

AN EXPERIMENTAL STUDY OF HABITAT SELECTION BY BIRDS IN A COFFEE PLANTATION

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Abstract. Unique components of tropical habitats, such as abundant vascular epiphytes, influence the distribution of species and can contribute to the high diversity of many animal groups in the tropics. However, the role of such features in habitat selection and demography of individual species has not been established. Understanding the mechanisms of habitat selection requires both experimental manipulation of habitat structure and detailed estimation of the behavioral and demographic response of animals, e.g., changes in movement patterns and survival probabilities. Such studies have not been conducted in natural tropical forest, perhaps because of high habitat heterogeneity, high species diversity, and low abundances of potential target species. Agroforestry systems support a less diverse flora, with greater spatial homogeneity which, in turn, harbors lower overall species diversity with greater numerical dominance of common species, than natural forests. Furthermore, agroforestry systems are already extensively managed and lend themselves easily to larger scale habitat manipulations than protected natural forest. Thus, agroforestry systems provide a good model environment for beginning to understand processes underlying habitat selection in tropical forest animals. Here, we use multistate, capture–recapture models to investigate how the experimental removal of epiphytes affected monthly movement and survival probabilities of two resident bird species (Common Bush-Tanager [*Chlorospingus ophthalmicus*] and Golden-crowned Warbler [*Basileuterus culicivorus*]) in a Mexican shade coffee plantation. We established two paired plots of epiphyte removal and control. We found that Bush-Tanagers were at least five times more likely to emigrate from plots where epiphytes were removed compared to control plots. Habitat-specific movement patterns were not detected in the warbler. However, unlike the Golden-crowned Warbler, Common Bush-Tanagers depend upon epiphytes for nest sites and (seasonally) for foraging. These dispersal patterns imply that active habitat selection based on the presence or absence of epiphytes occurs in *C. ophthalmicus* on our study area. Survival rates did not vary with habitat in either species. Interestingly, in both species, survival was higher in the nonbreeding season, when birds were in mixed-species flocks. Movement by Common Bush-Tanagers into areas with epiphytes occurred mostly during the breeding season, when mortality-driven opportunity was greatest.

Key words: *Basileuterus culicivorus*; *Chlorospingus ophthalmicus*; coffee plantations; Common Bush-Tanager; epiphytes; Golden-crowned Warbler; habitat manipulation; multistate capture–recapture models; tropical ecosystems.

INTRODUCTION

A strong gradient of increasing richness of bird species can be found between temperate and tropical forests (Terborgh 1980). What ultimate and proximate factors contribute to the development of latitudinal gradients in diversity remains a classic question of ecology: a question that has no single answer. A number of authors have argued that bird species are “added” to Neotropical over equivalent temperate systems because of the presence of stable habitat features or resources,

such as bamboo (Parker 1982, Kratter 1997), aerial leaf litter (Gradwohl and Greenberg 1982, Remsen and Parker 1984, Rosenberg 1997), and abundant epiphytic growth (Remsen 1985, Nadkarni and Matelson 1989, Sillett 1994, Sillett et al. 1997), not present in more depauperate, temperate zone habitats.

Patterns in community attributes, such as species richness, are based in the distribution of species across habitats that result, in part, from decisions of individual animals (Morris 2003). Habitat selection therefore integrates the behavior of individuals with ecological and evolutionary processes. Decisions about where to settle determine the distribution of a population across space (Jones 2001), and thus set the selective environment shaping adaptations. The term “habitat selection” is often used interchangeably with “habitat use,” a static description of a species’ distribution. However, the power of the concept of habitat selection lies in an

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understanding of the mechanisms by which individuals chose habitat and the consequences of that decision. Over the past 20 years, the traditional approach of correlating the abundance of individuals of a given species with specific habitat features or overall habitat gestalt has given way to studies that investigate the dynamic response of individuals (Martin 1985, Morse 1985, Wiens 1986, Jones 2001).

