Persistence of Forest Birds in the Costa Rican Agricultural Countryside

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Abstract: *Understanding the persistence mechanisms of tropical forest species in human-dominated landscapes is a fundamental challenge of tropical ecology and conservation. Many species, including more than half of Costa Rica's native land birds, use mostly deforested agricultural countryside, but how they do so is poorly known. Do they commute regularly to forest or can some species survive in this human-dominated landscape year-round? Using radiotelemetry, we detailed the habitat use, movement, foraging, and nesting patterns of three bird species,* Catharus aurantiirostris, Tangara icterocephala, *and* Turdus assimilis, *by obtaining 8101 locations from 156 individuals. We chose forest birds that varied in their vulnerability to deforestation and were representative of the species found both in forest and human-dominated landscapes. Our study species did not commute from extensive forest; rather, they fed and bred in the agricultural countryside. Nevertheless,* T. icterocephala *and* T. assimilis, *which are more habitat sensitive, were highly dependent on the remaining trees. Although trees constituted only 11% of land cover, these birds spent 69% to 85% of their time in them. Breeding success of* C. aurantiirostris *and* T. icterocephala *in deforested habitats was not different than in forest remnants, where* T. assimilis *experienced reduced breeding success. Although this suggests an ecological trap for* T. assimilis, *higher fledgling survival in forest remnants may make up for lower productivity. Tropical countryside has high potential conservation value, which can be enhanced with even modest increases in tree cover. Our findings have applicability to many human-dominated tropical areas that have the potential to conserve substantial biodiversity if appropriate restoration measures are taken.*

Keywords: avian ecology, countryside biogeography, home range, landscape ecology, Neotropical communities, radio tracking, restoration ecology

Persistencia de Aves en el Paisaje Agrícola de Costa Rica

Resumen: *El entendimiento de los mecanismos de persistencia de especies de bosques tropicales en paisaje dominados por humanos es un aspecto fundamental de la ecología y conservación tropical. Muchas especies, incluyendo más de la mitad de las especies de aves terrestres nativas de Costa Rica, principalmente utilizan campos agrícolas deforestados, pero se conoce poco sobre como lo hacen. ¿Se mueven regularmente al bosque o algunas especies pueden sobrevivir todo el año en este paisaje dominado por humanos? Utilizando radio telemetría, detallamos los patrones de uso de hábitat, movimiento, forrajeo y anidación de tres especies de aves,* Catharus aurantiirostris, Tangara icterocephala, *y* Turdus assimilis, *mediante la obtención de 8101 locaciones para 156 individuos. Seleccionamos especies de aves que variaban en su vulnerabilidad a la deforestación y que fueron representativas de las especies encontradas tanto en bosques como en paisajes dominados por humanos. Nuestras especies de estudio no se movían desde bosque extenso, sino se alimentaban y reproducían*

482

en el paisaje agrícola. Sin embargo, T. icterocephala *y* T. assimilis, *que son más sensibles al hábitat, dependían estrechamente de los árboles remanentes. Aunque los árboles sólo constituían 11% de la cobertura de suelo, estas aves pasaban entre 69 y 85% del tiempo en ellos. El éxito reproductivo de* Catharus *y* Tangara *en habitats deforestados no fue diferente al de los remanentes de bosques, en donde* Turdus *experimentó disminución en el éxito reproductivo. Aunque esto sugiere una trampa ecológica para* Turdus, *la campiña tropical tiene un valor de conservación potencialmente alto, que se puede reforzar aun con modestos incrementos de cobertura arbórea. Nuestros hallazgos son aplicables en muchas áreas tropicales que son dominadas por humanos y que tienen el potencial de conservar la biodiversidad si se toman las medidas de restauración apropiadas.*

Introduction

Tropical forests worldwide are being reduced to biologically impoverished remnants (Laurance & Bierregaard 1997) embedded in the agricultural countryside (hereafter "countryside"; Daily et al. 2001)—human-dominated and mostly deforested areas consisting of croplands, pasture, gardens, open second growth, and a scattering of forest fragments, riparian strips, and remnant trees. Even though human-dominated areas are the preferred habitat of <1% of the world's nearly 10,000 avian species (Sekercioglu et al. 2004), about one-third make some use of such habitats (Sekercioglu 2003). Given the high rate of tropical deforestation, the extent and ecological qualities of the heavily deforested countryside will determine whether some tropical forest species can persist in the absence of extensive forests. That, in turn, will affect the future of much biodiversity.

Unfortunately, protected areas alone are inadequate to protect the majority of tropical biodiversity and ecosystem services (Liu et al. 2001; Dirzo & Raven 2003). Ecological management of the countryside is essential for connecting, buffering, and reducing the pressure on protected areas (Schroth et al. 2004; Castellón & Sieving 2006). Thus, perhaps the most important questions in conservation ecology today are (1) to what degree can tropical forest organisms persist in human-dominated countryside? and (2) what can be done to make the countryside habitats more hospitable to forest species?

Previous studies have shown that many species of tropical forest birds use the countryside (e.g., Greenberg et al. 1997*a*; Gascon et al. 1999; Daily et al. 2001; Sodhi et al. 2005; Peh et al. 2006). Seventy-five percent of Costa Rica's native land birds also use heavily deforested areas to some extent, provided that some canopy trees and forest patches remain (Stiles 1985). Nevertheless, there have been few detailed and mechanistic investigations of the habitat use and movements of forest species in human-dominated tropical landscapes (e.g., Rappole et al. 1989; Graham 2001; Cohen & Lindell 2004; Powell & Bjork 2004; Castellón & Sieving 2006), and the ecological requirements of such species living in the countryside are virtually unknown. For example, certain seed-dispersing tropical bats can forage in mostly deforested habitats, but have to "commute" to mature forest for roosting (Evelyn & Stiles 2003). Similar behavioral traits can limit the ability of birds to persist far from such forests. Therefore, we addressed two key questions: (1) What habitat elements are essential for maintaining native forest birds found in deforested countryside? and (2) Do these birds mostly rely on extensive forest, commuting to the countryside only for opportunistic foraging?

Methods

Study Area

Our study was centered around the Las Cruces Biological Station of the Organization for Tropical Studies (8°47′N, 82°57′W) in the Coto Brus province of Costa Rica (map available from http://www.naturalphotos.com/sekercioglu/science/SekerciogluAppendix1.doc). This previously forested region of southern Costa Rica is now dominated by sparsely shaded coffee plantations and pasture, and is representative of human-dominated tropical areas that retain a substantial portion of their original biodiversity (Hughes et al. 2002). The area consists of fragments of Pacific premontane humid forest surrounded by pastures, plantations of sun coffee, other crops, and human settlements. Coffee plants (*Coffea arabica* L.) were 2–3 m tall, partially shaded by banana plants (*Musa* spp.), poro trees (*Erythrina poeppigiana* Walpers), and scattered remnant trees that did not form a continuous canopy. The forest fragments have been isolated since the mid-1950s, and Las Cruces forest is the largest midelevation fragment in the region (235 ha). Mean annual temperature is 22° C, and the yearly average rainfall is around 3500 mm.

