

Spatial Post-Breeding Segregation of 1st-Year and Adult Common Bush-Tanagers in a Guatemalan Cloud Forest

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Abstract: I captured birds in a central Guatemalan cloud forest (Sierra Yalijux) in two adjacent habitats, with different habitat structure to assess the influence of land use on bird populations. The regional population of Common Bush-Tanager (*Chlorospingus ophthalmicus*) showed a pattern of spatial separation of 1st-year individuals *vs.* adults, a pattern not shown so far for any bird species. During the early post-breeding season, I captured similar numbers of adult individuals in both natural and young secondary forest (38 *vs.* 43), while 1st-year individuals were captured mainly in young secondary vegetation (3 *vs.* 40). The findings indicate that inexperienced, young or less competitive individuals may use other habitats than adults, at least temporarily.

Keywords: *Chlorospingus ophthalmicus*, Common Bush-Tanager, Guatemala, habitat selection, habitat quality, juvenile age segregation, tropical montane cloud forest.

INTRODUCTION

Birds select a habitat to perform vital functions, like breeding, recovering during stopover, foraging during post-breeding, or wintering (Rappole 1988, 1995). The selection of habitat for these functions is determined mainly by the quality and availability of resources (Rappole 1995) and ability to disperse (Vega-Rivera *et al.* 1999). Habitat selection is strongly affected by competitive ability, which in turn is affected in part by individual experience in defending a territory against other individuals (Winkler *et al.* 1995) and experience learned or inherited from parents (Dingemanse *et al.* 2003). Habitat selection, and its associated density and frequency-dependent evolution, has a profound influence on the distribution of individuals.

Less experienced competitors such as juveniles should be expelled during post-breeding from their parents' high quality breeding grounds and may therefore show higher abundance in less-suitable habitat such as secondary vegetation. In many species, young and old individuals should hence segregate after breeding and forage in different areas (Winkler *et al.* 1995). However, it has not yet been shown that such segregation should occur in different habitats.

Here I present data indicating that during the early post-breeding period, young individuals of the Common Bush-Tanager (*Chlorospingus ophthalmicus*) show unequal between-habitat distribution, being more common than adults in a supposedly lower quality habitat.

METHODS

Study Area

The study site is located in the Sierra Yalijux and belongs to the north-easternmost slopes of the northern Cordillera of Guatemala (Municipio de Tucurú, south-east Alta Verapaz, central Guatemala; center coordinates: 15°22'N, 90°03'W; 1,950 to 2,550 m). In Guatemala, the lower altitudinal border of cloud forests is around 1,800 m a.s.l. The total natural (climax) forest above 1,800 m covers an estimated 5,500 ha in the Sierra Yalijux (Markussen 2004). In this region, the climate is tropical to sub-tropical (MAGA 2001, Markussen 2004).

I chose a 102 ha study plot in the Sierra Yalijux near the settlement of Chelemhá (Fig. 1) to determine and analyze the bird community and vegetation structure between natural forest and secondary vegetation (results on bird community and deforestation are summarized for instance in Renner 2005 and Renner *et al.* 2006). Bordering the 51-ha primary forest study plot was a similar-sized secondary vegetation section with dense bush, shrub and bracken. Young secondary forest is less favorable for a variety of forest birds in tropical areas (e.g., Sodhi 2002, Waltert *et al.* 2005) although this has been disputed (e.g., Winkler *et al.* 1995). The environment in Chelemhá, a Central Guatemalan cloud forest, consists mainly of two different habitat types, (1) natural forest and (2) different stages of young secondary forest re-growth.

