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# MIXED FLOCK COMPOSITION AND FORAGING BEHAVIOR OF INSECTIVOROUS BIRDS IN UNDISTURBED AND DISTURBED FRAGMENTS OF HIGH-ANDEAN *POLYLEPIS* WOODLAND

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**Resumen**. – **Comportamiento de forrajeo de aves insectivores en fragmentos no perturbados y perturbados de bosques alto-Andinos de *Polylepis*. –** Bandadas de forrajeo de especies mixtas de aves se encuentran en muchas comunidades de bosque, tanto en bosques templados como en bosques tropicales. Típicamente tales bandadas están altamente estructuradas en términos del comportamiento de forrajeo, con diferentes especies ocupando nichos de forrajeo diferentes con respecto a la posición y/o técnicas de forrajeo. En el Neotropico, la mayoría de los estudios se han enfocado en bandadas ricas en especies en bosques tropicales bajos, pero muy poco se ha publicado sobre comunidades menos diversas en bosques montanos Andinos. Cerca de Cochabamba, Bolivia, estudiamos la composición y el comportamiento de forrajeo de bandadas mixtas de aves insectívoras en dos pequeños fragmentos de bosques alto-Andinos de *Polylepis* (Rosaceae). Un sitio representaba un bosque muy poco perturbado, mientras que el otro estaba sujeto a influencias antropogénicas debido a corte, pastoreo y agricultura en pequeña escala dentro del bosque restante. Las bandadas eran pequeñas en ambos sitios (4–5 individuos por bandada), pero la composición de la bandada difería marcadamente entre los dos sitios. En el sitio no perturbado, las bandadas estaban dominadas por especialistas del hábitat *Polylepis*, mientras que los no-especialistas eran numéricamente dominantes en el sitio perturbado. En el sitio no perturbado, las especies estaban claramente separadas por el modo de forrajeo y preferían un substrato de forrajeo, lo cual no era así en el sitio perturbado. En el sitio no perturbado había evidencia de divergencia de nicho entre al menos un par de individuos de la especie principal de la bandada, mientras que en el sitio perturbado algunas especies tendieron a convergir en el comportamiento de forrajeo cuando se encontraban en presencia de las otras. Se concluye que tanto la composición como la estructura de la bandada en términos de la separación de nicho difieren marcadamente entre los dos sitios, tal vez debido a la abundancia más baja de especies especialistas en el sitio perturbado.

**Abstract. –** Mixed-species foraging flocks of birds are found in many forest communities, both in temperate and tropical forests. Such flocks are typically highly structured in terms of foraging behavior, with different species occupying different foraging niches with respect to foraging positions and/or techniques. In the Neotropics, most studies have focused on species-rich flocks in lowland tropical forest, but little has been published on less diverse communities in montane Andean forests. We studied the composition and foraging behavior of birds in mixed insectivorous flocks in two small fragments of high-Andean *Polylepis* (Rosaceae) woodland near Cochabamba, Bolivia. One site represented largely undisturbed forest, while the other was more subject to anthropogenic influences due to clearing, grazing and small-scale agriculture inside the remaining forest. Flocks were small in both areas (4–5 individuals per flock), but flock composition differed markedly between the two sites. In the undisturbed site, flocks were dominated by *Polylepis* habitat specialists, while non-specialists were numerically dominant in the disturbed site. Species were clearly separated by foraging mode and preferred foraging substrate in the undisturbed site, but not so in the disturbed site. In the undisturbed site there was evidence for niche divergence between at least one pair of the main flocking species, while in the disturbed site some species tended to converge in foraging behavior when in each other's presence. It is concluded that both flock composition and flock structure in terms of niche separation differ markedly between the two sites, perhaps due to the lower abundance of specialist species in the disturbed site. *Accepted 28 May 2008.*

**Key words:** Mixed flocks, foraging, fragmentation, montane forest, niche shift.

## INTRODUCTION

Mixed-species foraging flocks consisting primarily of insectivorous birds are one of the most conspicuous elements of many forest bird communities, both in temperate (Morse 1970, 1978; Suhonen 1993) and tropical forests on different continents (Buskirk *et al.* 1972, Moynihan 1979, Bell 1983, Hutto 1987, Eguchi *et al.* 1993, Lee *et al.* 2005). Birds participating in such flocks may increase benefits in terms of foraging success through copying, information sharing, or flushing prey, or in terms of lowered predation risk through shared vigilance and/or dilution effects (Buskirk *et al.* 1972, Barnard 1982, Waite & Grubb 1988, Terborgh 1990, Dolby & Grubb 1998, Jullien & Clobert 2000). On the other hand, participation in mixed flocks also results in costs through prey depletion and/or direct interference (food stealing; Morse 1974, Krause & Ruxton 2002).

