HABITAT AND FORAGING SUBSTRATE USE OF THREE *BASILEUTERUS* WARBLERS FROM CENTRAL BRAZIL

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Resumo. Descrevemos quatro componentes (tipo de floresta utilizada, altura de ocorrência e tipo e ângulo do substrato utilizado) dos nichos de três espécies de *Basileuterus* (*B. leucophrys, B. flaveolus*, e *B. hypoleucus*) em uma mata de galeria no ecossistema do Cerrado do Brasil central. As três espécies de *Basileuterus*, estudadas entre setembro de 1988 e abril de 1989 e entre julho e agosto de 1990, diferiram em pelo menos dois dos quatro componentes do nicho estudados. *B. hypoleucus* ocorreu em ambas as áreas (alagada e seca) da mata de galeria, enquanto que *B. flaveolus* ocorreu principalmente na área seca e *B. leucophrys* ocorreu somente na área alagada. *B. flaveolus* e *B. leucophrys* ocorreram principalmente no subbosque (< 3 m de altura) e utilizaram mais substratos secos. *B. hypoleucus* ocorreu principalmente no alto subbosque e baixa copa (até 15 m) e utilizou principalmente substratos verdes. *B. hypoleucus* e *B. flaveolus* utilizaram significativamente mais substratos horizontais do que *B. leucophrys*. As evidências obtidas através das observações no Brasil central e através de uma revisão da literatura disponível, dão suporte à exclusão competitiva como um fator responsável pelas diferenças de nicho encontradas entre espécies sintópicas de *Basileuterus*. Relatamos também que comunidades de aves raramente, ou nunca, possuem mais de duas espécies de *Basileuterus* sintópicas, e que a distribuição horizontal de forrageamento aparenta ser a característica mais importante da partição de nicho.

Abstract. We describe four niche components (type of forest used, height of occurrence, and type and angle of substrate used) of three *Basileuterus* warblers [White-striped (*B. leucophrys*), Flavescent (*B. flaveolus*), and White-bellied (*B. hypoleucus*)] in a gallery forest in the cerrado ecosystem of central Brazil. The three species of warblers differed in at least two of the four niche components studied between September 1988 and April 1989, and July through August 1990. The White-bellied Warbler occurred in both dry and flooded plots of the gallery forest, while the Flavescent Warbler occurred mostly in the dry plot, and the White-striped Warbler occurred only in the flooded plot. The Flavescent Warbler and the White-striped Warbler occurred mostly in the low understory (< 3 m high) and used more dry substrates. The White-bellied Warbler occurred mostly in high understory and low-canopy (up to 15 m) and used mostly green substrates. The White-bellied Warbler and the Flavescent Warbler used significantly more horizontal substrates than did the White-striped Warbler. The evidence obtained from the observations in central Brazil, and from a review of the literature available gives support to competitive exclusion as a factor responsible for niche differences among syntopic *Basileuterus* warblers. Also, bird communities rarely, if ever, have more than two syntopic species of *Basileuterus*, and vertical foraging distribution seem to be the most important characteristic of niche partitioning. *Accepted 23 March 1993.*

Key words: Habitat use, niche, Basileuterus, *warblers*, Emberizinae, *gallery forests, cerrado region, Brazil.*

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INTRODUCTION

The 21 species of *Basileuterus* warblers (Emberizinae: Sibley & Monroe 1990), even though relatively common and widespread in South and Central America, are still poorly known (but see Todd 1929; Skutch 1954, 1967; Olson 1975; Mees & Mees-Balchin 1990). The knowledge of habitat use by this genus of warblers is restricted to general short descriptions in faunistic books (e.g., Sick 1985, Hilty & Brown 1986). Even though several species of warblers have already been studied in relation to their distribution along varied niche dimensions (e.g., MacArthur 1958, Catchpole 1973, Garcia 1983, Rolando & Palestrini 1989, Price 1991), no detailed study of niche characteristics of Neotropical *Basileuterus* warblers has been conducted (but see Terborgh 1971, and Remsen 1985).

