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GROUND VERSUS CANOPY METHODS FOR THE STUDY OF BIRDS IN TROPICAL FOREST CANOPIES: IMPLICATIONS FOR ECOLOGY AND CONSERVATION

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Abstract. Birds of the forest canopy are important components of tropical forest ecosystems, but difficulty of access or viewing into the canopy complicates their study. If ground methods are biased against canopy birds, as has been suggested, this bias could affect our understanding of forest ecology as well as biological monitoring and conservation practices. This study is the first to quantitatively compare results from ground- and canopy-based methods of censusing canopy birds. I used three methods to assess differences in ground-based and canopy-based methods for detecting forest birds in a 100-ha plot of lowland forest in northern Honduras: (1) point counts from the ground, (2) 22 repeat censuses from two canopy trees, and (3) single censuses from 22 canopy trees. I counted birds for a full annual cycle from April 2006 to April 2007 and recorded 157 species in over 4000 individual detections. Ground methods significantly underestimated species and familial richness as well as abundance of individuals in the canopy stratum. On the basis of these results, I predict that the use of ground methods alone misses 25 to 50% of the species richness for some migrant and resident families and underestimates the density of some species by as much as 25%. These findings highlight the risk of relying on ground-based methods for bird studies in structurally complex tropical forests; reliance on ground-based methods may negatively affect long-term biological monitoring and the setting of conservation priorities for tropical forests.

Key words: *biological monitoring, birds, community composition, forest canopy, Honduras, rain forest.*

Muestreos desde el Suelo y en el Dosel para el Estudio de Aves en el Dosel de Bosques Tropicales: Implicaciones para el Monitoreo Biológico y la Conservación

Resumen. Las aves de dosel son componentes importantes de los ecosistemas de bosque en el Neotrópico, pero su estudio ha sido complicado por la dificultad de acceso al dosel o por la dificultad de observarlas desde el suelo. Si los muestreos desde el suelo son sesgados en contra de la detección de aves del dosel, como se ha sospechado, este sesgo podría afectar nuestra habilidad de entender la ecología de bosques como también el monitoreo biológico y las prácticas de conservación. El presente estudio es el primero que compara de manera cuantitativa los resultados de métodos de censo desde el suelo y desde el dosel para aves de dosel. En una parcela de 100-ha en el norte de Honduras usé tres métodos de censado para evaluar las diferencias entre los censos desde el suelo y desde el dosel: (1) conteos en puntos en el suelo, (2) 22 conteos en puntos repetidos desde dos árboles emergentes, y (3) 22 conteos en puntos no repetidos desde 22 árboles diferentes. Realicé los muestreos de aves durante un ciclo anual completo desde abril del 2006 hasta abril del 2007, periodo durante el cual detecté 157 especies en más de 4000 observaciones. Los métodos de conteo desde el suelo subestimaron la riqueza de especies y familias como también las abundancias en el estrato del dosel. Con base en estos resultados, predigo que entre el 25 y el 50% de la riqueza de especies de algunas familias migratorias y residentes no hubiese sido registrada si el estudio hubiese estado basado sólo en muestreos desde el suelo, y que la densidad poblacional de ciertas especies pudiese haber sido subestimada hasta en un 25%. Estos resultados demuestran el riesgo de basarse sólo en métodos de censo realizados desde el suelo en los estudios sobre aves en bosques tropicales estructuralmente complejos. Además, los métodos de muestreo de aves de dosel basados sólo en conteos desde el suelo no son adecuados para el monitoreo a largo plazo de las tendencias poblacionales, y pueden afectar la determinación de las prioridades de acciones para la conservación de bosques tropicales.

INTRODUCTION

As the rapid pace of tropical deforestation continues, improving our understanding of the processes that create and maintain forest biodiversity is increasingly essential for the continued preservation of the forests that remain (Millennium Ecosystem Assessment 2005). This understanding, in turn, is directly tied to the quality and variety of methods used to observe and study both processes and diversity. In tall and structurally complex tropical forests, a complete understanding of forest ecosystems must address diversity and ecological

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interactions at all levels of the forest (Lowman and Rinker 2004). Development of field methods for the study of forest canopies, however, has been hindered by the difficulty of gaining access or seeing into the forest canopy.

Birds are a conspicuous and important component of tropical forest ecosystems. Canopy bird communities include important functional groups, such as seed dispersers, pollinators, and top predators (Howe 1977, Nadkarni and Matelson 1989, Blake and Loiselle 2000, Holbrook and Smith 2000, Anderson 2001). Long-distance and elevational migrants also occur in the canopy, and their conservation requires an understanding of their ecology, distribution, and abundance (Loiselle 1987, Powell and Bjork 1995, Chaves-Campos et al. 2003). Of further conservation concern is the suggestion that canopy bird species may be disproportionately sensitive to forest fragmentation (Castelletta et al. 2000, Robinson et al. 2000, Sodhi et al. 2004), and several canopy species (e.g., large raptors, macaws, and some frugivores) are threatened or endangered in Middle America (Terborgh and Winter 1980, Kattan 1992, Levey and Stiles 1994). It follows that the conservation of tropical forests will depend in part on an accurate appreciation of canopy birds and their interactions within the forest ecosystem.

One of the methods used most frequently to study the abundance, distribution, and ecology of forest birds is the point count (Ralph et al. 1995). Point-count data are used to make inferences about the presence and abundance of birds, but an important consideration of this method is the probability of the birds' detection (Farnsworth et al. 2002), which can vary widely with species, habitat, and time of day or year, among other factors (Blake 1992, Ralph et al. 1995, Pacifici et al. 2008). The ability of an observer on the ground to detect birds in a tropical forest canopy varies dramatically because of (1) the range of conspicuousness of different species depending on size, coloration, vocalizations, and movements and (2) the dense foliage and distance that separate the observer from the canopy (Pacifici et al. 2008). In short, some canopy species should be harder to detect from the ground, in particular those that have soft vocalizations, call infrequently, or remain perched for long periods of time. The difficulty of detecting such species has led to the conclusion that canopy species are likely underrepresented in otherwise comprehensive studies of neotropical forest-bird assemblages that rely on ground-based sampling (Robinson et al. 2000, Blake 2007).

A few pioneering studies have advanced methods for studying birds in neotropical forest canopies (Greenberg 1981, Loiselle 1988, Naka 2004). Despite such advances, no attempt has been made to quantify the differences between ground-based and canopy-based data on canopy birds. Because of the continued reliance on ground-based methods, such a comparison is crucial to assessing their value for the study of canopy birds and to determine what biases or limitations may exist. Any substantial weaknesses that are revealed could have major implications for the understanding of forest bird communities, ecosystem processes, and the conservation of both.

