SURVEYING WINTERING WARBLER POPULATIONS IN JAMAICA: POINT COUNTS WITH AND WITHOUT BROADCAST VOCALIZATIONS[1]

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Abstract. Two independent methods were used to quantify abundances and population structure of two paruline wood warblers, the American Redstart (Setophaga ruticilla) and Black-throated Blue Warbler (Dendroica caerulescens), wintering in Jamaica, West Indies. One conventional 10-min point count was followed by 5 min each of redstart, then Black-throated Blue Warbler vocalizations (a mixture of territorial songs and chip notes recorded during the breeding season) at each of 585 points in 18 habitats. Age and sex composition of the target species were recorded along with observations of other species. Compared with conventional point counts, those supplemented with playback of vocalizations (1) detected 3.0 and 2.3 times more American Redstarts and Black-throated Blue Warblers, respectively, (2) disclosed significantly more individuals of three other migrant warbler species and one year-round resident species belonging to the "warbler guild," (3) facilitated identification of age and sex of target species by attracting them closer to the observer, and (4) confirmed that wintering individuals of both species of warbler were dispersed as expected for a territorial species. Compared with yearling males and with females, older redstart males were observed significantly more frequently during playbacks than predicted by pre-playback relative frequencies. No such sex bias was found for Black-throated Blue Warblers, a species in which age cannot be reliably determined except with hand-held individuals. Diurnal variation in surveyed abundances of both species was relatively minor, but was significantly less pronounced for playback counts than for pre-vocalization counts in Black-throated Blue Warblers. Our results indicate that broadcast territorial advertisement vocalizations provide a powerful tool to study the ecology and distribution of neotropical migrant songbirds in winter.

Key words: American Redstart; Black-Throated Blue Warbler; Dendroica; Jamaica; Parulinae; point count; Setophaga; territoriality; time of day; vocalization playbacks.

INTRODUCTION

Information about winter distributions and ecology of neotropical migrant birds was essentially restricted to labels of museum specimens and anecdotal field observations prior to 1970 (Terborgh 1989). Since then, knowledge about these birds has grown rapidly (see reviews in Keast and Morton 1981, Hagan and Johnston 1992). Despite increased interest in these birds, however, we still know far less about their ecology in winter than summer. The importance of further improving knowledge about neotropical migrant ecology in all seasons is emphasized by alarming population declines in many species (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990, Finch 1991).

One reason for the dearth of knowledge about winter distributions of neotropical migrants is the difficulty of censusing them during the non-breeding season. While breeding, many birds make frequent vocalizations associated with advertisement and defense of territories, and several methods to survey distribution and abundance take advantage of this conspicuousness, including territory mapping, point counts, and transect surveys (see references in Ralph and Scott 1981, Verner 1985). When vocalizations are in-

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frequent, as often the case in winter (Robbins 1981), most such techniques are relatively ineffective. However, the recent discovery of winter territoriality in many neotropical migrant species (Schwartz 1980, Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989), has led to the use of tape-recorded territorial songs, call notes, and other sounds for capturing and marking animals on the winter grounds (Rappole and Warner 1980, Lynch et al. 1985, Morton et al. 1987, Holmes et al. 1989). In a few cases, vocalization playbacks have been used effectively to supplement non-breeding season distributional surveys in diverse bird species (e.g., Gorski 1969, 1971; Johnson et al. 1981; Lynch 1989, in press; Varty, 1991). Vocalizations are an effective supplement even when wintering animals are non territorial, as illustrated by Lynch's (1989, in press) use of "*chip*" call notes, distress calls, and whistled imitations of a resident bird-hunting owl to supplement point count surveys in the Yucatan Peninsula. To our knowledge, however, no one has systematically surveyed wintering neotropical migrants using recordings of territorial advertisement vocalizations.

We took advantage of winter territoriality in two species of neotropical migrants, American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*), to study their distributions and demography across diverse habitats throughout Jamaica, West Indies. In this paper we analyzed the effectiveness of vocalization playbacks by comparing and contrasting detections of birds during 5-min vocalization playbacks with those during prior conventional 10-min point counts. Specifically, we asked five questions: (1) How effective were playbacks in detecting birds already detected in the 10-min point count, and in detecting new birds not previously detected? (2) Did playbacks influence age or sex classes differentially? (3) Was detection of redstarts or Black-throated Blue Warblers influenced by time of day during either pre-playback point counts or playbacks? (4) Did the two species respond differently to vocalization playbacks? And, (5) How were individuals of these populations dispersed among surveyed points—randomly, evenly (as predicted for territorial individuals), or aggregated (as predicted for some kinds of non-territorial behavior)? Answers to these questions help assess the advantages and disadvantages of the playback method compared with conventional point counts. We

present elsewhere (Sliwa 1991; Sliwa and Sherry, in prep.) the age- and sex-specific habitat-use and other distribution patterns of these species' populations in Jamaica.

