

BIASED DETECTION OF BIRD VOCALIZATIONS AFFECTS COMPARISONS OF BIRD ABUNDANCE AMONG FORESTED HABITATS¹

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Abstract. Community studies of birds often rely on abundance estimates that are obtained from counts of bird vocalizations, yet vocalizations are not equally detectable in all habitats. I broadcast vocalizations for nine bird species to evaluate biases in detection of bird vocalizations among four forested habitats (young, mature, and old aspen-dominated forests, and white spruce dominated forests), and in relation to height of the broadcast, whether the broadcast occurred before or after leaf formation, and the frequency of the broadcast vocalization. Virtually all of the broadcast vocalizations were detected at 50 m from the speaker. However, at 100 m from the speaker, 27% of the broadcast vocalizations were not detected and detection was highest in white spruce forest, lowest in young aspen forest, and intermediate in mature and old aspen forests. Detection of broadcasts was negatively related to the minimum frequency of the vocalization, higher for broadcasts from the canopy than for broadcasts from the shrub layer, and higher for broadcasts before than after leaf formation. I reanalyzed abundance data that were obtained from a study involving point counts of wild birds in young and old aspen-dominated forest. Biases among habitats in the detection of vocalizations had moderate influence on the resulting measures of habitat preferences for birds. I suggest that if a detection distance of more than 50 m is used for bird censuses within forested habitats, then comparisons among forest types should be interpreted cautiously unless the researchers demonstrate that biased detection of vocalizations does not affect their conclusions.

Key words: bird surveys, detection biases, sound attenuation, vocalizations.

INTRODUCTION

In many studies of bird communities, indices of abundance from point counts, line transects, or spot mapping are compared among habitats (e.g., Thiollay 1992, Warkentin et al. 1995). Implicit in these comparisons is the assumption that bird vocalizations are equally detectable in all habitats, although that probably is not true (Morton 1975, Marten and Marler 1977, Wiley and Richards 1982, Waide and Narins 1988). Sound attenuation may differ among habitats because objects and wind scatter and absorb some of the sound energy and the types of structures, surfaces of the structures, and atmospheric conditions vary among habitats (Morton 1975, Wiley and Richards 1978, Richards and Wiley 1980). In addition, interference from reflected sound waves differs among habitats because the type of ground surface differs among habitats (Wiley and Richards 1982). Scattering

and absorption of sound waves is most pronounced for frequencies greater than 2 kHz, whereas interference from reflected sound waves is most pronounced for frequencies less than 2 kHz (Morton 1975, Marten et al. 1982, Wiley and Richards 1982). Sound attenuation may vary among forest types (Morton 1975, Marten et al. 1982, Wiley and Richards 1982) or among seral stages (Marten and Marler 1977) because the density and size of trees, shrubs, and herbs vary, and the types and sizes of leaves vary. Differences in detection of vocalizations among forest types are further complicated by the height (Waide and Narins 1988) and the time of year vocalizations are produced (Marten and Marler 1977, Wiley and Richards 1978).

Differences among habitats in detection of vocalizations, however, do not make inter-habitat comparisons of bird abundance impossible. Detection of vocalizations will be unbiased up to a certain distance because all vocalizations will be heard (Wolf et al. 1995), but there is little information that can be used to determine that distance. Consequently, a wide

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range of detection distances have been chosen by investigators (e.g., 25 m in Warkentin et al. 1995, 50 m in Rudnický and Hunter 1993, 100 m in Hutto 1995, and unlimited distance in Gutzwiller 1991). If the detection distance used in a study is too short, then unbiased information will be discarded and the power of the test will be lower than necessary. Alternatively, if the detection distance is too long, biased information will be included and those biases may cause spurious results (Verner 1985).

In this study I broadcast bird vocalizations from a speaker in four different forest habitats, at both shrub and canopy height, and both before and after leaf formation on deciduous trees to determine how these factors affected the probability of detecting vocalizations at 50 and 100 m from the speaker. Vocalizations from nine bird species were used in the experiments so that I could evaluate biases in detection for the range of sound frequencies produced by birds in the area. To evaluate whether detection-biases found in the present broadcast experiment affected comparisons of bird communities among habitats, I reanalyzed point-count data that were collected as part of a study by Schieck et al. (1995).

METHODS

STUDY AREA AND VEGETATION

As part of a previous study, information on percent cover of canopy tree species was used to locate 12 stands of aspen-dominated mixed-wood forests in mesic upland areas near Lac La Biche, Alberta, Canada (55°N, 112°W). The stands had regenerated following wildfires, were greater than 80 ha, and were from one of three successional stages (young, 23–26 years; mature, 51–63 years; and old, >120 years). Although aspen was the most abundant tree species in the forest canopy, balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) also were present. For the present study, I extended the successional sequence by choosing four additional stands in the Lac La Biche area that were dominated by white spruce. White spruce often dominates mixed-wood stands on upland areas after aspen trees die and fall (Kelsall et al. 1977, Carleton and Maycock 1978), and based on species composition of canopy trees (see Results), the white

spruce stands chosen for this study were between 150 and 200 years old (Thorpe 1992). Three sites were positioned randomly in the interior of each of the stands (resulting in 12 sites within each successional stage) with the restrictions that sites were at least 300 m apart and both the broadcast equipment and the person detecting the broadcast were positioned at least 50 m from the edge of the stands.