The major goal of this study was to address the basic question of the relative validity of ground-based methods for the study of canopy birds. Therefore, I compared the results of ground point counts and two types of canopy point counts in a 100-ha plot in northern Honduras sampled over a complete annual cycle. To my knowledge, this study is the first to make such a comparison and the first to use canopy-based methods to sample canopy birds in a 100-ha plot. A quantitative definition of what constitutes a "canopy bird species" has remained elusive but should prove useful in discussions of canopy bird ecology and conservation. To compare canopy and noncanopy birds, I combined the data sets to define quantitatively the core canopy species of the study area. I then compared patterns of species richness, as well as family and species composition, as represented by the respective data sets derived from the three methods. Finally, I compared detection rates of canopy birds as a whole and of groups of quieter or less conspicuous species that I suspected would be underrepresented in ground-based data sets.

METHODS

STUDY AREA

I delineated a 100-ha study site (15° 43.40′ N, 86° 44.08′ W) in the Río Cangrejal valley on the humid north flank of Pico Bonito National Park, Honduras. The park encompasses 107 090 ha and elevations ranging from 50 to 2480 m (FUPNAPIB 2004). A majority of the park is primary forest with no recent history of human disturbance. Annual precipitation and mean temperature for the site are 2900 mm and 26° C, respectively. The wet and dry seasons are distinct: the driest months are April and May with an average monthly rainfall of 89 mm; the wettest months are November and December with an average monthly rainfall of 510 mm (FUPNAPIB 2004).

Slopes in the study area are nearly flat to moderately steep, and elevations range from 100 to 350 m. The forest averages 35–40 m high, and canopy emergents are rare. Primary and mature secondary moist forests are both present, with primary forests constituting about 60% of the study area. Common overstory tree species include *Symphonia globulifera, Vochysia guatemalensis, Virola koschnyi, Tapipira guianensis, Astronium graveolens, Bursera simaruba, Pouteria* spp., *Ficus* spp., *Calophyllum brasiliense, Dialium guianensis,* and *Schizolobium parahybum*. Numerous wind-snapped trees, gaps, and canopy vine tangles suggest a high incidence of weather-related disturbance.

SAMPLING METHODS

I tested three methods, one ground-based and two canopy-based, for their effectiveness in detecting canopy birds. The first method (henceforth ground) used point transects located along pre-existing trails. I established 30 count points along two trails that bisected the study area. Stations were separated by 100 m. This spacing was chosen because many neotropical species are hard to hear at distances >30 m (Terborgh et al. 1990, Robinson et al. 2000, Blake 2007). Censuses started 30 min after sunrise and typically lasted 3 hours, during which I normally covered approximately 1.3 km and 13 points. I selected the starting time to standardize sampling times with canopy censuses (see below). I rotated starting points to ensure, as much as possible, that all points were covered early in the morning when vocal activity was greatest. I conducted counts on days with no rain and little or no wind and terminated counts when rain or wind interfered with the detection of birds. I counted birds for 10 min at each point. Any individual detected from more than one point was noted as such, but only the first detection was used in analyses. The maximum number of individuals per species, summed for all points of a given census walk, was the datum used in analyses.

For the second method (repeat-tree method), I conducted repeat censuses from the crowns of two trees, a method similar to that of previous canopy-bird studies (Greenberg 1981, Loiselle 1988, Naka 2004). The first tree was a 45-m tall *Vochysia guatemalensis* in mature secondary forest at 115 m. The second tree was a 60-m tall *Virola koschnyi* in primary forest at 220 m. The trees were separated by 1 km. I conducted 22 censuses from these two trees. For the third method (single-tree method), I conducted single censuses from the crowns of 22 separate trees interspersed throughout the entire study area. I used a crossbow and single-rope technique to climb canopy trees (Sillett and Van Pelt 2000). I selected census trees on the criteria that they were safe to climb, had an open crown structure that allowed views out of the census tree, and were a minimum of 50 m from other census trees. Census trees closer than 100 m to each other were censused in different seasons (see below).

All canopy censuses began 30 min after sunrise and lasted 3 hours. Following the protocol of Loiselle (1988) and Naka (2004), I further subdivided the 3-hr censuses into 12 consecutive 15-min intervals. The use of short intervals facilitates tracking individual birds, which can be distinguished by differences in plumage and location in the forest, and avoids double counting (i.e., it is easier to follow individual birds and their direction of travel over 15 min than over 3 hr). The maximum number of individuals per species within a 15-min period was used for analysis of census results, unless additional individuals were identified on the basis of sex or plumage. Canopy census plots had a radius of 150 m and an area of 7.1 ha. Additionally, both repeat trees and eight single trees were paired with count points on the ground.

I recorded all birds seen or heard and categorized them into one of four forest strata: (1) *ground* (soil, leaf litter, and fallen logs), (2) *understory* (the space from the ground to 2 m), (3) *midstory* (the space between the understory and canopy), and (4) *canopy* (the sum of all tree crowns exposed to the sky above; Bongers 2001, Fig. 1C). Birds flying over the forest were noted as such and excluded from analyses. Finally, I noted for every observation whether the initial detection cue was by sight or sound.

I sampled birds over a complete annual cycle from April 2006 to April 2007. I subdivided the year into four seasons—early and late dry, and early and late wet—to compare seasonal variation in species abundance. This technique has been used in previous studies of neotropical forest birds (Greenberg 1981, Loiselle 1987, 1988, Blake 1992) to account for changes in forest phenology, principally the development and abundance of certain resources used by birds or their prey (e.g., flowers, nectar, fruit, insects, and leaves) that may affect the seasonal abundance and distributions of birds. Furthermore, seasonal changes in leaf density caused by leaf fall and regeneration, as well as natural levels of background noise, particularly cicadas, can affect the detectability of birds (Pacifici et al. 2008).

STATISTICAL ANALYSES

Because of differences in the spatial distribution, size, and number of plots used in each method, I do not attempt to estimate densities of species detected by each method. Rather, I present numbers of individual detections (by sight or sound) per method. This conservative approach focuses on the ability of each method to detect species and individuals in the canopy rather than to describe the canopy-bird community *per se* and is in line with the scope of the current study.

