

A COMPARISON OF TWO BIRD SURVEY TECHNIQUES USED IN A SUBTROPICAL FOREST¹

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Abstract. Mist netting and point counting have been used equally in the Neotropics for the purpose of surveying bird communities, although their effectiveness is poorly known. We compared mist netting and point counting data collected from the same survey points in a mature subtropical forest in Belize to assess their descriptions of a bird community within a small region and across many survey points. We surveyed each point for three consecutive days using one technique and then for three additional days using the other technique. Mist netting and point counting detected only 25% and 60%, respectively of all forest species. The species lists from mist netting and point counting had similar proportions of species in groupings based on families, abundance, and migratory status, and in diet, habitat use, and foraging substrate guilds. Species lists from mist netting had a greater proportion of understory and small species than the species list from point counting. Species lists from mist netting and point counting had smaller proportions of large-bodied and rare species than a local checklist. Point counting detected more species per point with greater time efficiency and more species per point in 25 of 28 guilds than did mist netting. Point counting detected three common species less frequently than mist netting, whereas mist netting detected 38 common species less frequently than point counting. Point counting detected understory species as frequently as mist netting did at individual points. The two methods had > 50% agreement on the presence of only four species at individual points. Both techniques detected different sets of common species with similar frequency, although point counting detected many more uncommon species. Although using both techniques was more effective than using either alone, point counting alone was significantly more efficient for conducting bird surveys.

Key words: Belize, bird community, inventory, mist nets, monitoring, point count, subtropical forest.

INTRODUCTION

Mist nets and point counts have been used equally in the Neotropics to survey birds. Both have been used more often than other techniques such as transects, spot mapping (Karr 1971), or plot searches (Thiollay 1992). The chief difference between the two techniques is that mist netting detects birds by capture, whereas point counting relies on an observer to detect birds by sight or sound. Although it has been suggested that both techniques are biased (Karr 1990), only two papers have compared their biases (Lynch 1989, Gram and Faaborg 1997). Lynch (1989) found that the number of migrant species detected by mist netting was significantly positively correlated with the number of migrant species detected by point counting, but he did not find a correlation for numbers of resident species. However, the lack of a relationship between the two techniques for resident species may have re-

sulted from not sampling the exact same locations with both techniques. Gram and Faaborg (1997) found that mist netting detected more species than point counting in tropical semi-deciduous forest. Simulations by Remsen and Good (1996), based on assumptions about bird behavior, also suggest significant sampling biases associated with mist netting, but they did not compare their simulations with real data or compare mist netting with other survey techniques to support their findings.

Surveying bird communities in tropical forest habitats has been problematic because these forests generally contain high species diversity (Karr et al. 1990). Counting techniques require skilled observers familiar with songs or calls of sometimes hundreds of bird species (Beehler et al. 1995), and still, they could miss secretive, nonvocal species which may be an important component of the avifauna (Karr 1981b). When skilled observers are not available, mist netting has been an attractive alternative for surveying birds. However, mist netting is ineffective for

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surveying species that are large and/or inactive within 2 m of the forest floor (Karr 1981b).

In this paper we compare data from mist netting and point counting at the same points in a mature subtropical forest to determine if one technique is better suited for surveying bird communities. Our results include a combination of mist netting and point counting data because the use of multiple methods together has been widely suggested as the best way to survey tropical bird communities (Karr 1971, Remsen and Parker 1983, Gram and Faaborg 1997). In our analysis, we compare each method based on the sum of data from an array of survey points (sum of points) and from data from each point (individual points). Each point was surveyed using both techniques with no more than three days between visits using either technique. We assumed that species present at a point when applying one survey technique also were present when applying the second survey technique.

METHODS

STUDY AREA

The study area is near Hill Bank (88°42'W, 17°36'N), Orange Walk District, northern Belize, in the Rio Bravo Conservation and Management Area, which is owned and managed by Programme for Belize, a nongovernment environmental organization. It is in the "subtropical moist" life zone and is 80 m above mean sea level. Annual rainfall is 1.5 m with 10% of the rain falling during the "dry" season, January to May. Rainfall in the dry and wet seasons can vary annually. The soils are moderately deep; bedrock is porous limestone. The topography is flat, punctuated with low hills and occasional small swamps. The forest is upland evergreen, broadleaf forest with a canopy height 15–20 m. It has been disturbed by occasional hurricanes, past deforestation by Maya during the period 0–1,000 AD, and low-intensity selective logging since the early 1800s (Brokaw and Mallory 1993). Dominant tree species include *Alseis yucatanensis*, *Pouteria reticulata*, *Aspidosperma cruenta*, *Manilkara chicle*, *Sabal mauritiformis*, *Attalea cohune*, *Ampelocera hottlei*, and *Terminalia amazonia*.

BIRD SURVEYS

From 14 February to 28 March 1993, we surveyed 60 haphazardly-selected points using both mist netting and point counting. Points were

spaced at least 200 m apart, which should provide adequate statistical independence for point counting (Hutto et al. 1986) and mist netting of most species (Gram and Faaborg 1997). This was part of a larger study comparing intact and selection-logged forests in northern Belize.