Experimental manipulations are the best approach for revealing the mechanisms of habitat selection. Laboratory experiments (Partridge 1974, Greenberg 1992) are most powerful for determining intrinsic preferences. Field experiments, although logistically difficult, are superior for examining habitat selection as it actually occurs under natural conditions, using more realistic spatial scales, and incorporating social interactions. The response of individuals to manipulations can be estimated by examining the patterns of immigration and emigration to and from the effected habitat patch. Furthermore, demographic parameters, such as fecundity and survival probability provide information about the consequences of habitat selection (Loery et al. 1997). Although experimental manipulations in the field are now frequently used to assess the influence of one particular habitat feature, like snags, understory cover, and leaf litter, on temperate bird assemblages (e.g., Scott 1979, Wiens 1986, Lohr et al. 2002), such studies have not been attempted in natural tropical forest. The paucity of field manipulations in tropical forest systems can be attributed to four factors: (1) local heterogeneity of forest composition (Condit et al. 2002) and structure, making the establishment of replicate plots difficult; (2) high tree species diversity; (3) low abundance of individual species (e.g., Loiselle 1988); and (4) overall structural complexity of the habitat.

Tropical agroforestry systems, such as those involved with the cultivation of coffee (*Coffea arabica*), can provide a simplified, model forest environment that allows habitat manipulations while circumventing the aforementioned complications. Even relatively diverse shaded coffee plantations have a far more depauperate tree flora, usually dominated by a few species, and possess a relatively simple and spatially homogeneous vegetative structure, with only two major layers of vegetation, compared to intact forest. Replicate control and experimental plots similar in initial habitat structure can therefore be readily established. Coffee agroecosystems can also exhibit ecological attributes that are qualitatively similar to those of natural forests. For example, coffee plantations in the highlands of eastern Mexico provide microclimates and pollinator assemblages, and enable reproductive success for vascular epiphytes that are comparable to those in intact forest (Solis-Montero et al. 2005).

In 1999, we initiated an experimental manipulation of avian habitat structure via epiphyte removal on a Mexican coffee plantation (see *Methods*). The effect of epiphytes on birds can be direct or indirect. Direct

effects include the use of epiphytes for nesting and foraging sites. Indirect effects include the influence on overall insect abundance and microclimate. As part of the epiphyte removal study, Cruz-Angón and Greenberg (*unpublished data*) determined through canopy-fogging that arthropods are both more diverse and numerous in trees with epiphytes compared to similar trees with epiphytes removed. Moreover, areas with epiphytes experienced greater canopy cover and hence a more buffered microclimate due to the shade provided by epiphytes. Cruz-Angón and Greenberg (2005) found that 15 forest bird species were significantly more abundant in sites with epiphytes, whereas only three open-habitat species were significantly more abundant in the sites where epiphytes were experimentally removed from shade trees.

Here, we test if the above patterns in avian diversity were a result of active habitat selection in individual birds. We focus our analysis on the two most abundant resident species, the Common Bush-Tanager (*Chlorospingus ophthalmicus*) and the Golden-crowned Warbler (*Basileuterus culicivorus*). Together these species comprised 35% of the resident birds surveyed on the plot (A. Cruz-Angón, *unpublished data*) and are the only two species with sufficient sample size to undertake the modeling approach described in this paper. Both species were more numerous in plots with epiphytes (Cruz-Angón and Greenberg 2005). However, Common Bush-Tanagers were 118% more abundant on plots with epiphytes relative to removal plots (mean per survey = 12.2 ± 0.5 vs. 5.6 ± 0.5 [mean \pm SE]), whereas only 20% more Golden-crowned Warblers were found on epiphyte-containing plots (4.2 ± 0.4 vs. 3.5 ± 0.4). Bush-Tanagers commonly used epiphytes for nesting and foraging. In contrast, the warbler nested on the ground and rarely foraged in epiphytes (Cruz-Angón and Greenberg 2005), so that any benefits of epiphytes to this species were probably indirect (such as humidity of the ground layer). We use systematic recapture and resighting of color-banded individuals and multistate, mark-recapture models (Hestbeck et al. 1991, Brownie et al. 1993, Nichols and Kendall 1995) to assess the role of habitat selection (movement) and its consequences (mortality) in these two species. We predicted that epiphyte removal would result in higher movement and lower survival probabilities in the bush-tanager compared to the warbler.

