VERTICAL DISTRIBUTION AND COMPETITIVE INTERACTIONS OF ANT-FOLLOWING BIRDS

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Abstract: Ant-following bird species display different foraging behaviors while following swarms of the army ant *Eciton burchelli*, which may influence where birds distribute themselves in the vertical strata above the swarm front. We hypothesized the existence of two main guilds within the ant-following birds: those that hunt in the air (aerial sallies) and those that hunt on the ground (ground sallies). We looked at height and competitive interactions within and between these strata as a way to evaluate the existence of these foraging guilds. We hypothesized that (1) ant-following bird species would be stratified according to the foraging guilds to which these bird species belong, and (2) that agonistic interactions would occur within the same height strata predicted by foraging guild. The results supported both hypotheses, suggesting that ant-following birds are vertically stratified based on partitioning of feeding zones between foraging guilds, and that the majority of agonistic interactions are within foraging guilds using shared resources.

Key Words: resource partitioning, foraging guilds, ant-following birds, competitive interactions, vertical stratification

INTRODUCTION

Ant-following birds are a group of unrelated insectivores that forage in areas disturbed by swarms of the diurnal army ants, *Eciton burchelli* (Janzen 1983). These birds generally track the front of the army ant swarm, where ground arthropods and other animals are flushed by the advancing ants. Antbirds, woodcreepers and other species compose mixed-species flocks, which draw from the same resource base of terrestrial invertebrates found at the swarm front (Stiles and Skutch 1989). This prompts speculation on how resources are divided between bird species. We propose, based on foraging behavior and life history traits, the existence of two major foraging guilds, ground and aerial foragers, which spatially partition insect resources (Table 1).

We developed two linked hypotheses of how bird behavior may indicate foraging guild. First, we predicted that vertical distribution over the ant

Table 1: Feeding habits and theoretical feeding guild assignments for ant-following species at La Selva Biological Station, Costa Rica.

Species	Feeding Habits[1]	Guild
Tawny-Winged Woodcreeper	Aerial sallies for spiders, insects, lizards	A
Ruddy Woodcreeper	Aerial sallies for spiders, insects; sometimes on ground	A
Chestnut-backed Antbird	Ground sallies for insects, spiders, lizards	B
Spotted Antbird	Ground sallies for smaller insects, spiders	B
Ocellated Antbird	Ground sallies for large insects, spiders, small vertebrates	B
Slaty Antshrike	Ground sallies for large insects, spiders, lizards	B
Plain Antvireo	Gleans insects and spiders from vegetation	B

[1] from Stiles and Skutch (1989)

swarm front of each species would be non-random, with each species found at the same level as other members of its foraging guild. Second, we hypothesized that agonistic interactions occur mainly between species in the same guild and therefore occur within the same vertical strata, indicating that competition exists mainly within foraging guild. Alternatively, vertical distribution may be random without these foraging guilds and all species compete equally for the same foraging position.

METHODS

We observed three different ant-following multi-species flocks at La Selva Biological Station, Costa Rica; one between 08:30 and 12:00 on February 14, 2006 and two between 8:30 and 11:00 on February 15, 2006. Following the army ant swarm front, we recorded the number of individuals of each bird species, their (visually estimated) height above ground, their foraging behaviors, and their agonistic interactions with other individuals. We considered an interaction agonistic when it involved one bird apparently forcing another bird to leave its perch or deviate from its foraging pattern.

RESULTS

We recorded 212 observations of ant-following birds, representing seven species (Chestnut-backed Antbird, *Myrmeciza exsul*; Ocellated Antbird *Phaenostictus Mcleannani*; Spotted Antbird, *Hylophylax naevioides*; Plain Antvireo *Dysithamnus Mentalis*; Ruddy Woodcreeper *Dendrocincla homochroa*; Tawny-winged Woodcreeper, *Dendrocincla anabatina*). We made 99 observations of members from guild A (ground sallying) and 113 observations of members from guild B (aerial sallying). We observed one Great Tinamou, which appeared disoriented. Height differed significantly by species ($F_{6,212} = 31.8$, $P < 0.001$) and guild (Fig. 1).