In the Neotropics, most research on the composition and structure of mixed-species flocks has focused on Central America and Amazonia (e.g., Buskirk *et al.* 1972, Wiley 1980, Gradwohl & Greenberg 1985, Munn 1985, Hutto 1987, Stouffer & Bierregaard 1995, Jullien & Thiollay 1998, Pomara *et al.* 2007), whereas Andean forests, despite their extraordinary species richness and highly structured bird communities, have been much less studied in this respect (Moynihan 1979, Poulsen 1996a, 1996b; Herzog *et al.* 2002). In this paper we focus on mixed-species foraging associations in high-altitude *Polylepis* (Rosaceae) woodland. *Polylepis* woodlands are currently extremely fragmented due to anthropogenic influences over many centuries (Kessler 1995, Fjeldså & Kessler 1996). While species richness is relatively low compared to lower-elevation montane forests, the bird community contains a high proportion of habitat specialists (Fjeldså & Kessler 1996, Cahill & Matthysen 2007). Due to its fragmented status and high degree of endemism, *Polylepis* forest is considered a high priority for conservation (Fjeldså & Kessler 1996). However, little information is available on the structure of bird communities in *Polylepis* forest and on the processes underlying community structure, in particular in relation to habitat quality and habitat degradation.

Mixed-species foraging flocks are typically highly structured in terms of foraging behavior, where different species specialize in different modes of foraging and/or use different foraging sites, thereby avoiding interference and competition (Morse 1970, Alatalo 1981, Alatalo *et al.* 1986, Bilcke *et al.* 1986). Foraging positions of individual species (and sometimes sex or age groups within species) are dynamically adjusted to the presence of competing species whereby species with similar foraging modes often restrict their foraging niches in each other's presence and, conversely, expand their niche in each other's absence (Alatalo *et al.* 1986, Cimprich & Grubb 1994, Latta & Wunderle 1996a, Jab³onski & Lee 2002). These patterns are modulated, however, by dominance/subordinance relationships among species or individuals (Morse 1974, Alatalo *et al.* 1986, Matthysen *et al.* 1991) and by location-specific predation risks. For example, Ekman (1986) and Suhonen (1993) showed that subordinate birds are forced to forage on the outside of tree canopies with higher predation risk. Thus, patterns of foraging behavior in mixed-species flocks of varying composition, and in particular shifts in niche use, may reveal important ecological processes that shape the community structure of insectivorous forest birds.

In this paper we report on the foraging behavior and flock composition of insectivorous birds participating in mixed-species flocks in two small remnants of *Polylepis* woodland. Previous studies in one of the two sites, a relatively intact woodland remnant, have already described seasonal changes in the overall bird community structure (Herzog *et al.* 2003) and provided a detailed description of mixed-flock composition and home-ranges of the core species in these flocks (Herzog *et al.* 2002). Here we focus in particular on the partitioning of foraging sites among species and look for evidence of foraging shifts of individual species in relation to flock composition. Furthermore we compare flock composition between the relatively undisturbed Sacha Loma site with a more disturbed *Polylepis* stand in the same region (San Miguel).

## STUDY AREAS AND METHODS

Both study sites are located in the department of Cochabamba, Bolivia, situated on the eastern slope of the tropical Andes. The first site is an 11-ha forest fragment located to the north of the small community of Sacha Loma (17°44'S, 65°34'W, 3710–3880 m elevation). The fragment consists of 9.3 ha of forest containing only *Polylepis besseri* trees, enclosing a 1.7-ha boulder field largely devoid of vegetation, and surrounded by *puna* grassland. Tree height inside the fragment varies from 4–10 m, shrubs (*Gynoxis*, *Berberis*, *Ribes*, *Baccharis*, *Brachyotum*) are distributed patchily, and the ground is largely covered by bunch grass (*Festuca*, *Stipa*, *Calamagrostis*) (see Fernández *et al.* 2001 for a general description). During the study there were only limited signs of anthropogenic disturbance such as occasional wood cutting and infrequent cattle grazing. The study fragment is connected to a less dense stand of *Polylepis* (c. 20 ha), and separated by c. 1 km from two other fragments of 35 and 47 ha.

The second study site is adjacent to the village of San Miguel (17°17'S, 66°20'W, 3600–3800 m) and is made up of two adjacent forest fragments separated by a small stream, together c. 12 ha. *Polylepis besseri* trees make up c. 66% of the tree cover, the remainder being mainly *Citharexylum punctatum*. Shrubs are more abundant than in the Sacha Loma site (same genera, also including *Passiflora*) while the herb layer is similar. Height and diameter of *Polylepis* trees are comparable between the two sites (Balderrama & Ramírez 2001, Fernández *et al.* 2001). Compared to the Sacha Loma site there was more intense anthropogenic disturbance in San Miguel with many sites showing evidence for recent tree removal, frequent cattle grazing inside the forest, and intrusion of many small fields into the forest (Balderrama & Ramírez 2001, Fernández *et al.* 2001). Outside the forested area, remnants of original vegetation (*Polylepis* and *Citharexylum* trees) were present along field boundaries.