METHODS

Experimental design

The study site was a 35-year-old, 200-ha shaded coffee plantation located in “La Orduña” (19°28'03" N, 96°55'58" W; 1220 m elevation), in Coatepec, near Xalapa, Veracruz, Mexico. Epiphyte removal from shade trees is part of normal management practices of coffee plantations in the Xalapa region. By convincing farm managers to remove epiphytes from two plots, we were able to document the ecological effects of this

procedure (see Cruz-Angón and Greenberg 2005). In 1999, we established two experimental sites located in the north and south sides of the coffee plantation, respectively, and separated by a distance of 1 km. Each site was divided into two adjacent 3-ha plots surrounded by a matrix of shaded coffee with epiphytes. Plantation workers removed the epiphytes from all shade trees between 1999 and early 2000 in one of the two plots at each site (hereafter "treatment": E+ = control, with epiphytes, E- = epiphytes experimentally removed); otherwise epiphytes were not manipulated in the rest of the farm. The four plots were delineated with flagging tape into a 25 × 25 m grid to facilitate mapping and resighting banded birds. Based on vegetation surveys (Cruz-Angón and Greenberg 2005), canopy cover was the only habitat structure variable, in addition to the presence or absence of epiphytes themselves, that significantly differed between experimental and control plots; the floristic composition of trees did not differ, with *Inga jinicuil* comprising 48–77% of total trees. Canopy cover was significantly higher in control plots, mostly due to the shading of the epiphytes themselves. Because bird abundance did not differ between sites (Cruz-Angón and Greenberg 2005), we pooled data for the north and south sites before modeling the effect of epiphytes on bird movement and survival.

Focal species

Common Bush-Tanagers are 15–20 g passerines that occur from central Mexico to northern Argentina and Bolivia in mid-elevation (1000–2500 m) primary and secondary forests (Isler and Isler 1987, Howell and Webb 1995). In coffee plantations of central Veracruz, bush-tanagers are most common in older and less managed coffee farms (A. Cruz-Angón, *personal observation*). This species is considered a generalist, but several authors associate them with abundant epiphytes (Isler and Isler 1987, Howell and Webb 1995, Richter 1998). In our study site, 30% of their foraging efforts are on epiphytic substrates and 80% of their nests are built inside clumps of vascular epiphytes (Cruz-Angón and Greenberg 2005). During the September–February nonbreeding (dry) season, bush-tanagers move in conspecific and mixed-species flocks, but during the March–August breeding (wet) season, pairs separate from flocks to defend territories of about 0.5–1 ha.

Golden-crowned Warblers are 9–12 g passerines that occur from the lowlands to 2100 m and are common in dense understory habitats in submontane humid forests, forest edges, second growth, and plantations from northeastern Mexico to northern Argentina (Curson et al. 1994). We did not observe any nesting association with epiphytes for this ground and understory-foraging species in central Veracruz (Cruz-Angón and Greenberg 2005). Golden-crowned Warblers occur in small conspecific groups and join mixed species flocks during the September–February nonbreeding season. Pairs defend

0.5–1 ha territories in the March–August breeding season.

Data collection

Birds were captured with mist nets and each individual was marked with a unique combination of colored plastic leg bands. We set up 14 12-m permanent mist net locations per plot and conducted nine mist-netting sessions per plot from 30 May 2000 to 15 March 2002, totaling 3276 mist net hours. Mist nets were open from 07:00–13:30 hours. Birds captured were aged by plumage characters, eye color, and skull ossification following Pyle et al. (1987) and Howell and Webb (1995). Reproductive state was determined by the condition of a brood patch or cloacal protuberance. However, both species are monomorphic, making sex determination at capture only possible for breeding adults.

