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FORAGING BEHAVIOR OF THE WHITE-BROWED (*BASILEUTERUS LEUCOBLEPHARUS*) AND THE GOLDEN-CROWNED (*B. CULICIVORUS*) WARBLERS IN A SEMIDECIDUAL FOREST IN SOUTHERN BRAZIL

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Resumo. – Comportamento de forrageio do Pula-pula-assobiador (*Basileuterus leucoblepharus*) e do Pula-pula (*B. culicivorus*) em uma floresta semidecidual no sul do Brasil. – A intenção deste trabalho foi de verificar se ocorrem diferenças comportamentais durante o forrageamento do Pula-pula-assobiador (*Basileuterus leucoblepharus*) e do Pula-pula (*B. culicivorus*) em diferentes estações do ano (inverno e verão). As variáveis avaliadas foram altura de forrageio, manobras de ataque a presas e tipo e ângulo do substrato de onde foram capturadas as presas. O período de estudo foi no inverno/2000 e no verão/2001. Os resultados mostraram que ocorreram diferenças significativas durante o forrageamento entre as espécies em ambas as estações do ano, sendo as variáveis de altura e tipo de substrato as que apresentaram os maiores valores de correlação para a ordenação das unidades amostrais. O Pula-pula-assobiador obteve seu alimento freqüentemente em alturas inferiores a 1 m, diferentemente, o Pula-pula forrageou em alturas superiores a 1 m. A manobra "glean" foi a mais freqüente dentre as utilizadas pelo Pula-pula-assobiador, enquanto que o Pula-pula mostrou um maior equilíbrio entre as principais manobras utilizadas ("sally-strike" e "reach-out"), sendo que durante o inverno houve uma maior utilização de manobras aéreas pela espécie. O principal substrato de forrageio utilizado pelo Pula-pula-assobiador foi o solo em ambas as estações, enquanto que o Pula-pula utilizou principalmente folhas verdes durante o forrageio e uma maior gama de outros substratos durante o inverno. Desta forma, os resultados demonstram que ocorre segregação, durante o forrageio, entre as duas espécies de *Basileuterus* estudadas tanto no inverno quanto no verão. Através deste estudo pode-se constatar também que o Pula-pula apresenta aspectos comportamentais mais generalistas quando comparado com o Pula-pula-assobiador.

Abstract. – This study intended to evaluate if differences occur in the foraging behavior of the White-browed (*Basileuterus leucoblepharus*) and the Golden-crowned (*B. culicivorus*) warblers during different seasons (winter and summer). The variables evaluated were foraging height, attack maneuvers and type and angle of substrate where the preys were attacked. The work was carried out in the winter/2000 and the summer/2001. The results show significant differences in the foraging behavior of these species in both seasons, with the variables of foraging height and substrate type presenting higher positive correlation coefficients with ordination axes. The White-browed Warbler caught prey frequently below 1 m, different from the Golden-crowned Warbler, which caught prey above 1 m. Gleaning was the most frequent maneuver used by the White-browed Warbler, while the Golden-crowned Warbler showed more equilibrium among the main maneuvers (sally-strike and reach-out) and used aerial maneuvers more often during the winter. The main foraging substrate used by the White-browed Warbler was the soil in both seasons, while the Golden-crowned Warbler used mainly green leaves during foraging and a greater variety of substrates during the winter. The results showed segregation between the two species of *Basileuterus* during foraging in both winter and summer. This study allowed to verify that Golden-crowned

Warblers present more generalist behavioral aspects when compared to White-browed Warblers. *Accepted 13 May 2003*.

Key words: *Basileuterus leucoblepharus*, White-browed Warbler, *Basileuterus culicivorus*, Golden-crowned Warbler, foraging behavior, niche, habitat partition, southern Brazil.