I used the method of Neu et al. (1974) to quantify birds' preference for the canopy stratum. I established 95% confidence limits, based on Bonferroni's adjustment of the significance level, around the observed frequency of detection in the canopy stratum for species with ≥4 detections. A significant preference for the canopy was indicated by expected values below the 95% confidence limits for the observed values (Haney and Solow 1992, Cardoso da Silva et al. 1996). I refer to species that met this criterion as core canopy species. I excluded from analyses nocturnal species and birds flying over the forest. Taxonomy follows AOU (1998) and supplements.

I used rarefaction analyses to compare rates of species accumulation among the three methods. Rarefaction curves are produced by repeatedly and randomly resampling the pool of observations and plotting the average number of species represented by *n* individuals; they are therefore a statistical representation of species-accumulation curves (Gotelli and Colwell 2001, Magurran 2004). I used Chao 1 and Chao 2 nonparametric estimators (Magurran 2004) to estimate species richness from each method. These analyses were conducted with EstimateS version 7.5 (Colwell 2005).

I followed the methods of Pitman et al. (2001) and Blake (2007) to compare the number of detections per family. This method tests the null hypothesis that the three methods are equivalent in terms of species or family composition. If two

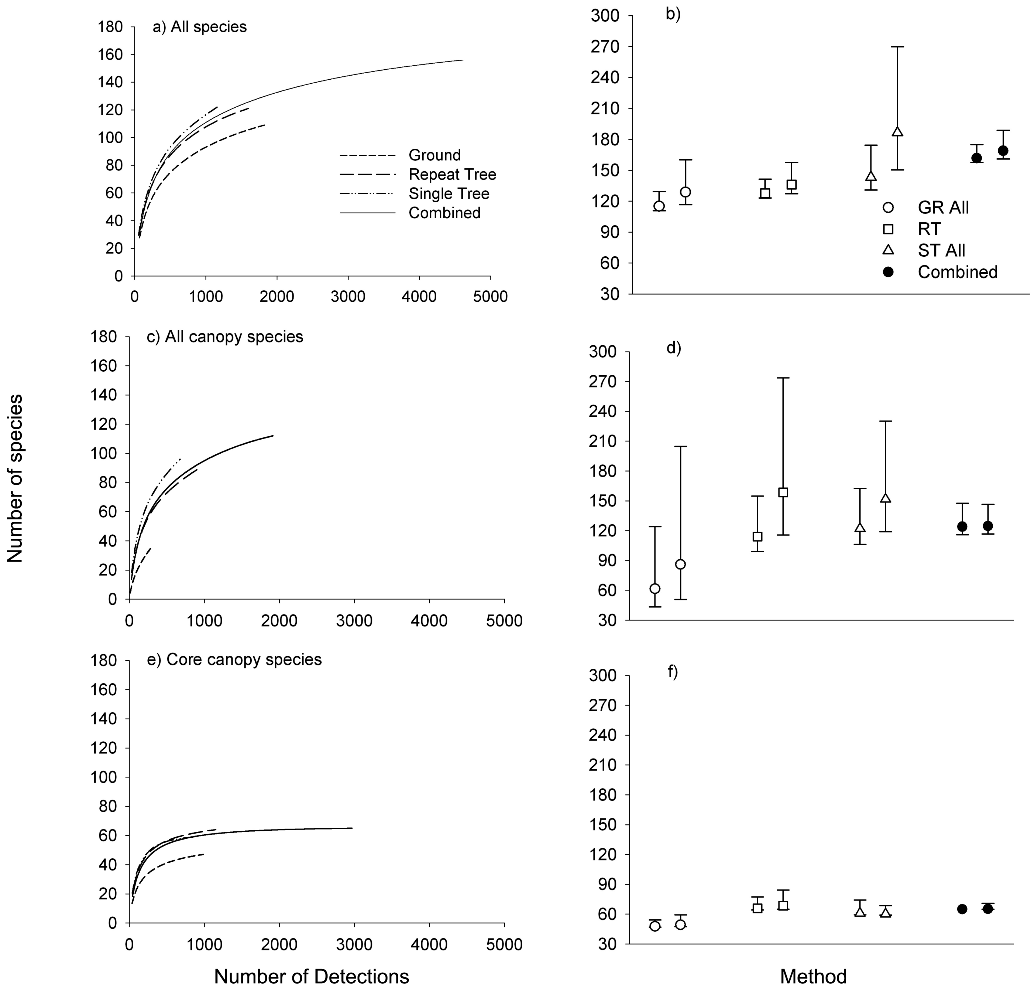

FIGURE 1. Sample-based rarefaction curves (left column) and corresponding estimates of species richness (right column) for three census methods and the combined data set, Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Each pair of cells depicts all detections of all species (a, b), canopy detections of all species (c, d), and all detections of core canopy species (e, f). Each duo in b, d, and f corresponds to richness estimates from Chao 1 and Chao 2 estimators, respectively. Shapes and vertical bars represent means and 95% confidence intervals, respectively.

methods are equivalent in the number of detections, then the slope of the regression line should be equal to 1 (Blake 2007). I used two subtly different approaches to compare my ability to detect canopy birds with each census method: (1) the hourly detection rate of all species and individuals in the canopy stratum and (2) the hourly detection rate of core canopy species and individuals in all forest strata. The first approach addresses the question, "are the methods equal in their ability to detect birds in the canopy?" The second approach addresses a different question, "are the methods equal in their ability to detect those species that spend a substantial portion of their time in the forest canopy?" I used mixed-model ANOVA to control for the effects of season and forest type and to test for an effect of method on the hourly detection rates of species and individuals. Data were first square-root transformed to meet assumptions of normality. I used post hoc Tukey's pairwise comparisons to test for significant differences between pairs of methods.

I used a two-step process to test for an effect of method on the hourly detection rates of three groups of inconspicuous canopy species, namely, (1) inconspicuous residents with soft or infrequent vocalizations, (2) inconspicuous migrants, and (3) canopy hummingbirds. For each group I considered only those species that qualified as core canopy species and compared the detection rate on the basis of all individuals within each group that were detected in any stratum. To test for differences, I first used a Kruskal–Wallis test to test for an overall effect of method on detection rates for each group. Upon finding a significant effect of method, I then used a Wilcoxon signed-rank test to make pairwise comparisons between methods. I used this same approach to test for differences between detection rates of highly vocal and conspicuous canopy

TABLE 1. Number of species and detections (by sight or sound) by three census methods in 100 ha near the Río Cangrejal, Pico Bonito National Park, Honduras.

