Species Richness and Pollen Loads of Hummingbirds Using Forest Fragments in Southern Costa Rica[1]

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ABSTRACT

In many areas of the humid tropics, relatively small patches of forest is the habitat most commonly available for forest-dwelling organisms. To assess resident hummingbird use of forest fragments near the Las Cruces Biological Station in southwestern Costa Rica, we mist-netted birds in five fragments (0.3–20 ha; *ca* 1300 m elev.) and the station's 226-ha forest preserve (*ca* 900–1280 m elev.). From January 1994 through mid-March 1999, we recorded 1069 captures of 21 hummingbird species during 49,900 net hours. Species richness, diversity indices, and capture rates increased asymptotically with patch size, as expected. We captured 16 hummingbird species in both the largest fragment (20 ha) and in the nearby forest preserve. Non-forest hummingbirds did not occur more frequently in the fragments than in the preserve, and all fragments supported a mixture of forest-interior and canopy-dwelling hummingbird species, along with a diverse group of hummingbird-pollinated plants. *Phaethornis guy* was common at all sites and visited >13 plant species in the fragments during the 1998 dry season (based on analyses of pollen collected from the birds' heads). In contrast, *Eutoxeres aquila* was found at only the largest three sites (10, 20, and 226 ha) and carried pollen from only one plant species during the 1998 dry season. *Lampornis castaneoventris*, a high-elevation hummingbird species, was far more common in the fragments than in the preserve, while three species typically found at lower elevations were rare in the fragments and common in the preserve. These distribution patterns could be influenced by local climatic differences because the fragments are higher and receive more cloud mist and annual precipitation than the preserve. Our data show that pollen loads on hummingbird species vary, and this has implications for gene flow among hummingbird-pollinated plants. Although our results are consistent with previous reports that hummingbird species may be less affected by deforestation than insectivorous avian species such as army ant followers, it is important to note that from the perspective of the genetics and demographics of hummingbird-pollinated plants, the important issue is whether appropriate pollinator species are able to move plant propagules among subpopulations of plants in fragmented landscapes. We conclude that the biodiversity of tropical forest fragments as small as 10 to 20 ha is high enough to warrant long-term preservation of these areas, especially if they are located near larger tracts of forest.

RESUMEN

En muchas áreas de los trópicos húmedos, parches de bosque que son relativamente pequeños son los hábitats más comunes para organismos que habitan en el bosque. Para evaluar la utilidad de los parches de bosque para las especies de colibríes residentes en el área cerca de la Estación Biológica Las Cruces en el sudoeste de Costa Rica, nosotros colocamos redes de niebla en cinco fragmentos (0.3–20 ha; *ca* 1300 m elevación) y también en la reserva de 226 ha de la Estación Las Cruces (*ca* 900–1280 m elevación). De enero 1994 hasta medio-marzo 1999, nosotros obtuvimos 1069 capturas de 21 especies de colibríes durante 49,900 horas-red. La riqueza de especies, los índices de diversidad, y las tasas de captura aumentaron asintoticamente con el aumento del tamaño del fragmento, tal como esperábamos. Capturamos 16 especies de colibríes en el fragmento mas grande (20 ha) y en la reserva (226 ha). Colibríes que no utilizan hábitats boscosos no se encontraron con mayor frecuencia en los fragmentos que en la reserva, y todos los fragmentos presentaron una mezcla de especies de colibríes del interior del bosque y del dosel; los fragmentos también tenían un grupo diverso de plantas que son polinizadas por colibríes. *Phaethornis guy* era común en todos los sitios y visitó >13 especies de plantas en los fragmentos durante la época seca de 1998 (basado en el análisis de polen colectado de las plumas

de la cabeza de las aves). En contraposición, encontramos *Eutoxeres aquila* solamente en los sitios mas grandes (10, 20, y 226 ha) y llevaba solamente polen de una especie de planta durante la época seca de 1998. *Lampornis castaneoventris*, una especie de colibrí de elevaciones altas, era mucho más común en los fragmentos que en la reserva, mientras tanto, tres especies que normalmente se encuentran en elevaciones bajas eran escasas en los fragmentos y comunes en la reserva. Estos patrones de distribución podrían ser influenciados por diferencias en climas locales, porque los fragmentos están a mayor elevación, son más nubosos y reciben un promedio de lluvia más alto por año que la reserva. Nuestros datos muestran que hay variación en el numero de especies de polen llevada por especies de colibríes, y esto podría afectar flujo genético en plantas polinizadas por colibríes. Aunque nuestros resultados coinciden con estudios previos que reportan que las especies de colibríes podrían ser menos afectadas por deforestación que las especies de aves insectívoras como los hormigueros, desde el punto de vista de la genética y demografía de plantas polinizadas por colibríes, lo que es importante es que los colibríes apropiados puedan mover propágulos entre sub-poblaciones de plantas en paisajes fragmentadas. Nosotros concluimos que la biodiversidad de fragmentos de bosque tropical tan pequeños como 10–20 ha es lo suficientemente alta que merecen ser preservadas a largo plazo, especialmente si estos fragmentos están cerca de bosques más extensos.

BECAUSE LARGE AREAS OF INTACT FOREST are being cleared and subdivided worldwide, conservation biologists have turned their attention to forest fragmentation and the potential utility of small, local forest fragments and nature preserves as reservoirs of biodiversity. In the tropics, forest fragments have been the subject of many studies aimed at preserving threatened species and identifying areas of potential conservation importance (refs. in Schelhas & Greenberg 1996; Laurance & Bierregaard 1997), but the richness of tropical biotas and the limited economic resources of developing countries make accurate assessments of biodiversity for prioritizing areas for conservation a daunting task.

In addition to the need for accurate assessment of biodiversity, the alteration and fragmentation of forests can disrupt coevolved ecosystem processes among forest organisms. In particular, because many animals are important dispersers of pollen and seeds (Fleming *et al.* 1987, Wheelwright 1988, Bawa 1990, Loiselle & Blake 1993, Levey *et al.* 1994, Tamboia *et al.* 1996), our understanding and conservation of dispersal mechanisms for plant propagules is important for maintaining gene flow and other genetic processes in many plants (Boshier *et al.* 1995, Gibson & Wheelwright 1995, Nason & Hamrick 1997, Nason *et al.* 1997, Aldrich & Hamrick 1998). Obviously, as landscapes continue to be altered, the mutualistic interactions between plants and their propagule dispersers can be affected, and these effects may manifest themselves genetically (Murawski *et al.* 1994) or demographically (Lande 1988). Although many tropical organisms respond to disturbances that are not human-induced, and in fact have evolved this ability (Feinsinger *et al.* 1987, 1988; Levey 1988), the level and rate of change caused by human-induced processes are usually greater than "natural" (*e.g.*,

treefall) disturbances. The dynamics of plant–animal interactions due to natural disturbances may differ substantially from those dynamics due to human-induced habitat alteration (Feinsinger *et al.* 1987), and therefore, predictions from one type of disturbance should not be deduced by studies of the other.

Thus, in areas of human-altered landscapes, the successful management and preservation of biodiversity and ecological processes depend on understanding how biological processes in remnants of forests are similar to and different from those of nearby, relatively unaltered areas. To this end, researchers have begun to evaluate the extent to which landscapes that have been converted to mixtures of crops, pasture, and fragmented forest can sustain native populations of forest-dwelling species over the long term (Guindon 1996, Greenberg *et al.* 1997, Daily in press). The preferred scenario would be to protect areas of biological importance from any disturbance; but in many parts of the world, the most feasible short-term goal may be to protect areas that have already suffered some alteration.

Costa Rica is renowned for its biological diversity and its extensive system of national parks (Gamez & Ugalde 1988, Boza 1993); however, in the past 50 years the country has lost >50 percent of its primary forest, which originally covered *ca* 85 percent of the landscape (Stiles 1985, Lutz *et al.* 1993). The inland county of Coto Brus in southwestern Costa Rica is typical of many areas in which mountainous terrain and inadequate roads delayed extensive settlement and deforestation until the mid-1900s. Now, with the exception of several high-elevation preserves, most of Coto Brus has been converted to a mosaic of medium intensity agriculture—pasture, coffee plantations, and small

plots of banana, cassava, beans, corn, sugarcane, and other crops—interspersed with small towns and remnant patches of forest. Scattered trees remain throughout much of the region, but isolated trees will eventually die off and valuable timber in remaining patches is harvested gradually, even in very steep terrain. In only 40 to 50 years, most large tracts of primary forest in the region have been replaced by scattered patches of secondary growth that sometimes contain elements of primary forest. These small patches of forest make up *ca* 20–25 percent of the land area in the county of Coto Brus (based on recent aerial photographs and satellite imagery; L. D. Gómez, pers. comm.; Daily *et al.* in press).