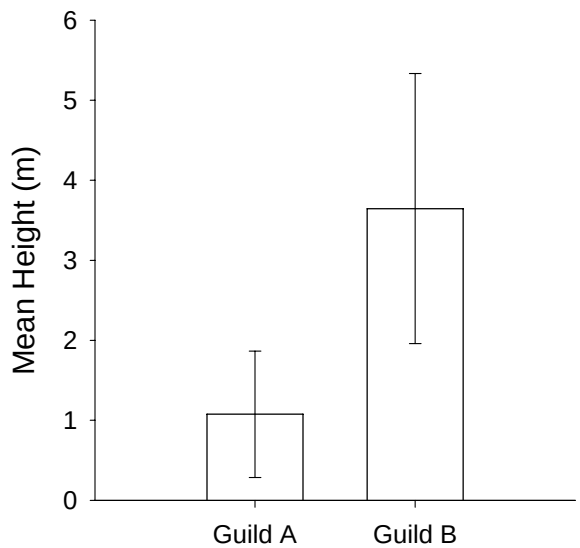

Figure 1: Relationship between foraging guild and the height (mean ± SD) above the ground at which it is typically found ($t = 5.96$, $df = 210$, $P < 0.0001$). Guild A represents five species (Chestnut Antbird, Ocellated Antbird, Plain Antvireo, Spotted Antbird and Slaty Antshrike), while Guild B represents two species (Ruddy Woodcreeper and Tawny-winged Woodcreeper).

We did not observe any agonistic interaction between individuals of guild A and guild B. We observed 18 agonistic interactions among individuals of guild A and 26 agonistic interactions among individuals of guild B (Table 2). We did not observe a substantial difference in agonistic interactions per observation between guild A (0.19 interactions/ observation) and guild B (0.23 interactions/ observation).

Table 2: Number of observed agonistic interactions between ant-following birds by species near La Selva Biological.Station, Costa Rica, with species generally found lower to the ground further to the upper left.

Species	Ocellated Antbird	Spotted Antbird	Chestnut Antbird	Plain Antvireo	Slaty Antshrike	Tawny -winged Woodcreeper	Ruddy Woodcreeper
Ocellated Antbird	1	0	1	0	0	0	0
Spotted Antbird		8	6	0	0	0	0
Chestnut Antbird			1	0	1	0	0
Plain Antvireo				0	0	0	0
Slaty Antshrike					0	0	0
Tawny –winged Woodcreeper						8	6
Ruddy Woodcreeper							12

DISCUSSION

Ant-following bird species at the front of an army ant swarm were distributed non-randomly with respect to height, as predicted by the guild assignments in Table 1. This suggests that vertical position of bird species is based on their foraging location and is not based on a dominance hierarchy of species that monopolize the best foraging space.

Agonistic interactions were also well correlated with foraging guild: interactions occurred exclusively within the strata but without regard to species. These agonistic interactions also support our foraging guilds because it is expected that birds in the same foraging guild are competing for access to the same resources. Since interactions are limited to vertical strata, we reject the alternative hypothesis that a more dominant species is excluding all other species from a certain strata. All species share a common resource: the terrestrial insects that are flushed from the forest floor by army ant swarms. However, the differentiation in height through resource partitioning by foraging guild appears to create niches and allows more species to co-forage than would be expected with one resource.

