

Mixed-species bird flocks in primary and regenerating montane forests in Ecuador

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Examinamos la riqueza de especies, composición y tamaño de los bandos mixtos de aves en bosques de elevación (>3.000 m), primarios y en regeneración, en los Andes del norte de Ecuador. En diciembre de 1998 se muestreó a diario a lo largo de senderos en la Reserva Biológica Guandera (de 1.000 ha), provincia de Carchi. Se observaron 50 bandos mixtos con un promedio de 18,92 ($\pm 1,46$ DS) individuos y 8,44 ($\pm 0,58$ DS) especies por bando. No hubieron diferencias significativas ni en la riqueza de especies ni el tamaño del bando, entre el bosque primario y en regeneración. La semejanza en el uso del tipo de bosque por el bando puede ser explicada, en parte, por la presencia de árboles emergentes a lo largo de gran parte del área en regeneración. Dado que los bandos mixtos se alimentaron frecuentemente en bosques en regeneración, nuestros hallazgos sugieren que las reservas de bosques montanos existentes pueden incrementar el hábitat disponible para bandos mixtos de forrajeo, adquiriendo tierras adyacentes, modificadas o en regeneración.

Introduction

Historic and contemporary habitat destruction at high elevations in the northern Andes has dramatically reduced montane forests to a small number of scattered reserves^{14,16}. Deforestation for agricultural development is expected to continue, making high-Andean forests among the most threatened ecosystems in the world⁵. Habitat loss is especially significant because the avifauna of cloud forests on the eastern slope of the Ecuadorian Andes is among the most diverse in the world at altitudes of 3,000–3,500 m¹¹. In addition, the north-central Andes of Colombia and Ecuador (>1,500 m) contain two Endemic Bird Areas holding 20 restricted-range bird species that require several key montane forest and páramo habitats¹⁶. However, the scarcity of undisturbed forests constrains efforts to establish additional reserves, and biologists should examine the degree to which disturbed or regenerating forests can contribute to bird conservation.

A relatively high proportion of birds in high-elevation forests join mixed-species foraging flocks. Although mixed-species bird flocks of Neotropical lowland^{4,7,8,17,18} and mid-elevation^{1,4,12} forests have been relatively well described, fewer studies have focused on mixed-species bird flocks in high-elevation (>2,500 m) Neotropical forests^{4,6,9,10,13}. In the high Andes of Ecuador, the behaviour and ecology of mixed-species flocks have been described in montane forest and scrub near Quito⁶, in southern forest fragments⁹, and in alder-dominated *Alnus acuminata* second-growth forest on the eastern slope¹⁰. The relative use of regenerating and primary forests by flocks has not been examined. To evaluate the potential that disturbed forest holds for the conservation of montane forest birds, we compared flock use of regenerating and primary forests in the Andes of northern Ecuador. Specifically, we

examined variation in flock species richness, composition and flock size between regenerating and primary high-elevation forests, and described use of forest strata by common species.

Study site and methods

We sampled mixed-species bird flocks in the 1,000-ha Guandera Biological Reserve (00°36'N 77°41'W), Carchi province, northern Ecuador, some of the last inter-Andean valley cloud forest extant in Ecuador. Recent avifaunal surveys recorded 140 bird species within the reserve, including Carunculated Caracara *Phalacrocorax carunculatus*, Black-thighed Puffleg *Eriocnemis derbyi*, Chestnut-bellied Cotinga *Doliornis remseni*, Crescent-faced Antpitta *Grallaricula lineifrons*, Masked Mountain-tanager *Buthraupis wetmorei* and Black-backed Bush-tanager *Urothraupis stolzmanni*³; these are restricted-range/endemic species classified as threatened or near threatened². Forest habitat (c.400 ha) in the reserve occurs at c.3,100–3,600 m elevation, and at higher elevations the forest grades into *Espeletia* páramo. We focused on two forest habitats within the reserve³: primary forest and regenerating forest. Primary forest (canopy height c.15–20 m) is dominated by *Weinmannia*, *Ocotea* and *Miconia* trees in the overstorey and has a dense understorey of shrubs and saplings. Epiphytes cover limbs of canopy trees, but are less dominant on understorey shrubs and saplings. Tree-fall gaps are common, and the forest structure is heterogeneous. Ridges are dominated by *Clusia flaviflora* and have ground cover primarily composed of bromeliads. Regenerating forests consist of abandoned agricultural clearings dominated by dense, tall (2–5 m) saplings and shrubs (e.g. *Weinmannia*, *Blechnum* tree ferns, Ericaceae, and Asteraceae) with scattered emergents or groups of trees. Mean canopy cover (>5 m tall) is approximately 10%, and