To quantify differences among the successional stages, nine vegetation characteristics were measured. With the aid of low-level aerial photographs (scale 1:1,000) and stereoscopes, height and species composition was determined for trees ≥ 5 m high at each of the sites. One 40 × 40 m quadrat that was centered on each of the sites was sampled in the aspen-dominated stands, whereas a 20 × 20 m quadrat was sampled in the white spruce stands (sampling intensity was lower in the white spruce stands because they were not part of the initial study). Canopy heights were determined as the heights of the 90th percentile live tree. Densities of tall shrubs and saplings were estimated based on the number of stems that were taller than 1 m within four 25 m² quadrats in aspen-dominated stands (two quadrats were sampled in white spruce stands). Percentage of the ground surface covered by herbs, grasses, mosses, and lichens was determined within 40, 0.11 m² quadrats in aspen-dominated stands (eight quadrats were sampled in white spruce stands). Shrub and ground vegetation quadrats were placed at random distances up to 100 m and in random directions from site centers.

Analyses. At each site I had multiple measures for densities of shrubs/saplings, and percentages of the ground surface covered by herbs, grasses, mosses, and lichens. Because the distributions of the vegetation data were not normal, I summarized each vegetation characteristic as its median value at the site (Conover 1980). Differences in vegetation characteristics among successional stages were evaluated using Kruskal-Wallis tests and *post hoc* multiple comparison tests (Conover 1980).

BROADCAST EXPERIMENT

Although I wanted to evaluate detection biases for all bird species that breed in the aspen-dominated forests in Alberta, logistic constraints limited the number of species I could use in the broadcast experiment. Consequently,

I chose to broadcast vocalizations for nine bird species whose vocalizations encompassed the range of sound frequencies, patterns, and durations (Fig. 1) that were found for bird species in the area. I chose to broadcast actual bird vocalizations, rather than simple pure tones, to make detection of the broadcasts similar to detecting natural vocalizations.

I used long-eared mini microphones (Applied Nature Systems, Gibsonia, PA), and a Sony portable dictator BM-15 tape-recorder (Sony of Canada Ltd. Willowdale, ON) to record vocalizations near the study areas. Only recordings with little background noise and obtained within 25 m of the vocalizing individual were used in the present broadcast experiment. For each species, I chose to broadcast its common territorial vocalization; for Pine Siskin (see Fig. 4 for scientific names) and Least Flycatcher I also included call notes because those were given frequently under natural conditions and were species specific.

Vocalizations used in the broadcast experiment were copied from the cassette tapes to a Macintosh Quadra 950 using Soundedit Pro at a sampling rate of 22.3 kHz (Macromind Paracomp 1991). The maximum intensity (dB), frequency (kHz) of maximum intensity, and the range from the lowest frequency with 50% of maximum intensity to the highest frequency with 50% of maximum intensity were determined for each species' vocalization (Fig. 1) using Soundedit Pro (size 128 points, offset 256 points). For each species a series of three vocalizations was created on the computer with a time separation of 2–5 sec between repetitions. The intensities of the vocalizations were adjusted so that when broadcast during the experiment they had intensities similar to those given by birds under natural conditions. During the broadcast experiment I was able to evaluate whether the intensities of the broadcast vocalizations were appropriate because wild birds often approached the speaker and vocalized. Based on subjective comparisons, broadcast vocalizations were within the range of intensities of vocalizations given by wild individuals.

Broadcast and detection of the vocalizations were carried out by a team of two people, the recorder who operated the tape recorder and the observer who listened for the broadcasts. The same observer was used during all broadcast experiments. Broadcast vocalizations were re-

corded as being detected if the observer heard the vocalization and identified the species. To ensure that the observer was not recording wild birds, the observer used a two-way radio to inform the recorder once a species had been detected and the recorder determined whether the broadcast was detected. The broadcast sequence of vocalizations for the nine species was determined using a random numbers table. In addition, the interval between broadcasts of the different species was varied randomly from between 2 and 18 sec. Broadcast experiments were conducted between sunrise and 09:00 and during calm and non-rainy weather because previous point counts were limited to those conditions (Schieck et al. 1995).