In central Brazil, there are three sympatric and partially syntopic species of *Basileuterus*. The White-striped Warbler (*B. leucophrys*) is an endemic species of central Brazil (see range map in Ridgely & Tudor 1989) that inhabits only flooded gallery forests (Sick 1985, Antas & Cavalcanti 1988, *pers. observ.*). Willis (1986) observed it usually over or near water, but even in dry sites. It searches for insects among leaves hopping on the ground or in shrubs and trunks up to 3 m high (Antas & Cavalcanti 1988, Willis 1986). Also, it may be the largest species of the genus *Basileuterus*, weighing twenty or more grams (Cavalcanti & Marini, *in press*). The White-bellied Warbler (*B. hypoleucus*) from central and southeastern Brazil (see range map in Ridgely & Tudor 1989) inhabits gallery forests, and "cerradão" (a 10 m high woodland), and searches for insects on leaves and branches above the ground (Antas & Cavalcanti 1988). Ridgely & Tudor (1989) stated that it inhabits lower growth of "deciduous woodland, gallery forest and shrubby overgrown borders". A third species, the Flavescent Warbler (*B. flaveolus*), has a more widespread geographical distribution (see range map in Ridgely & Tudor 1989) and inhabits gallery forests, "cerradão", and "caatinga" (a dry shrubland of northeast Brazil) (Sick 1985). In Colombia, it occurs in the undergrowth of dry or moist forest, shrubby or thorny thickets and woodland borders (Hilty & Brown 1986). It forages hopping on or near the ground (Sick 1985,

Hilty & Brown 1986, Mees & Mees-Balchin 1990). Willis (1986) observed these three species of *Basileuterus* following swarms of ants.

The main purpose of this paper is to estimate four niche components (use of type of forest, searching height, and type and angle of substrate used) of the three *Basileuterus* warblers in gallery forests in the "cerrado" (savanna) ecosystem of central Brazil. We also discuss potential factors underlying such niche differences, and a possible general pattern of species coexistence among *Basileuterus* warblers.

STUDY AREA AND METHODS

The study was conducted in gallery forest of the Córrego Capetinga , a creek, at the Ecological Station of the University of Brasília, Brasília, Distrito Federal (15°58'S, 47°56'W). We used two 2.5 ha plots, 5 km apart, each with a grid of 34 points at 30 m intervals. Plot A was in a flooded section, and plot B was in a dry section of the same gallery forest. The flooded plot has a continuous canopy formed by 14—20 m high trees, and a dense understory dominated by the 2.5—3.0 m high bamboo *Ichnanthus bambusiflorus* (Gramineae), whereas the dry plot has emergent trees up to 20—30 m high, with continuous canopy between 10 and 15 m high (Ratter 1980), and a more open understory. Ratter (1980), Eiten (1984) and Marini (1992) provide more details of the study area and region.

Observations were conducted only by M.Â.M. to avoid observer bias, and were made primarily in the morning (06:30—13:00), from September 1988 to April 1989 (rainy season), and during July through August 1990 (dry season).

Only the first searching height was recorded per sighting. We do not consider the first sighting biased because the birds seemed habituated to our presence in the study sites. Two consecutive samples of an individual bird searching height and type of substrate used were considered independent since they were always at least 7 min apart. This methodology was used to decrease temporal pseudoreplication (Hurlbert 1984) of the observations. Plant substrates used were considered either as dry (apparently dead) or green (apparently alive). A substrate was considered horizontal if it had less than 45° angle from horizontal, and vertical if 45° or more.

Even though birds encountered were usually searching for food, we refer to the heights sampled as searching height because birds were rarely seen attacking prey. We estimate that the observations were taken from approximately 10 individuals of each species in each 2.5 ha plot. This estimate is based on the numbers of birds banded, on the location of unbanded birds in the study plots, and on the spatial distribution of foraging observations.