Observations were collected by one of the authors (FC) during three 4–5 day visits to each study area between 11 July and 3 September 2001 in the dry winter season (see

Herzog *et al.* 2003 for more information on climate). The total observation time was c. 73 h in Sacha Loma and 79 h in San Miguel. Data were collected throughout the day by slowly walking through the forest and systematically covering the entire study area. Due to differences in size and topography, Sacha Loma could be covered in a single day, but San Miguel only in 2 days. We focused on insectivorous bird species that foraged on *Polylepis* or other trees and (at least occasionally) associated with mixed flocks. When a bird was found by visual or auditory contact, we determined flock composition as the total number of individuals observed foraging within 10 m or less of another flock member (Morse 1970, Lee *et al.* 2005) within a time period of maximum 15 min, which should be sufficient to detect all members of a small flock (Hutto 1987). For each individual per flock (including solitary individuals) we recorded foraging maneuver, tree or shrub species, substrate and foraging height. Foraging maneuvers were classified into the following general categories (Remsen & Robinson 1990): gleaning (picking food from the substrate, including hanging from branches), hover-gleaning (hovering while searching food on a substrate; "sally-hover" in Remsen & Robinson 1990), sallying (attacking aerial prey while flying from a perch) and prying in the bark (all subsurface maneuvers sensu Remsen & Robinson 1990). Foraging substrate was recorded as ground (GR), trunk (TR) above a diameter of 10 cm, large branch (LB) between 5 and 10 cm diameter, small branch (SB) below 5 cm diameter, and twig (TW) as a small branch bending under the weight of the bird (cf. Alatalo 1982, Bilcke *et al.* 1986). Height was assigned to three categories: low (below 2 m), middle (2 to 6 m) and high (above 6 m). Only one observation was taken per individual; additional observations from the same flock were only taken if at least 15 min had elapsed. The use of foraging sites per species was only analyzed when at least 20 observations were available for this species.

The degree of interspecific association was evaluated using pairwise coherence indices (Ekman 1979) which represent the proportion of flocks observed where species i and j were present together, relative to the total number of flocks observed with i and/or j: $X_{ij} = N_{ij}/(N_i + N_j + N_{ij})$ where $N_i$, $N_j$ and $N_{ij}$ represent the number of flocks containing species i but not j, species j but not i, and species i and j together, respectively. For this calculation we pooled all flock observations within each site, including flocks with a single individual. Note that this index is necessarily symmetrical between species but is also influenced by their relative abundance; thus, if species i is more abundant than species j, the coherence index may be low even if species j is always observed together with species i. Also note that this index does not take into account the number of individuals per flock. Since these numbers were typically low (see results), a coherence index on the basis of individuals would probably not be very different.

Niche overlap in substrate use and foraging height were calculated using Schoener's (1968) index of overlap. We tested whether species shifted their niches in the presence or absence or other species by comparing the use of foraging sites (substrate and height classes) by a focal species, with and without the presence of the other species, by means of Fisher's exact test. This was done separately for each study site, and only if at least 10 observations were available with and without the other species present.

## RESULTS

*Species observed and flock composition.* In total we collected 258 observations (70 flocks) on 9 insectivorous bird species in Sacha Loma, and

TABLE 1. Number of observations of insectivorous birds (n) and participation in mixed flocks (% MF) in the two study areas. Body mass data (mean ± SD, with sample size in parentheses) were collected from mist-net captures in the study sites or nearby areas (N/A = not available).

| Species | Body mass (g) | Sacha Loma | | San Miguel | |
|---|---|---|---|---|---|
| | | n | % MF | n | % MF |
| White-throated Tyrannulet (*Mecocerculus leucophrys*) | 10.5 + 1.3 (54) | 38 | 84 | 3 | 33 |
| Yellow-billed Tit-tyrant (*Anairetes flavirostris*) | N/A | 0 | - | 2 | 100 |
| Tufted Tit-tyrant (*Anairetes parulus*) | 6.4 + 0.6 (75) | 3 | 0 | 63 | 54 |
| D'Orbigny's Chat-tyrant (*Ochthoeca oenanthoides*) | 14.7 + 1.0 (58) | 0[a] | - | 5 | 60 |
| White-browed Chat-tyrant (*Ochthoeca leucophrys*) | 12.7 + 1.1 (223) | 5 | 40 | 11 | 27 |
| Rock Earthcreeper (*Upucerthia andaecola*) | 32.9 + 3.3 (16) | 4 | 100 | 0 | - |
| Brown-capped Tit-spinetail (*Leptasthenura fuligeniceps*) | 9.9 + 1.1 (23) | 5 | 100 | 24 | 100 |
| Tawny Tit-spinetail (*Leptasthenura yanacensis*) | 9.5 + 1.0 (215) | 80 | 86 | 51 | 80 |
| Cordilleran Canastero (*Asthenes modesta*) | 17.9 + 2.6 (9) | 4 | 100 | 0 | - |
| Creamy-breasted Canastero (*Asthenes dorbignyi*) | 18.8 + 1.4 (222) | 30 | 97 | 12 | 92 |
| Brown-capped Redstart (*Myioborus brunniceps*) | 8.8 + 0.9 (19) | 0 | - | 9 | 100 |
| Giant Conebill (*Oreomanes fraseri*) | 23.5 + 1.8 (155) | 89 | 84 | 11 | 100 |

[a] Observed in the area but not as part of the regular observations.