I conducted broadcast experiments throughout May and June to evaluate whether attenuation of sound increased throughout the spring. The first half of the broadcast experiment was conducted prior to 30 May to evaluate detection of vocalizations before full leaf formation on deciduous trees. The second half of the experiment was conducted after 9 June so that most leaves on deciduous trees were fully grown. At each site, vocalizations were broadcast from the shrub layer at 1.5 m above ground and again at approximately half-way between the lower branches and tops of the deciduous trees to evaluate differences in detection associated with birds vocalizing near the ground or in the canopy. Even though canopy heights varied among successional stages, I chose to broadcast vocalizations from the canopy because under natural conditions birds that vocalize from the canopy would be at different heights in each of the successional stages. The broadcast speaker was raised to the canopy on a rope that was looped over an appropriate branch with the aid of a sling-shot. Vocalizations were broadcast twice at each height, once when the observer was a horizontal distance of 50 m from the speaker and again when the observer was 100 m from the speaker. Vocalizations for each of the nine bird species were broadcast at six sites in each successional stage before leaf formation and at an additional six sites in each successional stage after leaf formation.

Analyses. I used logistic regression (SAS Institute 1989) to evaluate whether the probabilities of detecting broadcast vocalizations were related to successional stages in which they were broadcast, heights at which they were

broadcast, horizontal distances from the broadcast locations, whether the broadcasts were before or after leaf formation, and the frequencies of the vocalizations. Lower sound frequencies were expected to attenuate less than high frequencies (Wiley and Richards 1982), and thus I evaluated detection of broadcast vocalizations in relation to the minimum frequency that had at least 50% of the maximum intensity of the vocalization (hereafter called minimum frequency). A statistical model including the independent variables and all interactions was very complex and could not be evaluated due to some cells with zero frequencies. Consequently, I used log-linear modeling (SAS Institute 1989) and a forward stepwise procedure with backwards elimination to develop a model that included the main effects and interactions that were most highly related to the probability of broadcast vocalizations being detected (Hosmer and Lemeshow 1989). The likelihood ratio test was used to determine the sequence that main effects, then first-, second-, third-, fourth-, and fifth-order interactions were included in the model (Hosmer and Lemeshow 1989). Terms were added sequentially, starting with the term having the highest significance, with the restriction that terms had $P < 0.15$ to be included in the model. Terms were removed at any step if they no longer met the criterion of $P < 0.15$ with the added restriction that main effects could not be removed after first-order interactions had been entered, first-order interactions could not be removed after second-order interactions had been entered, etc. In the final analyses, the significance level of all main effects and interactions that had been included during the model-building process were tested simultaneously using maximum likelihood estimates of the log-linear model with chi-square approximation of the Wald statistic (SAS Institute 1989). Main effects and interaction were considered statistically significant if the probability of their relationship occurring by chance was < 0.05 .

BIASES IN DETECTION DURING POINT COUNTS

Relative abundance of birds within young and old aspen-dominated boreal forests was estimated from point counts (Schieck et al. 1995). In that study breeding bird surveys were conducted between mid-May and late-June during

both 1991 and 1992. Surveys were not conducted during windy or rainy conditions and began 30 minutes before sunrise and ended by 09:00. During each 10 minute survey all species that were seen or heard were recorded onto maps of the study areas (Schieck et al. 1995).

Analyses. All individuals detected during the point-count surveys were classified as within 50 m, between 50 and 100 m, or greater than 100 m from the point-count stations. To evaluate whether biased detection of distant vocalizations affected our interpretation of point-count data, I ordered species based on the ratio of number of detections in young successional stages to the number of detections in old successional stages, first using only information from within 50 m of the point-count stations and then using all information within 100 m of the point-count stations. Only species that were detected at least five times within 50 m of the point-count stations were included in the analyses because proportions may have been affected greatly by chance occurrences for species that were detected few times.

RESULTS

VEGETATION

Eight of the nine vegetation characteristics differed significantly among successional stages (Table 1). Density of white spruce trees increased, whereas density of aspen trees decreased throughout succession. Canopy height increased throughout succession. All other vegetation characteristics were not monotonically related to successional stage. Old aspen forests had higher density of non-aspen and non-white spruce trees than did young and mature aspen forests, and white spruce forests. Young and old aspen forests had higher densities of shrubs/saplings than mature aspen or white spruce forests. Percentage of the ground surface covered by moss and lichens was greater, and percentage of the ground surface covered by herbs was less, in white spruce forests than in all earlier aspen-dominated successional stages.

BROADCAST EXPERIMENT

Frequency range was greater than 2 kHz for vocalizations from five of the nine bird species and greater than 0.85 kHz for all bird species that were used in the broadcast experiment (Fig. 1). The minimum frequency was lowest for Northern Flickers (1.91 kHz) and highest for

TABLE 1. Differences in vegetation characteristics among successional stages of aspen mixedwood forests.