Bird measurements (estimated to the nearest 0.1 mm) were taken from banded individuals mist-netted from 1985 through 1990. Birds were captured on more than 30 mist-net sites in four areas of the gallery forest (at least 1 km apart), mostly from sunrise to 13:00. Beak width was measured at the mid-nostril. Body masses are from Cavalcanti & Marini (*in press*). Nomenclature of the species cited follows Sibley & Monroe (1990).

We used bird capture rates (number of individuals captured per 100 net-hours, where one mist net open for 1 h = 1 net-hour) as an approximate index of bird abundance in each forest plot. Recaptures were not included in the calculations. Capture rates were calculated based on 110.1 mist-net h in the flooded plot from March 1988 to January 1989, and 289.1 mist-net h in the dry plot from March 1988 to April 1989.

Niche breadth (B_j) and niche overlap (O_{jk}) were calculated following MacArthur (1972) and Pianka (1973), respectively:

$$B_j = 1/\sum(p_{ij}^2),$$

where p_{ij} represents the proportion of records for species j in each category (i) of a particular niche dimension; and

$$O_{jk} = \sum(p_{ij}p_{ik})/[\sum(p_{ij}^2)\sum(p_{ik}^2)],$$

where j and k are two species, p_{ij} is the proportion of species j's activity or diet recorded from category i of a particular resource dimension.

Because the searching heights of the birds were not distributed normally (Fig. 1), comparisons of mean values were restricted. Thus we used Wilcoxon two-sample tests, to test for differences in searching heights. Type and angle of substrate used were analyzed by Chi-square tests with Yates continuity correction, or by Fisher exact test. Differences among the means of the morphological characters were tested with one-way analyses of variance (ANOVA) and contrasted with Tukey tests.

RESULTS

Abundance by forest type. Only one species of *Basileuterus* warbler was abundant in the low understory (< 3 m) of each plot. The Flavescent Warbler was recorded more in the dry plot (1.4 individuals captured/100 mist-net h), and was very rare in the flooded plot, where it was never captured, but was observed twice on the edge of the flooded zone. The White-striped Warbler was relatively common in the flooded plot (5.5 individuals captured/100 mist-net h), but absent from the dry plot (Table 1). The White-bellied Warbler was a relatively common bird at both dry (2.1 individuals captured/100 mist-net h) and flooded (4.5 individuals captured/100 mist-net h) plots. The different mist-netting effort in each plot, however, compromises the comparison between plots and should be considered with care.

Searching height. Usually only one species of *Basileuterus* warbler was common at a given height in each plot. The White-striped Warbler used mostly (94.4 %, n = 56 observations) the

TABLE 1. Searching height in m (mean ± 1 SE, n) and capture rate (number of individuals captured/100 mist-net hours) of *Basileuterus* warblers in the dry and flooded gallery forest plots.

Species	Dry plot		Flooded plot	
	height of occurrence	capture rate	height of occurrence	capture rate
White-striped Warbler (*B. leucophrys*)	—	0	1.3 ± 1.4 (54)	5.5
Flavescent Warbler (*B. flaveolus*)	1.1 ± 1.4 (46)	1.4	0.8 ± 1.1 (2)	0
White-bellied Warbler (*B. hypoleucus*)	5.6 ± 3.3 (74)	2.1	8.0 ± 3.0 (36)	4.5

