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COMPOSITION AND STRUCTURE OF AVIAN MIXED-SPECIES FLOCKS IN A HIGH-ANDEAN *POLYLEPIS* FOREST IN BOLIVIA

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Resumen. Se determinó la composición y organización de bandadas mixtas de aves en un fragmento de bosque altoandino de *Polylepis besseri* (Rosaceae) (3710–3880 m.s.n.m., 11 ha), durante la época no-reproductiva, de abril a agosto de 2000, en el departamento de Cochabamba, Bolivia. Desde diciembre de 1999, se anillaron aves del bosque con anillos de color. Se registraron 63 observaciones de bandadas mixtas con un total de 10 especies y un promedio (\pm DS) de 2.8 ± 0.9 especies y 5.4 ± 1.8 individuos por bandada. La comunidad entera de aves del bosque presentó 30 especies núcleo. Debido al tamaño reducido del bosque, la mayoría de las bandadas contenía por lo menos algunos de los mismos individuos. Tres especies ocurrieron en $> 70\%$ (*Oreomanes fraseri*, *Leptasthenura yanacensis* y *Mecocerculus leucophrys*, con 2.6 ± 0.6 , 1.9 ± 0.6 y 1.6 ± 0.5 individuos por bandada respectivamente), una especie (*Asthenes dorbignyi* con 1.4 ± 0.5 individuos por bandada) en 21% y las restantes seis especies en $\leq 5\%$ de todas las bandadas. Todos los participantes de las bandadas, excepto uno, fueron insectívoros. Los individuos de *O. fraseri* mostraron alta fidelidad de agrupamiento intraespecífico o de pareja y a menudo, pero no siempre, actuaron como líderes de bandada, mientras el rol de centinela fue principalmente asumido por *L. yanacensis* o *A. dorbignyi*. Para las tres especies regularmente asociadas con bandadas mixtas, se determinaron los ámbitos de hogar de individuos anillados observados en bandadas. En promedio, los ámbitos de hogar (100% polígono convexo mínimo) fueron de 6.13 ± 0.87 ha para *O. fraseri* ($n = 4$), 2.13 ± 1.26 ha para *L. yanacensis* ($n = 6$) y 3.41 ± 2.73 ha para *M. leucophrys* ($n = 3$). El solapamiento intraespecífico en ámbitos de hogar fue de moderado a alto en todas las especies, no existió una clara asociación entre individuos de *L. yanacensis* y *M. leucophrys* con una pareja o grupo de *O. fraseri* y las interacciones agonísticas estuvieron casi ausentes excepto en agosto. En otras palabras, ni los individuos ni las bandadas fueron territoriales, y las bandadas fueron mucho menos estructuradas que aquellas estudiadas en tierras bajas neotropicales, similares en algunos aspectos a bandadas mixtas de zonas templadas del norte. Ventajas selectivas de bandadas mixtas en bosques de *Polylepis* son brevemente discutidas, encontrando apoyo solo para la hipótesis de evasión de predadores.

Abstract. We determined the composition and organization of avian mixed-species foraging flocks during the non-breeding season from April to August 2000 in a high-Andean forest fragment of *Polylepis besseri* (Rosaceae) (3710–3880 m a.s.l., 11 ha) in Cochabamba, Bolivia. Forest birds were color-banded monthly starting December 1999. Sixty-three observations of flocks were made containing a total of 10 species with a mean (\pm SD) of 2.8 ± 0.9 species and 5.4 ± 1.8 individuals per flock. The entire *Polylepis* bird community contained 30 core species. Since the forest was small, most flocks contained at least some of the same individuals. Three species occurred in $> 70\%$ (Giant Conebill *Oreomanes fraseri*, Tawny Tit-Spinetail *Leptasthenura yanacensis*, and White-throated Tyrannulet *Mecocerculus leucophrys*, with 2.6 ± 0.6 , 1.9 ± 0.6 , and 1.6 ± 0.5 individuals per flock respectively), one species (*Asthenes dorbignyi* with 1.4 ± 0.5 individuals per flock) in 21% , and the remaining six species in $\leq 5\%$ of all flocks. All flock participants except one were insectivores. Individuals of *O. fraseri* showed high intraspecific group or pair fidelity and often, but not always, acted as flock leader, whereas the sentinel role was mainly assumed by *L. yanacensis* or *A. dorbignyi*. For the three species regularly associated with mixed-species flocks, home ranges of banded individuals observed in flocks were determined. Mean home ranges (100% minimum convex polygons) were 6.13 ± 0.87 ha for *O. fraseri* ($n = 4$), 2.13 ± 1.26 ha for *L. yanacensis* ($n = 6$), and 3.41 ± 2.73 ha for *M. leucophrys* ($n = 3$). Intraspecific home range overlap was moderate to high in all species, clear associations of Tawny Tit-Spinetail and White-throated Tyrannulet individuals with one of the two Giant Conebill pairs/groups were lacking, and agonistic interactions were almost absent except in August. In other words, neither individuals nor flocks were territorial, and flocks were much more loosely structured than those studied in Neotropical lowlands, resembling in some respects mixed-species flocks in northern temperate zones. Selective advantages of mixed flocks in *Polylepis* forests are briefly discussed, finding support only for the predation avoidance hypothesis. Accepted 20 May 2002.

