# COMMUNITY ORGANIZATION AND ECOLOGY OF BIRDS OF HIGH ELEVATION HUMID FOREST OF THE BOLIVIAN ANDES

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ABSTRACT. The avian community composition, and foraging behavior and social organization of birds of two humid forest sites near timberline in the Bolivian Andes were studied and compared to the same features of montane communities in other regions, particularly New Hampshire. Most of the difference in species richness between the tropical and temperate latitude sites can be explained by the addition of "tropical" resources not specially used by, or unavailable to, temperate birds, i.e., fruit, nectar, epiphytic vegetation, and bamboo thickets. When Andean species using these resources are eliminated, the overall species richness between the two regions is very similar, as are other community characteristics, such as use of foraging strata of different heights. The foraging maneuvers used by Andean birds are also discussed in detail. Almost 50 percent of the Andean species are regular participants in mixed-species flocks. In this respect, as well as with regard to the finer categories of social organization, the Andean community is very similar to one in montane Costa Rica but differs in important ways from others in Venezuela and New Hampshire.

RESUMEN. Se estudió la composición de la comunidad avícola y los comportamientos de forraje y organización social de aves en dos sitios de bósques húmedos cercanos al límite superior boscoso ("timberline") en los Andes bolivianos y se los comparó con los de otras comunidades montañosas similares en otras regiones, particularmente en Nueva Hampshire, E.E.U.U. La mayoría de las diferencias en la riqueza de especies entre las áreas de latitudes templadas y tropicales se pueden explicar por la presencia de recursos "tropicales" adicionales no especialmente usados o fuera del alcance de las aves de regiones templadas (por ej. frutas, néctar, vegetación epífita y cañaverales). Cuando se eliminan las especies andinas que usan esos recursos ls riqueza total de especies entre las dos regiones es muy similar, así como lo son otras características de la comunidad tales como el uso de estratos de forraje de deferentes alturas. También se discuten en detalle las maniobras de forraje usadas por las especies andinas. Casi el 50% de las especies andinas participan de las bandadas de varias especies de manera regular. En este aspecto, así como con respecto a las categorías más detalladas de organización social, la comunidad andina es muy similar a una en montañas costarricences, pero diferente en aspectos importantes de otras en Venezuela y Nueva Hampshire, en el noreste de E.E.U.U.

The problem of latitudinal differences in bird species diversity has often been investigated by comparing properties of land bird communities of tropical lowland regions to those of communities at temperate latitudes (Ricklefs 1966; Orians 1969; Howell 1971; Karr 1971; Faaborg 1980; Terborgh 1980; Greenberg 1981). Only comparisons by Stiles (1978) for alder habitats and by Fjeldså (1981) for wetlands have focused on communities in the Neotropics other than those of lowland areas. My purpose in this paper is to provide insight into latitudinal diversity gradients by comparing relatively low diversity bird communities in montane forests of tropical and temperate regions, using methods similar to those of Karr (1975) and Terborgh (1980). I also present information on the foraging ecology of birds of high elevation forest of the humid Andes and compare it with that available from similar habitats elsewhere.

## STUDY SITES AND METHODS

Two localities in the upper "Temperate Zone" of the humid Andes of Dpto. La Paz, Bolivia were studied, 1 km south of Chuspipata, 3050 m (hereafter referred to as Chuspipata), and Cotapata, 4.5 km WNW Chuspipata, 3300 m (hereafter, Cotapata). Although these sites are within 5 km of one another, they differ in the following important ways, (1) air temperatures are substantially lower at the upper site (mean daily lows 2°C versus 8°C, mean daily highs 10°C versus 14°C); (2) average canopy height is lower at the upper site (5–12 m vs 14–17 m);

(3) tree species richness is much lower at the upper site, where only four species make up an estimated 90 percent of the trees more than 5 m tall.

Both sites are dominated by humid forest in which trees are heavily laden with moss and other epiphytes. The four common tree species at Cotapata are *Myrica pubescens* (Myricaceae), *Brunellia* sp. (Brunelliaceae), and two species of *Clusia* (Clusiaceae). Also present are two species of *Weinmannia* (Cunnoniaceae), *Freziera* sp. (Theaceae), several species of *Solanum* (Solanaceae), *Schefflera* sp. (Araliaceae), and *Gaiodendron* sp. (Loranthaceae). At Chuspipata, these latter species all become more common as *Myrica, Brunellia,* and *Clusia* become less dominant; *Tibouchina* and other Melastomaceae also become common. The dense undergrowth at both sites is dominated by bamboo (*Chusquea*), but the following shrubs and vines are also common, especially in edge situations: *Cavendishia* sp. (and many other Ericaceae), *Baccharis* sp. (Compositae), *Monnina* sp. (Polygalaceae), *Syphocampylus* sp. (Campanulaceae), *Gunnera* sp. (Haloragidaceae), and *Bomarea* sp. (Amaryllidaceae). At Chuspipata, *Munnozia* sp. and *Barnadesia* sp. (Compositae) are also common. The terrain at both sites was extremely steep. A dirt road bisected each site, creating a substantial edge effect. Between 1979 and 1982, both sites were altered considerably by human disturbance and deteriorated markedly in their suitability as study areas. Cotapata is no longer a tenable site, and Chuspipata will not last much longer.

In spite of the disturbance, the avifaunas at both sites seemed to be intact in 1980 and 1981. Birds sensitive to human disturbance, such as guans, raptors, and parrots, were present, and to our knowledge, no species that should have been absent if the area were disturbed, was missing. High elevation forest in the Andes is naturally disturbed by frequent landslides, and so even in its pristine state, the canopy is seldom continuous and the forest often patchy.

Typically, skies at Cotapata remained clear until 10:00 to 12:00 hours, after which clouds poured over the ridge from the east; low overcast or dense fog persisted the rest of the afternoon and into the evening. My visit, from 27 May to 25 June 1981, apparently coincided with the early part of the dry season; rain was recorded on only nine of 28 days, and on only one day did it rain hard. Nevertheless, dew soaked the vegetation each morning, and dense fog kept vegetation damp or wet during the afternoon. Skies were clear on only five days. Frost and ice covered the vegetation on many mornings.

My visit to Chuspipata, 22 July to 10 August 1982, coincided with the height of the dry season. Except for afternoon fog on the ridges several hundred meters above camp, skies were generally clear, although during the last six days a major southern storm brought light to moderate rain that lasted through most daylight hours.

During the months of my visits, most insectivorous and nectarivorous bird species were not breeding, but at least some fraction of the population of many frugivorous species were breeding (as indicated by gonad size data: Appendix I). Each site was sampled intensively by mist-netting; as many as 44 nets were operated simultaneously at each site, for a total of 11,221 daylight net hours at the upper site and 6366 at the lower site. Nets were not closed at night, and so an equivalent number of nighttime hours were accumulated. Species not prone to mist net capture were hunted selectively. Complete species lists for both localities are given in Appendix I; these are the first inventories available for high elevation Andean forests. Details on new distributional records for Bolivia and natural history observations on some poorly known species have been published elsewhere (Parker et al. 1980; Cardiff and Remsen 1981; Remsen 1981; Remsen et al. 1982; Schulenberg and Remsen 1982).

Foraging data and other natural history information were accumulated on a daily basis from dawn to dusk, giving approximately 450 man-hours observation time at the upper site and 625 at the lower site. Visual observations and mist net lanes encompassed elevations that extended approximately 50 m above and below the upper site and 100 m above and below the lower site. All data were gathered within a 0.5 km radius of the campsite. Each prey capture attempt by a bird was considered as a separate foraging observation. No more than three consecutive foraging observations for a given bird were analyzed. Sample sizes for foraging observations were low relative to most studies from temperate latitudes, partly because the precipitous terrain and impenetrable undergrowth precluded following birds away from trails and roadsides. Furthermore, the highly clumped spatial distribution (in flocks) of nearly half of the species resulted in "feast or famine" data collection; during the few minutes when a flock was visible, it was impossible to get data on all species or individuals, and intervening periods of an hour or more could be spent in search of another flock. Most species not in flocks were secretive or difficult to observe (e.g., antpittas, tapaculos, spinetails, cotingas,

TABLE 1

DIET CATEGORY MEMBERSHIP FOR BIRDS FROM STUDY SITES IN THE ANDES AND WHITE MOUNTAINS

| Diet | Number of species (% locality total) | | |
|---|---|---|---|
| | Chuspipata | Cotapata | Mt. Moosilauke |
| Fruit | 10 (13.5) | 8 (16.7) | 0 |
| Fruit + insects | 10 (13.5) | 6 (12.5) | 0 |
| Fruit + insects + nectar | 1 (1.4) | 1 (2.1) | 0 |
| Nectar + insects | 11 (14.9) | 8 (14.6) | 0 |
| Insects | 38 (51.4) | 22 (16.7) | 14 (82.3) |
| Insects + seeds | 3 (4.1) | 2 (4.2) | 3 (17.7) |
| Seeds | 1 (1.4) | 1 (2.1) | 0 |
| Total species | 74 | 48 | 17 |

and undergrowth tyrannids). Researchers accustomed to following passerines for extended periods in habitats at temperate latitudes will be discouraged by the low yield of data per hour in the Andes.