low understory (3 m or below) of the flooded plot, whereas the White-bellied Warbler used mostly (97.2 %, n = 36) high-understory and low-canopy (> 3 m) (Fig. 1A). The White-bellied Warbler had searching height 39 % broader than the White-striped Warbler (Table 2). The White-striped Warbler and the White-bellied Warbler differed significantly (Z = 5.237, P <
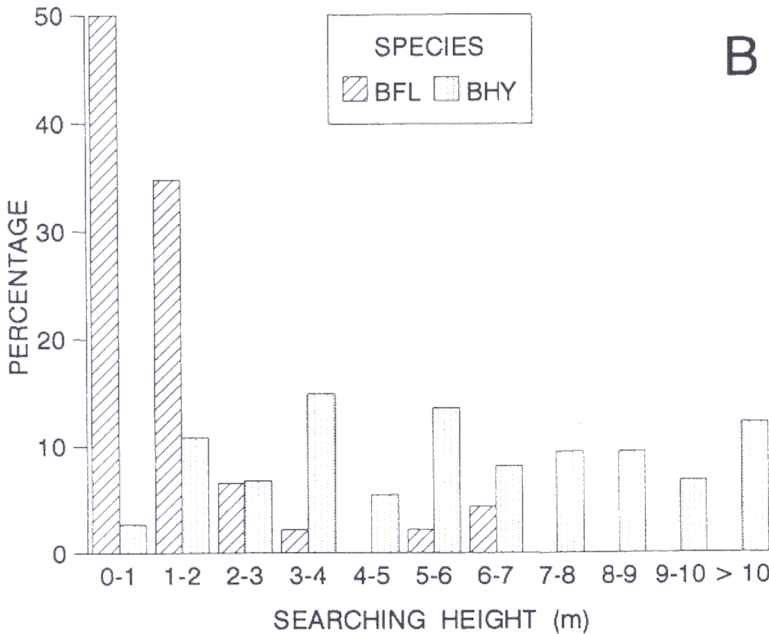

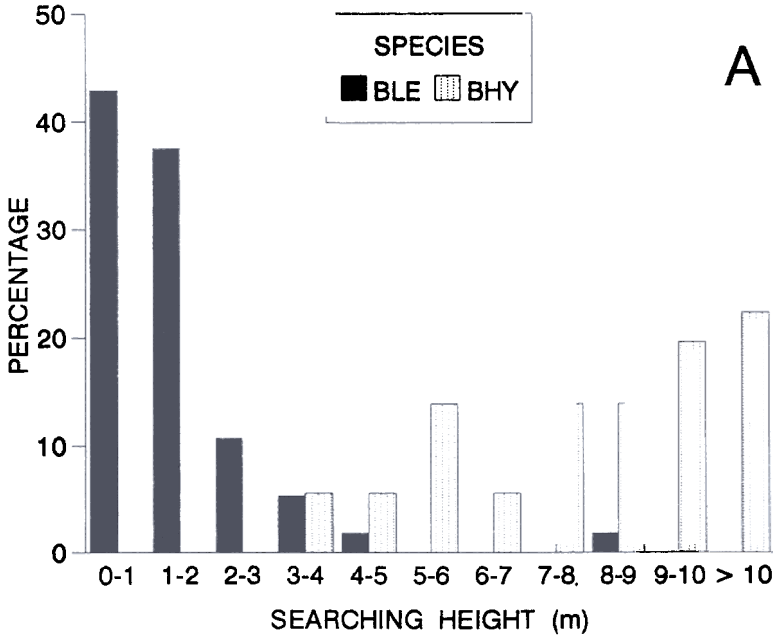
FIG. 1. Searching height of (A) *Basileuterus leucophrys* (BLE) (n = 56) and *B. hypoleucus* (BHY) (n = 36) in the flooded plot, and (B) *B. flaveolus* (BFL) (n = 46) and *B. hypoleucus* (BHY) (n = 74) in the dry plot.

TABLE 2. Niche breadth (B_j) and niche overlap (O_{jk}) for searching height in m, type of substrate and angle of substrate used by the White-striped (*Basileuterus leucophrys*) (BLE), the Flavescent (*B. flaveolus*) (BFL), and the White-bellied (*B. hypoleucus*) (BHY) warblers.

Forest type	Species	Searching height	Substrate	
			Type	Angle
Niche breadth (B_j)				
Flooded	BHY	7.45	1.32	1.18
	BLE	5.37	1.92	1.93
Dry	BHY	24.89	1.45	1.21
	BFL	4.62	1.60	1.00
Niche overlap (O_{jk})				
Flooded	BLE-BHY	0.20	1.09	1.32
Dry	BFL-BHY	1.81	0.80	1.09
Flooded-dry	BLE-BFL	4.70	1.69	1.15

0.000) in searching heights (Fig. 1, Table 1) which overlap very little (Table 2).