Within the Coto Brus area, the Organization for Tropical Studies maintains the Las Cruces Biological Station (LCBS), which owns 226 ha of protected forest (Las Cruces Biological Station Forest Reserve, LCBSFR) that includes *ca* 210 ha of primary forest and the adjacent Wilson Botanical Garden (10 ha of tropical plant collections). Although this forest is small and somewhat isolated, LCBSFR provides a focus for long-term biological studies and local reforestation efforts. The forest of LCBSFR and surrounding areas have been the subject of several studies on how habitat fragmentation impacts local biodiversity. These studies have included rapid assessments of diversity in beetles, moths, butterflies, and birds (Daily & Ehrlich 1995, 1996), mark–release–recapture studies of understory forest birds (Borgella 1995; R. Borgella & T. Gavin, pers. comm.), characterization of genetic diversity and gene flow in trees (Aldrich & Hamrick 1998, Aldrich *et al.* 1998) and birds (Brown 2000), ecology of herps (Schlaepfer 1998), and studies of natural succession in pastures (B. L. Haines & C. J. Peterson, pers. comm.).

More than 25 species of hummingbirds have been observed at LCBSFR, most of which are residents with no obvious altitudinal migrations (LCBS Bird Checklist). Here we report on the hummingbirds captured as part of a six-year mist-netting study of understory forest birds in LCBSFR and several nearby forest fragments. Hummingbirds are known as edge-tolerant species (Stiles 1985) and are expected to be less adversely affected by habitat fragmentation than many other birds, such as obligate army ant followers (Stouffer & Bierregaard 1995a, b). Nonetheless, many hummingbird species require vertically structured vegetation for foraging, nesting, and predator avoidance, and they need flowering plants for year-round sources of nectar. The objectives of this study of small forest fragments were to quantify: (1) hummingbird species richness and species diversity; (2) the relative abundances of hummingbird species; and (3) pollen loads on hummingbirds at these sites during the 1998 dry season.

METHODS

STUDY SITES.—LCBS (8°47′N, 82°57′W; *ca* 900–1280 m elev.) is located near the Panama border, 6.5 km south of the town of San Vito, on the slopes of a mountain ridge known as Fila Cruces (or Fila Zapote). The landscape surrounding LCBS was converted to agricultural use within the past 30–40 years and is now dominated by degraded cattle pasture, small coffee plantations (*ca* 0.5–5.0 ha; sun-grown coffee) mixed with banana and family garden plots, and small patches of forest. Forests larger than *ca* 10 ha are scarce at lower elevations in the Coto Brus valley, limiting the chance for wildlife to migrate seasonally to lower elevations.

The five study fragments, which were situated slightly higher in elevation and *ca* 0.4–1.3 km west of LCBSFR, were often shrouded in cloud mist by late morning, whereas LCBSFR is much drier. In fact, the central portion of LCBSFR receives *ca* 1000 mm less annual precipitation than the fragments, including Fragment 1, which was 400 m away from the LCBSFR boundary (Table 1; Fig. 1; R. Borgella, pers. comm.). Thus, there is a rather sharp climatic shift near the LCBSFR boundary, which is evident from the greater abundance of climbing aroids and epiphytes such as bromeliads, ericads, and bryophytes in the fragments when compared to LCBSFR (R. Borgella, pers. obs.). It is tempting to consider LCBSFR as a "control" for comparisons to the much smaller fragments, but differences in local climate and certain elements of the vegetation make this comparison a qualified one.

Mean annual temperature at LCBS is 21.7°C and mean annual precipitation is 3600 mm, with a distinct dry season from January to March (LCBS weather data averaged over 30 years). The LCBSFR is considered to be pre-montane (*i.e.*, below the frost line) wet forest, whereas the forests of the study fragments are pre-montane cloud forest (R. Borgella, pers. obs.; L. D. Gómez & B. Boyle, pers. comm.). According to Holdridge's (1967) life-zone classification system, climatic conditions at LCBSFR are transitional between pre-montane wet forest and pre-montane rain forest, which are distinguished by having less than or greater than *ca* 4000 mm of annual precipitation, respectively. The

TABLE 1. *Characteristics of forest fragments and the Las Cruces Biological Station Forest Reserve (LCBSFR). Sites are listed from east to west. Rainfall data are from Borgella (pers. obs.).*

	LCBSFR	Fragment 1	Fragment 2	Fragment 3	Fragment 4	Fragment 5
Area (ha)	ca 226	ca 10	ca 0.9	ca 0.9	ca 0.3	ca 20
Elevation (m)	ca 900–1283	ca 1273–1309	ca 1323	ca 1328	ca 1318	ca 1300–1327
Annual rainfall (mm)	1996: 3199 1997: 2009 1998: 3299	1996: 4311 1997: 2866 1998: 4433	1996: —[a] 1997: 3092	1996: —	—	1996: 4462 1997: 3261 1998: 4793
Distance from LCBSFR boundary (km)	—	ca 0.40	ca 0.83	ca 0.89	ca 1.17	ca 1.33
Other site characteristics	steep, with river and streams; no cattle use; includes ca 211 ha of primary forest	steep, with streams; low–medium cattle ingress; includes primary forest with frequent treefalls	less steep, no stream; medium–high cattle ingress; includes canopy trees but selectively logged in 1996	fairly flat, no stream; next to seasonal marsh; low–medium cattle ingress; disturbed primary and mid-age secondary forest	fairly flat, no stream; next to seasonal marsh; high cattle ingress; advanced secondary growth	steep, with streams; low cattle ingress; includes primary forest with frequent treefalls
Site ID in Daily and Ehrlich (1995, 1996)[b]	Las Cruces	Vaca Vaca	Lower Gamboa Swamp	Upper Gamboa Swamp	—	Ridge Road Ravine

[a] Data incomplete or not available.
[b] Site descriptions in Daily and Ehrlich (1995, 1996) differ somewhat from ours due to revised estimates of fragment size and elevation (elevations on government topographic maps are 100 m too high; L. D. Gomez, pers. comm.; R. Borgella, pers. obs.).
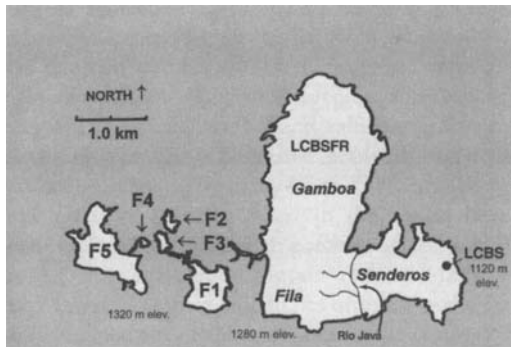
FIGURE 1.   Map of study area near the Las Cruces Biological Station (LCBS), Costa Rica (modified from Borgella [1995], based on a 1992 aerial photograph). Numbers (F1–F5) correspond to fragments and LCBSFR refers to the Las Cruces Biological Station Forest Reserve; sites are described in Table 1. The habitat surrounding the fragments is primarily active cattle pasture.

term "cloud forest" is typically used to describe the vegetation of pre-montane or montane rain forests that are exposed to daily periods of cloud mist.

The five fragments used in this study ranged in size from 0.3 to 20 ha, and were *ca* 97–400 m apart and surrounded by cattle pasture (Table 1; Fig. 1). All included canopy trees, with varying degrees of disturbance due to logging and intermittent cattle grazing along fragment edges, and several were linked by narrow corridors of scattered, remnant trees (Table 1; Fig. 1; Borgella 1995). For sampling purposes, we divided the LCBSFR into three adjacent sections: the Senderos (Spanish for "trails") area of mature forest closest to the botanical garden, the Fila (Spanish for "ridge") area of primary forest closest to the fragments and highest in elevation, and the Gamboa area, on the west side of the valley flanking the Rio Java (Fig. 1).

It is important to note that the topography of the study area is varied. Elevation at the Las Cruces Biological Station (LCBS), located at the extreme eastern end of LCBSFR (Fig. 1), is *ca* 1120 m. Heading due west from LCBS itself toward the Rio Java, the land generally slopes downward, reaching an elevation of *ca* 930 m at the Rio Java (Fig. 1). From the western bank of the Rio Java toward the western extreme of LCBSFR, elevation increases to 1280 m at the western edge of the LCBSFR (Fila area; Fig. 1). Similarly, from the northern end of the Gamboa area of LCBSFR (*ca* 950 m elev.), elevation increases as one approaches the Fila area. The five fragments that comprised the rest of the study sites were located due west of the Fila area

of LCBSFR, on a portion of the Fila Cruces ridg that has a much smaller elevational range thaɪ what occurs within the boundaries of LCBSFR Generally, elevations within each of these fragment range from 1300 to 1340 m (Fig. 1; Borgell. 1995). All of the LCBSFR area and the two large fragments, Fragments 1 and 5, have various stream, and associated ravines throughout. Treefall gaps blowdowns, and other natural disturbances occuɪ at all of our sites (R. Borgella, pers. obs.); thus, thɛ vegetation–air interface comes down to ground level at these stream edges, forest edges, and treefall gaps within each site.

