

MIXED-SPECIES BIRD FLOCKS IN A MONTANE CLOUD FOREST OF COLOMBIA

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Resumen. – **Bandadas mixtas de aves en un bosque nublado de montaña en Colombia.** – Las bandadas mixtas de aves fueron estudiadas durante un año en un bosque de niebla a 1800–2000 m de elevación, en el sur-occidente de Colombia. Las bandadas fueron observadas para registrar patrón anual, frecuencia de especies, composición de especies y tamaño de las bandadas. Un total de 71 especies fueron registradas en las bandadas, la mayor parte estuvieron presentes con uno o dos individuos por bandada. La mayoría de las bandadas tuvieron especies en todos los estratos verticales de la vegetación. Thraupinae fue el grupo que caracterizó las bandadas tanto en número de especies como en número de aves por especie presente en las bandadas. La Tangara Oscura de Monte (*Chlorospingus semifuscus*) fue la especie más frecuente en las bandadas y la principal especie nuclear. Una pequeña proporción de co-ocurrencias de especies fue no originada por el azar, sugiriendo que la composición de las bandadas es el resultado de la co-ocurrencia de especies en la misma área, y se encuentra relacionada con la abundancia de especies en La Planada. Aunque el número de bandadas mixtas fue similar a lo largo del año, las bandadas fueron más frecuentes durante el periodo no reproductivo en el patrón diario, lo que evidencia un balance evolutivo entre las actividades reproductivas y de alimentación social de las especies.

Abstract. – Mixed-species bird flocks were studied during one year in a cloud forest at 1800–2000 m a.s.l. in southwest Colombia. The annual pattern, frequency of species, species composition and size of mixed species bird flocks are described. A total of 71 species were recorded in the flocks, and most species were represented by one or two individuals in each flock. Most flocks had species in all vertical layers. Thraupinae was the most prevalent group in flocks, both in number of species and number of individuals per species. Dusky Bush-Tanager (*Chlorospingus semifuscus*) was the most frequent species in the flocks as well as the main nuclear species. A small proportion of the species co-occurrences were nonrandom, suggesting that the composition of flocks results from species which co-occur in the same area, and is related with the abundance of the species in La Planada. Although the number of flocks were similar year-round, the flocks were most frequent during the non-breeding period in a daily pattern; there appeared to be an evolutionary balance between the reproductive and social-feeding activities of flocking species. *Accepted 9 May 2002.*

Key words: Andes, cloud forest, Colombia, mixed species flocks.

INTRODUCTION

Flocking behavior is widespread in most families of birds, in most habitats and in most areas in the world. There are several advan-

tages to participation in mixed-species flocks, the principal ones are reduced predation risk and enhanced foraging efficiency (Powell 1985). Nevertheless, there is still need for more descriptive studies, particularly from the tropics, before evaluating different hypotheses about the selective advantages of flocking

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(Powell 1985; Hutto 1987, 1994).

Despite the complexity of mixed bird flocks in the Neotropics (Gill 1995), there are few studies about flocks in tropical montane forests (Buskirk *et al.* 1972, Moynihan 1979, Powell 1979, Remsen 1985; Poulsen 1996b, 1996c), and there are no studies about flocks in Colombia. The best known flock studies are from the Peruvian Amazon (Munn & Terborg 1979, Munn 1985, Powell 1985, Graves & Gotelli 1993). Studies on mixed-species flocks in the Andes have shown differences in species composition, territoriality, propensity of association, and vertical distribution in the vegetation, compared with the Amazon associations (Powell 1985, Poulsen 1996c). Differentiation between nucleus and attendant species is difficult for the flocks in the Amazon, because many species contribute in different degrees to flock cohesion (Powell 1985). Moynihan (1962) gave a definition for nuclear species as follows: a nuclear species is one whose behavior is capable of influencing the formation and cohesion of flocks, and has conspicuous color patterns, movements or vocalizations. Moynihan (1960) proposed that nucleus species have evolved conspicuous patterns of dull colors (neutral coloration) to make them less threatening to other species while still remaining conspicuous enough to be followed. Hutto (1994) summarizes the criteria for identification of a nuclear species as: they are joined and followed more often than they themselves join and follow others, have a strong flocking propensity, are intra-specifically gregarious, are regular participants of mixed flocks, are conspicuous, and are year-round residents.

