

MIXED-SPECIES FLOCK COMPOSITION IN A NORTHWESTERN ECUADORIAN CLOUD FOREST

Esteban A. Guevara, Juan C. Valarezo, Alexandra Onofa, & Fabián Cupuerán

Aves&Conservación – BirdLife en Ecuador, Casilla 17-17 906, Quito, Ecuador. *E-mail:*
eguevara@avesconservacion.org

Resumen. – Composición de bandadas mixtas en un bosque nublado del noroeste de Ecuador. –

Se estudió la composición de bandadas mixtas en cuatro localidades en el nor-occidente de Ecuador, en hábitat de bosque nublado, entre noviembre del 2006 y octubre del 2008. Se registraron 112 especies y 878 individuos participando en 53 bandadas mixtas. Las bandadas estuvieron compuestas en promedio por 16,6 (\pm 10,1) individuos y por 10,3 (\pm 4,8) especies, el número de individuos y especies estuvo directamente relacionado. Thraupidae fue la familia más frecuente y abundante en las bandadas mixtas, así como la más diversa. Catorce especies fueron registradas regularmente formando parte de las bandadas mixtas, de las cuales la Tangara-Montana Aliazul (*Anisognathus somptuosus*) y la Tangara-Montana Encapuchada (*Buthraupis montana*) fueron especies nucleares. El estrato vertical en el cual se registraron a los individuos participantes de las bandadas mixtas fue variable e individuos forrajeando en diferentes estratos fueron registrados en la misma bandada. Algunos patrones como la relación número de individuos vs número de especies fueron consistentes con estudios previos, mientras que otros como la composición de especies mostraron cierta variación.

Abstract. – The composition of mixed-species flocks was studied in four sites within northwestern Ecuadorean cloud forest between November 2006 and October 2008. A total of 112 species and 878 individuals were recorded participating in 53 mixed-species flocks. Mean numbers of individuals and species per flock were 16.6 (\pm 10.1) and 10.3 (\pm 4.8) respectively and flock size and species diversity were correlated. Thraupidae was the most frequent and abundant family within flocks as well as the most diverse. Fourteen species were recorded regularly participating in flocks and the Blue-winged Mountain tanager (*Anisognathus somptuosus*) and the Hooded Mountain-Tanager (*Buthraupis montana*) were regarded as nuclear species. Individuals foraging in different vertical strata were recorded in the same flock. Some patterns such as the relationship between number of individuals and species seemed to be consistent with previous studies whereas other factors such as species composition exhibited differences. *Accepted 21 June 2011.*

Key words: Cloud forest, mixed-flock composition, nuclear species, Ecuador.

INTRODUCTION

In Neotropical forests, some insectivorous and omnivorous passerines associate in mixed-species flocks throughout the year. Non-passerine species, such as hummingbirds, may join these foraging flocks opportunistically (Bohórquez 2003). Two major

selective advantages are hypothesized to favor the evolution of mixed-species flocking behavior: decreased predation and increased foraging efficiency (Powell 1985). The predation hypothesis suggests that flocking birds may reduce vigilance cost for each individual participating in the foraging group because early detection of an approaching predator is

increased (Elgar 1989). On the other hand, foraging benefits for flocking birds may include improved information on foraging tactics as well as food type and location (Krebs 1973, Valburg 1992). However, flocking individuals may also experience lower per-capita intake because of adjustments in movement patterns that are required to stay with the group or increased interspecific competition (Petit & Bildstein 1987, Hutto 1988).

Flocking behavior differs among species. According to Moynihan's (1962) definition, nuclear species, that promote group cohesion, can be identified by the following criteria: 1) nuclear species are joined and followed more often than they themselves join and follow others species (Moynihan 1962, Munn & Terborgh 1979); as a result, they tend to be positioned in the front of flocks (Greig-Smith 1978); 2) nuclear species are intraspecifically gregarious and are rarely seen away from other individuals of their own species; therefore, these species tend to always be recorded in flocks and are more numerous than other species within flocks; 3) they are regular participants of mixed-species flocks or, in other words, they are frequent species; 4) they are conspicuous by their plumage coloration, voice, or active behavior; and 5) nuclear species are year-round residents.