Mist netting. Three mist nets (2.6 × 12 m, 36-mm mesh) were used at each point. Mist nets were opened at sunrise (about 06:00), checked every hour, and closed 5 hr later. Six points were sampled with mist nets each day. Each point was sampled for three consecutive days immediately preceding or following the three days of point counting (below). Three days of netting are sufficient to detect most individuals of those species detectable with mist nets (Robbins et al. 1989). All birds were marked so that recaptured individuals would not be counted twice. The banding team included three people: one or two experienced banders who knew the local avifauna and one or two assistants.

Point counts. Fixed-radius point counts were conducted between sunrise and 3 hr later, as detection rates may decline 3 hr after sunrise (Lynch 1995). During a 15-min period, we recorded the species, distance from observer (≤ 50 m or > 50 m), and time of all birds heard or seen. A 15-min point-count period detects most vocal species (Hutto et al. 1986). Most singing or calling birds can be detected within 50 m, although soft-singing canopy species might be missed (Waide and Narins 1988). Six points were surveyed by point counting each day. Each point was sampled for three consecutive days immediately preceding or following the three days of mist netting (above). Each point was surveyed once each day for three consecutive days. The daily order of point sampling was changed so that each point was visited once in the first hour, once in the second hour, and once in the third hour of the morning sample period. The point count team included two people: an experienced bird census person, i.e., a birder with previous, limited tropical experience who had spent 2 weeks in the area learning bird songs and calls; and a data recorder. Steve Howell, a noted field ornithologist of Central American birds, evaluated the identification skills of the bird census person and found them to be very accurate before fieldwork began.

Checklist. We developed a checklist of forest birds during all field work, January to April, 1993–1996 (two field ornithologists for 16

weeks each year). We used the proportion of days detected as an index of abundance. The proportion of days detected was ascertained in part while mist netting and point counting; therefore, it is not completely independent of these data sets. The checklist is based on 896 person days (about 7,170 person hr), whereas mist netting and point counting is based on 30 mornings in the field (150 person hr or 2,700 net hr for mist netting and 45 person hr for point counting).

Groupings were based on families, abundance, migratory status, body size categories, and guilds. Family status was based on the AOU (1983) checklist. Species were grouped into abundance categories after DeSante and Pyle (1986). These categories were: extremely rare (10 or fewer records), rare (detected < 10% of days), uncommon (detected on 10–50% of days), common (detected on 51–90% of days), abundant (detected > 90% of days). Species also were assigned to groupings based on migratory status (Neotropical-Nearctic migrant or resident, O. Komar, pers. comm.) and body size (small < 22.5 g, medium 22.5–51 g, and large > 51 g; Stiles and Skutch 1990). Each size category included one third of the species in the study area. The medium body size category included species that were most likely to be caught in the 36-mm mesh mist nets of this study (Pardieck and Waide 1992). Finally, birds were assigned to guilds based upon foraging height strata, diet, foraging substrate (Karr et al. 1990), and habitat (Stiles and Skutch 1990).

STATISTICAL ANALYSES

We only statistically compared results based on mist netting and point counting data. We were not able to compare these data with mist netting + point counting data combined or the checklist because these latter data sets were not statistically independent of the former data sets. However, we present and comment on the data from the latter data sets as these results may be useful to future studies.

Sum of Points. We compared mist netting and point counting to determine if results were similar in terms of: (1) number of species (Sign Test, SAS 1990), (2) efficiency (using species-effort curves), (3) proportions of species in different groups (χ^2 goodness-of-fit test [Conover 1980]; see Table 1 for a list of groups and guilds), and (4) proportion of days a species was

detected (paired *t*-test). For species-effort curves, effort was measured in labor hours including labor to set up survey points, to collect data, and to enter data into a computer. We used a χ^2 goodness-of-fit test to determine if the proportions of species in different groupings as determined by mist netting fit the proportions of species in different groupings as determined by point counting. For sum of points analyses, we used all point count observations regardless of the distance of the observation.

Individual points. We compared mist netting and point counting data at 60 points in five ways: (1) number of species at each point (paired *t*-test, SAS 1990), (2) community composition at each point (Jaccard's index, paired *t*-test, SAS 1990), (3) efficiency, (4) number of species in different groups per point (Median Test), and (5) agreement on the presence/absence of species at points (analysis of discordant pairs, also known as McNemar's Test, SAS 1990). For the point count data, we only used observations within 50 m. Jaccard's index is the number of species at a point detected by both techniques divided by the sum total of species detected by either technique (Wilkinson 1990). The paired *t*-test was used because it is robust to heterogeneity of variances and departures from normality (SAS 1990). Median tests were used because the data did not meet the assumptions necessary for an analysis of variance. All statistical tests were two-tailed with the exception of one sample *t*-tests comparing Jaccard's Index of points to 0 or 1. Means \pm SD are reported.

RESULTS

SUM OF POINTS

Number of species. Neither mist netting, point counting, nor mist netting + point counting detected all of the 203 forest species on the checklist. Mist netting + point counting detected 125 species, point counting 119 species, and mist netting 58 species. Point counting detected 61 more species than mist netting (Sign test, $P < 0.001$). Point counting only failed to detect six species detected by mist netting.