Key words: Birds, Bolivian Andes, home range, *Leptasthenura yanacensis*, *Mecocerculus leucophrys*, mixed-species flocks, *Oreomanes fraseri*, *Polylepis* forest, predation avoidance hypothesis, social organization.

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INTRODUCTION

Mixed-species foraging flocks are one of the most conspicuous elements of many tropical forest bird communities. They often contain large numbers of species and individuals (Munn & Terborgh 1979, Powell 1985, Hutto 1987) and are composed predominantly of insectivorous birds (Moynihan 1962, Munn & Terborgh 1979, Gradwohl & Greenberg 1980, Bell 1983, Hutto 1987, Eguchi *et al.* 1993), although species with other diets (e.g., frugivores) are known to join such flocks occasionally when foraging for arthropods (Valburg 1992, Poulsen 1996a).

Mixed-species flocks have been studied throughout the tropics (Davis 1946, Winterbottom 1949, McClure 1967, Croxall 1976, Partridge & Ashcroft 1976, Macdonald & Henderson 1977, Bell 1983, Munn 1985, Eguchi *et al.* 1993). In the Neotropics, most research on the composition, structure, and organization of mixed-species flocks has focused on Central America (Wiley 1971, Buskirk *et al.* 1972, Buskirk 1976, Gradwohl & Greenberg 1980, Greenberg & Gradwohl 1985, Hutto 1987) and Amazonia (Munn & Terborgh 1979, Wiley 1980, Munn 1985, Jullien & Thiollay 1998), whereas the Andes (Moynihan 1979; Poulsen 1996a,b) have received less attention. To date there has been no account of mixed-species flocks in high-Andean *Polylepis* (Rosaceae) forests.

A number of studies on mixed-species flocks in the Neotropics have depended on observations of unmarked individuals (e.g., Short 1961, Hutto 1994), but a growing body of literature based on color-banded birds is now available (e.g., Munn 1985, Jullien & Thiollay 1998). Several studies quantifying the spatial structure of Neotropical mixed-species flocks and their component species have found that flocks are permanent associations of territorial birds and are stable in composition between seasons and years (Munn & Terborgh 1979, Powell 1979, Munn 1985, Jullien & Thiollay 1998). However, the evidence is strongly biased towards lowland evergreen forest, and Jullien & Thiollay (1998) concluded that this pattern may not be generalizable for all tropical forests.

The genus *Polylepis* is endemic to the Andes and forms high-elevation forests and woodlands with a highly fragmented, relict distribution, a result of strong, ongoing anthropogenic influences since early post-glacial times (Ellenberg 1958, 1996; Lægård 1992; Kessler 1995; Fjeldsø & Kessler 1996). In addition, *Polylepis* forests contain a number of avian

obligatory habitat specialists (see Fjeldsø & Krabbe 1990) and threatened species (BirdLife International 2000). They are therefore considered a high priority for conservation (Fjeldsø 1993, Fjeldsø & Kessler 1996). Ornithological studies in *Polylepis* have consisted mostly of rapid assessments of community parameters such as species richness and endemism (e.g., Fjeldsø 1993, Fjeldsø & Kessler 1996). Detailed data on community organization and population structure of species dependent on this habitat are lacking. The objectives of the present study were to determine (a) the relative importance of mixed-species flocks to the bird community of a *Polylepis* forest fragment in Bolivia, (b) the composition of such flocks, and (c) the spatial associations among individuals of regularly-participating species.