We used resighting surveys and mist net recaptures to generate data on individual survival and movement. Resighting surveys entailed intensive searching for color-banded individuals from 07:00 to 10:30 hours, and were conducted from 31 May 2000 to 23 April 2002, totaling 560 observation hours (140 hours per plot). We alternated survey days between plots, covering one plot day per survey period. Plots were surveyed in May, October, and December 2000, and at least once per month from May 2001 to April 2002. When a marked individual was resighted, we noted its color band combination and its location based on the nearest plot grid intersection. All mist-netting and resighting surveys were restricted to the four study plots; no individuals caught and banded in one side of the coffee plantation were seen or caught in the opposite side of the study area. In order to obtain robust parameter estimation, observations were pooled into 15 monthly encounter occasions: May, October, and December 2000, and May 2001–April 2002. A bird detected in more than one habitat in a given month was assigned to the habitat that had the most encounters within that month. If a tie existed, we assigned the bird to the habitat that minimized information loss on movements (Béchet et al. 2003).

Data analysis

We estimated monthly survival, movement, and recapture probabilities with open-population, multistate capture–recapture models implemented in program MARK (version 4.1; White and Burnham 1999). Our candidate model set contained four models (see Tables 1 and 2) that were chosen prior to data analysis based on our understanding of Common Bush-Tanager and Golden-crowned Warbler biology and on the sample size limitations of our data set. In all models, survival (S) and movement (ψ) were parameterized as functions of age class (adult, juvenile) and season (breeding, nonbreeding). Both S and ψ for individuals captured as juveniles were modeled as adults in March following

TABLE 1. Estimates of monthly survival probabilities, S (mean \pm SE) for Common Bush-Tanagers and Golden-crowned Warblers on a coffee plantation in Coatepec, Veracruz, Mexico, 30 May 2000–23 April 2002.

Species	Survival probability, S		
	Breeding† (Mar–Aug)	Nonbreeding† (Sep–Feb)	Transient‡
Common Bush-Tanager			
Adult	0.88 \pm 0.02	0.99 \pm 0.01	0.98 \pm 0.03
Juvenile	0.81 \pm 0.10	0.99 \pm 0.01	0.70 \pm 0.07
Golden-crowned Warbler			
Adult	0.89 \pm 0.03	0.99 \pm 0.01	0.93 \pm 0.14
Juvenile	0.95 \pm 0.29	0.94 \pm 0.04	0.96 \pm 0.04

† Resident individuals.

‡ S_i to S_{i+1} for adults in the nonbreeding season and for juveniles prior to their first breeding season, where i = initial capture occasion.

their hatch year (i.e., at the start of their first breeding season). We investigated if epiphyte removal affected survival or movement by modeling S and ψ as functions of habitat (E+, E–). To account for heterogeneity of capture and to provide unbiased estimates of resident survival, all models also included a transient parameterization of S for adults in the nonbreeding season and for juveniles prior to their first breeding season (Pradel et al. 1997, Hines et al. 2003). Recapture probability (p) was always parameterized as fully time dependent, but independent of age class or habitat. We tested the same candidate model set for both species. Models were fit using a sine link function and ranked by second-order Akaike's information criterion (AIC_c) scores; relative likelihood of each model was estimated with AIC_c weights (w_i ; Burnham and Anderson 2002). Results are given as a parameter estimate \pm 1 SE.

RESULTS

Patterns of monthly survival and recapture probabilities were similar between species. In both the bush-tanager and warbler, S differed by age and season (Table 1), but was not strongly affected by the presence or absence of epiphytes (Table 2). Adults had higher

monthly survival probabilities than juveniles, and mortality of both age classes was concentrated during the breeding season (Table 2). Monthly recapture probabilities for the bush-tanager ranged from 0.09 \pm 0.06 to 0.81 \pm 0.08, and from 0.09 \pm 0.04 to 0.48 \pm 0.09 for the warbler.

Based on Σw_i , habitat-specific movement (Table 2: models 1 and 3) in the Common Bush-Tanager was nine times more likely, given our data, than habitat-independent movement (Table 2: models 2 and 4). During the breeding season, adults were at least three times more likely to move from E– habitat to E+ habitat than in the opposite direction (Fig. 1). Adult movement probabilities during the nonbreeding season were lower than during the breeding season, but the probability of moving from E– habitat to E+ habitat was still higher than the probability of moving in the opposite direction (Fig. 1). High variability made interpretation of juvenile movement inconclusive. Juvenile movement probabilities were not appreciably different between habitats, but tended to be higher during the March–August breeding season ($\psi[E- \text{ to } E+] = 0.20 \pm 0.14$; $\psi[E+ \text{ to } E-] = 0.35 \pm 0.20$) than during the nonbreeding season ($\psi[E- \text{ to } E+] = 0.11 \pm 0.07$; $\psi[E+ \text{ to } E-] = 0.07 \pm 0.06$).