TABLE 2. Coherence indices representing the degree of association between the most commonly observed species (n ≥ 15) in the two study areas.

| Sacha Loma | Giant Conebill | Tawny Tit-spinetail | White-throated Tyrannulet |
|---|---|---|---|
| Tawny Tit-spinetail | 0.541 | | |
| White-throated Tyrannulet | 0.364 | 0.442 | |
| Creamy-breasted Canastero | 0.288 | 0.367 | 0.321 |
| San Miguel | Tawny Tit-spinetail | Brown-capped Tit-spinetail | |
| Brown-capped Tit-spinetail | 0.412 | | |
| Tufted Tit-tyrant | 0.259 | 0.200 | |

191 observations (67 flocks) on 10 species in San Miguel (Table 1). Seven of these species were observed in the two areas. Fourteen observations of birds that were present, but showed no foraging activity were included in data on flock composition but not the foraging observations. Observation frequencies per species differed considerably between the two sites. The only species that was frequently observed in both sites was Tawny Tit-spinetail (*Leptasthenura yanacensis*). Several species, including Giant Conebill (*Oreomanes fraseri*), White-throated Tyrannulet (*Mecocerculus leucophrys*) and Tufted Tit-tyrant (*Anairetes parulus*), were common in one site (15–30% of observations) but rare (< 6%) in the other. Mean flock sizes (including single individuals) were small in both areas, but significantly larger in Sacha Loma (3.69 ± SD 2.20, n = 70) than in San Miguel (2.85 ± SD 2.00, n = 67; Mann-Whitney test, $P = 0.02$). For comparison with data presented in Herzog *et al.*

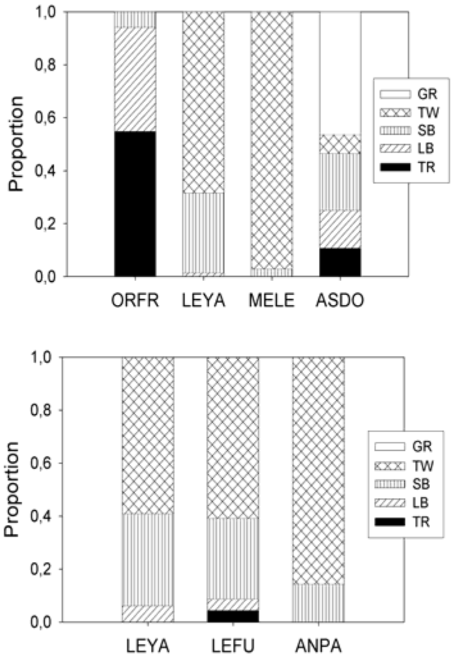

FIG. 1. Substrate use by the most commonly observed insectivorous bird species (n ≥ 20) in Sacha Loma (top) and San Miguel (bottom). GR = ground, TW = twig, SB = small branch, TB = thick branch, TR = trunk. ANPA = Tufted Tit-tyrant, ASDO = Creamy-breasted Canastero, LEFU = Brown-capped Tit-spinetail, LEYA = Tawny Tit-spinetail, MELE = White-throated Tyrannulet, ORFR = Giant Conebill.

(2002), we also calculated mean sizes of flocks with at least two species present, which yielded average values of 4.78 ± SD 1.87 for Sacha Loma, and 4.21 ± SD 2.03 for San Miguel. The number of species per flock was also higher in Sacha Loma (2.29 ± SD 1.17 vs 1.90 ± SD 1.13, $P = 0.035$). Degree of participation in flocks was high in most species with sufficient observations (80 to 100% of observations in mixed flocks; Table 1) with the exception of the two Chat-tyrant species and the Tufted Tit-tyrant, where 60% or less were observed in mixed flocks (Table 1).

Table 2 shows the association indices between the most commonly observed species (at least n = 20 observations). In Sacha Loma most species showed relatively high association indices (0.3 to 0.5) while in San Miguel the association index was rather low except between the two *Leptasthenura* species (0.41).