Study Plot Design

The study plot design in combination with capture-mark-recapture methods is adequate to measure age distribution of birds. Most studies with capture-mark-recapture methods intend to identify differences in diversity statistics (e.g., Terborgh *et al.* 1990, Sodhi 2002, Waltert and Mühlberg 2001, Waltert *et al.* 2005) and use spatially indepen-

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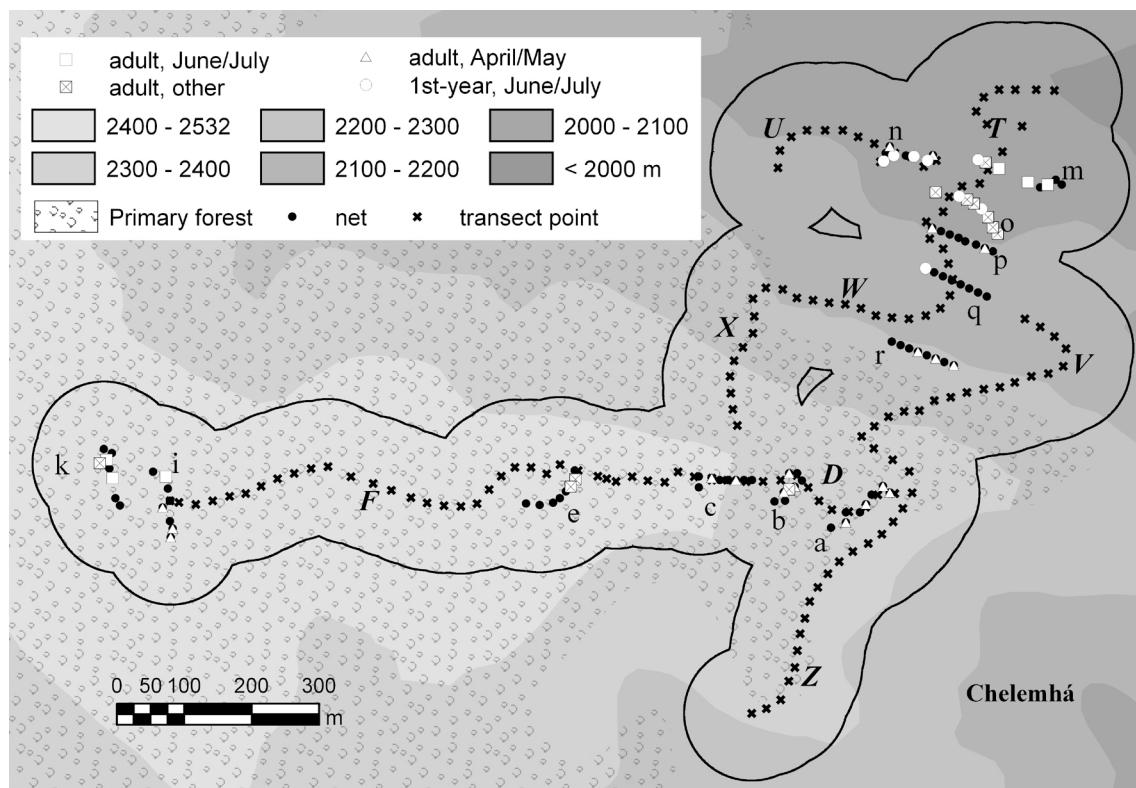


Fig. (1). Localities of 1st-year and adult captures of *Chlorospingus ophthalmicus*; study plot design with distribution of the 12 net-lines (small letters) and transects (capital letters, italics); black outline indicates 100 m buffer distance from transect point or mist net localities. Note, through projection of the 3D slope to 2D image, some net lines and transects appear closer to each other on map than they are; this is particularly true for the young secondary forest area.

dent samples to reduce pseudo-replication (Hurlbert 1984). Secondary forest and natural forest sample sites are separated by at least 250 m, but typically more than 5,000 m. Contrastingly, habitat selection can be revealed simply by plots of density in adjacent habitats or located closely to each other (Morris 2003). Thus, the two 51-ha plots in Chelemhá (natural forest vs. young secondary forest) are well suited to test the distribution of Common Bush-Tanagers in two different habitats.