TABLE 2. Models of monthly survival (S), recapture (p), and movement (ψ) probabilities for Common Bush-Tanagers ($N = 112$ birds) and Golden-crowned Warbler ($N = 80$ birds) on a coffee plantation in Coatepec, Veracruz, Mexico, 30 May 2000–23 April 2002.

Rank	Model	K	AIC_c	Δ_i	w_i
Common Bush-Tanager					
1	$S_{\text{age} \times \text{season}}, p_t, \psi_{\text{age} \times \text{season} \times \text{habitat}}$	28	986.29	0	0.89
2	$S_{\text{age} \times \text{season}}, p_t, \psi_{\text{age} \times \text{season}}$	24	990.66	4.37	0.10
3	$S_{\text{age} \times \text{season} \times \text{habitat}}, p_t, \psi_{\text{age} \times \text{season} \times \text{habitat}}$	34	996.39	10.10	0.01
4	$S_{\text{age} \times \text{season} \times \text{habitat}}, p_t, \psi_{\text{age} \times \text{season}}$	30	1000.49	14.20	0.00
Golden-crowned Warbler					
1	$S_{\text{age} \times \text{season}}, p_t, \psi_{\text{age} \times \text{season}}$	24	710.80	0	0.96
2	$S_{\text{age} \times \text{season}}, p_t, \psi_{\text{age} \times \text{season} \times \text{habitat}}$	28	717.35	6.56	0.04
3	$S_{\text{age} \times \text{season} \times \text{habitat}}, p_t, \psi_{\text{age} \times \text{season}}$	30	725.88	15.08	0.00
4	$S_{\text{age} \times \text{season} \times \text{habitat}}, p_t, \psi_{\text{age} \times \text{season} \times \text{habitat}}$	34	733.37	22.58	0.00

Notes: Columns provide model rank, model name, number of estimable parameters (K), second-order Akaike's information criterion values (AIC_c), AIC_c differences (Δ_i), and AIC_c weights (w_i). Subscripts indicate parameterizations for S , p , and ψ (see Methods).