INTRODUCTION

According to Cody (1985), similar portions of the same habitat may be used by several bird species, thus occurring the potential for ecologic segregation among these species through different foraging methods or the use of different prey capture tactics. Characteristics such as prey dispersion (Fitzpatrick 1981), prey type (Strong 2000), foliage structure (Whelan 2001), seasonality (Hutto 1981, Lovette & Holmes 1995), sex (Sodhi & Paszkowski 1995) and morphology (Fitzpatrick 1985, Morse 1985), among others, have influence upon the foraging behavior of birds. Many studies on birds were carried out taking into consideration the behavior related to food searching and some aspects of ecological niches (e.g., Rabenold 1978, Eckhardt 1979, Airola & Barrett 1985, Thiollay 1988, Martin & Karr 1990, Alves 1991, Marini 1992, Smith *et al.* 1998, Forstmeier & Keßler 2001, Mallet-Rodrigues 2001).

The sub-family Parulinae (Passeriformes) has representatives from Canada to Argentina, being exclusive from the American continent (Ridgely & Tudor 1989, Sick 1997). In Brazil, there are 19 species, of which 11 are resident (Sick 1997). According to Stotz *et al.* (1996), the genus *Basileuterus* includes 21 species that are widespread in Central and South of America. Ridgely & Tudor (1989) stated that this genus reaches its greater diversity in the Andes Mountains. According to Ridgely & Tudor (1989) and Sick (1997), the Golden-crowned Warbler (*Basileuterus culicivorus*), is distributed from Mexico to Uruguay, occurring mainly in eastern Brazil, while the White-browed Warbler (*Basileuterus leucoblepharus*), presents a more restricted distribution from southern Minas Gerais and Rio de Janeiro to Rio Grande do Sul (also Argentina, Paraguay and Uruguay). As said by Belton (1994) and Sick (1997), the Golden-crowned Warbler is smaller than the White-browed Warbler and, according to Silva (1991), the latter species presents greater morphological dimensions of tarsus, tail, wing and bill than the former. Belton (1994) considered the White-browed Warbler and the Golden-crowned Warbler as inhabitants of forest regions in most part of Rio Grande do Sul State. Ridgely & Tudor (1989), Belton (1994) and Sick (1997) considered these species as sympatric and frequently syntopic. Belton (1994) and Sick (1997) mentioned that the White-browed Warbler inhabits inside forests, hopping on the ground or flying at low heights, while the Golden-crowned Warbler uses the medium stratum of the forests. However, no work has been done in order to verify and quantify these statements.

Several studies on the ecology of parulids were carried out mainly in North America, but some were accomplished in Brazil. Silva (1991) studied the ecology, bioacoustics, biogeography and phylogenetic relationships of five species of genus *Basileuterus*, emphasizing the complex *B. culicivorus*. Marini & Cavalcanti (1993) investigated the habitat and foraging substrate of White-striped (*B. leucophrys)*, White-bellied (*B. hypoleucus)* and Flavescent (*B. flaveolus*) warblers in a "cerrado" region and verified that the horizontal distribution of foraging was the main characteristic involved in the niche partition among these species. Despite the studies mentioned above, most of the studies on foraging of parulids were con-

