Effects of Selection Logging on Birds in Northern Belize[1]

Andrew A. Whitman[2], John M. Hagan III, and Nicholas V. L. Brokaw

Manomet Center for Conservation Sciences, Division of Conservation Forestry, P.O. Box 1770, Manomet, MA 02345, U.S.A.

ABSTRACT

We compared bird diversity and frequency in selection logged and unlogged forest to determine the effects of recent selection logging on avian biodiversity in a subtropical, moist evergreen forest. We used a combination of mist netting and fixed-radius point counts to assess bird communities in February and March 1993 in northwestern Belize. Vegetation structure and composition was similar in logged and unlogged forest. The 66 most common species occurred with statistically similar frequency in logged and unlogged forest although 13 species were two times more frequent in intact forest. Numbers of total bird species were similar between logging gaps and the logged forest matrix, and between the logged forest matrix and unlogged forests. A comparison of numbers of species in 26 guilds based on migration strategy, diet, foraging substrate, and height strata also showed them to be similar regardless of logging history. Our results differed from previous studies that reported lower bird species richness and abundance of individual species in logged tropical forests than in unlogged forest. The differences might be explained by the lower logging intensity and/or greater levels of natural disturbance in our study area compared to previous studies.

Key words: Belize; disturbance; forest birds; forest management; Neotropical migrants; selection logging; subtropical moist evergreen forest.

MANY STUDIES HAVE EVALUATED SILVICULTURAL OR ECONOMIC EFFECTS of selection logging in tropical forest (Uhl & Viera 1989, Appanah & Weinland 1990, Uhl et al. 1991, Crome et al. 1992, Gullison & Hardner 1993); however, there are too few studies of selection logging impacts on biodiversity to predict how any taxonomic group might respond to different intensities of selection logging. Birds have been the most frequently studied taxonomic group (Johns 1991, Lambert 1992, Thiollay 1992, Lynch & Whigham 1995, Johns 1996) and may be appropriate biological indicators of landscape degradation because they respond to habitat changes at several scales (Wiens 1989), and they perform important ecological functions in Neotropical forests as predators, pollinators, and seed dispersers (Stiles 1983).

Previous studies have shown significant negative affects of selection logging on tropical bird communities (Wong 1986, Johns 1991, Lambert 1992, Thiollay 1992, Johns 1996). However, they did not always address two important points in their experimental design. First, some studies did not verify the similarity of control sites to treated sites before or after logging. Studies either had established unlogged forest sites 10 or more km away from the logged site (e.g., Lambert 1992), did not

quantitatively assess the vegetation of the logged and unlogged forests (e.g., Johns 1991), or found differences in the vegetation structure between logged and unlogged sites (e.g., Wong 1986). Differences between the birds of logged and unlogged forest found in these studies might have been the result of logging, or differences in forest type, tree species composition, or other site factors. Second, some studies restricted bird surveys to areas most affected by logging: logging gaps (where trees were removed) and logging trails (e.g., Johns 1986, Thiollay 1992). These studies did not address the important conservation question, which is whether the bird communities in the forest matrix surrounding logging gaps were also affected.

We surveyed birds in logged and unlogged forests to determine how selection logging affected bird communities, guilds, and species. Our surveys included points in logged forest with undisturbed canopy (50–200 m from logging disturbance) to determine the effects of logging on the bird community in the forest matrix surrounding logging gaps and trails. These areas are important because selection logging typically disturbs <50 percent of the stand area (Gullison & Hardner 1993). We also compared the vegetation in logged and unlogged forests.

MATERIALS AND METHODS

STUDY LOCATION.—The study was conducted near the southwestern tip of the New River La-