Previous authors (Powell 1985, Hutto 1988, 1994, Latta & Wunderle 1996, Bohórquez 2003) have emphasized on the need of descriptive studies of mixed-species flocks, especially for the Neotropics, as a necessary tool to test whether foraging efficiency increases or decreases as a result of flocking behavior. Data on mixed-species flocks' composition, movements, and behavior can give us important insights into understanding the costs and benefits related with flocking behavior.

Studies on Neotropical mixed-species flocks' composition and organization have concentrated mainly on the tropical humid

lowland forest (Davis 1946, Munn 1985, Terborgh *et al.* 1990, Graves & Gotelli 1993, English 1998, Develey & Stouffer 2001), with a minor extent on the montane cloud forest or other type of habitat in South America (e.g., Poulsen 1996, Bohórquez 2003). These studies have shown differences in species composition, territoriality and propensity of association between mixed-species flocks of lowland Amazonian and montane habitats (Powell, 1985, Poulsen 1996) and these reported differences are worth special attention.

In this paper, we contribute data on mixed-species flock composition and foraging substrates in a northwestern cloud forest of Ecuador to the existing knowledge on mixed-species flocks in Neotropical montane habitats.

STUDY SITE AND METHODS

Study site. At least two persons conducted audiovisual field surveys in Pichincha Prov, northwestern Ecuador, at four sites: Cerro Guarumos (00°02'S, 78°38'W, 2700 m a.s.l.) Cerro El Campanario (00°03'S, 78°39'W, 2500 m a.s.l.), Sachatamia (00°01'S, 78°45'W, 1670 m a.s.l.) and San Luis (00°02'S, 78°40'W, 2200–2300 m a.s.l.). All sites are located in the vicinity of the Crude Oil Pipeline (OCP, Spanish acronym) route, which transports oil from eastern Ecuador to Esmeraldas city on the Pacific Coast.

The four localities are located within the natural formation montane cloud forest of the western Andes (Sierra *et al.* 1999), characterized by abundant epiphytes, especially orchids, ferns, and bromeliads. Forest canopy heights vary between 25–30 meters. Habitats covered by our study included primary forest, second growth forest, forest edge, and bamboo stands. At Guarumos, Campanario, and San Luis, surveys were carried out at ridge tops where the terrain was dominated by

steep slopes of more than 45 degrees. At Sachatamia, the observations were performed in flat terrain.

Field observations. We observed mixed-species flocks while walking along 2-km transects in each site, birds were counted within a lateral band of 0–35 m. Cerro Guarumos was visited in November and December 2006 and in February, March, May, June, and December 2007. Cerro El Campanario site was visited in November and December 2006 and in February, May, and June 2007. Sachatamia was surveyed in June and December 2007 and during March 2008. Finally, San Luis was visited during January and October 2008. Each monthly visit lasted from one to four days and observations were performed from 09:00 to 12:00 h each day. A rough total effort of 150 hours was invested in observations and an average of 1.34 hours was invested in describe each flock. In order to avoid recounting flocks along the same transect we settled a minimum distance of 500 m between each separate observation to consider it an independent flock. Upon encountering a flock we followed it and recorded species and quantified individuals, as well as foraging height, substrate (leaf, branch, moss, flower, bark) and sex of each individual participating (whenever possible). We considered a bird as a flock participant if it was observed foraging along with different species individuals at least within a c.10 m radius, and moved alongside other members of the flock for at least 15 m (Hutto 1994). For species taxonomy we followed Ridgely & Greenfield (2001).

Data analyses. We summarize our observations through descriptive statistics on species composition, flock size (mean number of birds/flock, \pm SD, minimum and maximum), as well as frequency of occurrence and abundance (mean number of individuals/flock, \pm SD, minimum and maximum) of species encoun-

tered more than 25% within flocks. We considered membership frequency as the number of times that a species or family was recorded in a mixed flock divided by the total number of observations, and we considered abundance as the total number of individuals of a given species recorded within mixed flock divided by the number of flocks in which that species was recorded.

We performed simple regression analyses between the number of species and the number of individuals per flock on square-root transformed data. Analyses were run in BioEstat 5.0 software.