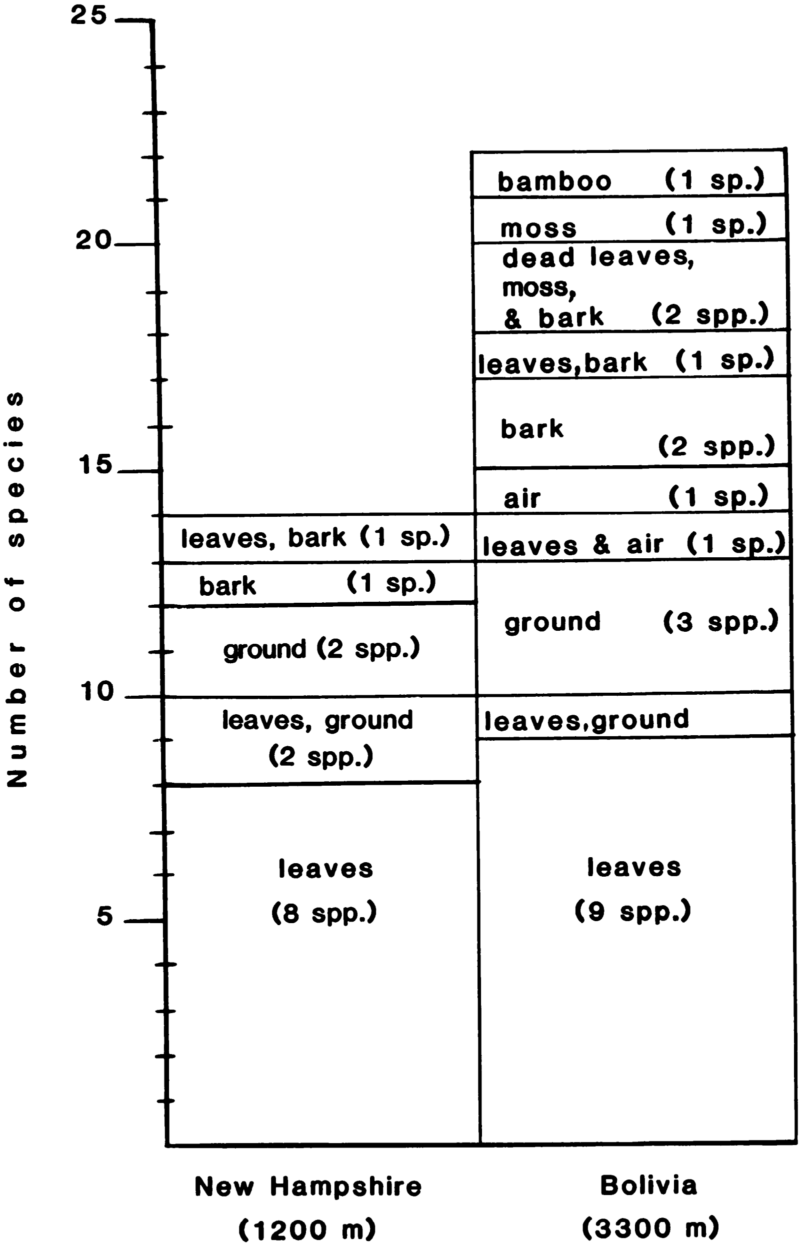
For general comparisons with a high elevation temperate community, I chose Sabo's (1980) data from the White Mountains of New Hampshire, primarily because of the volume of foraging information available for the insectivorous species. For specific comparisons, I used a hypothetical community constructed by S. R. Sabo (in litt.) for a similar census effort in an area of similar size at 1200 m (approximately the same number of meters below timberline as Cotapata in Bolivia). The 18 species at 1200 m were: Sharp-shinned Hawk (*Accipiter striatus*), Spruce Grouse (*Dendragapus canadensis*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Common Raven (*Corvus corax*), Boreal Chickadee (*Parus hudsonicus*), Red-breasted Nuthatch (*Sitta canadensis*), Winter Wren (*Troglodytes troglodytes*), Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*C. minimus*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Nashville Warbler (*Vermivora ruficapilla*), Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler (*D. coronata*), Blackpoll Warbler (*D. striata*), White-throated Sparrow (*Zonotrichia albicollis*), Dark-eyed Junco (*Junco hyemalis*), and Purple Finch (*Carpodacus purpureus*). The forest at 1200 m is dominated by two conifers (*Abies balsamea, Picea rubens*) and two broadleaf trees (*Betula papyrifera, Sorbus americana*); the canopy height is similar to that at the Bolivian sites (Sabo 1980).

## COMMUNITY COMPOSITION, SPECIES DIVERSITY, AND FORAGING SITE SELECTION

Excluding raptors and nocturnal species, resident bird species at the Bolivian and New Hampshire localities were assigned to one of seven diet categories (Table 1; Appendices I and II for details). Four diet categories that involve heavy use of fruit and nectar are strongly represented in the tropical latitude communities but are absent from the temperate latitude community. These four categories encompass 43 percent (at 3050 m) and 48 percent (at 3300 m) of all resident species at the tropical latitude localities. Thus, nearly half of the species in the Andean communities are dependent on resources not used in and virtually unavailable to the White Mountains community (S. R. Sabo, pers. comm.). When species in these four diet categories are eliminated, the species richness of the temperate and tropical latitude communities is much more similar, although the temperate community is still less speciose.

A further breakdown of the insectivorous species into foraging substrate categories (Fig. 1) shows that the five substrate categories in New Hampshire either have the identical number of species in Bolivia or differ by only one species. The eight "extra" insectivores at Cotapata all use one of five substrate categories not used by or unavailable to birds at the Mt. Moosilauke (White Mountains) site. Two of these substrates ("air" and "leaves and air") are obviously available at the New Hampshire site but are not used. Aerial foraging swifts and swallows are only rare visitors at such elevations, and the Olive-sided Flycatcher (*Contopus borealis*) is a scarce and local resident.

The other three substrate categories ("bamboo," "moss," and "dead leaves, moss, and bark") are more "tropical" in character in being largely unavailable for specialized use by



**Substrate Use by Insectivores**

FIG. 1. Number of insectivorous species in various substrate use categories at near-timberline sites in the White Mountains and the Andes. Foraging substrates for each Andean species are those from Appendix II necessary to include at least 60% of a species' foraging observations; assignment to substrate category for White Mountains species was based on data from Sabo (1980). The "moss" category includes all epiphytic vegetation, but only one species, *Pseudocolaptes boissonneautii,* was recorded feeding in epiphytes other than mosses.

temperate latitude birds. Bamboo thickets throughout the Neotropics support a unique avifauna (Parker 1982; Parker and Remsen, unpubl. data), only one species of which, *Catamblyrhynchus diadema* (Hilty et al. 1979), occurs as high as 3300 m. *Hemispingus calophrys* also forages primarily in bamboo, as does *Cranioleuca albiceps* when gleaning foliage. The Andean subspecies of *Cacicus holosericeus* may also be a bamboo thicket specialist, but our observations are too few to make this certain. Although mosses and other epiphytes occur at most latitudes (lichen growth is heavy at Mt. Moosilauke; S. R. Sabo, pers. comm.), apparently only in the tropics do some birds specialize upon this substrate (Remsen and Parker, unpubl. data). At Cotapata, only one species, *Margarornis squamiger,* is a specialized moss-searcher, although *Delothraupis castaneoventris* forages almost exclusively on moss-covered branches when not feeding on fruit. At Chuspipata, three additional epiphyte-searching specialists are *Lepidocolaptes affinis, Pseudocolaptes boissonneautii,* and *Troglodytes solstitialis* (the latter two are rare visitors to Cotapata). *Chlorornis riefferii, Buthraupis montana, Tangara vassorii,* and *Cacicus chrysonotus* also search moss frequently at the two Bolivian sites, but none is exclusively insectivorous. Finally, two species, *Cranioleuca albiceps* and *Atlapetes rufinucha,* use a combination of substrates (dead leaves, moss, bark, and green leaves). The "tropical" nature of dead leaves suspended above ground is discussed elsewhere (Remsen and Parker 1984).

Once those species dependent on resources not available (at least on a year-round basis or to a degree that would allow specialization) at temperate latitudes are excluded, the timberline sites in Bolivia and New Hampshire are very similar in species richness. The New Hampshire site, however, contains both coniferous and broadleaf vegetation. These two types of vegetation are structurally very different, each with characteristic bird species, and so species richness would almost certainly be somewhat reduced at a site at 1200 m with only coniferous or only broadleaf vegetation. No such heterogeneity exists at the Bolivian sites, although, as S. R. Sabo (pers. comm.) has pointed out, frugivore diversity must be at least partly dependent on floristic diversity. Also, the analysis of the insectivorous species ignores those frugivorous and nectarivorous species that include insects in their diet. It it fair to exclude these species? For all but four of the 23 species involved at Cotapata, the answer is "probably." Except for *Cacicus chrysonotus,* the nectarivores are either hummingbirds or flowerpiercers, most of which take insects mainly from or near the flowers upon which they feed, or in the case of sallying and gleaning hummingbirds, capture insects that are presumably smaller than those used by other species at either the Andes or White Mountains sites. Among the six frugivores that also feed on insects, two species (*Buthraupis montanus* and *Delothraupis castaneoventris*) search for insects primarily in moss on tree branches, a substrate not used at the White Mountains site. This leaves only four frugivorous/insectivorous species (three flycatchers and a thrush) that search for insects in substrates (foliage, ground) used by White Mountains birds.

Why the pronounced difference in species richness between the 3300 and 3050 m sites in Bolivia (48 vs 74 resident species)? The species at the higher elevation site are mainly a subset of the species from the lower elevation site (with 16 of the residents at 3050 m also occurring as visitors to the 3300 site). Only six species (*Metallura aeneocauda, Myiophobus ochraceiventris, Turdus serranus, Hemispingus trifasciatus, Iridosornis jelskii,* and *Diglossa lafresnayii*) are residents at the 3300 m site but absent from or only visitors at 3050 m. *Turdus serranus* is common at elevations below 3050 m (LSUMZ specimens at 2575 m at Sacramento Alto, only a few km away), and so its rarity at 3050 m is puzzling. Of the five species truly restricted to the upper site, direct competition can possibly be invoked for restriction to upper elevations for only one, *Hemispingus trifasciatus.* At about 3100 m, this species is replaced by *H. superciliaris,* which is extremely similar in morphology and almost all aspects of foraging behavior, e.g., substrate selection (Appendix I), foraging maneuvers, and foraging position (see below). The only substantial difference between the two is in foraging height, and this is merely a consequence of differing canopy heights at the two elevations. Both species are seen in the same flocks at about 3100 m. For the remaining four species restricted to upper elevations, no congeneric ecological counterpart replaces them at the 3050 m site.

The proportional decrease in species in each of the major diet categories from 3050 to 3300 m is very similar to the overall proportional decrease, 34 percent, in species richness (Table 1). The decreases within diet categories range from 30 percent for "nectar and insects" to 42 percent for "insects." Thus, the depauperization of the avifauna is spread rather evenly among the diet categories, in contrast to the findings of Terborgh (1977) over a broader elevational gradient in the Peruvian Andes. A similar analysis for foraging substrate categories is made difficult by the fewer species per category. The decreases, however, in species in two categories,

TABLE 2

DEGREE OF SPECIALIZATION OF SOME COMMON INSECTIVORES ON UPPER OR LOWER LEAF SURFACES AT ANDEAN STUDY SITES

| | Percent of foraging on upper surface[1] |
|---|---|
| Undergrowth species | |
| *Hemispingus calophrys* | 50 N.S. |
| *Thlypopsis ruficeps* | 23*** |
| *Basileuterus luteoviridis* | 20*** |
| *Basileuterus signatus* | 26* |
| Canopy species | |
| Gleaners | |
| *Hemispingus superciliaris* | 46 N.S. |
| *Hemispingus trifasciatus* | 54 N.S. |
| *Conirostrum sitticolor*[2] | 44 N.S. |
| Sallyers | |
| *Mecocerculus leucophrys* | 24** |
| *Mecocerculus stictopterus* | 21** |
| *Myiophobus ochracieventris* | 47 N.S. |
| *Myioborus melanocephalus* | 31** |
| Edge species | |
| *Ochthoeca rufipectoralis* | 82** |

[1] The percent of all foraging bouts observed directed at upper surface is followed by significance levels for a two-tailed Binomial Test: N.S. = $P > 0.05$; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

[2] Moynihan (1963) considered this species to be an undergrowth species that frequently fed at flowers (in Ecuador).

"moss" and "air," do seem disproportionately high (75%). Not much significance can be attached to the difference in aerial foragers, because one is a nocturnal caprimulgid that could have been missed at the upper site, and two other species at the lower site were rare. The difference in moss-searchers, however, is more noteworthy, especially because as a substrate, moss is at least as extensive at the upper site as at the lower. Perhaps insects within moss become disproportionately depleted at the upper site.