Almost every major habitat of the Andes has its characteristic associations, so information on mixed-species flocks from different altitudinal places and habitats can help us to understand the evolution of mixed flocking behavior. In this study, I present data on frequency, annual pattern, species composition

and size of mixed-species flocks from a cloud forest in southwest Colombia. My major goals are to describe flock composition and to determine whether there are nonrandom patterns of association within flocks.

STUDY AREA AND METHODS

From July 1995 to July 1996, I studied mixed-species bird flocks at La Planada Natural Reserve, Mun. of Ricaurte, Depto. of Nariño, southwestern Colombia ($01^{\circ}10'N$, $78^{\circ}00'W$). Situated on the Pacific slope of the Western Andes between 1300 and 2200 m a.s.l., the reserve has a central plateau at 1800 m, flanked by taller ridges to the N and E, and valleys to the S and W. The average annual rainfall is 4800 mm with a single (relatively) dry period between June and August, and a mean annual temperature of $19.3^{\circ}C$. The vegetation is mostly disturbed forest and 16–21 year old second growth on the plateau; on the ridges and in the lower part of the reserve, the forest is lightly disturbed to nearly pristine, save that, at several points on the N boundary, pastures extend right up to the reserve boundary. The forest canopy is 20–25 m tall, with very high densities of epiphytes and hemi-epiphytes (Gentry 1988). The reserve is located in the premontane rain forest life zone *sensu* Holdridge (1967), and may be considered cloud forest since it is shrouded in clouds and mist for several hours daily during most of the year.

Mixed flocks were located during walks along 8 km of trails between 1800 and 2000 m a.s.l., following ridges, areas of secondary forest and heavily to lightly disturbed primary forest. The observations were made during eight days per month (except September, December, March and June), between 05:30 and noon, walking slowly (c. 1.5 km/h) through the forest, listening for bird vocalizations and watching for movements. Due to frequent rain after midday, few data are avail-

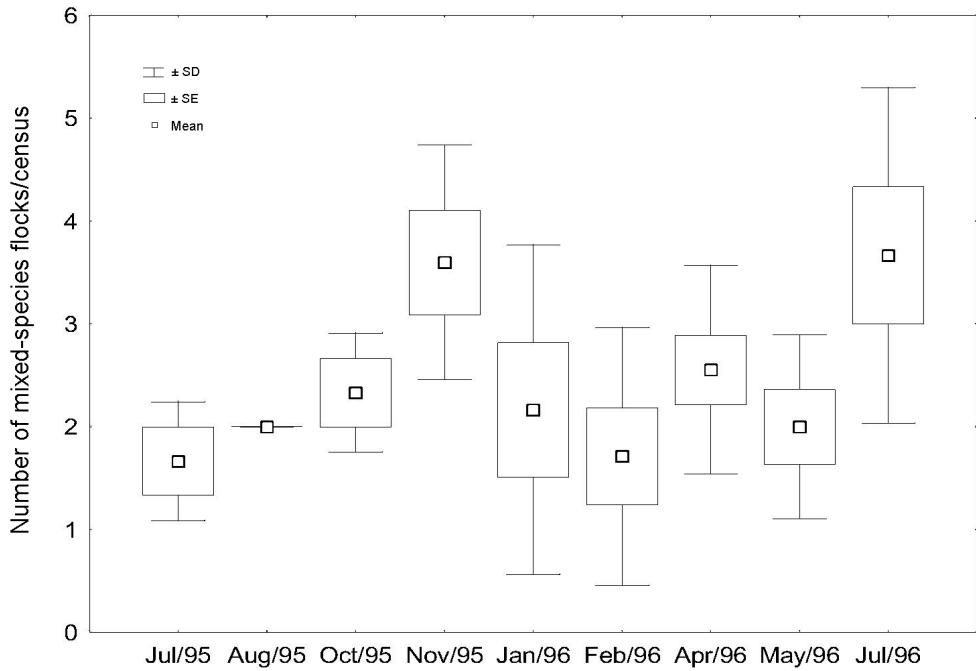


FIG. 1. Number of mixed species flocks per census for each month, between July 1995 and July 1996.

able for the afternoon hours. To reduce the possibility of encountering a flock more than once, each trail was never censused more frequently than once a week. For each flock sighted, locality, time, size and composition were recorded, but due to the limited view in the forest the majority of flock records probably were under-sampled. A distinction was made between flocks in which all species and individuals were recorded and those in which only some species and individuals were recorded. The first type of data was used to calculate frequency, mean flock size, number of flock species, mean number of individuals for each species, and co-occurrences. I classified the flocks as canopy, understory and combined flocks. The classification of species and families (or subfamilies) follow Stotz *et al.* (1996).