METHODS

This study was conducted from 22 October to 21 December 1989, over a broad range of elevations and habitats in Jamaica. To obtain representative results from throughout Jamaica, we conducted 585 point counts in eighteen habitats, which were recognized on the basis of differences in vegetation physiognomy and floristics, elevation, and human agricultural activities. Habitats included dry limestone and wet limestone forests, elfin woodland and montane mist forests, mangrove woodlands, agricultural lands (banana, citrus, coconut, coffee, and pine plantations), and secondary and hurricane-disturbed habitats (see Sliwa [1991] for detailed descriptions of habitat structure and composition, point count dates, elevations, number of counts per habitat, and locations).

Upon arrival at a point, the observer waited 5 min to allow birds to return to normal activity after any disturbance created upon arrival, then conducted one 10-min point count, followed by 5 min of vocalization playbacks of each target species, always in the order American Redstart (RS), then Black-throated Blue Warbler (BW). We used a modified point count method (Hutto et al. 1986, Wunderle and Waide 1992) to record birds during the pre-playback, 10-min period. This method was deemed particularly effective for the conditions found in Jamaica, because many habitats were small in extent, yet differed structurally and floristically. Unlimited-radius point counts (Blondel et al. 1981) were used because habitat types differed markedly in structure. Using 10 × 50 power binoculars, we recorded every bird heard or seen, except nocturnal species, wading birds, and aerial foragers such as swifts and vultures (Hutto 1980, Lynch 1989). The minimum distance of a bird from the observer was estimated, and movements of all birds were followed to avoid recording the same bird twice. We used vocalization playbacks to increase the likelihood of detecting birds that had been missed during the point count, and to help identify sex and age of the two focal species as accurately as possible at close range. RS playbacks consisted of a 5-min, tape-recorded segment of continuous RS song and chip notes re-
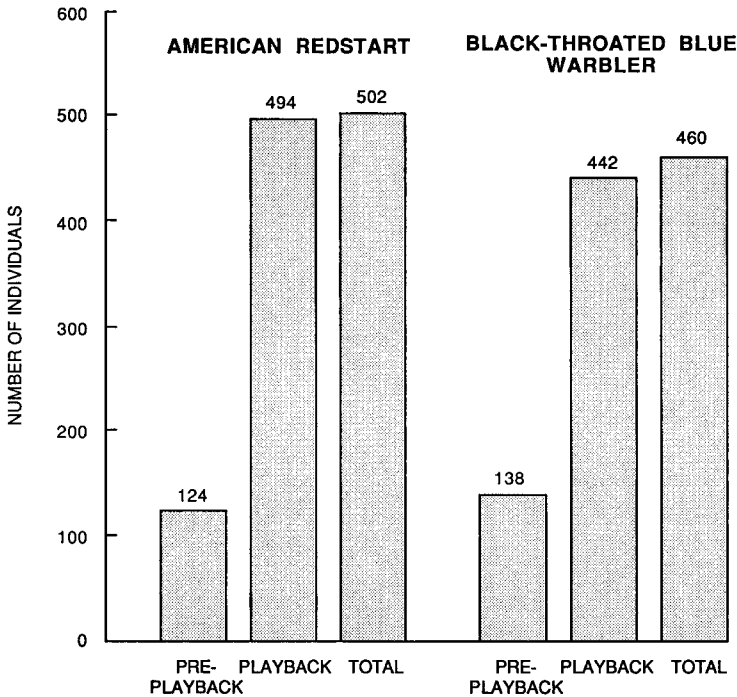
FIGURE 1.   Number of American Redstarts and Black-throated Blue Warblers detected during all point counts, divided into pre-playback, during playback, and total observation periods within 18 habitats throughout Jamaica. "Playback" refers to the 5-min period that either American Redstart or Black-throated Blue Warbler vocalizations were broadcast, beginning immediately after the 10-min point count. "Total" is the sum of all individuals detected by one method plus those detected only by the other method.

corded by TWS in the Hubbard Brook Experimental Forest, N.H.; RS songs were "accented ending" (Ficken 1962), given in "repeat-mode" (Lemon et al. 1985). BW playbacks consisted of a loop tape with song and chip notes recorded in North America by the Cornell Laboratory of Ornithology (Laboratory of Natural Sounds). Point counts mostly involved birds that had never previously been exposed to playbacks, except for birds on about 50 counts located on sites used by Holmes et al. (1989). We used an SP5 Mineroff Electronics Inc. (Elmont, New York 11003) loudspeaker connected with a short cable to a Sony TCS-430 cassette-recorder.

Points were located at least 25 m from the nearest habitat edge, and successive points were separated by at least 100 m from the previous point in heavily forested habitats or 200 m in more open habitats. A separation of 100 m has proved sufficient to avoid double recording individuals of small, territorial bird species, both in western Mexico (Hutto et al. 1986) and Jamaica (Wunderle and Waide 1992). Habitats were generally surveyed on consecutive days, and as

many as 52 point counts were done in one habitat at a particular site. Sampling occurred from sunrise 06:05 to 11:30, and from 15:00 to 17:45 Eastern Daylight Time. No point counts were conducted during rain or high winds. In dense habitats, sampling was done from trails or roads, whereas in more open habitats we used a compass bearing to locate new points. Birds detected, but not identified to species or age and sex during any point count or playback period, were pursued afterwards for closer examination. Hypotheses were tested with chi-squared statistics as described in the tables.

