hansell 2000).

In our analyses, multiple ecological factors are associated with the decline of bird species at La Selva and all could be interrelated. Unfortunately, we were unable to test for interactions among factors (e.g., with log-linear models) because of low cell frequencies in the contingency tables. Nevertheless, we can infer that interactions exist because of shared ecological categorizations among declining species. Almost all the species associating in mixed-species flocks that declined had insects in their diet, and all but one of the understory specialist species that declined were strict insectivores. Also, almost half the insectivores that declined were associated with mixed-species flocks.

## Evaluation of Methods

Both the census and literature data probably underestimated changes in the La Selva avifauna. Greater sampling effort would have been necessary to detect changes in species that were already rare in the 1970s. Many species declined to zero in the 1990s censuses, but too few individuals were detected in the 1970s to categorize them as decreasing (e.g., *M. sulphureipygius*), a trend confirmed by another analysis (C. Leumas, T.W.S., and B.J.S., unpublished data). Although rarity may be an important determinant of extinction proneness in birds (e.g., Goerck 1997; Manne & Pimm 2001), even formerly abundant La Selva species such as antwrens declined to zero in our survey, emphasizing that other ecological factors (e.g., insectivory and/or flock participation) were important in the local declines we documented.

Published qualitative abundances may also be conservative. Authors of subsequent assessments of abundance most likely used the previously published assessments when assigning species to abundance category, especially between Stiles (1983) and Levey and Stiles (1994). Later authors may have been hesitant to change assignments without strong evidence, contributing to nonindependence of assignments. We suspect that during the 40-year period covered by our analysis, detection ability of ornithologists has improved because of increased knowledge of tropical birds and their vocalizations via audio recordings. This would have biased results by underestimating declines, or overestimating increases, especially among already rare species. We attempted to mitigate effects of variable bird detectability in our data by using multiple independent methods to detect trends and conservative interpretation. Two-hour surveys on the 0.25-ha plots should have increased detectability compared with standard point counts, although we did not compare the two methods. We advocate more intensive surveys of the La Selva avifana to increase the power and precision of future inferences.

Our two methods differed in their identification of which species increased. Most of the discrepancy between the two methods can be explained by the restricted location of the census plots. All censuses were conducted in forest, whereas the literature data are based on the entire La Selva reserve, which includes nonforested habitat. During the period covered by this study, OTS purchased additional property, consisting of mostly nonforested habitat, thereby increasing the relative amount of this habitat type. Accordingly, several of the species that increased in the analysis of published data are found in open habitats. Those that increased in the census data tended to be forest generalists and omnivores, which may represent a true increase of generalist species at La Selva because of a greater area of disturbed habitats surrounding the study area.

Some species decreased in the censuses, but did not do so in the qualitative data (e.g., *Myiozetetes granadensis*, *Campylorhynchus zonatus*, *Thryothorus nigricapillus*) (Table 3). These changes most likely result from the maturation of second growth and old plantations immediately adjacent to the old-growth forest at La Selva. Although these species declined in the maturing forest, they are still common to abundant at La Selva (hence their unchanged status in the qualitative data), especially in second growth and cleared areas around buildings (B.J.S., personal observation). Such cases may have made it more difficult to find patterns in the census data and further justify the use of the two independent assessments of abundance in our analyses.

## Study Implications and Areas for Further Research

Although La Selva has long been considered a flagship tropical research site, our data show that the bird community there has changed significantly in the past 40 years. Possible effects of change in the bird community on the forest community as a whole have not been documented, but recent evidence suggests that insectivorous birds have a significant impact on levels of herbivory (Greenberg et al. 2000; Van Bael et al. 2003). The removal of top predators in the tropics can have dramatic top-down effects (e.g., Terborgh et al. 2001; Letourneau et al. 2004). If a significant fraction of an entire guild, specifically forest understory insectivores, is lost, as our data suggest, then top-down trophic cascades could alter arthropod and plant communities and ultimately biodiversity (Schmitz et al. 2000; Rao et al. 2001). Investigators working in tropical forest fragments, even those as large as La Selva, must take into account such changes, especially when using La Selva as a control site for smaller fragments (e.g., Gibbs 1991).

