ECOLOGICAL RELATIONSHIPS OF TWO TODIES IN HISPANIOLA: EFFECTS OF HABITAT AND FLOCKING[1]

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Abstract. We studied microhabitat use, foraging and social behavior of Broad-billed (*Todus subulatus*) and Narrow-billed (*T. angustirostris*) Todies in two areas of sympatry in the Cordillera Central of the Dominican Republic. Solitary Broad-billed and Narrow-billed Todies occupied distinct microhabitats in both shade coffee plantations and native pine forest while generally sharing similar foraging strategies. In both habitats, Broad-billed Todies foraged higher in the vegetation and occurred in more outer horizontal positions with lower foliage density than did their congener. Movement rates and feeding rates differed significantly between the two species, with the Narrow-bill being the more active species. Changes in foraging behavior by both species of todies were observed when they associated with mixed-species flocks in pine forest. We noted a decrease in some measures of spatial overlap of todies in interspecific flocks, but other feeding behaviors tended to converge.

Key words: foraging behavior; mixed-species flocks; Hispaniola; Todus; *insectivores; habitat use.*

Sinopsis. Estudiamos el uso del microhábitat, comportamiento alimenticio y social de *Todus subulatus* y *T. angustirostris* en dos áreas simpátricas de la Cordillera Central de la República Dominicana. Aves solitarias de ambas especies ocupan distintos microhábitates en plantaciones de café de sombra y en los bosques nativos, mientras comparten estrategias de forrajeo generalmente similares. En ambos habitates *T. subulatus* se alimenta más alto en la vegetación mientras se encuentra en posiciones horizontales más hacia afuera, con una densidad de follaje menor que su congénere. Las razones de movimiento y alimentación difieren grandemente entre las dos especies, siendo el *T. angustirostris* la especie más activa. Se observaron los cambios en el comportamiento de alimentación cuando estas especies se asociaban en bandadas de especies mixtas en los bosques de pinos. Notamos una merma en el solapamiento espacial en las bandadas interespecíficas, pero otros comportamientos de alimentación mostraron una tendencia a converger.

INTRODUCTION

Patterns of resource use among avian sympatric congeners may change in the presence of mixed-species foraging flocks. Flocking behavior, hypothesized to increase fitness through enhanced foraging or decreased likelihood of predation (reviewed by Powell 1985, Hutto 1994), may facilitate the exploitation of foraging locations or tactics that a bird would not otherwise use (Krebs 1973, Buskirk 1976, Valburg 1992), or may force a bird to modify foraging behavior because of potential competition with so many birds in close proximity (Hutto 1988). Changes in foraging behavior have been suggested in studies comparing

solitary individuals with individuals in mixed-species flocks (Morse 1970, Austin and Smith 1972, Alatalo 1981), and color-banded birds which forage solitarily and as group members (Valburg 1992). Flocking may result in the convergence of foraging behavior of flock participants (Pearson 1971, Buskirk 1972 cited in Powell 1985, Valburg 1992) and a reduction in resource partitioning (Morse 1970, Powell 1985), indicating possible social learning and copying (Krebs 1973, Morse 1978). Decreased foraging overlap in flocks is generally interpreted as indicating interference competition (Alatalo 1981). Studies of how resource partitioning is affected by the interaction of species, social organization, and habitat have not been published for the tropics (but see With and Morrison 1990).

Hispaniola supports two closely related species of todies and provides an ideal system for studying resource partitioning and the effects of habitat

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and social organization on foraging behavior of congeners. Broad-billed (*Todus subulatus*) and Narrow-billed (*T. angustirostris*) Todies, thought to have evolved in isolation when Hispaniola was separated into two islands during Pleistocene glacier melts (Kepler 1977), continue to be geographically isolated over much of the island (Kepler 1977, Dod 1981). The Broad-billed Tody occurs from sea level to 1700 m and prefers xeric scrub habitats and broadleaf and pine forests. The Narrow-billed Tody is found at higher elevations (800–3,200 m) and most often occurs in moist forests and ravines. The two species are sympatric, however, in mangroves and wet forest on the Samaná Peninsula, over a broad range (465–1,730 m) in the Sierra de Baoruco, and in portions of the Cordillera Central (Kepler 1977; pers. observ.). Both species most frequently occur as single birds or in pairs throughout their ranges, but join mixed-species flocks in the pine forests of the Cordillera Central (Latta and Wunderle 1996).

In this study we compared the foraging behavior of Broad-billed and Narrow-billed Todies in two areas of sympatry in the Cordillera Central of the Dominican Republic to determine if resource use and foraging behavior varied by species, habitat, or social organization of the birds. We compared foraging behavior between the two species in shade coffee plantations and native pine forest, and within species when foraging solitarily and in mixed-species flocks in pine forests. We hypothesized that flocking allows similar species to copy foraging locations and behaviors, and that todies gain foraging benefits from such behavior. We predicted that (1) when foraging solitarily in similar habitat each species would occupy a distinct microhabitat and interspecific behavioral differences would be consistent between habitats, (2) foraging behavior and microhabitat use by the two species would converge in mixed-species flocks, and (3) foraging rates would increase in the presence of mixed-species flocks.