RESULTS

During our surveys we recorded 878 individuals of 112 species participating in 53 mixed-species flocks, including three Neotropical migrants, sighted during the non-breeding season (October to April): Black-and-white Warbler (*Mniotilta varia*), Blackburnian Warbler (*Dendroica fusca*), and Swainson's Thrush (*Catharus ustulatus*). Mean numbers of individuals and species per flock were 16.6 ± 10.1 (range 3–55) and 10.3 ± 4.8 (range 3–28) respectively. Flock size in terms of number of individuals was positively correlated with the number of species present ($r^2 = 0.802$, $n = 53$, $P < 0.001$, Fig. 1). Flocks were composed mainly by Thraupidae which was the most abundant and frequent family in flocks (391 individuals 98.1%), followed by Parulidae (131 individuals 73.6%) and Tyrannidae (99 individuals 83.0%). Fourteen species were recorded as occurring regularly (present in = 25% of the flocks; Table 1) including the Blue-and-black Tanager (*Tangara vassorii*) which was the most abundant species recorded in flocks. Foraging heights of individuals participating in flocks ranged from 0.4 to 20 m (6.39 ± 4.061 , $n = 590$ observations). The preferred foraging substrate of the four most frequent and abundant species in flocks were branches

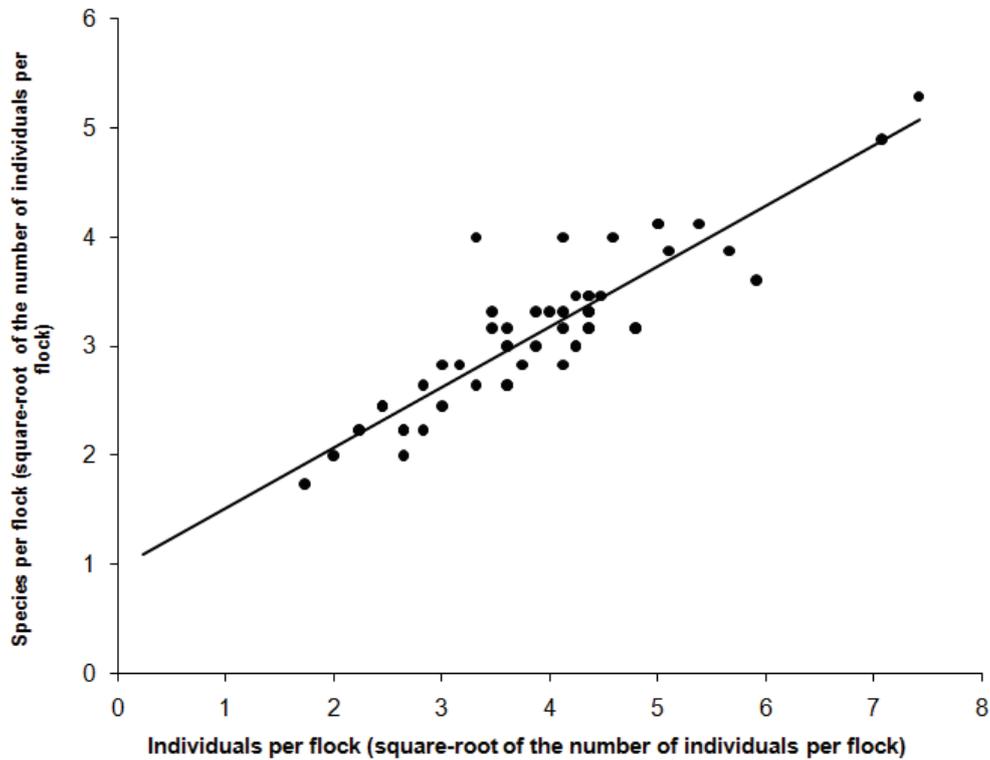


FIG. 1. Relationship between the number of species and number of individuals recorded in mixed-species flocks. The equation of the regression line is $y = 0.55x + 0.97$; $r^2 = 0.802$, $P < 0.001$, and $n = 53$.

(72.2 %, $n = 82$ out of 115 observations, Fig. 2).

We detected occasional participation in flocks of taxa that were regarded by Ridgely & Greenfield (2001) as solitary and non-flocking species, like Buff-tailed Coronet (*Boissonneana flavescens*), Club-winged Manakin (*Machaeropterus deliciosus*), and Golden-winged Manakin (*Masius chrysopterus*).

