*Wilson Bull.*, 114(3), 2002, pp. 342–348

# FORAGING BEHAVIOR AND MICROHABITAT USE OF BIRDS INHABITING COASTAL WOODLANDS IN EASTCENTRAL ARGENTINA

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ABSTRACT.—We examined foraging behavior and microhabitat use of four passerine bird species inhabiting an old growth coastal woodland in Buenos Aires Province, Argentina. Based on foraging maneuvers, we identified two groups: (1) nonaerial foragers formed by Tropical Parulas (*Parula pitiayumi*) and Masked Gnatcatchers (*Polioptila dumicola*) that hopped on branches and twigs while searching and gleaning prey from the nearby foliage, and (2) aerial foragers formed by White-crested Tyrannulets (*Serpophaga subcristata*) and Small-billed Elaenias (*Elaenia parvirostris*) that searched for and detected prey while perched, and captured it from foliage or in the air. Nonaerial foragers found prey primarily in the canopy while aerial foragers captured prey at all heights in the woodland. Tree species selection was similar among the four species. All bird species disproportionately foraged in *Scutia buxifolia* and avoided the use of *Ligustrum lucidum* trees. Our results indicate that these bird species differed in microhabitat selection in old growth coastal woodland, and that nonaerial foragers were more sensitive to foliage architecture and foliage height distribution than aerial foragers. These results illustrate the importance of woodland logging to bird densities, and provide basic information for effective management. *Received 19 September 2001, accepted 5 June 2002.*

RESUMEN.—Nosotros estudiamos el comportamiento de alimentación y el uso de microhábitats de cuatro especies passeriformes que habitan bosques costeros maduros de la Provincia de Buenos Aires, Argentina. Considerando las maniobras de alimentación encontramos dos grupos: (1) las recolectoras, formado por Pitiayumí (*Parula pitiayumi*) y Tacuarita Azul (*Polioptila dumicola*), las cuales saltando por las ramas y ramitas buscan y recolectan presas desde el follaje cercano, y (2) las cazadoras por revoloteo, formado por Piojito Común (*Serpophaga subcristata*) y Fiofío Pico Corto (*Elaenia parvirostris*), que buscan y detectan presas desde una percha y, usando tácticas aéreas, capturan las presas desde el follaje o en el aire. Las especies recolectoras capturan sus presas principalmente en el dosel del bosque, mientras que las cazadoras por revoloteo se alimentan en todas las alturas. El uso de las especies arbóreas del bosque fue similar para las cuatro especies de aves. Todas seleccionaron alimentarse en árboles de *Scutia buxifolia* y evitaron usar los de *Ligustrum lucidum*. En general, las especies de aves difieren en su selección de los microhábitats en el bosque costero maduro; las especies recolectoras fueron más afectadas por la arquitectura del follaje y la abundancia de cobertura en altura que las especies cazadoras por revoloteo. Los resultados obtenidos ayudan a comprender los efectos del talado del bosque sobre la densidad de aves, y proveen información básica para su efectivo manejo.

Studies of foraging behavior show how birds use their habitat and allow identification of environmental features that could be influencing bird populations. Vegetation structure provides opportunities and constraints that determine how and where birds detect and capture their prey (Holmes 1990). Leaf morphology, arrangement of leaves on branches, foliage height distribution, and other aspects of foliage architecture have a strong influence on bird foraging behavior (Sabo 1980, Franzreb 1983, Robinson and Holmes 1984, Holmes and Recher 1986, Robinson 1992). These patterns, mostly identified through detailed field studies, also have been supported by experimental aviary studies (Emlen and DeJong 1981; Whelan 1989, 2001; Parrish 1995). As a consequence of these influences, bird species selectively forage in certain tree species, plant life forms, and at particular heights (Holmes and Robinson 1981, Airola and Barrett 1985, Morrison et al. 1986, Adams and Morrison 1993, Sodhi and Paszkowski 1995, Gabbe et al. 2002). These choices ultimately can determine which species survive in a particular habitat.