MIST-NETTING PROCEDURES.—We sampled understory birds using standard mist nets (*ca* 2 × 9 m, four-shelf, 32 mm) deployed along grid systems within the fragments and LCBSFR areas (Borgella 1995). Sampling of birds was carried out at regular intervals from January 1994 through mid-March 1999 (Appendix I). The total sampling effort (49,900 net hours over 460 days, where each net hour represents one mist-net sampling for one hour) was partitioned so that all six sites (each fragment plus LCBSFR) were included during each round of sampling, thereby controlling for possible variation due to time of year. We established net lanes with minimal clearing of the vegetation and without regard to steep terrain, placing parallel lanes *ca* 30–60 m apart; in the Senderos area of LCBSFR, nets were placed both along existing trails and in areas away from the trails. To minimize possible biases associated with specific net locations, we occasionally relocated nets along these lanes and trails. At each sampling station, we used 20 nets/d, sampling at each sampling station for two (usually consecutive) days during each round of sampling. We established one station in each of the three small fragments and the Fila area, several stations in other areas of LCBSFR, four stations in Fragment 1, and four stations (later increased to eight) in Fragment 5 (Appendix I). Thus, the two large fragments and the LCBSFR were sampled during more days than the smaller fragments, but the cumulative number of net hours per unit area was greatest in the three small fragments and lowest in LCBSFR (Appendix I). At each station, we attempted to sample all habitat types (as well as changes caused by treefalls and other events) that occurred within a given sampling area (each station).

On each sampling day, mist nets were opened by 0600 h, checked for captured birds at 30-min intervals, and closed at *ca* 1100 h. Captured hum-

mingbirds were identified to species and sex (if adults), weighed, offered sugar water, and released immediately without marking them. Because hummingbirds were not marked, it was impossible to know how often the same individual was recaptured. On any given morning, however, differences in the species, sex, and weight of the few hummingbirds that were caught indicated that we rarely captured the same bird twice on the same day.

To investigate plant–pollinator interactions in the fragments during the dry season, we sampled pollen from the heads of hummingbirds captured from January to March 1998. Clear Scotch® tape was dabbed on the bird's upper mandible, forehead, lower mandible, and chin feathers (as in Feinsinger 1992), and then placed on a glass microscope slide for later analyses of pollen morphospecies (see below). To obtain larger sample sizes, we also collected pollen from birds that were captured in several additional small fragments (<1 ha) nearby as part of another study. Bill lengths of a subset of captured birds were measured to the nearest millimeter using calipers. For species with decurved bills, we also used a ruler to measure a few bills along the curve to calculate a correction factor; thus all reported bill lengths include curvature.

FLOWERING PLANTS.—From January to May 1998, we made weekly observations of flowering plants that were known or presumed to be visited by hummingbirds. These were not exhaustive surveys of the study areas, but they provided general information about common understory species and higher-strata plants that dropped flowers onto the forest floor. To estimate the bill lengths that legitimate pollinators would need to obtain nectar, we measured *ca* 5 fresh flowers/species to determine the length of the enclosed corolla, including corolla curvature, if any. We also collected fresh pollen, which was mounted on microscope slides using clear Scotch® tape. These collections were used to develop criteria for pollen identification (by AAS), and characteristics of pollen from different plant families were compared with those of Panamanian species illustrated in Roubik and Moreno (1991). In most cases, pollen grains preserved on tape and viewed with a compound microscope could not be identified to species; so they were assigned to distinct morphospecies based on their size, shape, pores, presence of tetrads, and any distinctive exine sculpturing. These assignments were conservative, so the number of pollen species reported is likely to be an underestimate of the actual number of plant species visited by hummingbirds. A few genera had very distinctive pollen (*e.g., Macleania, Razisea,* and *Aphelandra*), in which case pollen samples from hummingbirds could be identified to genus. Pollen from *Malvaviscus arboreus* was easily recognized by its large size and spiny exine.

ANALYTICAL PROCEDURES.—We used our capture data to estimate the relative abundance of each species, expressed as the number of captures per 1000 net hours. We calculated Shannon's diversity index (Shannon & Weaver 1949, Magurran 1988) using $H' = -\Sigma \, n_i (ln \, n_i)$, where n_i is the proportion of the *i*th species in the total sample. We used the general linear models procedure in the SAS statistical package (SAS 1996) to test for significant coefficients in least squares regressions between H' and the log(area) of each site. Because every sampling method can have sampling biases, we examined the possibility that our enumeration of total number of hummingbird species at each site was biased by comparing our actual counts of captured species at each site to a nonparametric bootstrapped estimate of species richness at each site, as well as across all sites. We calculated each species richness estimate using: $S^* = S_{obs} + \Sigma_{k=1}^{obs} (1 - P_k)^m$, where S^* is the estimated richness, S_{obs} is observed number of species in original data, P_k is proportion of the samples that contain species k, and m is the total number of samples (Smith & van Belle 1984; R. K. Colwell pers. comm.). We computed each site's richness estimate by running the bootstrap with samples added in random order and randomized 500 times. One could also use a jackknife approach to generate an estimate of species richness; however, bootstrap procedures perform better than jackknife estimates when there is a large number of quadrats (samples; Smith & van Belle 1984), as in our data set.

RESULTS

HUMMINGBIRD SPECIES RICHNESS AND DIVERSITY.— We had a total of 1069 hummingbird captures representing 21 species (Appendix II). Every species in the final tally, except one (*Florisuga mellivora*), was caught at least once by 1996. A total of 18 species was captured at all of the fragments combined as compared to 16 at LCBSFR (Appendix II). At LCBSFR, our sampling effort per unit area was lower than at the other sites (Appendix I); so total species richness was more likely to be underestimated. The number of species detected per site increased asymptotically with forest area, from a low
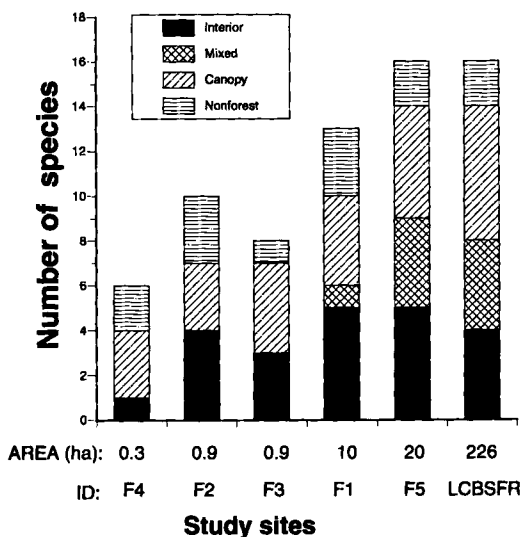
FIGURE 2. Number of hummingbird species captured at each of the five fragments and LCBSFR during the 1994–1999 period. Species are grouped by habitat preference (Stiles 1985).

of 6 species at Fragment 4 (0.3 ha), the smallest site, to highs of 16 species at Fragment 5 (20 ha) and 16 species at LCBSFR (226 ha; Fig. 2; Table 2). At two other small fragments, each 0.9 ha, 10 and 8 species were captured, respectively. The correlation between species richness and log(area) was statistically significant ($P < 0.006$, $R^2 = 0.87$; Table 2; considering just the five fragments, $P < 0.006$, $R^2 = 0.95$). Species richness from the three smallest sites combined (12 spp.) was 92 percent of the species richness of the 10-ha fragment (Fragment 1) and 75 percent of the species richness of the 20-ha fragment (Fragment 5). Shannon's diversity indices ranged from 1.39, at the smallest fragment, to 2.25 at LCBSFR (Table 2), and like species richness, increased significantly with log(area) (Table 2).

Four hummingbird species (*Elvira cupreiceps,*

Chlorostilbon canivetii, Doryfera ludoviciae, and *Colibri thalassinus*) were unique to the fragments and three species (*F. mellivora, Phaeochroa cuvierii,* and *Heliothryx barroti*) were unique to LCBSFR, but there were very few captures (≤ 3) of each of these species (Appendix II). *Lampornis castaneoventris* was captured at fragment sites and LCBSFR, but of 200 captures, only 4 were at LCBSFR (Appendix II). Five additional hummingbird species recorded as present in the 1998 LCBS Checklist were not detected, but these species are considered rare or accidental occurrences at this site (LCBS Bird Checklist).

Our bootstrap estimate for total species richness across sites was 23.6 hummingbird species, which was similar to our enumerated tally of 21 species captured. Bootstrap estimates of species richness at each study fragment were also similar to observed richness (Table 2), suggesting that our sampling effort was sufficient to detect nearly all resident understory species at each of our sites.