emergent trees are 10–20 m tall. Although some epiphytes persist on emergent trees within the regenerating forest, epiphytic vegetation is less abundant than within primary forest. Of approximately 400 ha searched for mixed-species flocks, we estimate that 60% was primary forest, 30% regenerating forest, and 10% forest–páramo transition (not included in our sampling). Both primary and regenerating forest habitat occurred at comparable elevations, slopes and aspects.

In December 1998, flocks were sampled daily along established trails between 06h00 and 18h00, but 77% of observations occurred at 06h00–12h00. These trails covered c.8–10 km within the reserve and ranged from c.3,100 to 3,600 m elevation. Most days were overcast to partially cloudy, with daytime temperatures ranging from c.3°C to 20°C. Flocks were not sampled during periods of rain or strong wind. To reduce the possibility of sampling the same flock more than once per day, observations were separated by 250 m distance or five hours in time. Because we did not band (ring) birds, we cannot be certain that different individuals were sampled within flocks. Indeed, some individuals were probably sampled more than once. However, Andean mixed-species flocks exhibit frequent turnover in species composition and individuals¹⁰, reducing the

likelihood that we repeatedly sampled the same individuals within flocks.

A mixed-species flock was defined as a group of individuals of at least two species moving together and within 25 m of each other⁴. Flocks were located either vocally or visually. To minimise bias towards detecting larger flocks or flocks in more open habitats, we attempted to locate each bird seen or heard to determine whether or not a flock was present. Two experienced observers simultaneously collected data on each flock for a mean of 20 minutes. Based on visual estimation, we categorised each species' vertical position in the vegetation as: understory (lower third of strata), midstorey (middle third), canopy (upper third), or as a combination of adjacent strata (e.g., midstorey and canopy). Differences in flock size (number of individuals per flock) and species richness (number of species within a flock) between the forest types were analysed separately using an analysis of covariance with time of day as a covariate¹⁵. The relationship between flock size and species richness was examined using a correlation analysis¹⁵.

Results

Fifty mixed-species flocks were observed during the period with a mean of 18.92 (± 1.46 SE) individuals

Table 1. Mean (\pm SE) abundance per flock and frequency (%) of occurrence within flocks for 22 species recorded in primary and regenerating forests in Guandera Reserve, northern Ecuador, December 1998. Species encountered in fewer than five flocks are listed below.