STUDY AREA AND METHODS

Todies were studied in fourteen shade coffee plantations in the vicinity of Manabao and Jarabacoa, La Vega Province, Dominican Republic at elevations of 540–850 m. Shade coffee plantations were characterized by a predominant overstory of *Inga vera,* although mango (*Mangifera indica*), avocado (*Persea americana*), var-

ious citrus species (*Citrus* spp.), and banana or plantains (*Musa* spp.) were also scattered throughout some plantations where they provided an intermediate layer above the coffee. In a few plantations, an occasional pine (*Pinus* sp.) or palm (*Roystonea* sp.) extended into the overstory. The predominant variety of coffee (*Coffea arabica*) in the plantations was the traditional "tipica" variety, although "caturra" predominated in some of the larger plantations. Most of the shade coffee plantations were relatively small ($\bar{x}$ = 1.9 ha, range = 0.1–9.7 ha).

Coffee is cultivated in areas that were originally pine (*P. occidentalis*) forest. Pine forests, many of which have been selectively logged, remain on the steeper slopes and ridge-tops, with variable amounts of broadleaf understory that may be affected by fire, cutting, or grazing. Broadleaf species were not sampled but included *Ribes* sp., *I. vera,* mango (*M. indica*), citrus (*Citrus* sp.), *Cecropia* sp., *Syzygium jambos, Clusia* sp., *Miconia* sp., as well as numerous unidentified shrubs. Pine forest was sampled at six sites on slopes near Manabao (905–1,050 m) and six sites near Jarabacoa (643–779 m). Although the area of the pine forest was not measured, the remnant patches were all estimated to be >100 ha.

Foliage height profiles were determined for each habitat where feeding observations were collected (Wunderle and Latta, in press). Foliage height profiles for the two habitat types showed general structural similarity with a fairly open canopy, a denser coffee or mixed broadleaf understory, and very little in the way of an intermediate layer. In the shade coffee plantations, *Inga* provided most of the shade overstory, with greatest cover in the 10–12 m height category. Pine foliage predominated in the canopy of the pine forest, although scattered broadleaf trees also extended into the canopy, and pine sites had a slightly higher canopy with greatest cover in the 15–20 m height category. The broadleaf understory of the pine forest provided a sparser foliage cover within the different height categories than that provided by coffee in the shade coffee plantations, except within the first 1.0 m where foliage cover was greater in the pine sites.

FEEDING BEHAVIOR

Foraging observations were made in the non-breeding season from October–March 1993–1995 while walking slowly through the sites. Obser-

vations were made from 07:00–12:00 in coffee plantations, but extended to 18:00 in pine forests where feeding activity occurred all day. Foraging observations were made by walking slowly through the habitat until a foraging bird was located. The first foraging event five seconds after an individual was initially detected was recorded to avoid a bias toward the more conspicuous feeding techniques. Only a single foraging event was recorded per individual per day to reduce the problem of autocorrelation inherent in sequence data (Wagner 1981). In all cases, the "social organization" of the bird (i.e., whether the bird was solitary or a member of a mixed-species flock) was noted. A mixed-species flock was defined as comprising at least two heterospecifics within 25 m of one another and moving together for at least five minutes.

Terminology for foraging maneuvers and foraging site classifications was derived from Remsen and Robinson (1990). Aerial foraging maneuvers encountered included sally-strike, sally-stall, sally-hover, sally-pounce, and jump-up (leap). All perch maneuvers were combined into a single category (glean) and included reach-up, reach-out, probe, and glean. For each foraging maneuver in the coffee plantations, the direction of the feeding maneuver (upwards, downwards, horizontal) was noted, and the distance moved by the bird (from the perch site to the food item) was estimated by eye to the nearest 0.15 m.

At each foraging site (i.e., the location of the food item when attacked by the bird) the following were noted: (1) estimated height of the bird above the ground, (2) estimated height of the tallest tree within 15 m (canopy height), (3) horizontal position of the bird (1 = inner 1/3 of tree, 2 = middle 1/3 of tree, 3 = outer 1/3 of tree), (4) the estimated amount of light passing through an imaginary 2 m diameter sphere surrounding the foraging site (0 = 100% of light passes through, 1 = 95%–99% of light passes through, 2 = 75%–94% of light passes through, 3 = 25%–74% of light passes through, 4 = 5%–24% of light passes through, and 5 = 0–4% of light passes through), (5) the location of the prey item, or the "primary substrate type" (for example a tree species or air), and (6) the "secondary substrate" or the location of the food item within or on the primary substrate (for example leaf, twig, trunk, fruit, flower). In coffee plantations we also noted (7) substrate side (top or bottom) and (8) substrate condition (live or dead).

Because canopy heights varied somewhat between sites, bird height relative to canopy height was calculated and used in further analyses. In all statistical analyses foliage density scores of 0–2 and 4–5 were combined to reduce the number of sparse cells. Similarly, for analyses of feeding behavior in pine forests and analyses comparing behavior in pine to behavior in coffee, sample sizes within a cell were increased with the following condensations: (1) foraging methods were combined into three categories: sally-strike, sally-stall and sally-hover, and all others, (2) primary substrates were reclassified as either broadleaf or pine, (3) secondary substrates were reclassified as broadleaf-related (leaves or twigs) or pine related (needles or twigs) and then eliminated as a habitat variable in pine forests as the test became identical to that of the primary substrate, and (4) horizontal positions 1 and 2 were combined.