DISCUSSION

Flock size and species richness were positively related in our study, which is consistent with a previous research performed in Andean cloud forest (Bohórquez 2003). The plot of flock

size vs. species numbers (Fig. 1) shows that, on average, flocking species tended to occur singly or in pairs, although some tanager species like *Tangara vassorii* seemed to occur in small family groups of 2–5 individuals per flock (Table 1). In other words, the increase in flock size responded to the presence of additional species rather than individuals of the already participant species. As pointed out by Bohórquez (2003), this phenomenon could be related to species territoriality that produces high turnover of conspecific individuals every time a flock moved across the territories. On the other hand the addition of conspecific individuals to pairs participating in mixed flocks might be explained by the pres-

TABLE 1. Species recorded in mixed flocks in four sites at northwestern cloud forest of Ecuador. Summary of frequency, mean individuals per flock, standard deviation and minimum/maximum values of species recorded in more = 25 % of the mixed flocks recorded (n = 53).

Family/species	Frequency (%)	No. ind./flock	SD	Min/Max
Picidae				
<i>Campephilus pollens</i>	25	1.231	0.122	1–2
Furnariidae				
<i>Margarornis squamiger</i>	26	1.133	0.091	1–2
Tyrannidae				
<i>Mecocerculus poecilocercus</i>	34	1.222	0.129	1–3
Corvidae				
<i>Cyanolyca turcosa</i>	28	1.444	0.202	1–4
Parulidae				
<i>Myioborus melanocephalus</i>	40	1.233	0.114	1–4
<i>Basileuterus nigrocristatus</i>	34	1.261	0.094	1–2
<i>Basileuterus coronatus</i>	30	1.875	0.086	1–2
Thraupidae				
<i>Conirostrum albifrons</i>	34	1.750	0.260	1–6
<i>Diglossopsis cyanea</i>	28	1.267	0.118	1–2
<i>Tangara nigroviridis</i>	25	2.385	0.331	1–4
<i>Tangara vassorii</i>	32	2.762	0.275	1–5
<i>Anisognathus somptuosus</i>	53	2.180	0.179	1–4
<i>Butoraptes montana</i>	47	1.500	0.128	1–4
<i>Chlorospingus semifuscus</i>	32	1.647	0.284	1–5

ence of dependent juveniles during certain months of the year. However, the aforementioned results might not be completely conclusive, considering the extreme survey conditions in montane cloud forests, such as extreme topography, very dense undergrowth, and prevalence of foggy conditions, making it difficult to obtain complete counts of all flock members. Moreover previous research on montane pine-oak forest in Central America (King & Rappole 2000) demonstrated that an average time of 1.5 h is necessary to record all species in a mixed-species flock, therefore we feel that additional survey effort would be required to confirm our results.

Contrary to lowland Amazonian forest, where canopy and understory flocks were described as clearly separated (Munn 1985, Terborgh *et al.* 1990), our observations suggest that this was not the case in our study

area, especially in the Guarumos and Campanario sites. As previously reported for montane forest (Poulsen 1996) our observations show that canopy and understory birds tended to flock together, likely due to forest height and structure, and the steep sloping terrain that motivated some species to switch strata frequently.

Thraupidae were the dominant group in mixed flocks. The frequency and abundance of tanagers can be related to the fact that the Andes constitute a major center of radiation for this group (Isler & Isler 1999, Sedano & Burns 2010) and that syntopic tanager species tend to travel together in mixed-species flocks. The great diversity of Thraupidae species within the same mixed-species flocks may be explained by the fact that species within this group frequently differ in arthropod acquisition techniques, avoiding interspecific