Point counting always detected more species than mist netting at any level of effort (Fig. 1). The accumulation of new species leveled off with 1,000 person-hours of mist netting (or about 3,600 net hr); thus, it is unlikely that ad-

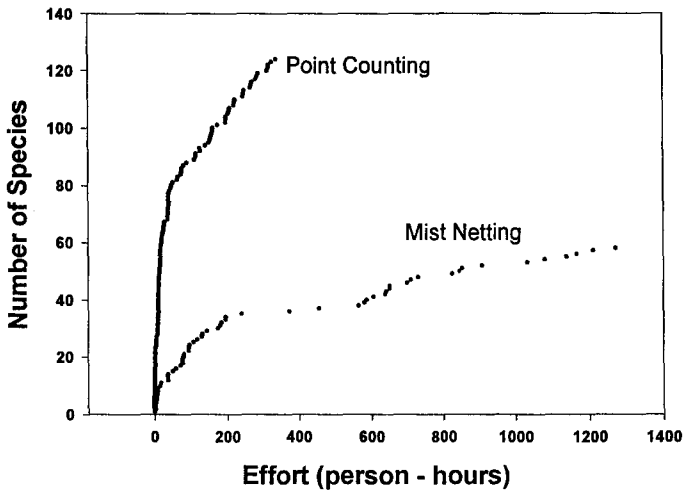


FIGURE 1. Cumulative number of species detected by mist netting and point counting with increasing effort. Effort was equal to the total amount of time spent to set up points, and collect and enter data into a computer.

ditional netting would yield many more species. However, for point counting, the accumulation of new species continued to increase at 200 person-hours (or about 20 field census hours) and it might take up to 1,000 person-hours (or about 100 field census hours) before most species are detected.

Proportion of species in groups based on families, abundance, body sizes, migratory status, and guilds. The mist netting and point counting data sets had similar proportions of species in groupings based on families ($\chi^2_{35} = 34.6$, $P = 0.45$), abundance, and migratory status, and different diet, foraging substrates, and habitats guilds (Table 1). However, mist netting detected a significantly greater proportion of medium and small bodied species than point counting. The proportion of species in different abundance categories was similar for mist netting and point counting, and perhaps mist netting + point counting, but these seemed to differ from the checklist. The checklist had a greater proportion of rare species (species detected on less than 10% of the days). Also, the proportion of species in each height stratum guild detected by mist netting was significantly different from that detected by point counting, and seemed different from mist netting + point counting and the checklist, whereas the later three data sets appear similar to each other. Mist nets detected a greater proportion of mid-story species than

point counting but not a greater proportion of ground species.

Proportion of days detected for individual species. The mean proportion of days detected for each species was significantly greater for point counting (0.43 ± 0.34 , $n = 119$; 30 mornings of effort) than for mist netting (0.28 ± 0.29 , $n = 58$; 30 mornings of effort; paired t -test, $t = 4.39$, $P < 0.001$) and these appear to be less than found using point counting + mist netting (0.46 ± 0.33 , $n = 125$; 30 mornings of effort) or the checklist (0.49 ± 0.42 , $n = 203$; 896 person days of effort). The proportion of days detected for each species was significantly positively correlated between mist netting and point counting ($r = 0.26$, $P < 0.05$). In other studies, pairwise positive correlations between abundances of migrant species based on mist netting and point counting data were sometimes significant: Robbins et al. (1992, $r = 0.46$, $n = 19$, $P < 0.05$), and at one site ($r = 0.37$, $n = 24$, $P < 0.05$), but not at three other sites ($r < 0.32$, $n = 24$, $P > 0.05$) in Blake and Loiselle (1992).

INDIVIDUAL POINTS

Number of species and similarity of communities. Point counting detected nearly four times as many species per point as mist netting (Table 2). Point counting also detected more species hr^{-1} (1.4 versus 0.1 species hr^{-1} of data collection) and required less time (7.2 versus 12.6 hr

TABLE 1. Proportion of species in different categories detected by mist netting, point counting, mist netting + point counting (both), and occurring on the checklist of forest birds near Hill Bank, Belize. The statistical test results only apply to comparisons between mist netting and point counting.

Group/category	Mist netting	Point counting	Both	Checklist
Abundance ($\chi^2_4 = 5.0, P > 0.25$)				
Abundant	58.6	55.5	53.6	37.6
Common	0.0	5.8	5.6	3.5
Uncommon	29.3	23.5	24.0	23.3
Rare	12.1	14.3	16.0	31.2
Extremely rare	0.0	0.8	0.8	4.4
Migratory status ($\chi^2_1 = 0.1, P > 0.95$)				
Migrant	15.5	15.1	15.2	17.8
Resident	84.5	84.9	84.8	82.2
Body size ($\chi^2_2 = 7.3, P > 0.25$)				
Large	12.1	27.7	27.2	33.7
Medium	22.4	16.8	16.0	15.8
Small	65.5	55.5	56.8	50.5
Height strata ($\chi^2_4 = 26.5, P < 0.001$)				
Air	0.0	0.9	0.8	2.9
Canopy	6.9	36.2	35.3	39.5
Mid-story	41.4	34.5	34.4	27.9
Shrub	39.7	20.7	22.1	18.6
Ground	12.1	7.8	7.4	11.1
Diet ($\chi^2_7 = 12.9, P > 0.15$)				
Carrion and vertebrates	1.7	3.5	4.1	2.9
Fruits and seeds	10.3	16.4	16.4	14.0
Insects and vertebrates	12.1	9.5	9.8	11.6
Large insects and fruits	1.7	8.6	8.2	6.4
Nectar	8.6	4.3	4.9	5.2
All foods	1.7	1.7	2.5	2.3
Small insects	51.7	37.1	36.1	34.3
Small insects and fruits	12.1	19.0	18.0	18.0
Foraging substrate ($\chi^2_6 = 5.8, P > 0.25$)				
Air	6.9	5.2	4.9	5.8
Ant following	5.2	2.6	2.5	0.7
Branch	8.6	9.5	9.8	9.9
Dead foliage	1.7	3.5	3.3	2.3
Alive foliage	60.3	69.0	68.9	66.9
Ground	13.8	8.6	8.2	10.5
Trunk	3.5	1.7	2.5	1.7
Preferred habitats ($\chi^2_2 = 4.0, P > 0.10$)				
Forest edge	19.0	31.1	31.2	41.9
All forest	67.2	58.0	57.6	48.2
Mature forest	13.8	10.9	11.2	9.9