METHODS

Study area. We studied an 11-ha fragment of *Polylepis berterii* near the small community of Sacha Loma, dpto. Cochabamba, Bolivia (17°44'S, 65°34'W, 3710–3880 m a.s.l.). Canopy height was 4–10 m, and *P. berterii* was the only tree species with admixed shrubs of *Gynoxis*, *Berberis*, *Ribes*, *Baccharis*, and *Brachyotum*. The fragment, ca. 600 m long and 150–200 m wide, consisted of 9.3 ha of forest and completely contained a 1.7-ha boulder field largely devoid of vegetation. Most of the ground was covered by bunch grass (*Festuca*, *Stipa*, *Calamagrostis*). Moss cover on trees or boulders was patchy and primarily found at the lowest elevation. Although a few spots were densely vegetated, most of the vegetation was open enough to allow unobstructed passage on foot.

The fragment was embedded in a landscape mosaic of high-Andean *puna* grassland (with locally abundant *Puya naimondii*) and more or less isolated *Polylepis berterii* fragments. Forest patches varied in size (from ca. 0.01 to 100 ha), vegetation density, canopy height, and human impact. The selected fragment had the overall densest vegetation structure and also some of the biggest trees in the Sacha Loma area. Current human impact was low to moderate on most forest patches but strong on the surrounding grassland. The latter was used intensively for sheep grazing, especially during the rainy season, resulting in sparse vegetation cover. Small numbers of cattle sometimes grazed inside the study fragment, and branches or single trees were occasionally cut for firewood and construction. Although we did not observe any grassland fires (peasants often set such fires in the Andes; see Læg-

gaard 1992, Kessler & Herzog 1998, Kessler 2000), c. 1 ha of the study fragment showed clear signs of a recent fire.

The study area is located in the transition zone from the rain-drenched *yungas* on the east-Andean slope to the dry intermontane valleys of southern Bolivia. Pronounced climatic differences between the rainy and dry seasons exist (authors' pers. obs.). The rainy season (c. November to March) is characterized by often complete cloud cover and frequent rain showers that occasionally result in torrential flash floods. During the dry season (c. May to September) clouds are rare and it may not rain for several weeks; nightly frost, especially during the influence of southern polar storm fronts, and gusting wind during the daytime occur frequently. Brief periods of transition between both seasons occur in April and October.

Fieldwork. Birds were captured with mist nets for several days per month starting in December 1999, and all individuals of forest-dependent species captured were color-banded. No fieldwork was conducted in February and March 2000. We defined a mixed-species flock as comprising at least two heterospecific individuals within a radius of 10 m that moved together for at least five minutes. Mixed-species flocks and banded birds outside of flocks were observed from mid-April to early August 2000 for four to eight days per month from sunrise to sunset (07:00–18:00 hrs). This period corresponds to the nonbreeding season of the forest birds (authors' pers. obs.). Two larger fragments nearby were visited occasionally to check for the presence of marked individuals from the study fragment. Observers usually worked in pairs and covered all sections of the fragment more or less evenly with respect to effort and time of day. Each flock encountered was followed until its exact composition (number of species and individuals per species) had been determined (mostly for 5–15 min). For individuals (both banded and unbanded) outside of mixed flocks, data on intraspecific associations and group size were taken.

To determine the relative importance of mixed-species flocks to the entire *Polylepis* bird community we compiled a list of all species observed during each field session from April to August 2000 (Herzog *et al.*, unpubl. data). Based on the relative abundance and frequency of observation of each species we then determined the core species (*sensu* Remsen 1994) of the *Polylepis* patch. Core species are those that regu-

larly breed, winter, or migrate through a given habitat (Remsen 1994).

We used a Global Positioning System (GPS) to map observations of color-banded birds, taking the mean of 10 repeated measurements during nine minutes. To ensure accuracy, the GPS unit had to capture at least five satellites with a measurement error of <20 m. In the few cases where these conditions were not met, the spot in question was marked and revisited later. When flocks contained banded individuals we first completed the determination of flock composition and then returned to measure the positions where each banded bird had first been observed. To ensure the absence of systematic GPS errors, fixed points at the fragment perimeter were measured repeatedly throughout the study period.