Vegetation characteristic	Habitat				Kruskal-Wallis test	
	Young aspen	Mature aspen	Old aspen	White spruce	χ^2	<i>P</i>
Density of aspen trees [~] (stems/ha)	6,140 ± 200 ^a	2,200 ± 130 ^b	520 ± 60 ^c	270 ± 50 ^d	41.3	< 0.001
Density of white spruce trees [~] (stems/ha)	0 ± 0 ^a	15 ± 12 ^{ab}	31 ± 14 ^b	750 ± 110 ^c	35.4	< 0.001
Density of other trees [~] (stems/ha)	33 ± 33 ^a	33 ± 30 ^a	147 ± 38 ^b	98 ± 37 ^b	18.3	< 0.001
Canopy height [#] (m)	10 ± 1 ^a	20 ± 1 ^b	26 ± 1 ^c	33 ± 1 ^d	42.6	< 0.001
Density of shrubs/saplings* (stems/25 m ²)	26 ± 1 ^a	12 ± 1 ^b	27 ± 2 ^a	10 ± 1 ^b	34.5	< 0.001
Herb cover (%)	54 ± 7 ^a	70 ± 5 ^b	59 ± 5 ^{ab}	19 ± 2 ^c	27.0	< 0.001
Grass cover (%)	5 ± 1	3 ± 1	5 ± 1	5 ± 1	5.3	0.15
Moss cover (%)	2 ± 1 ^a	1 ± 1 ^b	1 ± 1 ^b	31 ± 5 ^c	32.9	< 0.001
Lichen cover (%)	0 ± 0 ^a	0 ± 0 ^a	0 ± 0 ^a	5 ± 1 ^b	43.3	< 0.001

Tests were calculated using χ^2 approximation for the Kruskal-Wallis tests (SAS Institute 1989), *df* = 3 for all tests. Successional stages with similar superscripts indicate that the vegetation characteristic was not statistically different among those stages based on a multiple comparison test (Conover 1980).

[~] number of stems \geq 5 m tall.

[#] height of the 90th percentile canopy tree.

* number of stems \geq 1 m tall and less than 10 cm diameter at breast height.

Black-and-white Warblers (4.69 kHz). Maximum intensity and minimum frequency tended to be negatively related although that relationship was not quite statistically significant (Fig. 2; Person's correlation $r = -0.65$, $n = 9$, $P = 0.06$).

All main effects were included during the model building process. Consequently, I present general patterns of differences in detection among categories for each of the main effects. Probability of detection was high for all broadcast vocalizations at 50 m from the speaker and lower for broadcasts at 100 m (Table 2; percentage detected \pm SE, 96 ± 1 and 73 ± 1 , respectively; $\chi^2_1 = 127.4$, $P < 0.001$). At 100 m from the speaker, detection of vocalizations varied in a complex manner: (1) probability of detecting broadcast vocalizations was lowest in young aspen-dominated forests, moderate in mature and old aspen-dominated forests and highest in white spruce forests (Table 2; 60 ± 3 , 75 ± 3 , 74 ± 3 , 85 ± 2 , respectively; $\chi^2_3 = 35.1$, $P < 0.001$), (2) detection of broadcasts from the shrub layer was lower than that for broadcasts from the canopy (Table 2; 69 ± 2 and 78 ± 2 , respectively; $\chi^2_1 = 9.1$, $P = 0.01$), (3) detection of broadcasts was higher before than after leaf formation (Table 2; 79 ± 2 and 69 ± 2 , respectively; $\chi^2_1 = 12.0$, $P < 0.001$), and (4) detection of broadcasts was negatively related to the minimum frequency of the vocalization

(Fig. 3; $\chi^2_1 = 212.5$, $P < 0.001$). Results of the last test were confounded because intensity of the vocalizations tended to be negatively related to the minimum frequency of the vocalizations. Vocalization intensities, however, were similar for six of the species (Fig. 2; Black-capped Chickadee, Pine Siskin, Connecticut Warbler, Least Flycatcher, Black-throated Green Warbler, and Black-and-white Warbler); when only these six species were included in the analyses, there still was a negative relationship between the probability of detecting the broadcast vocalizations and the minimum frequencies of the vocalizations ($\chi^2_1 = 183.2$, $P < 0.001$).

In the final model, probability of detection was significantly related to four of the five main effects and two of the 2-way interactions that were included during the model building process (Table 3). Two of the 3-way interactions were marginally significant ($P < 0.10$; Table 3). In the final model, probability of detection did not appear to be related to distance from the broadcast speaker, but that was due to a highly significant interaction between distance from the broadcast speaker and minimum frequency of the broadcast vocalization (Table 3). Broadcast vocalizations that had minimum frequencies lower than 2.5 kHz were detected well at both 50 and 100 m from the speaker, broadcast vocalizations with minimum frequencies between 2.5 and 3.5 kHz had slightly lower prob-