The Flavescent Warbler used mostly (93.5 %, n = 46) the low-understory (3 m or below) of the dry gallery forest, whereas the White-bellied Warbler used mostly (71.6 %, n = 74) high understory and low canopy (> 3 m) (Fig. 1B). The White-bellied Warbler had a broad range of searching heights (0–15 m). As in the flooded plot, the White-bellied Warbler occurred at significantly (Z = 5.736, P < 0.000) greater heights than its syntopic congener. These two species overlapped more in searching height than the White-bellied and the White-striped warblers did in the flooded plot (Table 2).

The White-striped Warbler and the Flavescent Warbler did not differ (Z = 1.428, P = 0.153) in the heights they used in the flooded and dry plots (Fig. 1B). The searching height overlap between these two species was relatively high compared with the overlap between the other two pairs of species. The White-striped and the Flavescent warblers used a narrower range of searching heights (Table 2) whereas the White-bellied Warbler used a broader range of heights (Table 2, Fig. 1). We can not compare differences in height between dry and wet seasons because of small (n < 20 for the three species combined) sample sizes during the dry season.

Type and angle of substrate used. The White-striped Warbler used dry and green substrates more evenly (greater niche breadth) than did the White-bellied Warbler (Table 2). This difference was statistically significant (Chi² = 10.99, P = 0.001) (Fig. 2). The Flavescent Warbler used

more dry substrates whereas the White-bellied Warbler used more green substrates in the dry plot than expected by chance (Chi² = 11.08, P = 0.001) (Fig. 2). The White-striped and the Flavescent warblers used dry and green substrates with similar frequency (Chi² = 0.31, P = 0.575) in the flooded and dry plots, respectively.

The White-bellied Warbler used significantly (Chi² = 5.74, P = 0.017) more horizontal substrates than did the White-striped Warbler, which used both angles of substrate similarly (Table 2, Fig. 3). The Flavescent and White-bellied warblers, however, did not differ (Fisher Exact test, P = 0.156) in the use of horizontal vs. vertical
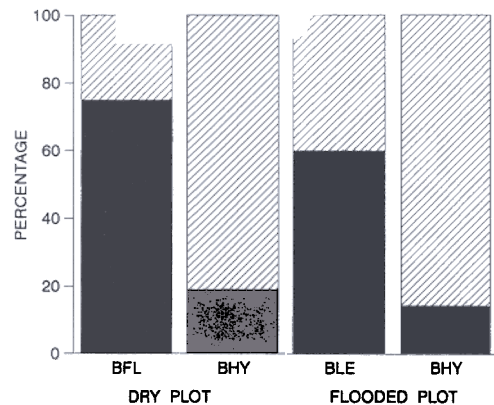

FIG. 2. Dry (solid bars) and green (cross-hatched bars) substrates used by the Flavescent (*Basileuterus flaveolus*) (BFL) (n = 12) and by the White-bellied (*B. hypoleucus*) (BHY) (n = 42) warblers in the dry plot, and the White-striped (*B. leucophrys*) (BLE) (n = 30) and the White-bellied (*B. hypoleucus*) (BHY) (n = 28) warblers in the flooded plot.
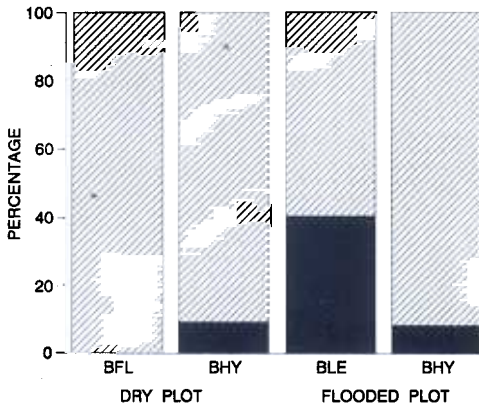
FIG. 3. Horizontal (cross-hatched bars) and vertical (solid bars) substrates used by the Flavescent (*Basileuterus flaveolus*) (BFL) (n = 11) and the White-bellied (*B. hypoleucus*) (BHY) (n = 32) warblers in the dry plot, and by the White-striped (*B. leucophrys*) (BLE) (n = 32) and the White-bellied (*B. hypoleucus*) (BHY) (n = 24) warblers in the flooded plot.