A Kolmogorov-Smirnov one-sample test was applied to test for differences in number

of mixed flocks through the year. A regression analysis was made to correlate number of species with flock size; data were square root transformed to stabilize variances. To determine if the species co-occurrence patterns were nonrandom, I compared the observed patterns to those expected under the null hypothesis of random, using the number of species combination index (Gotelli & Entsminger 2001). I used a matrix that represents the occurrence of a particular species on a particular mixed flock, in which the rows are species and the columns are the different flocks, this matrix was randomized 1000 times.

A 2×2 test of independence with a Yate's corrected Chi square test was used to test for the independence of each pair of species co-occurrences within flocks. In tests where cells were less than five, a Fisher's test was used. To evaluate the influence of the most com-

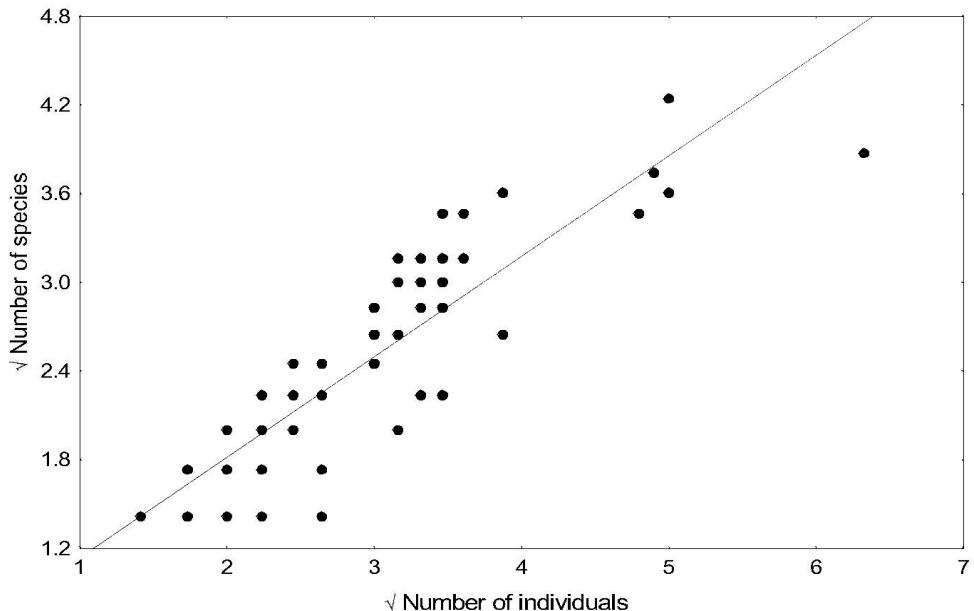


FIG. 2. Relationship between the number of species and the number of individuals per flock. The equation of the regression line is: $y = 0.46 + 0.68x$, $r^2 = 0.795$, $n = 77$, $P < 0.05$.

mon species on the species richness of the flocks, I compared species numbers of each flock observed, with and without the species, by means of Mann-Whitney U -tests.

RESULTS

Mixed-species flocks were common throughout the year, although flocks tended to be more frequent in November and July 1996. However, there was no significant difference in the number of mixed flocks encountered through the year (Kolmogorov-Smirnov test, $D_{max} = 1.29$, $P > 0.05$; Fig. 1). The mean numbers of individuals and species per flock were 8.3 ($SD = 6.3$) and 5.8 ($SD = 3.6$), respectively ($n = 77$ flocks); the ranges of individuals and species were 2–40 and 2–18, respectively. Flock size was positively correlated with the number of species present ($r = 0.892$, Fig. 2). Most observations had species

in all vertical layers (59% of 102 flocks); 39% of the flocks were seen in the forest canopy, and only 2% were restricted to the understorey. The flocks were observed searching mainly for insects, although when they passed nearby a fruit source many of the omnivorous species consumed fruits.