goon, Orange Walk District, Belize (17°36'N, 88°42'W), in the Rio Bravo Conservation and Management Area. The area is owned and managed for conservation and sustainable use by the Programme for Belize, a nonprofit organization. The study area is in the "subtropical moist" life zone at 80 m elev. Annual rainfall is 1.5 m with 10 percent of the rain falling during the "dry" season, January to May. However, 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. It has been disturbed by occasional hurricanes, past deforestation by Maya during the period 0–1000 AD, and low-intensity selective logging since the early 1800s (Brokaw & Mallory 1993). Logging occurred February to April 1992, and removed on average one mahogany tree per 2.0 ha and 2 percent of the canopy (Whitman et al. 1997). Most logging gaps were created when single trees were cut (43 of 45 gaps) and only two gaps had been enlarged due to blowdowns by 1995. We surveyed birds in two 3 km^2 areas (Botas and Marimba) that were separated by 10 km and had both logged and unlogged forest. In Botas, the forest was 18.8 m (SE = 2.4) tall, with emergents to 25 m; in Marimba, the forest was 21.8 m (SE = 2.0) tall with emergents to 28 m. The 5 most common bird species were: Lesser Greenlet (*Hylophilus decurtatus*), Northern Bentbill (*Oncostoma cinereigulare*), White-breasted Wood-wren (*Henicorhina leucosticta*), Tawny-crowned Greenlet (*Hylophilus ochraceiceps*), and Thrushlike Manakin (*Schiffornis turdinus*) (Vallely & Whitman 1998).

STUDY DESIGN.—Between 14 February and 28 March 1993, we surveyed birds and vegetation in both study areas at a total of 60 points. We sampled logged and unlogged forest in both areas. We sampled two habitats in logged forest: logging gaps and logged forest. Points at logging gaps (N = 6, Botas; N = 6, Marimba) were on the edge of treefall gaps created by loggers cutting and removing single trees. Bird and vegetation surveys at these points encompassed the treefall gaps as well as the adjacent intact forest. Points in logged forest (N = 6, Botas; N = 18, Marimba) were 50–200 m from logging disturbance and had intact forest canopy overhead. Six points in Marimba and six points in Botas in logged forest were paired with logging gap points in each area.

Second, we sampled points in unlogged forest that had not been logged within 10 years and had an intact canopy (N = 12, Botas; N = 12, Marimba). We were unable to sample uncut forest because of its rarity and inaccessibility; however, past selection logging has not altered the forest significantly (Brokaw & Mallory 1993). Furthermore, we were only interested in the immediate effects of logging disturbance and how it affects bird diversity and frequency. Points in logging gaps and logged forest were interspersed amongst each other within a 1 km^2 area, whereas points in unlogged forest were located 2 km away. Survey points were at least 200 m apart. Using semivariograms to determine spatial autocorrelation (Turner et al. 1991), neither the number of bird species nor the number of species in each guild at each point were spatially correlated ($P > 0.25$). Gutzwiller (1991) and Hutto et al. (1986) also found that 200 m was adequate spacing for statistical independence. Thus, all points were considered to be statistically independent.

VEGETATION SURVEY TECHNIQUES.—We assessed vegetation along randomly placed transects 10 m from each point to avoid vegetation clipped for mist nets. We measured the DBH (diameter at 1.4 m) of trees ≥8 cm DBH and counted logs in a 10 × 50 m plot. DBHs of *Acacia cookii, Alseis yucatanensis, Ampelocera hottlei, Bursera simaruba, Calophyllum brasiliense, Cryosophila argentea, Coccoloba* spp., all liana spp., *Manilkara chicle, Orbignya cohune, Pimenta dioica, Sabal mauritiiformis*, and *Swietenia macrophylla* were recorded separately from other species because inexperienced observers were able to identify these species. Other tree species were measured but not identified.

We counted all stems <8 cm DBH within a 2 × 50 m plot inside the 10 × 50 m plot. The number of stems were tallied for *Acacia cooksii, Alseis yucatanensis, Ampelocera hottlei, Bactris* spp., bambusoid grasses, *Cryosophila argentea, Desmoncus* sp., *Chamaedorea* spp., all liana spp., *Orbignya cohune, Piper* spp., species in the family Myrtaceae, and *Sabal mauritiiformis* because these species could be learned and reliably identified by inexperienced observers. Stems of remaining species <8 cm DBH were counted but not identified to species. Stems were tallied in five height classes: 0.5–1 m, 1–2 m, 2–4 m, 4–6 m, and >6 m. At logging gaps, the vegetation plot was bisected by the gap edge, with half of the plot in the gap and the other half in the forest. Data from the gap and forest halves were recorded separately so that we could compare halves.