			Number of species/number of detections			
			All species		Core canopy species	
Method	Censuses	Census hours	All strata	Canopy stratum	All strata	Canopy stratum
Ground	27	66.7 (2.4 ± 0.56)	110/1824	36/300	47/986	31/329
Repeat-tree	22	66 (3.0 ± 0)	121/1598	91/936	64/1149	64/900
Single-tree	22	66 (3.0 ± 0)	123/1191	96/675	59/863	59/614
Total	71	198.7	157/4613	112/1911	65/2998	65/1843

species. Results of all statistical tests were assumed significant at $P < 0.05$.

RESULTS

NUMBERS OF DETECTIONS AND SPECIES

I conducted a total of 71 censuses from April 2006 to April 2007, resulting in 4613 individual detections of 157 species, 112 of which I observed in the canopy (Table 1). I recorded an additional 27 species outside standardized surveys but excluded these from analyses. Sixty-five species (60% of all species detected in the canopy) qualified as core canopy species. Species-accumulation curves for all species suggest that most species on the plot were detected by the combination of methods but that sampling by any single method was less complete (Fig. 1a). Curves for detections in the canopy stratum do not reach asymptotes, suggesting that some species observed in lower strata would eventually be encountered in the canopy stratum (Fig. 1c). Sampling of core canopy species was more complete, with all curves quickly reaching asymptotes (Fig. 1e). The actual number of species estimated for the study area by the combined data set lies between 162 and 189, not significantly greater than the 156 actually observed (Fig. 1b). Richness estimates for core canopy species by the canopy methods and the combined data set did not differ, but all three of these estimates were significantly higher than those derived from ground censuses (Fig. 1f). Repeat-tree and single-tree censuses detected nearly the full complement of core canopy species, whereas the ground censuses detected only 47 (72%) of all core canopy species. On the basis of the level of sampling I achieved, richness estimates for all canopy species did not differ regardless of census method (Fig. 1d).

Distributions of abundances of the core canopy species according to canopy and ground censuses differed significantly when comparisons were limited to canopy detections only (Kolmogorov–Smirnov two-sample tests; Fig. 2b, Table 2). Most of the curve for ground censuses lies below the curves for canopy censuses, indicating (1) larger differences in abundance by species and (2) a greater predominance of common species and an omission of rare ones. These patterns disappear when detections of core canopy species in all strata are considered (Fig. 2a, Table 2), in which case there were no significant differences between methods.

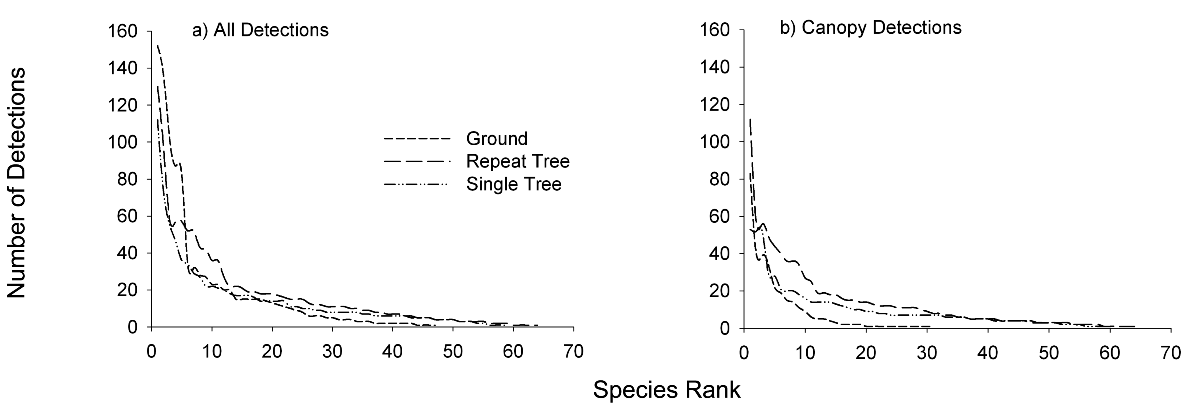

FIGURE 2. Rank-abundance curves based on numbers of detections (by sight or sound) of core canopy species in all strata (a) and the canopy stratum only (b) on the 100-ha Río Cangrejal study plot, Pico Bonito National Park, Honduras, April 2006–April 2007.

TABLE 2. Kolmogorov–Smirnov two-sample significance tests for differences between census methods of rank-abundance distributions of core canopy species.

Comparison	KS statistic	*P*
Detections in the canopy stratum		
Ground–repeat-tree	0.16	0.014
Ground–single-tree	0.18	0.006
Repeat-tree–single-tree	0.08	0.489
Detections in all strata		
Ground–repeat-tree	0.05	0.906
Ground–single-tree	0.07	0.638
Repeat-tree–single-tree	0.05	0.904

FAMILY COMPOSITION

I observed 27 families in the canopy stratum (Table 3). Ground censuses detected eight fewer families in the canopy than repeat-tree censuses and nine fewer families than single-tree censuses. The pattern of species richness per family was the same for the repeat-tree and single-tree methods, as indicated by the slope of the regression being equal to 1.0 (Fig 3c). In contrast, the pattern of species richness per family by either canopy method differed significantly from that by the ground method, as indicated by slopes deviating substantially from 1.0 (Fig. 3a, b). With only two exceptions, species richness per family was greater for both canopy methods than for the ground method. Patterns of detections per family were less precise, with no relationship between methods approaching a slope of 1.0 (Fig. 3d, e, f), although once again the canopy methods were most similar. Substantially more individuals were detected in the canopy during canopy censuses than during point counts from the ground.

SPECIES COMPOSITION

I found important differences among dominant species as detected by the three census methods. Eleven of the top 20 species were detected by all three methods, but in no case were species ranked the same in numbers of detections by the three

TABLE 3. Numbers of species and individual detections (*n*) by sight or sound in the canopy stratum for each of three census methods at Pico Bonito National Park, Honduras, April 2006 to April 2007.