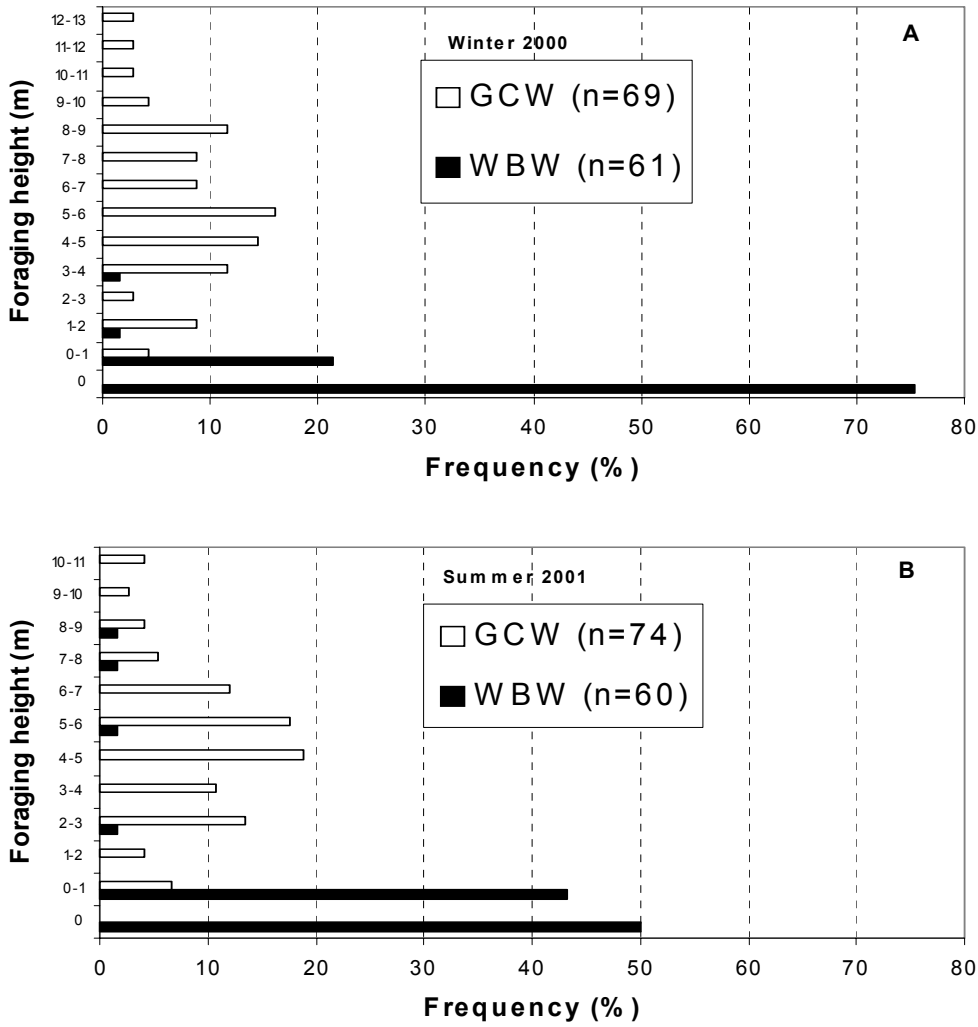

FIG. 1. Distribution of foraging height frequencies of White-browed (WBW) and the Golden-crowned (GCW) warblers in a semidecidual forest of southern Brazil.

duted in North or Central America (e.g., MacArthur 1958, Morse 1971, 1973; Rabenold 1980, Hutto 1981, Martin & Karr 1990, Sodhi & Paskowski 1995, Lovette & Holmes 1995, Keane & Morrison 1999, Smith *et al.* 1998, Strong 2000, Whelan 2001). When comparing to what has already been studied, a lack of data on behavior and habitat partition of parulids from South America is obvious, mainly of species from Atlantic forest, where this study was conducted.

Due to the lack of information about the two species of *Basileuterus* focused in this study, our aim was to verify if there are differences in the foraging behavior between the Golden-crowned and the White-browed war-