Movement rates (i.e., changes in perch position) and feeding rates were determined by following feeding todies and recording the time of each feeding attempt into a cassette recorder. Birds were followed for up to 10 min or as long as consecutive feeding attempts could be observed. Rates were calculated as the average time between moves or feeding attempts, but no rates were determined unless there were at least four consecutive moves or feeding attempts. Rates were log-transformed to achieve normality prior to statistical testing.

Both Broad-billed and Narrow-billed Todies are sexually monomorphic, so data from both sexes were lumped. Lumping of the sexes may be justified because in the closely related Puerto Rican Tody (*T. mexicanus*), which are reliably sexed by eye color, Kepler (1977) did not find any difference in body size or morphology.

STATISTICAL ANALYSES

The software package SYSTAT Version 5.2 (Wilkinson 1992) was used to perform various statistical tests described in Sokal and Rohlf (1981). A probability of Type I error of 0.05 or less was accepted as significant but greater values are shown for descriptive purposes. Where data were not normally distributed nonparametric statistics were used. A Pearson's correlation matrix was used to verify the independence of all variables associated with foraging behavior in coffee and pine habitats.
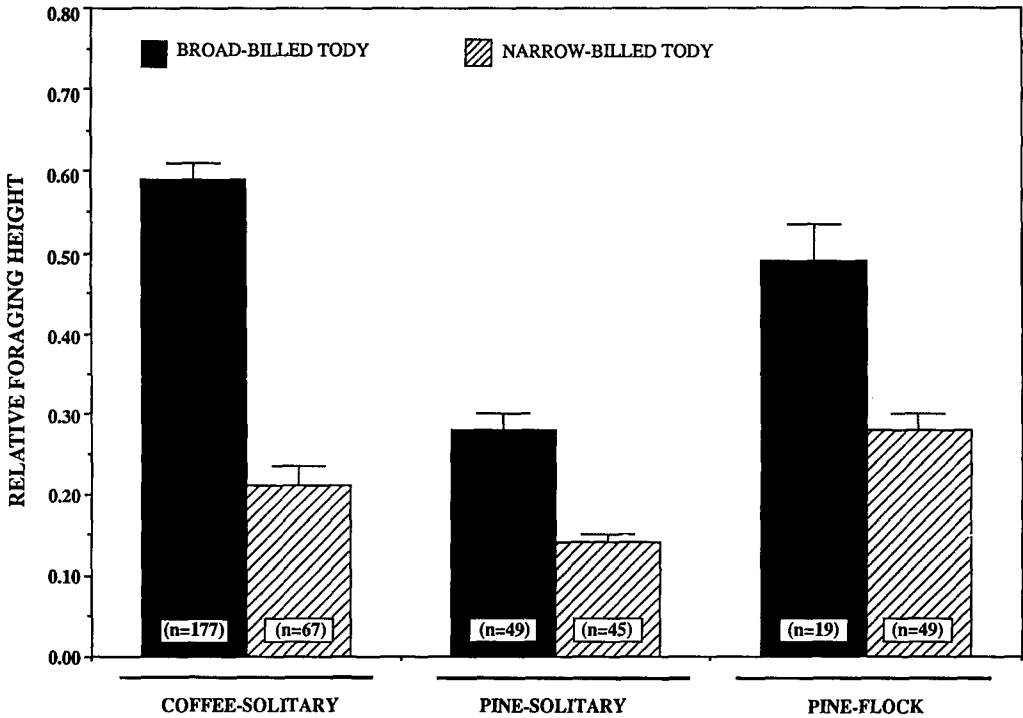
Independent samples *t*-test (with pooled var-

FIGURE 1. Mean relative foraging height (± SE) of Broad-billed and Narrow-billed Todies in shade coffee habitat, and as solitary birds and flock participants in native pine forest. Relative foraging height is calculated by dividing absolute foraging height by maximum canopy height within 15 m of the foraging bird.

iances) was used to test for interspecific differences in the means of attack distances, and to test for interspecific and intraspecific differences in the means of foraging heights, movement rates, and feeding rates. A 2 × 2 Test of Independence with a χ^2 statistic or a Row × Column Test of Independence with a G-statistic was used to test for the independence of various feeding behaviors and feeding site characteristics among species and among social organizations within a species. In tests where cells were sparse (< 5) a G-test with Yates' correction for continuity was used. Log-linear models were used to examine the degree of association between species (Broad-billed or Narrow-billed), social organization (flocking or solitary), and each of four variables describing feeding behavior in pine forest habitat: foraging method, horizontal position, foliage density, and substrate type. Where a three-factor interaction was not present, tests for conditional independence were also run.

RESULTS

Broad-billed and Narrow-billed Todies were found to inhabit shade coffee plantations and native pine forest in the northern Cordillera Central. Todies of both species appeared to be territorial in these habitats, as evidenced by singing and territorial displays, and by recaptures of color-banded birds within the non-breeding season and up to two or more years post-banding. In pine forests, where insectivorous mixed-species foraging flocks of migrant and resident birds are common (Latta and Wunderle 1996), todies join these flocks as the flocks move through tody territories (pers. observ.). Similar foraging flocks were never observed in coffee plantations.