RESULTS

BIRDS DETECTED BEFORE VERSUS DURING PLAYBACKS

The first question we asked concerned how effective the 5-min playbacks were in detecting new birds that had not been detected previously during the pre-playback (10-min) point counts, as well as in revealing birds that had already been detected during the pre-playback point counts.
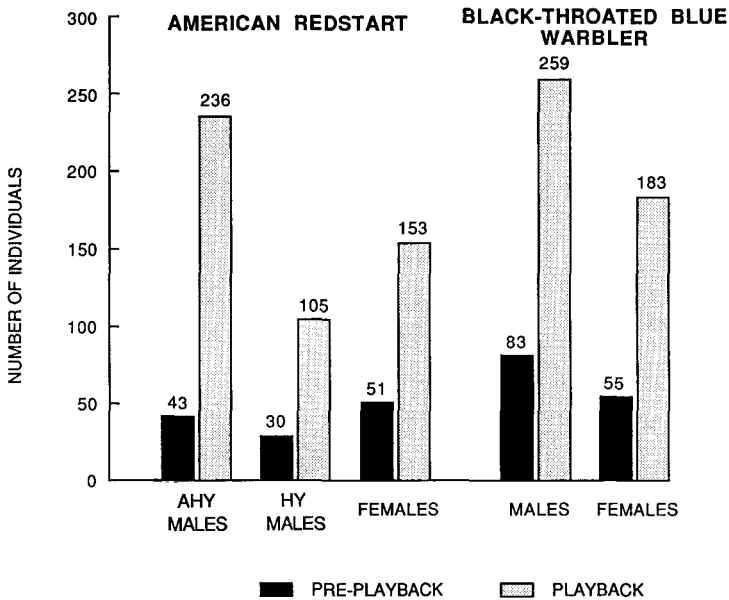
FIGURE 2. Number of American Redstart and Black-throated Blue Warbler individuals detected during pre-playback versus playback periods, partitioned by sex and age classes, and pooled for all 18 habitats included in 585 points surveyed throughout Jamaica.

Playbacks revealed 494 individual American Redstarts, 378 more than the 124 detected during the point counts (Fig. 1). This represents just over three times more birds detected during playbacks than in pre-playback point counts. In only eight cases (1.6% of 502 RS individuals seen in total) was an individual missed during playbacks that had been detected during pre-playback point counts. The null hypothesis that equal numbers of redstarts were observed during playbacks as during pre-playback periods was rejected ($\chi^2 = 159.3$, df = 1; $P < 0.001$).

Playbacks revealed 442 individual Black-throated Blue Warblers, 322 more than detected during the preceding point counts (Fig. 1). This represents just over 2.3 times more birds than the 138 seen during the pre-playback period. In only eighteen cases (3.9% of 460 BW individuals seen in total) was a BW missed during playbacks that had been detected during pre-playback point counts. The null hypothesis that the same number of BWs was observed during playbacks as during pre-playback periods was again rejected ($\chi^2 = 159.3$, df = 1; $P < 0.001$).

AGE- AND SEX-SPECIFIC EFFECTS OF PLAYBACKS

Hypotheses concerning relative responsiveness of age or sex classes of individuals were tested by comparing frequencies of individuals detected during playback periods to frequencies predicted by the relative proportion of these same classes detected prior to playbacks (see Fig. 2). Effects of playbacks on RS age and sex classes depended on the particular comparison. Older (after-hatch-year, henceforth "AHY") males responded significantly more frequently to playbacks than young ("hatch-year," henceforth "HY") males ($\chi^2 = 14.9$, df = 1; $P < 0.001$). In this case, 236 AHY males and 105 HY males responded to playbacks compared with the 201 and 140 individuals predicted to respond from the 43 and 30 AHY and HY males detected, respectively, prior to playbacks (Fig. 2). Similarly, older males responded to playbacks significantly more frequently than females ($\chi^2 = 34.8$, df = 1; $P < 0.001$) based on the 236 and 153 males and females, respectively, detected compared with 178 and 211 males and females predicted (Fig. 2). In contrast, yearling male and female RSs did not differ significantly in their reaction to playbacks ($\chi^2 = 1.5$, df = 1; $P > 0.05$), based on 105 and 153 playback counts of HY males and females, respectively, and 95.6 and 162.4 predicted counts. To summarize these results, older males responded proportionately more strongly to playbacks than did either yearling males or females, which did not differ from each other.