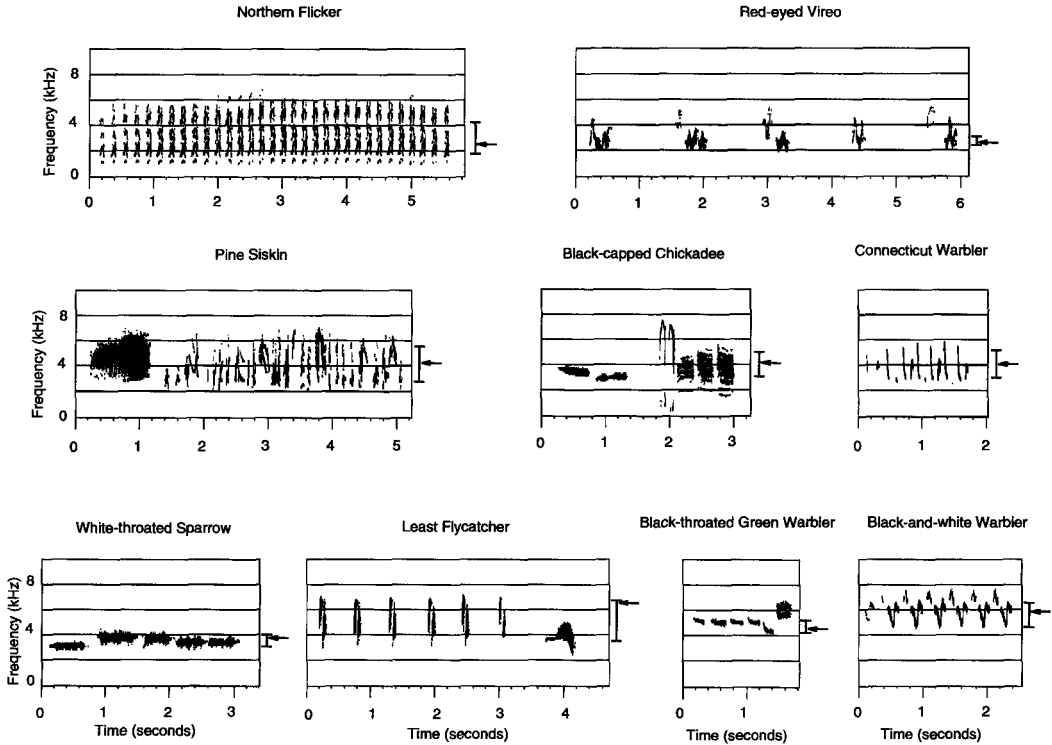


FIGURE 1. Sonograms for the vocalizations of the nine bird species used in the broadcast experiment. For each species the arrow at the right side of the sonogram indicates the frequency with maximum intensity and the bar indicates the range of frequencies with $\geq 50\%$ of the maximum intensity. Species were ordered based on their minimum frequency (see text).

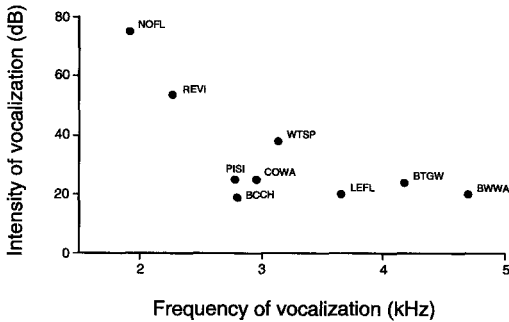


FIGURE 2. Maximum intensity of the broadcast vocalizations in relation to the minimum frequency with 50% of the maximum intensity of the vocalization. Maximum intensities were calculated from the vocalizations on the broadcast tape, but do not include the amplification that occurred in the speaker during the actual broadcast. Codes identify vocalizations for each of the bird species: NOFL = Northern Flicker, REVI = Red-eyed Vireo, PISI = Pine Siskin, BCCH = Black-capped Chickadee, COWA = Connecticut Warbler, WTSP = White-throated Sparrow, LEFL = Least Flycatcher, BTGW = Black-throated Green Warbler, and BWWA = Black-and-white Warbler.

abilities of detection at 100 m than at 50 m, and broadcast vocalizations with minimum frequencies higher than 3.5 kHz had much lower probabilities of detection at 100 m than at 50 m. The significant interaction between successional stage and timing of the broadcast experiment indicates that although the probability of detecting vocalizations was lower after than before leaf formation in all successional stages, that difference varied among successional stages. In agreement with that, leaf formation appeared to have a greater negative effect on the probability of detecting broadcast vocalizations in old aspen-dominated forests than in any other successional stage. The two marginally significant 3-way interactions may indicate that detection of broadcast vocalizations varied in complex ways among the categories of all main effects.

BIASES IN DETECTION DURING POINT COUNTS

In the study of native bird communities in young and old aspen-dominated forests, slightly

TABLE 2. Percentage of the broadcast vocalizations that were detected at each distance, at each height, and before and after leaf formation. Data have been presented separately for each species with the species ordered based on their minimum frequency with 50% of their maximum intensity (see Methods).