We radio tracked birds from 6 June to 15 September 2002 (wet season) and from 27 January to 10 April 2003 (dry season, main breeding period) near the towns of San Bosco, San Francisco, San Gabriel, and Santa Teresa. To investigate the importance of tree cover, we chose four 1-km² study sites (elevations 980–1080 m) that exhibited a

range of typical arboreal cover (forest fragments, riparian strips, and remnant trees). Arboreal cover was higher at more-forested sites San Bosco (11.5%) and Santa Teresa (14.2%) than in less-forested San Francisco (5.1%) and San Gabriel (9.2%), which, unlike the more-forested sites, did not include any forest fragments >1 ha. Because we were studying forest birds that are now frequently found in the countryside, all birds were captured in partially shaded coffee plantations, the most prevalent form of agriculture in the region.

Study Species

Nearly half of the bird species native to this area presently occur in deforested countryside (Hughes et al. 2002). In order to have large sample sizes, we chose three focal species that are common in both extensive forest and the countryside. According to Stiles (1985), Orange-billed Nightingale-Thrushes (*Catharus aurantiirostris*, hereafter *Catharus*) have low dependence on forest and prefer forest edge, second growth, thickets, plantations, and gardens (Stiles & Skutch 1989). Silver-throated Tanagers (*Tangara icterocephala*, hereafter *Tangara*) are intermediately dependent on forest (Stiles 1985) and are found in forest canopy, forest edge, and agricultural areas around Las Cruces. White-throated Thrushes (*Turdus assimilis*, hereafter *Turdus*) are highly dependent on forest (Stiles 1985), but although they prefer forests, also use bordering thickets, riparian corridors, secondary growth, pastures, and coffee plantations (Stiles & Skutch 1989; Cohen & Lindell 2004).

Capturing and Marking Birds

At each site, we operated 16 to 20, 12 × 2.7 m, 30- to 36-mm mesh mist nets between 0500–1100 hours. We placed the nets between rows of coffee and checked them every half hour. We rotated daily between sites to minimize the drop in capture rate as a result of birds learning and avoiding net locations. Captured individuals of the study species were weighed, measured, banded with a steel numbered band and a unique combination of color bands, and fitted with a BD-2 model radio transmitter (Holohil Systems, Carp, Ontario). We glued a piece of silk to each transmitter to improve adhesion and attached the transmitter to the interscapular area of each bird with skin-compatible eyelash glue. We trimmed the feathers in the way and glued some of the surrounding feathers to the transmitter so as to maximize adhesion and mobility of the bird (Kenward 2001). The transmitters weighed 0.7 g, 1.0 g, and 1.5 g, respectively for *Tangara* (21 g), *Catharus* (28 g), and *Turdus* (64 g) and were <3.6% of the mean body mass of each study species.

To check for any behavioral changes, we observed the birds for a few hours after release. Additionally, we did not collect data for 2 days after release to allow habituation to the transmitter. After some preening in the first half hour

following placement of the transmitter, the birds resumed their usual behavior, flew and fed normally, and were apparently not hindered by the transmitters. Results of previous studies on transmitter effects on passerines show that transmitters have negligible effects (Wells et al. 2003). In 2003 we recaptured 31 of the birds we had tagged in 2002, and except for their leg bands, none showed any sign of having carried a radio tag.

Radio Tracking

We located birds between 0500–2200 hours (sunrise: 0515–0545, sunset: 1730–1800) with R-1000 receivers (Communications Specialists, Orange, California) and RA-14 (Telonics, Mesa, Arizona), 3-element Yagi, 5-element Yagi, and vehicle-mounted omnidirectional antennas (Wildlife Materials International, Murphysboro, Illinois). We radio tracked birds continuously except during episodes of heavy rain when birds ceased activity and sought shelter. Our objective was to observe an individual regularly every 30 minutes, and we were mostly within 15 minutes of this objective. Each bird was tracked for an average of 45 hours distributed across an average of 10 days. Each day we rotated among sites and birds as evenly as possible. We confirmed 63% of our radio-tracking locations visually and confirmed the rest with containment and short-distance triangulation. For example, we surmised that a bird was in a tree by going around the tree, observing that all the signals pointed to the center, and seeing substantial and irregular signal change, which indicates an attached tag on a moving bird. We did not use long-distance triangulation because average error was too large compared with home range sizes. We lost only 5 of 156 birds before expected battery death, likely because of premature tag failure (Rappole et al. 1989).

The tracking procedure differed slightly based on the species. Continuous tracking was almost impossible for *Catharus* because they prefer dense thickets and are hard to approach without flushing. Even when it was possible to follow them, we sometimes were flushing them rather than observing their natural movements. Therefore, we rotated between the tagged *Catharus* in an area, getting a location from a bird and then finding the next one. Because each site had 4–7 tagged *Catharus* at any one time, we returned to the same bird within 90 to 120 minutes and did not appear to affect its behavior excessively. For *Tangara* and *Turdus*, we conducted continuous tracking and behavioral monitoring (Altmann 1974).

When a bird was observed, we noted time, GPS location (waypoint) with a Garmin 12 global positioning device (Garmin International, Olathe, Kansas), bird's height above ground, behavior, vegetation type, food type if possible, topography, and direction and distance of any movement. The GPS location error was almost always under 10 m, and frequently under 5 m. When we could not see the bird (or we could see a bird, but not its color bands) but

were confident that the bird was within 10 m, we noted most of the variables except behavior and occasionally height above ground. In the rare cases when we could not get GPS coverage under dense vegetation cover, we noted location of the bird, walked away until there was coverage, measured direction with a compass and distance with a Bushnell Yardage Pro laser rangefinder (Bushnell Performance Optics, Overland Park, Kansas), and were able to assign a waypoint to the initial location.

Vegetation categories were coffee (<3 m plant height, including shade coffee, which was negligible), pasture (<1 m), second growth (<5 m, little or no canopy cover), riparian strips (10–25 m, consisting of trees along rivers), remnant trees (5–30 m), forest (15–30 m, regenerating forest and original forest fragments), and other human use (<3 m, including gardens, corn, yucca, beans, settlements, and roads). At times we refer collectively to coffee, pasture, and other human use as "agricultural" cover and pool riparian strips, remnant trees, and forest fragments into "arboreal" cover. We divided vegetation height into four categories: 0–2 m, 2–5 m, 5–15 m, and >15 m. Topography categories were flat, hilly, and steep.