Little is known about bird foraging ecology in old growth forest and woodlands of southern South America. Such information is important because human activities could be promoting bird population declines in some areas

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(Willson et al. 1994, Aleixo 1999, Cueto and Lopez de Casenave 2000a). Thus, basic understanding of the ecological requirements of bird species inhabiting forest habitats, critical for effective management decisions, is lacking. In this paper, we examine foraging behavior and microhabitat use of White-crested Tyrannulets (*Serpophaga subcristata*), Small-billed Elaenias (*Elaenia parvirostris*), Masked Gnatcatchers (*Polioptila dumicola*), and Tropical Parulas (*Parula pitiayumi*), four species common in coastal woodlands of eastcentral Argentina (Cueto and Lopez de Casenave 2000b). We analyzed frequency of use of different tree species and foliage height where birds captured their prey, and compared this use with relative abundance of tree species and vertical distribution of foliage in an old growth coastal woodland of eastcentral Argentina. We addressed the following questions. (1) Do bird species use the same foraging maneuvers to detect and attack prey? (2) Are there differences in foraging substrate among bird species? (3) Do bird species use the same tree species to search and capture prey? (4) Are there differences in foraging height among bird species?

## METHODS

*Study area.*—We conducted this research in old growth woodland of the Private Reserve El Destino (35° 08′ S, 57° 25′ W; 2,400 ha) on the shore of de la Plata River, Buenos Aires Province, Argentina. This reserve is part of the Biosphere Reserve Parque Costero del Sur. Dominant tree species in El Destino are *Scutia buxifolia* (Rhamnaceae) and *Celtis tala* (Ulmaceae); other less abundant tree species include *Ligustrum lucidum* (Oleaceae), *Schinus longifolius* (Anacardiaceae), *Jodina rhombifolia* (Santalaceae), and *Sambucus australis* (Caprifoliaceae; Cueto and Lopez de Casenave 2000a). A detailed description of the vegetation of El Destino is presented in Cagnoni et al. (1996). The climate is wet, warm temperate, with hot summers and mild winters. Frosts are infrequent because of the proximity to the river. Mean annual precipitation is 88.5 cm ($n$ = 10 years); the rainiest months are January and February (summer). Mean maximum temperature (January) is 27.5° C and the mean minimum temperature (July) is 5.9° C.

*Vegetation measurements.*—We quantified vegetation structure and composition during December 1992 and March 1993. Eight plots (30 × 30 m) were randomly located in the old growth woodland. In the center of each plot, we established a 15-m transect in each of the four cardinal directions. We sampled vegetation at 30 random points along each transect by erecting a rod marked at 1-m intervals at each point and recording the height and species identity of vegetation contacting the rod. The horizontal cover of each tree species was calculated as the percentage of points at which the species was present. We estimated a mean value over the four transects for each plot. We depicted a profile of foliage cover as the percentage of points with contacts at 1-m intervals.

*Bird foraging behavior.*—We recorded the foraging behavior of White-crested Tyrannulets, Small-billed Elaenias, Masked Gnatcatchers, and Tropical Parulas during the breeding season (October to March) during 1994–1995 and 1995–1996, and on occasional visits during autumn and winter, 1995. During each sampling period, we systematically walked through the study area and observed as many different birds as possible. When a foraging bird was sighted, we recorded foraging maneuver, substrate from which food was taken or toward which the attack was directed, height above ground (to the nearest m), plant species, and (when possible) prey taken. We defined the following foraging maneuvers: (1) glean, when a perched or walking bird took prey items from the surface of a nearby substrate; (2), probe, when a bird's beak penetrated the substrate in pursuit of subsurface prey items; (3) hover, when a flying bird took prey items from the surface of a substrate; and (4) sally, when a flying bird pursued aerial prey items. Substrates considered were foliage, twigs, branches, and air. We recorded only the first attack for each individual encountered, because sequential observations of repeated foraging maneuvers by the same individual are not independent (Hejl et al. 1990, Recher and Gebski 1990).