A. AMERICAN REDSTART

B. BLACK-THROATED BLUE WARBLER
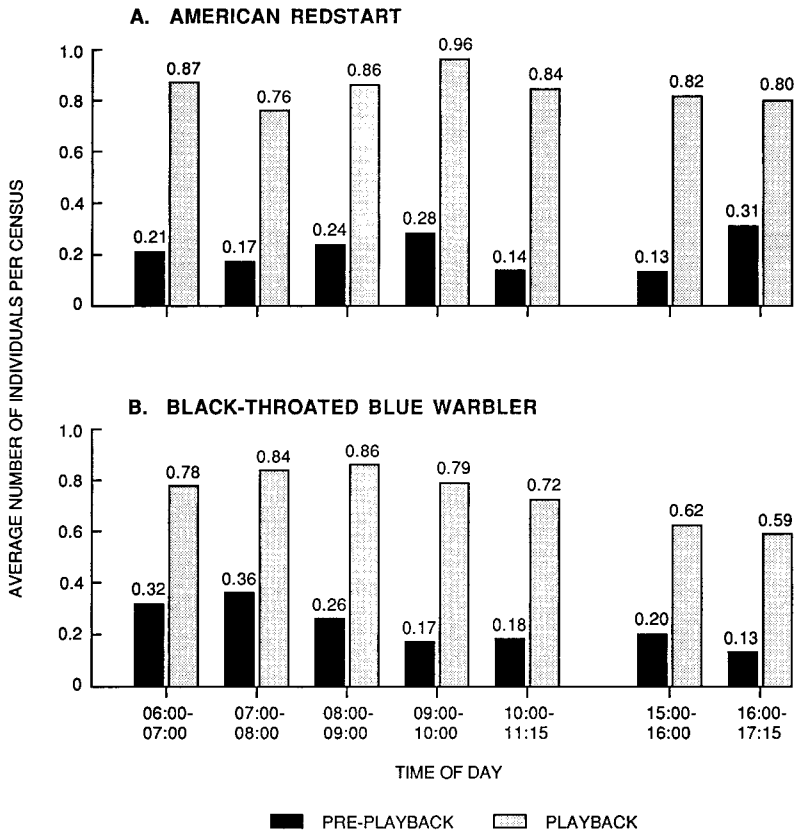
PRE-PLAYBACK   PLAYBACK

FIGURE 3. Number of individual birds detected during pre-playback versus playback periods as a function of time of day for (A) American Redstarts, and (B) Black-throated Blue Warblers.

In contrast to redstarts, male and female BWs were attracted in nearly the same relative frequencies during playbacks as they had been detected before the playbacks ($\chi^2 = 0.5$, df = 1; $P > 0.1$), based on 259 observed versus 266 expected BW males, and 183 observed versus 176 expected females (Fig. 2). BW age classes cannot be distinguished reliably in the field, so we could not analyze age differences in responsiveness to playbacks in this species.

INFLUENCE OF TIME OF DAY

Our third question concerned RS and BW reactions to playbacks at different times of day. Analyses were based on times of day divided into seven point count periods equal to, or slightly in excess of, 1 hr: 06:00–07:00, 07:00–08:00, 08:00–09:00, 09:00–10:00, 10:00–11:15, 15:00–16:00, 16:00–17:20 hr. No point counts were conducted during the very hottest times of day, i.e., from 11:15–15:00 hr.

Based on pre-playback detection frequencies, peak activity of RSs occurred in the 09:00–10:00 and 16:00–17:20 time periods, and low activity from 10:00–11:15 (Fig. 3A). This activity lull in later morning continued into the midday period (unpubl. observ.). However, these apparent diurnal activity differences were not statistically significant from frequencies generated according to the null hypothesis of no diurnal differences ($\chi^2 = 10.7$, df = 6; $P > 0.05$). Frequencies of RSs observed during playbacks peaked at 09:00–10:00, but again these diurnal differences were not significant ($\chi^2 = 2.5$, df = 6; $P > 0.05$). Thus the null hypothesis could not be rejected for either data set, although less diurnal variation was observed for playback responses than for pre-playback detections. We cannot determine from available data whether significant diurnal variation would be found if midday observations had been made.

In the BW the difference between pre-playback

TABLE 1. Responses of selected species of migrant warblers and resident birds to American Redstart and Black-throated Blue Warbler vocalization playbacks, as indicated by detections during versus prior to playbacks. Bold-faced numbers indicate time periods in which significantly more birds were detected than predicted by the null hypothesis. Latin names of species given in text.