Nest Monitoring

During March–July 2004 and March–June 2005, we monitored 73 *Catharus*, 52 *Tangara*, and 60 *Turdus* nests. In addition to monitoring the nests of birds with radio transmitters, we also searched suitable nesting sites intensively and observed all individuals of the study species for any signs of nesting. We used established protocol (Ralph et al. 1993), marked and monitored nests so as to minimize disturbance, and visited them every 3–4 days as recommended. We did not monitor the 20 nests we found as a result of radio tracking in 2002 and 2003 and report only on their habitat associations in the section on habitat use.

Vegetation Surveys

Ninety-one percent of all bird locations were within 500 m of the mist-net lanes. Therefore, at each of the four study sites, we surveyed the vegetation in a 1-km^2 grid centered on mist-net locations. We divided each survey grid into 50 × 50 m plots (21 × 21 plots in each grid, 1764 plots at all sites) and uploaded the coordinates for the center of each plot to a GPS unit. We then visited each plot and recorded the dominant vegetation types, using the same criteria we used for classifying vegetation for bird observations. We then compared vegetation preferences of our study species with the survey results.

Microclimate Data

We placed Hobo Pro temperature and humidity data loggers (Onset Corporation, Pocasset, Massachusetts) in coffee plantations, forest fragments, riparian strips, and second growth at each site. By recording these data every

minute, we were able to assign habitat temperature and humidity values to bird observations that occurred in those vegetation types. In the wet season we collected data only from coffee plantations and riparian strips. In the end, 4760 radio-tracking locations had associated temperature and humidity data from the same site, habitat, and minute. We used these data to calculate average habitat temperature and humidity values for the three species.

Data Analyses

We used ArcView 7.0 and the extension Animal Movement 2.0 (Hooge & Eichenlaub 1997) to calculate 95% fixed kernel and 95% minimum convex polygon (MCP) home range sizes (Kenward 2001). Even though kernel estimators are superior in general (Kernohan et al. 2001), in highly fragmented landscapes, they often exclude potentially important areas between high concentrations of activity (Riley et al. 2003). In addition, MCP is the most frequently reported type of home range in telemetry studies (Kenward 2001), and we included them to enable comparisons with other studies.

We used compositional analysis (Aebischer et al. 1993), based on the log-ratio analysis of compositions (Aitchison 1986), to compare radio locations with the habitat composition of the surveyed areas where 91% of bird observations took place. Compositional analysis, which calculates the proportion of an animal's trajectory contained within each habitat it visited, corrects for the nonindependence of proportional data that result from continuous radio tracking (Aebischer et al. 1993).

We first subtracted, for each vegetation pair, the natural log of the ratio of those vegetation types' percent cover of the study area (e.g., ln[% coffee cover/%pasture cover]) from the natural log of the ratio of radio locations in those vegetation types in each individual's home range (e.g., ln[% locations in coffee/% locations in pasture]). We then calculated the mean of this difference for all individuals to create and transform the matrices necessary for calculating Λ (Aebischer et al. 1993). Lambda is used to test whether habitat use is significantly nonrandom because $\chi^2 = N * \ln(\Lambda)$, where N is the number of radio-tracked animals. Then t tests are used to determine the habitat types where nonrandom use occurs. If Λ shows habitat use is nonrandom, Aebischer et al. (1993) recommends using standard significance levels of t values rather than Bonferroni corrections.

The unit of replication was the number of individuals with >25 locations because the observation curves for home range area reached asymptotes around 25 locations. We obtained 26 dry-season, 14 wet-season, and 31 total home ranges for *Catharus*; 29, 21, and 43 home ranges for *Tangara*; and 22, 6, and 28 home ranges for *Turdus*, respectively, that met this criterion. We compared habitat preferences among species and between sexes and seasons (dry [breeding] vs. wet [nonbreeding]).

To test for the differences in habitat preferences, resource use, movements, home range sizes, and microclimatic preferences, we used analysis of variance (ANOVA), binomial, Wilcoxon (Mann-Whitney U), Tukey-Kramer HSD, t, and chi-square tests as appropriate (Zar 1999). We calculated nest survivorship with the Mayfield method (Mayfield 1975) and used the Z test (Nur et al. 1999) to compare the daily mortality rates of nests between different habitats.

Results

Between June–September 2002 (wet season) and January–April 2003 (dry season), mist nets were deployed for 13,300 net hours. We caught, radio tagged, and followed 58 *Catharus* (21 females, 24 males, 3 immatures, and 10 birds of unknown sex or age), 61 *Tangara* (22, 28, 10, and 1, respectively), and 37 *Turdus* (9, 15, 4, and 9, respectively) during 6960 hours of radio tracking. We obtained 2137 (52% visual), 3814 (78% visual), and 2150 (53% visual) locations, respectively (Fig. 1). We had enough locations to calculate home range sizes for 31 *Catharus* (median = 53 locations, range = 25–171), 43 *Tangara* (median = 74, range = 25–211), and 28 *Turdus*
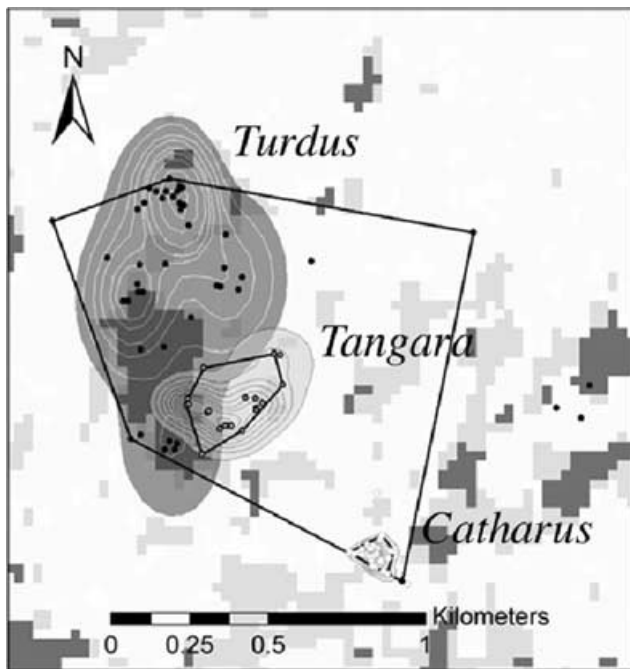

Figure 1. Examples of 95% kernel (contours) and 95% minimum convex polygon (black lines) home ranges of radio-tracked birds in Las Cruces area, excluding 5% outliers. Some points represent multiple locations. Dark gray squares represent arboreal cover (forest fragments, riparian strips, and remnant trees), gray is scrub and second growth, and white is human-dominated habitats (coffee plantations, pastures, other agriculture, and towns). Resolution is 30×30 m.

(median = 78, range = 30–148). Home range size stabilized beyond 25 locations and was not correlated with the number of locations (all $r < 0.16$, all $p > 0.206$).