Data analysis. Consecutive observations of mixed-species flocks had to be either one hour or 50 m apart to be considered independent. Despite the low canopy and, in most places, relatively open vegetation structure, which greatly facilitated observations, occasionally we were uncertain whether all participants of a mixed flock had been detected. These observations were excluded from the analysis of flock composition. Because the forest was small, most flocks inevitably contained at least some of the same individuals. Therefore most flocks are not independent in the strict sense. This attribute is not the result of a flawed study design, but rather a constraint imposed by the high degree of anthropogenic fragmentation of *Polylepis* forests. Small patches of only a few hectares are the rule rather than the exception in Bolivia (see Fjelds  & Kessler 1996). To avoid spatial autocorrelation as much as possible, observers generally moved away from a given flock after its composition had been determined.

Home range sizes of color banded birds that participated in flocks were determined with Ranges V (Kenward & Hodder 1996). For any given bird, observations within and outside of mixed flocks were combined and those separated by less than one hour or 50 m were excluded from the analysis. Positions of net captures were generally included, but captures in December 1999 and January 2000 (as well as opportunistic observations of banded birds during that time) were only included if located inside the April-to-August home range of the individual concerned. Maximum home ranges were estimated with 100% minimum convex polygons (MCP, Mohr 1947), and incremental area plots were used to determine the

number of locations necessary to calculate home range size. Home range areas became asymptotic only for six individuals of three species, for which we also computed 90% MCPs based on the harmonic mean (Dixon & Chapman 1980) to minimize inclusion of unused areas due to outlying fixes (Kenward 1987, Meretsky 1987) and core areas using 80% hierarchic cluster polygons. Although home range size was probably somewhat underestimated for the remaining individuals, we nonetheless present these results as no such data have been published previously.

For one species (Giant Conebill *Oreomanes fraseri*) we obtained sufficient sample sizes (> 20 observations) for several individuals to calculate an index of intraspecific association, i.e., the number of times two birds are seen together divided by the total number of observations of these two individuals (alone and together) (Ekman 1979).

RESULTS

We recorded 30 core species of the *Polylepis* bird community and made 63 observations of mixed-species flocks that contained a total of 10 species (Table 1) and averaged (\pm SD) 2.8 ± 0.9 species and 5.4 ± 1.8

individuals. Of the 10 species observed as participants in mixed-species flocks, three (Tawny Tit-Spinetail *Leptasthenura yanacensis*, Giant Conebill, White-throated Tyrannulet *Mecocerculus leucophrys*) occurred in most flocks (> 70%), one (Rusty-vented Canastero *Asthenes dorbignyi*) was an occasional (6–25%), and six were accidental (\leq 5%) participants (Table 1). Of the three regular mixed-flock participants, the former two are obligate *Polylepis* specialists (Fjelds  & Krabbe 1990, Fjelds  & Kessler 1996). Nine of the 10 flock participants were insectivores (except for Chiguanco Thrush *Turdus chiguanco*, a frugivore), whereas the entire core species community contained 13 insectivores. On average, no species except Giant Conebill had more than two individuals per flock, and no mixed-species flock contained more than three individuals of the same species (Table 1), but we once observed a single-species flock (not included in these data) of five Giant Conebills.

Flocks were detected at all hours of the day, but two activity peaks were observed: an extended period of flock activity from early to mid-morning and a brief, lower peak in the late afternoon (Fig. 1). Direction of flock movement was generally initiated by Giant Conebill and occasionally by Tawny Tit-Spine-

TABLE 1. Composition of 63 avian mixed-species flocks observed from April to August 2000 in an 11-ha fragment of high-Andean *Polylepis* forest at Sacha Loma, Bolivia.