BIRD SURVEY TECHNIQUES.—We used point counts

and mist nets to survey birds at each point because both methods together provide a more complete survey of the avifauna than either alone (Remsen & Parker 1983). We selected this time of year because Neotropical-Nearctic migrants were present and breeding activity (including singing and calling) began at this time in Belize (Mallory & Brokaw 1993). During this period, we alternated surveying different forest tracts weekly to avoid surveying all points in one forest type at the same time. Fixed-radius point counts were conducted between 0600 and 0900 h when detections for many species may be the greatest (Lynch 1995). All birds heard or seen within 50 m during a 15-minute period were recorded. Six points were surveyed each day. 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. Three NEBBA ATX mist nets also were used at each point. Mist nets were opened at sunrise (about 0600 h), checked every hour, and closed five hours later. Six points were surveyed each day. Each point was sampled for three consecutive days, immediately preceding or following the three days of point counting. All birds were marked so that data from recaptures were only used once.

VEGETATION DATA.—To compare the three habitats, we used multivariate techniques to reduce 48 vegetation variables into three principal component analysis (PCA) scores (SAS 1990). First, because the tree species composition data were highly skewed and hence not suited to PCA (Gauch 1982), we reduced these data to a presence/absence data and transformed them into a matrix of Jaccard's indices (% of species in common) between all combinations of pairs of points. The matrix was analyzed using multidimensional scaling (MDS) to determine point scores on two axes indicating the floristic composition of each point (Wilkinson 1990). The MDS analysis accounted for 94.3 percent of the variance in the matrix of Jaccard's similarity indices. MDS scores were used to characterize the species composition of each point. Second, we conducted a PCA without tree species abundance. It accounted for only 26 percent of the variation in the vegetation data. Finally, we eliminated variables with low explanatory value and conducted a second PCA using the 13 variables with the highest loadings from the second analysis (loadings > 0.15) and the MDS scores from the first two axes.

BIRD DATA.—We used point counting and mist netting data to determine the presence or absence of a species, the total number of species, and the number of species within each guild at each point. We used Fisher's exact test to determine if a species occurred more frequently in logged or unlogged forest (SAS 1990). We arbitrarily restricted this analysis to the 66 species that occurred at 10 or more of the 60 points because analyses for species with lower frequencies meant that the power of this analysis was low. However, we recognize that rare species potentially might be most sensitive to logging disturbance. We did not compare density estimates because we rarely detected >1 individual of a species at a point and so the data were too skewed.

Point counts next to logging gaps where visibility was greater yielded significantly more visual detections than counts at other points (Fisher's exact test, $P = 0.006$). Because this bias might have affected our comparisons, we excluded point count detections made by sight, repeated all analyses, but found the same results and so do not report them here. However, the number of aural detections was similar among points (Fisher's exact test, $P = 0.15$).

We compared total number of species and the number of species in different guilds at logging gaps and paired logged forest points using paired t-tests (SAS 1990). We compared total number of species and the number of species in different guilds in logged forest and unlogged forest at each point using ANOVA for unbalanced replication with logging history and area (Botas and Marimba) as fixed effects. Area was included as a variable because their vegetation was different. In 80 percent of the tests, residuals were normally distributed and in all cases a visual inspection of the variances indicated that they were homogeneous. Therefore, we only used ANOVA to minimize the kinds of statistical tests presented and to maximize power.

Birds were assigned to guilds based on foraging height strata (Karr et al. 1990), diet (Karr et al. 1990), foraging substrate (Karr et al. 1990), migratory status (O. Komar pers. comm.), and habitat (Stiles & Skutch 1989). We analyzed foraging height strata, diet, and foraging substrate guilds to determine if certain ecological groups were particularly sensitive to selection logging. We analyzed migratory status and habitat guilds because of special conservation concerns for Nearctic-Neotropical migrants and forest-dependent species. We made Bonferroni adjustments to the alpha levels because so many guild and species analyses were conducted. We assessed the similarity of the bird commu-

nity among the three pairwise combinations of the three habitats (unlogged forest—logged forest, unlogged forest—logging gaps, logged forest—logging gaps), using Jaccard's similarity index ([a/(a + b + c)] where a = number of species in common, b = number of species restricted to one habitat, and c = number of species only restricted to the other habitat; Ludwig & Reynolds 1988). We compared the observed Jaccard's index with a simulated distribution of indices that would be expected if there were no effect of logging. For the simulation, each survey point, regardless of its actual logging history, was randomly assigned to a logging history. Then, a species list was generated for each simulated logging history and a Jaccard's similarity index was calculated. We repeated the simulation 300 times to generate the distribution of potential Jaccard's indices if there were no logging effect. A 95 percent confidence interval was calculated for the simulated distribution. An observed Jaccard's similarity index between two types of logging histories was considered significantly different from random if it fell outside the 95 percent confidence interval. These analyses were run using 12 points from each habitat type so that sample sizes would be equal. The number of species in each guild and frequency of each species in forests of different histories, and guild assignments are available from the authors.