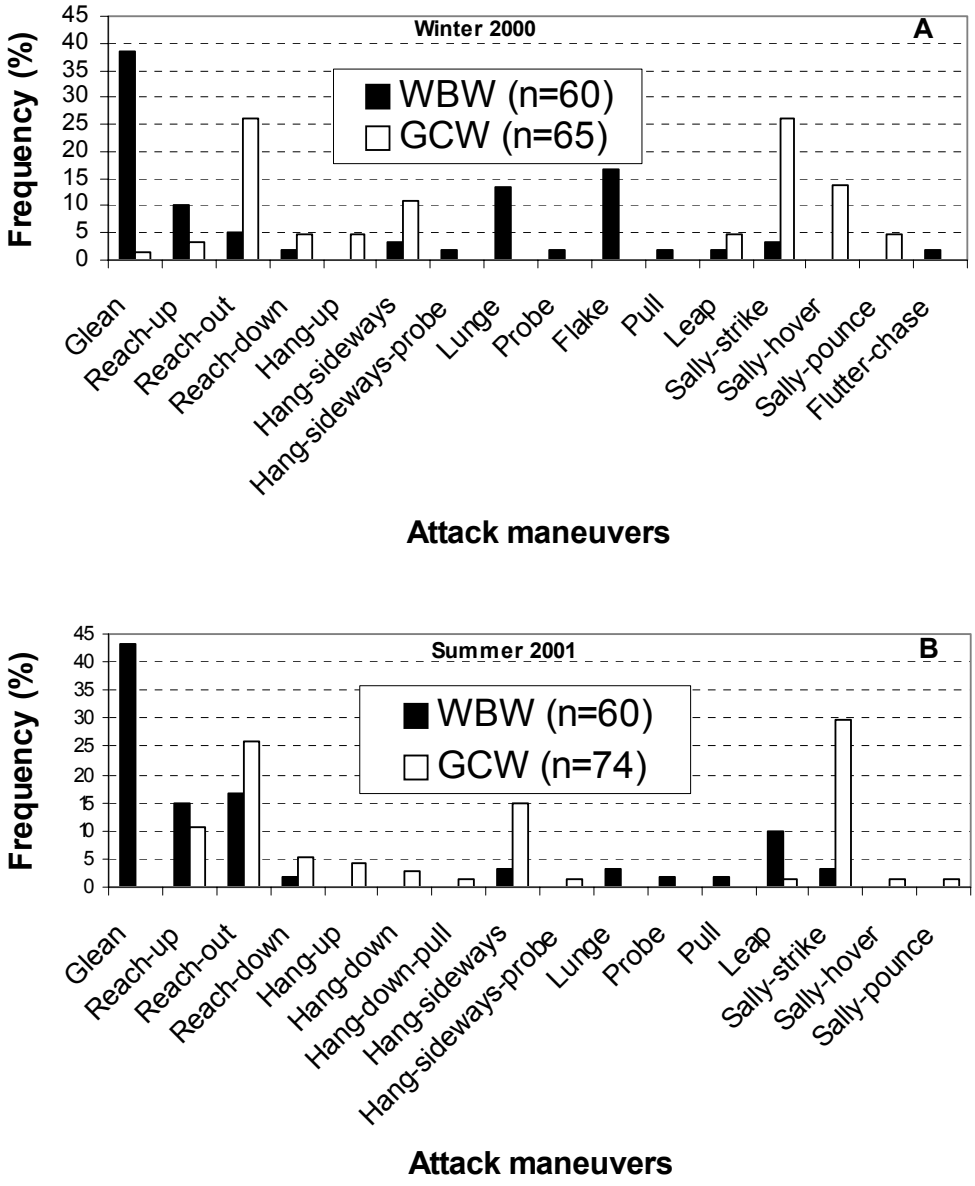

FIG. 2. Frequency distribution of prey attack maneuvers by White-browed (WBW) and Golden-crowned (GCW) warblers in a semidecidual forest of southern Brazil.

blers in a semidecidual forest using height, substrate and substrate angle where prey are catched and attack maneuvers as comparative variables. We also intended to observe if there are seasonal differences of foraging strategies within each species.