Species		Mean (\pm SE) abundance per flock	Primary forest	Regenerating forest
Pearled Treerunner	<i>Margarornis squamiger</i>	2.7 (0.21)	46	69
Streaked Tuftedcheek	<i>Pseudocolaptes boissonneautii</i>	1.2 (0.20)	8	12
Cinnamon Flycatcher	<i>Pyrrhomyias cinnamomea</i>	1.7 (0.14)	13	31
White-throated Tyrannulet	<i>Mecocerculus leucophrys</i>	2.1 (0.17)	63	73
White-banded Tyrannulet	<i>M. stictopterus</i>	2.2 (0.16)	71	58
Agile Tit-tyrant	<i>Anairetes agilis</i>	1.8 (0.20)	4	15
Rufous-breasted Chat-tyrant	<i>Ochthoeca rufipectoralis</i>	1.2 (0.17)	13	12
Blackburnian Warbler	<i>Dendroica fusca</i>	1.4 (0.12)	42	46
Spectacled Redstart	<i>Myioborus melanocephalus</i>	2.8 (0.26)	71	85
Black-crested Warbler	<i>Basileuterus nigrocristatus</i>	1.2 (0.12)	4	46
Citrine Warbler	<i>B. luteoviridis</i>	1.1 (0.14)	17	12
Slaty Brush-finch	<i>Atlapetes schistaceus</i>	1.6 (0.15)	46	35
Blue-backed Conebill	<i>Conirostrum sitticolor</i>	2.0 (0.16)	50	65
Black-capped Hemispingus	<i>Hemispingus atopileus</i>	1.6 (0.24)	13	8
Superciliaried Hemispingus	<i>H. superciliaris</i>	2.4 (0.29)	21	31
Black-headed Hemispingus	<i>H. verticalis</i>	2.2 (0.23)	13	46
Hooded Mountain-tanager	<i>Buthraupis montana</i>	2.0 (0.58)	4	8
Lacrimose Mountain-tanager	<i>Anisognathus lacrymosus</i>	1.8 (0.14)	63	62
Scarlet-bellied Mountain-tanager	<i>A. igniventris</i>	1.6 (0.12)	63	62
Buff-breasted Mountain-tanager	<i>Dubusia taeniata</i>	1.9 (0.31)	21	19
Glossy/Black Flowerpiercer	<i>Diglossa</i> spp.	1.3 (0.24)	21	35
Masked Flowerpiercer	<i>Diglossa cyanea</i>	1.7 (0.19)	46	23

Species recorded in fewer than five mixed-species flocks were: Flavescent Flycatcher *Myiophobus flavicans*, Barred Becard *Pachyrhamphus versicolor*, Black-capped Tyrannulet *Phyllomyias nigrocapillus*, Red-eyed Vireo *Vireo olivaceus*, Pale-naped Brush-finch *Atlapetes pallidinucha*, Black-chested Mountain-tanager *Buthraupis eximia*, Blue-and-black Tanager *Tangara vassorii*, Golden-crowned Tanager *Iridosornis rufivertex*, and White-sided Flowerpiercer *Diglossa albilatera*.

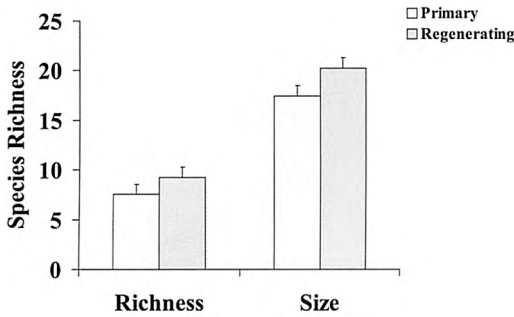


Figure 1. Mean species richness and size of flocks within primary and regenerating forest for 50 mixed-species bird flocks in Guandera Reserve, northern Ecuador, December 1998.

and $8.44 (\pm 0.58 \text{ SE})$ species per flock. Neither flock species richness ($F_{1,47} = 1.90, P = 0.175$) nor flock size ($F_{1,47} = 0.64, P = 0.429$) significantly differed between primary and regenerating forests (Fig. 1). However, both species richness ($F_{1,47} = 5.52, P = 0.023$) and flock size ($F_{1,47} = 5.99, P = 0.018$) were negatively related to time of day, such that flocks were larger and more diverse earlier than later in the day. As expected, flock size and species richness were positively correlated ($r = 0.924, P < 0.001$).