Thus, except for moss-searchers, the decrease in species richness within various diet and foraging categories is more or less proportional to the overall decrease in species richness. This implies that the overall decline reflects general resource depletion (as a result of colder temperatures?) at upper elevations.

Greenberg and Gradwohl (1980) pointed out that many lowland tropical bird species distribute their search efforts unequally with respect to upper and lower surfaces of leaves, with a majority of species, particularly those of the undergrowth, specializing on lower surfaces. Their preliminary data from higher elevations showed a shift in insect abundance from lower to upper leaf surfaces, and their model consequently predicts a shift in searching effort by birds toward the upper surface as one moves up in elevation.

Comparison of upper surface versus lower surface searching by birds at the Bolivian sites (Appendix II, Table 2) with similar data for lowland species from Panama (Greenberg and Gradwohl 1980) shows that (1) undergrowth species at both sites have similar (low) percent upper surface values; the exception among the Andean species is *Hemispingus calophrys,* which forages primarily in bamboo, the leaves of which are very differently shaped and arranged from those of woody undergrowth plants; (2) sallying species at the Andean sites have higher percent upper surface values than Panamanian sallying species (= "hoverers" in terminology of Greenberg and Gradwohl 1980); (3) canopy foliage-gleaners at the Andean sites show no demonstrable upper or lower surface preference. Trends 2 and 3 are consistent with the hypothesis that insects themselves show less preference for the lower surface at high than at low elevations. Unfortunately, too few bird species are involved for statistical analysis.

## FORAGING MANEUVERS

The maneuvers used by the birds in gathering food and the frequency with which they were used were recorded for each species (Table 3). Most of the discussion below pertains only to those 33 species for which more than 10 observations were obtained. Data from other species about which nothing has been published are also included in Table 3.

Six species (19%) used only one type of maneuver. Sixteen species (49%) used four or more maneuver types. Using Levins (1968) niche breadth formula (NB = $1/\Sigma\,[p_{ij}]^2$), the three most generalized species in terms of foraging maneuvers were the flycatchers *Myiophobus ochraceiventris* (NB = 2.5), *Mecocerculus leucophrys* (2.6), and *M. stictopterus* (3.0). The latter was the only species to use more than 50 percent (6 of 10) of the maneuver types (but it also had one of the largest sample sizes of observations). That three flycatchers should rank the highest in foraging maneuver "niche breadth" will surprise many investigators accustomed to the stereotyped foraging behavior exhibited by most temperate latitude tyrannids. Unfortunately, the small sample sizes for observations make interpretations of the NB values tenuous.

The maneuvers were ranked on a subjective scale of increasing acrobatic complexity and accompanying requisite morphological specialization (Table 3, from left to right). At one end of the scale is "pick," the maneuver in which the bird picks its food from a substrate without extending its legs or wings. Seventeen species (51%) used this maneuver for 50 percent or more of the observations. Thus, most species use most frequently the maneuver that requires the lowest degree of agility and energy expenditure. Although 50 percent of the species used the "reach out/up" maneuver (fully extending body by extending legs and neck to reach prey), only one species, *Basileuterus signatus,* used this more than any other maneuver. Two other species of the dense undergrowth, *Basileuterus luteoviridis* and the warbler-like tanager *Thlypopsis ruficeps,* used this maneuver frequently.

Only the bamboo-stem-climbing *Catamblyrhynchus diadema* used the "pull/rip" maneuver frequently. This species feeds primarily by opening bamboo stem and leaf nodes (Hilty et al. 1979). The moss-and-epiphyte-searching furnariid, *Pseudocolaptes boissonneautii,* regularly used the "probe" maneuver (thrusting bill deep into substrate with extension of neck). Its allospecies *P. lawrenceii* exhibits similar behavior in Costa Rica (Skutch 1969). *Cacicus chrysonotus* may also use this maneuver regularly (but N = only 5 foraging records).

Only *Basileuterus luteoviridis* frequently used the "lunge" maneuver (rapid lateral movement that appears to combine rapid leg movements and some wing propulsion; differs from "reach out/up" in that the bird moves along a perch rather than remaining stationary). The "reach down" maneuver is one in which the bird leans down, stretching much of its body below the level of the perch to search a substrate. The feet still grasp the upperside of the perch. It is similar to the "reach out/up" maneuver but is directed downward. This maneuver is employed by more than half (52%) of the species examined and is the predominant maneuver used by the tanager *Buthraupis montana.* It is also heavily used by another mossy-branch-searching tanager, *Delothraupis castaneoventris,* and a hummingbird, *Metallura tyrianthina.* (*M. aeneocauda* and the several *Diglossa* species may also use this maneuver frequently, but sample sizes of observations were small.)

The "hang" maneuver differs from "reach down" in that most of the bird's body is suspended below the level of the feet, and the feet grasp the underside of the perch. Although this maneuver is used by more species (19) than "reach down," it is a prominent part of the foraging repertoire of only *Conirostrum sitticolor,* which uses this maneuver in the majority of its foraging maneuvers, primarily to reach the tips and curled portions of *Brunellia* leaves (c.f. Moynihan 1963), and *Margarornis squamiger,* which frequently hitches along the undersides of mossy branches.

The "sally" maneuver (flight from perch to pick object from substrate or out of the air) is used by fewer than half (46%) of the species, but it is the second most frequently used foraging maneuver after "pick" when mean percent use over all 33 species is calculated.

The "hover-glean" maneuver is the same as "sally" except that the bird hovers briefly in front of the target substrate before returning to a perch. Both in terms of number of species that use it and mean percent use over all 33 species, it is much less widely used than "sally," presumably because of the difficulty and high energy expenditure of hovering flight. Only the flycatchers *Mecocerculus leucophrys* and *Mionectes striaticollis* employ "hover-glean" frequently.

The "hawk" maneuver is the searching and pursuing of prey in continuous flight. Only a swift and two swallows, hawking specialists, use this maneuver (the only one that they use). Presumably, the extremely high wing length to body weight ratio required for hawking flight would make other foraging maneuvers very difficult.

## TABLE 3
### Foraging Maneuvers Used by Birds in the Humid Temperate Zone of the Bolivian Andes[1]

| Species | Proportion total foraging maneuvers | | | | | | | | | Mean sally or hover-glean distance (m) | Hawk | Hover | N |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pick | Reach out/up | Pull/rip | Probe | Lunge | Reach down | Hang | Sally | Hover-glean | | | | |
| *Cypseloides rutilus* | | | | | | | | | | | 1.00 | | 19 |
| *Pterophanes cyanoptera* | | | | | | | | | | | | 1.00 | 11 |
| *Coeligena violifer* | | | | | | | | | | | | 1.00 | 37 |
| *Heliangelus amethysticollis* | | | | | | .12 | | .12 | | | | .76 | 17 |
| *Chalcostigma ruficeps* | | | | | | .20 | | | | | | .80 | 5 |
| *Metallura aeneocauda* | | | | | | .60 | | | | | | .40 | 5 |
| *M. tyrianthina* | | | | | | .39 | | | | | | .61 | 28 |
| *Lepidocolaptes affinis* | 1.00 | | | | | | | | | | | | 11 |
| *Schizoeaca harterti* | .60 | .10 | | | | .10 | .20 | | | | | | 20 |
| *Cranioleuca albiceps* | .92 | | | | | .05 | | .03 | | | | | 36 |
| *Margarornis squamiger* | .73 | | | | | | .27 | | | | | | 30 |
| *Pseudocolaptes boissonneautii* | .59 | | | .38 | | | .03 | | | | | | 32 |
| *Phyllomyias uropygialis* | .44 | .22 | | | | | .22 | | .11 | | | | 9 |
| *Elaenia albiceps* | .50 | | | | | | .08 | .42 | | 0.3 | | | 12 |
| *Mecocerculus leucophrys* | .13 | | | | | | .03 | .51 | .33 | 0.6 | | | 30 |
| *M. stictopterus* | .14 | .06 | | | | | .09 | .51 | .20 | 0.3 | | | 35 |
| *Mionectes striaticollis* | .56 | | | | | | .11 | | .33 | 0.6 | | | 18 |
| *Myiophobus ochraceiventris* | .12 | .02 | | | | .02 | .08 | .60 | .16 | 0.6 | | | 51 |
| *Ochthoeca rufipectoralis* | .03 | | | | | | | .89 | .08 | 1.0 | | | 36 |
| *O. frontalis* | | | | | | .20 | | .80 | | 1.1 | | | 5 |
| *Myiotheretes fuscorufus* | | | | | | | | 1.00 | | 2.0 | | | 3 |
| *Notiochelidon murina* | | | | | | | | | | | 1.00 | | 128 |
| *N. flavipes* | | | | | | | | | | | 1.00 | | 26 |
| *Troglodytes solstitialis* | .69 | .13 | | | | .19 | | | | | | | 16 |
| *Atlapetes rufinucha* | .61 | .13 | | | | .10 | .10 | .06 | | | | | 31 |
| *Catamblyrhynchus diadema* | .32 | | .57 | | | | .11 | | | | | | 19 |
| *Hemispingus calophrys* | .64 | .14 | | | | .07 | .11 | .04 | | | | | 28 |
| *H. superciliaris* | .73 | .12 | | | | .09 | .06 | | | | | | 34 |
| *H. trifasciatus* | .87 | .05 | | | | .03 | .03 | .02 | | | | | 58 |
| *Thlypopsis ruficeps* | .56 | .33 | | | | .10 | .01 | | | | | | 40 |
| *Buthraupis montana* | .22 | .09 | .09 | | | .54 | .06 | | | | | | 35 |
| *Anisognathus igniventris* | .73 | .10 | | | | .10 | .02 | .05 | | | | | 42 |
| *Delothraupis castaneoventris* | .53 | | | | | .39 | .08 | | | | | | 13 |

## TABLE 3
CONTINUED

| Species | Proportion total foraging maneuvers | | | | | | | | | Mean sally or hover-glean distance (m) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pick | Reach out/up | Pull/rip | Probe | Lunge | Reach down | Hang | Sally | Hover-glean | | Hawk | Hover | N |
| *Tangara vassorii* | .67 | | | | | .33 | | | | | | | 6 |
| *Diglossa baritula* | .20 | | | .20 | | .40 | | .20 | | | | | 10 |
| *D. lafresnayii* | .67 | | | | | .33 | | | | | | | 9 |
| *D. carbonaria* | | .17 | | | | .33 | .50 | | | | | | 6 |
| *D. cyanea* | .64 | | | | | .18 | .18 | | | | | | 17 |
| *Conirostrum sitticolor* | .24 | .04 | | | | .11 | .57 | .04 | | | | | 54 |
| *Myioborus melanocephalus* | .25 | .05 | | | | .01 | | .61 | .08 | 1.1 | | | 88 |
| *Basileuterus luteoviridis* | .62 | .23 | | | .01 | | | .10 | .04 | | | | 70 |
| *B. signatus* | .26 | .42 | | | | | | .32 | | | | | 19 |
| *Cacicus chrysonotus* | .83 | | | .17 | | | | | | | | | 5 |
| Mean frequency for all species | .36 | .05 | .02 | .02 | <.01 | .12 | .07 | .15 | .03 | | .07 | .11 | |
| Mean frequency for species for which N > 10 observations | .40 | .06 | .02 | .01 | <.01 | .08 | .07 | .13 | .04 | | .09 | .10 | |

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[1] Data for 3050 m and 3300 m sites combined; see text for descriptions of maneuvers.