CAPTURE RATES AND SEX RATIOS.—Overall capture rates generally increased with area (*ca* 14 captures/ 1000 net hours at the three smallest sites, *ca* 20/ 1000 net hours at the two larger fragments, and *ca* 30/1000 net hours at LCBSFR [Fig. 3]). Stiles (1985) had noted that all of the hummingbird species we recorded can use forest edges, and he described their habitat preferences as non-forest, canopy, interior, or a mixture of canopy and interior habitats (Appendix II). These four groups of species were represented at all of the study sites with the exception of those classified as "mixed," which were not detected at the smallest three sites (Fig. 2; Appendix II). We expected that non-forest species would be most common at the three smallest fragments, but this was not the case (Fig. 3). Instead, hummingbirds captured at Fragments 2, 3, and 4 were mostly canopy and interior species (Fig. 3; Appendix II). In the 10-ha (Fragment 1) and 20-ha sites (Fragment 5), the number of canopy

TABLE 2. *Hummingbird species richness and Shannon's diversity (H') at the study sites, listed from smallest to largest. Values in brackets are bootstrapped estimates of species richness (see Methods for explanation of bootstrap methods and diversity estimates). P values refer to significance of correlations between log(area) and number of species and Shannon's H'; R^2 values are in parentheses.*

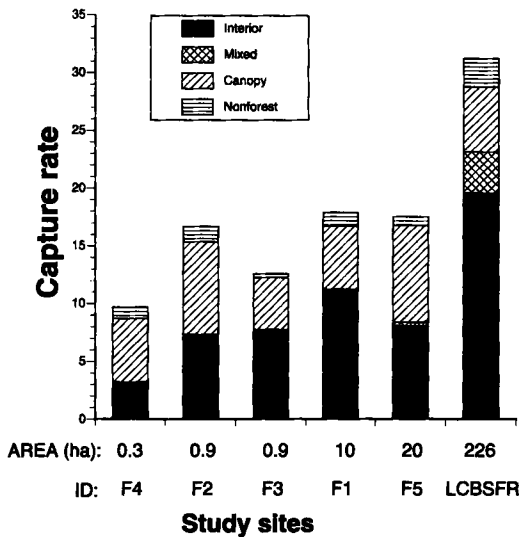|	Fragment 4	Fragment 2	Fragment 3	Fragment 1	Fragment 5	LCBSFR	P
Area (ha)	0.3	0.9	0.9	10	20	226	—[a]
Number of species	6	10	8	13	16	16	
	[6.9]	[11.6]	[9.1]	[14.5]	[17.9]	[15.9]	0.006 (0.87)
Shannon's H'	1.386	1.737	1.701	1.877	1.867	2.251	0.003 (0.91)

[a] Not calculated.

FIGURE 3.   Relative hummingbird abundance in each of the five fragments and LCBSFR during the 1994–1999 period. Capture rates are number of individuals captured per 1000 net hours. Species are grouped by habitat preference (Stiles 1985).

species and their capture rates were similar to what was found at our smallest sites (Figs. 2 and 3; Appendix II); but the avifauna at these two larger fragments also included more interior species as well as the addition of species in the mixed category (Figs. 2 and 3; Appendix II). Overall, canopy species were more predominant (*i.e.,* in absolute numbers of captures and percentage of all captures) at the fragments when compared to LCBSFR, while interior and mixed interior/canopy species were captured more frequently at LCBSFR than at the other sites (Fig. 3; Appendix II). In fact, at LCBSFR, the capture rate for interior species was about the same as the combined capture rates for all species types (interior, mixed, canopy, and nonforest) at each of the other sites.

The relative abundance of *Eutoxeres aquila*, an interior forest species, generally increased with forest size, as expected, although *Eutoxeres* was uncommon in the fragments (Table 3). In contrast, two canopy species, *L. castaneoventris* and *Heliodoxa jacula*, were unexpectedly common in the fragments and rare at LCBSFR (Table 3). It is also noteworthy that these two canopy species reached their greatest abundance in Fragment 4 (0.3 ha) and Fragment 5 (20 ha; Table 3), both of which occurred at higher, wetter elevations and farther west along Fila Cruces than any of the other study sites (Fig. 1). Three species that typically occur at

elevations <1200 m, *E. aquila, Amazilia decora,* and *Thalurania colombica,* were much more common at LCBSFR than in the fragments (Table 3; Appendix II).

For five common species, 61–77 percent of the birds captured were females, while sex ratio differences in the *Campylopterus hemileucurus* that we captured were not significantly different from 1:1 (Table 3). Sex ratios were generally consistent across seasons and sites (data not shown).

POLLEN LOADS AND NECTAR SOURCES.—Most of the plant species we observed during weekly observations from January to May 1998 occurred in both LCBSFR and the fragments, although species in the genera *Satyria, Razisea,* and *Pitcairnia* were not seen in the LCBSFR. We found 35 species in flower during this period (40% with curved corollas), which included most of the annual dry season and the transition to the longer wet season in mid-April. Although intermittent cattle grazing probably reduces the abundance of understory plants in some areas of the fragments, the frequency of understory plants with hummingbird-pollinated flowers appeared to be higher in the fragments than in LCBSFR, especially during the wet season (A. Snow, pers. obs.).

One of the most common and longest-blooming species at all sites was the understory herb *Heliconia tortuosa,* which is an important source of nectar for *Phaethornis guy* and *C. hemileucurus* (Stiles & Skutch 1989; R. Borgella, A. Snow, & T. Gavin, pers. obs.). *Calathea, Besleria,* and *Columnea* spp. also bloomed throughout the study period. *Aphelandra, Malvaviscus,* and *Macleania* spp. flowered mainly during the dry season, while *Renealmia, Palicourea, Satyria,* and bromeliad species began flowering in the early wet season. These and other species listed in Appendix III represent a continuum of flower types, from large flowers (enclosed corollas of 40 to 50 mm), which often have curved corollas, to smaller flowers (enclosed corollas <20 mm), such as *Palicourea* spp. (a shrub or small tree) and the canopy tree *Symphonia globulifera* (Appendix III). We also observed hummingbirds visiting flowering species in nearby pastures and farmland, including flowers of living fence post trees (*Erythrina cochleata,* and *Spathodea campanulata*), banana and other *Musa* cultivars, introduced *Hibiscus rosasinensis,* and isolated individuals of *S. globulifera.*

Phaethornis guy, C. hemileucurus, and *E. aquila,* the three interior hummingbird species, and *L. castaneoventris,* a canopy species, carried pollen more

TABLE 3.   Capture data for the seven most common species captured in the five fragments and LCBSFR. Sites refer to fragment numbers and LCBSFR, listed from smallest to largest (areas in Table 1). Preferred habitat is from Stiles (1985); elevational range is from Stiles and Skutch (1989). Complete species names are Phaethornis guy (PHGU), Campylopterus hemileucurus (CAHE), Eutoxeres aquila (EUAQ), Lampornis castaneoventris (LACA), Heliodoxa jacula (HEJA), Elvira chionura (ELCH), and Amazilia tzacatl (AMTZ).

Species:	PHGU	CAHE	EUAQ	LACA	HEJA	ELCH	AMTZ
Preferred habitat	Interior	Interior	Interior	Canopy	Canopy	Canopy	Non-forest
Proportion female[a]	0.69	0.54	No data	0.61	0.71	0.64	0.77
	$P \ll 0.001$	NS		$P = 0.004$	$P \ll 0.001$	$P = 0.010$	$P = 0.011$
(N)	(314)	(87)		(177)	(166)	(87)	(22)
Elevational range (m)	500–2000	1500–2400	300–1200	>1000	700–2000	1000–1700	0–1850
Capture rate (number captured per 1000 net hrs) Site:							
F4	3.2	0.0	0.0	5.2	4.2	0	0.6
F2	5.7	1.0	0.3	6.3	1.7	1.7	0.7
F3	5.5	1.9	0.0	3.0	2.3	1.3	0.3
F1	8.0	1.8	0.9	3.0	3.4	2.2	1.0
F5	5.6	1.5	0.6	6.1	4.6	2.2	0.7
LCBSFR	9.7	4.1	3.7	0.6	2.5	2.5	1.1
Percent of all hummingbird captures at each site comprised of this species Site:							
F4	23	0	0	37	30	0	5
F2	38	5	2	35	9	9	4
F3	37	13	0	20	15	9	2
F1	38	8	4	14	16	10	5
F5	25	7	3	27	21	10	3
LCBSFR	30	13	11	2	8	8	3

[a] Chi-square tests were used to compare proportion of birds that were female with expected proportion of 0.50 (NS indicates not significant); N refers to number of adult birds that could be sexed with confidence (male and female EUAQ could not be distinguished). Percent captures at each site do not sum to 100 percent because this table summarizes only the data of the seven most commonly captured species.

often than the other three species examined (Table 4). Pollen was collected from >90 percent of the captures of each of these interior species and 78 percent of the captures of *L. castaneoventris*. We found pollen on only 56, 11, and 0 percent of *Amazilia tzactl, H. jacula*, and *Elvira chionura*, respectively. These differences could have been due to the difficulty of obtaining pollen from smaller bills and/or the possibility that *E. chionura* and *H. jacula* often visited flowers without contacting the anthers.