	Ground		Repeat-tree		Single-tree		Combined	
Family	Spp.	*n*	Spp.	*n*	Spp.	*n*	Spp.	*n*
Cracidae (guans)	1	2	0	0	1	1	1	3
Accipitridae (hawks)	2	2	1	5	2	8	2	15
Columbidae (pigeons)	1	9	3	5	1	4	3	18
Psittacidae (parrots)	2	50	2	46	3	74	3	170
Cuculidae (cuckoos)	0	0	2	16	2	8	2	24
Trochilidae (hummingbirds)	0	0	9	36	6	34	9	70
Trogonidae (trogons)	3	4	2	9	4	14	4	27
Momotidae (motmots)	0	0	1	1	1	2	1	3
Galbulidae (jacamars)	0	0	0	0	1	4	1	4
Bucconidae (puffbirds)	0	0	1	2	0	0	1	2
Ramphastidae (toucans)	2	43	4	90	3	50	4	183
Picidae (woodpeckers)	1	1	5	26	3	15	5	42
Funariidae (ovenbirds)[a]	0	0	3	7	5	7	5	14
Thamnophilidae (antbirds)	0	0	2	2	3	8	3	10
Tyrannidae (tyrant flycatchers)[b]	5	18	16	108	20	94	21	220
Cotingidae (cotingas)	0	0	1	11	1	4	1	15
Pipridae (manakins)	0	0	1	1	2	3	2	4
Vireonidae (vireos)	3	89	7	141	7	86	7	316
Corvidae (jays)	1	5	1	25	1	12	1	42
Troglodytidae (wrens)	0	0	1	4	1	7	1	11
Polioptilidae (gnatcatchers)	1	5	2	39	2	33	2	77
Turdidae (thrushes)	1	4	1	3	3	7	3	14
Parulidae (wood-warblers)	5	8	11	64	8	46	12	118
Thraupidae (tanagers)[c]	3	4	7	99	7	60	8	163
Cardinalidae (grosbeaks)	1	12	2	50	2	6	2	68
Icteridae (blackbirds)	2	41	3	128	4	63	4	232
Fringillidae (euphonias)	2	3	3	18	3	25	4	46
Total families	17		25		26		27	

[a]Includes Dendrocolaptidae.
[b]Includes *Tityra*, *Pachyramphus*, and *Schiffornis*.
[c]Includes *Piranga*.

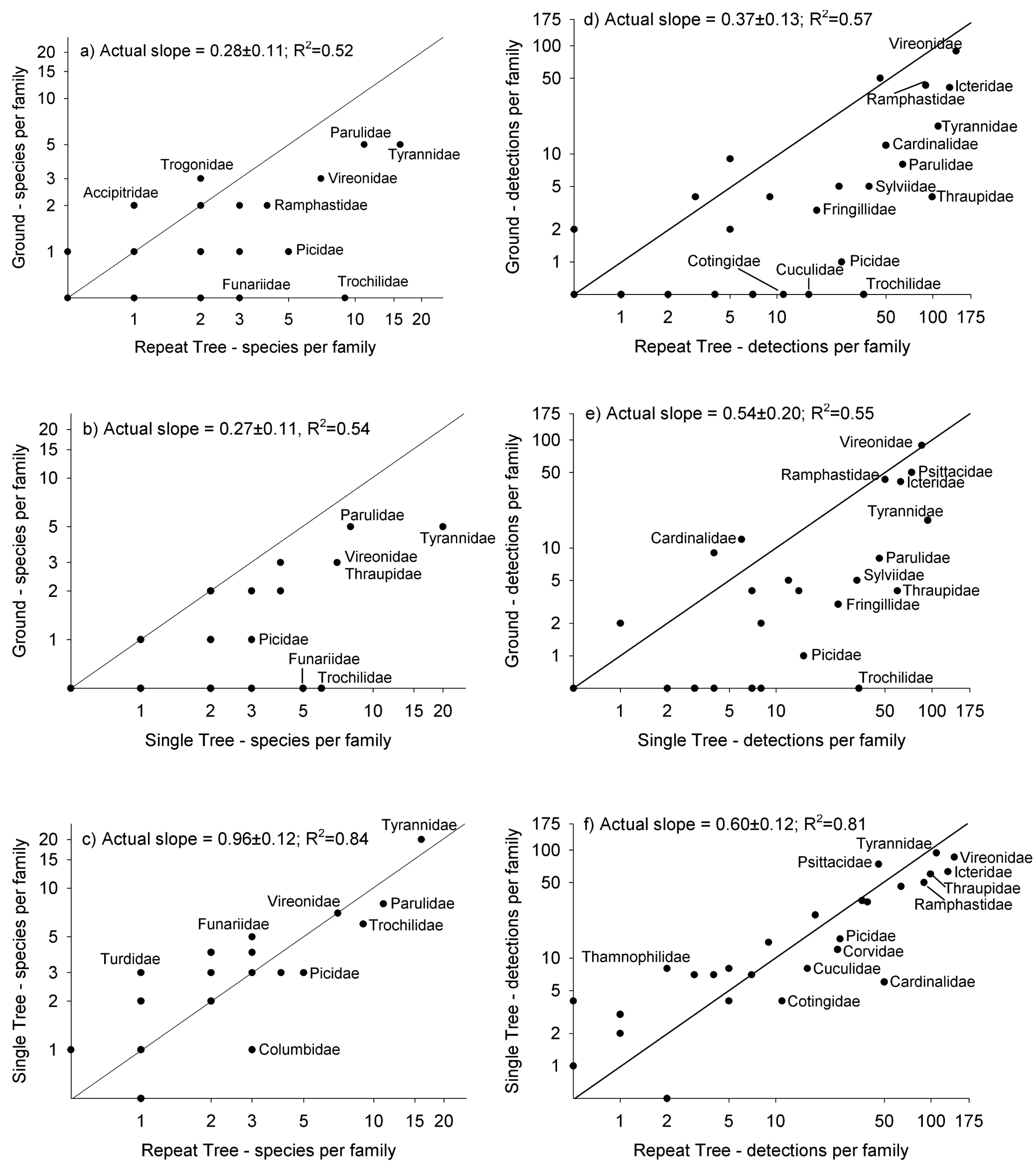

FIGURE 3. Number of species (a–c) and detections (by sight or sound; d–f) per family estimated by three census methods in the Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Data represent detections from the canopy stratum only. Straight lines indicate a 1:1 relationship between values for two methods. Actual slopes are given.

methods (Table 4). Species that were more evenly distributed across the study area (e.g., *Hylophilus decurtatus*, *Cyanocorax morio*, *Polioptila plumbea*) or that were highly conspicuous (e.g., *H. decurtatus*, *Ramphastos sulfuratus*, *Psarocolius wagleri*) ranked similarly by all methods. Species that were either less common or less conspicuous (e.g., *Thalurania colombica*, *Piranga rubra*, *Chlorophanes spiza*) tended to rank very differently by different methods. The top 20 species accounted for a greater percentage of canopy observations made from the ground (96%) than they did in canopy observations made from the canopy (76% and 70% for the repeat-tree and single-tree methods, respectively). This pattern signals that fewer species were detected in the canopy during ground censuses and that the evenness of dominant species by this method was also less. This is evident in the inclusion of *Penelope purpurascens*, not characteristically a canopy species, in the list of dominant canopy species for ground censuses.