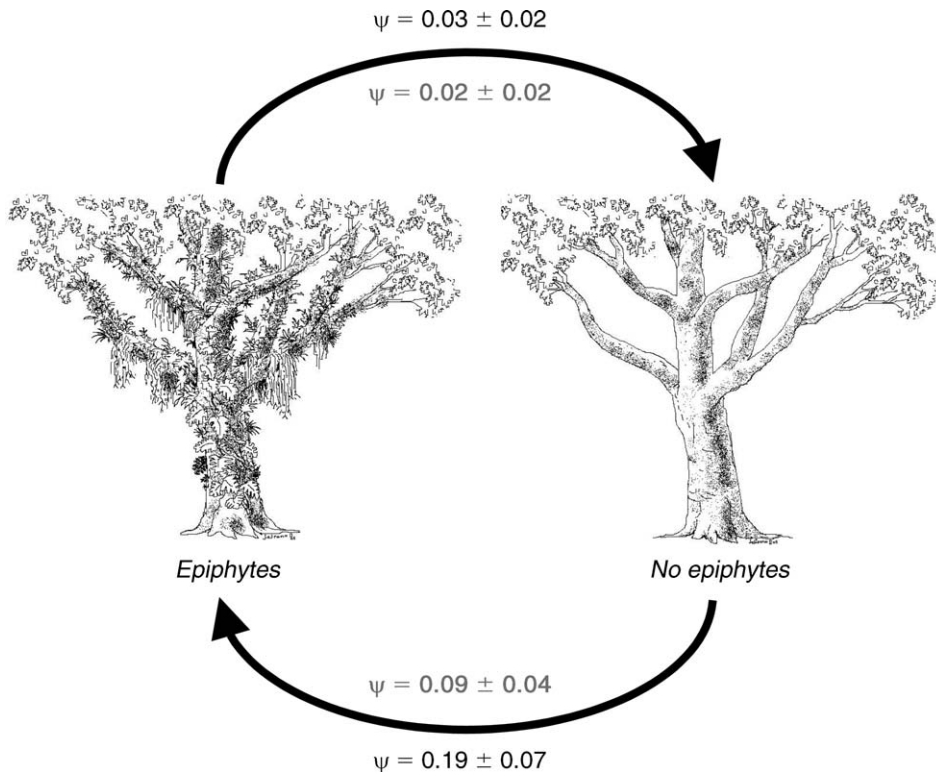


FIG. 1. Based on the best-fit model (Table 1), estimated monthly transition probabilities ($\psi \pm 1$ SE) for adult Common Bush-Tanagers differed between experimental shade coffee plots with epiphytes (left) and without epiphytes (right). Values in black indicate transition probabilities during the breeding season; nonbreeding season values are in gray.

Monthly movement probabilities of the Golden-crowned Warbler did not differ between habitats: based on $\sum w_i$, habitat-independent movement (Table 2: models 1 and 3) was 24 times more likely than habitat-

specific movement (Table 2: models 2 and 4). Like the bush-tanager, adult warblers tended to move between habitats more during the breeding season than during the nonbreeding season (Fig. 2). Juvenile warblers were

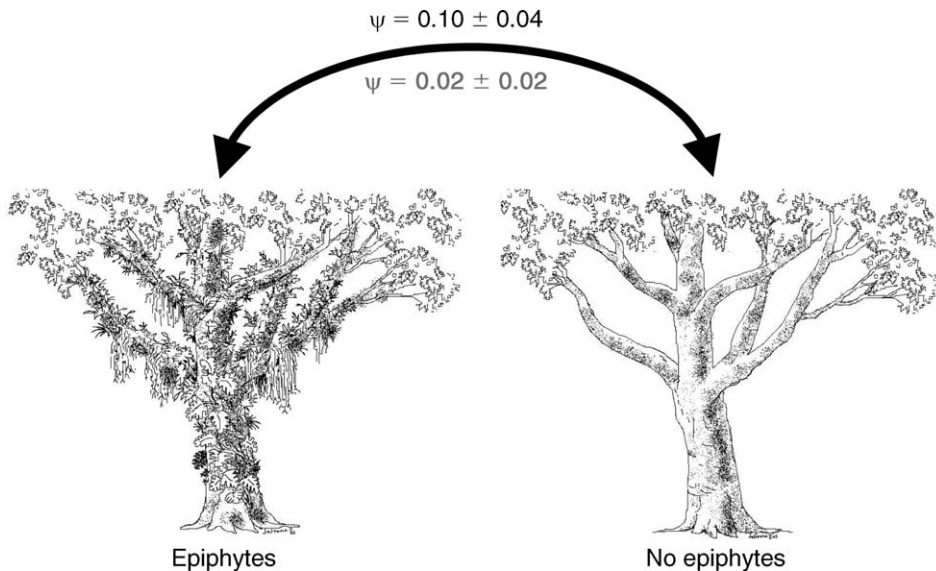


FIG. 2. Based on the best-fit model (Table 1), estimated monthly transition probabilities ($\psi \pm 1$ SE) for Golden-crowned Warblers did not differ between experimental shade coffee plots with epiphytes (left) and without epiphytes (right). Values in black indicate transition probabilities during the breeding season; nonbreeding season values are in gray.

never observed moving between habitats during the breeding season ($\psi[\text{Mar–Aug}] = 0$) and seldom moved during the nonbreeding season ($\psi[\text{Sep–Feb}] = 0.03 \pm 0.02$).