Our largest and most consistent pollen collections came from *P. guy*, an interior species that traplines at widely spaced plants with large flowers (Stiles 1975, Stiles & Skutch 1989). Based on pollen morphospecies, *P. guy* visited at least 13 species of flowering plants, including species in the genera *Heliconia, Aphelandra, Razisea*, and *Malvaviscus*. Individual birds often carried pollen from as many as 4 to 6 species ($\bar{x}$ = 2.8/bird, N = 32, SD = 1.4). In contrast, the other 2 interior species were more specialized. *Campylopterus hemileucurus* carried 4 pollen morphospecies, but >90 percent of the pollen on these birds appeared to be from *Heliconia* (N = 11 birds). *Eutoxeres aquila* (N = 5 birds) carried only 1 type of *Heliconia*-like pollen from an unidentified species that was different from that found on *C. hemileucurus* or *P. guy. Lampornis castaneoventris* carried only 3 types of pollen, 1 of which was from the understory shrub *Razisea* and 1 from a canopy epiphyte in the Ericaceae, probably *Macleania* (both males and females foraged at these two species). *Amazilia tzactl* carried a total of 9 pollen morphospecies, also including *Razisea* and *Macleania* (N = 9 birds). Only 3 *H. jacula* had pollen on them, all of the same morphospecies, even though the birds were caught in two different fragments.

DISCUSSION

This study demonstrated that Fragments 1 and 5, the two largest sites near LCBSFR, were used by at least as many hummingbird species (17) as the 226-ha LCBSFR, in which 16 species were detected. Species diversity indices and capture rates of hummingbirds generally were lower in the fragments than at LCBSFR, but differences between the two largest fragments and LCBSFR were relatively small. Therefore, fragments as small as 10 to 20 ha appear to represent valuable habitat for supporting local hummingbird populations in this agriculturally dominated landscape. Smaller fragments of 0.3 to 0.9 ha were less diverse, but none-

theless, these fragments were used by 6 to 10 hummingbird species. A key issue, however, is whether small forest fragments actually sustain viable local populations, function as demographic "sinks" in which birds attempt to nest but are unsuccessful (*sensu* Pulliam 1988), or serve only as foraging (but not breeding) sites. This question requires long-term mark–release–recapture and breeding data, but we speculate that hummingbirds move to and from forest fragments relatively easily, using them as foraging (if not breeding) areas as well. Within the fragments, we have observed lekking behavior of *C. hemileucurus* and *P. guy*, as well as nests of these two species and a nest of an *Elvira* species, probably *E. cupreiceps*, but the breeding status within our study area for the majority of these hummingbirds is unknown.

In a related study of hummingbird diversity in small patches of forest, Stouffer and Bierregaard (1995a) documented effects of localized deforestation at several 1 and 10-ha moist-forest fragments in Brazil. Unlike our landscape matrix of pastures and mixed agriculture, the cleared area around their study fragments was often <100 m wide and adjacent to continuous primary forest. Also, cleared areas were allowed to regenerate immediately after cutting and became reforested with secondary growth species within five to ten years. At all periods of the study, however, hummingbirds showed little response to fragment size (intact forest vs. 1- or 10-ha patches). Three understory species were captured prior to fragmentation and five additional species were captured after logging occurred. The latter five were canopy species that had been present prior to logging but were not caught in earlier sampling. The three understory species remained common after fragmentation, and one, *Phaethornis superciliosus*, increased in abundance after clearing occurred. Because the vegetation between some of the fragments in Stouffer and Bierregaard's study (1995a) was allowed to regenerate, the Brazil fragments are different from our forest fragments, which have been separated continuously for several decades. Nevertheless, their results are consistent with others suggesting that common hummingbird species are able to persist in patchy forest and secondary growth (Stiles 1975; Linhart *et al.* 1987, Feinsinger *et al.* 1988).

We documented a linear increase in species richness and diversity as a function of log(area), a finding that was reported also for other avian species at these sites (Borgella 1995, Daily *et al.* in press). *Eutoxeres aquila* and *Phaethornis longuemareus*, species characterized as using interior forest

TABLE 4. *Characteristics of the seven most common hummingbird species captured in the five fragments and LCBSFR. Bill length is the average of three to ten birds per species. Elsewhere, N = number of birds sampled. Complete hummingbird species names are listed in Table 3.*

	Hummingbird species						
	PHGU (interior)	CAHE (interior)	EUAQ (interior)	LACA (canopy)	HEJA (canopy)	ELCH (canopy)	AMTZ (non-forest)
Weight (g) $\bar{x}$ (male, female)	5.8, 5.7	11.5, 9.2	9.4	5.6, 4.8	8.9, 7.7	3.2, 3.0	5.0, 4.9
SD	0.3, 0.5	0.7, 0.6	0.7	0.5, 0.4	0.5, 0.5	0.4, 0.3	0.5, 0.3
N	36, 95	20, 25	24	37, 40	20, 64	16, 27	3, 11
Bill type	Curved	Curved	Very curved	Straight	Straight	Straight	Straight
Bill length (mm)	40	33	35	21	21	14	22
(SD, N)	(1.1, 11)	(1.6, 10)	(1.0, 3)	(0.8, 7)	(0.9, 9)	(0.4, 4)	(1.0, 10)
Proportion of birds with pollen	0.94	0.92	1.00	0.78	0.11	0.00	0.56
(N)	(33)	(12)	(5)	(23)	(28)	(11)	(9)
Number of pollen morphospecies per hummingbird species	13	4	1	3	1	No pollen	8
(N; range)	(31; 1–6)	(11; 1–2)	(5; 1)	(18; 1–2)	(3, 1)		(5, 1–4)
Number of pollen morphospecies per individual [$\bar{x}$; SD]	[2.84; 1.44]	[1.36; 0.50]	[1.0; 0.0]	[1.39; 0.49]	[1.0; 0.0]		[3.0; 1.0]

habitat (Stiles 1985), were found exclusively or primarily at our larger sites (LBCSFR, Fragment 1, and Fragment 5; Table 3; Appendix II). These data suggest there may be a minimum patch size that is required for these hummingbird species, or for the plants at which these hummingbirds forage. For example, we collected only one type of pollen from *E. aquila* and *H. jacula* during the 1998 dry season, which suggests that they may be specialized feeders during the dry season. The bill morphology (strongly decurved) of *E. aquila* dictates that it would be a legitimate pollinator on a select group of plants with appropriately shaped corollas. Gene flow and population structure of plant species that depend on a pollinator with a suitably sized- or shaped-bill may be affected if such a pollinator is not available. In contrast, species such as *H. jacula*, *P. guy*, and *E. chionura* were captured at similar rates across most of the sites, regardless of size (Table 3; Appendix II). These ubiquitous species have straight or curved bills that range from 14 to 40 mm long and they probably serve an important role in dispersing pollen for a variety of species (*e.g.*, ≥13 pollen morphospecies moved by *P. guy* at our sites).

Our data also suggest that species occurrences were influenced by factors other than the size of the forest fragment. Indeed, it is difficult to ascertain whether area is the most important determinant of species' abundances because our six sites also differed in elevation, climate, topography, presence of streams, and level of disturbance (Table 1). Several species' occurrences may be strongly influenced by elevation and rather dramatic gradients in local climate (Table 1; R. Borgella, pers. obs.). For example, *L. castaneoventris* typically occurs at elevations of >1000 m (Stiles & Skutch 1989), and was more common in all of the fragments (*ca* 1300 elev.) than in the much larger LCBSFR (mostly ≤1280 m; Table 3). Of the 200 captures of *L. castaneoventris*, all but 4 were in the fragments; the 4 captures that occurred in LCBSFR were all from the Fila area, the portion of the LCBSFR with the highest elevation. *Florisuga mellivora* typically occurs at elevations of <1000 m, and the 2 captures of this species were in the lower-elevation Senderos portion of LCBSFR. Hummingbird capture data for the 1997–1999 interval from four other forest fragments that are not presented here support this pattern of distribution: *L. castaneoventris* was not captured at the single pre-montane rain forest (lower elevation) site, but was captured at the three pre-montane wet forest (higher elevation) sites. Likewise, data from the 1994–1999 interval suggest

that the distribution of *A. decora* and *T. colombica* were primarily centered at elevations below *ca* 1200 m; they were common at LCBSFR but rare in the fragments, regardless of fragment area. Because these two species were not captured at another large (*ca* 5000 ha) pre-montane wet forest (high elevation) site (*ca* 7 km west of LCBS; R. Borgella & T. Gavin, pers. comm.), it is probable that the distribution of *A. decora* and *T. colombica* reflect their climatic/habitat affinities rather than a lack of tolerance for smaller forest patches.