DETECTION RATES

I found important differences between detections rates of individual species as well as between groups of species. Secretive migrant and resident species (Table 5) were detected at significantly greater hourly rates by canopy methods than from the ground, but between canopy methods detection rates did not

TABLE 4. Percentage of detections and rank for the 20 most frequently detected species in the forest canopy, by method, Río Cangrejal, Pico Bonito National Park, Honduras.

	Method					
	Ground		Repeat-tree		Single-tree	
Species	%	Rank	%	Rank	%	Rank
Penelope purpurascens	0.7	12	0.0		0.1	
Patagioenas nigrirostris	3.0	7	0.2		0.6	
Aratinga nana	3.7	6	1.3		3.0	6
Pyrilia haematotis	13.0	3	3.6	8	7.7	2
Piaya cayana	0.0		1.5	15	1.0	
Florisuga mellivora	0.0		0.3		1.5	13
Thalurania colombica	0.0		1.6	14	2.1	9
Trogon violaceus	0.7	12	0.5		0.6	
Pteroglossus torquatus	3.7	6	4.7	5	4.1	4
Ramphastos sulfuratus	10.7	4	4.3	6	3.1	5
Melanerpes pucherani	0.0		2.0	11	1.0	
Ornithion semiflavum	1.0	11	1.9	12	1.9	10
Zimmerius vilissimus	0.7	12	1.3		1.3	14
Megarynchus pitangua	0.0		0.1		1.6	12
Tityra semifasciata	3.7	6	2.9	9	2.1	9
Vireo olivaceus	0.3		6.0	3	2.4	8
Hylophilus decurtatus	26.7	1	6.1	2	7.7	2
Vireolanius pulchellus	2.7	8	1.7	13	0.3	
Cyanocorax morio	1.7	9	2.7	10	1.8	11
Polioptila plumbea	1.7	9	3.8	7	4.3	3
Catharus ustulatus	1.3	10	0.3		0.7	
Dendroica pensylvanica	1.3	10	1.9	12	2.1	9
Piranga rubra	0.3		1.5	15	3.0	6
Chlorophanes spiza	0.0		2.0	11	1.2	
Cyanerpes cyaneus	0.7	12	3.8	7	2.7	7
Cyanerpes lucidus	0.0		1.6	14	0.0	
Caryothraustes poliogaster	4.0	5	5.2	4	0.7	
Psarocolius wagleri	13.3	2	12.0	1	7.9	1
Euphonia hirundinacea	0.3		0.2		1.5	13
Euphonia gouldi	0.7	12	1.2		2.1	9
Percentage of total canopy detections	95.7		76.4		70.1	

TABLE 5. Groups of core canopy species used in comparisons of hourly detection rates by the three census methods.

Groups/species
Secretive or inconspicuous species
Migrants
Myiarchus crinitus
Vireo flavifrons
Vireo philadelphicus
Vireo olivaceus
Dendroica petechia
Dendroica pensylvanica
Dendroica magnolia
Dendroica virens
Dendroica castanea
Mniotilta varia
Setophaga ruticilla
Piranga olivacea
Icterus galbula
Residents
Notharchus macrorhynchos
Tolmomyias sulphurescens
Cotinga amabilis
Chlorophanes spiza
Hummingbirds
Florisuga mellivora
Thalurania colombica
Amazilia tzacatl
Heliothryx barroti
Tilmatura dupontii
Highly detectable, conspicuous species
Piaya cayana
Ramphastos sulphuratus
Attila spadiceus
Cyanocorax morio
Thryothorus maculipectus

differ (Fig. 4). I found no statistical difference among any of the methods in the hourly detection rate of canopy hummingbirds (Table 5), perhaps because of the overall low detection rate of this group. Ground censuses, however, detected only four of seven core canopy hummingbirds, and none in the canopy stratum. I found that the choice of method significantly affected the hourly detection rates of both species ($F_{2,86}$ = 31.1, $P < 0.0001$) and individuals ($F_{2,86}$ = 21.9, $P < 0.0001$) in the canopy stratum (Fig. 5). Similarly, the choice of method significantly affected the hourly detection rates of core canopy species ($F_{2,86}$ = 20.4, $P < 0.0001$) and individual core canopy birds ($F_{2,86}$ = 9.5, P = 0.0002) when detections in all strata were considered (Fig. 5). For core canopy species, detection rates were significantly greater for ground censuses than by either canopy method and and did not differ between the repeat-tree and single-tree methods (Fig. 5). For core canopy individuals the relationship was more complex, although again the detection rate by ground censuses was greatest (Fig. 5).

DISCUSSION

OVERVIEW

Because a major goal of this study was to test methods for the study of canopy birds, I chose to focus specifically on methods that are either widely available to forest ecologists or which have been used in past studies of canopy birds. Ground-based point counts remain the primary tool for observing forest birds in all levels of the forest because they are easy to conduct and because they are readily adaptable to different environments or particular questions of interest (Ralph et al. 1995). Repeated censuses from one or a small number of canopy viewpoints, as used in pioneering studies of canopy birds (Greenberg 1981, Loiselle 1988, Naka 2004), will continue to be important when canopy access is constrained by the availability of canopy towers or cranes. An important consideration

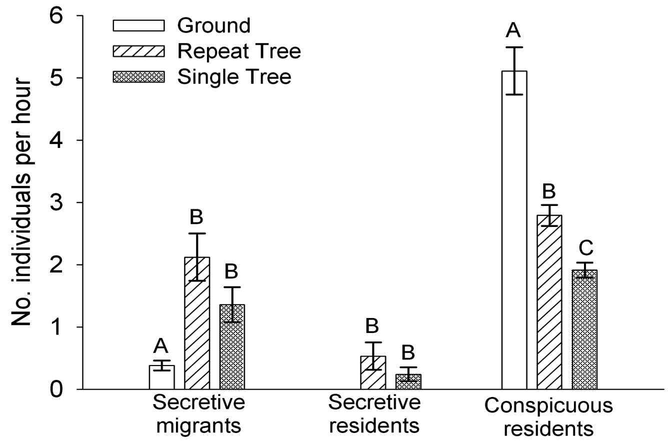

FIGURE 4. Hourly detection rates for numbers of individuals of secretive migrant, secretive resident, and conspicuous resident species observed (by sight or sound) by three census methods, Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Means ± 1 SE are shown. Different letters indicate significant differences between groups.