substrates (Fig. 3). The White-striped and Flavescent warblers used horizontal and vertical substrates with different (Chi^2 = 4.62, P = 0.032) frequencies in the flooded and dry plots respectively.

Species morphology. The White-striped Warbler is the largest of the three species, followed by the Flavescent and by the White-bellied warblers (Table 3). There was a significant difference among the three species (One-way ANOVA, P < 0.000) and the respective contrasts (Tukey tests, P < 0.05) for all five morphological characters measured. The only exception was the marginal difference (P = 0.054) in beak width between the White-striped and Flavescent warblers.

DISCUSSION

The findings show that the three species of *Basileuterus* warblers differ in at least two of the four niche components analyzed (use of type of forest, searching height, and type and angle of substrate used). Differences in vertical distribution (Tables 1, 2, and Fig. 1) and type of habitat used (Table 1) seem to be the most important variables of niche partitioning in the gallery forests studied. The two species (Flavescent and White-striped warblers) which forage mostly below 3 m are not syntopic, whereas the species (White-bellied Warbler) that forages primarily

over 3 m occurs syntopically with either one of the former two species. Differences in type and angle of substrate used (Table 2, Figs. 3, 4), seem to be less pronounced. Remsen (1985) also observed greater differences between foraging heights than between substrate type between the Citrine Warbler (*B. luteoviridis*) and the Pale-legged Warbler (*B. signatus*) in Bolivia. The availability of each type and angle of substrate and the vegetation density, however, may also influence searching height in central Brazil. For example, the less frequent occurrence of the White-bellied Warbler below 3 m in the flooded plot (Fig. 1A) coincides with the presence of the White-striped Warbler, but also with the height of the bamboo shoots, which reach 3 m. Other variables, such as type and size of prey, and specific foraging tactic should also be estimated.

The morphological overlap among the three warblers is small with the White-striped Warbler being almost twice as heavy as the White-bellied Warbler (Table 3). Also, the White-striped Warbler has the smallest wing chord/body mass ratio (3.64), followed by the Flavescent Warbler (4.54), then by the White-bellied Warbler (5.15), showing different morphological adaptations of the wing. Different morphological adaptations may reflect different levels of use of the wing in foraging (Fitzpatrick 1985), and hence different foraging niches.

Vertical replacement within the same habitat, as seen here (Fig. 1) may be a common pattern among *Basileuterus* species with the heavier species occurring at lower heights, but with exceptions. A similar case of vertical partitioning was suggested by Sick (1985) who commented that the White-browed Warbler (*B. leucoblepharus*) [body mass = 15.1 g (Marini, Reinert, Pinto & Coleto, unpubl.)] occurs on the ground or at lower heights whereas the Golden-crowned Warbler (*B. culicivorus*) [body mass = 9.7 g (Marini, Reinert, Pinto & Coleto, unpubl.)] occurs higher in the vegetation of the same forest. Remsen (1985), however, found in Bolivia that the lighter (males: 11.5 g, females: 11.1 g) species (Pale-legged Warbler) foraged lower (1.4 ± 2.0 m), and the heavier (males: 13.7 g, females: 12.2 g) species (Citrine Warbler) foraged higher (3.3 ± 2.5 m). These two species used the same type of substrate (green foliage) but had different proportional use of foraging tactics (Remsen 1985).