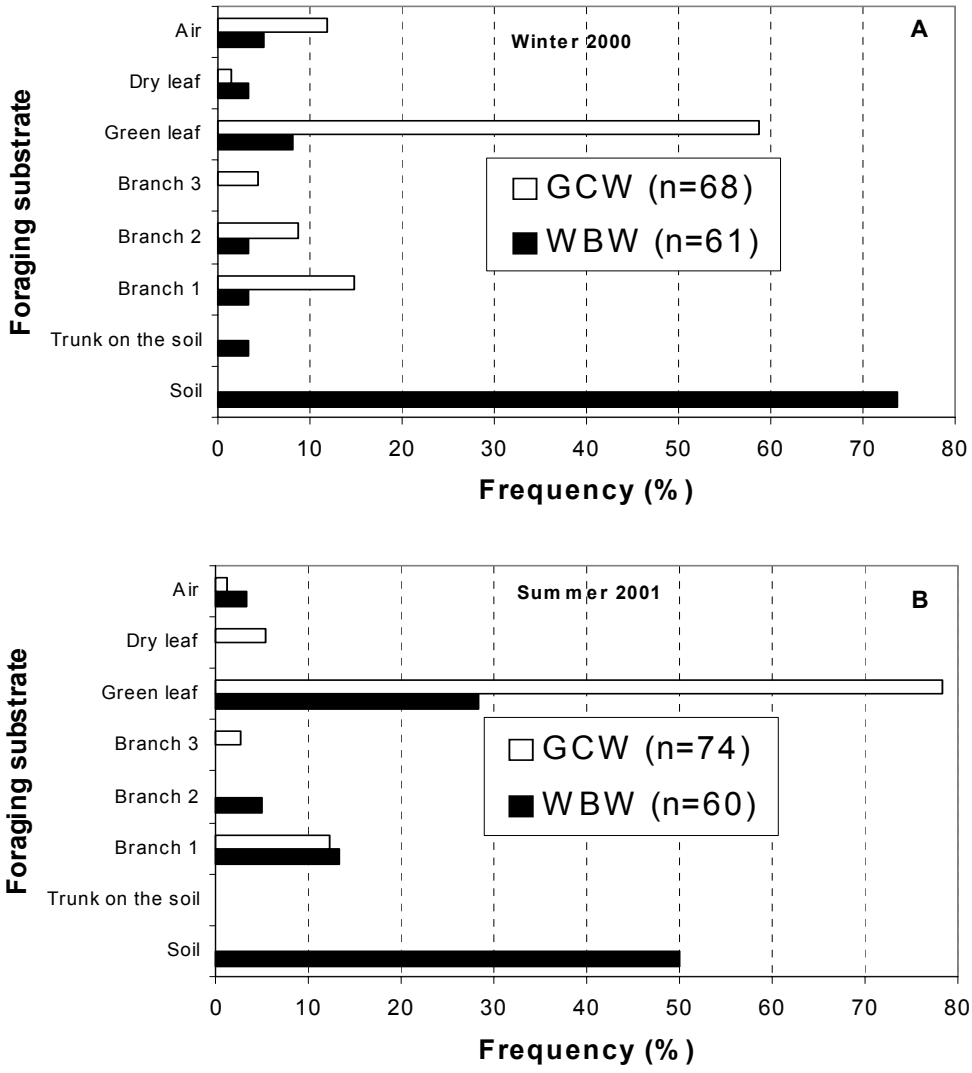

FIG. 3. Frequency of use of different foraging substrates by White-browed (WBW) and Golden-crowned (GCW) warblers in semidecidual forest of southern Brazil. Branch 1 (≤ 1 cm), branch 2 (1 cm < branch ≤ 5 cm), branch 3 (> 5 cm).

METHODS

Study area. The study area was defined inside a 2.2-ha remnant of seasonal forest (IBGE 1986) within the coordinates 50º29'28"–50º59'20"W and 30º16'14"–30º16'18"S. The climate is humid subtropical (cfa) according to the Koeppen's classification; the annual mean temperature is 19.5ºC and the mean precipitation is 1300 mm/year (Ferraro & Hasenack 1995).

The forest canopy was between 7 m and

14 m height, but some emerging trees reached 16 m and presented a high frequency of *Sebastiania commersoniana* (Euphorbiaceae), *Guapira opposita* (Nyctaginaceae), *Casearia sylvestris* (Flaucortiaceae) and *Diospyrus inconstans* (Ebenaceae), corresponding to a secondary succession stage. The understory was composed by young individuals of the larger trees and by shrubs like *Psychotria leiocarpa* (Rubiaceae), *P. carthagenensis* (Rubiaceae), *Faramea marginata* (Rubiaceae), *Sorocea bomplandii* (Moraceae), *Myrciaria cuspidata* (Myrtaceae), *Garcinia gardneriana* (Guttiferae). Herbaceus plants like *Pharus glaber* (Poa- ceae), *Olyra humilis* (Poaceae), *Doryopoteris* sp. (Pterydaceae), *Peperomia* sp. (Piperaceae), *Aechmea* sp. (Bromeliaceae), *Bromelia antiacantha* (Bromeliaceae) and *Calliandra tweediei* (Mimosaceae) predominated in the lower strata (Mendonça-Lima 2002). Granitic outcrops where common within the forest remnant.