*Statistical analysis.*—We evaluated tree species use with the Chi-square goodness-of-fit test. We estimated expected frequencies of tree use from the relative cover of each tree species. We tested the hypothesis that observed distribution of foraging maneuvers among tree species for each bird species was the same as the expected distribution generated from relative cover of tree species.

We also evaluated foraging height use with the Chi-square goodness-of-fit test. We segregated foraging height data into 1-m height categories. We estimated expected frequencies of height use from the profile of foliage cover. The lowest category (0–1 m above the ground) was not included in these estimates because the birds we observed did not forage at this height. We tested the hypothesis that observed distribution of foraging heights for each bird species was the same as the expected distribution of foraging height generated from the profile of foliage cover.

Chi-square goodness-of-fit tests should not be used if >20% of the cells of expected frequencies are <5, or when any expected frequency is <1 (Siegel and Castellan 1988). To avoid that problem, we combined adjacent categories in some cases to raise the expected values. A consequence of that procedure was the reduction of degrees of freedom. Statistical significance was set at $P \leq 0.05$.

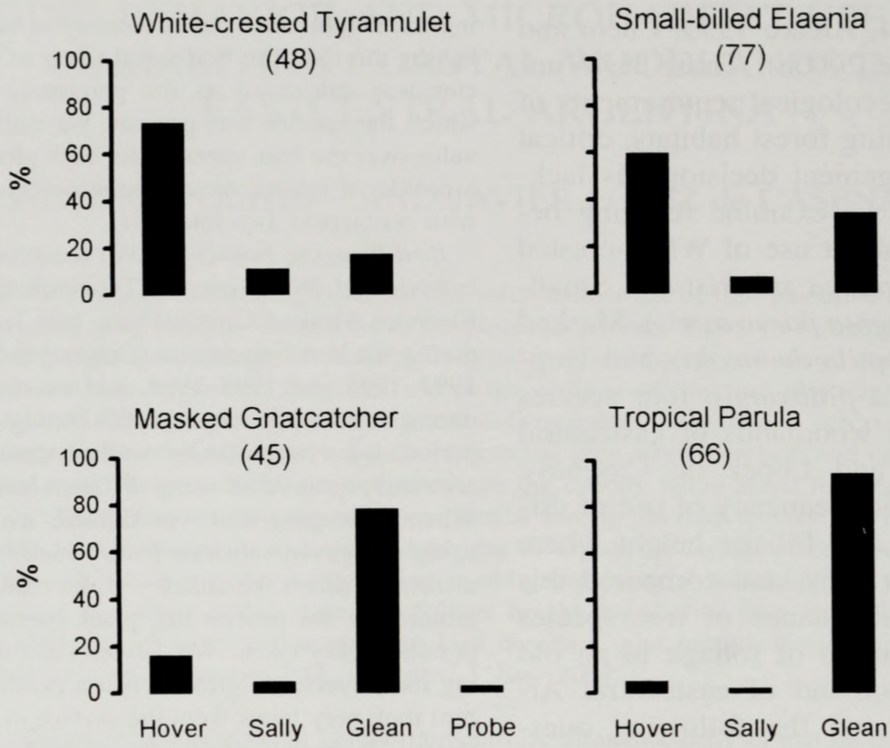


FIG. 1. White-crested Tyrannulets and Small-billed Elaenias most frequently hovered to capture prey, while Masked Gnatcatchers and Tropical Parulas captured prey mostly by gleaning. Data are from old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Numbers of individual birds are in parentheses.

## RESULTS

Bird attacks were directed mainly at non-flying prey (i.e., glean and hover; Fig. 1). Tropical Parulas and Masked Gnatcatchers used glean as their principal maneuvers, although the first was more stereotyped (>90% of attacks were performed using glean maneuvers). The Masked Gnatcatcher was the only species to probe for prey. White-crested Tyrannulets and Small-billed Elaenias most frequently hovered to capture prey.

The four species concentrated their foraging mainly on foliage (Fig. 2). Twigs also were used, but in low frequencies. White-crested Tyrannulets and Small-billed Elaenias frequently captured prey in the air, and Masked Gnatcatchers used branches more than the other three species.