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BOTTOM-UP AND TOP-DOWN EFFECTS ON ARTHROPOD COMMUNITIES ACROSS A SUCCESSIONAL GRADIENT

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Abstract: Understanding mechanisms of community change during succession is important for understanding biotic regeneration following disturbance. Both top-down and bottom-up effects may drive changes in herbivorous arthropod community structure across a successional gradient. Bottom-up effects may include increasing plant species richness, which may drive increasing herbivore richness, or decreasing leaf quality, which may drive decreasing herbivore richness. Arthropod predators may act as a top-down effect; in the extreme case predator biomass would be inversely proportional to herbivore biomass over a successional gradient. We sampled arthropod communities in three plots (cleared 1 year, 3 years, and 5 years ago) in a lowland tropical rainforest to examine patterns in plant, arthropod herbivore and predator communities. Plant species richness increased with time since disturbance, while herbivore richness decreased. Herbivore biomass was not inversely related to predator biomass. Thus, bottom-up effects based on leaf quality may drive changes in arthropod herbivore communities.

Key Words: succession, arthropods, herbivores, predators

INTRODUCTION

Understanding the mechanisms by which community characteristics change during succession is important for understanding community regeneration following disturbance. Tropical systems experience extremely rapid early succession, and therefore are excellent systems to study the effects of succession on community structure. The herbivore-based trophic system can be abstracted into three levels: plants (primary producers), arthropod herbivores and predators (here we ignore vertebrate herbivores. Herbivore communities may be influenced by plant communities ("bottom-up") and by predatory arthropods ("top-down").

Increases in plant species richness with succession may exert bottom-up effects on herbivore communities (Connell 1978). Increased plant species richness may lead to a greater variety of plant resources available to herbivores and thus a greater richness of herbivores with plot age. Alternatively, changes in plant tissue quality across a successional gradient may exert bottom-up effects on herbivore communities. According to the resource availability hypothesis of plant defense theory, fast growing, gap specialists (early colonizers) will have fewer chemical and structural defenses and are therefore more palatable to herbivores than slow growing, late successional plant species (Coley et al. 2003). Thus, leaf quality may decrease across a successional gradient, decreasing herbivore species richness by eliminating many generalist species.

In contrast to bottom-up effects, top-down effects may influence herbivore communities by reducing herbivore biomass. In extreme cases, total predator biomass would be inversely related to total

herbivore biomass. We tested these broad predictions for how bottom-up versus top-down effects influence arthropod communities across a successional gradient in a lowland tropical rainforest at La Selva, Biological Station.

METHODS

We examined 3 successional plots on the morning of 12 February 2006, along Holdrige trail in La Selva National Park, Costa Rica. The plots were 100 x 100 m areas cleared 1, 3 and 5 years ago. We sampled six 3-m radius subplots within each plot, three at 10 m and three at 20 m from the edge. We collected arthropods using sweep netting, with 20 aggressive passes in a circular pattern off the ground within each subplot. We also collected arthropods from ≈40 g of randomly selected dead leaves suspended within reach. We sorted all arthropods to family and feeding guild (herbivore, predator, or detritivore), and measured volume as a proxy for biomass (mm^3).

To determine how time since disturbance influences the species richness and biomass of plants, herbivores, predators, and detritivores, we ran a one-way ANOVA, followed by a linear contrast when appropriate to test the directionality of the relationship. We used JMP 5.0.1 for all analyses.

RESULTS

In total, we collected 205 arthropods in 13 orders and 60 families. Plant species richness increased with plot age (Fig. 1; $F_{2,15} = 29.61$, $P < 0.001$) while herbivore species richness decreased with plot age (Fig. 2; $F_{2,15} = 2.50$, $P = 0.12$). Predator species richness did not change with increasing plot age