RESULTS

VEGETATION.—The first 3 components of a PCA based on the 15 most important vegetation variables explained 57 percent of the variance in the vegetation data, with the first, second, and third components explaining 27.8 percent, 19.2 percent, and 10.2 percent of the variance, respectively. Measures of shrub height diversity and indices of size distributions of tree stems had the highest loadings and thus were the most important variables for explaining variation in the vegetation data (Table 1). Most plots in logging gaps had a few large trees remaining, with an open canopy and little shrub height diversity, whereas controls, logged forest with intact canopy, and logged forest next to logging gaps were more toward the other extreme and similar to each other (Fig. 1).

BIRDS.—The frequency in occurrence of the 66 most common species did not show differences (P > 0.20) between logging gaps and logged forest or between logged and unlogged forest. Species not showing differences included migrants, Kentucky Warbler (*Oporornis formosus*) and Wood Thrush

(*Hylocichla mustelina*). In the constant effort sample (12 points in each of the three habitat types), 5 of 113 species (4.4%) were only in unlogged forest, including: Golden-crowned Warbler (*Basileuterus culicivorus*), Golden-masked Tanager (*Tangara larvata*), Great Curassow (*Crax rubra*), Royal Flycatcher (*Onychorhynchus coronatus*), and Tody Motmot (*Hylomanes momotula*). Six species (5.3%) were only in logged forest, including: Crested Guan (*Penelope purpurascens*), Mottled Owl (*Ciccaba virgata*), Vaux's Swift (*Chaetura veauxi*), Vermiculated Screech-Owl (*Otus guatamalae*), Wedge-billed Woodcreeper (*Glyphoryncus spirurus*), and Worm-eating Warbler (*Helmitheros vermivorus*). Three species (4.0%) were only in logging gaps, including Red-legged Honeycreeper (*Cyanerpes cyaneus*), Wedge-tailed Sabrewing (*Campylopterus curvipennis*), and Yellow-bellied Elaenia (*Elaenia flavogaster*). These species were rare (occurring at fewer than 6 of the 36 constant effort points).

Although we did not find statistical differences in the frequency of occurrence for common species in the different habitats, 13 common species occurred twice as frequently in unlogged and logged forest than in logging gaps (Table 2). These were three dove species, an Amazon parrot, and several understory species. Nine occurred twice as frequently in logged forest and/or logging gaps than in unlogged forest. Five occurred more frequently in logged forest and logging gaps than in unlogged forest. The four occurred more frequently in logging gaps than in unlogged or logged forest and were canopy species. None of the 26 guilds showed differences ($P > 0.5$) in the number of species between logging gaps and logged forest or between logged and unlogged forest.

The mean number of species per point was similar between logging gaps and logged forest (Botas $x = 26.2 \pm 9.1$/species point versus 24.3 ± 4.5, Marimba $x = 30.2 \pm 4.1$ versus 29.3 ± 6.5; ($t_5 = < 0.72$, $P > 0.5$), logged and unlogged forest (29.1 ± 5.7/species point versus 25.3 ± 5.7; $F_{1,23} = 0.28$, $P > 0.100$), or between sites ($F_{1,23}$, $P = 0.09$). In the constant effort sample (12 points in each of the three habitat types), we detected a total of 113 bird species with similar numbers being found in the three habitat types (Sign test, P > 0.15): 97 in logging gaps, 91 in unlogged forest, and 101 in logged forest.