A total of 71 species were recorded in 184 mixed flocks (Appendix 1). Five species were the most common species (present in more than 25% of the flocks): Dusky Bush-Tanager (*Chlorospingus semifuscus*), Blue-winged Mountain-Tanager (*Anisognathus flavinucha*), Orange-bellied Euphonia (*Euphonia xanthogaster*), Golden Tanager (*Tangara arthus*) and Beryl-spangled Tanager (*Tangara nigroviridis*). Sometimes these species were observed in intra-specific groups within the flocks. Only the Dusky Bush-Tanager was present in more than 50% of the flock encounters. Some 36 species (50%) were observed exclusively in

TABLE 1. Relative importance of different groups as participants in mixed-species flocks at La Planada, from a total of 77 flocks. Rank refers to the index A/B; A = total number of birds seen per family (or subfamily), B = total number of species observed in flocks.

Family or subfamily	No. of flocks seen	% of total flocks	Bird flocks seen (A)	No. of species observed (B)	Index A/B	Rank
Thraupinae	75	97.4	359	22	16.3	1
Parulinae	34	44.7	61	5	12.5	2
Furnariidae	22	28.9	36	12	3	5
Tyrannidae	21	27.6	25	10	2.5	6
Dendrocolaptidae	14	18.4	15	3	5	4
Formicariidae	11	14.5	18	2	9	3
Vireonidae	10	13.2	10	2	5	4
Troglodytidae	4	5.3	5	2	2.5	6
Trochilidae	3	3.9	3	2	1.5	8
Picidae	2	2.6	4	2	2	7
Pipridae	2	2.6	3	1	3	5
Cotingidae	2	2.6	2	2	1	9
Trogonidae	1	1.3	1	1	1	9
Turdinae	1	1.3	1	1	1	9
Emberezinae	1	1.3	3	2	1.5	8
Catamblyrhynchinae	1	1.3	1	1	1	9
Tersininae	1	1.3	1	1	1	9

flocks with this species.

Most species that participated in flocks were present by one or two individuals in each flock, while a minority of species occurred in small groups, with only five of the species participating in flocks with group size > 2 (Appendix 1). In some of these species juveniles accompanied the adults. Most species encountered were permanent residents (97.2%). Just two Nearctic migratory species were seen in flocks during the period of overwintering (September to April): Black-and-white Warbler (*Mniotilla varia*) and Blackburnian Warbler (*Dendroica fusca*). The latter species was especially common in the flocks, and its frequency of participation in flocks (25.6%) was truly higher during this period: 36% (19 encounters in 53 flocks from September to April).

The most common species in the flocks were Thraupinae; 97.4% of all complete flocks (n = 77) included species of this sub-

family. Species of others families (or subfamilies) were in less than a half of the encounters (Table 1). Thraupinae and Tyrannidae are the most common groups in La Planada, with 28 and 19 species observed for each, respectively (pers. observ.). Thraupinae had almost twice as many flock-species (n = 22) as Furnariidae (n = 12) and Tyrannidae (n = 10). Considering the number of birds seen in flocks per species in the flocks as an index (Index = A/B, Poulsen 1996b), Thraupinae characterized flocks more than any other group (Table 1). Two species of hummingbirds, Empress Brilliant (*Heliodoxa imperatrix*) and Hoary Puffleg (*Haplophaedia lugens*), and the Golden-winged Manakin (*Manis chrysopterus*), typically regarded as solitary (Hilty & Brown 1986), were occasionally seen joining mixed flocks at La Planada. Species observed as nuclear in the flocks were: Dusky Bush-Tanager, Golden Tanager, Beryl-spangled Tanager and Blue-winged Mountain-Tanager, all

72 TABLE 2. The number of 77 mixed-species flocks in which each species was recorded (n), the number of occasions in which each of the other species was also recorded, and the mean species richness of flocks occupied and not occupied by each of the species. Number of positive co-occurrences that are significantly greater than expected appear underlined and bold, the number of significant negative co-occurrences are underlined and italicized.