Habitat Use

Catharus preferred coffee plantations and second growth, whereas *Tangara* and *Turdus* spent more time in arboreal remnants, forest fragments, riparian strips, and single trees, and less time in coffee plantations and other open habitats (Fig. 2; Table 1). Unlike *T. assimilis* 40 km away (Cohen & Lindell 2005), Las Cruces *Turdus* almost never visited pastures. Despite equal effort, at the more-forested sites we caught significantly more *Turdus* than at the less-forested sites (31 vs. 6, respectively; binomial test, $p < 0.001$), confirming the high forest dependence of *Turdus* (Stiles 1985). Captures of the two other species did not differ ($p > 0.10$). All three species exhibited strong habitat selection and were found in vegetation types out of proportion to their landscape cover (Fig. 2 and Table 1; compositional analysis test of radio locations vs. total study area: $\Lambda = 0.025$–0.126; goodness-of-fit test for vegetation types, subscript indicates degrees of freedom: $\chi^2_{5-42} = 21$–156, all $p < 0.001$), except for *Catharus* in the wet season ($\Lambda = 0.285$; $\chi^2_{13} = 17.6$, $p > 0.1$). Habitat use differed significantly among species (all $\chi^2 > 49.7$, all $p < 0.0001$) and between seasons within each species (all $\chi^2 > 31.7$, all $p < 0.0001$).

Sedentary *Catharus* mostly inhabited coffee plantations, although females preferred dense secondary growth during the breeding season (Fig. 2a; Table 1). In contrast, arboreal patches were more important for *Tangara* and *Turdus*, which frequently moved between these patches. Both *Tangara* (Fig. 2b; Table 1) and *Turdus* (Fig. 2c; Table 1) spent 69% to 85% of their time in 11% arboreal cover, especially in the dry season when many remnant trees were fruiting and birds were breeding. *Tangara* ($\chi^2_1 = 38.2$, $p < 0.0001$) and *Turdus* ($\chi^2_1 = 25.3$, $p < 0.0001$) also preferred to nest in trees (of 20 nests of radio-tracked individuals, 70% were in the 11% of the land covered by trees), despite the abundance of coffee and banana plants. *Catharus* sample size was insufficient to allow us to draw any conclusions (three nests in coffee; $\chi^2_1 = 2.07$, $p > 0.11$). Compared with *Tangara* or *Turdus*, most of which spent >60% of their time in trees, *Catharus* showed more variation in habitat use (Fig. 3).

Key Resources

None of the species consumed resources in the same proportion they occurred in the landscape. Each species also differed from the other two in its resource use (all $\chi^2 > 120$, all $p < 0.0001$; top 10 resources can be seen on http://www.naturalphotos.com/sekercioglu/science/SekerciogluAppendix1.doc). *Catharus*, observed foraging on 14 plant taxa, was mainly insectivorous and mostly foraged on or near the soil. *Catharus* often fed on rotting
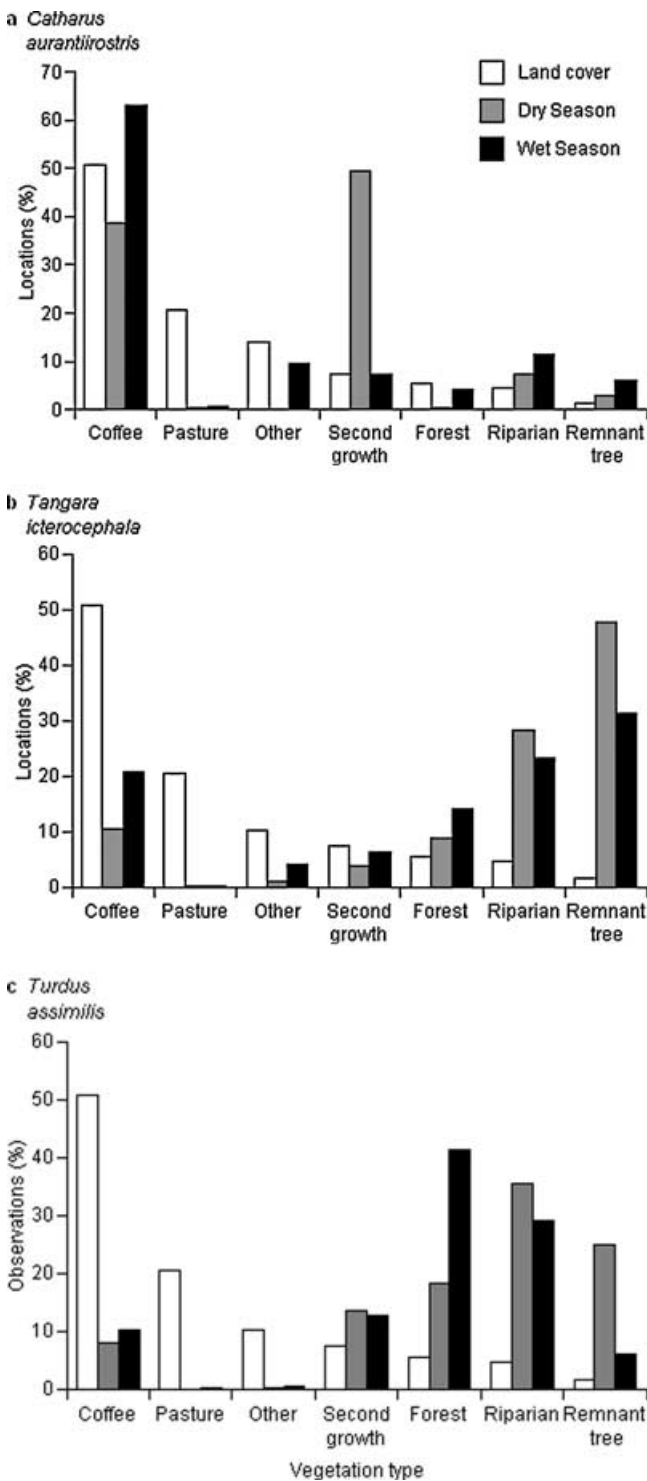
Figure 2. Habitat use of study species (a, b, c) compared with land cover of available vegetation types. All birds were caught and radio tagged in coffee plantations. White bars are the percentage of vegetation survey plots that belong to the respective land cover. Dry season is also the nesting season for the study species. See "Methods" for the descriptions of vegetation types.

bananas, but might have been eating invertebrates feeding on bananas. *Tangara* and *Turdus* mostly consumed fruits and foraged on 71 and 45 taxa, respectively. Fruits of *Cecropia peltata* L., *Ficus* spp., and *Syzygium malacanse* Merr. & Perry, among others, were significantly favored by both species (binomial test; all $p < 0.0001$).