Field observations. Sampling was carried out in ten visits to the area in the winter (July to August) 2000 and eleven visits in the summer (December, January and February) 2001, beginning 30 min after the daybreak; the total sampling efforts were 62 h (winter) and 74:20 h (summer). Data on only one species were recorded each day. We searched for the birds and observed them from distance using binoculars (10x50) when necessary. After the first sighting of the bird, the record of data started when it first attacked a prey, always taking care to not disturb the bird during foraging. When this was perceptible (e.g., attention directed to the observer, more frequent and nervous vocalizations), the distance of observation was increased and after the bird retook its usual behavior, the records were resumed. Two or more observations of the same individual were valid only when they were separated by a minimum interval of seven min, following Marini & Cavalcanti (1993).

Data on the position of the individual in relation to the soil (height), attack maneuvers to prey (Remsen & Robinson 1990), the substrate type where the attack happened, and the substrate angle were recorded. The position of the birds in relation to the soil was defined by visual estimation in 1-m intervals. The foraging substrate was classified as: soil (including litter), trunk on the soil, green leaf, dry leaf, branch with diameter equal or thinner than 1 cm, branch with diameter thicker than 1 cm and thinner than 5 cm, branch with diameter thicker than 5 cm and air. The substrate angle was divided into vertical (more or equal to 45º in relation to soil) and horizontal (less than 45º in relation to soil). The field data were first recorded in a portable tape-recorder and later transferred to field tables.

Statistical procedures. Data about niche overlap were analyzed using the indexes as follow: Morisita, Pianka, Czekanowski and overlap percentage (Krebs 1989). Since each sampling day corresponded to one species, a frequency matrix of sampling units (columns) and various classes of attack maneuvers, heights, foraging substrates and angles (lines) was created. A multivariate comparison between species and seasons using all data was performed by means of variance analysis with randomization test (Manly 1991, Pillar & Orlóci 1996). Chord distance was used as the similarity measure between sampling units. A principal coordinates analysis (Manly 1994) was made in order to establish comparisons between the species in the same season and for each species in different seasons. All data were analyzed using the statistical package MULTIV 2.1 (Pillar 2001).

RESULTS

During the winter, 1.5 and 3.1 records/h were obtained for the White-browed and the

TABLE 1. Niche overlap indexes for prey attack maneuvers, foraging height and substrate used by White-browed and the Golden-crowned warblers in winter/2000 and summer/2001 in southern Brazil.

Overlap indexes	Maneuver	Height	Substrate
Winter			
Overlap percentage	19.1%	7.5%	21.1%
Morisita	0.19	0.03	0.13
Pianka	0.35	0.07	0.35
Czekanowski	0.37	0.18	0.39
Summer			
Overlap percentage	37.1%	13.5%	41.9%
Morisita	0.34	0.12	0.48
Pianka	0.42	0.23	0.52
Czekanowski	0.44	0.23	0.40

Golden-crowned warblers, respectively, compared to 1.4 records/h and 2.4 records/h for the summer. The Golden-crowned Warbler foraged higher than the White-browed Warbler in both seasons. The mean foraging height in the winter was 0.18 m (SD = ± 0.44 m, n = 61) for the White-browed and 5.77 m (SD = ± 2.9 m, n = 69) for the Golden-crowned warblers (Fig. 1A). The mean foraging height in the summer was 0.61 m (SD = ± 1.58 m, n = 60) for the White-browed Warbler, compared to 4.85 m (SD = ± 2.4 m, n = 74) for the Golden-crowned Warbler (Fig. 1B).

During the winter the White-browed Warbler used 13 attack maneuvers to prey, compared to 10 for the Golden-crowned Warbler (Fig. 2A). The Golden-crowned Warbler used attack maneuvers that involved flight more often than the White-browed Warbler. During summer, White-browed and Golden-crowned warblers used 10 and 12 attack maneuvers, respectively (Fig. 2B). Both species often used maneuvers in which the bird reached the prey on the perch surface (in 86.7% and 66.4% for the White-browed and the Golden-crowned warblers, respectively).