FEEDING BEHAVIOR IN COFFEE

Broad-billed and Narrow-billed Todies occupied distinct microhabitats in shade coffee plantations while sharing generally similar foraging strategies. Broad-billed Todies foraged higher in the vegetation (t = 11.0, df = 242, P < 0.001; Fig. 1) and occurred in more outer horizontal positions (G = 14.3, df = 2, P = 0.001; Fig. 2), with lower foliage density (G = 23.5, df = 2, P < 0.001; Fig. 3) than did Narrow-billed Todies. Foraging substrates of the two species differed (G = 74.3, df = 3, P < 0.001; Fig. 4), with the
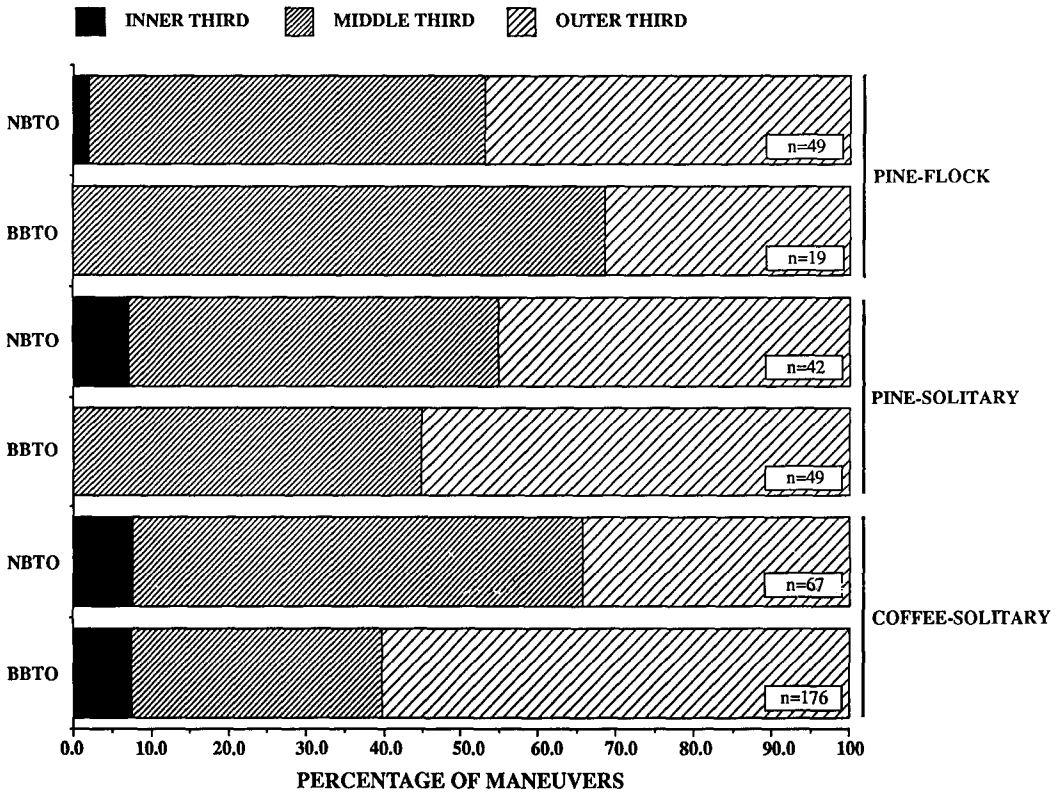
FIGURE 2. Horizontal position of foraging Broad-billed (BBTO) and Narrow-billed (NBTO) Todies in shade coffee plantations, and as solitary birds and flock participants in native pine forest.

Broad-bill most often (69.3% of feeding movements) found in the *Inga* overstory, while the Narrow-bill fed primarily (61.2%) in the coffee. There was no difference ($\chi^2 = 0.9$, df = 1, $P = 0.35$), however, in the use of secondary substrates, with both species using leaves far more frequently (94.0% and 89.4%, respectively) than branches or trunks as attack sites. The two species did not differ in their foraging maneuvers ($G = 7.1$, df = 4, $P = 0.13$; Fig. 5), and there was no interspecific difference in use of live as opposed to dead substrates ($\chi^2 = 0.0$, df = 1, $P = 1.00$), or lower as opposed to upper substrate surfaces ($\chi^2 = 1.5$, df = 1, $P = 0.22$). Attack flight directions, however, differed significantly ($G = 6.9$, df = 2, $P = 0.03$), with Broad-bills directing attacks nearly equally both horizontally (48.9%) and upwards (42.2%), whereas most (73.9%) of the attacks by Narrow-bills were directed horizontally. Attack flight distances also differed ($t = 3.4$, df = 111, $P = 0.001$), with mean attack distances of 0.86 m and 0.49 m, respectively. Movement rates differed significantly ($t = 7.7$, df

$= 103$, $P < 0.001$; Fig. 6) between the species, as did feeding rates ($t = 4.9$, df = 66, $P < 0.001$; Fig. 6), with the Narrow-billed Tody being the more active species.