Movement

Our study species' movements were mostly local, and none of them regularly moved ("commuted") between study sites and large (>10 ha), distant (>1 km) forest patches. Of daily movements, 97% were <500 m and 74% were <100 m. Movements of *Catharus* were the smallest (mean = 75.4 ± 3.4 m, range = 0–1186 m, $n = 1998$), followed by *Tangara* (mean = 101 ± 3.7 m, range = 0–3027 m, $n = 3655$) and *Turdus* (mean = 126 ± 10 m, range = 0–5809 m, $n = 2057$). These values were significantly different (Wilcoxon test, all $p < 0.0001$). *Catharus* movements were greater (ANOVA: $F_{1999} = 3.73$, $p = 0.024$) at more-forested sites (84.6 m; $n = 854$) than those with less tree cover (72.3 m; $n = 1146$). In contrast, shorter movements at more-forested sites were observed for *Tangara* (95.9 m vs. 118 m; $F_{3654} = 4.99$, $p = 0.007$) and *Turdus* (122 m vs. 127 m; $F_{2056} = 3.44$, $p = 0.032$). *Catharus*, being mostly terrestrial, moved less in areas with steeper topography ($F_{1972} = 3.44$, $p < 0.0001$), whereas there was no difference for the other species.

Home Range Size

Both kernel and MCP home ranges of *Catharus* were significantly smaller than those of *Tangara* or *Turdus* (all $Z > 3.44$, all $p < 0.001$; Fig. 4), whose average kernel home range sizes did not differ from each other ($Z = 1.253$, $p = 0.21$), but MCP home range sizes did ($Z = 2.27$, $p = 0.024$). Home range sizes did not differ between the sexes of any species (Wilcoxon test: all $Z < 1.32$, all $p > 0.187$; see "Data Analyses" for n). The MCP home range sizes differed between seasons for all the species, whereas kernel home range size differences were more varied (Fig. 4). There was no correlation between kernel or MCP home range size and percent arboreal cover for any species (all $r^2 < 0.063$, all $p > 0.1$; Fig. 3). Average kernel home ranges of *Tangara* in less-forested sites ($n = 19$) were significantly larger than those in more-forested sites ($n = 24$; 24.5 ha vs. 9.3 ha; $Z = 2.14$, Wilcoxon test, $p = 0.032$), however, there were no differences for *Catharus* or *Turdus*.

Breeding Success

Neither clutch size nor the number of per nest (Table 2) differed between *Catharus* nesting in deforested (coffee, pasture, second growth without trees) versus forested (Las Cruces forest, forest fragments, riparian strips)

Table 1. Matrix of ranked habitat preferences of *Catharus aurantiirostris*, *Tangara icterocephala*, and *Turdus assimilis* individuals radio tracked during the study.[a]

Vegetation[b]	Coffee	Pasture	Other	S.G.	Forest	Riprn.	Remnt.
Catharus aurantiirostris							
coffee plantation	5	D: +++ W: +++	D: +++ W: +++	D: −−− W: +++	D: +++ W: +++	D: ++ W: +	D: + W: +
cattle pasture	F: −−− M: −−−	0	D: − W: ++	D: −−− W: −−−	D: + W: ++	D: −−− W: −−−	D: −−− W: −−−
other agriculture	F: −−− M: −−−	F: + M: −	1	D: −−− W: −	D: +++ W: −	D: −−− W: −−−	D: −−− W: −
second growth	F: +++ M: +	F: +++ M: +++	F: +++ M: +++	6*	D: −−− W: −−	D: −−− W: +	D: −−− W: +
forest fragment	F: −−− M: −−−	F: − M: −	F: − M: +	F: +++ M:+++	2	D: −−− W: −−−	D: −−− W: −−−
riparian strip	F: − M: −	F: +++ M: +++	F: +++ M: +++	F: +++ M: +	F: ++ M: +++	4	D: + W: −
remnant tree	F: − M: −	F: +++ M: +++	F: +++ M: +++	F: +++ M: +	F: +++ M: +++	F: + M: −	3*
Tangara icterocephala							
coffee plantation	3*	D: +++ W: +++	D: +++ W: +++	D: + W: +++	D: − W: +	D: −−− W: −−−	D: −−− W: −−−
cattle pasture	F: −−− I: −−− M: −−−	0	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−
other agriculture	F: −−− I: −−− M: −−−	F: +++ I: + M: +++	1*	D: −−− W: −−−	D: −−− W: −−	D: −−− W: −−−	D: −−− W: −−−
second growth	F: ++ I: − M: +	F: +++ I: +++ M: +++	F: + I: + M: +++	2*	D: − W: −	D: −−− W: −−−	D: −−− W: −−−
forest fragment	F: − I: +++ M: +	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: + I: ++ M: +	4	D: −−− W: −	D: −−− W: −−−
riparian strip	F: +++ I: − M: +++	F: +++ I: ++ M: +++	F: +++ I: + M: +++	F: +++ I: − M: +++	F: +++ I: − M: +++	5*	D: −−− W: −−−
remnant tree	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	6*
Turdus assimilis							
coffee plantation	2*	D: +++ W: +++	D: +++ W: +++	D−−− W: −	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−
cattle pasture	F: −−− I: − M: −−−	0	D: −−− W: −	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−
other agriculture	F: −−− I: − M: −−−	F: + I: − M: +	1*	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−	D: −−− W: −−−
second growth	F: + I: ++ M: +++	F: +++ I: ++ M: +++	F: +++ I: ++ M: +++	3*	D: − W: −	D: −−− W: −−	D: −−− W: −
forest fragment	F: +++ I: ++ M: +++	F: +++ I: +++ M: +++	F: +++ I: +++ M: +++	F: + I: ++ M: +	4	D: −−− W: +	D: −−− W: +
riparian strip	F: +++ I: +++ M: +++	F: +++ I: ++ M: +++	F: +++ I: ++ M: +++	F: ++ I: +++ M: +++	F: + I: − M: ++	5*	D: −−− W: +
remnant tree	F: +++ I: +++ M: +++	F: +++ I: ++ M: +++	F: +++ I: ++ M: +++	F: +++ I: ++ M: +++	F: ++ I: + M: +	F: ++ I: ++ M: −	6