Species	Frequency in flocks	Mean (\pm SD) no. of birds per flock ¹	Min./max. no. of birds per flock ¹	No. of marked birds in all flocks
Furnariidae				
<i>Leptasthenura yanacensis</i>	0.92	1.9 ± 0.6	1/3	6
<i>Asthenes dorbignyi</i>	0.21	1.4 ± 0.5	1/2	3
<i>A. punensis</i>	0.02	1.0 ± 0.0	1/1	0
<i>Phacellodomus striaticeps</i>	0.05	1.7 ± 0.6	1/2	2
Tyrannidae				
<i>Mecocerculus leucophrys</i>	0.71	1.6 ± 0.5	1/3	3
<i>Anairetes parulus</i>	0.03	1.5 ± 0.7	1/2	1
<i>Ochthoeca oenanthoides</i>	0.03	1.0 ± 0.0	1/1	0
<i>O. leucophrys</i>	0.03	1.0 ± 0.0	1/1	0
Turdidae				
<i>Turdus chiguanco</i>	0.02	1.0 ± 0.0	1/1	0
Thraupidae				
<i>Oreomanes fraseri</i>	0.76	2.6 ± 0.6	1/3	5

¹ based only on those flocks containing a given species

tail (primarily when no Giant Conebills were present). These two species also appeared to contribute to the maintenance of flock cohesion through vocalizations. Sentinel behavior was shown primarily by Tawny Tit-Spinetail and occasionally by Rusty-vented Canastero. White-throated Tyrannulet was a typical attendant species (Rand 1954, Powell 1985) that rarely vocalized and that did not contribute appreciably to the maintenance of flock cohesion. We observed no intraspecific agonistic interactions from April to July, but such apparently territorial behavior was fairly common in the regular participant species in early August.

We obtained home range estimates for six Tawny Tit-Spinetails, three White-throated Tyrannulets, and four Giant Conebills (Table 2). One of the five banded Giant Conebills observed in flocks (Table 1) was located too few times for analysis and appeared not to be resident in the study fragment after April 2000. We banded an additional three Tawny Tit-Spinetails, four White-throated Tyrannulets, and four Giant Conebills, but these birds were not observed in mixed-species flocks and, in most cases, were never observed at all after they had been released. On average, 100% MCP home ranges were largest and least variable in size for Giant Conebill, varying from 5.10 to 6.97 ha, whereas those of Tawny Tit-Spinetail were the smallest and varied from 0.47 to 3.80 ha (Table 2). Three White-throated Tyrannulets had home ranges of 1.55 to 6.55 ha. Detailed home range analyses were made for four Giant Conebills, one Tawny Tit-Spinetail, and one White-throated Tyrannulet (Table 2). For all Giant Conebills, 90% MCP home ranges were roughly half the size of the respective 100% MCP. This difference was less pronounced for the single individuals of Tawny Tit-Spinetail and White-throated Tyrannulet. Core areas of Giant Conebill varied in size from 0.29 to 1.38 ha, and this range also included core area sizes of the single individuals of Tawny Tit-Spinetail and White-throated Tyrannulet (Table 2).

It should be noted here that unbanded birds of all three species were present at Sacha Loma and participated in mixed-species flocks throughout the study period (i.e., we were unable to capture all resident individuals). Up to three unbanded Giant Conebills were sighted irregularly (probably representing visitors from nearby *Polylepis* patches), and one unmarked individual was commonly observed together with two banded Giant Conebills (see below). On four occasions two to three unbanded Giant Conebills par-

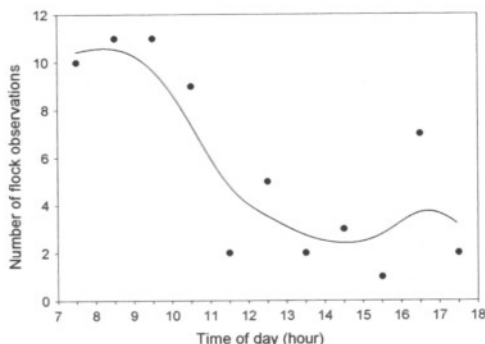


FIG. 1. Diurnal variation in mixed-species flock activity during the nonbreeding season 2000 at Sacha Loma, Bolivia. The curve was fitted by distance-weighted least-squares smoothing.

ticipated in a mixed-species flock inside the home ranges of absent marked conspecifics. Numbers of Tawny Tit-Spinetails and White-throated Tyrannulets appeared to be more stable, and we conservatively estimated the number of resident individuals at approximately 14–16 and 8–10 respectively.

Home range overlap for the six Tawny Tit-Spinetails varied from as low as 7.2% to complete overlap, and all six home ranges coincided in a small area near the center of the fragment (Table 3, Fig. 2A). We obtained similar results for White-throated Tyrannulet (Table 4, Fig. 2B). For the latter species, the large home range of individual CN in combination with the low number of locations (Table 1) is noteworthy. Four of the eight observations were made before August 2000 and approximately comprised the northern one-third of the bird's home range, whereas the remainder of fixes was taken on 5 to 6 August 2000 in the southern one-third. It therefore seems possible that the bird shifted from a winter home range to a breeding territory.