Species	No. of birds detected			χ^2 statistic[1]
	Pre-playback period	Playback period	Expected frequency[2]	
Jamaican White-eyed Vireo	108	**145**	126.5	5.4*
Black-and-white Warbler	**157**	69	113	34.3**
Parula Warbler	38	**122**	80	44.1**
Yellow Warbler	38	51	44.5	1.9^{ns}
Cape May Warbler	9	17	13	2 5^{ns}
Prairie Warbler	62	**88**	75	4.5*
Arrow-headed Warbler	25	27	26	0.08^{ns}
Ovenbird	72	**102**	87	5.2*
Common Yellowthroat	97	59	78	9.3**
Bananaquit	**210**	104	157	35.8**
Orangequit	**97**	31	64	34.0**

[1] χ^2 values calculated with one degree of freedom from observed and expected frequencies, the latter calculated according to null hypothesis that a species was equally likely to be detected in pre-playback and playback periods. ns indicates not statistically significant at 0.05 level, and number of asterisks indicates level of significance: * $P < 0.05$, ** $P < 0.01$.
[2] Expected frequencies of sightings for both pre-playback and playback periods represent the average of the two frequencies observed during the pre-playback and playback periods.

and playback frequencies was more dramatic. Pre-playback activity levels of BWs were significantly greater earlier in the day, especially in the three hours after sunrise (06:00–09:00 hr) than during other time periods ($\chi^2 = 15.8$, df = 6; $P < 0.05$; Fig. 3B). Responses of BWs to playbacks, on the other hand, did not differ significantly among time periods ($\chi^2 = 6.5$, df = 6; $P > 0.05$; Fig. 3B). Although BWs showed stronger diurnal differences in activity than did RSs, and were less likely to exhibit a resurgence of activity late in the day, both species were equally responsive to playbacks during all time periods under consideration.

INTERSPECIFIC DIFFERENCES IN RESPONSES TO PLAYBACKS

Pre-playback frequencies of RSs (124 individuals) and BWs (138 individuals) were compared to frequencies of individuals detected during playbacks (494 RSs and 442 BWs; Fig. 1). The null hypothesis of equal responsiveness was rejected ($\chi^2 = 12.6$, df = 1; $P < 0.001$). Thus RSs responded significantly more strongly to playbacks than BWs.

Just as the two species targeted in this study responded differentially to playbacks of their own vocalizations (even though in some cases BWs responded to RS vocalizations, and vice versa), we noticed that a variety of other species also appeared to be attracted to the source of the vocalizations, or to the increased vocal activity of RSs or BWs that the vocalization playbacks induced. We thus tested the null hypothesis that a variety of species were equally likely to be observed during the playbacks compared with the pre-playback periods. We confined statistical tests to the relatively common migrants and residents that are similar in size and diet to RSs and BWs, and we used the standard procedure of generating expected frequencies such that the total observed detections were distributed in a 50:50 ratio between pre-playback and playback periods. Results of these tests indicate that indeed some species were more likely to be detected during playbacks than before, but a variety of species were also less likely to be detected during the playback period (Table 1). Specifically, Ovenbird (*Seiurus aurocapilus*), Parula Warbler (*Parula americana*), Prairie Warbler (*Dendroica discolor*), and Jamaican White-eyed Vireo (*Vireo modestus*) individuals were all detected significantly more frequently during than before playbacks, whereas Black-and-white Warbler (*Mniotilta varia*), Common Yellowthroat (*Geothlypis trichas*), Bananaquit (*Coereba flaveola*), and Orangequit (*Euneornis campestris*) individuals were detected significantly less frequently during than before playbacks (Table 1). Since these are *a posteriori* statistical tests, we caution against attributing too much significance to these results.

NUMBERS OF INDIVIDUALS OBSERVED PER POINT COUNT

Our final question concerned dispersion of conspecific individuals among the point counts.

TABLE 2.   Observed and expected (Poisson) frequency distributions of number of individuals seen per point count for American Redstarts and Black-throated Blue Warblers during 585 point counts throughout Jamaica. See text for description of methods of calculation.

No. birds seen per point count	Observed frequency	Expected frequency
American Redstart		
0	207 (35.4%)	248.0
1	269 (46.0%)	212.8
2	94 (16.1%)	91.3
3	15 (2.5%)	26.1
≥4	0	6.7
	585 (100%)	585

Mean no. birds/point count = 0.86; χ^2 = 33.1, on 4 df, $P < 0.001$.

Black-throated Blue Warbler		
0	229 (39.1%)	266.5
1	261 (44.6%)	209.5
2	88 (15.0%)	82.4
3	5 (0.9%)	21.6
≥4	2 (0.3%)	5.0
	585 (100%)	585

Mean no. birds/point count = 0.79; χ^2 = 32.9, on 4 df, $P < 0.001$.

Based on data pooled from pre-playback and playback periods, and from all habitats and times of day, 207 points had no RSs and 378 (64.7%) had at least one RS (Table 2). Comparable figures for BWs were 234 points without birds and 356 (60.9%) with at least one bird. Most individuals were observed singly in both species. We observed on average 0.86 RS and 0.79 BW per point.