*Foraging behavior*. The four furnariid species [Brown-capped Tit-spinetail (*Leptasthenura fuliginiceps*), Tawny Tit-spinetail, Creamy-breasted Canastero (*Asthenes dorbignyi*), Cordilleran Canastero (*A. modesta*)] foraged by gleaning from branches or, in the case of the Canasteros, from the ground. Tufted Tit-tyrants practiced mainly gleaning (71%) but also hover-gleaning (29%, n = 66 observations). Brown-capped Redstart (*Myioborus brunniceps*) used gleaning (56%), hover-gleaning (22%) and sallying (22%; n = 9). White-browed Chat-tyrant (*Ochthoeca leucophrys*) mainly foraged by sallying but occasionally by gleaning as well (6%; n = 16). White-throated Tyrannulet also spent most of its time sallying, and occasionally hover-gleaning (8%, n = 38). Giant Conebill was most specialized in foraging maneuver since it exclusively foraged by prying in the leafy *Polylepis* bark, and was the only species doing so (see Table 1 for number of observations of this and other species). The remaining species were not observed sufficiently frequently to characterize their foraging maneuver.

*Tree species*. In Sacha Loma, all species were only seen foraging on *Polylepis* trees (no other tree species were available), with the exception of Creamy-breasted Canastero which frequently foraged on the ground (46%, n = 30). In San Miguel, most birds foraged on *Polylepis* trees as well, but a small proportion of observations was on other trees or shrubs, notably on *Cytharexylum punctatum* (Tawny Tit-spinetail: 8%, Tufted Tit-tyrant: 13%, Brown-capped Tit-spinetail: 22%) and a few other

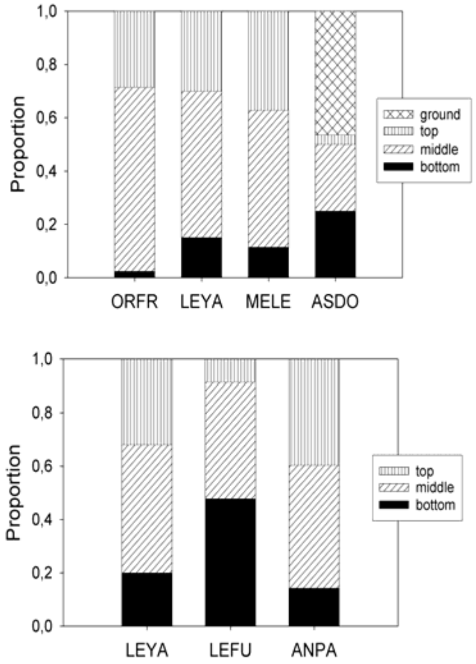

FIG. 2. Foraging height of the most commonly observed species (n ≥ 20) in Sacha Loma (top) and San Miguel (bottom). ANPA = Tufted Tit-tyrant, ASDO = Creamy-breasted Canastero, LEFU = Brown-capped Tit-spinetail, LEYA = Tawny Tit-spinetail, MELE = White-throated Tyrannulet, ORFR = Giant Conebill.

species such as *Bacharis* sp. and *Gynoxis* sp. (in total: 12%, 2% and 17% for the same bird species; see Table 1 for sample sizes).

*Substrate.* In Sacha Loma, the four most common species showed clear differentiation in substrate use (Fig. 1). Giant Conebill foraged mainly on trunks and thick branches, while Tawny Tit-spinetail used both thin branches and (mainly) twigs, and White-throated Tyrannulet foraged almost exclusively on twigs. Creamy-breasted Canastero used various substrates and was the only species to forage regularly on the ground. Niche-overlap in substrate use was rather high for Tawny Tit-spinetail and White-throated Tyrannulet (0.71), but low for the other combinations (all ≤ 0.3; details not shown). In San Miguel, in contrast, the three most common species all foraged mainly on twigs and thin branches (Fig. 1) which resulted in high values for niche-overlap (0.94 Tawny vs Brown-capped Tit-spinetail, 0.73 Tawny Tit-spinetail vs Tufted Tit-tyrant, 0.75 Brown-capped Tit-spinetail vs Tufted Tit-tyrant). The substrate use of Tawny Tit-spinetail in the two study sites was highly similar (Fig. 1); none of the other species was observed sufficiently frequently in both areas to make this comparison.

*Foraging height.* All species in both sites spent half to two thirds of their time in the middle part of the trees (43–69%), except for Creamy-breasted Canastero, which was often seen on the ground (Fig. 2). Creamy-breasted Canastero and Brown-capped Tit-spinetail foraged to a similar extent in the lower and middle part of the trees, and rarely visited the upper part, while the other species seemed to avoid the lowest zone and spent considerable time in the upper parts (Fig. 2). This pattern was reflected in very high niche-overlap values for most species combinations (all > 0.82), except those involving Creamy-breasted Canastero in Sacha Loma (0.3–0.44) and Brown-capped Tit-spinetail in San Miguel (0.72 with Tawny Tit-spinetail and 0.66 with Tufted Tit-tyrant). The modest overlap in foraging height between Tawny Tit-spinetail and Brown-capped Tit-spinetail (0.72) was remarkable given their very similar use of substrates (0.94, see above). A Fisher exact test confirmed that this differentiation in foraging height between the two Tit-spinetail species was statistically significant ($P = 0.02$).