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Species	Species																		Mean species richness			
	n	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	With the sp.	Without the sp.	U	P
<i>Chlorospingus semifuscus</i>	51	21	16	15	15	11	<u>15</u>	11	9	<u>11</u>	9	<u>11</u>	9	6	<u>2</u>	6	7	4	6.75	3.88	341.5	0.0005*
<i>Tangara nigroviridis</i>	33	11	13	10	8	5	4	<u>2</u>	5	3	5	7	5	3	1	6	3	6.09	5.54	656	n.s.	
<i>Tangara arthus</i>	26		6	8	8	3	6	5	4	2	<u>8</u>	5	4	1	1	2	2	7.00	5.16	502.5	n.s.	
<i>Euphonia xanthogaster</i>	22			8	7	3	5	2	5	<u>7</u>	4	5	3	4	2	3	2	8.18	4.82	333.5	0.002*	
<i>Anisognathus flavinucha</i>	21				5	3	5	3	5	5	3	1	3	1	1	2	4	8.09	4.91	288.5	0.0006*	
<i>Tangara labradorides</i>	17					3	5	3	3	3	2	3	2	3	2	2	2	8.76	4.93	278.5	0.004*	
<i>Basileuterus tristriatus</i>	17						2	5	1	4	1	1	1	0	2	3	1	6.12	5.68	502.5	n.s.	
<i>Dendroica fusca</i>	13						3	<u>7</u>	<u>5</u>	2	2	1	1	2	1	1	8.77	5.17	195.5	0.003*		
<i>Premnornis guttuligera</i>	12							1	2	2	2	2	0	0	1	2	7.08	5.54	290	n.s.		
<i>Anisognathus notabilis</i>	12								4	2	1	2	2	1	0	2	8.33	5.31	210.5	0.012*		
<i>Drymophila caudata</i>	11									1	1	1	1	1	0	0	7.91	5.42	197	0.016*		
<i>Chlorochrysa phoenicotis</i>	11										<u>4</u>	1	1	1	2	0	8.64	5.3	135.5	0.0009*		
<i>Lepidocolaptes affinis</i>	10										2	0	1	<u>4</u>	1	7.90	5.46	185	0.023*			
<i>Tangara parzudakii</i>	10											3	0	1	2	6.60	5.66	264	n.s.			
<i>Tangara ruficervix</i>	8												1	0	0	5.87	5.77	262	n.s.			
<i>Myioborus miniatus</i>	8													2	1	6.12	5.74	275.5	n.s.			
<i>Vireo leucophrys</i>	8														0	7.62	5.56	198.5	n.s.			
<i>Tangara xanthocephala</i>	7															7.14	5.64	170	n.s.			

* The mean species richness with the species differs significantly from the mean richness without the species, based on 77 flocks ($P < 0.05$).

thraupids. To a lesser degree, Three-striped Warbler (*Basileuterus tristriatus*) was a nuclear species in the understory and medium-layer flocks. These species were also the most common species in the flocks. Although in some flocks I observed all flock species actively singing and moving and there were flocks with two or three of these species singing and very active at the same time, most flocks had Dusky-bush Tanager as the leader.

I calculated the number of species combination index for a matrix with 77 mixed species flocks and 71 species. The observed number of species combination was 75, and the average of the simulated matrices was 76.11. The observed number did not differ significantly than expected by chance ($P = 0.25$), and there is no reason to reject the null hypothesis that the number of species combination is random. It suggests that most of the species co-occurrences are random.

Co-occurrences for each pair of species were calculated for 18 species that occurred in more than 5 flocks ($n = 77$; Table 2). Of 153 possible pair comparisons, 11 were significantly different than the expected number by random (7.2%). Nine of these significant comparisons were positive, indicating that these pairs of species co-occurred together more frequently than expected. Dusky Bush-Tanager and Glistening-green Tanager (*Chlorochrysa phoenicotis*) were involved in three positive relations each. Two pair-wise combinations were negative suggesting that these species pairs may be avoiding one another. These data indicate that not all birds are joining flocks independently, although most of species associations are random.

For nine species, the average species richness of flocks occupied by each was significantly greater than the mean richness without that species (Table 2). No species (from these 18) participated in flocks that averaged fewer than the overall mean number of participant species (5.8), it means, no species occurred

exclusively in small flocks and many of them preferred the join larger flocks.