Studied birds diverged concerning the substrate type used in both winter and summer (Figs. 3A and 3B). The White-browed Warbler frequently directed its maneuvers to the soil, while the Golden-crowned Warbler used mainly green leaves as substrate in both seasons. The substrate angles differed; the Golden-crowned Warbler used vertical substrates (22.4%, n= 15) more often than the White-browed Warbler (9.8%, n= 6). The Golden-crowned Warbler presented differences in the use of substrates with different angles between the two seasons, with higher frequency of vertical substrates in the winter (22.4%, n = 15) than in the summer (11.1%, n = 8).

According to the four niche overlap indexes (Table 1), height was the dimension with the smaller overlap, hence resulting in the greater segregation between the two species both during winter and summer. The variance analysis did not show significant difference (sum of squares = 0.2089, $P = 0.5717$) for each species in different seasons. However, a significant difference was found between species in both seasons (sum of squares = 4.3234, $P = 0.0001$). The dispersion diagram for the principal coordinates analysis clearly showed this differences (Fig. 4). Variables of foraging height and substrate type presented the higher positive correlation coefficients (height until 1 m = 0.98, soil = 0.98) between original descriptors and the first

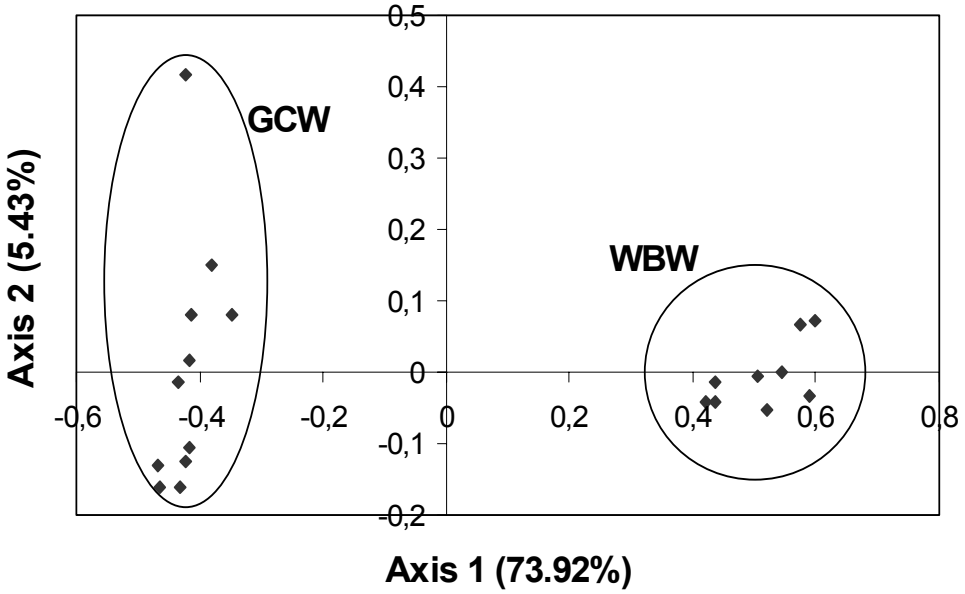

FIG. 4. Dispersion diagram for the ordination scores (PCA) of the sampling units (20) and all variables measured (34) of White-browed (WBW) and the Golden-crowned (GCW) warblers in semidecidual forest of southern Brazil.

ordination axis. On the other hand, the green leaf (substrate category) was negatively correlated (r = –0.94) with the axis 1, showing the importance of these variables for the segregation of foraging habits among species.

DISCUSSION

Data show segregation between both species of *Basileuterus* studied. Either during winter or in the summer, analyzed parameters resulted effective in evaluating the differences among the niche dimensions of White-browed and the Golden-crowned warblers. When niche overlap indexes of winter and summer are compared, segregation between both species increased in winter. This fact could indicate (1) that, due to greater scarcity of food, the birds forage in locations where prey are more easily caught or (2) that, even if prey density is the same in both seasons, the need for saving energy while foraging in winter induces the birds to search for food in more limited areas than in summer when energetic costs of self-maintenance are lower.