In addition, several non-hummingbird species are largely restricted to distinct life zones along this same climatic gradient at our sites (Borgella 1995; R. Borgella & T. Gavin, pers. obs.). The following species pairs occurred predominantly in either the fragments (pre-montane rain forest life zone) or LCBSFR (pre-montane wet), respectively: *Platyrinchus mystaceus* and *P. coronatus*; *Mionectes olivaceus* and *M. oleagineus*; and *Henicorhina leucophrys* and *H. leucosticta*. These distributions adhere to distribution patterns of Costa Rican birds described by Stiles (1985) as species found primarily in either "Tropical Evergreen" habitat (pre-montane wet forest life zone) or "Subtropical Evergreen" (pre-montane rain forest) habitat. Young *et al.* (1998) reported a similar pattern of congeneric elevational species replacement in Monteverde, Costa Rica. Karr and Freemark (1983) found that understory forest birds were distributed according to a microclimatic gradient in lowland forest of Panama. Our observations of plant distributions suggest that some "cloud forest" plant species (Gentry 1993; *e.g.*, *Razisea*, *Pitcairnia brittoniana*, *P. atropurpurea*, *Satyria* sp., and *Burmeistera*; Appendix III) also followed a pattern of being present at our fragment sites (pre-montane rain forest) but absent from the LCBSFR (wet forest).

Climatic differences among these sites also may affect local distributions of butterfly species. Fruit-eating butterflies appear to reach their greatest diversity at lower elevations, based on results from short-term trapping efforts with fruit bait. Daily and Ehrlich (1995, 1996) recorded >20 butterfly species at each of two lower sites, LCBSFR, and a nearby 25-ha fragment, compared to only 9 species in Fragment 1 and 12 species in Fragment 5. In contrast, moth diversity was high (*ca* 50–100 spp.) at both LCBSFR and the smaller fragments, with no apparent effect of fragment size on the number of moth species captured in light traps. Daily and Ehrlich (1996) attributed differences between moth and butterfly distribution patterns to the fact that moths are nocturnal and therefore better able

to cross open areas (potentially stressful due to abiotic factors) than butterflies. We suggest that differences in local climate also could play a role in limiting butterfly use of higher elevation fragments, given that many moth species are endothermic and butterflies are not (Heinrich 1981). Thus, we suggest that for butterflies, plants, and birds in these study fragments and LCBSFR, local species' distributions may be influenced by the prevalence of cloud forest conditions, the sizes of the forest fragments, or both.

It is important to note that with fragments as small as these (including the LCBSFR), edge effects are probably also an important factor. It is likely that edge effects are a factor throughout most, if not all, of the smaller fragments, and at least portions of the larger fragments, especially the odd-shaped Fragment 5. The LCBSFR, although much larger than the other sites, is probably also affected by edge effects because of its L-shape, wherein a greater amount of its interior habitat (volume) is exposed to edge (surface) than if it were a more symmetrically shaped fragment. Therefore, although in this study we did not explicitly distinguish among edge and area (or size) effects, we believe that the two types of effects may exist at a particular site. For the purposes of this study, however, we have referred to the suite of effects from area and edge effects simply as fragmentation effects.

In the fragments, the common occurrence of interior hummingbird species with curved bills and canopy species with shorter, straight bills ensures that a variety of hummingbird-dependent plant species can be pollinated. Hummingbirds are especially important for plant species with long, curved corollas because other animals such as bees or butterflies are unable to pollinate them (Bawa 1990). Therefore, for some plant species, plant population structure and gene flow can be affected by hummingbird presence or movements. In this regard, it is fortunate that *P. guy*, which carried diverse pollen morphospecies, was common at all of the fragments and LCBSFR, and has been seen crossing open pastures nearby (Daily *et al.* in press). Like its lower-elevation congener, *P. superciliosus*, this widespread species appears to be able to thrive in secondary growth and partially deforested landscapes. *Campylopterus hemileucurus*, another common species with a curved bill, also occurs in agricultural habitats and sometimes forages for nectar at banana flowers growing away from forested areas (Stiles & Skutch 1989; R. Borgella & T. Gavin, pers. obs.).

Of the seven most common hummingbird species captured, three were interior species with long, curved bills (ca 30–40 mm; *P. guy*, *C. hemileucurus*, and *E. aquila*), three were canopy species with shorter, straight bills (ca 14–21 mm; *L. castaneoventris*, *H. jacula*, and *E. chionura*), and one was a "non-forest" species with a short, straight bill (ca 22 mm; *A. tzacatl*; Table 4). The interior species often forage widely at plants such as *Heliconia*, *Aphelandra*, *Drymonia*, and *Columnea* spp., whereas the canopy species are more often territorial, depending on the local availability of flowers that are easily pierced or bearing short corollas (Stiles 1975, 1978; Stiles & Skutch 1989). Birds with smaller bills are likely to be both legitimate pollinators and nectar robbers that obtain nectar through holes in the sides of corollas or unopened buds. For example, *P. longuemareus*, a less common interior species with a short, curved bill (ca 24 mm), was seen pollinating *Calathea crotalifera* and robbing nectar from *Aphelandra golfodulcensis*.

Our findings regarding pollen loads contrast to those of Feinsinger *et al.* (1986), wherein the short-billed pollinator (*Lampornis castaneoventris calolaema*) had pollen from 15 plant species and a long-billed pollinator (*P. guy*) had pollen from 16. We collected pollen of 3 and 13 plant species from these same hummingbird species (respectively) throughout the January–March 1998 interval. We also found that our data did not support the suggestion by Feinsinger *et al.* (1988) that long-billed hummingbirds would be found more frequently in undisturbed habitats than short-billed species, which they predicted would be found more commonly in secondary growth habitat. At our study sites, the long-billed species *P. guy* and *C. hemileucurus* were found at all sites, although *C. hemileucurus* was not captured in the smallest site, Fragment 4 (Appendix II). As for short-billed species, three were found in all of the fragments and two of these were also found at LCBSFR. Interestingly, the species with the shortest bill-length and no pollen (*E. chionura*) was captured primarily at the larger sites (LCBSFR, Fragment 1, and Fragment 5); of 95 captures, all but 9 were in these three larger sites. Thus, in our sites, the expectation that short-billed hummingbirds would be more common in secondary-growth forest than in primary forest was not supported.

Our mist-netting results may have been biased against capturing canopy-dwelling hummingbird species, because this technique is known to sample the understory avifauna more accurately than the forest canopy avifauna (Karr 1981a, b; Remsen &

Good 1996). This bias could also influence apparent sex ratios within species because male hummingbirds sometimes forage in higher strata than females (*e.g., E. chionura*; Stiles & Skutch 1989). Female-biased capture rates could be due also to the presence of lek sites (display areas for breeding males) that reduce the males' chances of being sampled or be due to seasonal altitudinal movements that differ between males and females; however, these behaviors are not well described for these species in our study area.

Because canopy hummingbirds are known to forage at lower levels wherever the air–vegetation interface comes down lower at edges, ravines, and streamsides (Stiles & Skutch 1989), one might also expect to have higher detection probabilities of canopy hummingbirds at our smaller fragments. Therefore, it is possible that our results are biased because canopy species may have foraged closer to the nets in the fragments than in the LCBSFR due to a more open canopy layer (the density of canopy trees appeared to be somewhat higher at LCBSFR); however, the proportion of birds captured at LCBSFR that were canopy species was nonetheless substantial (22%), along with 14 percent that used a mixture of canopy and interior foraging areas. In addition, an examination of Figures 2 and 3 suggests that number of species and capture rates of canopy hummingbird species did not differ substantially across all sites, regardless of size. Another possible bias is that the numbers of captures per unit effort may not reflect actual abundance if the probability of being detected (*i.e.,* captured) varied among species or sites (a problem of all sampling methods). For example, very small and highly maneuverable species such as Little Hermits (*P. longuemareus*) may escape capture more often than larger species.

Because our bootstrapped estimates of species richness do not depend *a priori* on data that follow any particular statistical distribution, and because bootstrapping allows for accurate estimation even when detection probabilities differ among species, our species richness estimates at each site were not affected by any of the potential shortcomings of data obtained by using mist nets. As seen in Table 1, observed numbers of species at each site closely corresponded to the bootstrap estimates, suggesting that our mist-net samples adequately represented the hummingbird communities at each site.

Considering the abundances of hummingbird species and hummingbird-pollinated plants observed in the 10- and 20-ha fragments, we conclude that these areas are valuable satellites of

LCBSFR in terms of the biodiversity they support. This is especially true because the natural vegetation of the fragments is cloud forest, whereas LCBSFR consists of drier pre-montane wet forest, and some species occur more frequently in one climatic zone or the other. Therefore, an added benefit of these particular fragments is that they support several plant and avian species that are rare at LCBSFR. Nonetheless, it is important to note that for hummingbird-pollinated plants, population structure and gene flow could be affected if appropriate pollinating species are not available (Rathcke & Jules 1993, Buchmann & Nabhan 1996, Kearns *et al.* 1998), a situation that is more likely to occur in the smaller fragments. For example, these data demonstrate that an important difference among the avifauna at our sites is that the largest of the sites, LCBSFR, had a substantially higher capture rate of interior hummingbirds than any of the other sites (Fig. 3). This is even more notable given that the actual number of interior hummingbird species at LCBSFR was not significantly greater than at most of the other sites (Fig. 2). It seems then that visitation rates at hummingbird-pollinated plants of the forest interior may be more affected by fragmentation than are visitation rates at canopy plants. This is important to the extent that the appropriate pollinator species is available at a density that ensures that plant's viability.