DISCUSSION

The flocks at La Planada were uniform along year. Mixed-species flocks are generally most frequent and large during the non-breeding season (Moynihan 1962, Powell 1979). The breeding season at La Planada seems to occur in the dry season (Orejuela *et al.* 1982, pers. observ.), between May and August. With the Dusky Bush-Tanager, the singing season of males also occur between May and August (Bohórquez & Stiles in press). Nevertheless, all the species seem to participate along year in mixed species flocks. This pattern could be related to the high rainfall in La Planada, which can make feeding difficult for birds. Especially at sites as La Planada with very high rainfall throughout the year and dense mist, mixed flocks could be a solution for foraging activities in adverse weather conditions, when the searching for insects increases (Poulsen 1996a).

In a daily pattern the flock activity at La Planada was reduced in the early morning and late afternoon (Bohórquez & Stiles in press). This uneven distribution of flock activity suggests that birds join flocks during an optimal foraging time, advocating that feeding may be an important aspect of mixed-species flock formation. The period of lowest flock activity could provide a time available to the species for reproductive activities. In fact, at this time in which flocks were scarce, Dusky Bush-Tanager's singing period occurs (Bohórquez & Stiles in press). These patterns seem to evidence a balance between the reproductive and social-feeding activities of flocking species, in an evolutionary sense.

The majority of flocking species occurred singly or in pairs, and the increase in flock size was a result of the addition of species rather than individuals of species already

present. This could be related to a relative stability of species, and a high turnover of conspecific individuals whenever the flock moved across territories, as is the case in flocks from montane forest in Costa Rica and Ecuador (Powell 1979, Poulsen 1996c). Systematic study of banded individuals is needed to establish whether or not flocks occupied stable home ranges and any compositional changes.

In the taller lowland forests as in the Amazon, flocks are clearly differentiated into canopy and understory flocks (Powell 1979, Munn 1985, Terborgh *et al.* 1990). It is unlikely that in montane forest both canopy and understory birds flock together (Powell 1985). In this study, a large part of the flocks observed included members from all vertical levels. Similar results were found from montane forest in Ecuador (Poulsen 1996b, 1996c), although these forests are structurally different from the La Planada forest.

Flocks at La Planada were comprised mainly of Thraupinae species, while in other studies in tropical montane forest the flocks were characterized by Furnariidae and Parulinae (Powell 1979, Poulsen 1996b), although Thraupinae was the group with more species participating in these flocks (Poulsen 1996b). This is the most remarkable feature of La Planada flocks. The major presence of Thraupinae could be related to the high component of canopy flocks, which are mainly formed by omnivorous tanagers (Moynihan 1962, 1979; Munn 1985, Powell 1985 pers. observ.). In addition, the Andes are a major center of tanager radiation (Isler & Isler 1987). At the elevation of La Planada there were no ant-following flocks encounters involving mainly sub-oscines that are more common at lowland forests.

The nuclear species observed meet Hutto's quantitative criteria (Hutto 1994), because: they were observed rarely foraging alone, were mainly joined and followed by

others and vocalized frequently, were intra-specifically gregarious and relatively numerous in the flocks, were the most common flock participants, were conspicuous by their calls and their active behavior, and are year-round residents. The presence of the nuclear species Dusky Bush-Tanager and Blue-winged Mountain-Tanager was related with an increase in the size and number of species in the flocks. The most frequent species in the flocks, the Dusky Bush-Tanager, possesses the full set of characteristics described by Moynihan (1962) as typical of nuclear species: has a dull plumage and is nervously active and noisy. One could expect that the nuclear species had positive associations with many of the other flock species. However, only three associations showed a significant relationship with the Dusky Bush-Tanager and none with Blue-winged Mountain-Tanager and Beryll-spangled Tanager. Moreover, Glistening-green Tanager was never observed as nuclear species in the flocks, but it was also significantly involved in three positive associations. This suggests that the species composition of the flocks may be related with the abundance of the species in La Planada and with species which co-occur in the same area, rather than nonrandom associations. In fact, most species are distributed independently of one another within flocks and most of the species co-occurrences are random. Nevertheless, these mixed-species flocks may need one or more nuclear species to maintain flock cohesion and structure (Bell 1983). These positive interactions are not fully explained by the role of nuclear species, and more studies must be made to understand these associations.

ACKNOWLEDGMENTS

WCS-FES fellowship program and La Planada Natural Reserve through the MacArthur foundation fellowship program provided financial support for this study. I thank D.