Either in winter or in summer, foraging height was the dimension that most influenced the ecological segregation of both warbler species. According to Keast (1980), one of the mechanisms that allow the coexistence of small insectivorous species in the Neotropical region is the use of different vertical zones for foraging. Although the differences were not statistically significant, during the winter the Golden-crowned Warbler used a greater height range. This fact may be related to higher difficulty in finding prey during the winter period. As a consequence, the smaller height range used in summer may have resulted (1) from easier finding of abundant

or less hidden prey, or (2) from the influence of arriving migrant insectivorous birds that forage in the understory (e.g., Euler's Flycatcher, *Lathrotriccus euleri*). For the White-browed Warbler, this relationship was inverse, that is, the greater height range was observed in summer. This fact may be explained by a more constant prey density the year round in the litter (Ford *et al.* 1990), and by the use of conspicuous food items in other heights during summer. Similarly, Marini & Cavalcanti (1993) observed the White-bellied Warbler foraging more frequently in higher substrates than the White-striped Warbler and the Flavescent Warbler, thus resulting in the fact these species did not occur in the same habitats. According to Silva (1991) and Sick (1997), the White-bellied Warbler is a subspecies of the Golden-crowned Warbler, being evident that this species is a characteristic forager of higher strata. Tramer & Kemp (1980), working in Costa Rica, indicated that the *Basileuterus* species were exclusive of understory, and that the Golden-crowned Warbler foraged from the ground up to 12 m. Several works mentioned the importance of height in the segregation of closely related species (e.g., MacArthur 1958, Ficken *et al.* 1968, Cody 1974, Hutto 1981, Airola & Barrett 1985).

Hutto (1981) stated that the foraging location, rather than the foraging methods may be relatively more important in promoting ecological isolation among parulids. In our study, this was verified because the attack maneuvers variables showed correlation coefficients smaller than other variable types. Even using different parts of the same habitat, studied birds differed in foraging tactics probably because of differences in the structures of their microhabitats or their prey types. Regarding attack maneuvers, Fitzpatrick (1985) informed that flight maneuvers are less precise than those in which prey is in the reach of the bird's bill. Remsen & Robinson (1990) and Thiollay (1988) also stated that aerial maneuvers result in higher energetic costs than maneuvers in which food items are removed from a near substrate, avoiding the need of flight. Taking that into account, Golden-crowned Warblers, besides using less precise maneuvers, would spend more energy than White-browed Warblers when attacking prey. On the other hand, Whelan (1989) stated that birds might vary their foraging tactics depending on prey types. Thus, the frequency of use of attack maneuvers could be based on the prey type that is available in such moment. This could indicate that the studied *Basileuterus* species probably used different food resources, with Golden-crowned Warblers taking larger preys with a greater energetic content in both seasons of the year. Thus, the type of preys might be more important than the seasonal abundance of them for the studied warbler species due the fact that there are no significant differences between summer and winter for the both species.

As a conclusion, present results show that White-browed and the Golden-crowned warblers segregate in their winter and summer foraging niche dimensions. This conclusion corroborates Sick (1997) statement that White-browed Warblers use lower strata than Golden-crowned Warblers. Golden-crowned Warblers besides having greater foraging plasticity than White-browed Warblers, do not show seasonal differences in the use of the studied dimensions. Based on these results, it could be predicted that, in forest patches heavily used as roosting sites by cattle or urban areas where the shrubby, herbaceous and litter strata are disturbed or removed (e.g., squares and parks), White-browed Warblers would probably disappear, since these birds are closely related to the lower strata of the forests. Golden-crowned Warblers, although predominantly foraging in the understory, due to their greater plasticity, perhaps could adjust their food search to higher strata and thus be less sensible to habitat disturbances like those

mentioned above. Other habitat requirements (e.g., nesting sites) could however determine the disappearance of both species under those conditions.

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