point⁻¹) to establish points and collect data than mist netting. There was no relationship between the number of species detected at a point by mist netting and the number detected by point counting when considering the total number of species, only species detectable by both techniques, or only common species (detected by both techniques at over 50% of the points; $r < 0.20, n = 60, P > 0.10$). The mean similarity (Jaccard's Index) in the species lists per point was low be-

tween mist netting and point counting and significantly less than 1, i.e., complete similarity ($t_{60} = 52.8, P < 0.001$). Mist netting and point counting shared on average about $8.6 \pm 6\%$ ($n = 60$) of the species per point.

Number of species in groups based on families, abundance, body sizes, migratory status, and guilds. Point counts detected significantly more species than mist netting in 25 of 28 groups (Table 2). In the three remaining groups

TABLE 2. Mean \pm SD number of forest species detected per point in different guilds by mist netting, point counts, and both techniques near Hill Bank, Belize. Within a row, values with different letters had different medians (Median Test, $P < 0.005$). The statistical results apply only to comparisons between mist netting and point counting.

Group/category	Mean \pm SD number of species		
	Mist netting	Point counting	Both
Total	6.3 \pm 2.4a	24.7 \pm 6.3b	28.5 \pm 6.6
Abundance			
Abundant	8.3 \pm 2.3a	22.0 \pm 5.3b	26.4 \pm 5.0
Common	0.0 \pm 0.0a	0.2 \pm 0.4b	0.2 \pm 0.4
Uncommon	1.4 \pm 1.3a	2.3 \pm 1.5b	3.6 \pm 1.8
Rare	0.6 \pm 0.8a	0.7 \pm 0.8b	1.3 \pm 1.1
Extremely rare	0.0 \pm 0.0a	0.2 \pm 0.4b	0.2 \pm 0.4
Migratory status			
Resident	4.9 \pm 1.9a	20.2 \pm 5.4b	23.5 \pm 5.6
Migrant	1.4 \pm 1.0a	5.2 \pm 1.8b	5.9 \pm 1.9
Body size			
Large	0.3 \pm 0.4a	3.9 \pm 2.0b	4.2 \pm 2.2
Medium	2.3 \pm 1.2a	4.7 \pm 1.8b	6.1 \pm 1.8
Small	3.8 \pm 2.0a	16.7 \pm 4.9b	18.2 \pm 5.1
Height strata			
Air	0.0 \pm 0.0a	0.1 \pm 0.4b	0.1 \pm 0.4
Canopy	0.3 \pm 0.5a	6.6 \pm 2.4b	6.9 \pm 2.4
Mid-story	2.0 \pm 1.2a	10.4 \pm 3.4b	11.8 \pm 3.3
Shrub	3.4 \pm 1.7a	7.1 \pm 2.2b	9.1 \pm 2.5
Ground	0.6 \pm 0.6a	1.2 \pm 0.9b	1.5 \pm 1.0
Diet			
Carrion and vertebrates	0.0 \pm 0.2a	0.1 \pm 0.3a	0.1 \pm 0.3
Fruits and seeds	0.5 \pm 0.7a	3.5 \pm 1.7b	3.9 \pm 1.7
Insects and vertebrates	0.8 \pm 0.7a	1.4 \pm 1.0b	2.0 \pm 1.2
Large insects and fruits	0.0 \pm 0.0a	1.1 \pm 1.0b	1.1 \pm 1.0
Nectar	0.2 \pm 0.4a	0.8 \pm 0.8b	0.9 \pm 0.9
All foods	0.0 \pm 0.0a	0.2 \pm 0.4b	0.2 \pm 0.4
Small insects	3.7 \pm 2.0a	13.7 \pm 3.9b	16.0 \pm 4.0
Small insects and fruits	1.2 \pm 0.8a	4.7 \pm 1.6b	5.3 \pm 1.8
Foraging substrate			
Air	0.6 \pm 0.7a	1.0 \pm 0.9b	1.5 \pm 1.1
Ant following	0.5 \pm 0.6a	0.3 \pm 0.5a	0.8 \pm 0.6
Branches	0.8 \pm 0.7a	1.9 \pm 1.1b	2.5 \pm 1.2
Dead foliage	0.0 \pm 0.1a	0.1 \pm 0.3a	0.1 \pm 0.3
Alive foliage	3.7 \pm 1.9a	20.2 \pm 5.2b	22.1 \pm 5.4
Ground	0.6 \pm 0.7a	1.4 \pm 0.9b	1.8 \pm 1.0
Trunk	0.1 \pm 0.4a	0.6 \pm 0.5b	0.7 \pm 0.6
Habitat			
Forest edge	0.3 \pm 0.5a	7.0 \pm 2.9b	7.3 \pm 3.0
All forest	4.7 \pm 1.9a	15.1 \pm 4.5b	18.3 \pm 4.9
Mature forest	1.4 \pm 1.0a	3.3 \pm 1.2b	3.9 \pm 1.2