Because all of the hummingbird species in our area sometimes forage along forest edges and in secondary-growth forest, they are probably more resilient to habitat fragmentation than other birds that are largely confined to forest interiors (Borgella 1995; Stouffer & Bierregaard 1995a, b). On the other hand, we do not know whether fragments as small as 10 to 20 ha can support viable populations of hummingbirds over the long term. Indeed, if it were not for the high mobility of hummingbirds and the presence of larger biological preserves in the region, it is possible that certain species would be locally extinct.

ACKNOWLEDGMENTS

LITERATURE CITED

ALDRICH, P. R., AND J. L. HAMRICK. 1998. Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. Science 281: 103–105.

————, ————, P. CHAVARRIAGA, AND G. KOCHERT. 1998. Microsatellite analysis of demographic genetic structure in fragmented populations of the tropical tree *Symphonia globulifera*. Mol. Ecol. 7: 933–944.

BAWA, K. S. 1990. Plant–pollinator interactions in tropical rainforests. Annu. Rev. Ecol. Syst. 21: 399–422.

BORGELLA, R., JR. 1995. Population size, survivorship, and movement rates of resident birds in Costa Rican forest fragments. M.S. thesis. Cornell University, Ithaca, New York.

BOSHIER, D. H., M. R. CHASE, AND K. S. BAWA. 1995. Population genetics of *Cordia alliodora* (Boraginaceae), a Neotropical tree. 3. Gene flow, neighborhood, and population substructure. Am. J. Bot. 82: 484–490.

BOZA, M. A. 1993. Conservation in action: past, present, and future of the national park system in Costa Rica. Conserv. Biol. 7: 239–247.

BROWN, L. M. 2000. Population genetic structure of understory birds in a fragmented tropical forest. Ph.D. dissertation. Cornell University, Ithaca, New York.

BUCHMANN, S. L., AND G. P. NABHAN. 1996. The forgotten pollinators. Island Press, Washington, DC.

DAILY, G. C. Countryside biogeography and the provision of ecosystem services. *In* P. Raven (Ed.). Nature and human society: the quest for a sustainable world. National Academy of Sciences, Washington, DC. In press.

————, AND P. R. EHRLICH. 1995. Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. Biodiv. Conserv. 4: 35–55.

————, AND ————. 1996. Nocturnality and species survival. Proc. Natl. Acad. Sci. 93: 11,709–11,712.

————, ————, AND G. A. SÁNCHEZ-AZOFEIFA. Countryside biogeography: utilization of human-dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. In press.

FEINSINGER, P. 1992. Trapping and marking birds. *In* A. Dafni (Ed.). Pollination ecology: a practical approach, pp. 223–230. IRL Press, Oxford, England.

————, J. H. BEACH, Y. B. LINHART, W. H. BUSBY, AND K. G. MURRAY. 1987. Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. Ecology 68: 1294–1305.

————, W. H. BUSBY, K. G. MURRAY, J. H. BEACH, W. Z. POUNDS, AND Y. B. LINHART. 1988. Mixed support for spatial heterogeneity in species interactions: hummingbirds in a tropical disturbance mosaic. Am. Nat. 131: 33–57.

————, K. G. MURRAY, S. KINSMAN, AND W. H. BUSBY. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated cloud forest plant species. Ecology 67: 449–464.

FLEMING, T. H., R. BREITWISCH, AND G. H. WHITESIDES. 1987. Patterns of tropical vertebrate frugivore diversity. Annu. Rev. Ecol. Syst. 18: 91–109.

GAMEZ, R., AND A. UGALDE. 1988. Costa Rica's national park system and the preservation of biological diversity: linking conservation with socioeconomic development. *In* F. Almeda and C. M. Pringle (Eds.). Tropical rainforests: diversity and conservation, pp. 131–142. California Academy of Sciences, San Francisco, California.

GENTRY, A. H. 1993. A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. Conservation Biology Series, contribution no. 1. Conservation International, Washington, DC.

GIBSON, J. P., AND N. T. WHEELWRIGHT. 1995. Genetic-structure in a population of a tropical tree *Ocotea tenera* (Lauraceae): influence of avian seed dispersal. Oecologia 103: 49–54.

GREENBERG, R., P. BICHIER, A. CRUZ ANGNON, AND R. REITSMA. 1997. Bird populations in shade and sun coffee plantations in central Guatemala. Conserv. Biol. 11: 448–459.

GUINDON, C. F. 1996. The importance of forest fragments to the maintenance of regional biodiversity in Costa Rica. *In* J. Schelhas and R. Greenberg (Eds.). Forest patches in tropical landscapes, pp. 168–186. Island Press, Washington, DC.

HEINRICH, B. (Ed.). 1981. Insect thermoregulation. John Wiley and Sons, New York, New York.

HOLDRIDGE, L. R. 1967. Life zone ecology, revised edition. Tropical Science Center, San Jose, Costa Rica.

KARR, J. R. 1981a. Surveying birds with mist nets. Stud. Avian Biol. 6: 62–67.

————. 1981b. Surveying birds in the tropics. Stud. Avian Biol. 6: 548–553.

————, AND K. E. FREEMARK. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. Ecology 64: 1481–1494.

KEARNS, C. A., D. W. INOUYE, AND N. M. WASER. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annu. Rev. Ecol. Syst. 29: 83–112.

LANDE, R. 1988. Genetics and demography in biological conservation. Science 241: 1455–1460.

LAURANCE, W. F., AND R. O. BIERREGAARD JR. (Eds.). 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois.

LEVEY, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69: 1076–1089.

————, T. C. Moermond, and J. S. Denslow. 1994. Frugivory: an overview. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). La Selva: ecology and natural history of a Neotropical rain forest, pp. 282–294. University of Chicago Press, Chicago, Illinois.

Linhart, Y. B., P. Feinsinger, J. H. Beach, W. H. Busby, K. G. Murray, W. Z. Pounds, S. Kinsman, C. A. Guindon, and M. Kooiman. 1987. Disturbance and predictability of flowering patterns in bird-pollinated cloud forest plants. Ecology 68: 1696–1710.

Loiselle, B. A., and J. G. Blake. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a Neotropical lowland wet forest. Vegeratio 107/108: 177–189.

Lutz, E. M., W. Vedova, H. Martínez, L. San Román, R. Vazquez L., A. Alvarado, L. Merino, R. Celis, and J. Husing. 1993. Interdisciplinary fact-finding on current deforestation in Costa Rica. The World Bank Sector Policy and Research Staff Report Environment Working Paper No. 61. World Bank, Environment Dept., Washington, D.C.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

Murawski, D. A., I. A. U. N. Gunatilleke, and K. S. Bawa. 1994. The effects of selective logging on inbreeding in Shorea megistophylla (Dipterocarpaceae) from Sri Lanka. Conserv. Biol. 8: 997–1002.

Nason, J. D., P. R. Aldrich, and J. L. Hamrick. 1997. Dispersal and the dynamics of genetic structure in fragmented tree populations. In W. F. Laurance and R. O. Bierregaard Jr. (Eds.). Tropical forest remnants, pp. 304–320. University of Chicago Press, Chicago, Illinois.

————, and J. L. Hamrick. 1997. Reproductive and genetic consequences of forest fragmentation: two case studies of Neotropical canopy trees. J. Hered. 88: 264–276.

Pulliam, H. R. 1988. Source, sinks, and population regulation. Am. Nat. 132: 652–661.

Rathcke, B. J., and E. S. Jules. 1993. Habitat fragmentation and plant pollinator interactions. Curr. Sci. 65: 273–277.

Remsen, J. V., Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 381–398.

Roubik, D. W., and J. E. Moreno. 1991. Pollen and spores of Barro Colorado Island. Missouri Botanical Garden Monographs in Systematic Botany. Vol. 36. Missouri Botanical Garden, St. Louis, Missouri.

SAS. 1996. Version 6.12. SAS Institute, Cary, North Carolina.

Schelhas, J., and R. Greenberg. (Eds.). 1996. Forest patches in tropical landscapes. Island Press, Washington, DC.

Schlaepfer, M. A. 1998. Edge effects on lizards (Norops) and frogs (Eleutherodactylus) in Neotropical forest fragments. M.S. thesis. Cornell University, Ithaca, New York.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, Illinois.

Smith, E. P., and G. van Belle. 1984. Nonparametric estimation of species richness. Biometrics 40: 119–129.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology 56: 285–301.

————. 1978. Temporal organization of flowering among the hummingbird food plants of a tropical wet forest. Biotropica 10: 194–211.

————. 1985. Conservation of forest birds in Costa Rica: problems and perspectives. In A. W. Diamond and T. E. Lovejoy (Eds.). Conservation of tropical forest birds, pp. 141–168. International Council for Bird Preservation Technical Publication No. 4, Cambridge, England.

————, and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.

Stouffer, P. C., and R. O. Bierregaard Jr. 1995a. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. Conserv. Biol. 9: 1085–1094.

————, and ————. 1995b. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76: 2429–2445.