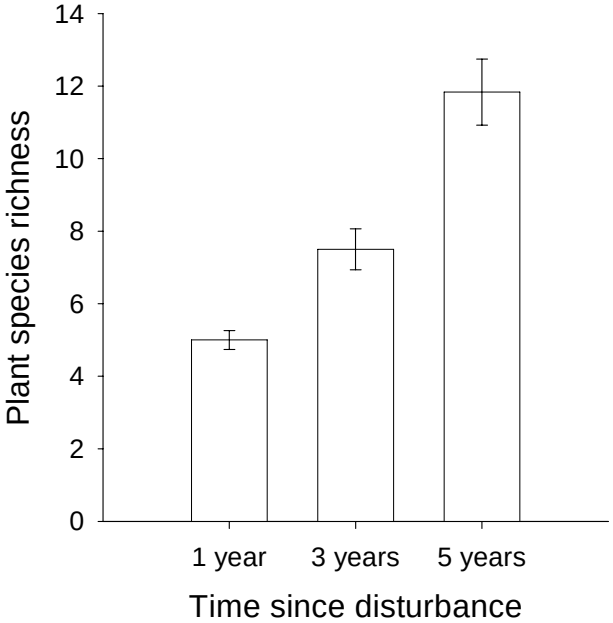

Figure 1. Plant species richness (mean ± SE) across 3 successional plots (cleared 1, 3, and 5 years ago) at La Selva Biological Station, Costa Rica ($F_{2,15} = 29.61$, $P < 0.0001$; $P < 0.0001$ for linear trend).

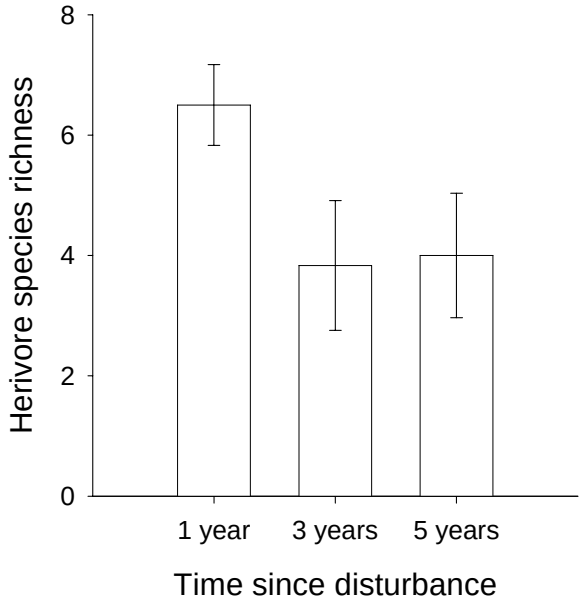

Figure 2. Arthropod herbivore species richness (mean ± SE) across 3 successional plots (cleared 1, 3, and 5 years ago) at La Selva Biological Station, Costa Rica ($F_{2,15} = 2.50$, $P = 0.12$; $P = 0.081$ for linear trend).

Table 1. Comparison of alpha taxa richness (mean ± SE, n = 6) plots to total taxa richness in three successional plots at La Selva Biological Station, Costa Rica. Total taxa richness was based on the pooled samples for a plot.

Plot age (years)	Alpha Herbivore Richness	Total Herbivore Richness	Alpha Predator Richness	Total Predator Richness
1	6.50 ± 0.95	29	3.83 ± 0.95	4
3	1.67 ± 0.32	16	1.67 ± 0.32	5
5	0.67 ± 0.25	13	0.50 ± 0.25	3

($F_{2,15}$ = 0.09, P = 0.91). All three successional plots showed evidence of β diversity as species richness increased with additional subplots (Table 1). Herbivore biomass did not change with plot age ($F_{2,15}$ = 1.22, P = 0.32). Predator biomass did not change with plot age ($F_{2,15}$ = 0.88, P = 0.44). As our sampling techniques were designed to sample arthropod herbivores and predators we did not analyze the incidental captures of detritivores.

Discussion

Results indicated the importance of bottom-up effects on herbivore richness. Plant species richness increased with time since disturbance as predicted for areas during early succession (Connell, 1978). However, herbivore species richness decreased with time since disturbance. One possibility is that decreased plant nutritional quality drives decreased herbivore species richness. We found no relationship between herbivore and predator biomass. Thus, as is generally found in terrestrial communities (Shurin et al. 2002), bottom-up effects on herbivore communities appear more important than top-down for early successional tropical forest at La Selva.