TABLE 3. Measurements (mean ± 1 SE, n) of body mass, wing chord, tarsus, culmen and beak width of the White-striped (*Basileuterus leucophrys*), Flavescent (*B. flaveolus*), and White-bellied (*B. hypoleucus*) warblers.

Measurement [1]	White-striped	Flavescent	White-bellied
		13.63 ± 0.27 (12)	
		61.80 ± 1.04 (11)	
		23.47 ± 0.25 (11)	
		12.18 ± 0.15 (10)	
		4.83 ± 0.07 (10)	

[1] Measurements in mm except for mass (g).   Data from Cavalcanti & Marini (*in press*).

Evidence of a general pattern of niche partitioning among *Basileuterus* species, possibly resulting from competitive exclusion is the observation that bird communities rarely, if ever, have more than two syntopic species of *Basileuterus*. This pattern is in agreement with the old argument (Elton 1946) that communities are taxonomically restricted, with only one or two species present per genus. This is true in the several habitats in Brasília, and near Curitiba, Paraná state, Brazil (pers. observ.). In São Paulo state, Brazil, there are five species of *Basileuterus*. Of thirteen sites visited by Willis & Oniki (1981), however, all but two had only two species of *Basileuterus*. The other two sites had three sympatric (but maybe not syntopic) species. The information given in the literature usually enables the reader to evaluate whether the species are sympatric, but is not sufficient to evaluate if they are syntopic and synchronic. In Mexico (Edwards 1968), four *Basileuterus* species never have more than one sympatric congener. The range maps shown in Narosky & Yzurieta (1989) show similar pattern in most areas of Argentina. Only two syntopic *Basileuterus* species were also reported by Terborgh (1971), Remsen (1985), and Wiedenfeld et al. (1985). The generality of the pattern of niche partitioning among *Basileuterus* warblers is best supported by Terborgh's (1971) data on the distribution of five Peruvian species. He found only two abundant species per altitudinal zone between 500 and 3500 m. When a third species was also present, it had very low abundance. Also, at one of the elevation zones, the two recorded species differed in habitat, foraging height and size.

There are several cases of parapatric distributions among *Basileuterus* species, which may also be related to competitive exclusion. The White-striped and White-browed warblers represent one case from southeast Brazil (Sick 1985, Willis 1986). Wetmore et al. (1984) stated that the Gol-

den-crowned Warbler "was replaced by *B. tristriatus* at higher elevations", and also that the Three-striped Warbler (*B. tristriatus tacarcunae*) may be replaced by the Black-cheeked Warbler (*B. melanogenys ignotus*) in some regions of Panama. Also, several species of *Basileuterus* seem to have parapatric distributions and to replace each other altitudinally in Colombia (see range maps in Hilty & Brown 1986) and in Peru (Terborgh 1971, Parker et al. 1985).

Further studies should evaluate alternative explanations (suggested and discussed by a number of authors) to patterns of habitat partitioning, such as: (1) resource (arthropod) abundance in different habitats, vegetation heights, and types of substrates, (2) species adaptation to different climates, habitats or substrates, (3) competition from congeners or unrelated species, (4) non-nest predation, which would make species living in darker (or with denser vegetation) parts of the forest more protected, or (5) differential resistance to parasites. Density-dependent nest predation (all species of *Basileuterus* nest on the ground) could explain the small number of *Basileuterus* species per habitat, but not differences in foraging height. To test (see review in Connell 1983) these hypotheses one may need additional data such as on: (1) habitat use of each species where they occur in sympatry and in allopatry, (2) prey (arthropod) abundance, (3) survivorship or predation risk, and nesting success, (4) the behavior of species after the experimental removal of syntopic species, (5) habitat use in the laboratory or field cages, where confounding factors can be controlled or manipulated, and (6) response of one species to song/call play-backs of sympatric species. A clarification of which factors are responsible for this niche partitioning, however, awaits additional tests, not only for the species studied here, but for the *Basileuterus* genus as a whole.

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