Jaccard's similarity index of bird communities between logging gaps and logged forest, and between logged and unlogged forest was not different from what was expected by chance ($P > 0.20$). Unlogged and logged forest shared 73 percent of

TABLE 1. *Loading of 15 vegetation variables on first three PCA axes.*

| | Loadings on axes | | |
Variable	First	Second	Third
Canopy cover	0.318	−0.041	0.237
Number of logs	−0.285	0.019	−0.139
Indices indicating size distributions			
Proportion of large tree stems	−0.376	−0.238	−0.003
Proportion of small tree stems	0.388	0.238	0.053
Indices of shrub height diversity			
Hill's modified index	0.310	−0.371	−0.111
Reciprocal of Simpson's index	0.347	−0.354	−0.145
Log of Shannon index	0.350	−0.367	−0.133
Indices of floristic composition			
MDS first axis score	0.123	0.306	0.075
MDS second axis score	0.064	0.219	−0.597
Number of shrub stems			
Orbignya cohune	0.046	−0.090	0.318
Sabal mauritiiformis	−0.117	0.166	0.297
Other species	−0.107	−0.300	0.250
Numbers of tree stems			
All stems	0.251	0.279	0.142
Other species	0.200	0.068	0.513
Sabal mauritiiformis	0.191	0.214	−0.256

the species occurring in either habitat, logged forest and logging gaps shared 82 percent of the species occurring in either habitat, and unlogged forest and logging gaps shared 74 percent of the species occurring in either habitat.

DISCUSSION

VEGETATION.—Traditional selection logging (removal of one tree per 2 ha) at our site had little effect on the forest vegetation. Vegetation structure and composition was similar in logged and unlogged forest except inside logging gaps. The only logging impacts on vegetation were collateral damage around logging gaps and on the skid trails (Whitman *et al.* 1997.). Thus, at small scales (10sm²), logging affected vegetation surrounding skid trails and logging treefall gaps but logging impacts on vegetation at large scales (km²) was small.

BIRD SPECIES.—We did not find statistically significant effects of selection logging on the frequency of any species. In contrast, other studies found between 14 percent (Johns 1996) and 61 percent (Thiollay 1992) of the bird species were statistically negatively affected by selection logging in Neotropical forests. The large impact of logging on birds in Thiollay's (1992) study may have been observed because he primarily sampled within logging gaps created by selection logging where the damage is most severe. By sampling only the high-impact ar-

eas, his study might have overestimated the logging impacts on the avifauna of the forest as a whole. However, Thiollay (1992) estimated a wood volume harvest density of 11.0 m³/ha, nearly six times the harvest density in our study (1.8 m³/ha).

Seven rare species were only found in unlogged forest. Although their exclusive presence in controls could have been due to chance, populations of species that occur at low densities may be especially vulnerable to habitat degradation. Low densities of one of these species, the Great Curassow, probably reflected inherent uncommonness of large-bodied species, but may also be the result of hunting associated with the improved access created by logging (Johns 1991).

Thirteen of 66 common species were twice as likely to be found in unlogged and/or logged forest than in logging gaps. These included forest doves and other understory species that may tend to avoid high-impact areas. We speculate that these species might be significantly affected by selection logging at greater intensities. Although eight other species were twice as likely to be found in logged forest or logging gaps, these species might not respond favorably to logging at greater intensities as they might benefit only from small disturbances in the forest.