Foraging height distribution differed significantly among bird species (Fig. 3). Tropical Parulas and Masked Gnatcatchers captured prey predominantly in the canopy of the woodland ($\chi^2_6 = 38.4$, $P < 0.0001$, and $\chi^2_4 = 15.9$, $P = 0.003$, respectively). In contrast, White-crested Tyrannulet and Small-billed Elaenia foraging heights were similar to the available foliage height distribution ($\chi^2_4 = 3.0$, $P = 0.56$, and $\chi^2_6 = 10.4$, $P = 0.11$, respectively).

Tree species were not used by birds in proportion to their availability (Table 1). *Scutia buxifolia* was used to a much greater degree than its relative abundance, and *Ligustrum lucidum* was avoided by the four species. *Celtis tala* frequently was used by Tropical Parulas and White-crested Tyrannulets and in proportion to its availability by Small-billed Elaenias and Masked Gnatcatchers. The other tree species had low cover and rarely were used by the four bird species.

## DISCUSSION

The birds we studied in the old growth woodland of El Destino located and captured prey mainly in the tree foliage, using two maneuvers. Tropical Parulas and Masked Gnatcatchers hopped along the branches and twigs capturing prey by gleaning them from nearby foliage. White-crested Tyrannulets and Small-billed Elaenias searched and detected prey while perched, and captured them from foliage using aerial maneuvers. These prey attack maneuvers are common behaviors of foliage-dwelling birds in a variety of woodland

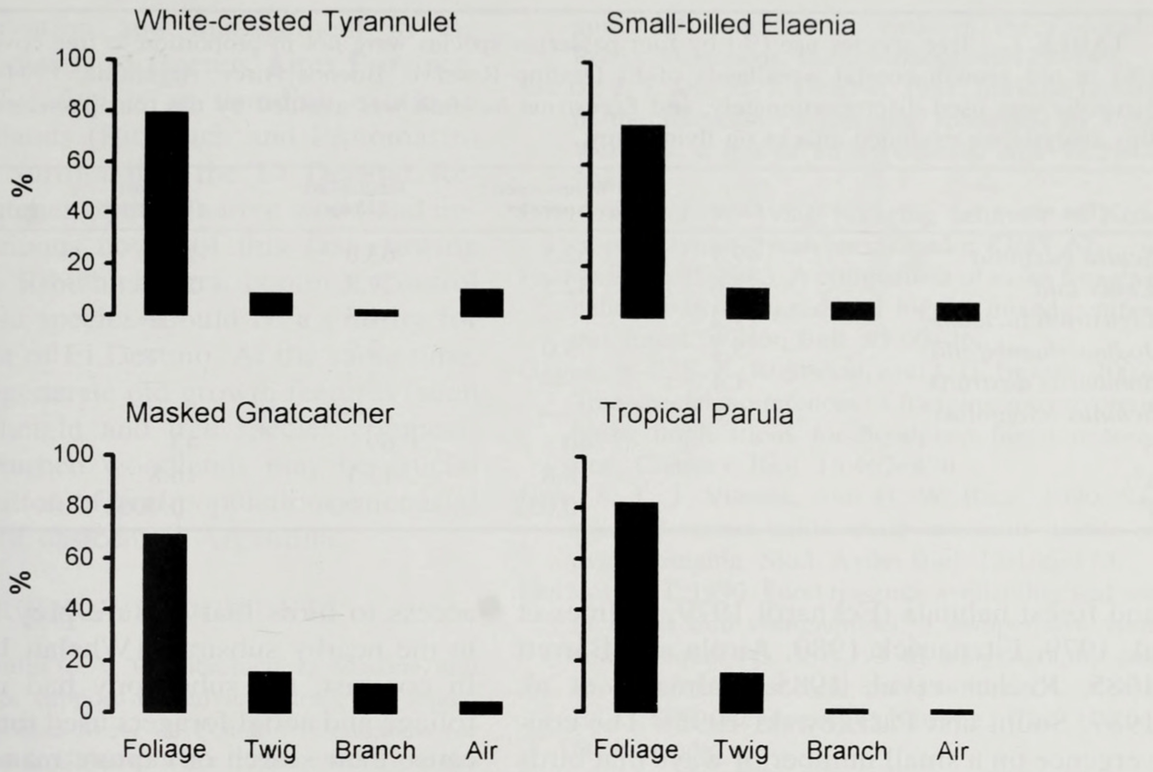


FIG. 2. The four passerine species concentrated their foraging mainly on the foliage substrate in old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Sample sizes are the same as in Fig. 1.