*Niche shifts.* We tested the existence of niche shifts for nine combinations of species where sufficient data were available for a focal species both in presence and absence of another

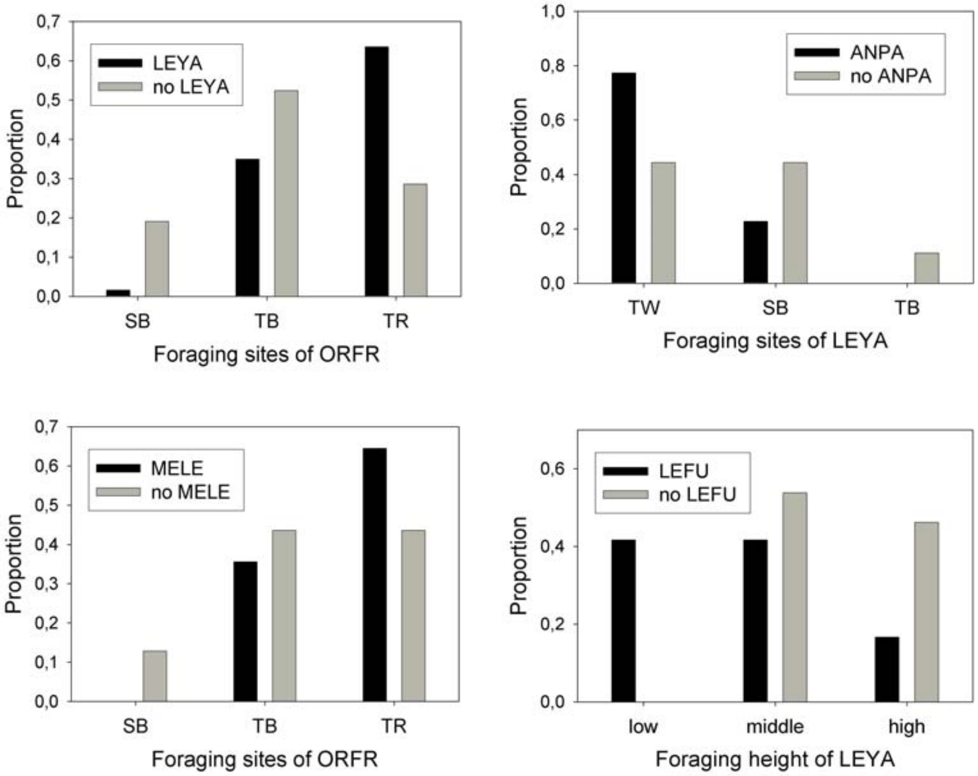

FIG. 3. Niche shifts as evidenced by differences in foraging behavior in the presence or absence of another species. Only combinations with significant effects are shown (out of nine tested). Sample sizes are given in brackets and significance test results (Fisher exact test) are indicated on each panel. Left panels: differences in substrate use in Sacha Loma by Giant Conebill (ORFR) in relation to presence/absence of Tawny Tit-spinetail (LEYA) and White-throated Tyrannulet (MELE). Right: differences in substrate use and height in San Miguel by Tawny Tit-spinetail (LEYA) in relation to presence/absence of Tufted Tit-tyrant (ANPA) and Brown-capped Tit-spinetail (LEFU).

species that was actively foraging (each n $\geq$ 10). We found significant shifts in four out of nine comparisons (Fig. 3); two of these comparisons remained significant after Bonferroni correction for multiple testing ($\alpha$ = 0.006). In Sacha Loma, Giant Conebill foraged more often on trunks in the presence of Tawny Tit-spinetail than in its absence (Fig. 3). The same pattern was shown in relation to the presence of White-throated Tyrannulet (Fig. 3) but this was not significant after Bonferroni correction. Moreover, the effects of the two species were possibly confounded since the presence of White-throated Tyrannulet nearly always (43 of 45 cases) implied the presence of Tawny Tit-spinetail as well (though not vice versa). Since Tawny Tit-spinetail as well as White-throated Tyrannulet rarely or never forage on trunks, our observations imply that Giant Conebill shifted its niche away from these species in their presence. In San Miguel, Tawny Tit-spinetail foraged more often on twigs in the presence of Tufted Tit-tyrant, and foraged at lower heights in the presence of Brown-capped Tit-spinetail (Fig. 3); only the latter shift was significant after Bonferroni correction. Since Tufted Tit-tyrant forages mainly on twigs and Brown-capped Tit-spinetail forages lower than Tawny Tit-spinetail (see above), both shifts imply niche convergence rather than divergence between Tawny Tit-spinetail and its companion species.