The "hover" maneuver is the searching for food while hovering continuously (in contrast to "hover-glean," in which actual hovering is only a small component of the total maneuver). Hummingbirds are the only species that use this maneuver.

Climbing and hitching up branches were not included among the maneuvers because they are used more for moving between foraging sites than for prey capture itself. *Lepidocolaptes affinis* and *Margarornis squamiger* are specialized bark-climbers, and *Pseudocolaptes boissonneautii* and *Cranioleuca albiceps* are almost exclusively "hitchers" that use a combination of climbing and hopping motions to ascend stems but not large vertical branches. *Catamblyrhynchus diadema* also uses the hitching technique frequently.

Sabo's (1980) foraging data were taken in a way differing sufficiently from that in the present study to preclude formal comparisons. Nevertheless, it seems clear that all maneuvers used by the tropical latitude birds are also used by those at the temperate latitude site, except "hawk" and "hover" (as defined above). These are absent from the Mt. Moosilauke birds' repertoires only because swifts, hummingbirds, and swallows do not occur at the White Mountains study site (Sabo, in litt.).

## FORAGING POSITIONS

Foraging position here refers to the location of feeding sites with respect to the ground and the canopy (Table 4). Very few deep undergrowth or terrestrial foragers were considered because of difficulty in observing these species. The discussion that follows is restricted to species for which I had more than 10 observations unless stated otherwise.

Except for the swallows and swift, the three species with greatest mean foraging heights are *Hemispingus superciliaris, Delothraupis castaneoventris,* and *Troglodytes solstitialis.* The three species with the smallest mean distance-to-canopy measures are the bush-top flycatcher *Ochthoeca rufipectoralis* and two hummingbirds (*Pterophanes cyanopterus, Coeligena violifer*) that characteristically feed in flowers on the outer surface of shrubs, mostly at forest edges.

The relative position (RP) of most canopy species in the foliage column (height above ground/height above ground + distance to canopy) ranges from .75 to .90 (Table 4). The values for most undergrowth species are biased upward by the relative ease of detection of these species when in edge situations, where canopy height is reduced.

Species foraging in the densest foliage (Table 4) are *Elaenia albiceps,* which feeds in the densest sections of the canopy, and three small insectivores that maneuver through dense foliage, *Thlypopsis ruficeps, Hemispingus trifasciatus,* and *H. superciliaris.* Bias against observations in dense undergrowth is responsible for the unexpectedly low values (open areas) for some insectivores of dense foliage (e.g., *Schizoeaca harterti, Basileuterus luteoviridis, B. signatus, Hemispingus calophrys*). Other than species with a high aerial component to their foraging, the species with the lowest foliage density values are the bark-foraging *Lepidocolaptes affinis* and the bush-top hummingbirds *Pterophanes cyanopterus* and *Coeligena violifer.*

To determine if foraging sites of bird species in the tropical and temperate sites differed with respect to distance above ground, I assigned primarily insectivorous species to a category based on the heights most frequently used (Table 5). For the Andes, only data from the 3300 m site were used because canopy height at the 3050 m was substantially greater than that at the 3300 m site or at Mt. Moosilauke, preventing meaningful comparisons using absolute heights.

The only notable difference between the tropical and temperate sites (Table 5) was the number of species in the understory zone, five in the Andes versus none in the White Mountains (although 10 of 13 insectivores at the White Mountains site used the understory on occasion). Otherwise, the two sites are very similar, but sample sizes of species per category are too small for statistical comparison.

## FORAGING SOCIAL SYSTEMS

Using Buskirk's (1976) categories, I characterized the foraging social system of each resident species at the two Andean sites (Appendix I). As expected, almost every species was seen solitarily on occasion, and many species characterized as solitary were occasionally seen to accompany mixed-species flocks. Thus, I considered only the most frequently observed system, although two or more designations are given for particularly flexible species.

At both sites, nearly half of the species participated regularly in mixed-species flocks (Table 6), and because the small passerines that predominate in such flocks are for the most part the most abundant birds at the sites, a large majority of the individual birds seen were found in

TABLE 4

CHARACTERISTICS OF FORAGING SITES USED BY ANDEAN FOREST BIRDS

| | Height (m) above ground ± s.d. | Distance (m) to canopy ± s.d. | Relative position[1] | Foliage density[2] | N |
|---|---|---|---|---|---|
| *Pterophanes cyanoptera* | 2.2 ± 2.0 | 0.3 ± 0.4 | .88 | 2.0 ± 0.9 | 11 |
| *Coeligena violifer* | 2.2 ± 2.4 | 0.3 ± 0.6 | .88 | 2.1 ± 1.0 | 37 |
| *Heliangelus amethysticollis* | 3.2 ± 3.0 | 0.6 ± 1.4 | .84 | 1.8 ± 1.0 | 17 |
| *Chalcostigma ruficeps* | 3.7 ± 1.5 | 1.9 ± 3.3 | .66 | 2.4 ± 0.6 | 5 |
| *Metallura aeneocauda* | 1.2 ± 0.3 | 1.5 ± 1.1 | .44 | 2.4 ± 1.1 | 5 |
| *M. tyrianthina* | 1.7 ± 1.0 | 1.0 ± 1.6 | .63 | 2.4 ± 0.6 | 29 |
| *Piculus rivolii* | 6.6 ± 1.5 | 0.8 ± 1.0 | .89 | 2.2 ± 1.0 | 6 |
| *Lepidocolaptes affinis* | 8.2 ± 5.0 | 3.7 ± 3.4 | .69 | 1.6 ± 0.5 | 12 |
| *Margarornis squamiger* | 4.9 ± 3.8 | 2.4 ± 1.4 | .67 | 2.6 ± 1.1 | 31 |
| *Cranioleuca albiceps* | 2.5 ± 1.1 | 4.4 ± 2.0 | .36 | 3.0 ± 0.9 | 37 |
| *Pseudocolaptes boissonneautii* | 8.5 ± 3.4 | 4.0 ± 2.3 | .68 | 2.7 ± 0.7 | 34 |
| *Schizoeaca harterti* | 1.4 ± 1.0 | 1.9 ± 2.0 | .42 | 2.9 ± 1.2 | 33 |
| *Ochthoeca rufipectoralis* | 2.6 ± 3.2 | 0.0 ± 0.5 | 1.00 | 1.3 ± 1.1 | 38 |
| *O. frontalis* | 1.6 ± 0.9 | 3.2 ± 1.2 | .33 | 2.4 ± 0.5 | 7 |
| *Myiotheretes fuscorufus* | 12.2 ± 0.0 | 0.5 ± 0.9 | 1.04 | 0.7 ± 1.2 | 3 |
| *Myiophobus ochraceiventris* | 4.7 ± 1.8 | 0.8 ± 0.9 | .85 | 2.2 ± 0.7 | 52 |
| *Phyllomyias uropygialis* | 6.2 ± 5.4 | 4.3 ± 2.9 | .59 | 2.6 ± 0.7 | 9 |
| *Elaenia albiceps* | 6.3 ± 2.3 | 0.7 ± 0.3 | .90 | 3.3 ± 0.7 | 12 |
| *Mecocerculus leucophrys* | 6.2 ± 2.3 | 1.5 ± 0.9 | .81 | 2.4 ± 0.8 | 31 |
| *M. stictopterus* | 8.3 ± 2.9 | 2.4 ± 2.5 | .78 | 2.9 ± 0.4 | 35 |
| *Mionectes striaticollis* | 5.3 ± 1.7 | 1.0 ± 1.0 | .84 | 2.8 ± 0.6 | 19 |
| *Troglodytes solstitialis* | 9.6 ± 5.9 | 3.1 ± 2.5 | .76 | 2.8 ± 0.7 | 17 |
| *Atlapetes rufinucha* | 4.9 ± 4.2 | 3.2 ± 2.6 | .60 | 2.4 ± 1.0 | 31 |
| *Catamblyrhynchus diadema* | 2.0 ± 1.3 | 3.4 ± 1.7 | .37 | 2.9 ± 0.8 | 19 |
| *Hemispingus calophrys* | 3.4 ± 1.3 | 3.0 ± 2.8 | .53 | 2.9 ± 0.4 | 28 |
| *H. superciliaris* | 10.6 ± 4.7 | 2.0 ± 1.5 | .84 | 3.1 ± 0.8 | 34 |
| *H. trifasciatus* | 6.0 ± 2.4 | 1.4 ± 1.3 | .81 | 3.1 ± 0.7 | 58 |
| *Thlypopsis ruficeps* | 4.1 ± 2.8 | 1.9 ± 2.5 | .68 | 3.2 ± 0.7 | 40 |
| *Buthraupis montana* | 6.6 ± 2.3 | 1.8 ± 1.2 | .79 | 2.5 ± 1.0 | 35 |
| *Anisognathus igniventris* | 5.8 ± 2.9 | 1.5 ± 1.3 | .80 | 3.0 ± 0.9 | 42 |
| *Delothraupis castaneoventris* | 10.1 ± 3.6 | 2.5 ± 1.4 | .80 | 2.3 ± 1.0 | 14 |
| *Tangara vassorii* | 8.9 ± 3.5 | 1.6 ± 1.4 | .85 | 2.8 ± 0.8 | 6 |
| *Diglossa baritula* | 6.9 ± 2.5 | 3.1 ± 3.3 | .69 | 1.9 ± 1.5 | 10 |
| *D. lafresnayii* | 2.1 ± 1.2 | 0.8 ± 1.5 | .75 | 2.6 ± 0.9 | 9 |
| *D. carbonaria* | 6.4 ± 1.1 | 0.5 ± 0.3 | .93 | 3.2 ± 0.8 | 6 |
| *D. cyanea* | 3.9 ± 2.8 | 1.4 ± 1.7 | .73 | 2.6 ± 0.9 | 18 |
| *Conirostrum sitticolor* | 5.7 ± 2.9 | 1.1 ± 1.6 | .84 | 2.2 ± 0.6 | 54 |
| *Myioborus melanocephalus* | 7.0 ± 3.6 | 2.1 ± 3.9 | .77 | 1.7 ± 1.3 | 88 |
| *Basileuterus luteoviridis* | 3.3 ± 2.5 | 3.0 ± 2.4 | .52 | 2.6 ± 0.8 | 71 |
| *B. signatus* | 1.4 ± 2.0 | 1.8 ± 1.8 | .44 | 2.8 ± 0.5 | 19 |
| *Cacicus chrysonotus* | 8.2 ± 5.5 | 3.9 ± 1.1 | .68 | 2.0 ± 1.0 | 5 |
| *Notiochelidon murina* | 21.4 ± 14.2 | +10.5 ± 7.2 | 1.49 | 0.0 ± 0.0 | 128 |
| *N. flavipes* | 18.3 ± 9.2 | +3.3 ± 2.7 | 1.18 | 0.0 ± 0.0 | 26 |
| *Cypseloides rutilus* | 85.7 ± 34.5 | +61.0 ± 29.3 | 1.71 | 0.0 ± 0.0 | 19 |

[1] Relative position in the foliage column is measured by dividing the height above ground at which a bird is recorded by the height of the canopy at that point; species with values close to 1.00 are high canopy foragers and those with values close to 0 are near-ground foragers.