Conservationists have expressed concerns about the effect that tropical forest degradation might have on Neotropical-Nearctic migrants (Terborgh 1980, Rappole & McDonald 1994). The Kentucky
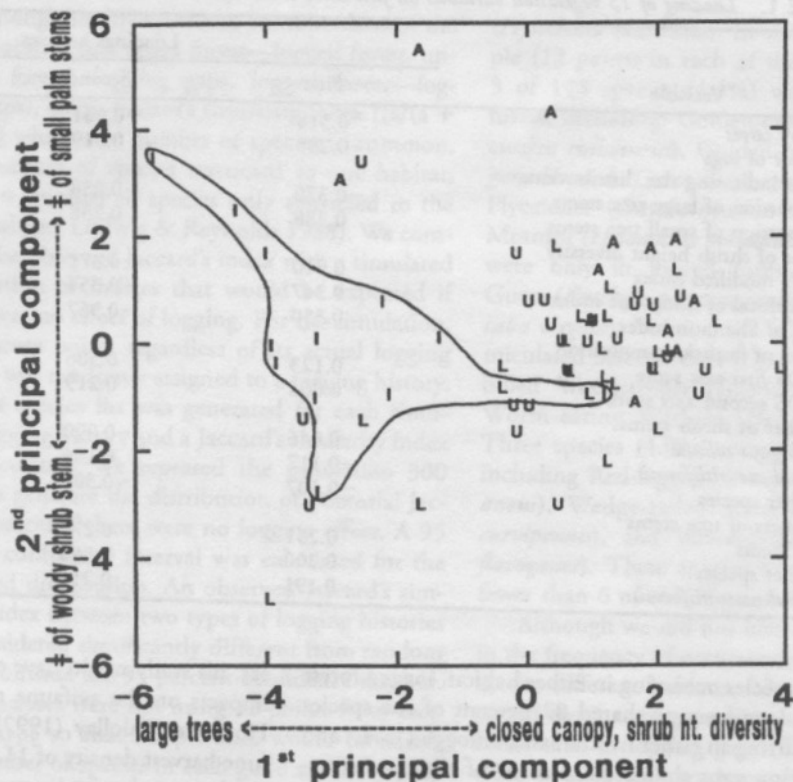
FIGURE 1.   Plot of first two principal component scores of the vegetation of survey points near Hill Bank, Belize. The first axis depicts a gradient from points dominated by large trees to points with closed canopy and much shrub height diversity. The second axis depicts a gradient of points from an understory dominated by woody plants to an understory dominated by palms. U = unlogged forest (logged >10 yr), L = logged forest with intact canopy, A = forest adjacent to logging gaps, and I = interior of logging gaps. The hand drawn line includes all of the interior logging gap points.

Warbler and Wood Thrush were of particular concern because these species seem most dependent on unlogged forest in Belize (Petit *et al.* 1992, Robbins *et al.* 1992) and the nearby Yucatan (Greenberg 1992, Lynch 1992) as wintering habitats. Our study indicates that selection logging at low intensities did not affect these species. Selection logging may positively affect the Hooded Warbler, another Neotropical-Nearctic migrant, given that it can reach its highest densities in disturbed forest (Petit *et al.* 1992). Thus, selection logging at the levels we observed may maintain adequate habitat for Neotropical-Nearctic migrants that use tropical forest.

Selection logging at our site in Belize had no demonstrable effect on 26 avian guilds or forest bird communities as indicated by composite statistics. Logged and unlogged forest also had similar numbers of bird species and species' composition. By contrast, other researchers found a reduction in the number of forest bird species ranging between 29 percent (Thiollay 1992) and 53 percent (Lambert 1992) in logged areas (except see Lynch & Whigham 1995). Overall, most common species occurred with similar frequency in the different habitats, although habitats had slightly different rare species.

WHY NO APPARENT EFFECT?—Three factors may explain why selection logging in our study did not affect the bird community: (1) low harvest density of selection logging; (2) high levels of natural background disturbance; and (3) past disturbance by Maya. Other studies may have demonstrated a significant effect because the harvesting intensity was greater. For example, the intensity of wood harvest by selective logging and corresponding effects on birds in other studies (Thiollay 1992, Johns 1991, Lambert 1992) was greater than in our study area:

TABLE 2. *Frequency of common species found twice as frequently in forest (unlogged and logged) than logging gaps, in logged forest (logged forest and logging gaps), or logging gap than forest (unlogged or logged). Only species occurring at 10 or more of 60 points are listed. No species were twice as frequent in unlogged forest than logged forest or logging gaps.*

| | Frequency | | |
Habitat type	Unlogged forest (N = 24)	Logged forest (N = 24)	Logging gap (N = 12)
Forest			
Scaled Pigeon (*Columba speciosa*)	0.250	0.292	0.083
Short-billed Pigeon (*Columba nigrirostris*)	0.083	0.250	0.000
Gray-fronted Dove (*Leptotila plumbeiceps*)	0.292	0.167	0.083
Mealy Parrot (*Amazona farinosa*)	0.167	0.167	0.083
Little Hermit (*Phaethornis longuemareus*)	0.167	0.250	0.083
Scaly-throated Leaftosser (*Sclerurus guatemalensis*)	0.167	0.125	0.083
Wedge-billed Woodcreeper (*Glyphoryncus spirurus*)	0.167	0.167	0.000
Barred Woodcreeper (*Dendrocolaptes certhia*)	0.292	0.208	0.000
Dot-winged Antwren (*Microrhopias quixensis*)	0.333	0.375	0.167
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	0.417	0.667	0.333
Rufous Piha (*Lipaugus unirufus*)	0.125	0.167	0.083
Black-throated Shrike Tanager (*Lanio aurantius*)	0.292	0.333	0.083
Red-crowned Ant Tanager (*Habia rubica*)	0.583	0.625	0.250
Logged forest			
Squirrel Cuckoo (*Piaya cayana*)	0.125	0.333	0.333
Rufous-tailed Hummingbird (*Amazilia tzacatl*)	0.042	0.292	0.250
Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*)	0.208	0.458	0.417
Clay-colored Robin (*Turdus grayi*)	0.083	0.375	0.167
Hooded Warbler (*Wilsonia citrina*)	0.333	0.667	0.750
Logging gap			
Red-lored Parrot (*Amazona autumnalis*)	0.042	0.208	0.417
Dusky-capped Flycatcher (*Myiarchus tuberculifer*)	0.125	0.125	0.250
Yellow-throated Euphonia (*Euphonia hirundinacea*)	0.167	0.125	0.333
Montezuma Oropendola (*Psarocolius montezuma*)	0.000	0.167	0.417