For Giant Conebill home range overlap was high (73–99%) between individuals of two pairs, i.e., AR and ZV as well as BB and AA, and was low (10–18%) for the remaining combinations, but all four ranges had a common area of overlap (Table 5, Fig. 2C). Overlap of core areas was lower than that of home ranges for all combinations except one (overlap of AR by BB), including one case (overlap of AA by BB) where the reduction was extreme, from 92.4% to

19.5% (Table 5). Intraspecific association indices (Table 6) revealed the same trend as the analysis of home range overlap, i.e., AR and ZV as well as BB and AA were often seen together (note, however, that BB was once associated with AR and a third, unbanded individual). On 28 occasions, AR and ZV were found in a group of three together with an unbanded adult (Table 6) that, based on the behavior of the four banded birds, we presume to have been the same individual, at least throughout most of the study period.

From the data presented so far it may appear that the study area contained two mixed-species flocks that had some spatial overlap and each of which formed around a pair or group of Giant Conebills. However, only 44 flock observations (70%) actually contained at least one of these four banded conebills. Individual AR was present on 28 occasions and was associated at least once with every one of the six banded Tawny Tit-Spinetails and on 15 occasion with unmarked tit-spinetails. The situation was similar for individual ZV except that it was never seen with tit-spinetail indi-

vidual RR. Conebill individuals BB and AA were observed during 13 and 12 mixed-species flock observations respectively, where they associated with three and two respectively of the six banded tit-spinetails, as well as with unmarked tit-spinetails on four and five occasions respectively. Thus, three of the six color-banded Tawny Tit-Spinetails (and possibly one or more of the unbanded tit-spinetails) were observed with both Giant Conebill pairs. Similarly, all four cone-bills associated with two of the three banded White-throated Tyrannulets (the third tyrannulet associated only with conebills AR and ZV) as well as with unbanded White-throated Tyrannulets.

Among Tawny Tit-Spinetails, individuals ZZ and BB each associated at least once with four, individuals AR and CC with three, and individual ZV with two of the other five banded conspecifics. Individual RR was observed on only three occasions in a mixed-species flock, where it never associated with a banded tit-spinetail.

Fifteen mixed-species flock observations (24%) did not contain Giant Conebill individuals (during

TABLE 2. Home ranges (minimum convex polygon = MCP) of color-banded individuals of three species regularly participating in mixed flocks. Ninety % MCPs are based on the harmonic mean, and core area was determined using 80% hierarchic cluster polygons.

Species/Individual	Number of locations	100% MCP (ha)	90% MCP (ha)	Core area (ha)
<i>Leptasthenura yanacensis</i>				
RR	12	3.80	—	—
ZZ	33	3.41	2.14	1.28
AR	14	2.01	—	—
CC	8	1.55	—	—
BB	13	1.51	—	—
ZV	8	0.47	—	—
Mean \pm SD	14.7 \pm 9.3	2.13 \pm 1.26	—	—
<i>Mecocerculus leucophrys</i>				
CN	8	6.55	—	—
BJ	21	2.13	1.68	0.50
AR	16	1.55	—	—
Mean \pm SD	15.0 \pm 6.6	3.41 \pm 2.7	—	—
<i>Oreomanes fraseri</i>				
BB	24	6.97	3.57	0.29
AR	38	6.73	3.18	1.38
AA	23	5.72	2.81	0.72
ZV	29	5.10	2.55	0.98
Mean \pm SD	28.5 \pm 6.9	6.13 \pm 0.87	3.03 \pm 0.44	0.84 \pm 0.46

TABLE 3. Home range (100% MCP) overlap for six *Leptasthenura yanacensis*. Range areas in rows are overlapped by range areas in columns.