[2] Foliage density was estimated for each observation on a subjective scale from 0 to 5. A value of 0 indicates no vegetation within a ½ m radius sphere around the foraging site and a value of 5 indicates extremely dense vegetation: no light passes through this sphere.

mixed-species flocks. One can often walk for an hour without seeing a bird until a mixed-species flock is encountered.

At the 3300 m site, four types of mixed-species flocks were noted, (A) small insectivores in the canopy, (B) small frugivores in the canopy, (C) small insectivores in the undergrowth, and (D) large omnivores in the canopy.

A typical Type A flock consisted of *Hemispingus trifasciatus* (4–8 individuals), *Myiophobus ochraceiventris* (4–5), *Myioborus melanocephalus* (2), *Conirostrum sitticolor* (2), *Margarornis squamiger* (2), and *Delothraupis castaneoventris* (1). A typical Type B flock included *Aniso-*

TABLE 5

FORAGING HEIGHT STRATA OF INSECTIVOROUS BIRDS AT STUDY SITES IN THE ANDES AND WHITE MOUNTAINS

| Vertical zone[1] | No. of species (% locality total) | |
|---|---|---|
| | Andes (3300 m)[2] | White Mtns. |
| Forest floor | 3 (14) | 3 (23) |
| Understory, 0.1–2 m | 6 (29) | 0 |
| Midstory, 2–5 m | 6 (29) | 4 (31) |
| Midcanopy, 5–8 m | 6 (29) | 5 (38) |
| Upper canopy, 8 m | 0 (0) | 1 (8) |
| Total | 21 | 13[3] |

[1] See text for explanation of assignment of species to categories.

[2] "Visitors" (Appendix I) and aerial foragers were not included in the analysis, but several species not listed in Table 4 were included: *Grallaria squamigera, G. rufula,* and *Scytalopus magellanicus* in the "forest floor" category; *Anairetes parulus* and *Cacicus holosericeus* in the "understory" category; and *Veniliornis nigriceps* in the "midstory" category.

[3] *Corvus corax* was not included in the analysis because of lack of data.

*gnathus igniventris* (4–8), *Iridosornis jelskii* (2), *Diglossa cyanea* (1–4), *Mionectes striaticollis* (1), and often *Elaenia albiceps* (1–2). A typical Type C flock included *Basileuterus luteoviridis* (4), *Atlapetes rufinucha* (4), *Cranioleuca albiceps* (2), and *Catamblyrhynchus diadema* (2–4); these were often accompanied by *Ochthoeca rufipectoralis* (2) in edge situations, and *Hemispingus calophrys* (4–8). The boundaries between these first three flock types were not rigid, and two or more types often mingled temporarily, especially A and B in *Myrica* trees. Type D flocks, however, did not intermingle with the others and were much less frequently noted. A typical Type D flock included *Buthraupis montana* (6–12), *Cacicus chrysonotus* (5–10), *Piculus rivolii* (1), and often *Cyanolyca viridicyana* (2–4). All but *Piculus rivolii* were seen frequently in monospecific flocks as well.

Within A, C, and D flocks, ecological differences in feeding behavior between member species were obvious. For example, in Type A flocks, *Hemispingus trifasciatus* gleaned leaves in dense foliage, particularly *Myrica* trees; *Conirostrum sitticolor* hung acrobatically to reach leaves, particularly those of *Brunellia,* generally out of reach of a "normal" foliage-gleaner; *Myiophobus ochraceiventris* sallied to foliage, especially *Clusia* leaves, for insects and to dehiscent fruit clusters of *Brunellia*; *Margarornis squamiger* searched moss on branches of all sizes and inclinations; *Delothraupis castaneoventris* searched horizontal mossy branches; and *Myioborus melanocephalus* pursued flushed insects through the air, often for many meters. As expected, the relative abundance of each species within a flock seemed in proportion to the available volume of favored substrate. Thus, *Hemispingus trifasciatus,* the most common bird, foraged primarily in the most abundant tree, *Myrica,* and *Delothraupis castaneoventris,* which focused most of its effort upon a relatively scarce substrate, horizontal mossy branches, was the least common.

Ecological segregation within Type B flocks was less obvious, because all species except *Iridosornis jelskii* ate the small fruits of *Myrica.* The sallying tyrannids presumably were able to reach fruit that the perch-gleaning tanagers could not.

At the 3050 m site, the same four flock types were noted, with similar but richer species composition. The greatest differences in composition between the two sites were in Type A flocks, which at 3050 m included *Hemispingus superciliaris* (4–6), *H. xanthophthalmus* (2–4), *Myioborus melanocephalus* (2), *Mecocerculus leucophrys* (2), *M. stictopterus* (2), *Delothraupis castaneoventris* (1), *Troglodytes solstitialis* (1), and regularly, *Lepidocolaptes affinis* (2; below 3100 m only), *Margarornis squamiger* (2; above 3000 m only), *Pseudocolaptes boissonneautii* (1–2), *Chlorornis riefferii* (1), and *Veniliornis nigriceps* (2). A typical Type B flock was composed of *Anisognathus igniventris* (4–8), *Tangara vassorii* (2–4), *Diglossa cyanea* (1–4), and often *Thraupis cyanocephala* (4–6). A typical Type C flock was similar to one at 3300 m except that *Thlypopsis ruficeps* (1–2), and, often, in edge situations, *Myioborus melanocephalus* (2) were added. A typical Type D flock was the same as that at 3300 m, but usually more *Buthraupis montana* were present, sometimes as many as 25.

During the breeding season, when Sabo's (1980) Mt. Moosilauke study was conducted,

## TABLE 6
## SUMMARY OF AVIAN SOCIAL FORAGING SYSTEMS FOR STUDY SITES IN THE ANDES AND COASTAL MOUNTAINS OF VENEZUELA

| Interspecific[1] | Intraspecific[2] | Chuspipata | Cotapata | Costa Rica[3] | Guatopo[4] |
|---|---|---|---|---|---|
| N | N | 18 (24.7) | 14 (29.2) | 24 (42.1) | 64 (33.0) |
| N | N, P; P | 7 (9.6) | 4 (8.3) | 2 (3.5) | 32 (16.5) |
| N | N, S; P, S; N, P, S | 7 (9.6) | 5 (10.4) | 0 | 0 |
| N | S; L; S, L; P, L | 7 (9.6) | 2 (4.2) | 4 (7.0) | 35 (18.0) |
| F | N; P; N, P | 16 (21.9) | 9 (18.8) | 18 (31.6) | 38 (19.6) |
| F | N, S; P, S; P, L | 3 (4.1) | 4 (8.3) | 2 (3.5) | 1 (0.5) |
| F | S; L; S, L | 8 (11.0) | 4 (8.3) | 7 (12.3) | 16 (8.2) |
| N, F | N; N, P; P; N, S; P, S; N, P, S | 4 (5.5) | 4 (8.3) | 0 | 6 (3.1) |
| N, F | S; L; S, L | 3 (4.1) | 2 (4.2) | 0 | 2 (1.0) |
| Total species | | 73 | 48 | 57 | 194 |

[1] Refers to interspecific sociality: N = does not form flocks with other species; F = flocks with other species.

[2] Refers to intraspecific sociality: N = not social, solitary; P = pairs; S = small flocks, 3–5 birds; L = large flocks, 6+ birds; see Appendix I.

[3] Data from Buskirk (1976).

[4] Data from Morton (1979).

virtually all species are paired and defending territories; thus, mixed-species flocks are nearly non-existent during the temperate summer, at least until the end of the breeding season.

Buskirk's (1976) analysis of social systems of the avifauna of a tropical montane locality in Costa Rica provides an excellent comparison for the Bolivian sites. The proportion of species that participate in mixed-species flocks at the Bolivian sites is virtually identical to that in Costa Rica. Eliminating rare transients, predators, and North American migrants from Buskirk's Monteverde list leaves 57 species, of which 27 (47%) are interspecifically gregarious; this compares with 34 (47%) and 23 (48%) at the 3050 m and 3300 m sites, respectively (Table 6). Differences between the sites in proportion of the avifauna within finer subdivisions of foraging system categories are probably due primarily to differences in scoring technique—I was more liberal in giving multiple categories for each species. Even so, the overall similarity between the Bolivian and Costa Rican sites is impressive, especially because the montane forest of the Costa Rican site differs from that in Bolivia in not being near timberline and because the sites share only two species and 18 of 53 genera.

In light of these ecological and taxonomic differences, and the tremendous geographic distances between the two areas, it is noteworthy that in 15 of 18 cases the shared resident congeners were independently characterized as having the same foraging social system (with allowance for my more liberal dispensing of multiple categories for a species). The three conflicting cases differed only in flock size category (*Columba, Amazona,* and *Chlorospingus*), and in two of these, the Bolivian species (*Amazona mercenaria* and *Chlorospingus ophthalmicus*) were only marginal community members at 3050 m and at lower elevations have larger flock sizes similar to their Costa Rican counterparts. Thus, the constancy of foraging social systems over geographic and taxonomic distance is impressive. This contrasts with the extensive intraspecific geographic variation perceived by Moynihan (1979) for Andean birds.

Morton (1979) presented similar data for foraging social systems of birds of the coastal mountains of northern Venezuela at Guatopo National Park, and I have summarized his findings with predators and North American migrants removed (Table 6). Of Morton's 194 species, 63 (33%) are regular participants in mixed-species flocks. This is significantly lower ($\chi^2 < 3.9$, $P < 0.05$) than the percentage of mixed-species flocking birds at the Costa Rican and Bolivian sites.

Inspection of the proportion of the avifauna in various foraging social system categories reveals that most of this difference is due to a higher proportion of the Guatopo avifauna in two categories: single-species flocks and non-interspecifically-gregarious species that forage in pairs (Table 6). The Guatopo avifauna has a higher proportion of flocking parrots, doves, and icterids than the other three sites; this is to be expected, because the habitat at Guatopo consists of much second-growth forest at low elevation, where such birds are more common. The ultimate reasons for the higher proportion of single-species flocking birds presumably lies with the greater patchiness of food distribution in more open, seasonal areas (Crook 1965), but pertinent data on dispersion patterns of food are not available. As for the higher proportion at Guatopo of non-interspecifically social species that forage in pairs, no plausible hypothesis is immediately evident.

Patterns of presumed food dispersion and vulnerability to predators with respect to foraging social system yield results very similar to and supportive of the analysis of Buskirk (1976), as would be expected from the great similarity in foraging social organization between the Costa Rican and Bolivian avifaunas (Table 6). Species that feed on clumped resources tend to be either in single-species flocks or sentinel foragers, species that feed on dispersed resources in the canopy tend to be in mixed-species flocks, and species with good anti-predator surveillance that feed on dispersed resources tend to be solitary.