(species that use dead foliage, follow ants, and eat carrion and vertebrates), mist netting and point counting detected similar numbers of species. However, the number of species detected by mist netting + point counting was much greater than point counting in 11 of 28 guilds. For these 11 guilds, mist netting detected the same number of species as point counts or sig-

nificantly increased the number of species detected. These included the common and uncommon species abundance categories, two of the three body size categories, both migratory status groups, four of the five height strata guilds, the diet guild with the most species (small insects), and the habitat guild with the most species (all forest).

Detection of each species. Mist netting only detected three common and nonvocal species more frequently than point counting (Appendix 1): Ochre-bellied Flycatcher (*Mionectes oleagineus*, $P \leq 0.001$), Ruddy Woodcreeper (*Dendrocincla homochroa*, $P \leq 0.001$), and Tawny-winged Woodcreeper (*Dendrocincla anabatina*; $P < 0.02$). Point counting failed to detect these species at more than 90% of the points where they occurred. Point counting also failed to detect three uncommon species, Long-tailed Hermit (*Phaethornis superciliosus*), Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*), and Ruddy-Quail Dove (*Geotrygon montana*), at more than 90% of the points where they occurred ($P > 0.05$). Except for the Long-tailed Hermit, these species are not territorial, not strongly vocal, and use the ground and shrub layers of the forest. In total, 31 species were detected more frequently by mist nets than point counts, and 18 of these species were uncommon, occurring only at 10 or fewer points.

Point counting detected 38 species more frequently than mist netting ($P < 0.004$), including six common species (Appendix 1): Lesser Greenlet (*Hylophilus decurtatus*), Tawny-crowned Greenlet (*Hylophilus ochraceiceps*), Greenish Elaenia (*Myiopagis viridicata*), Northern Bentbill (*Oncostoma cinereigulare*), Magnolia Warbler (*Dendroica magnolia*), and American Redstart (*Setophaga ruticilla*). Two of these, Tawny-crowned Greenlet and Northern Bentbill, use the understory, and the greenlet can be caught by mist nets. The other four are canopy species. Thirty-four other species were not detected by mist netting at 90% of the points where they occurred. A total of 91 species were detected more frequently by point counts than mist nets, although 56 of these species occurred at 10 or fewer points. Species more frequently detected by one technique were generally uncommon.

Point counting failed to detect a species when present about 25% of the time (single-sample t -test, $t_{121} = 7.1$, $P < 0.001$). Moreover, the mean agreement (proportion of points where a species was detected by both techniques) between both techniques for species presence was low, 0.06, and not significantly different from 0 (Fisher's Exact Test, $P > 0.20$). The two techniques agreed on the presence of only four species for more than 50% of the points where they were detected: White-breasted Wood-wren (*Henicor-*

hina leucosticta), Stub-tailed Spadebill (*Platyrinchus cancrominus*), Wood Thrush (*Hylocichla mustelina*), and Blue Bunting (*Cyanocompsa parellina*).

For the 52 species detected by both methods and the 16 most common species (occurring at $> 50\%$ of points), the proportion of points where a species was detected by mist netting and by point counting were negatively correlated ($r = -0.80$, $n = 52$, $P < 0.001$; $r = -0.81$, $n = 16$, $P < 0.001$, respectively). Thus, species well detected by one technique were poorly detected by the other. The mean proportion of points for common species was similar for point counting and mist netting (paired t -tests, $t_{15} = 0.5$, $P = 0.63$). Overall, both techniques detected different sets of common species equally well.

Twelve common understory species were detected much more often by mist netting + point counting than either technique alone: Tawny-winged Woodcreeper, Olivaceous Woodcreeper (*Sittasomus griseicapillus*), White-breasted Wood-wren, Thrush-like Manakin (*Schiffornis turdinus*), Red-capped Manakin (*Pipra mentalis*), Stub-tailed Spadebill, Ruddy-tailed Flycatcher (*Terentotriccus erythrurus*), Sulfur-rumped Flycatcher (*Myiobius sulphureipygius*), Wood Thrush, Kentucky Warbler (*Oporornis formosus*), Hooded Warbler (*Wilsonia citrina*), and Red-throated Ant-Tanager (*Habia fuscicauda*).

LABOR COSTS

The number of hours of field work and data entry point⁻¹ for mist netting was nearly twice that of point counting (12.6 versus 7.2 hr). Point counting took less time point⁻¹ to collect data (3 versus 9 hr including travel time), detected more species point⁻¹ (24.7 versus 6.3), generated more data, and required more data entry time point⁻¹ (2 hr versus 20 min). In our sampling scheme, point counting detected nearly seven times as many species hr⁻¹ point⁻¹ than mist netting.