Surveying Methods

Bird surveys employing standardized mist netting were conducted during the main breeding season between March and September in 2001 and 2002. In the Sierra Yalijux, the Common Bush-Tanager is breeding mainly in May (own observations) and 1st-year individuals are present from about late May to July (own data). I established six mist net lines in each part of the study plot, six in natural forest and further six in secondary vegetation (Fig. 1). All net lines were distributed randomly along a path with distances between 100 and 900 m. Each net line consisted of eight nets, with each net 12.0 m long and 2.5 m high. I kept a distance of 12 m gaps between nets. Nets were opened for 8.5 h per capture day. I captured for two days at each line in 2001 and for four days in 2002 with a total of 4,896 net hours (hours as per 12 m net). Each capture day at any given net line was separated by at least two weeks. Bird identification was made using Howell and Webb (1995). During mist-netting procedures, each individual was banded with an individually numbered,

aluminum leg band for capture-mark-recapture experiments. Body mass of each individual was determined with spring scales (Pesola 100 g) weighing the bird in a clean and airy cotton bag and subtracting the bag's mass afterwards. Differences in numbers of adults vs. 1st-year birds were compared with the non-parametric Mann-Whitney-U-Test, with the significance level set to $P = 0.05$. Capture sequence was altered between natural forest and young secondary forest to sample both habitats during the breeding and non-breeding seasons. The capture effort was equal in both habitats and conducted at the same time intervals.

Common Bush-Tanager Plumage Characteristics and Biology

In Central America, the Common Bush-Tanager 1st-year individuals (young fledged in about May of any given year) are easily distinguishable from adults by their different plumage until late post-breeding (Howell and Webb 1995). In the study region, 1st-year Common Bush-Tanager were distinguishable and present from late May until July. After that period, they had undergone post-juvenile molt, rendering them indistinguishable from adults. Heads of immature individuals are more olive and throats and underparts are washed and appear less colorful than those of adults (Howell and Webb 1995).

Common Bush-Tanagers are frequent residents in Central American rainforest between 1,000-3,500 m and sometimes move to lower elevations during northern winter. They are abundant in closed and open forests but rare or absent in

arable land and farmland without denser vegetation or bushes. Some Common Bush-Tanagers occur in flocks during their non-breeding season in the study area.

RESULTS

Capture-Mark-Release

I captured Common Bush-Tanagers 218 times in total in all 12 mist net lines over the two breeding and post-breeding seasons in 2001 and 2002 (Table 1). Of these, I banded 148; the remainders were recaptures, or birds released prior to banding for different reasons (see below for recaptures).

While I captured similar numbers of adult individuals in natural forest and the bordering secondary vegetation (38 vs. 43 1st captures, respectively; Table 1, Fig. 1), 1st-year individuals were captured significantly more often in secondary vegetation (3 vs. 40, $P = 0.02$). The remaining captures (24) were not aged since captured when age determination was no longer possible.

Adult Common Bush-Tanagers were almost absent in young secondary forest during June/July. Hence, while adults were quite abundant prior to and after breeding in young secondary forest, very few adults were present in young secondary forest during the presence of 1st-year individuals (June/July; Fig. 1). I recorded adults only once at net line 'm' in young secondary forest in June/July (Fig. 1) within a troop of 1st-year individuals.

Recaptures

I recaptured 13 Common Bush-Tanager individuals in total (of which some were recaptured twice or more, Table

1). Same-day recaptures were excluded from analyses since these same-day recaptures occurred in the same or the immediately neighboring nets in the same net line.

Twelve individuals were recaptured within 150 m from the original capture site. The body mass of these 12 recaptures (11 out of these with body mass from capture and recapture) did not change significantly and the mean body mass of all 1st-captures was 17.02 g (± 3.1 s. d.); mean body mass of the same individuals at final recapture increased slightly to 17.56 g (± 3.4 s. d.). One banded individual (Ring # 030-056) captured on 17 July 2001, identified as a 1st year bird, at the young secondary forest net line 'm', was recaptured about 1,000 m away (Fig. 1) on 17 April 2002 at the natural forest net line 'a' and lost 51 % of the original body mass (16.5 g \rightarrow 8.5 g). None of the other individuals recaptured change their habitat type (seven were captured and recaptured in young secondary forest, five in natural forest).