Species/Habitat	50 m				100 m			
	Shrub		Canopy		Shrub		Canopy	
	Before leaf	After leaf	Before leaf	After leaf	Before leaf	After leaf	Before leaf	After leaf
Pine Siskin								
Young aspen	100	100	100	100	67	67	83	50
Mature aspen	100	100	100	83	67	67	83	100
Old aspen	100	100	100	100	100	50	100	100
White spruce	100	100	100	100	100	100	100	100
Black-capped Chickadee								
Young aspen	100	100	100	100	67	83	83	83
Mature aspen	100	100	100	100	83	100	100	100
Old aspen	100	100	100	100	100	83	100	83
White spruce	100	100	100	100	100	100	100	100
Connecticut Warbler								
Young aspen	67	100	83	100	67	33	100	67
Mature aspen	100	83	100	100	83	33	100	83
Old aspen	100	67	100	100	83	33	100	100
White spruce	100	100	100	100	100	100	100	100
Least Flycatcher								
Young aspen	83	100	100	83	17	0	50	17
Mature aspen	100	100	100	100	50	17	100	67
Old aspen	100	67	83	83	83	0	100	33
White spruce	100	100	100	100	83	33	100	83
Black-throated Green Warbler								
Young aspen	100	83	100	67	17	0	0	0
Mature aspen	83	83	100	100	33	33	50	33
Old aspen	100	100	100	83	67	33	50	33
White spruce	100	83	100	100	83	33	50	50
Black-and-white Warbler								
Young aspen	67	83	83	83	0	0	0	17
Mature aspen	67	83	83	100	33	0	33	67
Old aspen	83	83	100	83	33	0	0	17
White spruce	100	100	100	100	67	17	33	50

Results from Northern Flicker, Red-eyed Vireo, and White-throated Sparrow were not presented because all broadcast vocalizations were detected.

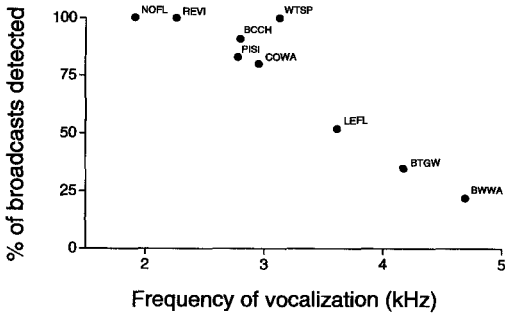


FIGURE 3. Percentage of the broadcast vocalizations that were detected at 100 m from the speaker in relation to the minimum frequency with 50% of maximum intensity for each of the vocalizations. See Figure 2 for bird species' codes.

fewer individuals were detected between 50 and 100 m from the point-count stations than were expected based on the area between 50 and 100 m from the point-count stations (30% and 70% of the individuals were detected <50 m and between 50 and 100 m, respectively, of the point-count stations, whereas 25% and 75% of the area was <50 m and between 50 and 100 m, respectively). Thus, some individuals that vocalized between 50 and 100 m from the point-count stations probably were not detected. When species were ranked based on the ratio of their relative abundances in young and old forests, nine species had exactly the same rank using all detections within 100 m as they did when using only detections within 50 m of the point-count stations (Fig. 4). Eleven, five, three, and one species changed ranks by one, two, three, and four, respectively, when all detections from within 100 m were used as compared to that found using only detections within 50 m of the point-count stations (Fig. 4).

DISCUSSION

Detection of vocalizations was expected to vary among forest types (Marten and Marler 1977, Wiley and Richards 1982), and I found that the probability of detection was lowest in young aspen-dominated forests, highest in white spruce forests, and intermediate in mature and old aspen-dominated forests. Three of the vegetation characteristics that I evaluated (density of aspen trees, density of white spruce trees, and canopy height) also varied monotonically throughout succession. These, or other vegetation characteristics that varied in a monotonic

TABLE 3. Analyses of variance table from the logistic regression evaluating differences in detection of broadcast vocalizations among successional stages (HABITAT), heights of the broadcast (HEIGHT), whether the broadcast was before or after leaf formation (LEAF), distances from the broadcast speaker (DISTANCE), and in relation to the minimum frequency of the vocalization that had 50% of its maximum intensity (FREQUENCY). Only variables and interactions that were included during the model-building stage (see text) were included in the analyses.

Source	χ^2	df	P
Intercept	92.4	1	< 0.001
HABITAT	23.6	3	< 0.001
DISTANCE	0.3	1	0.66
HEIGHT	3.9	1	0.05
LEAF	4.8	1	0.03
FREQUENCY	131.1	1	< 0.001
HABITAT \times DISTANCE	5.0	3	0.17
HABITAT \times HEIGHT	2.2	3	0.54
HABITAT \times LEAF	9.9	3	0.02
DISTANCE \times FREQUENCY	11.9	1	< 0.001
HEIGHT \times FREQUENCY	1.7	1	0.19
LEAF \times FREQUENCY	1.8	1	0.18
HABITAT \times DISTANCE \times FREQUENCY	5.3	3	0.15
HABITAT \times HEIGHT \times LEAF	6.7	3	0.09
HABITAT \times HEIGHT \times FREQUENCY	2.3	3	0.51
DISTANCE \times HEIGHT \times LEAF	2.3	1	0.13
HEIGHT \times LEAF \times FREQUENCY	3.7	1	0.06
HABITAT \times DISTANCE \times HEIGHT \times LEAF	3.2	3	0.37