As a consequence of the Costa Rican-Bolivian similarities, most differences between the foraging social organization of Costa Rican and Venezuelan avifaunas revealed by Morton's (1979) thorough analysis are mirrored in a comparison of the Bolivian and Venezuelan avifaunas, and will not be repeated here. Similar community-wide analyses in various habitats throughout the Neotropics are needed to test the generality of these interhabitat and interregional differences.

Because the categorization of foraging social systems presented here for several Andean species differs from that of Vuilleumier (1970, 1982) for a site in central Peru, I feel that it is necessary to address the discrepancies: (1) *Diglossa lafresnayii* is listed by Vuilleumier as a participant in mixed-species flocks; in Bolivia, this species is solitary, only occasionally and temporarily participating in mixed-species flocks; (2) *Buthraupis montana* and (3) *Thraupis cyanocephala* are listed by Vuilleumier as mixed-species flock members; in Bolivia both species are also commonly found in single-species flocks; (4) *Troglodytes solstitialis* is listed as a single-species flock member; in Bolivia this species is found primarily in pairs or solitarily in mixed-species flocks; (5) *Mionectes striaticollis* is listed among the solitary species; in Bolivia this species is a regular, frequent participant in mixed-species flocks; (7) *Mecocerculus stictopterus* is listed as a non-social species; in Bolivia this species is found primarily in mixed-species flocks, usually in pairs. Among species not found or not resident at the Bolivia sites, Vuilleumier lists *Entomodestes leucotis* as a mixed-species flock member; in Bolivia this species is solitary (Remsen, unpubl. data) as it is also in Peru (T. A. Parker, pers. comm.). *Saltator cinctus* (= "?*Arremon*" from the 1970 paper) is listed as a mixed-species flock member; because virtually nothing is known about this species in the field (O'Neill and Schulenberg 1979), this classification is premature at best. *Haplospiza rustica* is listed as a mixed-species flock member; in Peru, this species is found primarily as singles or in single-species flocks (T. A. Parker, pers. comm.).

At first one might explain these differences as simply due to geographic variation in foraging social systems (Moynihan 1979). However, I know of only two such examples; *Margarornis squamiger* and *Chlorornis riefferii* in central and northern Peru, Ecuador, and Colombia are frequently seen in small flocks within mixed-species flocks (T. A. Parker, R. S. Ridgely, T. S. Schulenberg, pers. comms.), but at my sites in Bolivia they occur primarily as pairs or singles. Vuilleumier's (1970) conclusions were based on three days of fieldwork and observation of eight flocks; at least three of these flocks had five or fewer birds and another included canopy species (*Tangara nigroviridis*) with undergrowth species (*Basileuterus luteoviridis*). Additionally, of the 24 species listed by Vuilleumier (1970), four were not positively identified and nine others were noted only once. Thus, Vuilleumier's categorizations and subsequent analyses must remain suspect.

## GENERAL CONSIDERATIONS

When ornithologists discuss tropical species diversity, they almost always focus on tall, lowland tropical forest with its impressively large avifauna—as many as 550 species have been recorded in a two km$^2$ area after only a few years of fieldwork (Parker 1982). The bird diversity at tropical latitudes near timberline in the Andes in cold, fog-shrouded, stunted forest is almost as impressive. In the Bolivian Andes at 3300 m, an elevation at which only a handful of breeding birds are found at temperate latitudes, nearly 50 resident species are present in a 20 hectare area. This is at least 10 more species than coexist in some of the tallest, richest forests of eastern North America (Terborgh 1980). Even compared to tropical regions, the diversity of the Andean avifauna is impressive. For example, in forested montane New Guinea one must descend below 1800 m to reach an avifauna with 50 species (Diamond 1972). It also must be kept in mind that northern Bolivia is far south of the center of Andean bird diversity; an inventory in northern Peru similar to the one presented here would yield a community richer by another 10 species or more (LSUMZ collecting locality data).

As discussed in a previous section, most of this increased species richness of the Andes relative to temperate latitudes can be accounted for by the addition of "tropical" resources. Also, Stiles' (1978) data for alder forests in Washington and Costa Rica indicate that once nectarivores and epiphyte-searchers are removed from the species lists, species richness is very similar (17 vs 18) at the temperate and tropical sites. In contrast, Terborgh (1980) found that only 34 percent of the increase in species number in a lowland tropical forest in Peru could be accounted for in such a manner, with the remaining difference best explained by larger tropical niches (broader resource spectra within a guild) or increased species-packing within guilds. Karr (1975) found that approximately 70 percent of the "excess" species in a lowland forest in Panama could be accounted for by addition of "tropical" resources.

At least two hypotheses exist to explain the difference between the montane and lowland results. Terborgh (1980) is one of many (e.g., especially Haffer 1974; Karr 1976; Pearson 1977, 1982) who have invoked historical factors, primarily increased numbers of speciation events, to explain increased species-packing in the tropics. Because the Andes are geologically recent relative to the South American lowlands, one would predict that if historical factors are important, they would be more important in the lowlands than in the Andes. The results of the montane-lowland comparison are consistent with this hypothesis. Also predicted by this hypothesis, therefore, is a decrease in the importance of historical factors with increasing elevation along a lowland-to-highland gradient at a given latitude. This follows from Chapman's (1917, 1926) analysis of the origin of the forest avifauna of the Andes: avifaunas at higher elevations are more recent in origin, because the species at a given elevation are derived primarily from those of the next lowest elevational "zone." This hypothesis needs to be tested.

Although the influence of historical factors is undeniable, perhaps the importance of reduced extinction rates in the tropics, rather than increased speciation rates, should be emphasized. A speciation event can be considered analogous to reproduction by fission, and so with only two refugia, one parental species potentially can produce over 100 "off-spring" species in just seven "generations." Hypothetically, therefore, only a handful of allopatric speciation episodes are necessary to generate an avifauna far more diverse than currently exists in the forests of North America, and certainly, the number of geographic isolating events over the last 20 million years has been far, far greater than this minimum number. Proponents of the importance of speciation rates in determining species richness need to consider why current species numbers are so small relative to the hypothetical upper limit.

Obviously, time is needed between speciation events for the ecological and morphological changes required before syntopy of recently speciated forms can be achieved (and single-point diversity thereby increased). This period, however, may be much shorter than once thought. For example, the adaptive radiation of the Drepanidinae of Hawaii in just a few million years or so (Amadon 1950; Olson and James 1982; Sibley and Ahlquist 1982) attests to the speed with which secondary morphological changes can occur if ecologically stimulated by lack of competitors, i.e., if the resources are available.

The large number of speciation events that have apparently occurred in the Amazon Basin did nothing but fragment parental species into allopatric component species, i.e., produce superspecies, and this does not directly increase single-point diversity. Clearly, the proponents of the importance of historical factors do not take such a narrow view of the mechanism by which historical factors increase species diversity. Nevertheless, I think it is useful to take such a view briefly to emphasize that to increase single-point diversity, the resources that promote coexistence must be available. Thus, trying to separate historical from ecological factors may not be a realistic way of looking at the process of species enrichment.

If it is true that there has been time for far more speciating events and subsequent morphological change than needed to generate today's avifauna, then differential extinction rates become critical. Although no one any longer believes that the tropics are climatologically and ecologically stable, certainly their stability in these respects is greater than that of temperate regions, and this stability could reduce extinction rates, thereby "buying time" for ecological and morphological changes that promote survival of species and syntopy. On the other hand, as Darwin pointed out, species diversity in a stable equilibrium state may be reduced by competitive exclusion.

An alternative hypothesis to the importance of historical factors is that the degree of species-packing in the lowlands has been overestimated because our knowledge of the natural history of the birds is very incomplete. In other words, perhaps many of the species currently assigned to a guild also found at temperate latitudes are really specializing on different resources and should form their own separate guild. Could we be overlooking many examples of resource specialization? Lowland avifaunas are notoriously complex and inherently difficult to study. Many species exist in very low densities or are extremely difficult to observe. Our knowledge of diets through analysis of stomach contents is virtually nil. Certainly the conspicuous "tropical" resources, such as year-round fruit and nectar (Karr 1971; Morton 1973) and army ants (Willis and Oniki 1978), have already been identified and their contribution assessed. The contribution of other foraging substrates, habitats, and microhabitats, such as dead leaves suspended in the foliage (Terborgh 1980; Remsen and Parker, 1984), vine tangles (Terborgh 1980), tree falls (Schemske and Brokaw 1981), oxbow lakes and flooded forest (Remsen and Parker, 1983), bamboo thickets (Parker 1982; Parker and Remsen, unpubl. data), and epiphytic vegetation (Orians 1969; Remsen and Parker, unpubl. data), has only recently been identified or assessed. It thus seems likely that many more resources found in, or exploited only in, the tropics are yet to be discovered and that the degree to which tropical species diversity can be explained by additional or expanded resources is still to be resolved.

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# APPENDIX I

## SPECIES FOUND AT EACH STUDY SITE WITH ECOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF EACH SPECIES

| | Relative[1] abundance | | Foraging[2] system | | | | Mean body weight (g)[5] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3050 m | 3300 m | Intersp. | Intrasp. | Diet[3] | Breeding[4] condition | ♂ (N) | ♀ (N) | Juv. ♂ (N) | Juv. ♀ (N) |
| CATHARTIDAE | | | | | | | | | | |
| *Cathartes aura* | (V) | (V) | | | | | | | | |
| *Vultur gryphus* | | (V) | | | | | | | | |
| ACCIPITRIDAE | | | | | | | | | | |
| *Accipiter striatus* | | (V) | | | | | | | | |
| *Buteo leucorrhous* | | (V) | | | | | | | | |
| ?*Buteo albigula* | (V) | | | | | | | | | |
| *Buteo polyosoma* | | (V) | | | | | | | | |
| FALCONIDAE | | | | | | | | | | |
| *Phalcoboenus megalopterus* | (V) | V | | | | | | | | 740 (1) |
| *Falco sparverius* | (V) | V | | | | | 105 (1) | | | |
| CRACIDAE | | | | | | | | | | |
| *Chamaepetes goudotii* | R | R | N | P, S | f | ±, +, − | 730 (3) | 773 (3) | | |
| PHASIANIDAE | | | | | | | | | | |
| *Odontophorus balliviani* | (R) | | N | ? | (i, f) | | | | | |
| SCOLOPACIDAE | | | | | | | | | | |
| *Gallinago stricklandii* | | V | | | | | 252 (1) | | | |
| COLUMBIDAE | | | | | | | | | | |
| *Columba fasciata* | FC | C | N | L | f | +, − | 265 (1) | 280 (1) | | |
| *Geotrygon frenata* | (V) | | | | | | | | | |
| PSITTACIDAE | | | | | | | | | | |
| *Hapalopsittaca melanotis* | R | (V) | N | S, N | f | +, − | 158 (2) | | | |
| *Pionus tumultuosus* | (U) | | N | S, L | f | | | | | |
| *Amazona mercenaria* | (U?) | (V) | N | P, S | (f) | | | | | |
| STRIGIDAE | | | | | | | | | | |
| ?*Otus albogularis* | | (V) | | | | | | | | |
| ?*Ciccaba albitarsus* | (V) | | | | | | | | | |
| *Glaudicium jardinii* | FC | (V) | N | N | i (c) | −, + | 63.7 (3) | 73.5 (2) | | |
| CAPRIMULGIDAE | | | | | | | | | | |
| ?*Uropsalis segmentata* | (R) | | N | ? | (i) | | | | | |