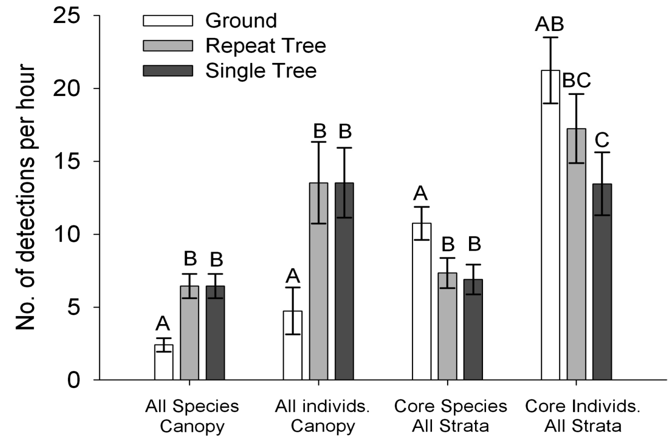

FIGURE 5. Hourly detection rates of all species and individuals detected in the canopy stratum and in all forest strata by three census methods in the Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Means ± 1 SE are shown. Different letters indicate significant differences between groups.

with canopy-based methods is the high temporal and spatial variability of food resources in the canopy (Leigh et al. 1996), which could influence the number of species and individual birds available to the observer. For this reason I incorporated single censuses from trees scattered throughout the study area for comparison with my repeat-tree method. Although a more direct comparison of bird detectability from the canopy and ground could have been obtained by paired canopy and ground observations of equal length, the intended scope of the study was a quantitative comparison of methods. The study design and statistical methods therefore reflect the larger goals of the study.

DETECTION PROBABILITIES

The spatial distribution, population density, and behavior of a species combined with the choice of method can affect how the proportional abundance of that species at a site is characterized. In this study *Hylophilus decurtatus* was disproportionately predominant in ground censuses and was detected more than twice as often from the ground as from the canopy. This finding is consistent with results from ground-based censuses in central Panama, where Robinson et al. (2000) found *H. decurtatus* to be one of the eight most abundant species. Despite being considered one of the more abundant species at La Selva, Costa Rica (Levey and Stiles 1994), it was not ranked among the most abundant species when canopy-based data alone were used (Loiselle 1988). In contrast, quieter species were systematically overlooked. During ground censuses I failed to detect 67% of all canopy species, including 28% of core canopy species, a result that biased the pattern of familial richness as well.

Two factors, vegetation density and distance between observer and bird, increase dependence on auditory detections (Pacifici et al. 2008). This balance comes with a tradeoff. Increasing vegetation density decreases sound transmittance, and increasing distance between the observer and bird lessens probability of detection (Bibby et al. 2000, Ellinger and Hödl 2003). In tropical forests, the vocalizations of many species are hard to detect at distances >30 m, and other species call infrequently (Robinson et al. 2000, Blake 2007). These factors increase the dependence on visual detections. Ellinger and Hödl (2003) found that sound waves are scattered by the uneven canopy surface and that species with high-frequency vocalizations compensate by singing above the canopy. In the Río Cangrejal study area the forest averaged 35 to 40 m tall with some trees reaching heights of over 50 m. The combination of forest height and foliage density with the habit of small species with high-frequency voices to sing at the top of the forest undoubtedly decreased the probability of birds in the upper foliage layers being detected. Species underrepresented by ground censuses frequented upper levels of the forest and were disproportionately harder to detect through auditory cues. This result is independent of observer skill, which cannot reduce the amount of obstruction or the distance between a bird at the top of the forest and an observer on the ground. Furthermore, the terrain of the Río Cangrejal study area is uneven and sloping, facilitating viewing into the canopy from the ground. In portions of Amazonia and wherever the terrain is uniformly flat, a ground-based observer is at an even greater disadvantage.

My results also highlight that the probability of detecting birds in the canopy is a function of both census method and bird behavior. Canopy and ground point counts differ in that a canopy point count is conducted at a single point over a long period, whereas a ground transect consists of many distinct point counts of short duration. Remaining at a single station in the canopy for several hours resulted in rates of detection of birds in the canopy higher than by ground censuses. Species richness by canopy methods was also substantially higher. Ground methods detected conspicuous canopy species more often, partly because during any transect the observer walks through multiple territories of vocal species.

ESTIMATES OF POPULATION DENSITY

Robinson et al. (2000) used multiple ground-based methods to estimate population densities for 165 of 252 species in central Panama. Their density estimates for three groups of species were likely affected by the use of ground-based census data. The first group comprised 41 diurnal interior-forest species for which they attempted no estimates because of the birds' high mobility or small sample sizes resulting from difficulty of observation from the ground. Twenty of these species are characteristic of the canopy, including raptors (*Leucopternis albicollis, Falco rufigularis*) and visually conspicuous but otherwise secretive residents (e.g., *Cotinga nattererii*). In contrast, some of these species are readily observed from canopy viewpoints. In Honduras *L. albicollis* may be the single bird most easily observed from the canopy (this study, Anderson 2001); some other raptors are easily observed as well. Canopy-dwelling hummingbirds are notoriously difficult to detect from the ground, yet from my tree vantage points I could often identify and track individual hummingbirds at distances up to 80 m. The second group consisted of some quiet canopy species, (e.g., *Heliothryx barroti, Dendroica pensylvanica, Chlorophanes spiza*), and Robinson et al. (2000) estimated population densities for these. Given that these species are either largely silent or best heard at short distances and are difficult to view from the ground, my results suggest that Robinson et al. (2000) may have underestimated densities of some of them by up to 50%. It is likely that the ground methods of Robinson et al. missed a third group of species altogether, particularly certain nearctic migrants, further canopy hummingbirds, and quiet residents. In my study ground censuses revealed 30% fewer species than either canopy method, and the mean estimate of species richness for the study area was approximately 10% lower when the canopy methods were excluded.