Tests were calculated using the χ^2 approximation for the Wald's statistic (SAS Institute 1989).

fashion throughout succession (Lee et al. 1995), may have caused the monotonic increase in detection of vocalizations that occurred among successional stages. Surprisingly, however, differences in detection between young and mature/old aspen-dominated forests were as great as differences in detection between mature/old aspen-dominated forests and white spruce forests. Thus, detection of broadcasts differed as greatly between successional stages that had similar canopy tree species as it did between successional stages that had different canopy tree species.

In aspen-dominated forests the physical structures of deciduous trees, shrubs, and herbs change throughout the spring (Peterson and

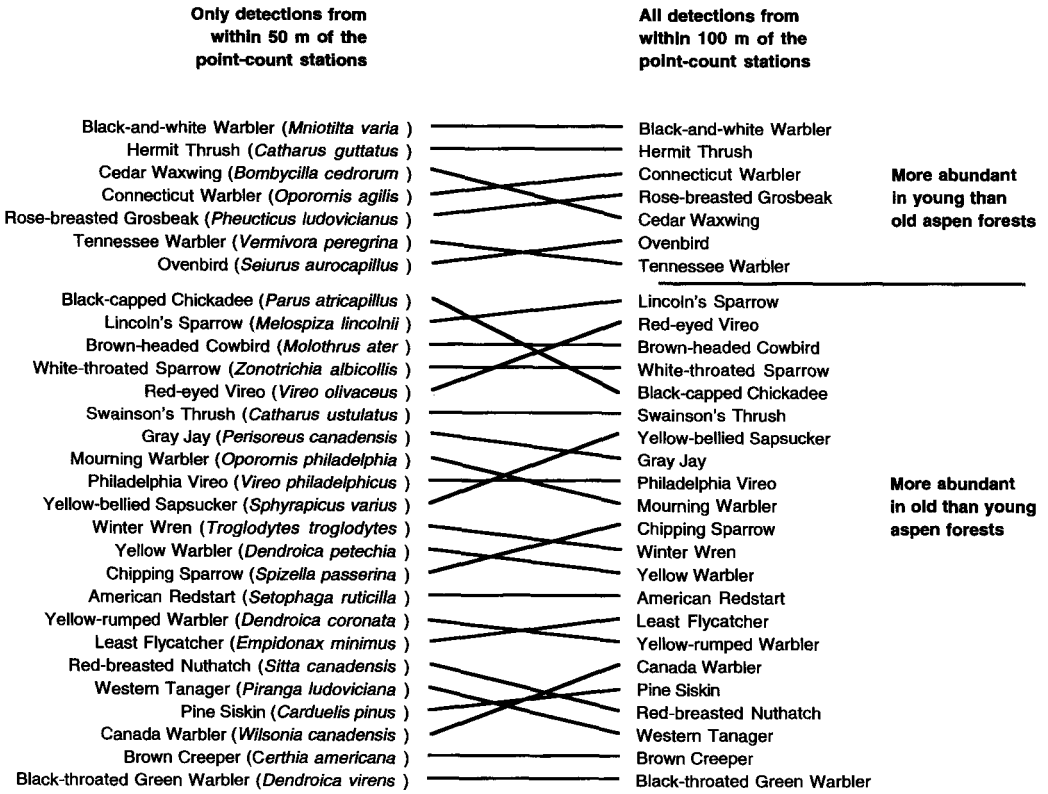


FIGURE 4. Rank order preference ratios of bird species for young versus old aspen-dominated forests in Alberta. Preference ratios were determined based on the number of detections during point counts. The rank order of preference ratios that was determined based on detections within 50 m of the point-count stations (left-hand side) is compared to the rank order of preference ratios that was determined based on detections within 100 m of the point-count stations (right-hand side).

Peterson 1992), and as expected (Marten and Marler 1977), detection of broadcast vocalizations was lower after than before leaf formation. Seasonal differences in detection within old aspen-dominated forests, however, were greater than the seasonal differences found in the other three successional stages. Larger seasonal differences in detection in old, than in young or mature, aspen-dominated forests was unexpected because aspen was the dominant tree in all three of these successional stages and leaf formation should have been similar in each. However, more leaves may have grown in old aspen-dominated forests than in the younger successional stages because the distance between the bottom and top of the canopy was greatest in old forests (Schieck, unpubl. data). Alternatively, a complex set of interactions between the growth of leaves and the abundance of deciduous trees, density of shrubs/saplings,

and height of the canopy may have affected reflection, refraction, and diffraction of sound under the canopy (Wiley and Richards 1978) which may have resulted in old aspen forests having relatively low detection of broadcast vocalizations after leaf formation.