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TROPICAL BIRD COMMUNITY STRUCTURE IN FLOWERING AND FRUITING TREES

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Abstract: Bird species may use flowering and fruiting trees differently in time and space, as a consequence of either niche-partitioning or a dominance hierarchy. At La Selva Biological Reserve, Costa Rica, we observed birds foraging on flowering and fruiting trees to evaluate whether the spatial or temporal distribution of birds on these trees was nonrandom. We found that some species are distributed nonrandomly in space, but temporal distribution was random. The nonrandom distribution did not seem to be a result of an established dominance hierarchy; rather, structure probably results from niche partitioning.

Key Words: Quararibea cordata, Ficus pertusa, *bird community structure, niche partitioning, dominance hierarchy*

INTRODUCTION

Many tropical bird species are attracted to fruiting and flowering trees, which are ephemeral sources of concentrated resources. At La Selva Biological Reserve, Costa Rica, we observed an introduced, cauliflorous Bombacaceae tree, *Quararibea cordata* that supported an abundance and richness of colorful bird species that fed on its nectar (even though the tree was only 10 m tall). We hypothesized that with the high concentration of birds and resources in a small area, species would segregate spatially or temporally. Alternatively, species could be distributed randomly in space and time.

Nonrandom distribution of bird species in space or time could be due to either niche partitioning or a dominance hierarchy. According to the niche partitioning hypothesis, bird species will use a common resource in different ways, and a species' use will not be affected by the presence of other species. In contrast, the dominance hierarchy hypothesis suggests that dominant birds will displace subdominant species to lower quality areas in the tree. These trends may apply on the temporal scale as well. Thus, by comparing how subdominant species behave in the presence and absence of dominant species, we can distinguish whether a dominance hierarchy influences foraging locations.

METHODS

We conducted our study 12 - 14 February at the OTS biological station, La Selva, Costa Rica. We searched extensively for flowering trees, but found only two trees (*Quararibea cordata* and *Erythrina* sp.) with birds visiting flowers. We also observed a fruiting tree, *Ficus pertusa*. We visited each of the three trees eight times daily. For each observation period, we recorded the time, what species were present, and the location of individuals in the tree at that moment in time. Vertical location was categorized as low, middle, or high and horizontal location was categorized as either interior or peripheral.

We evaluated our data for evidence of structure, and for evidence of mechanisms that could produce structure. To compare the mean abundance of birds and the mean species richness between trees, we ran t-tests. We performed a chi-square test of vertical position (low, middle, or high) by bird species, and another chi-square test of horizontal position (interior or periphery) by bird species. To evaluate temporal structure, we performed a chi-square test of the relative abundance of each bird species by the time of day. We evaluated whether the dominance hierarchy hypothesis explains structural arrangement in the trees, we used a chi-squared test to evaluate whether subdominant birds distribute differently in the presence of high or low abundances of dominant birds. We used JMP 5.0.1 for all analyses.

RESULTS

In 46 observations, we recorded 448 birds of 30 species in the three trees (Appendix A). We observed 17 species at *Q. cordata*, 14 species at *F. pertusa*, and five species at *Erythrina*. There was little overlap between the species represented on the three trees; one species overlapped between *Q. cordata* and *F. pertusa* and four species overlapped between *Q. cordata* and *Erythrina*. The number of birds on *Erythrina* was too low to evaluate structure, so we limited our comparisons to *Q. cordata* and *F. pertusa*. *Q. cordata* had more birds per observation (13.2 ± 1.8, mean ± SE) than *F. pertusa* (6.0 ± 2.3; $t_{1,33}$ = 2.47, P = 0.02), and more species per observation (5.1 ± 0.46) than *F. pertusa* (2.8 ± 0.60; $t_{1,33}$ = 3.10, P = 0.004).