FUNCTIONAL ECOLOGY

Understanding the roles of birds in an ecosystem is a central component of tropical forest ecology. For example, much importance has been placed on the role of birds in seed dispersal and in the natural regeneration of forests after disturbance (Cardoso da Silva et al. 1996, Howe 1996, Silva et al. 2002, Cordiero and Howe 2003). Evaluating the potential of the local avifauna to disperse seeds of varying sizes and characteristics requires an accurate depiction of the seed-dispersing guild. My study found that the functional composition of the avifauna was severely misrepresented by census data from the ground only. Among the core canopy birds alone three of seven species of nectarivores, two of four obligate frugivores, and seven of 33 other potential seed dispersers went undetected during ground censuses. For example, *Cotinga amabilis*, a medium-sized frugivore of the forest canopy, was observed frequently during canopy censuses. My observations suggest that, by regurgitating seeds onto tree branches, it plays an important role in seed dispersal of certain Loranthaceae (principally *Psittacanthus rhyncanthus*), hemiparasitic mistletoes that grow on canopy trees. Fruits of these plants are in turn fed on by at least 19 species of migrant and resident birds, and their flowers are favored by hummingbirds (unpubl. data). Despite the brilliant plumage of the male cotinga, my ground censuses did not to detect it, and all interactions between birds and the Loranthaceae were viewed exclusively from canopy viewpoints. Furthermore, many canopy species detected from the ground through auditory cues were seldom, if ever, observed visually. Understanding the foraging ecology and behavior of canopy species is best accomplished from canopy viewpoints.

IMPLICATIONS FOR CONSERVATION

Results of this study demonstrate that estimates of population density, species distributions, and local species richness can all be biased by exclusively ground-based methods. I offer two scenarios in which data from ground-based censuses alone could affect conservation practices:

1. Estimates of species richness of birds are often used to determine the conservation importance of particular sites. In sites with identical species richness, differences in forest stature and structure may affect detectability of birds in upper strata and, therefore, bias estimates of richness and the prioritization of conservation potential.

2. Ground-based censuses are often used to describe effects of disturbances, such as selective logging and storm damage, on population densities of birds. Disturbances may affect an observer's ability to detect canopy birds in two ways. First, a disturbance that reduces the amount of foliage in a forest can enhance the observer's ability to see and hear birds at greater heights. Second, a disturbance may affect movement patterns of birds and render them more detectable by the observer. In either case, estimates of population density may be erroneously biased upward. Although forest disturbance may favor some species of birds, changes in detectability may lead to this conclusion when it is actually false.

Canopy-based censuses may be critical for biological monitoring in several respects. Thirty-five species listed as endangered, threatened, or vulnerable by the International Union for the Conservation of Nature (IUCN) inhabit canopies of lowland neotropical forests (Stotz et al. 1996, BirdLife International 2000). Of these, six are raptors whose population densities are often naturally low and which may be highly visible from canopy viewpoints. Another 13 are frugivores or omnivores that may be important seed dispersers. One is a hummingbird and likely difficult to detect from the ground. If my results have general applicability, then ground-based surveys will underestimate the densities of these and other inconspicuous species. Additionally, canopy-based censuses may be necessary for monitoring long-term changes in community composition, including species loss following forest fragmentation, as on Barro Colorado Island, Panama, where the difficulty of detecting canopy species may affect estimates of species extirpation and recolonization (Robinson 1999).

RECOMMENDATIONS

Canopy-based methods offer obvious advantages for studies of canopy birds, but the question remains as to what circumstances justify the added effort and expense that field work in the canopy requires. Cohn-Haft et al. (1997) demonstrated how canopy surveys from a single canopy tower improve the understanding of an otherwise well-known avifauna. Consequently, long-term data sets at sites of high biological interest, such as tropical field stations, should include canopy methods for a better understanding of trends in canopy bird communities. Rapid ecological assessments may also justify canopy methods, or, if canopy methods are not used, need to state explicitly that ground-based assessments likely miss or underestimate the density of core canopy species.

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APPENDIX 1. Common and scientific names of birds referenced in the text and tables.

Scientific name	Common name	Scientific name	Common name
Penelope purpurascens	Crested Guan	*Cotinga nattererii*	Blue Cotinga
Leucopternis albicollis	White Hawk	*Vireo flavifrons*	Yellow-throated Vireo
Falco rufigularis	Bat Falcon	*Vireo philadelphicus*	Philadelphia Vireo
Patagioenas nigrirostris	Short-billed Pigeon	*Vireo olivaceus*	Red-eyed Vireo
Aratinga nana	Olive-throated Parakeet	*Hylophilus decurtatus*	Lesser Greenlet
Pyrilia haematotis	Brown-hooded Parrot	*Vireolanius pulchellus*	Green Shrike-Vireo
Piaya cayana	Squirrel Cuckoo	*Cyanocorax morio*	Brown Jay
Florisuga mellivora	White-necked Jacobin	*Thryothorus maculipectus*	Spot-breasted Wren
Thalurania colombica	Violet-crowned Woodnymph	*Polioptila plumbea*	Tropical Gnatcatcher
Amazilia tzacatl	Rufous-tailed Hummingbird	*Catharus ustulatus*	Swainson's Thrush
Heliothryx barroti	Purple-crowned Fairy	*Dendroica petechia*	Yellow Warbler
Tilmatura dupontii	Sparkling-tailed Hummingbird	*Dendroica pensylvanica*	Chestnut-sided Warbler
Trogon violaceus	Violaceous Trogon	*Dendroica magnolia*	Magnolia Warbler
Notharchus macrorhynchos	White-necked Puffbird	*Dendroica virens*	Black-throated Warbler
Pteroglossus torquatus	Collared Aracari	*Dendroica castanea*	Bay-breasted Warbler
Ramphastos sulfuratus	Keel-billed Toucan	*Mniotilta varia*	Black-and-white Warbler
Melanerpes pucherani	Black-cheeked Woodpecker	*Setophaga ruticilla*	American Redstart
Ornithion semiflavum	Yellow-bellied Tyrannulet	*Piranga rubra*	Summer Tanager
Zimmerius vilissimus	Paltry Tyrannulet	*Piranga olivacea*	Scarlet Tanager
Tolmomyias sulphurescens	Yellow-olive Flycatcher	*Piranga leucoptera*	White-winged Tanager
Attila spadiceus	Bright-rumped Attila	*Chlorophanes spiza*	Green Honeycreeper
Myiarchus crinitus	Great Crested Flycatcher	*Cyanerpes lucidus*	Shining Honeycreeper
Megarynchus pitangua	Boat-billed Flycatcher	*Cyanerpes cyaneus*	Red-legged Honeycreeper
Schiffornis turdina	Thrushlike Schiffornis	*Caryothraustes poliogaster*	Black-faced Grosbeak
Pachyramphus aglaiae	Rose-throated Becard	*Icterus galbula*	Baltimore Oriole
Tityra semifasciata	Masked Tityra	*Psarocolius wagleri*	Chestnut-headed Oropendola
Tityra inquisitor	Black-crowned Tityra	*Euphonia hirundinacea*	Yellow-throated Euphonia
Cotinga amabilis	Lovely Cotinga	*Euphonia gouldi*	Olive-backed Euphonia