DISCUSSION

SUM OF POINTS

Mist netting was not an effective technique for the purpose of describing bird communities at our site and was much less efficient than point counting. It failed to detect many species and indicated a distribution of species among family and body size groupings and height strata guilds that was different from that of point counting

and the checklist. Mist netting did not detect large, rare, or canopy species, and underestimated the frequency of species (Lynch 1989); and so its data did not accurately describe either the total or the understory bird community. In contrast, Gram and Faaborg (1997) found that mist netting detected twice as many species and migrant species as point counting in tropical semi-deciduous forest and was more effective than point counts at detecting ground and shrub dwelling species.

Point counting was more effective and time efficient at describing bird communities at our site than mist netting, but like mist netting it did not provide a complete description. It did not detect all species and indicated a distribution of species among guilds that was different from the local checklist. Like mist netting, point counting did not detect large-bodied or rare species well and underestimated the frequency of all species (Lynch 1989), although this may not always be the case (Hutto et al. 1986).

Together mist netting and point counting yielded a more accurate description than mist netting alone and a slightly more complete description than point counting, but the effort involved with mist netting was much greater than point counting alone. Therefore, point counting alone would be the most time efficient, least costly, and a relatively complete technique for the purpose of describing bird communities in the tropics (Beehler et al. 1995). However, Gram and Faaborg (1997) found that both mist netting and point counting were necessary to detect most species at sites in Tamaulipas, Mexico. About 1,000 total person-hours (or 200 hr of census time) of effort by moderately-experienced observers at about 300 points in a 20 km² area might yield a list of most species detected by point counting. Our results may be useful for researchers in the selection of methods for the purpose of conducting inventories or describing individual sites. However, other techniques such as plot searches (Thiollay 1992), mapping, or transects (Verner 1985), also may be useful for describing bird communities at a site.

INDIVIDUAL POINTS

Mist netting also was less effective than point counting for surveying birds at points. It only detected three common, understory species more frequently than point counting: Tawny-winged Woodcreeper, Ruddy Woodcreeper, and Ochre-

bellied Flycatcher. These nonterritorial species are less vocal than territorial or lekking species, and thus are poorly detected by counting techniques (Hutto et al. 1986, Gram and Faaborg 1997). They may be more easily captured by mist netting than territorial species (Remsen and Good 1996). However, mist netting's chief advantage over point counting is that marking birds makes it possible to ascertain repeat detections. Repeat detections are problematic for three kinds of species: (1) species with large territories, (2) nonterritorial species (ant-swarm following or lekking species), which are common in the tropics (Karr 1981) and can move widely during a morning, and (3) species with such small territories that disputes between birds of adjacent territories are mis-identified as being single birds. Also, mist netting may be well suited for studies other than those needing survey data, for example, studies estimating population parameters and assessing food habitats. However, a single mist netting protocol may not successfully meet different research goals simultaneously (Remsen and Good 1996).

Mist netting clearly has several drawbacks. It poorly detects large bodied species and species that are active greater than 3 m above the ground (Karr 1981, Lynch 1989). Detection by mist nets is affected by variation in habitat structure (Remsen and Good 1996). Canopy species may be caught more often in nets in short forest than in tall forest even though the species is equally abundant in both habitats (Petit et al. 1992). Flight distance and frequency also might affect detectability by mist nets (Remsen and Good 1996), but we do not have species-specific data on these behaviors.

In our study, point counting detected more species and more species in most guilds than mist netting. Each technique detected different groups of common species with equal frequency, but many less common species only were detected by point counting, especially canopy species. Although mist netting has been promoted as a good survey technique for understory species (Petit et al. 1989, Karr 1990, Blake and Loiselle 1992), this study found point counting equally or more effective than mist netting at surveying such species. This is not surprising considering that few tropical species spend all of their time within 2 m of the ground (Remsen and Good 1996).

However, point counting is not free of bias

and has weaknesses. Point counting was poor at detecting nonterritorial species that are less vocal than territorial or lekking species (see also Hutto et al. 1986). Detection by point counting can be biased by the height strata of the bird because height influences aural and visual detection (Waide and Narins 1988). When surveying different habitats, point counting may be subject to detection rates that are habitat specific; a given species may not always be equally detectable in all habitats (Verner 1985). Potential errors by a data recorder and in observer training were more problematic for point counting than mist netting. Moreover, identification errors and observer bias are time-consuming to assess for point counting (Verner 1985). Further discussion about the biases of point counting and mist netting can be found in Verner (1985) and Remsen and Good (1996).

Combining mist netting and point counting increased the total number of species detected and the number of species in over one-third of the guilds. Together, mist netting and point counting was superior to mist netting alone or point counting alone (Remsen and Parker 1983, Lynch 1989, Gram and Faaborg 1997) particularly because the combined detection rates for understory and canopy species were higher than for either technique alone. However, mist netting and point counting together detected few large-bodied or rare species because these species occurred at low densities. Other species with few detections were nocturnal (families Caprimulgidae and Strigidae) or associated with forested wetlands, a rare habitat on our study plots. The remaining species with few detections may be uncommon and rarely detected because they are not vocal. These species may require special survey techniques such as play backs to elicit vocalizations. When experienced observers are available, point counting alone may be the most efficient of the two techniques.