We found non-random vertical spatial structure of bird species on both *Q. cordata* (χ^2 =43.99, df = 10, P = <0.0001), and *F. pertusa* (χ^2 = 10.03, df = 2, P = 0.01). On *Q. cordata*, Montezuma Oropendolas and Northern Orioles were higher in the tree, Green Honeycreepers were lower in the tree, and White-necked Jacobins and Rufous-tailed Hummingbirds favored the middle relative to other birds (Table 1). In *F. pertusa*, Olive-backed Euphonia preferred the middle, while Silver-throated Tanagers were higher in the tree (Table 1). The distribution of birds did not differ between the interior and periphery in either *Q. cordata* (χ^2 = 7.81, df = 5, P = 0.16) or *F. pertusa* (χ^2 = .54, df = 1, P = 0.46). Birds were also randomly distributed in time in both *Q. cordata* (χ^2 = 10.83, df = 10, P = 0.30) and in *F. pertusa* (χ^2 = 0.50, df = 2, P = 0.78).

We observed only four agonistic interactions between species. Montezuma Oropendolas were involved in two of these interactions; the other two interactions were between hummingbird species. We tested the dominance hierarchy hypothesis using the Montezuma Oropendolas as a dominant species, and Green Honeycreepers as the subdominant species because they were the most common species observed, and were smaller than the oropendolas.

There was a marginally significant shift in spatial arrangement of Green Honeycreepers, depending on the higher or lower abundance of Montezuma Oropendolas. Montezuma Oropendolas tended to be high in the tree. When there was a higher abundance of Montezuma

Oropendola on *Q. cordata*, Green Honeycreepers were concentrated in the top and bottom of the tree; in the absence of oropendola, a greater percentage of honeycreepers were found in the middle of the tree ($\chi^2 = 5.16$, df = 2, P = 0.06).

Table 1. Observations of vertical locations of birds in flowering (*Q. cordata*) and fruiting (*F. pertusa*) trees at La Selva, Costa Rica. Expected values for each strata are given in parantheses, and are based on the overall distribution of all bird species in each tree. A chi-squared test showed that the arrangement of birds in both trees was non-random, with certain species tending to be found in certain strata.

Quararibea cordata

Bird Species	Number	Low	Middle	High	Chi-square
Green Honeycreeper	81	28 (18.1)	23 (28.0)	30 (34.9)	7.0
Montezuma Oropendola	69	7 (15.4)	18 (23.9)	44 (29.7)	12.9
White-necked Jacobin	41	12 (9.1)	20 (14.2)	9 (17.7)	7.5
Northern Oriole	28	1 (6.2)	10 (9.7)	17 (12.1)	6.4
Shining Honeycreeper	23	9 (5.1)	9 (8.0)	5 (10.0)	5.5
Rufous-tailed Hummingbird	18	1 (4.0)	10 (6.2)	7 (7.8)	4.6
Totals	*260*	*58*	*90*	*112*	*44.0* *P<0.001*

Ficus pertusa

Bird Species	Number	Low	Middle	High	Chi-square
Olive-backed Euphonia	37	7 (4.8)	23 (20.6)	7 (11.6)	3.2
Silver-throated Tanager	17	0 (2.2)	7 (9.4)	10 (5.4)	6.9
Totals	*54*	*7*	*30*	*17*	*10.0* *P=0.003*

DISCUSSION

Birds were arranged non-randomly in our two sample trees, possibly due to niche partitioning. We found no evidence of a dominance hierarchy. Green Honeycreepers did not move into the space occupied by Montezuma Oropendola when the Montezuma Oropendolas were less abundant. Furthermore, we observed few agonistic interactions between species which would support a dominance hierarchy, and none of the species we observed are described as aggressive (Stiles & Skutch 1989).