FEEDING BEHAVIOR IN PINE

Interspecific differences in feeding behaviors of solitary birds observed in coffee plantations were similar to those of solitary birds in pine forest habitat. Broad-billed Todies foraged higher in the vegetation ($t = 5.7$, df = 92, $P < 0.001$; Fig. 1) and occurred in positions with lower foliage density ($\chi^2 = 7.3$, df = 2, $P = 0.025$; Fig. 3) than did Narrow-billed Todies, but there was no significant difference in horizontal positions ($\chi^2 = 0.9$, df = 1, $P = 0.35$; Fig. 2) or use of foraging substrates ($\chi^2 = 0.3$, df = 1, $P = 0.56$; Fig. 4) by the two species. Interspecific differences in foraging maneuvers was found ($G = 20.8$, df = 3, $P < 0.001$; Fig. 5), with the Broad-bill using more sally-strikes and sally-hovers than the Narrow-bill which used a higher proportion of near-perch jumps when feeding. There was no interspecific
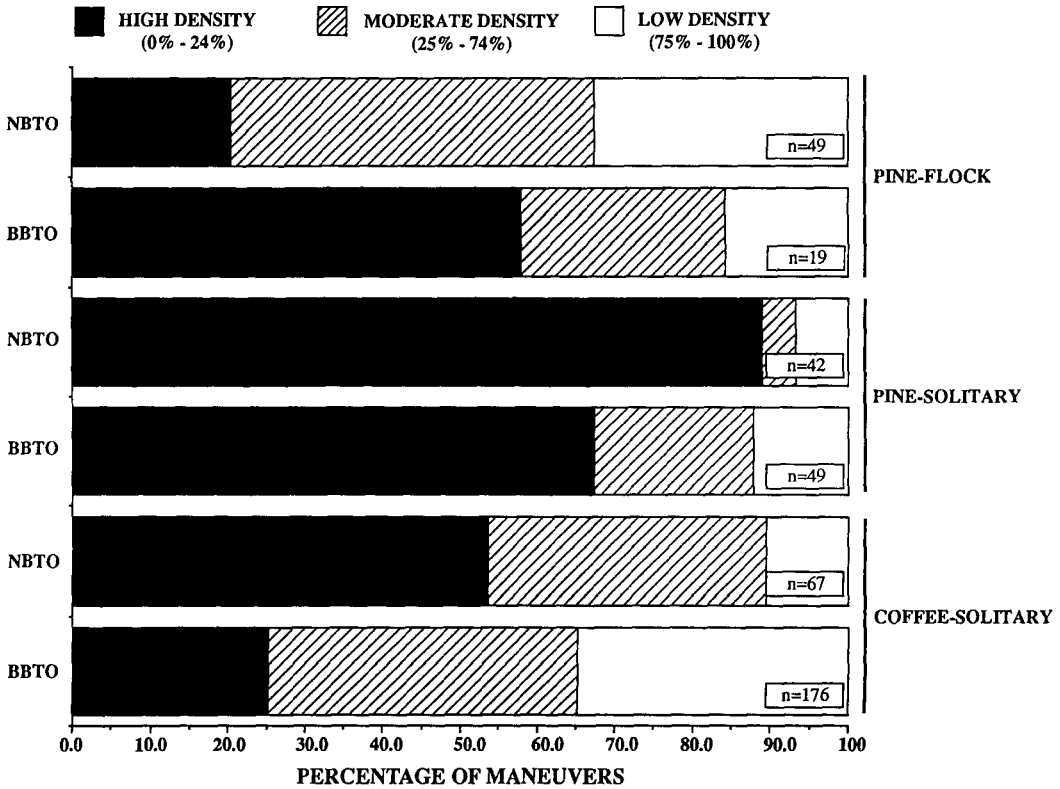
FIGURE 3. Foliage density surrounding foraging Broad-billed (BBTO) and Narrow-billed (NBTO) Todies in shade coffee plantations, and as solitary birds and flock participants in native pine forest. Foliage density was measured as the percentage of light passing through an imaginary sphere 2.0 m around the foraging site and ranged from 0–100%.

difference in use of live as opposed to dead substrates ($\chi^2 = 0.4$, df = 1, $P = 0.52$), or lower as opposed to upper substrate surfaces ($\chi^2 = 0.3$, df = 1, $P = 0.58$). Movement ($t = 7.8$, df = 41, $P < 0.001$; Fig. 6) and feeding rates ($t = 4.3$, df = 27, $P < 0.001$; Fig. 6) differed significantly between the species, as they did in coffee habitat, with the Narrow-bill being the more active tody.

EFFECTS OF SOCIAL ORGANIZATION ON FORAGING BEHAVIOR

Flocking birds foraged significantly higher than solitary individuals in the same pine habitat (Broad-billed Todies: $t = -5.2$, df = 66, $P < 0.001$, Narrow-billed Todies: $t = -5.6$, df = 92, $P < 0.001$; Fig. 1). Intraspecific comparisons also showed a significant increase in the mean movement rate ($t = -3.2$, df = 31, $P = 0.003$), but not the mean feeding rate ($t = -1.6$, df = 17, $P = 0.12$) of flocking vs. solitary Broad-bills. Cor-

responding increases in the movement and feeding rates of flocking Narrow-bills were recorded, but these increases were non-significant ($t = 1.5$, df = 33, $P = 0.14$; $t = 0.8$, df = 29, $P = 0.45$), respectively.