## APPENDIX I

### CONTINUED

| | Relative[1] abundance | | Foraging[2] system | | Diet[3] | Breeding[4] condition | Mean body weight (g)[5] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3050 m | 3300 m | Intersp. | Intrasp. | | | ♂ (N) | ♀ (N) | Juv. ♂ (N) | Juv. ♀ (N) |
| APODIDAE | | | | | | | | | | |
| *Cypseloides rutilus* | (R) | | N | L | i | | | | | |
| TROCHILIDAE | | | | | | | | | | |
| *Colibri corruscans* | | V | | | | | 7.8 (1) | 6.8 (2) | | |
| *C. thalassinus* | R | | N | N | n, i | – | 5.0 (1) | | | |
| *Pterophanes cyanopterus* | U | U | N | N | n, i | – | 10.2 (3) | 8.4 (3) | 10.1 (3) | |
| *Ensifera ensifera* | R | | N | N | n, (i) | – | 10.2 (3) | 8.4 (3) | 10.1 (3) | |
| *Coeligena torquata* | FC | V | N | N | n, i | – | 7.3 (4) | 6.4 (5) | 6.6 (1) | |
| *C. violifer* | C | FC | N | N | n, i | | 7.7 (44) | 7.1 (23) | 7.9 (1) | |
| *Heliangelus amethysticollis* | FC | FC | N | N | n, i | –, + | 5.3 (15) | 4.8 (11) | | |
| *Chalcostigma ruficeps* | U | (V) | N | N | n, i | –, + | 3.8 (1) | 3.3 (2) | | |
| *Metallura aeneocauda* | V | FC | N | N | n, i | –, + | 5.3 (16) | 5.0 (9) | 5.3 (19) | |
| *M. tyrianthina* | FC | FC | N | N | n, i | +, – | 3.5 (18) | 3.4 (10) | 3.5 (4) | |
| TROGONIDAE | | | | | | | | | | |
| *Trogon personatus* | V | | | | | | 64.0 (1) | | | |
| RAMPHASTIDAE | | | | | | | | | | |
| *Aulacorhynchus coeruleicinctus* | V | | | | | | 225 (1) | | | |
| *Andigena cucullata* | U | R | N | S, N | f | ±, – | 272 (4) | | | |
| PICIDAE | | | | | | | | | | |
| *Piculus rivolii* | U | R | F | N | i, (f) | – | | 91.5 (2) | | |
| *Veniliornis nigriceps* | U | R | F | P | i | – | 46.0 (2) | 42.8 (5) | | |
| DENDROCOLAPTIDAE | | | | | | | | | | |
| *Lepidocolaptes affinis* | (U) | | F | P, N | i | | | | | |
| FURNARIIDAE | | | | | | | | | | |
| *Cinclodes fuscus* | V | V | | | | | 26.7 (4) | | | |
| *Synallaxis azarae* | FC | | N | P | i | – | 12.6 (5) | 12.0 (3) | | |
| *Schizoeaca harterti* | FC | C | N | N, P | i | –, ± | 13.2 (11) | 12.7 (21) | | |
| *Cranioleuca albiceps* | FC | FC | F | P | i | –, + | 15.0 (15) | 15.2 (8) | | |
| *Asthenes urubambensis* | V | | | | | | | 16.0 (1) | | |
| *Margarornis squamiger* | U | U | F | P | i | – | 15.5 (8) | 15.1 (6) | | 13.0 (1) |
| *Pseudocolaptes boissonneautii* | U | V | F | N, P | i | –, + | 45.5 (4) | 42.7 (3) | | |

## APPENDIX I
CONTINUED

| | Relative[1] abundance | | Foraging[2] system | | Diet[3] | Breeding[4] condition | Mean body weight (g)[5] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3050 m | 3300 m | Intersp. | Intrasp. | | | ♂ (N) | ♀ (N) | Juv. ♂ (N) | Juv. ♀ (N) |
| FORMICARIIDAE | | | | | | | | | | |
| *Chamaeza mollissima* | U | | N | N | g, i | – | 71 (1) | 65 (1) | | |
| *Grallaria squamigera* | (R?) | R? | N | N | i | – | | 166 (1) | | |
| *G. erythrotis* | R | | N | N | i | – | 53 (1) | 61 (1) | | |
| *G. rufula* | FC | R | N | N | i | – | 35.3 (6) | 34.7 (3) | | |
| *G. ferrugineipectus* | R | | N | N | i | – | 17.0 (3) | 16.0 (2) | | |
| RHINOCRYPTIDAE | | | | | | | | | | |
| *Scytalopus magellanicus* | FC | C | N | N | i | – | 14.6 (7) | 14.6 (4) | | 12.0 (1) |
| COTINGIDAE | | | | | | | | | | |
| *Ampelion rubrocristatus* | (V) | R | N | N | f | – | 69.9 (7) | 65.6 (4) | 60.0 (1) | 61.0 (1) |
| *Pipreola intermedia* | R | V | N | N, P | f | – | 52.8 (4) | 57.0 (2) | | |
| *P. arcuata* | U | U | N | N, P | f | +, – | 117.3 (3) | 111.3 (2) | | |
| TYRANNIDAE | | | | | | | | | | |
| *Phyllomyias uropygialis* | U | R | N | N | i | – | 9.4 (11) | 8.6 (8) | | |
| *Elaenia albiceps* | U | U | N, F | N, S | f, i | – | 16.2 (14) | 16.3 (9) | | |
| *E. pallatangae* | V | V | | | | | 13.7 (1) | | | |
| *Mecocerculus leucophrys* | FC | R | F | P | i | ±, – | 12.2 (3) | 10.0 (1) | | |
| *M. stictopterus* | FC | | F | P | i | – | 8.8 (1) | 8.7 (2) | | |
| *Anairetes parulus* | R | R | N | P | i | –, ± | 6.4 (5) | 6.9 (1) | | |
| *Mionectes striaticollis* | R | FC | F | N | f, (i) | – | 15.2 (60) | 12.6 (18) | | |
| *Pseudotriccus ruficeps* | R | | N | N | i | – | 9.9 (2) | 9.8 (4) | | |
| *Hemitriccus granadensis* | | V | | | | | 7.7 (1) | 6.6 (1) | | |
| *Myiophobus ochraceiventris* | V | FC | F | S | i, f | –, ± | 11.2 (11) | 9.8 (3) | 11.0 (1) | |
| *Pyrrhomyias cinnamomea* | (V) | | | | | | | | | |
| *Ochthoeca frontalis* | FC | FC | N | N | i | | 10.4 (34) | 9.6 (36) | | |
| *O. pulchella* | V | | | | | | | 10.2 (1) | | |
| *O. rufipectoralis* | FC | U | F, N | P | i | – | 10.5 (4) | 9.5 (10) | | |
| *O. fumicolor* | | V | | | | | 13.4 (2) | 13.5 (1) | | |
| *Myiotheretes fuscorufus* | R | V | N | P | i | – | 32.4 (2) | 31.0 (3) | | |
| *Myiarchus* (sp.) | | (V) | | | | | | | | |

## APPENDIX I
CONTINUED

| | Relative[1] abundance | | Foraging[2] system | | Diet[3] | Breeding[4] condition | Mean body weight (g)[5] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3050 m | 3300 m | Intersp. | Intrasp. | | | ♂ (N) | ♀ (N) | Juv. ♂ (N) | Juv. ♀ (N) |
| HIRUNDINIDAE | | | | | | | | | | |
| *Notiochelidon murina* | R | C | N | L | i | – | 11.8 (7) | 11.6 (7) | | 10.4 (3) |
| *N. cyanoleuca* | (V) | | | | | | | | | |
| *N. flavipes* | (R) | | N | L | i | | | | | |
| CORVIDAE | | | | | | | | | | |
| *Cyanolyca viridicyana* | U | V | N | S | i | –, ± | 93.8 (6) | 89.0 (2) | | |
| TROGLODYTIDAE | | | | | | | | | | |
| *Cinnycerthia peruana* | R | | N | S | i | –, + | 18.0 (1) | 15.1 (6) | | 14.0 (1) |
| *Troglodytes solstitialis* | FC | (V) | F | N, P | i | – | 11.6 (4) | | | |
| TURDINAE | | | | | | | | | | |
| *Myadestes ralloides* | (V) | | | | | | | | | |
| *Entomodestes leucotis* | | V | | | | | | 69.0 (1) | | |
| *Catharus fuscater* | V | | | | | | | 28.0 (1) | | |
| *Turdus chiguanco* | V | | | | | | 100 (1) | | | |
| *T. fuscater* | FC | FC | N | N, S | f, (i) | –, ± | 126 (4) | 139 (5) | | 118 (2) |
| *T. serranus* | V | R | N | N | f | – | 92.3 (3) | 90.5 (4) | | 76.0 (1) |
| EMBERIZINAE | | | | | | | | | | |
| *Zonotrichia capensis* | C | FC | N | N, P, S | g | – | 24.0 (3) | 21.9 (2) | 23.0 (2) | |
| *Catamenia homochroa* | | V | | | | | 12.1 (2) | | | |
| *C. analis* | V | | | | | | | 12.7 (1) | | |
| *Atlapetes rufinucha* | C | U | F | S, P | g, i, f | – | 22.2 (9) | 20.9 (16) | | |
| *A. torquatus* | R | | N | P, S | i, g | – | 41.7 (3) | | | |
| CATAMBLYRYHNCHINAE | | | | | | | | | | |
| *Catamblyrhynchus diadema* | FC | R | F | S | i, v | – | 14.9 (16) | 13.4 (8) | 13.5 (2) | 12.5 (1) |
| THRAUPINAE | | | | | | | | | | |
| *Chlorornis riefferii* | R | | F | N | f, i | – | 55.0 (1) | 54.0 (1) | | |
| *Chlorospingus ophthalmicus* | R | | F | S | i, f | – | 18.0 (1) | | | |
| *Hemispingus calophrys* | FC | R | N, F | S | i | –, ±, + | 17.0 (17) | 16.4 (10) | | 15.0 (1) |
| *H. superciliaris* | FC | (V) | F | S | i | – | 13.3 (2) | 12.5 (1) | | |
| *H. xanthophthalmus* | FC | | F | S | i | –, ± | 11.4 (3) | 11.3 (3) | | |
| *H. trifasciatus* | R | C | F | S | i | +, – | 14.9 (10) | 13.3 (11) | 14.0 (5) | |