Individual	AR	ZV	RR	ZZ	BB	CC
AR	—	22.4	71.3	55.2	43.1	38.4
ZV	94.7	—	57.7	100.0	90.6	35.9
RR	38.0	7.2	—	36.6	13.7	27.4
ZZ	32.4	14.1	42.0	—	39.2	38.1
BB	57.6	28.3	34.2	88.4	—	21.3
CC	49.3	11.0	67.1	82.4	20.7	—

the remaining four flock observations all participating cone-bills were unbanded, see above). Two to three Tawny Tit-Spinetail individuals were always present (including all banded individuals) and associated with one to three White-throated Tyrannulets on 13 occasions (also including all banded individuals), one to two Rusty-vented Canasteros on five occasions, and a single Tufted Tit-Tyrant *Anairetes parulus* and White-browed Chat-Tyrant *Ochthoeca leucophrys* on one occasion each.

DISCUSSION

In accordance with the low overall core species richness of the *Polylepis* forest fragment, its mixed-species flocks also contained less species and individuals than

flocks in other tropical areas (see Greig-Smith 1978, Munn 1985, Latta & Wunderle 1996, King & Rappole 2001). However, mixed-species flocks at our study site also were exceptionally species-poor relative to the entire bird community: only 33% of all core species joined mixed-species flocks and only 10% were regular participants. Considering the insectivore guild alone, only 23% of all insectivores regularly formed mixed-species flocks. Several other studies have shown that most members of a given community often participate in mixed-species flocks (e.g., Latta & Wunderle 1996, King & Rappole 2001).

Mixed-species flocks in *Polylepis* also differ with respect to the social organization of its members from other flocks in tropical habitats where color-banded

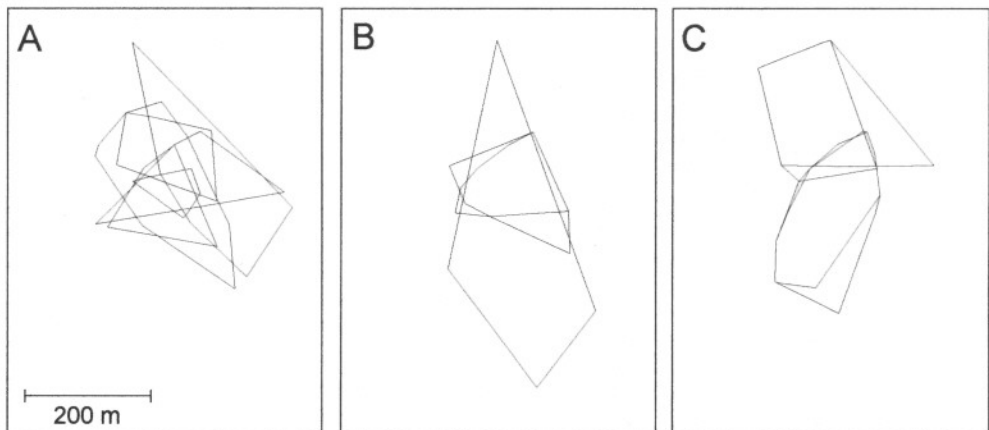


FIG. 2. Home ranges of (A) six *Leptasthenura yanacensis* (100% MCP), (B) three *Mecocerculus leucophrys* (100% MCP), and (C) four *Oreomanes fraseri* (90% MCP). Range outlines in all panels are drawn to scale.

TABLE 4. Home range (100% MCP) overlap for three *Myiozetetes similis*. Range areas in rows are overlapped by range areas in columns.

Individual	AR	BJ	CN
AR	—	95.7	89.6
BJ	69.2	—	87.2
CN	21.1	28.2	—

individuals were studied (Munn & Terborgh 1979, Powell 1979, Gradwohl & Greenberg 1980, Greenberg & Gradwohl 1985, Munn 1985, Jullien & Thiollay 1998). Moderate to extensive intraspecific home range overlap, the lack of clear associations of Tawny Tit-Spintail and White-throated Tyrannulet individuals with one of the two Giant Conebill pairs/groups, and the absence of agonistic interactions throughout most of the study period in all three species that regularly formed mixed-species flocks, indicate that little to no territoriality occurred and that flocks lacked a rigid spatial structure. Similarly, a well-defined nuclear species as reported from Amazonia (Munn & Terborgh 1979; Munn 1985, 1986) was absent in mixed-species flocks in *Polytlpis*, where the roles of flock leader and sentinel were shared by three different species. The onset of territorial behavior in early August further suggests that the social organization of at least some members of the *Polytlpis* bird

TABLE 5. Percentage overlap of home ranges (90% MCP) and core areas (80% hierarchic cluster polygons) for four *Oreomachus frater*. Range areas in rows are overlapped by range areas in columns.