[a]*Above the diagonal are dry- (D) and wet- (W) season preferences and below are differences between males (M), females (F), and immatures (I) for both seasons combined. A plus (+) indicates row vegetation is preferred over the column vegetation. A minus (−) indicates avoidance. Three signs, p < 0.05; two signs, 0.05 < p < 0.10; one sign p > 0.10. Numbers on the diagonal indicate the overall order of preference; higher numbers indicate greater affinity, and an asterisk (∗) indicates a significant preference over the lower-ranked vegetation types (S.G., second growth; riprn., riparian; remnt., remnant tree).*
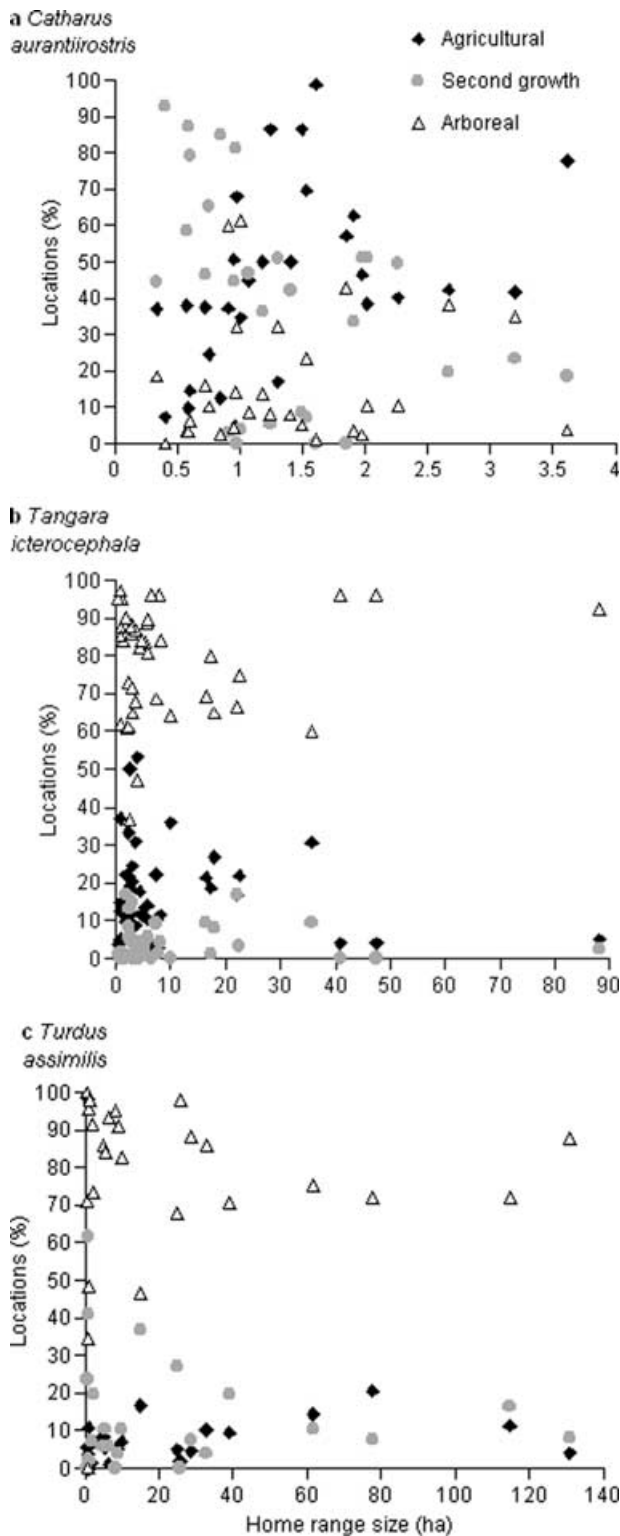[b]*Vegetation types are listed from most to least land cover.*

Figure 3. Variation in home range composition with respect to the home range sizes of the study species (a, b, c) in southern Costa Rica. For each individual, three different symbols that sum up to 100% represent percentages of that individual's locations in respective vegetation types. Three Catharus *home ranges >5.8 ha, two* Tangara *ranges > 130 ha, and one 240-ha* Turdus *home range were excluded for purposes of clarity.*
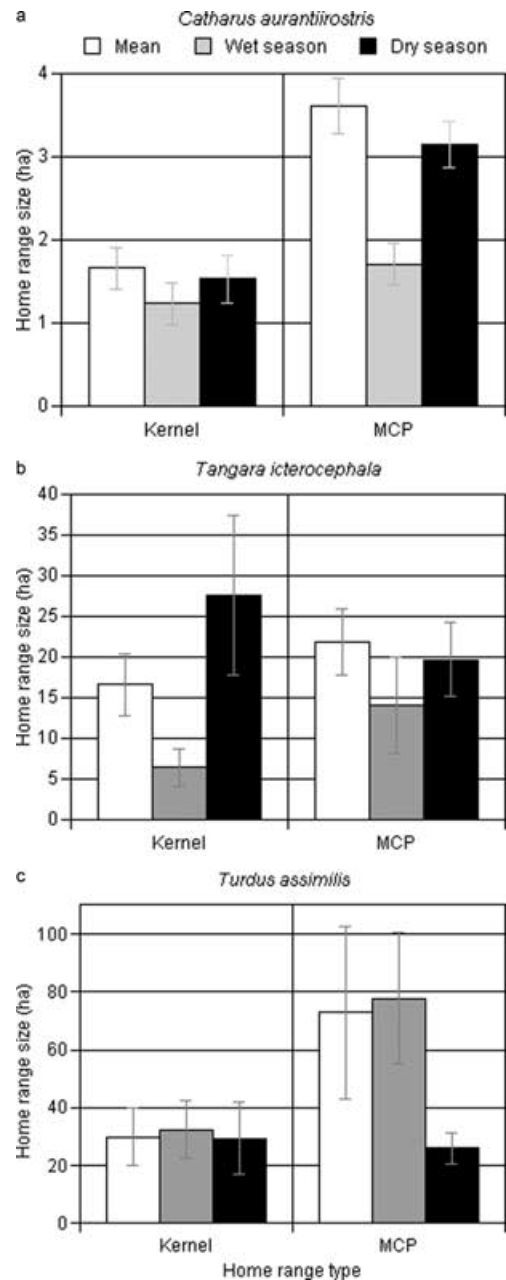
Figure 4. Mean (±SE), dry season, and wet season kernel and minimum convex polygon (MCP) sizes of home ranges of Catharus aurantiirostris, Tangara icterocephala, *and* Turdus assimilis *radio tracked around Las Cruces, southern Costa Rica: (a) kernel = 1.7 ± 0.4 ha, range = 0.3–6.2 ha, wet versus dry Wilcoxon test, Z = 0.55, p = 0.58; MCP = 3.6 ± 0.6 ha, range = 0.6–8.1 ha, wet versus dry Z = 3.53, p = 0.0004; (b) kernel = 16.7 ± 5.3 ha, range = 0.4–174 ha, wet versus dry Z = 1.68, p = 0.091; MCP = 21.8 ± 4.3 ha, range = 1.3–121 ha, wet versus dry Z = 2.13, p = 0.033; (c) kernel = 29.9 ± 10.0 ha, range = 0.5–240 ha, wet versus dry Z = 1.93, p = 0.053; MCP = 72.9 ± 29.9 ha, range = 3.5–363 ha, wet versus dry Z = 2.44, p = 0.015. Mean home range size is based on all home ranges from both seasons.*

Table 2. Comparative breeding success measures for *C. aurantiirostris*, *T. icterocephala*, and *T. assimilis* based on monitored nests in deforested (coffee plantation, pasture, and second growth) and forested (Las Cruces forest, riparian strips, and small fragments) habitats.