## DISCUSSION

This study provides the first quantitative description of foraging behavior of insectivorous birds in high-Andean *Polylepis* woodland, including several species considered as *Polylepis* specialists. It also documents marked differences in flock composition between two different *Polylepis* woodlands (one of them studied earlier by Herzog *et al.* 2002) in the same region and at similar altitudes. By lack of replicated study sites it is difficult to attribute these differences to particular environmental or geographic factors. Nevertheless, the most striking difference between the two sites is the higher anthropogenic disturbance in the San Miguel site with accompanying higher floristic and structural diversity, and we propose that this is the main reason for the difference between the sites. We found that flock composition as well as foraging niche structure differed markedly between the two areas. Even though most species were observed in the two sites, only a single species (Tawny Tit-spinetail) was common in the two areas. Most of the individuals observed in the Sacha Loma site belonged to species generally considered as *Polylepis* specialists (Giant Conebill*,* Tawny Tit-spinetail*,* White-throated Tyrannulet) or having a high affinity for *Polylepis* (Herzog *et al.* 2003 based on Fjeldså & Kessler 1996). Together these made up 92% of all observations, while in San Miguel this was only 43% [including the rarely observed *Polylepis* specialist D'Orbigny's Chat-tyrant (*Ochthoeca oenanthoides*)]. The common occurrence of several *Polylepis* specialists in Sacha Loma is in agreement with the relatively pristine nature of the woodland relicts in this area compared to the San Miguel site which, on the other hand, has a higher floristic diversity, including different species of trees and shrubs (Balderrama & Ramírez 2001, Fernández *et al.* 2001). Remarkably, most insectivorous birds in San Miguel – including the habitat specialists – were observed in mixed *Polylepis-Citharexylum* stands or in scattered *Polylepis* trees, rather than in the denser *Polylepis* stands (74% of all observations in two visits when this was explicitly recorded). Earlier, Hjarsen (1998) had concluded from surveys in different *Polylepis* stands in the Tunari Parc that overall bird diversity was highest in moderately disturbed sites such as San Miguel, but that *Polylepis* specialists responded in a different way to disturbance. His study showed that Giant Conebill was more abundant in the least disturbed sites within the park, and this pattern is supported by our present observations, and also by surveys in other undisturbed *Polylepis* fragments in the Sacha Loma area (Cahill & Matthysen 2007). Thus, we suggest that the differences in bird community composition are not only shaped by geographic factors or by random variation, but to some extent represent differences in the disturbance regime of the studied *Polylepis* woodlands.

In both sites, mixed-species flocks were typically small with few individuals and species. This confirms an earlier report on the Sacha Loma area (Herzog *et al.* 2002) where flocks contained the same species as reported here, and mean flock size was 5.4 birds (only flocks with at least two species present). The somewhat smaller flock sizes in our study (corresponding value = 4.7) could be due to annual or seasonal variation (but see Herzog *et al.* 2003), or to a difference in observation protocol, since the earlier study focused explicitly on flock composition including the reading of individual color-bands, and flocks were probably observed for a longer timespan. Most of the species had high flock propensity with > 80% of all observations in mixed flocks, except for the two Chat-tyrants and the Tufted Tit-tyrant. Both study sites contained a number of other insectivorous birds that never participated in flocks, most of them non-arboreal foragers associated with open areas or specific microhabitats such as wet areas (see Herzog *et al.* 2002, 2003 for details of the Sacha Loma bird community). Thus, small flock sizes represent a low diversity of small arboreal insectivores rather than a low propensity to join flocks. High flock propensities have also been noted in other neotropical mixed flocks (Hutto 1994, Latta & Wunderle 1996a, Pomara *et al.* 2007; but see Powell 1979). Flocks were markedly smaller than in other montane tropical forests such as in Mexico, Panama and Hispaniola with typically 7 to 18 species per flock and 10 or more individuals (Powell 1979, Hutto 1987, Latta & Wunderle 1996a, Pomara *et al.* 2007). Poulsen (1996b, 1996a) also reported larger and more species-rich flocks from Ecuadorian primary and secondary montane forest. The relatively small and species-poor flocks in our study can be explained by the low species diversity in *Polylepis* woodland (Herzog *et al.* 2003). One of the reasons for this is the absence of northern migrants which are an important component of some other neotropical montane flocks (Hutto 1994, Latta & Wunderle 1996a; but see Powell 1985).

Coherence indices in Sacha Loma were relatively high (0.3–0.5) for the three arboreal *Polylepis* specialists (Giant Conebill, Tawny Tit-spinetail, White-throated Tyrannulet) but somewhat lower with the more terrestrial Creamy-breasted Canastero. From 47 flock observations with more than a single species present, no less than 41% had all three species present, and 72% had Giant Conebill and Tawny Tit-spinetail present. In San Miguel, flocks were not only smaller on average, but also less predictable in composition as shown by low pairwise coherence indices, except between the two Tit-spinetail species. For example, among the 33 flocks with more than a single species, only 18% had the three most common species (both Tit-spinetails plus Tufted Tit-tyrant) present together. A possible explanation for the lower coherence indices in San Miguel might be the absence of a clear nuclear species, since this may prevent facultative flock members from joining (Stouffer & Bierregaard 1995). Observations in Sacha Loma suggest that Giant Conebill may act as nuclear species by initiating flock movements (Herzog *et al.* 2002). Another explanation could be the more diverse bird community in San Miguel with less marked numerical dominance of a few species. If birds associate randomly thigh might lead to lower coherence indices in the more diverse community, but this in itself does not explain the smaller flocks in San Miguel. While more behavioral data are necessary to elucidate the patterns of flock cohesion, we suggest that the observed differences reflect a genuine difference in association behavior between insectivorous species.