Individual	AR	ZV	BB	AA
Home range				
AR	—	79.2	11.4	15.1
ZV	98.7	—	13.2	18.4
BB	10.2	9.5	—	73.2
AA	16.9	16.4	92.4	—
Core area				
AR	—	51.6	8.3	2.7
ZV	72.4	—	0.1	0.2
BB	37.9	0.1	—	46.2
AA	5.3	0.1	19.5	—

community varies between seasons. Although mixed-species flocks in other *Polytlpis* fragments need to be studied to determine whether such a lack of spatial structure is a general pattern, our study nonetheless indicates, as already suggested by Jullien & Thiollay (1998), that conclusions on mixed-species-flock structure and organization drawn from Neotropical lowland forests are not generalizable.

In some respects the flocks studied here bear more resemblance to mixed-species flocks observed in northern temperate zones. Several studies in these areas have described winter flocks of insectivorous, mainly bark-foraging birds, containing on average less

TABLE 6. Intraspecific association indices for four *Oreomachus frater* and an unbanded individual presumed to be the same during the study period (see text).

Individual	AR	ZV	BB	Unbanded
AR (n = 33)	—	—	—	0.91
ZV (n = 28)	0.83	—	—	0.93
BB (n = 22)	0.04	0.00	—	—
AA (n = 18)	0.00	0.00	0.77	—

than 10 individuals of only two to four species (Herrera 1979, Berner & Grubb 1985, Morrison *et al.* 1987), although other studies reported larger flocks with on average 10 to 20 birds from a greater number of species (e.g., Austin & Smith 1972; Morse 1970, 1978; Suhonen 1993). These flocks typically have tits (*Parus*) as nuclear species. Intraspecific sociality among these species usually varies seasonally, with pair territories in the breeding season and small groups in winter that may or may not be territorial and vary in degree of coherence (see Matthysen 1990, 1993 for reviews).

Powell (1985) discussed in detail the adaptive significance of insectivorous mixed-species flocks with special reference to the Neotropics. We found very little support for the foraging enhancement hypothesis, which includes various aspects, amongst them flushing cryptic prey, imitative foraging, and facilitation of niche separation (see Powell 1985). The three species that regularly participated in mixed flocks show considerable differences in foraging behavior:

whereas Giant Conebill pries and probes the flaky *Polylepis* bark, especially on trunks and major branches (George 1964, Parker & O'Neill 1980, Fjeldsá & Krabbe 1990, authors' pers. obs.). Tawny Tit-Spinetail primarily foliage-gleans along thinner branches and twigs, and White-throated Tyrannulet mainly obtains its prey by performing short aerial sallies to foliage and by hover-gleaning (authors' pers. obs.). Thus, among these insectivorous *Polylepis* birds mixed-species flocking is unlikely to serve as a mechanism for reducing foraging niche overlap and interspecific competition (see Morse 1967, 1970). Likewise, it is improbable that mixed-species flock species in *Polylepis* act as beaters, flushing cryptic insects for each other (see Belt 1874). One example of imitative foraging – a Rusty-vented Canastero copying Giant Conebill and visually inspecting, but not probing, *Polylepis* bark – represents our only observation in support of the foraging enhancement hypothesis.

By contrast, we obtained anecdotal evidence for a potential role of flocking in avoiding predation (see Powell 1985, Terborgh 1990). Once we observed two Tawny Tit-Spinetails persistently and successfully mobbing a Yungas Pygmy-Owl *Glaucidium bolivianum*, the main predator of small birds in the area (del Hoyo *et al.* 1999, König *et al.* 1999, authors' pers. obs.). This species was once captured in a mist net closely surrounded by entangled individuals of three passerine species (none were regular flock participants, however) that probably tried to escape the predator's attack. One flock reacted to a passing Mountain Caracara *Phalcoboenus megalopterus*, a scavenger that does not prey on live birds, with alarm calls (by Rusty-vented Canastero) and immediate escape behavior by all flock participants. Although largely anecdotal, these observations nonetheless indicate that predation pressure influences the behavior of *Polylepis* birds and is likely to promote flocking in this high-Andean habitat.

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