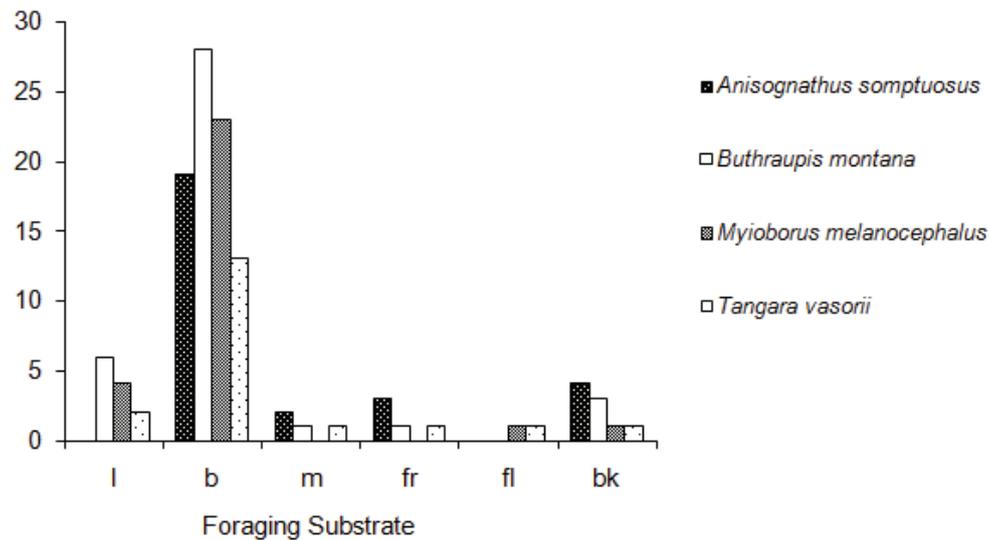


FIG. 2. Foraging substrate used by the most common species attending mixed species flocks in NW Ecuador. Substrates: l = leaf, b = branch, m = moss, fr = fruit, fl = flower, bk = bark.

competition (Naoki 2003). However, because tanager species also rely in fruit items, the partitioning on fruit resources in flocking tanager species might also be considered. Previous evidence suggest that tanager species that frequently join the same mixed-species flocks differed largely in arthropod foraging but overlapped greatly in fruit foraging (Naoki 2003).

Based on our results we determine that Blue-winged Mountain tanager (*Anisognathus somptuosus*), Hooded Mountain-Tanager (*Buthraupis montana*), and Spectacled Whitestart (*Myioborus melanocephalus*) are nuclear species in the flocks we studied, since they meet the aforementioned criteria regarding nuclear species, according to Moynihan's (1962) definition. Moreover, these species have been recorded as common elements in mixed flocks also further south on the eastern slope of the Ecuadorean Andes (A. Soria unpubl. data).

Optimizing the capture of spatially dispersed prey like insects is one of the benefits

regarded to flocking behavior (Powell 1985). Our observations on preferred foraging substrates of nuclear species seem to be typical for insectivorous species (branches, live and dead leaves), suggesting that there is a possible benefit in arthropod acquisition due to flocking behavior. Nuclear species rely mostly on branches as a substrate for food acquisition (Fig. 2), suggesting that ecological niche segregation comes from differences in food type or foraging techniques, as well as body size and bill shape. However, because our observations concentrated on flock participants but not on recording solitary individuals, our data could be useful to describe behavior of nuclear species within mixed flocks only, but not necessarily reflects these species propensity to join mixed flocks. Therefore, our assessment of foraging benefits of flocking behavior should be regarded as preliminary.

As mentioned earlier, the nuclear or attendant status of a species within flocks has been

defined by the frequency of their participation. In this sense, nuclear species that promote the cohesion and participate in flocks for large periods of time are clearly distinguishable from those that follow nuclear species for shorter periods, regarded as “attendants” (Powell 1985). Our results place *Machaeropterus deliciosus* and *Masius chrysopterus* as attendants, recorded occasionally within foraging groups. Recent research also report the occasional participation of two species of manakins in understory mixed flocks in Ecuadorian Amazonia (Buitron-Jurado 2008), supporting the idea that manakins may occasionally join mixed-species flocks. In order to properly assess the status of secretive species like green-plumaged manakins within mixed flocks, it is important to consider the potential bias caused by the uneven detectability between flock-joining taxa.

ACKNOWLEDGMENTS

We deeply thank Aves & Conservación staff for their kind support during the study, we are specially grateful with Adriana Lara, Sandra Loo-Vela, Irina Muñoz, Luis Muñoz, and Tatiana Santander. We are also grateful for funding provided by the Consorcio OCP to FC's and AO's fieldwork. Advice on initial stages of the data collection was provided by Tatiana Santander. We thank Adrian Soria for sharing comments on his own data. Earlier drafts of this manuscript benefited from comments of Juan F. Freile, Olaf Jahn, Paulo C. Pulgarín-R., and Ernesto Ruelas Inzunza. Finally, we would like to thank Sonia Onofa, Jorge Correa, and Gabriela Villares for field assistantship.

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