These results may be useful to researchers who are selecting methods for studies that survey, monitor, or census birds. Other survey techniques such as roost surveys, mark-resighting methods (Casagrande and Beissinger 1997), plot searches (Thiollay 1992), mapping, or transects (Verner 1985), also may be useful. However, plot searches and transects also rely on aural detections and may have the same biases as point counting. Mapping and mark-resighting have the advantage of yielding a more accurate and pre-

cise abundance estimate than point counting (Casagrande and Beissinger 1997).

Some might argue that our results do not apply to other sites. Wet tropical forests may be rich in secretive species that are especially difficult to survey by aural techniques, thus mist netting may still be well suited for surveying birds in these forests. Gram and Faaborg's (1997) study suggests that our results do not apply in central Mexico or in tropical semi-deciduous forest, cloud forest, and oak-pine forest habitats. Additional studies in other locations would be necessary to verify advantages of mist netting over other survey techniques.

Our paper emphasizes differences in the ability of point counting and mist netting to detect individual species. We did not consider other factors that affect the detectability of a species by either survey technique (for example, length of count period, time-of-day, effort, etc.), and this may confound our comparison. Our comparison was appropriate because the number of field days spent with each technique was the same, and the same points were sampled with both techniques. However, other sampling issues such as statistical efficiency and effect of sample size should be investigated to completely appreciate differences in the effectiveness of mist netting and point counting for surveying tropical bird communities.

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APPENDIX 1

A list of forest species and number of points where detected by mist netting, point counting, and both techniques, respectively ($n = 60$). *Tinamus major*, 0, 1, 1; *Casmerodius albus*, 0, 1, 1; *Leptodon cayanensis*, 0, 1, 1; *Micrastur ruficollis*, 0, 1, 1; *M. semitorquatus*, 0, 1, 1; *Ortalis vetula*, 1, 0, 1; *Penelope purpurescens*, 0, 1, 1; *Crax rubra*, 0, 1, 1; *Columba speciosa*, 0, 8, 8; *C. nigrirostris*, 0, 6, 6; *Leptotila cassinii*, 0, 6, 6; *L. plumbeiceps*, 2, 0, 2; *Geotrygon montana*, 13, 1, 13; *Aratinga astec*, 0, 18, 18; *Pionopsitta haematotis*, 0, 17, 17; *Pionus senilis*, 0, 17, 17; *Amazona autumnalis*, 0, 14, 14; *A. farinosa*, 0, 4, 4; *Piaya cayana*, 0, 12, 12; *Otus guatemalae*, 0, 1, 1; *Ciccaba virgata*, 1, 0, 1; *Chaetura veauxi*, 0, 3, 3; *Panyptila cayennensis*, 0, 1, 1; *Phaethornis superciliosus*, 5, 0, 5; *Phaethornis longuemareus*, 1, 5, 6; *Campylopterus curvipennis*, 5, 1, 5; *Amazilia candida*, 2, 22, 22; *A. tzacatl*, 2, 7, 9; *Heliothryx burroti*, 0, 1, 1; *Trogon melanocephalus*, 0, 23, 23; *T. violaceus*, 0, 4, 4; *T. collaris*, 0, 1, 1; *T. massena*, 0, 5, 5; *Hylomanes momotula*, 5, 0, 5; *Malacoptila panamensis*, 4, 4, 7; *Pteroglossus torquatus*, 1, 2, 3; *Ramphastos sulfuratus*, 0, 1, 1; *Melanerpes pucherani*, 0, 4, 4; *Veniliornis fumigatus*, 1, 17, 18; *Picus rubiginosus*, 0, 3, 3; *Celeus castaneus*, 0, 10, 10; *Campophilus guatemalensis*, 0, 6, 6; *Automolus ochrolaemus*, 0, 2, 2; *Xenopus minutus*, 13, 34, 40; *Sclerurus guatemalensis*, 2, 5, 7; *Dendrocincla anabatina*, 42, 13, 44; *D. homochroa*, 35, 3, 36; *Sittasomus griseicapillus*, 17, 15, 27; *Glyphorhynchus spirurus*, 8, 0, 8; *Dendrocolaptes certhia*, 6, 2, 8; *Xiphorhynchus flavigaster*, 17, 23, 30; *Microrhopias quixensis*, 1, 15, 16; *Formicarius analis*, 10, 21, 27; *Zimmerius villissimus*, 0, 2, 2; *Ornithion semiflavum*, 0, 19, 19; *Myiopagis viridicata*, 1, 36, 36; *Elaenia flavogaster*, 0, 1, 1; *Mionectes oleagineus*, 22, 2, 23; *Leptopogon amauroce-*