Forero for support during the writing of this manuscript and for his comments. I thank the ecotourism guides and personnel of La Planada for facilitating the research. I thank D. Knapp and C. Torres for their help with the English version. The manuscript benefited from the comments by two anonymous reviewers.

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APPENDIX 1. Species participating in mixed-species flocks at La Planada, frequency (as percent of total flocks), mean number of individuals and resident status. Nomenclature of birds follows Stotz *et al.* (1996) except for *Diglossopis*, and *Diglossa* (Bock 1985).

Family/Species	Proper names	Frequency in flocks (%)	Mean number of individuals	Resident status ^a
TROCHILIDAE				
<i>Heliodoxa imperatrix</i>	Empress Brilliant	1.3	1.00	PR
<i>Haplophaedia lugens</i>	Hoary Puffleg	1.3	1.00	PR
TROGONIDAE				
<i>Trogon personatus</i>	Masked Trogon	1.3	1.00	PR
PICIDAE				
<i>Veniliornis dignus</i>	Yellow-vented Woodpecker	2.6	1.00	PR
<i>Piculus rubiginosus</i>	Golden-olive Woodpecker	6.5	2.40	PR
DENDROCOLAPTIDAE				
<i>Dendrocitta tyrannina</i>	Tyannine Woodcreeper	3.9	1.33	PR
<i>Glyptorhynchus spirurus</i>	Wedge-billed Woodcreeper	1.3	1.00	PR
<i>Lepidocolaptes affinis</i>	Spot-crowned Woodcreeper	13	1.00	PR
FURNARIIDAE				
<i>Cranioclewa erythrops</i>	Red-faced Spinetail	1.3	1.00	PR
<i>Margarornis stellatus</i>	Fulvous-dotted Treerunner	3.9	1.00	PR
<i>Premnornis guttuligera</i>	Rusty-winged Barbtail	15.6	1.25	PR
<i>Premnoplex brunnescens</i>	Spotted Barbtail	2.9	1.00	PR
<i>Pseudocolaptes boissonneautii</i>	Streaked Tuftedcheek	3.9	1.00	PR
<i>Pseudocolaptes lawrencii</i>	Buffy Tuftedcheek	1.3	1.00	PR
<i>Syndactyla subalaris</i>	Lineated Foliage-gleaner	2.6	1.00	PR
<i>Anabacerthia striaticollis</i>	Montane Foliage-gleaner	1.3	1.00	PR
<i>Anabacerthia variegaticeps</i>	Spectacled Foliage-gleaner	6.5	1.00	PR
<i>Philydor rufus</i>	Buff-fronted Foliage-gleaner	1.3	1.00	PR
<i>Thripadectes ignobilis</i>	Uniform Treehunter	1.3	1.00	PR
<i>Thripadectes virgaticeps</i>	Streak-capped Treehunter	3.9	1.33	PR
FORMICARIIDAE				
<i>Drymophila caudata</i>	Long-tailed Antbird	14.3	1.64	PR
<i>Terenura callinota</i>	Rufous-rumped Antwren	1.3	1.00	PR
TYRANNIDAE				
<i>Zimmerius viridiflavus</i>	Golden-faced Tyrannulet	5.2	1.25	PR
<i>Mionectes striaticollis</i>	Streak-necked Flycatcher	2.6	1.00	PR
<i>Phylloscartes ophthalmicus</i>	Marble-face Bristle-Tyrant	1.3	1.00	PR
<i>Pseudotriccus pelzelni</i>	Bronze-olive Pygmy-Tyrant	1.3	1.00	PR
<i>Platyrinchus mystaceus</i>	White-throated Spadebill	1.3	1.00	PR

APPENDIX 1. Continued.