Log-linear models used to analyze data on microhabitat characteristics and foraging behavior in pine forests showed no significant three-way interaction ($G = 2.1$, df = 1, $P = 0.15$) between species, social organization, and horizontal position of feeding todies, and tests for conditional independence also were non-significant. A significant interaction was found between species and horizontal position ($G = 16.8$, df = 4, $P = .002$), indicating that species occupy distinct horizontal positions regardless of social organization. Log-linear analysis found the presence of a three-way interaction ($G = 5.4$, df = 1, $P = 0.02$) between species, social organization, and substrate use. This suggests that the degree of as-
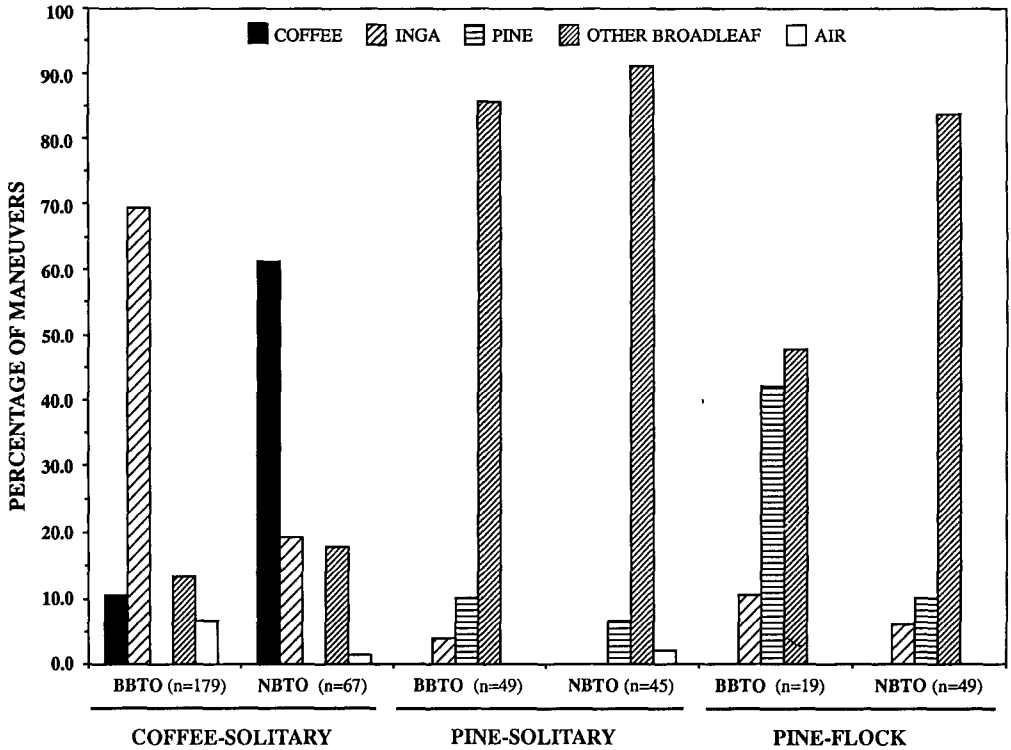
FIGURE 4.   Substrate use by foraging Broad-billed (BBTO) and Narrow-billed (NBTO) Todies in shade coffee plantations, and as solitary birds and flock participants in native pine forest.

sociation between species and social organization differed for different substrates. A test for a three-way interaction between species, social organization and foliage density was not significant ($G = 3.7$, df $= 2$, $P = 0.16$), but tests for conditional independence found significant interactions between social organization and foliage density for each species ($G = 13.3$, df $= 4$, $P = 0.01$), and species and foliage density for a given social organization ($G = 17.9$, df $= 4$, $P = 0.001$). A final log-linear analysis showed a strong three-way interaction between species, social organization and foraging method ($G = 10.2$, df $= 2$, $P = 0.006$), again indicating the degree of association between species and foraging methods differed with social organization.

DISCUSSION

RESOURCE PARTITIONING AMONG SOLITARY BIRDS

Broad-billed and Narrow-billed Todies appear to forage in a generally similar manner charac-

terized by short sallies to the undersides of live, broadleaf leaves. The two species are ecologically segregated, however, because of the use of different foraging strata. Narrow-billed Todies consistently foraged lower than their congener, using denser vegetation both in shade coffee plantations and in pine forests. Different foraging strata dictated the use of different substrates in coffee plantations where Narrow-billed Todies were found virtually always in the coffee understory, whereas Broad-billed Todies, foraging higher, did not use coffee (which generally reaches no more than 3–4 m in height), and were more often seen in the *Inga* overstory. This was not the case in pine forest where the deciduous understory is taller and where some deciduous trees even reach into the canopy.