phalus, 1, 5, 6; *Oncostoma cinereigulare*, 1, 44, 44; *Rhynchocyclus brevirostris*, 3, 21, 23; *Platyrinchus cancrinus*, 38, 28, 44; *Onychorhynchus coronatus*, 2, 1, 3; *Terenotriccus erythrus*, 15, 7, 19; *Myiobius sulphureipygus*, 17, 7, 22; *Tolmomyias sulphureus*, 0, 7, 7; *Empidonax flaviventris*, 1, 24, 25; *Attila spadiceus*, 6, 4, 9; *Rhytipterna holerythra*, 0, 3, 3; *Myiarchus tuberculifer*, 0, 5, 5; *M. crinitus*, 0, 1, 1; *Myiozetetes similis*, 0, 2, 2; *Pachyrhamphus aglaiae*, 0, 2, 2; *Tityra semifasciata*, 0, 1, 1; *Lipaugus unirufus*, 0, 5, 5; *Schiffornis turdinus*, 40, 26, 47; *Manacus candei*, 4, 0, 4; *Pipra mentalis*, 27, 18, 35; *Cyanocorax morio*, 0, 2, 2; *Thryothorus maculipectus*, 4, 18, 20; *Uropsila leucogastra*, 1, 28, 28; *Henicorhina leucosticta*, 33, 40, 48; *Ramphocaelus melanurus*, 1, 14, 15; *Poliptila plumbea*, 0, 14, 14; *Hylocichla mustelina*, 40, 44, 51; *Turdus grayi*, 2, 8, 9; *Dumetella carolinensis*, 24, 45, 50; *Vireo griseus*, 0, 5, 5; *Hylophilus ochraceiceps*, 14, 40, 43; *H. decurtatus*, 0, 57, 57; *Vireolanius pulchellus*, 0, 5, 5; *Vermivora pinus*, 0, 2, 2; *V. peregrina*, 0, 1, 1; *Dendroica pensylvanica*, 0, 3, 3; *D. magnolia*, 0, 48, 48; *D. virens*, 0, 5, 5; *Mniotilta varia*, 6, 5, 10; *Setophaga ruticilla*, 0, 37, 37; *Helmitheros vermivorus*, 4, 1, 5; *Seiurus aurocapillus*, 6, 4, 9; *S. noveboracensis*, 6, 2, 7; *Oporornis formosus*, 35, 27, 44; *Wilsonia citrina*, 21, 24, 33; *Basileuterus culicivorus*, 0, 1, 1; *Granatellus sallaei*, 0, 3, 3; *Tangara larvata*, 0, 1, 1; *Cyanerpes cyaneus*, 0, 4, 4; *Euphonia affinis*, 0, 1, 1; *E. hirundinacea*, 0, 13, 13; *E. gouldi*, 0, 9, 9; *Eucometis penicillata*, 6, 1, 7; *Lanio aurantius*, 0, 8, 8; *Habia rubica*, 5, 27, 28; *H. fuscicauda*, 29, 14, 35; *Piranga rubra*, 0, 1, 1; *Caryothraustes poliogaster*, 0, 16, 16; *Cyanocompsa cyanoides*, 8, 12, 17; *C. parvella*, 1, 1, 1; *Passerina cyanea*, 1, 0, 1; *Arremonops chloronotus*, 1, 2, 3; *Icterus dominicensis*, 0, 4, 4; *Psarocolius montezuma*, 0, 8, 8.

APPENDIX 2

Fifty-one forest species were never detected by mist netting or point counting in this study or in subsequent

field seasons: *Tigrisoma mexicanum*, *Butorides striatus*, *Jabiru mycteria*, *Coragyps atratus*, *Cathartes burrovianus*, *Sarcoramphus papa*, *Leptodon cayanensis*, *Agriocarus ocellata*, *Elanoides forficatus*, *Harpagus bidentatus*, *Ictinia plumbea*, *Leucopternis albicollis*, *Buteo magnirostris*, *B. nitidus*, *Falco ruficularis*, *Claravis pretiosa*, *Amaurolimnas concolor*, *Amazona farinosa*, *A. ochrocephala*, *Glaucidium minutissimum*, *Nyctidromus albicollis*, *Otophanes yucatanicus*, *Caprimulgus badius*, *Phaeochroa cuvierii*, *Florisuga mellivora*, *Chloroceryle aenea*, *C. americana*, *Bucco macrorhynchus*, *Sphyrapicus varius*, *Lepidocolaptes souleyetii*, *Contopus borealis*, *Laniocera rufescens*, *Pitangus sulphuratus*, *Myiodynastes luteiventris*, *Pachyrhamphus aglaiae*, *P. cinnamomeus*, *Tityra inquisitor*, *Vireo pallens*, *V. magister*, *Vermivora peregrina*, *Parula americana*, *Dendroica dominica*, *D. virens*, *D. caerulescens*, *Protonotaria citrea*, *Chlorophanes spiza*, *Piranga ludoviciana*, *Salpinctes obsoletus*, *Sporophila torqueola*, *Icterus spurius*, and *I. galbula*.

Fifteen forest species were never detected by mist netting or point counting in this study and were only detected by point counting in subsequent field seasons included: *Crypturellus boucardi*, *Geranoospiza caerulescens*, *Buteogallus urubitinga*, *Spizaetus ornatus*, *S. tyrannus*, *Falco peregrinus*, *Odontophorus guttatus*, *Aramides cajaneus*, *Columba cayennensis*, *C. flaviventris*, *Galbula ruficauda*, *Xiphocolaptes promeropirhynchus*, *Tolmomyias sulphureus*, *Cyanocorax yncas*, and *Turdus grayi*.

Seven forest species were never detected by mist netting or point counting in this study but were only detected by mist netting in subsequent field seasons included: *Chloroceryle amazona*, *Synallaxis erythrorhax*, *Dysithamnus mentalis*, *Cercomacra tyrannina*, *Myiarchus crinitus*, *Catharus ustulatus*, and *Limnithlypis swainsonii*.

Three forest species were never detected by mist netting or point counting in this study but were detected by mist netting and point counting in subsequent field seasons: *Thamnophrus doliatius*, *Vireo flavifrons*, and *Amblycercus holosericeus*.