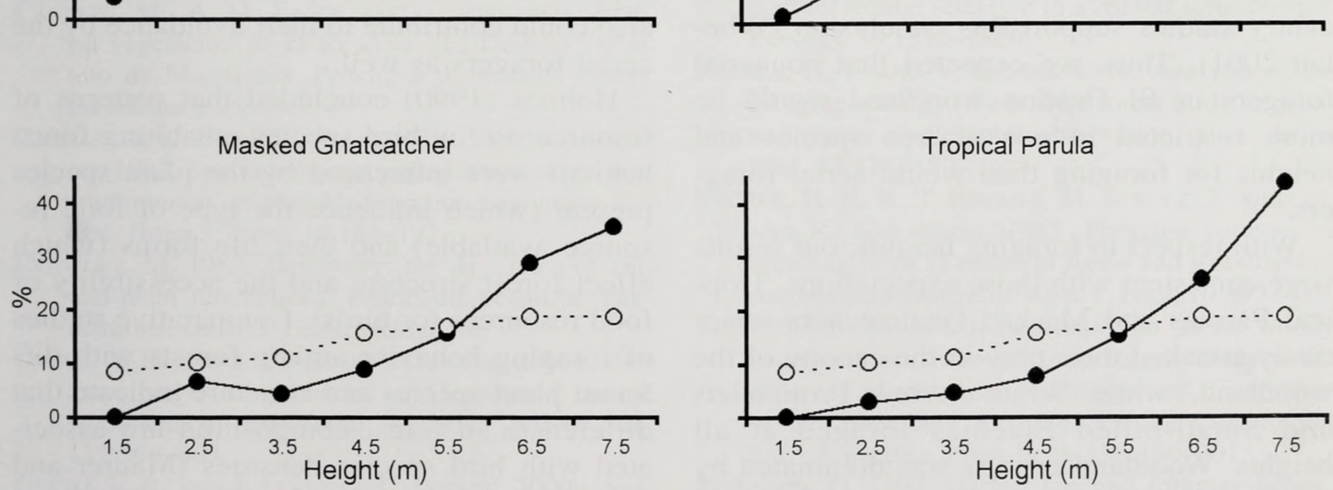


FIG. 3. The distribution of foraging heights (solid circles) of White-crested Tyrannulets and Small-billed Elaenias were similar to the height distribution of available foliage (open circles), while Masked Gnatcatchers and Tropical Parulas captured prey predominantly in the canopy. Data are from old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. Sample sizes are the same as in Fig. 1.

TABLE 1. Tree species use (%) by four passerine species were not in proportion to tree cover availability (%) in old growth coastal woodlands of El Destino Reserve, Buenos Aires, Argentina, 1994–1996. *Scutia buxifolia* was used disproportionately, and *Ligustrum lucidum* was avoided by the four passerine species. For this analysis we excluded attacks on flying prey.