Broadcast vocalizations with minimum frequencies less than 2.5 kHz were always detected at 100 m, whereas vocalizations with minimum frequencies between 2.5 and 3.5 kHz usually were detected at 100 m, and vocalizations with minimum frequencies higher than 3.5 kHz often were not detection at 100 m from the speaker. This pattern was present even for the species that have vocalizations of similar intensity. In addition, when pure tones were broadcast at a constant intensity in other studies within forested habitats, detection was negatively related to frequency (Morton 1975, Marten et al. 1982, Wiley and Richards 1982). High

frequencies may have had relatively short detection distances in forests because the stems and leaves of trees are large enough to absorb, diffract, and reflect the short wavelengths of high frequencies but not the longer wavelengths of low frequencies (Wiley and Richards 1978).

As found in previous studies (e.g., Morton 1975, Marten and Marler 1977, Marten et al. 1982, Wiley and Richards 1982), detection of bird vocalizations in this study was positively related to height of the broadcast. Relatively low detection of broadcasts from the shrub layer may have been due to wind and temperature gradients near the ground resulting in greater reflection, refraction, and diffraction of sound than in the canopy (Wiley and Richards 1982). Additionally, broadcasts from the shrub layer may have had lower detection because the many saplings, shrubs, and herbs in the understory increased the reflection and diffraction of sound (Wiley and Richards 1978). This latter possibility is less probable, however, because mature aspen-dominated forests and white spruce forests had relatively few shrubs and saplings in comparison to young and old aspen-dominated forests, yet broadcasts from the shrub layer did not have relatively high detection in mature aspen and white spruce forests (i.e., the interaction between height of the broadcast and successional stage was not significant).

Based on results from this and other broadcast experiments, detection of bird vocalizations vary in complex ways among forested habitats. Consequently, it will be difficult to develop correction factors that can be used to compare abundances among habitats. Correction factors would need to be specific for each of the many forest habitats, and within each of the habitats specific for each successional stage because vegetation is unique for each successional stage in each habitat. In addition, correction factors would need to be different before and after leaf formation because detection varies seasonally. As a further complication, correction factors would need to be bird species-specific because the minimum frequency of vocalizations differs among species. Finally, if birds vocalize from different heights in different habitats, then correction factors also must account for differences in detection that are related to height of the vocalization.

Based on the above complexity, it may not be feasible to calculate correction factors that

allow comparison of species densities among habitats. However, abundances will be directly comparable, and it will not be necessary to use correction factors, if the sampling distance is short enough that all vocalizations will be heard in all habitats. In a study involving wild birds in a forested habitat in Wisconsin, 83% and 61% of the 18 bird species that were studied had all their vocalizations detected at 50 m and 100 m, respectively (Wolf et al. 1995). In that study, at least half of the vocalizations for all species were detected at 75 m. In a comparable study of wild birds in a different Wisconsin forest, Emlen and DeJong (1981) found that at least half of the vocalizations for all of the 11 species that they studied could be detected at 75 m. In the present study, detection of broadcast vocalizations were evaluated in four different forested habitats. Although most of the vocalizations were detected at 50 m, five of the nine species that I studied had at least one of their broadcast vocalizations not detected at 50 m. At 100 m from the speaker only 73% of the broadcast vocalizations were detected. In addition, at 100 m six of the nine species had at least one of the broadcast vocalizations not detected and two of the nine species had less than 50% of their broadcast vocalizations detected. Thus, the suggestion by Petit et al. (1995) and Ralph et al. (1995) to use a 50 m detection distance when comparing bird communities among forested habitats appears reasonable, although 50 m may be conservative and 75 m may be appropriate. In studies involving bird species that have relatively loud and/or low frequency vocalizations, detection biases may not be present until at much greater distances (Emlen and DeJong 1981, Wolf et al, 1995, this study); sampling distances of between 100 and 250 m may be appropriate in those species.

Surprisingly, when I reanalysed information from a previous study of bird communities in boreal forests, habitat preference ranks for the bird species using all detections within 100 m were similar, but not identical, to the ranks found using only detections within 50 m of the point-count stations. Thus, results from studies that used a detection distance of 100 m may indicate general patterns. Habitat preferences, however, differed greatly among many of the bird species in that study (Schieck et al. 1995). If habitat preferences had not differed as greatly among species, then the relative ranks of spe-

cies that were calculated including detections between 50 and 100 m of the point-count stations may have been less accurate. I suggest that, among-habitat comparisons of bird communities should be interpreted cautiously unless the researcher(s) demonstrates that biased detection of vocalizations did not affect the results. Thus, it may be necessary to analyze the data twice; first using a detection distance of 50 m so that data have little bias among forest habitats and a second time using a detection distance of 100 m so that more, but potentially biased, data are included. Results could then be compared among those two analyses.

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