Mean intraspecific group size within flocks was greatest (in decreasing order) for Spectacled Redstart *Myioborus melanocephalus*, Pearled Treerunner *Margarornis squamiger*, Superciliaried Hemispingus *Hemispingus superciliaris*, Black-headed Hemispingus *H. verticalis* and White-banded Tyrannulet *Mecocerculus stictopterus* (Table 1). Feeding of dependent young within flocks was recorded for Spectacled Redstart, Superciliaried Hemispingus, Blue-backed Conebill *Conirostrum sitticolor*, Pearled Treerunner and Slaty Brush-finch *Atlapetes schistaceus*.

In both primary and regenerating forest, common species that primarily used the canopy while in flocks included Blackburnian Warbler *Dendroica fusca* (96% of observations), Masked Flowerpiercer *Diglossa cyanea* (88%), Black-headed Hemispingus (71%), Pearled Treerunner (70%), Blue-backed Conebill (68%) and Black/Glossy Flowerpiercer *Diglossa* spp. (50%). Species that primarily occurred in the midstorey within flocks were White-banded Tyrannulet (72%) and White-throated Tyrannulet *Mecocerculus leucophrys* (68%), whereas Black-crested Warbler *Basileuterus nigrocristatus* (83%) and Slaty Brush-finch (65%) used understorey habitat most frequently. Spectacled Redstart, Superciliaried Hemispingus, Lacrimose Mountain-tanager *Anisognathus lacrimosus* and Scarlet-bellied Mountain-tanager *A. igniventris* were regularly seen in all vertical strata.

Discussion

We recorded larger and more diverse flocks than reported at other high-elevation Andean sites from Venezuela to Bolivia^{6,10,13}. Even so, flocks at Guandera Reserve still shared 9–23 species with flocks reported in other studies. Thus, our findings may provide insight into habitat use patterns of montane flocks in other regions. Size and species richness of flocks were similar between primary and regenerating forests within Guandera Reserve. The similarity in use of the forest types by flocks may be explained, in part, by the presence of emergent trees throughout most of the regenerating forest area. For example, many common flock participants that primarily used canopy trees in primary forests (e.g. Pearled Treerunner, Masked Flowerpiercer, Blue-backed Conebill, Black-headed Hemispingus and Blackburnian Warbler) typically foraged in large emergents in regenerating forest. Species that regularly occurred in other vertical strata within primary forest (e.g. White-banded and White-throated Tyrannulets, Spectacled Redstart and Scarlet-bellied Mountain-tanager) are probably less dependent on emergents in regenerating forests, although we have no data to support, nor refute this possibility. An important limitation of our data is that no birds were banded and, therefore, we cannot exclude the possibility that the same individuals were not repeatedly encountered, and which may not be representative of the breadth of habitat use typical for the species as a whole.

Our results suggest that regenerating forest can provide important foraging habitat to mixed-species bird flocks in the montane forests of northern Ecuador. As a result, existing montane forest reserves may be able to increase available habitat for mixed-species foraging flocks in the short term by acquiring adjacent farmland and promoting forest regeneration, especially if emergent native trees are present. This is a particularly important management option given that the availability of primary montane forest is extremely limited and only small remnants remain. One caveat is that, although the detection of large and diverse flocks in regenerating forests is encouraging for conservation, the presence of such flocks does not necessarily indicate quality habitat. For example, birds using regenerating forest may encounter less-suitable food resources or may be unable to breed successfully in those areas. In addition, retention of a mature forest matrix adjacent to regenerating forest at Guandera Reserve was likely an important factor that promoted use by flocks. Loss or degradation of mature forest surrounding the regenerating forest patch could render it unsuitable for many of the birds we detected. Likewise, forest birds may avoid regenerating forest within extensively fragmented landscapes. Without information on food availability and breeding

productivity, the suitability of these forest types cannot be fully assessed. Although our study was brief, these results represent some of the only empirical data comparing flock use of primary and regenerating high-elevation montane forests. Given that many montane forest bird species at Guandera Reserve and other high-elevation Andean forests regularly occur within mixed-species flocks, a better understanding of habitat use and ecology of flocks is required for the development of robust conservation plans for the region.

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