| Tree species | Cover | White-crested Tyrannulet | Small-billed Elaenia | Masked Gnatcatcher | Tropical Parula |
|---|---|---|---|---|---|
| *Scutia buxifolia* | 49.3 | 62.5 | 63.8 | 76.7 | 58.5 |
| *Celtis tala* | 27.6 | 32.5 | 27.5 | 23.3 | 40.0 |
| *Ligustrum lucidum* | 17.2 | — | 1.5 | — | 1.5 |
| *Jodina rhombifolia* | 3.7 | 5.0 | 2.9 | — | — |
| *Sambucus australis* | 1.4 | — | 4.3 | — | — |
| *Schinus longifolius* | 0.8 | — | — | — | — |
| *n* | | 40 | 69 | 43 | 65 |
| $\chi^2_3$ | | 8.8 | 13.1 | 16.8 | 17.8 |
| *P* | | 0.032 | 0.004 | 0.0008 | 0.0005 |

and forest habitats (Eckhardt 1979, Holmes et al. 1979, Fitzpatrick 1980, Airola and Barrett 1985, Recher et al. 1985, Carrascal et al. 1987, Sodhi and Paszkowski 1995). The convergence on a small number of ways that birds capture prey suggests that forest structure constrains how birds encounter and attack prey and, in combination with food abundance, provides a set of foraging opportunities that determines which bird species inhabit a given forest habitat. Thus, forest structure could influence the composition of bird assemblages (Holmes and Robinson 1981, Whelan 2001).

Robinson and Holmes (1982, 1984) suggested that prey detectability for gleaning birds is strongly affected by leaf morphology and arrangement (e.g., size, shape, petiole length, and distribution along branches), while birds capturing prey by hovering are less affected by foliage architecture. Experimental aviary studies support this conclusion (Whelan 2001). Thus, we expected that nonaerial foragers in El Destino woodland would be more restricted in use of tree species and heights for foraging than would aerial foragers.

With respect to foraging heights, our results were consistent with those expectations. Tropical Parulas and Masked Gnatcatchers selectively attacked their prey in the canopy of the woodland, while White-crested Tyrannulets and Small-billed Elaenias foraged at all heights. Woodland canopy was dominated by *Scutia buxifolia* and *Celtis tala* (Cueto and Lopez de Casenave 2000a), which have dense foliage of small leaves on short petioles. These features of the foliage could facilitate access to birds that capture prey by gleaning in the nearby substrate (Whelan 1989, 2001). In contrast, the subcanopy had more sparse foliage and aerial foragers used these areas because their search or capture maneuvers were facilitated.

The selection of tree species was partly consistent with our expectations, because all bird species selected *Scutia buxifolia* for capturing prey and avoided *Ligustrum lucidum*. The avoidance of *Ligustrum lucidum* by nonaerial foragers could be related to the morphology and arrangement of leaves of this tree. *Ligustrum lucidum* foliage has large (7–13 cm) leaves with long (1–2 cm) petioles distributed in isolated form along the branches. In addition, *Ligustrum lucidum* also has coriaceous leaves which is an antiherbivore defense (Crawley 1983), so their foliage may support a lower arthropod abundance. This also could contribute to their avoidance by the aerial foragers as well.

Holmes (1990) concluded that patterns of resource use by bird species inhabiting forest habitats were influenced by the plant species present (which influence the type of food resource available) and their life forms (which affect forest structure and the accessibility of food resources for birds). Comparative studies of foraging behavior among forests with different plant species and structure indicate that differences in forest composition are associated with bird species densities (Maurer and Whitmore 1981, Franzreb 1983, Sabo and Holmes 1983).

Our data on bird foraging behavior and microhabitat use have important implications for bird conservation and management in the coastal woodlands of Buenos Aires Province. *Ligustrum lucidum* is an invading exotic in these woodlands (Ribichich and Protomastro 1998), and surrounding the El Destino Reserve are patches of dead native woodland under a continuous cover of this fast-growing tree (A. M. Ribichich pers. comm.). Control of this exotic species should be a priority for management of El Destino. At the same time, efforts to regenerate old growth features (such as canopy height and tree species composition) in disturbed woodlands may be crucial for conservation of bird populations in coastal woodlands of eastcentral Argentina.

## ACKNOWLEDGMENTS

We are grateful to A. M. Ribichich, L. Marone, and J. P. Pelotto for support and advice during this study. We thank the Elsa Shaw de Pearson Foundation for permission and facilities to work in the reserve and the staff of "El Destino" for their kindness. We received much useful and critical revision of a draft of the manuscript from C. J. Whelan.

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