If the number of individuals seen at each point were influenced by territoriality, then we would expect more cases of single birds being observed per point and fewer cases of zero, two, three, and four birds than predicted by chance, as modeled by the Poisson distribution (e.g., Whittaker 1975). We calculated the Poisson frequencies using the standard formula,

$$P[X] = (M^X)(e^{(-M)}/X!)$$

where P[X] is the probability of observing X birds, X is the number of birds seen per point count and takes on values from 0 to 4 or more in our case, e is the base of natural logarithms, and M is the mean number of birds seen per point count. For both species we observed birds in significantly different frequencies from those predicted by chance ($P < 0.001$; Table 2). In particular, we observed many more cases of one bird and a

few more cases of two birds per point count than predicted by chance, and fewer cases of zero, three, and four birds, as predicted for a territorial species. This is a robust result obtained even in tests done separately by habitat (for all habitats with sample size ≥30 individual birds). In the RS, for example, fit to a Poisson model was rejected for six of nine possible habitats ($P < 0.05$), and in the BW for five of six habitats; and deviations of observed from expected frequencies in all these 15 tests showed the same pattern as in Table 2. This pattern supports the hypothesis that both RSs and BWs wintering in diverse habitats throughout Jamaica are strongly dispersed by territoriality.

We tested the same null hypothesis of random dispersion among points for just the pre-playback point count data. The number of counts at which zero, one, and two RSs were seen were 469, 104, and 12, respectively (mean = 0.22 RS per point; χ^2 = 0.93, $P > 0.05$). The number of counts at which zero, one, and two BWs were seen were 462, 109, and 14, respectively (mean = 0.23 BW per point; χ^2 = 1.19, $P > 0.05$). Thus dispersion patterns of these two warblers obtained from conventional point count data without playbacks were random, and certainly provide no hint of the strong winter territoriality suggested by the responses to playbacks.

DISCUSSION

METHODOLOGICAL ADVANTAGES OF PLAYBACKS

A major advantage of vocalization playbacks was that they detected many more individuals than traditional point counts (3.0 and 2.3 times as many in RSs and BWs, respectively). Similar increases in responses to playbacks have been noted in several species of birds (references in Johnson et al. 1981). This advantage could have resulted in our study from any of several factors. First, an AHY male American Redstart foraging high in forest canopy (e.g., in tall primary wet limestone forest) may become more conspicuous through visual displays (increased frequency of movement—personal observations) and "*chip*" note calls given in response to playbacks. In the dense cover of leaves, and at heights of up to 30 m, a redstart is difficult to spot, so that a playback might attract it closer to the observer. The same hypothesis could operate in the Black-throated Blue Warbler by attracting an individual out from dense forest undergrowth, where visibility is of-

ten low. Second, playbacks may have attracted birds from across their territories. Our studies at Luana Point, Jamaica, showed that redstarts were often attracted by vocalization playbacks to the edge of their territories, where conflicts with neighbors often ensued (Holmes et al. 1989). Third, playbacks could in theory have attracted birds from beyond their normal territories. This hypothesis is unlikely to be true in practice, given the accumulating evidence for strong winter territoriality in the two species under study: Individuals of both species remain on small areas (<1 ha, based on numbers of birds seen in Jamaican sites per 10 ha) throughout the winter (Holmes et al. 1989); and individually color-banded birds are essentially never seen off these "territories," even when extensive playbacks are conducted nearby as part of territory-mapping procedures (T. W. Sherry and R. T. Holmes, unpubl. observ.). In the present study we observed single birds during point counts significantly more frequently than predicted by chance (Table 2), a result that is not predicted if birds leave territories frequently. This evidence for territoriality based on dispersion among survey points was only revealed during playbacks, and was not evident in data from just the pre-playback, 10-min point counts. We conclude that breeding season song and call note vocalizations significantly increased our detections of birds because the playbacks both attracted birds from parts of their territories where they would have been difficult to observe, and from distant parts of their territories. We cannot say precisely how many more birds we detected because of playbacks than we would have detected without the playbacks because we did not conduct any non-vocalization point counts after the initial 10-min count period as a control for the added 10-min (5 min for RS plus 5 min for BW) period available to detect birds during the playbacks. We doubt that we would have detected many more individuals of either target species had we extended the pre-playback period beyond 10 min, because individuals of both study species tend to be silent for many minutes at a time, and tend to spend long periods foraging in one area rather than moving constantly throughout their territories (T. W. Sherry, unpubl. observ.). A 10-min period is sufficient to detect most species and individuals from a census point unless individuals move rapidly throughout their territory or home range (Scott and Ramsey 1981; Hutto et al. 1986; Lynch, in press). We tried to avoid double-count-

ing birds by noting the direction from which individuals approached the speaker, and by noting distinctive plumage characteristics of individual redstarts. We suggest that in practice the distance between consecutive survey points should be at least as large as twice the maximum home-range or territory diameter of the species under consideration.

The first playback advantage, namely increasing detectability of birds, could be particularly important in studies of species that are rare or otherwise difficult to detect with conventional methods. Swainson's Warblers (*Lymnothlypis swainsonii*), for example, are widely dispersed and cryptic while wintering in Jamaica (Lack 1976), as well as of potential interest to conservationists (e.g., Terborgh 1989). Preliminary playbacks of breeding season songs elicited strong responses from individual Swainson's Warblers wintering in Jamaica (I. Lovette, pers. comm.).