Choice of microhabitat may have an effect on some foraging methods. Robinson and Holmes (1982) suggested that vegetation structure may limit foraging maneuvers by affecting how a bird moves through its environment, how the vege-
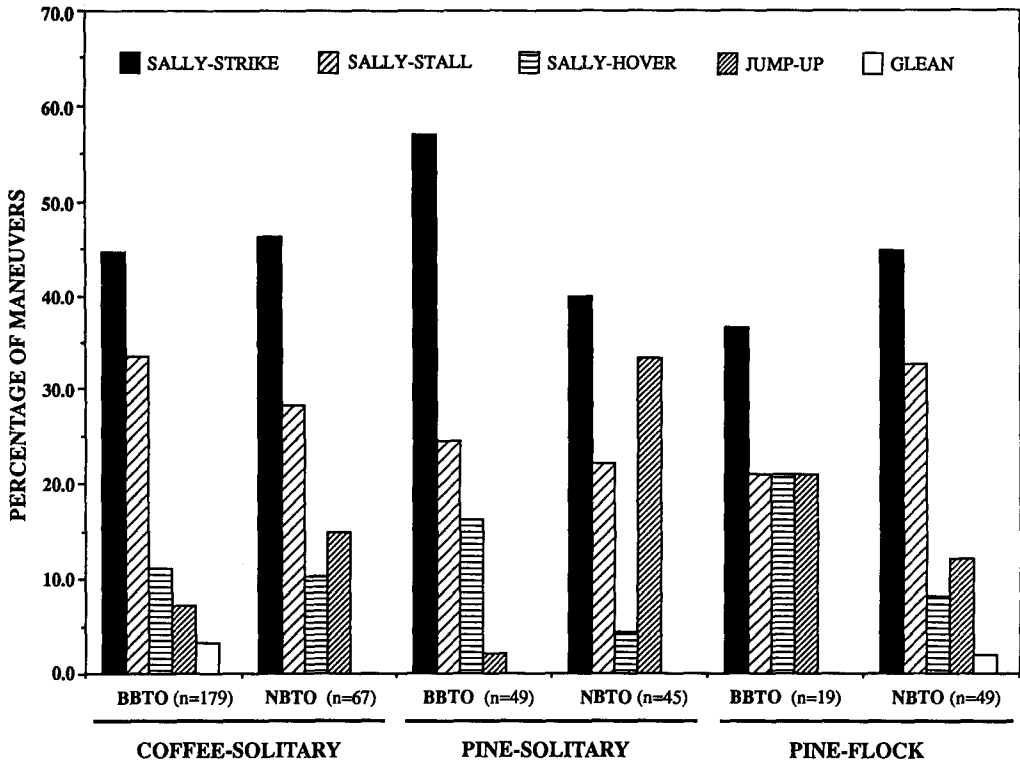
FIGURE 5.   Foraging maneuvers utilized by foraging Broad-billed (BBTO) and Narrow-billed (NBTO) Todies in shade coffee plantations, and as solitary birds and flock participants in native pine forest.

tation can be searched and at what rate, and how easily prey can be captured. In this study, coffee-dwelling Narrow-billed Todies exhibited shorter, and more often horizontal, attack flights than Broad-billed Todies—foraging behavior that may be expected in microhabitats with denser foliage. Similarly, in pine forest, Narrow-bills used a higher proportion of near-perch jumps than the longer sallies of the Broad-bill.

Differences in foraging behavior and differential use of substrates may be related to the use of different food types. Hespenheide (1973) showed that larger birds can be expected to select larger prey, and this may be assumed to be the case for the todies. Food items were rarely seen in this study, but Kepler (1977) reported that the Puerto Rican Tody feeds primarily on dipterans and coleopterans, and may take nearly any small insect. Insect surveys in these same habitats (Wunderle and Latta, in press) show a similar range of prey available. Broad-billed Todies were seen on occasion to prey on larger orthopterans, lepidopterans, and lepidopteran caterpillars—

prey that did not appear to be taken by the smaller Narrow-billed Tody. Different food types also may be reflected in the variation between species in bill size (Greenberg 1985, Moermond and Denslow 1985, Sherry 1990).

EFFECTS OF SOCIAL ORGANIZATION ON FORAGING BEHAVIOR

Both Broad-billed and Narrow-billed Todies have a high propensity to join mixed-species foraging flocks in pine forest in the Cordillera Central. In a related study (Latta and Wunderle 1996), 71% of encounters with Narrow-billed Todies and 61% of encounters with Broad-billed Todies were with individuals foraging in flocks. Both species averaged 1.3 birds/flock when the species was present. Mixed-species flocks in this habitat averaged 7.1 ± 0.2 different species and 11.3 ± 0.5 individuals. Seventy percent of birds encountered in mixed-species flocks were permanent residents and 64% of all flocking individuals were insectivores. Although most individuals were not color-banded, our impression was that Broad-
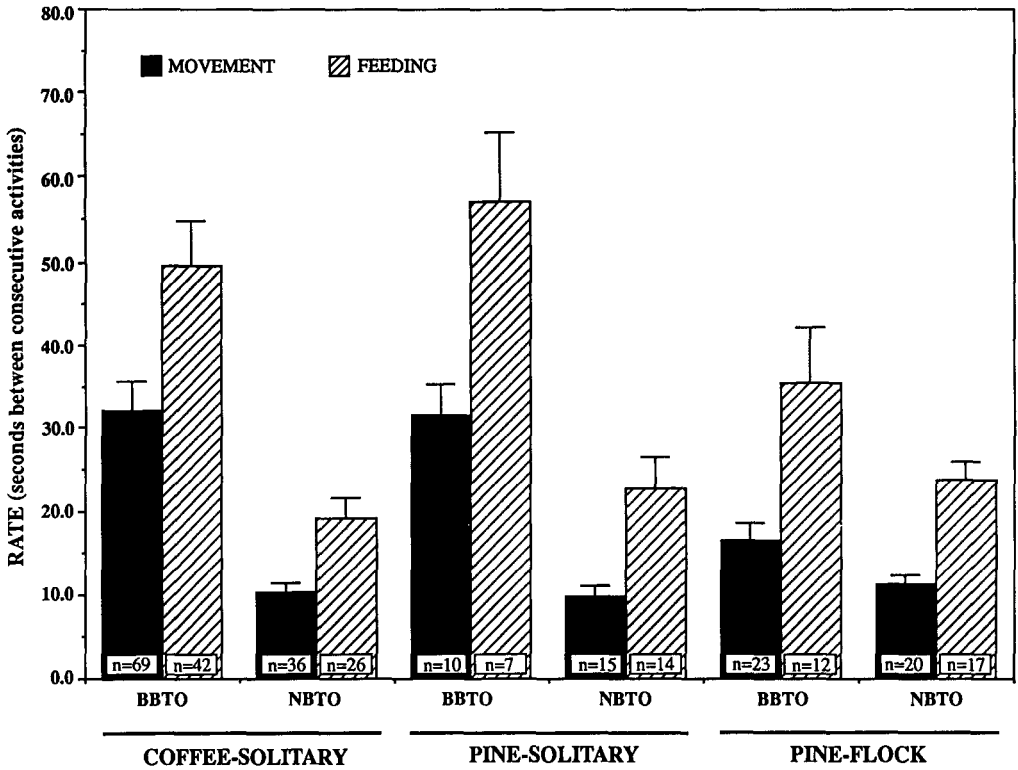
FIGURE 6.   Mean movement and feeding rates (± SE) by foraging Broad-billed (BBTO) and Narrow-billed (NBTO) Todies in shade coffee plantations, and as solitary birds and flock participants in native pine forest. Rates are calculated as the mean time between consecutive activities.