DISCUSSION

Epiphytes as a cue for habitat selection

Multistate, mark–recapture models in conjunction with a field manipulation allowed us to infer, for the first time, habitat selection in a tropical bird species based on a single habitat feature. Our results provide strong evidence that Common Bush-Tanagers actively select habitat on the basis of the presence or absence of epiphytes. As predicted, bush-tanagers selectively moved from coffee plots where epiphytes were removed from shade trees to plots with intact epiphyte cover. In contrast, Golden-crowned Warblers showed no difference in the probability of movement towards or away from plots with epiphytes. In Coatepec, Common Bush-Tanagers nest and forage in epiphytes, whereas Golden-crowned Warblers do not regularly use epiphytic substrates. Our habitat selection results are therefore consistent with the importance of epiphytes in the foraging and breeding requirements of the two species. Higher bird occupation and use of the epiphyte plots may be based on an additional effect of epiphyte presence: canopy-fogging experiments (A. Cruz-Angón and R. S. Greenberg, *unpublished data*) showed that arthropods were twice as abundant in tree canopies with epiphytes than in those with epiphytes removed.

Fitness consequences of habitat selection

Contrary to our prediction, monthly survival probabilities of both species, at least in the short term, were unrelated to the presence or absence of epiphytes, despite the fact that bush-tanagers selected habitat with intact epiphyte cover. One explanation for this pattern would be an ideal free distribution (Fretwell and Lucas 1970) for Common Bush-Tanagers. Epiphytes could be a cue for preferred habitat, but under the conditions of our experiment, density-dependent factors might limit the benefits of occupying such habitat. Alternatively, annual fecundity of bush-tanagers, not quantified in this study, rather than survival, could be the key vital rate associated with epiphytes. A complete understanding of the consequences of habitat selection by Common Bush-Tanagers requires further study and additional years of mark–recapture data.

Seasonal patterns of movement, survivorship, and habitat selection

Movement and survival probabilities of both species differed between the breeding and nonbreeding seasons. Movements between E+ and E– habitats by Common Bush-Tanagers occurred primarily in the breeding season, when individuals were territorial. Adult and hatch-year mortality for both species was also concentrated during the breeding season. To our knowledge,

these are the first estimates of seasonal survival probabilities for a tropical resident bird species. Higher breeding-season mortality might be the result of higher levels of starvation and predation during that season (Martin 1987). Adult Common Bush-Tanagers and Golden-crowned Warblers do not join mixed-species flocks while breeding, which can be an important antipredation strategy of tropical birds (Powell 1985). The benefits of flocking might be enhanced in coffee plantations, where a simplified habitat structure may favor predator success. Indeed, we observed an unusual number of attacks by predators, such as accipiter hawks, in the coffee plots, and most of these occurred during the breeding season (A. Cruz-Angón, *personal observation*). Finally, juvenile passerines appear to be most vulnerable to predation and starvation immediately after fledging (e.g., Anders et al. 1997, Cohen and Lindell 2004), which could contribute to lower survival probabilities of juveniles that we documented between March and August.

Common Bush-Tanagers and Golden-crowned Warblers are territorial toward conspecifics when breeding in our study system. Thus, successful immigration into preferred breeding habitat probably depends, in part, upon mortality-driven turnover of territory holders. Both species show a peak in local habitat occupancy during the breeding season and this is, therefore, the time of the year where active habitat selection should primarily occur. In fact, our models and data demonstrate that in Common Bush-Tanagers, movement into epiphyte-containing habitat occurs during the breeding season. We conclude that habitat selection in the bush-tanager comes at the nexus of behavior and demographic opportunity.

Studying avian habitat selection in agroforestry systems

Our results demonstrate the usefulness of studies in agroforestry systems and the power of multistate mark–recapture models to understanding habitat selection. Mechanistically determining the role of individual factors in habitat selection is largely impossible, especially in complex, heterogeneous tropical habitats where many ecological processes covary. Taking advantage of a common practice of epiphyte removal in coffee plantations, we were able to single out this important habitat character as a determinant of the habitat selection of one bird species, and not important for habitat selection of another. Moreover, our data revealed the seasonal context in which habitat selection occurs. Similar studies of individually marked animals in agroecosystems could elucidate the operation and timing of habitat selection mechanisms for a broad range of tropical and temperate species.

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