A second advantage of point counts supplemented by playbacks compared with conventional point counts was that the former equalized detection rates at different times of day (see below). Birds that normally would remain undetected due to inactivity during particular diurnal periods were apparently attracted to playbacks equally strongly at the times of day under study. Winter bird activity levels, by contrast, are generally much lower in midday (Hutto et al. 1986, Wunderle and Waide 1992), a time when we conducted no point counts. In North American winter bird counts, most smaller passerine species are detected more often in the first few hours of the morning (Robbins 1981, Rollfinke and Yahner 1990).

A third advantage of vocalization playbacks was their effectiveness in attracting birds often to within a few meters of the observer, at which range even subtle age- or sex-specific differences could be distinguished, a benefit noted by Lynch et al. (1985). Gorski (1969) was able to identify the sex of Willow Flycatchers (*Empidonax traillii*, i.e., "*fitz-bew*" songform of the former Traill's Flycatchers) wintering in Panama by observing the vocal response of territorial birds to playback of songs recorded during the summer in Connecticut. Hand-held birds can often be aged and sexed readily in many of these species (Pyle et al. 1987), but capturing birds with mist nets is often time- and labor-intensive. Thus, identification of age and sex of birds visually, without need of mist-netting facilitates wide-scale demographic studies, which can help identify pop-

ulation processes and habitats critical for winter population survival.

A fourth potential advantage of using vocalization playbacks to detect wintering warblers is that the combination of song and chip notes apparently aroused other bird species, increasing their detectability. The Prairie Warbler, Northern Parula Warbler, and Ovenbird, among migrants, and the resident Jamaican White-eyed Vireo all approached the playbacks or vocalized more frequently during playbacks than during pre-playback periods (Table 1). Other species tended to approach the speaker more closely during playbacks, including the resident Yellow Warbler (*Dendroica petechia*) and Bananaquit, but this difference was not statistically significant. Because as many species were detected *less* frequently than expected during playbacks as were detected *more* frequently (Table 1), one can argue that the playbacks did not on average increase the conspicuousness of birds in the vicinity of the playbacks. However, many species may have been less conspicuous during playbacks because they may have become habituated to the observer's presence during a pre-playback period, then returned to their often inconspicuous foraging locations. More research is needed to verify the effects of species-specific playbacks on non-target species.

DISADVANTAGES OF PLAYBACKS

AHY-male American Redstarts were detected proportionately more frequently during playbacks than either HY males or females, based on predictions from pre-playback relative frequencies. Any estimates of population age- or sex-structure that are based on responses to playbacks would thus be biased towards males. One possible explanation of this result is that AHY males are more aggressive than HY males or females, perhaps because AHY males are behaviorally dominant (e.g., Sherry and Holmes 1989, Marra et al., unpubl. manuscript), or relatively experienced in contests due to breeding season contests with other males (Bent 1953, Ficken 1962, Sherry and Holmes 1989), or both. In many chases observed during this study, AHY males dominated HY males and females. In addition, Sherry and Holmes (1989) reported several instances of older males on the breeding grounds displacing yearling males from territories the latter had held for several days. A second possible reason for the AHY-biased redstart responses to playbacks could be that AHY males

are more difficult to detect in densely foliated habitat. There could thus be a stronger bias against detecting AHY males in conventional point counts than against detecting HY males or females during playbacks. AHY males may forage higher in the canopy and be less easily detected without playbacks, for example, than HY males or females. Although the study of Holmes (1986) did not reveal significant differences in foraging height between redstart sexes, there could be a preference of AHY males for winter habitats with tall, dense forest structure (e.g., Morton 1990).

In the Black-throated Blue Warbler, males and females responded about equally to playbacks, so one can assume that either their degree of aggressiveness or their detectability prior to playbacks are indistinguishable. We do not know why we obtained no differential response to playbacks by BW sexes, whereas we did in RS comparisons. If male warblers were somehow primed more than females to respond strongly to song in winter just because males alone sing in summer, then we would predict that BW males would have responded more than BW females to the playbacks, which was not the case. Male BWs appear to be more tolerant of females than RSs, judging from the relatively high frequency of male-female pairs detected foraging together in this study (see also Holmes et al. 1989), an observation possibly related to differences in winter social behavior and diet (see below).

A second disadvantage of the playback method is that its usefulness may be restricted to those wintering birds that are highly territorial. Many migrants such as Bay-breasted Warblers (*Dendroica castanea*) are not territorial in winter (Greenberg 1984), and such species may not respond strongly to vocalization playbacks. This prediction has not been tested formally. Even in non-territorial species, however, vocalizations of one kind or another can effectively supplement point counts of wintering neotropical migrants (Lynch 1989, in press).