Species	Eggs and hatching success[a]		Nestlings and fledging success[a]		Fledglings/nest[b]	
	deforested	forested	deforested	forested	deforested	forested
Catharus	30/45 (457)	6/13 (120)	21/41 (319)	4/6 (69)	0.61	0.54
	1.90 ± 0.09	1.86 ± 0.14	1.85 ± 0.08	1.75 ± 0.25	0.65 ± 0.13 (48)	0.62 ± 0.24 (13)
Tangara	14/27 (230)	1/3 (18)	20/32 (124)	1/2 (7)	0.56	0.17
	1.79 ± 0.11	2	1.65 ± 0.11	1	0.48 ± 0.17 (25)	0 (2)
Turdus	15/28 (309)	6/16 (71.5)	18/21 (217)	6/11 (62)	0.80	0.31
	1.93 ± 0.15	1.33 ± 0.21	1.72 ± 0.14	1.50 ± 0.22	0.77 ± 0.16 (30)	0.24 ± 0.14 (18)
Total (%)[c]	59/100 (59)	13/32 (41)	59/94 (63)	11/19 (58)	0.64 ± 0.09 (103)	0.38 ± 0.13 (32)

[a]*First line for each species: number of nests that successfully hatched eggs or fledged nestlings/the total number of nests with eggs and nestlings (nest days of observation); second line for each species: average number of eggs or nestlings per nest $\pm$ SE.*

[b]*First line for each species: fledglings/nest calculated by multiplying hatching success, fledging success, and average number of eggs per nest; second line for each species: fledglings/nest $\pm$ SE based on all the nests that were monitored from before the eggs hatched until the nest fate was known (sample size).*

[c]*All species combined. Columns 2–5: successful nests/all nests (% success); columns 6–7: fledglings per nest (sample size).*

habitats (clutch: $Z = 0.138$, $p = 0.89$; fledgling: $Z = 0.420$, $p = 0.68$). *Turdus* clutch size in deforested habitats was higher (clutch: $Z = 1.99$, $p = 0.046$; nestlings: $Z = 0.770$, $p = 0.44$). We could not do these comparisons for *Tangara* because we only recorded one successful nest in forested habitats. Percentages of *Catharus* nests that successfully hatched ($\chi^2_1 = 0.80$, $p = 0.37$) or fledged ($\chi^2_1 = 0.66$, $p = 0.42$) young in deforested habitats were not different than those of nests in forest remnants (Table 2). This was also the case for the daily survival rates of eggs (97% in deforested vs. 95% in forested, $Z = 0.80$, $p > 0.05$) and nestlings (93% vs 97%, $Z = -1.5$, $p > 0.05$). The *Tangara* nests did not have higher hatching ($\chi^2_1 = 0.45$, $p = 0.50$) or fledging success ($\chi^2_1 = 0.13$, $p = 0.72$) in deforested habitats (Table 2). Daily survival rates of *Tangara* eggs (94% in deforested vs. 89% in forested, $Z = 0.72$, $p > 0.05$) or nestlings (90% vs. 86%, $Z = 0.34$, $p > 0.05$) also did not differ. Although hatching success (Table 2) of *Turdus* nests did not differ between deforested and forested habitats ($\chi^2_1 = 0.83$, $p = 0.36$), fledging success of nests in forest remnants was lower ($\chi^2_1 = 3.74$, $p = 0.053$). This was also the case for daily egg survival (96% in deforested vs. 86% in forested, $Z = 2.30$, $p = 0.014$) and nearly so for daily nestling survival (99% vs. 92%, $Z = 1.88$, $p = 0.078$). *Turdus* productivity (average number of fledglings per nest; Table 2) was three times lower in forest remnants ($z = 2.08$, $p = 0.037$).

Microclimate

Catharus individuals were found in the hottest and driest microclimate (daily average temperature 23.0° C, humidity 85.7%), followed by *Turdus* (22.2° C and 89.9%) and *Tangara* (22.0° C and 91.1%). All differences were significant (Tukey-Kramer HSD test: all $q^* > 2.43$, all $p < 0.04$), except average habitat temperatures of *Turdus* and *Tangara* ($q^* = 1.24$, $p = 0.42$). Coffee was the hottest and driest vegetation type in general, especially during

midday (1000–1459 hours; average midday temperature 27.6° C, average noon humidity 63.6%), followed by second growth (27.0° C and 72.7%), riparian strips (23.5° C and 85.9%), and forest fragments (23.1° C and 85.8%; all $q^* > 4.38$, all $p < 0.0001$, except between forest and riparian humidity, $q^* = 1.30$, $p = 0.99$). When we compared average habitat temperature and humidity values of birds using the same vegetation type, *Tangara* locations had consistently lower habitat temperature and higher habitat humidity than *Catharus* locations for each vegetation type (all $t > 2.33$, all $p < 0.01$). There were no consistent differences between *Turdus* and other species. Especially in the dry season, all three species, particularly *Tangara*, used cooler vegetation types (such as forest fragments and riparian strips) than coffee plantations during hot and dry midday, and vice versa during cool and humid mornings (all $\chi^2 > 3.86$, all $p < 0.05$; Table 3). Pasture and other agricultural areas were avoided all together.

Discussion

Remnant trees, riparian strips, and small forest patches in the mostly deforested Costa Rican agricultural countryside provided essential dietary, microclimatic, and nesting resources for our focal species, which exhibited a range of sensitivity to deforestation. Arboreal remnants were favored for nesting and foraging, especially during the dry season, perhaps because of their cooler and more humid microclimates (Karr & Freemark 1983). Additional habitat use data from radio tracking the same species in 2004 and 2005 conformed to the pattern we found here (C.H.S., unpublished data). These species persisted in human-dominated countryside on a multiannual time scale without regular recourse to large forest patches, and arboreal remnants played more important roles than their percent land cover would indicate. These birds exhibited two fundamentally different ways of dealing with the loss and fragmentation of their native forest habitat:

Table 3. Habitat preferences of radio-tracked birds in major vegetation types, based on time of day and season (dry/wet).*

Habitat	Catharus aurantiirostris		Tangara icterocephala		Turdus assimilis	
	morning	midday	morning	midday	morning	midday
Coffee	+/+	−/−	+/+	−/−	+/0	−/0
Second growth	−/0	+/0	0/0	0/0	0/0	0/0
Forest	0/0	0/0	−/−	+/+	−/0	+/0
Riparian	0/−	0/+	−/−	+/+	0/0	0/0
Remnant tree	+/0	−/0	0/0	0/0	0/0	0/0

*Morning is between 0500–0959 hours, and midday is between 1000–1459 hours. All $\chi^2 > 3.86$, all $p < 0.05$. For dry season/wet season: +, significant preference; −, significant avoidance; 0, neither preference nor avoidance.

sedentary usage of agricultural areas and high mobility among arboreal remnants.