11, 20, and 90 m³/ha respectively versus estimated 1.8 m³/ha in our study. Based on this study and others (Lynch & Whigham 1995, Johns 1996), wood harvesting at low intensities may not affect bird communities. However, further studies at multiple sites varying in frequency of harvesting, bird and plant communities, and disturbance regime are necessary to determine this relationship.

Natural disturbance levels in Belize may also account for the lack of effect from selection logging on forest bird communities. The area of canopy disturbance created by selection logging was similar to that created by natural treefall gaps for this area (Whitman *et al.* 1997). The Yucatan area (Lynch 1991) has been frequently struck by hurricanes and occasionally by subsequent fire. Bird communities seem to recover rapidly from such disturbances (Lynch 1991, Lynch & Whigham 1995). Broad scale, intensive disturbance by hurricanes and Maya activity that occurred with moderate frequency over long time intervals may have eliminated habitat for disturbance-sensitive species, thereby win-

nowing out these species or creating barriers of habitat unsuitable to their dispersal into the area. This would yield a community of bird species that are insensitive to low-impact disturbances (*e.g.*, Miller 1982, Lugo 1988). As a result, bird communities in frequently-disturbed forest may not be sensitive to low levels of selection logging.

Given that virtually all forest in Belize has been selection logged or struck by hurricane, it was impossible to find primary, undisturbed forest for comparison. More importantly, given the current condition of the forest, low-intensity selection logging does not appear to significantly reduce the number of bird species, if past selection logging has had an effect. It is more likely that centuries of large-scale disturbance by hurricanes and land clearing by Maya has had a greater effect than low-intensity selection logging (*e.g.*, Lynch & Whigham 1995). Thus, low-intensity selection logging may not significantly disturb forest bird communities.

Three alternative hypotheses might explain why we observed such a small effect of logging on birds.

First, failure to detect effects of logging in our study could be an artifact of small sample size. We sampled 12 points in logging gaps, 24 points in logged forest, and 24 points in unlogged forest. However, we gained accuracy by intensively sampling each point for three consecutive days with both mist netting and point counting. The mean species detection probability was high (70%, $N = 115$, $SD = 26$) after two days of sampling at each point.

Second, most studies rely on frequency of occurrence to evaluate species response to logging. Ultimately, one should consider measures of a species' survivorship or productivity (Van Horne 1983) to best assess effects; however, these measures are difficult to obtain and expensive. Therefore, we cannot rule out effects of logging on population metrics other than frequency.

Third, it may take more than one year before selection logging significantly affects bird populations because effects may not be immediate. Although differences in frequency generally were not observed, logging may still reduce bird populations locally. Reproduction in unlogged forest near the logged area may have yielded a surplus of young ("source" populations). These surpluses may have dispersed and have been maintaining populations

in logged forest ("sink" populations) which are not self-sustaining due to logging effects (*sensu* Brown & Kodric-Brown 1977). Testing this hypothesis would require a widespread and long-term effort to monitor reproduction and dispersal. We also do not know what the effects would be if this intensity of selection logging were applied over large areas (>10 km^2) for a few years. However, short-term declines would be expected if disturbance was significant. Birds may avoid logged areas immediately after disturbance because few food resources are available and predation risk is great (Schupp *et al.* 1989).

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