Family/Species	Proper names	Frequency in flocks (%)	Mean number of individuals	Resident status ^a
<i>Myiophobus flavicans</i>	Flavescnt Flycatcher	1.3	1.00	PR
<i>Myiophobus pulcher</i>	Handsome Flycatcher	1.3	1.00	PR
<i>Contopus sp.</i>	Pewee	1.3	1.00	M
<i>Pachyramphus polychopterus</i>	White-winged Becard	1.3	1.00	PR
<i>Pachyramphus versicolor</i>	Barred Becard	3.9	1.13	PR
PIPRIDAE				
<i>Masius chrysopterus</i>	Golden-winged Manakin	2.6	1.50	PR
COTINGIDAE				
<i>Pipreola riefferii</i>	Green-and-black Fruiteater	1.3	1.00	PR
<i>Lipaugus cryptolophus</i>	Olivaceous Piha	1.3	1.00	PR
TROGLODYTIIDAE				
<i>Troglodytes solstitialis</i>	Mountain Wren	2.6	1.00	PR
<i>Henicorhina leucophrys</i>	Gray-breasted Wood-Wren	2.6	1.50	PR
TURDINAE				
<i>Myadestes ralloides</i>	Andean Solitaire	1.3	1.00	PR
EMBERIZINAE				
<i>Atlapetes brunnineucha</i>	Chesnut-capped Brush-Finch	1.3	2.00	PR
<i>Atlapetes tricolor</i>	Tricolored Brush-Finch	1.3	1.00	PR
CATAMBLYRHYNCHINAE				
<i>Catamblyrhynchus diadema</i>	Plush-capped Finch	1.3	1.00	PR
THRAUPINAE				
<i>Chlorospingus semifuscus</i>	Dusky-bellied Bush-Tanager	66.23	2.04	PR
<i>Creurgops verticalis</i>	Rufous-crested Tanager	5.2	1.25	PR
<i>Thraupis cyanocephala</i>	Blue-capped Tanager	1.3	1.00	PR
<i>Anisognathus flavinucha</i>	Blue-winged Mountain Tanager	27.3	1.33	PR
<i>Anisognathus notabilis</i>	Black-chinned Mountain-Tanager	15.6	1.18	PR
<i>Iridosornis porphyrocephala</i>	Purplish-mantled Tanager	6.5	1.00	PR
<i>Pipraeidea melanonota</i>	Fawn-breasted Tanager	2.6	1.00	PR
<i>Euphonia xanthogaster</i>	Orange-bellied Euphonia	28.6	1.45	PR
<i>Chlorophonia flavirostris</i>	Yellow-collared Chlorophonia	1.3	1.00	PR
<i>Chlorophonia pyrrhoptera</i>	Chestnut-breasted Chlorophonia	1.3	1.00	PR
<i>Chlorochrysa phoenicotis</i>	Glistening-green Tanager	14.3	1.18	PR
<i>Tangara arthus</i>	Golden Tanager	33.8	1.23	PR
<i>Tangara heinei</i>	Black-capped Tanager	6.5	1.20	PR
<i>Tangara labradorides</i>	Metallic-green Tanager	22.1	1.59	PR
<i>Tangara nigroviridis</i>	Beryl-spangled Tanager	42.9	1.66	PR
<i>Tangara parzudakii</i>	Flame-faced Tanager	12.99	1.00	PR
<i>Tangara pulcherrima</i>	Golden-collared Honeycreeper	1.3	3.00	PR
<i>Tangara ruficervix</i>	Golden-naped Tanager	10.4	1.25	PR
<i>Tangara rufigula</i>	Rufous-throated Tanager	3.9	1.00	PR
<i>Tangara xanthocephala</i>	Saffron-crowned Tanager	9.1	1.00	PR

APPENDIX 1. Continued.

Family/Species	Proper names	Frequency in flocks (%)	Mean number of individuals	Resident status ^a
<i>Diglossopis cyanea</i>	Masked Flower-piercer	2.6	1.00	PR
<i>Diglossa indigotica</i>	Indigo Flower-piercer	5.2	1.00	PR
TERGININAE				
<i>Tersina viridis</i>	Swallow-Tanager	1.3	1.00	PR
PARULINAE				
<i>Mniotilla varia</i>	Black-and-white Warbler	1.3	1.00	M
<i>Parula pitiayumi</i>	Tropical Parula	2.6	1.00	PR
<i>Dendroica fusca</i>	Blackburnian Warbler	16.9	1.00	M
<i>Myioborus miniatus</i>	Slate-throated Whitestart	10.4	1.13	PR
<i>Basileuterus tristriatus</i>	Three-striped Warbler	22.1	2.18	PR
VIREONIDAE				
<i>Cyclarhis nigrirostris</i>	Black-billed Peppershrike	2.6	1.00	PR
<i>Vireo leucophrys</i>	Brown-capped Vireo	10.4	1.00	PR

^aResident status: PR = permanent resident, M = Nearctic migratory winter resident.