Both sites contained species covering a range of foraging maneuvers including gleaning, hover-gleaning and sallying, though not necessarily by the same species. For example, the role of White-throated Tyrannulet, a common species in Sacha Loma (mainly sallying, also hover-gleaning) was partly filled in by White-browed Chat-tyrant and Brown-capped Redstart in San Miguel. By far the most specialized species in terms of foraging maneuvers in both sites is Giant Conebill, which takes up a niche comparable to the nuthatches (Sittidae) of boreal and temperate forests (and incidentally, shows remarkable morphological convergence with this family). Apart from foraging maneuvers, there is also a clear separation in actual foraging sites, particularly in the Sacha Loma community where the four most common insectivores show relatively low overlaps in foraging substrate. In San Miguel there is higher overlap between the most common species, in particular between Tufted Tit-tyrant and the two Tit-spinetail species. The latter both forage by gleaning and use the same substrates, but show significant separation by foraging height with Brown-capped Tit-spinetail foraging more often at lower heights, and also tend to forage more often on *Cytharexylum* trees in addition to *Polylepis*.

We found some evidence for shifts in foraging behavior in relation to the presence or absence of other species, suggesting that birds actively avoid food competition by modifying their behavior (Alatalo *et al.* 1986, 1987). In Sacha Loma we found Giant Conebill foraging more often on trunks in the presence of Tawny Tit-spinetail. Somewhat surprisingly, Tawny Tit-spinetail showed no such response even though it is the smaller of the two species (Table 1), and studies on temperate flocks have shown repeatedly that larger and more dominant species tend to force subdominant competitors into less preferred microhabitats (Alatalo *et al.* 1986, Jab³onski & Lee 2002). Another possible reason is that Giant Conebill can retreat to a more specialized niche (i.e., bark-probing on trunks) while Tawny Tit-spinetail, in shifting away from Giant Conebill, might increase overlap with other species, notably White-throated Tyrannulet. The data also showed a non-significant tendency for Giant Conebill to reduce its niche width in the presence of White-throated Tyrannulet, but the data did not allow to separate this effect from the presence of Tawny Tit-spinetail. In the San Miguel community we found no evidence for divergent niche shifts; on the contrary, Tawny Tit-spinetail appeared to shift towards the two other species in their presence. The observed convergence between the morphologically very similar Tit-spinetail species is remarkable since Alatalo *et al.* (1986) found that species similar in body weight are more likely to show niche divergence. Niche convergence may be due to enhanced foraging opportunities through copying, social learning or other means of facilitation (Alatalo *et al.* 1986, Waite & Grubb 1988, Latta & Wunderle 1996b) or foraging or might be a mechanism to maintain contact and maximize flock integrity (Nour *et al.* 1997). Our results on niche convergence and divergence should be treated with caution because the number of observations is limited and because we treated each flock as a separate unit of observation, even though many individuals were probably included several times in the dataset. In a previous study in the Sacha Loma site, Herzog *et al.* (2002) estimated the numbers of different individuals as up to 8 Giant Conebills, 16 Tawny Tit-spinetails and 10 White-throated Tyrannulets, but no such estimate is available for the San Miguel site and for other species.

In conclusion, our observations show marked differences in flock composition and also suggest differences in flock coherence and foraging niche structure of arboreal insectivorous birds between two high-Andean *Polylepis* sites. The Sacha Loma community, in relatively undisturbed conditions, has flocks with highly predictable composition that are dominated by *Polylepis* specialists with well-segregated foraging niches, possibly maintained by active niche segregation in at least one species pair (Giant Conebill vs Tawny Tit-spinetail). The flocks in the more disturbed and structurally more diverse San Miguel site are smaller and less predictably in composition, contain only one *Polylepis* specialist (Tawny Tit-spinetail) as a common member, and show no clear evidence of foraging niche segregation. Studies in other tropical forests have similarly found that disturbance or fragmentation lead to smaller flocks and/or less predictable flock composition (Telleria *et al.* 2001, Maldonado-Coelho & Marini 2004, Lee *et al.* 2005, Pomara *et al.* 2007). While in the absence of replicated studies the interpretation of these differences is speculative, we suggest that both the lower flock coherence and the weaker structure of foraging niches in the more disturbed San Miguel area are due to the higher presence of generalists, whose niches have not co-evolved to the same degree as those of specialist species (Taper & Case 1992). Further research should bring more clarity in the community structure of these relatively species-poor tropical montane bird communities.

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