Tamboia, T., M. L. Cipollini, and D. J. Levey. 1996. An evaluation of vertebrate seed dispersal syndromes in four species of black nightshade (Solanum sect Solanum). Oecologia 107: 522–532.

Wheelwright, N. T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. Trends Ecol. Evol. 3: 270–274.

Young, B. E., D. DeRosier, and G. V. N. Powell. 1998. Diversity and conservation of understory birds in the Tilarán Mountains, Costa Rica. Auk 115: 998–1016.

APPENDIX I.   Details of sampling and net hours per site from January 1994 through mid-March 1999. Months when each area was sampled are indicated; the number of stations in Fragment 5 increased from four in 1994 and 1995, to six then eight in 1997, and eight in 1998–1999.

	LCBSFR	Fragment 1	Fragment 2	Fragment 3	Fragment 4	Fragment 5
Total net hours	9300	12,800	3000	3100	3100	18,600
Area (ha)	226	10	0.9	0.9	0.3	20
Net hours/area	41	1280	3333	3444	10,333	930
No. of banding stations	13	4	1	1	1	4–8
Months sampled in this year:						
1994	Jan., Feb., May	Jan., Feb., Apr.	Apr., May	Feb., Apr.	Feb., Apr.	Mar., Apr., May
1995	Jan., Apr.	Jan., Feb.	Jan., Feb.	Jan., Feb.	Jan.	Jan., Feb.
1996	Feb., Mar., Jul., Dec.	Jan., Feb., May, Oct., Nov.	Jan., Feb., Jun., Nov.	Jan., Feb., May, Nov.	Jan., Feb., Jun., Nov.	Jan., Feb., Jun., Nov., Dec.
1997	Feb., Nov., Dec.	Jan., Feb., Mar., Sep.	Jan., Feb., Oct.	Jan., Feb., Oct.	Jan., Feb., Oct.	Jan., Feb., Oct.
1998	Feb., Mar.	Jan., Feb.	Jan., Feb., Mar.	Jan., Feb., Mar.	Jan., Mar.	Jan., Feb., Mar.
1999	Feb., Mar.	Feb., Mar.	Feb., Mar.	Feb., Mar.	Feb., Mar.	Jan., Mar.

APPENDIX II.   List of species names, habitat preferences, and occurrences of hummingbird species at LCBSFR and the five fragments (F1–F5). Habitat preferences are from Stiles (1985): C = forages in forest canopy; I = forages in forest interior; and NF = primarily a non-forest species. Numbers are forest dependency classes: 1 requires >50 percent forest cover; 2 occurs in patchy forest; and 3 does not need forest. Blank cells in the table are zeroes.

Common name	Scientific name	Habitat	Number of captures						
			LCBSFR	F1	F2	F3	F4	F5	Total
Green Hermit	Phaethornis guy	I; 2	71	102	17	17	10	105	322
Variable Mountain-gem	Lampornis castaneoventris	C; 2	4	38	19	9	16	114	200
Green-crowned Brilliant	Heliodoxa jacula	C; 2	18	44	5	7	13	86	173
White-tailed Emerald	Elvira chionura	C; 2	18	28	5	4		40	95
Violet Sabrewing	Campylopterus hemileucurus	I; 2	30	23	3	6		28	90
White-tipped Sicklebill	Eutoxeres aquila	I; 1, 2	27	11	1			11	50
Rufous-tailed Hummingbird	Amazilia tzacatl	NF; 3	8	13	2	1	2	13	39
Little Hermit	Phaethornis longuemareus	I; 2, 3	15	5	1			5	26
Beryl-crowned Hummingbird	Amazilia decora	C, I; 2	15	4		1	1	2	23
Crowned Woodnymph	Thalurania colombica	C, I; 2	18	1				1	20
Bronzy Hermit	Glaucis aenea	NF; 3	2	1	1	1		1	6
Steely-vented Hummingbird	Amazilia saucerrottei	C; 2, 3	5				1		6
Long-tailed Hermit	Phaethornis superciliosus	I; 2		1				2	3
Green-fronted Lancebill	Doryfera ludoviciae	C; 2						3	3
Stripe-tailed Hummingbird	Eupherusa eximia	C, I; 2	1					2	3
Scaly-breasted Hummingbird	Phaeochroa cuvierii	C; 2, 3	2						2
White-necked Jacobin	Florisuga mellivora	C; 2	2						2
Coppery-headed Emerald	Elvira cupreiceps	C, I; 1, 2						2	2
Purple-crowned Fairy	Heliothryx barroti	C; 2	2						2
Green Violet-ear	Colibri thalassinus	NF; 2, 3			1				1
Fork-tailed Emerald	Chlorostilbon canivetii	NF; 3		1					1
Total per site:			238	272	55	46	43	415	1069

APPENDIX III.   *Corolla characteristics, location, and season of peak flowering of known or putative nectar sources for hummingbirds at the study sites in the vicinity of Las Cruces Biological Station, Costa Rica. Locations refer to all fragments (F) or LCBSFR. Corolla length is the length of the enclosed corolla; Y = curved corolla, and N = not curved. Color refers to the main color of the corolla; "other" refers to the main color of the calyx, adjacent bracts, or other structures that are part of the floral display.*

	Location	Season	Corolla length (mm)	Curved	Color (corolla/other)
ACANTHACEAE					
Aphelandra golfodulcensis	F, LCBSFR	Dry	46–50	Y	Red
Razisea sp.	F	Dry	35–40	Y	Magenta
Unidentified herb	F, LCBSFR	Dry, Wet	23–25	N	Red
APOCYNACEAE					
Stemmadenia donnellsmithii	LCBSFR	Dry	29–30	N	Yellow
BALSAMINACEAE					
Impatiens walleriana	F, LCBSFR	Dry, Wet	28	N	Pink, Orange, White
BROMELIACEAE					
Guzmania sp.	F, LCBSFR	Wet	31–33	N	Yellow/Yellow
Pitcairnia brittoniana	F	Wet	40–45	Y	Orange/Red
P. atropurpurea	F	Wet	*ca* 60	Y	Yellow/Red
CAMPANULACEAE					
Burmeistera sp.	F	Dry, Wet	13–15	Y	Maroon
Centropogon sp.	F, LCBSFR	Dry, Wet	34–37	Y	Red
Unidentified sp.	LCBSFR	Wet	42–45	Y	Cream/Green
CLUSIACIAE					
Symphonia globulifera[a]	F, LCBSFR	Dry, Wet	9–10	N	Red
COSTACEAE					
Costus sp.	F, LCBSFR	Dry, Wet	45	Y	Yellow/Red
CUCURBITACEAE					
Gurania makoyana	F, LCBSFR	Dry	19	N	Orange
ERICACEAE					
Cavendishia bracteata	F, LCBSFR	Dry, Wet	22	N	White/Pink
Macleania ovata	F, LCBSFR	Dry	24–26	N	White/Red
Satyria sp.	F	Wet	30–35	N	White/Red
GESNERIACEAE					
Alloplectus sp.	F, LCBSFR	Dry, Wet	45–47	Y	Red/Red
Besleria alloplectoides	F	Wet	11	N	Orange, Yellow
Besleria sp. 1	F, LCBSFR	Dry, Wet	15–17	N	Orange
Besleria sp. 2	F	Wet	12–14	N	Orange
Columnea consanguinea	F, LCBSFR	Dry, Wet	45–47	Y	Orange
C. consanguinolenta	F, LCBSFR	Dry, Wet	24–25	N	Orange/Orange
C. nicaraguensis	F, LCBSFR	Wet	36–40	Y	Maroon
Macrantha sp.	F	Dry, Wet	42–47	Y	Yellow/Orange
M. turrialvae	F, LCBSFR	Dry	40–43	N	White/Purple
HELICONIACEAE					
Heliconia tortuosa	F, LCBSFR	Dry, Wet	32–35	Y	Yellow/Red
H. wilsonii	F, LCBSFR	Dry, Wet	32–36	Y	Yellow/Red
MALVACEAE					
Malvaviscus arboreus	F, LCBSFR	Dry	48–50	N	Red
MARANTACEAE					
Calathea crotalifera	F, LCBSFR	Dry, Wet	18–20	N	Yellow/Yellow
Calathea sp., *lutea* group	F, LCBSFR	Dry, Wet	45–48	N	Yellow/Yellow

APPENDIX III.   *Continued.*

	Location	Season	Corolla length (mm)	Curved	Color (corolla/other)
RUBIACEAE					
Palicourea discolor	F, LCBSFR	Dry, Wet	15–18	N	Lavender/Purple
P. vestita	F	Wet	13–14	N	Yellow
P. padifolia	F, LCBSFR	Dry, Wet	8–10	N	Red/Yellow
ZINGIBERACEAE					
Renealmia cernua	F, LCBSFR	Dry, Wet	19–20	N	Orange/Orange

[a] P. R. Aldrich, pers. comm.
[b] A brief description of the fragments and some of the plant species observed therein is given in Appendix I of Borgella (1995).