DISCUSSION

This study establishes significant differences in habitat distribution of adult and 1st-year Common Bush-Tanager. During post-breeding, adult birds were distributed in natural as well as young secondary forest in similar numbers, while young birds were found mainly in secondary forest. Such a difference in distribution has not been shown before. Young birds disperse after breeding and may be forced by adults to leave their native habitats and search for foraging areas elsewhere (e.g., Winkler *et al.* 1995, Moller 1995). Age-specific distribution and habitat selection are two still hardly understood processes in ecology (Walters 2000, Skarpaas *et al.* 2005).

Table 1. Initial Captures for 1st-Year Individuals and Adult Common Bush-Tanager per Net Line in the Sierra Yalijux

Net line	Adult		1 st -year		Undetermined	Total
	1 st Capture	Recapture	1 st Capture	Recapture	1 st Capture	(1 st Captures only)
Natural Forest						
a	9	6	1	0	0	10
b	13	1	0	0	0	13
c	3	0	1	0	10	14
e	2	0	0	0	6	8
i	7	1	1	0	0	8
k	4	1	0	0	0	4
a-k	38	9	3	0	16	57
Young Secondary Forest						
m	17	0	10	0	3	30
n	3	0	6	0	0	9
o	14	4	21	4	3	38
p	4	0	0	1	1	5
q	0	2	1	0	1	2
r	5	2	2	0	0	7
m-r	43	8	40	5	8	91
Total	81	17	43	5	24	148

The observed differences in distribution between old and young birds could have several explanations: (1) adults expelling 1st-years from natural forest habitats (e.g., Fretwell 1972); (2) different resource needs of 1st-year individuals that are only present in young secondary forest (Vega-Rivera *et al.* 1999); (3) different breeding success in the two habitats; and/or (4) different foraging success (Rappole 1988). The methods applied do not enable me to distinguish between these possibilities. Since Common Bush-Tanagers are quite aggressive (judging from their behavior during capture) and mobile (recaptures up to 1 km), it is likely that either adults expel 1st-year individuals from natural forest, or that food resources needed by 1st-year individuals are more abundant in young secondary forest during the early post-breeding period. The expelling behavior would support an Ideal Despotic Distribution Theory (Fretwell 1972), which states that inexperienced or less competitive individuals should be expelled from higher quality habitat. These individuals are typically found in less-suitable habitats. While plankton (e.g., Lampert *et al.* 2003) and invertebrates (e.g., Ohashi and Yahara 2002) typically follow an ideal free distribution, many vertebrate species conform to a despotic distribution, including Spotted Owls (*Strix occidentalis*; Franklin *et al.* 2000, Zimmermann *et al.* 2003) and Common Cranes (*Grus grus*; Bautista *et al.* 1995). However, this prediction has not been rigorously tested, since observations of interactions have not been available, or observation of spatial distribution by different age classes was limited. If juveniles are all found in one habitat while adults in another one, we can assume, that the first is less suitable than the second (compare Fretwell 1972).

Habitat selection and post-breeding foraging are relevant for the understanding of dispersal and related ecological processes in conservation (Skarpaas *et al.* 2005). Factors determining habitat selection are numerous and controversial, but include density effects (e.g., Morris 2003), patch size (e.g., Moller 1995), habitat quality (e.g., Winker *et al.* 1995), fitness (Greene and Stamps 2001, Haugen *et al.* 2006), and competition (e.g., Winker *et al.* 1995, Skarpaas *et al.* 2005).

Age separation is an important issue for conservation. The key reproductive generations of Common Bush-Tanagers are found in habitat types considered as less important for conservation in the region (K. Eisermann and D. Unger, pers. com. 2005). This implies older secondary vegetation with dense bushes is also essential for the most abundant species in the Sierra Yalijux. The at least temporary stop-over of young Common Bush-Tanagers in habitat types less valuable for conservation needs to be reconsidered in any future local conservation strategy, to guarantee the long-term survival of this species.

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