Forest dependence of our study species (Stiles 1985) positively correlated with home range size and movement distance. By using coffee plantations extensively, *Catharus*, an edge and second-growth species, despite being sedentary and mostly insectivorous (http://www.naturalphotos.com/sekercioglu/science/Sekercioglu Appendix1.doc), fared better in the countryside (Fig. 2a) than most insectivorous forest birds, which have disappeared from this habitat (Sekercioglu et al. 2002). Although most tolerant of deforestation, this species was the least mobile and least frugivorous, traits that limit its function as a seed disperser (Sekercioglu 2006). The more forest-dependent *Tangara* and *Turdus* spent most of their time in arboreal remnants and moved between trees on a regular basis. These birds consumed the fruits of dozens of taxa, likely dispersing the seeds of keystone plants such as *Cecropia*, *Inga*, and *Ficus* spp. (Peres 2000). Probably due to their diverse frugivorous diets and the highly heterogeneous distribution of fruiting trees, these two species showed much greater variation in home range size than did *Catharus* (Fig. 3). Furthermore, *Tangara* home ranges were larger at sites with lower forest cover, potentially increasing seed dispersal in these areas, but likely raising birds' energetic costs and exposure to predators. There were few *Turdus* at less-forested sites, confirming that most *T. assimilis* do not use countryside far from sizable forest patches (Luck & Daily 2003), possibly due to reduced fledgling survival in coffee plantations (Cohen & Lindell 2004).

Because of the scarcity of trees in the area, 69% to 85% of *Tangara* and *Turdus* activity was concentrated in 11% of the landscape that consisted of trees. Even if the deforested countryside around Las Cruces has adequate dietary resources for birds, reduced arboreal cover may increase nest (Robinson et al. 1995), fledgling (Cohen & Lindell 2004) or adult (Gotmark & Post 1996) predation of forest birds. That only 5 out of 156 birds we radio tracked were preyed upon (one *Catharus* in a pasture, two *Tangara* in riparian strips, one *Tangara,* and one *Turdus* in remnant trees) suggests that adult predation is not a major source of mortality. Although some *Catharus* nests

in coffee plantations experienced parasitism by Bronzed Cowbirds (*Molothrus aeneus*), nest predation rates and overall breeding success of *Catharus* or *Tangara* did not differ between forested and deforested habitats (Table 2). Possibly because some forest nest predators decline in agricultural areas with increased human activity (Tewksbury et al. 1999), breeding success of *Turdus* was lower in forested habitats, which Snow and Snow (1963) also observed for *T. fumigatus* in Trinidad. That radio-tracked *T. assimilis* preferred nesting in forest remnants where these birds experienced higher nest predation suggests that these remnants may be "ecological traps" (Schlaepfer et al. 2002). Nevertheless, benefits of higher breeding success in coffee plantations may be negated by lower fledgling survival in this habitat, as observed 40 km away from our study side (Cohen & Lindell 2004) and supported by our pilot study in 2006 (C.H.S., unpublished data).

If nest or fledgling predation rates are high enough, some populations of forest birds in the countryside might not be viable in the long term without regular dispersal from source populations in more extensive forests. Even though we did not observe long-distance movements on a regular basis, these birds can cover 1.2 km (*Catharus*), 3.0 km (*Tangara*), and 5.8 km (*Turdus*) in <2 hours, suggesting that recolonization events are possible. Therefore, even if deforested habitats comprise population sinks for one or more of these species, these sinks can still be beneficial by providing a steady stream of dispersers that colonize vacant territories in forested habitats (Murphy 2001), by increasing the regional population size (Foppen et al. 2000; Murphy 2001), and by increasing the stability and resilience of populations in source patches (Foppen et al. 2000).

The heterogeneous nature of this landscape and the high diversity of fruiting trees are important factors in the persistence of *Turdus* and *Tangara* in the countryside. Because forest bird species also use trees extensively as stepping stones between forest patches (Graham 2001), remnant trees and forest patches are important in increasing landscape connectivity and improving avian survival (Rappole et al. 1989; Taylor et al. 1993; Powell & Bjork 2004; Peh et al. 2006).

In addition to providing food, sheltering birds from predators, and increasing landscape connectivity, Las Cruces arboreal remnants were also microclimatic refuges (Table 3), particularly in the dry season (Greenberg et al. 1997*a*). In our study area 10- to 20-m-wide riparian strips embedded in hot coffee plantations had the same temperature and humidity profile as the forest interior >100 m from the edge, likely due to the year-round presence of water in these riparian strips. Not only did *Tangara* and *Turdus* prefer microclimates similar to those of forest patches and riparian strips, *Tangara* individuals were consistently tracking lower temperatures and higher humidity levels, differing from *Catharus* even in identical vegetation types.

Arboreal remnants in the countryside connect bigger forest fragments and serve as important habitats in their own right, enabling some mobile or habitat opportunist forest bird species, at least in the medium term, to persist in human-dominated areas. If managed effectively, these remnants can provide many resident and migrant species with additional territories (Greenberg et al. 1997*b*) and connect the populations of more sedentary, specialized, and forest-restricted species (Powell & Bjork 1994; Sieving et al. 2000; Renjifo 2001; Sekercioglu et al. 2002; Harvey et al. 2005). Although the protection of extensive natural vegetation is essential for the preservation of major elements of biodiversity (Bruner et al. 2001; McKinney 2002), particularly habitat specialists with limited mobility (Owens & Bennett 2000; Sekercioglu et al. 2002; Sekercioglu et al. 2004), protected areas alone are not adequate in the face of humanity's growing demands (Liu et al. 2001; Dirzo & Raven 2003).

The crucial question remains whether arboreal resources can be maintained or augmented sufficiently to ensure the long-term survival of diverse tropical countryside avifaunas. In our study region, already heavily deforested, remnant trees are regularly cut for timber or firewood, valuable tree species in fragments are extracted as needed, and riparian strips and forest fragments are frequently degraded by cattle. Our results suggest that the conservation value of working landscapes in the tropics can be boosted significantly with relatively little investment and conflict because remnant trees, riparian strips, forest fragments, and their residents also supply people and domestic animals with fruits, shade, clean water, crop pollination, and other ecosystem services (Daily 1997; Ricketts et al. 2004; Harvey et al. 2005; Sekercioglu 2006). A good example can be seen in Monteverde, Costa Rica, where a combination of conservation easements, local education, reforestation, and economic incentives for landowners, including birdwatching ecotourism (Sekercioglu 2002), has successfully reconnected and expanded the habitat of Resplendent Quetzals (*Pharomacrus mocinno*) in the countryside (Powell & Bjork 1994). Similar initiatives are urgently needed to restore tropical countrysides with ecological approaches (Lamb et al. 2005), such as agroforestry schemes (Schroth et al. 2004). These will reduce the pressures on reserves, maintain essential ecosystem services, improve the biodiversity-carrying capacity of agricultural landscapes, and help integrate them with protected areas. We recommend that significantly more conservation effort be directed at enhancing the conservation value of tropical countryside, thus providing disappearing species with more options.

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