Barro Colorado Island, Panama (BCI), is roughly the same size as La Selva. Sixty years after isolation the site had lost 45 (22%) of all bird species (Willis 1974), and by the mid-1990s it had lost an additional 20 (Robinson 1999). La Selva appears to have an advantage relative to BCI in that it is not truly an island because of its connection to Braulio Carillo National Park. Our data demonstrate, however, that over the 40 years during which La Selva has become increasingly isolated from large tracts of forest, up to 38 species have declined in abundance (Table 3) and some may have become extirpated. If BCI can be used as a model, La Selva will continue to lose forest species. To protect biological communities of the Central American Caribbean lowlands, we recommend continuing efforts to enlarge the La Selva Reserve and to establish a forested corridor to the largely intact Rio Indio-Maíz forest in southern Nicaragua. Our work also highlights the need for (1) continued monitoring of bird populations using standardized methods, (2) intensified investigation

**Table 3.  Birds that decreased in abundance at La Selva Biological Station, Costa Rica, according to quantitative and qualitative analyses.**

| Scientific name | Quantitative abundance* | Quantitative frequency | Qualitative |
|---|---|---|---|
| *Spizaetus ornatus* | — | — | decrease |
| *Trogon clathratus* | no change | no change | decrease |
| *Malacoptila panamensis* | decrease | decrease | decrease |
| *Monasa morphoeus* | decrease | decrease | decrease |
| *Pteroglossus torquatus* | decrease | decrease | no change |
| *Celeus loricatus* | decrease | decrease | decrease |
| *Sclerurus guatemalensis* | — | — | decrease |
| *Cymbilaimus lineatus* | — | — | decrease |
| *Taraba major* | — | — | decrease |
| *Thamnistes anabatinus* | — | — | decrease |
| *Dysithamnus striaticeps* | decrease | decrease | no change |
| *Myrmotherula fulviventris* | decrease | decrease | decrease |
| *Myrmotherula axillaris* | decrease | decrease | decrease |
| *Microrhopias quixensis* | decrease | decrease | decrease |
| *Gymnocichla nudiceps* | — | — | decrease |
| *Myrmeciza exsul* | decrease | no change | no change |
| *Hylopezus perspicillatus* | no change | no change | decrease |
| *Oncostoma cinereigulare* | no change | no change | decrease |
| *Platyrinchus coronatus* | decrease | no change | decrease |
| *Terenotriccus erythrurus* | decrease | decrease | decrease |
| *Aphanotriccus capitalis* | no change | no change | decrease |
| *Rhytipterna holerythra* | decrease | decrease | no change |
| *Myiozetetes granadensis* | decrease | no change | no change |
| *Schiffornis turdina* | no change | no change | decrease |
| *Piprites griseiceps* | — | — | decrease |
| *Lipaugus unirufus* | decrease | no change | no change |
| *Tityra semifasciata* | decrease | no change | no change |
| *Querula purpurata* | decrease | decrease | no change |
| *Vireolanius pulchellus* | — | — | decrease |
| *Campylorhynchus zonatus* | decrease | decrease | no change |
| *Thryothorus nigricapillus* | decrease | no change | no change |
| *Cyphorhinus phaeocephalus* | decrease | decrease | decrease |
| *Microbates cinereiventris* | decrease | decrease | decrease |
| *Phaeothlypis fulvicauda* | decrease | no change | no change |
| *Mitrospingus cassinii* | decrease | no change | no change |
| *Chlorothraupis carmioli* | no change | no change | decrease |
| *Tachyphonus delatrii* | — | — | decrease |
| *Cacicus uropygialis* | decrease | no change | no change |

*Dashes indicate that these species were not detected in the 1970s and 1990s censuses.*

of the mechanisms causing population declines and extirpation in tropical forest fragments, and (3) studies that address cascading community and ecosystem effects of bird species and guild loss in tropical forest fragments.

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