## APPENDIX I
### CONTINUED

| | Relative[1] abundance | | Foraging[2] system | | Diet[3] | Breeding[4] condition | Mean body weight (g)[5] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3050 m | 3300 m | Intersp. | Intrasp. | | | ♂ (N) | ♀ (N) | Juv. ♂ (N) | Juv. ♀ (N) |
| *Thlypopsis ruficeps* | FC | (V) | F | N | i | – | 12.0 (1) | 11.4 (5) | | |
| *Thraupis cyanocephala* | FC | (V) | F | S | f, i | –, ± | 40.0 (6) | 37.0 (4) | | |
| *T. bonariensis* | V | | | | | | | | 32.0 (1) | |
| *Buthraupis montana* | C | U | N, F | L | f, i | –, ±, + | 79.3 (16) | 77.5 (9) | 70.3 (3) | |
| *Anisognathus igniventris* | C | C | F | S | f | –, ±, + | 34.9 (37) | 32.8 (17) | | |
| *Iridosornis jelskii* | | U | F | S, N | f | –, ± | 19.3 (15) | 19.2 (13) | | 16.0 (1) |
| *Delothraupis castaneoventris* | U | U | F | N, P | i, f | – | 26.4 (7) | | | |
| *Tangara vassorii* | U | V | F | S | f, i | – | 17.6 (3) | 17.5 (4) | 16.3 (1) | |
| *Diglossa baritula* | R | V | F | N | n, i | – | 9.3 (1) | 8.6 (1) | | |
| *D. carbonaria* | FC | U | N | N | n, i | | 13.1 (12) | 12.1 (9) | 11.8 (16) | 10.9 (16) |
| *D. lafresnayii* | V | FC | N | N | n, i | –, ± | 16.5 (17) | 15.0 (11) | 14.9 (25) | 14.2 (19) |
| *D. cyanea* | FC | FC | F | N, S | i, f, n | –, ± | 17.6 (12) | 16.6 (20) | 16.5 (5) | 15.5 (9) |
| CARDINALINAE | | | | | | | | | | |
| *Pheucticus aureoventris* | U | V | N, F | N | f | – | | | 47.0 (2) | |
| PARULIDAE | | | | | | | | | | |
| *Myioborus melanocephalus* | FC | U | F | P | i | – | 10.5 (9) | 10.6 (3) | | |
| *Basileuterus luteoviridis* | FC | FC | F | S, P | i | – | 13.7 (18) | 12.2 (11) | | 10.5 (1) |
| *B. signatus* | C | U | N, F | P, S | i | – | 11.5 (21) | 11.1 (16) | | |
| *Conirostrum sitticolor* | R | U | F | P | i | –, ± | 11.0 (2) | 10.8 (3) | | |
| ICTERIDAE | | | | | | | | | | |
| *Psarocolius atrovirens* | (V) | | | | | | | | | |
| *Cacicus chrysonotus* | FC | U | N, F | S | i, n | – | 99.0 (2) | 63.3 (4) | 80.5 (2) | |
| *C. holosericeus* | R | R | N | N, P | i | – | 58.5 (2) | 49.5 (4) | | |
| FRINGILLIDAE | | | | | | | | | | |
| *Carduelis* (sp.) | | (V) | | | | | | | | |

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[1] C = common (>10 noted/day), FC = fairly common (3–10/day), U = uncommon (1–2/day), R = rare (<1 detection/day), and V = visitor (only a few records; not part of the resident avifauna). When the relative abundance symbol is put in parentheses, no specimen was obtained from that site. For visitors, the only additional data presented are body weights, when available.

[2] Terminology for foraging social system follows Buskirk (1976): N = no sociality, F = flocks, P = pairs, S = small flocks (3–5 individuals), and L = large flock (>5 individuals).

[3] i = insectivore (includes all invertebrate prey), f = frugivore, n = nectarivore, v = unidentifiable vegetable matter, and g = granivore. Symbols in parentheses indicate that the diet category is inferred from morphology in the absence of feeding observations or stomach contents analysis. When more than one diet category is listed, the one observed most frequently is listed first.

[4] + = enlarged gonads (arbitrarily, testes >7 × 4 mm for birds under 50 g or >10 × 5 mm for birds over 50 g; largest ova >1 mm diameter for birds under 50 g or >2 mm for birds over 50 g); – = nonreproductive gonads (arbitrarily, testes <4 × 3 mm for birds under 50 g or <7 × 4 mm for birds over 50 g; largest ova ≤1 mm in diameter); ± = intermediate testis size. When more than one condition was noted, the most frequent is given first.

[5] Body weights taken only from specimens from the two study sites.

## APPENDIX II

### FORAGING SUBSTRATE USE AND CHARACTERISTICS FOR BIRDS AT TWO FORESTED SITES IN THE HUMID TEMPERATE ZONE OF THE BOLIVIAN ANDES[1]

| | | Frequency of substrate use | | | | | | | | Characteristics of substrates | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | N | Green foliage | Dead foliage | Bark/stem | Moss[2] | Ground | Fruit | Flower | Air | % Upper-side green leaves | x̄ leaf length (cm) | x̄ leaf width (cm) | x̄ diam. branch (cm)[3] | x̄ diam. fruit (cm) | x̄ corolla length (cm) |
| *Cypseloides rutilus* | 19 | | | | | | | | 1.00 | | | | | | |
| *Pterophanes cyanopterus* | 11 | | | | | | | 1.00 | | | | | | | 5.0 |
| *Coeligena violifer* | 37 | | | | | | | 1.00 | | | | | | | 5.5 |
| *Heliangelus amethysticollis* | 17 | | | | | | | .88 | .12 | | | | | | 2.3 |
| *Chalcostigma ruficeps* | 5 | | | | | | | 1.00 | | | | | | | 2.1 |
| *Metallura aeneocauda* | 5 | | | | | | | 1.00 | | | | | | | 2.7 |
| *M. tyrianthina* | 28 | | | | | | | 1.00 | | | | | | | 1.2 |
| *Piculus rivolii* | 6 | | | .33 | .17 | | .50 | | | | | | | | |
| *Lepidocolaptes affinis* | 11 | | | .18 | .82 | | | | | | | | 10.4 | | |
| *Schizoeaca harterti* | 20 | .55 | | .40 | .05 | | | | | .90 | 8.5 | 2.1 | 3.2 | | |
| *Cranioleuca albiceps* | 36 | .33 | .24 | .27 | | | | | | .25 | 8.6 | 2.9 | 3.5 | | |
| *Margarornis squamiger* | 30 | | .03 | .20 | .77 | | | | | | | | | | |
| *Pseudocolaptes boissonneautii* | 32 | .06 | .06 | | .82 | | | | | | | | | | |
| *Phyllomyias uropygialis* | 9 | .44 | | .22 | .11 | | | .22 | | .00 | | | | | |
| *Elaenia albiceps* | 12 | | | | | | 1.00 | | | | | | | 0.3 | |
| *Mecocerculus leucophrys* | 30 | .73 | | .10 | | | | .10 | .07 | .24 | 6.8 | 3.1 | | | |
| *M. stictopterus* | 35 | .94 | | .03 | .03 | | | | | .21 | 7.8 | 4.8 | | | |
| *Mionectes striaticollis* | 18 | .06 | | | | | .94 | | | | | | | 0.3 | |
| *Myiophobus ochraceiventris* | 51 | .59 | | .02 | | | .35 | | | .47 | 10.9 | 5.9 | | 0.3 | |
| *Ochthoeca rufipectoralis* | 36 | .47 | | | | .36 | | | .17 | .82 | 8.0 | 3.4 | | | |
| *O. frontalis* | 5 | .80 | | .20 | | | | | | 1.00 | | | | | |
| *Myiotheretes fuscorufus* | 3 | .33 | | | | | | | .67 | | | | | | |
| *Notiochelidon murina* | 128 | | | | | | | | 1.00 | | | | | | |
| *N. flavipes* | 26 | | | | | | | | 1.00 | | | | | | |
| *Troglodytes solstitialis* | 16 | .13 | | | .87 | | | | | | | | 11.0 | | |
| *Atlapetes rufinucha* | 31 | .26 | .03 | .19 | .26 | .10 | .03 | .10 | | .63 | 9.7 | 3.7 | | | |
| *Catamblyrhynchus diadema* | 19 | .16 | | .84 | | | | | | | | | 0.6 | | |
| *Hemispingus calophrys* | 28 | .81 | .04 | .11 | .04 | | | | | .50 | 11.8 | 2.6 | | | |
| *H. superciliaris* | 34 | 1.00 | | | | | | | | .46 | 5.6 | 2.7 | | | |
| *H. trifasciatus* | 58 | .96 | | .02 | | | | .02 | | .54 | 7.1 | 3.6 | | | |
| *Thlypopsis ruficeps* | 40 | .86 | .03 | .03 | | | | .08 | | .23 | | | | | |
| *Buthraupis montana* | 35 | .20 | .03 | | .40 | | .37 | | | | | | 4.4 | 0.5 | |

## APPENDIX II
CONTINUED

| Species | N | Frequency of substrate use | | | | | | | | Characteristics of substrates | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Green foliage | Dead foliage | Bark/stem | Moss[2] | Ground | Fruit | Flower | Air | % Upper-side green leaves | $\bar{x}$ leaf length (cm) | $\bar{x}$ leaf width (cm) | $\bar{x}$ diam. branch (cm)[3] | $\bar{x}$ diam. fruit (cm) | $\bar{x}$ corolla length (cm) |
| *Anisognathus igniventris* | 42 | .07 | | | | | .91 | | .02 | | | | | 0.3 | |
| *Delothraupis castaneoventris* | 13 | .15 | | .08 | .77 | | | | | | | | 5.8 | | |
| *Tangara vassorii* | 6 | | | | .33 | | .67 | | | | | | | 0.3 | |
| *Diglossa baritula* | 10 | | | | | | | .80 | .20 | | | | | | 3.6 |
| *D. lafresnayii* | 9 | | | | | | .11 | .89 | | | | | | | 0.8 |
| *D. carbonaria* | 6 | | | | | | | 1.00 | | | | | | | 3.9 |
| *D. cyanea* | 17 | .06 | | | .06 | | .06 | .82 | | | | | | | 2.5 |
| *Conirostrum sitticolor* | 54 | .96 | | | .02 | | | .02 | | .44 | 13.0 | 5.3 | | | |
| *Myioborus melanocephalus* | 88 | .49 | .01 | .02 | .05 | | | .05 | .38 | .31 | 10.9 | 4.7 | | | |
| *Basileuterus luteoviridis* | 70 | .98 | .01 | | | | | | .01 | .20 | 10.4 | 4.9 | | | |
| *B. signatus* | 19 | 1.00 | | | | | | | | .26 | 14.4 | 3.6 | | | |
| *Cacicus chrysonotus* | 5 | | | .20 | .60 | | | .20 | | | | | | | |

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[1] Data for 3050 m and 3300 m sites combined.

[2] Includes other epiphytic vegetation.

[3] Branch diameters include observations from "moss" substrates, all of which were moss-covered branches, as well as "bark/stem" substrates (bare branches).