billed and Narrow-billed Todies often occurred in pairs and were among the few flock-joining species to maintain smaller individual territories—joining the flock only when the flock passed through their territory.

Most measures of the impact of interspecific flocking behavior on resource partitioning indicate that flocking results in a reduction or convergence in foraging niche diversity (Powell 1985). Changes in spatial parameters—especially decreases in foraging height diversity—have been most frequently reported when birds join mixed-species flocks (Pearson 1971, Buskirk 1972 cited in Powell 1985). In this study, however, we did not observe a reduction in all measures of spatial overlap among tody species in mixed-species flocks. Both Broad-billed Todies and Narrow-billed Todies foraged significantly higher in the vegetation when participating in mixed-species flocks, but the height at which one tody species foraged relative to the other increased. In con-

trast, the use of horizontal positions by the two species in flocks tended to converge. Narrow-billed Todies continued to occupy less exposed horizontal positions (inner) relative to the Broad-bill, but showed a trend towards the use of the more exposed (outer) positions. Broad-billed Todies showed an opposite trend, though this may reflect movement from the outer canopy of the broadleaf understory to feeding locations in the lower reaches of pine trees.

Log-linear analysis suggested the presence of changes in substrate use and density of foliage used by flocking todies, which are parameters that may have been related to these spatial shifts. A strong interaction between species, social organization, and substrate use was probably a result of the upward vertical shift of the flocking birds in the vegetation, and the corresponding increased use of substrate-types by Narrow-billed Todies that were previously used primarily by solitary Broad-billed Todies. A similar reasoning

likely explains the result of the log-linear analysis of foliage density. In the presence of mixed-species flocks both species moved higher in the vegetation. Narrow-billed Todies generally remained in the broadleaf understory, but in more exposed (outer) horizontal positions where foliage density scores were lower. The Broad-billed Tody, in moving upwards, increased its use of pine (particularly the inner positions), where foliage density scores decreased only marginally.

Several studies have reported changes in avian feeding behavior resulting from association with mixed-species flocks (Morse 1970, Valburg 1992), including the convergence of the foraging behavior of individuals within the flock (Turner 1965, Buskirk 1976, Morse 1978, Herrerra 1979, Valburg 1992), but only Buskirk (1972, cited in Powell 1985) has recorded convergence of foraging maneuvers by insectivores. The data presented here suggest that todies in mixed-species flocks may not only adjust some spatial parameters, but some foraging maneuvers may converge as well. The observed three-way interaction between species, level of social organization, and foraging method reflects the presence of interspecific differences in foraging maneuvers in pine habitat, with Narrow-billed Todies using more near-perch maneuvers than Broad-billed Todies, but these differences decrease among flocking birds when both species more commonly utilize a sally-hover or sally-stall technique.

This trend towards convergence of some spatial parameters and foraging behaviors by two species of todies in the presence of mixed-species flocks suggests that todies find enhanced foraging opportunities amidst flocks. Movement rates and feeding rates did increase for both Broad-billed and Narrow-billed Todies in flocks in this study, but the increase was significant only for movement rates of Broad-billed Todies. Convergence of foraging behavior as well as rate increases may indicate that the birds benefit from the flushing of insects by the activity of other flock members, supporting the food facilitation hypothesis of interspecific flock formation (Powell 1985). But todies may also benefit from predator avoidance. Sharp-shinned Hawks (*Accipiter striatus*), which occur in the pine and shade coffee habitats, regularly prey on small birds. In the more sparsely foliated pine forest tody foraging behavior may be constrained by this predator. Protection afforded todies by way of mutual vigilance or the confusion of large flocks (Powell 1985) may allow

todies to forage in more exposed sites and utilize riskier behavior—foraging faster with less vigilance. Caution must be taken in interpreting these results in terms of flocking advantages, however, as environmental conditions were uncontrolled and may have differed independently of flocking behavior.

In conclusion, we found that the coexistence of two species of todies in shade coffee and pine habitats was facilitated by the use of distinct foraging strata, the use of different foraging substrates (in coffee plantations), and different foraging maneuvers (in pine forest). Behavioral differences may have reflected constraints imposed by microhabitat differences within these strata. The occurrence of todies in mixed-species foraging flocks resulted in the convergence in measures of some spatial parameters and in feeding behavior, indicating potential shifts in resource utilization, but the use of distinct strata by the species was maintained. Further studies that elucidate behavioral differences between flocking and non-flocking individuals, and the costs and benefits of flock association, are warranted.

ACKNOWLEDGMENTS

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