The structure we observed appears to result from niche partitioning. On *Q. cordata*, birds that flew into the tree from above the canopy (Montezuma Oropendola and Northern Oriole) tended to forage high in the tree, whereas birds that flew to the tree from below the canopy (honeycreepers and hummingbirds) tended to forage in the low or middle section.

However, if niche partitioning alone is the mechanism driving structure, we would expect honeycreepers to remain in the same place in the tree regardless of the abundance of oropendolas. Because Green Honeycreepers changed positions in the absence of Montezuma Oropendolas (in the opposite direction predicted by the dominance hierarchy hypothesis), the relationship between Montezuma Oropendolas and Green Honeycreepers is more complicated than predicted by the niche portioning hypothesis, and it may be influenced by other bird species which we could not include in our test. This result suggests that structure in trees is caused by more than niche partitioning alone. More data from more bird species is needed to rigorously evaluate the mechanisms driving structure.

It is also possible that there is structure on scales we did not measure. Birds may partition flowers based on flower position on the branch, branch size, orientation of the branch, etc. Structure on other scales could also result from a dominance hierarchy.

Additionally, *Q. cordata* is an introduced species, but birds showed highly significant structure in their spatial arrangement. Future studies could evaluate if and how structure differs between similar introduced and native species.

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Appendix 1. Bird species observed feeding on nectar or fruit on three trees, Feb 12-14, 2006, at La Selva, Costa Rica. *Quararibea cordata* and *Erythrina* spp. provided nectar for birds, and *Ficus pertusa* provided fruit. Birds are arranged taxonomically.

Common name	Taxon	Tree(s) on which birds were found
Unidentified Parakeet	Family Psittacidae	*Erythrina*
Red-footed Plumeleteer	*Chalybura urochrysia*	*Q. cordata*
White-necked Jacobin	*Florisuga mellivora*	*Q. cordata*
Rufous-tailed Hummingbird	*Amazilia tzacatl*	*Q. cordata*
Chestnut-colored Woodpecker	*Celeus castaneus*	*Q. cordata*
Black-cheeked Woodpecker	*Melanerpes pucherani*	*Q. cordata*
White-ruffed Manakin	*Corapipo leucorrhoa*	*F. pertusa*
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	*F. pertusa*
Mistletoe Tyrannulet	*Zimmerius vilissimus*	*F. pertusa*
Pale-vented Robin	*Turdus obsoletus*	*F. pertusa*
White-throated Robin	*Turdus assimilis*	*F. pertusa*
Bananaquit	*Coereba flaveola*	*Q. cordata*
Black-cowled Oriole	*Icterus dominicensis*	*Q. cordata*
Northern Oriole	*Icterus galbula galbula*	*Q. cordata*
Montezuma Oropendola	*Psarocolius montezuma*	*Q. cordata*, *Erythrina*
Chestnut-headed Oropendola	*Psarocolius wagleri*	*Q. cordata*, *Erythrina*
Scarlet-rumped Cacique	*Cacicus uropygialis*	*Q. cordata*, *Erythrina*
Olive-backed Euphonia	*Euphonia gouldi*	*F. pertusa*
Shining Honeycreeper	*Cyanerpes lucidus*	*Q. cordata*
Red-legged Honeycreeper	*Cyanerpes cyaneus*	*Q. cordata*
Emerald Tanager	*Tangara florida*	*F. pertusa*
Silver-throated Tanager	*Tangara icterocephala*	*F. pertusa*
Green Honeycreeper	*Chlorophanes spiza*	*Q. cordata*, *F. pertusa*
Bay-headed Tanager	*Tangara gyrola*	*F. pertusa*
Golden-hooded Tanager	*Tangara larvata*	*Q. cordata*, *F. pertusa*
Scarlet-rumped Tanager	*Ramphocelus passerinii*	*Q. cordata*, *F. pertusa*
Buff-throated Saltator	*Saltator maximus*	*F. pertusa*
Black-faced Grosbeak	*Caryothraustes poliogaster*	*F. pertusa*