A third, potentially serious disadvantage of playbacks is that the same species may respond differently to playbacks in different habitats or locations. Neotropical migrant warblers appear to respond more strongly to playbacks in lowland than high-elevation sites in Mexico, for example (R. T. Hutto, pers. comm.). Thus, the number of birds detected in different locations could be more a function of responsiveness to playbacks than of abundance of birds. We doubt that elevation was an important factor in the present

study. Black-throated Blue Warblers are a higher-elevation species than redstarts while wintering in Jamaica, yet responded to vocalization playbacks even at the highest elevations available (almost 2,300 m). We have not, however, analyzed responsiveness as a function of elevation. The important unanswered question from a methodological perspective is whether or not biases associated with playbacks are stronger than biases of other methods in the detectability of birds in different geographic locations, different elevations, and different habitats.

A final potential disadvantage of playbacks could result from their excessive repetition. Birds could become habituated, so that their responsiveness to playbacks would decline over time. Alternatively, playbacks could contribute to exhaustion and possible disruption of birds' reproduction or other activities.

Responsiveness by birds to playbacks could depend on a variety of other factors, such as the quality of the recordings, the particular song types used (e.g., repeat versus serial mode songs in RS, Lemon et al. 1985), or the race of birds from which the recordings are taken on the breeding grounds (see also Johnson et al. 1981). Differences in strength of response by RS and BW to playbacks might be attributable to better tape-recorded vocalizations used for RS than for BW, since RS tapes had more vocal variations (see Methods) or to a greater frequency of "*chip*" call notes on RS tapes. Alternatively, the species difference we documented could be an order artifact, since RS vocalizations were invariably played before those of BW. This would have given RS individuals 10 min to respond to vocalization playbacks, whereas BWs had only 5 min to respond. BW individuals may also have habituated to playbacks by the time their own vocalizations were conducted.

In summary, we argue that advantages outweigh disadvantages when care is taken in protocol and quality of recordings. Playback of various kinds of vocalizations could in fact overcome to some extent detectability biases inherent in other methods. Breeding season territorial vocalizations, such as we used, are probably most efficient when used in studies of one or a few targeted species, rather than as a standardized survey tool for community-wide studies. Some species were in fact deterred by the playbacks we used (Table 1), whether because of the species identification of the playbacks *per se* or because of habituation to the recorder.

IMPLICATIONS OF RESULTS FOR WINTER TERRITORIAL BEHAVIOR

A growing number of studies have recently been conducted on territoriality of neotropical migrant bird species on their wintering grounds (Rappole and Warner 1980, Faaborg and Arendt 1984, Lynch et al. 1985, Morton et al. 1987, Lynch 1989, Holmes et al. 1989). Redstarts and Black-throated Blue Warblers in Jamaica, for example, respond aggressively to vocalizations and decoy birds, defend small areas of winter habitat against conspecifics (especially of the same sex) using stereotyped display behaviors, remain on the same small area throughout the winter, and return to the same small area in subsequent years (Holmes et al. 1989, 1992). Another line of evidence for territoriality in these wintering warbler species is that their dispersion is consistent with that predicted for a territorial species (Table 2). Recent data suggesting that RS tend to flock during the winter in the Virgin Islands (Ewert and Askins 1991), if confirmed, could be the result of *aggregations* of multiple warbler species, given the high densities of migrant warblers observed; and each interspecific flock could consist of one or two RS individuals. Mixed-species flocking is not incompatible with intraspecific territoriality.

Various authors have taken advantage of the existence of winter territoriality by using vocalization playbacks to capture birds with the help of decoys (e.g., Holmes et al. 1989), but only a few studies have used playbacks regularly during censusing of migrant birds. Gorski (1969, 1971) used vocalizations recorded in summer to locate a limited number of wintering Willow Flycatchers in Panama and of Alder Flycatchers (*Empidonax alnorum*) in Peru. Individuals of both species defended non-overlapping winter territories about equal in size to summer ones, and responded vigorously to playbacks with both visual and auditory behaviors traditionally associated with breeding territories. Gorski's results thus reinforce the potential utility of song playbacks as a tool to survey wintering populations, and in a distinctive taxon (passerine suborder) from the paruline warblers we studied. Lynch (1989) used broadcast territorial chip notes of two common migrant warblers, imitations of distress squeaks of small passerines, and the whistle of a small bird-hunting owl, to attract birds in the Yucatan Peninsula, Mexico. He found that migrant warblers and vireos showed only a mi-

nor response and most resident species did not respond at all. His results thus suggest milder effects of playbacks, in contrast with the very strong responses of RSs, BWs, and other migrant warbler species and small resident passerines in the present study. Our data suggest that migrants wintering in Jamaica are more responsive in general, perhaps in part because of time of the season when playbacks were conducted. Our playbacks were conducted early in winter (October–December), when migrants are relatively more responsive to playbacks (Lynch, in press). Alternatively, Caribbean birds may be relatively responsive to playbacks, or territorial song combined with chip notes targeted at specific migrant species may be more effective vocalizations than the distress squeaks and predator calls used by Lynch.

Holmes et al. (1989) reported a lower BW than RS response to playbacks. A stronger reaction to playbacks by RS than BW was noted in the present study. Also, a greater percentage of BWs than RSs detected in the pre-playback period in the present study did not remain or return during the playbacks (13% in BW versus 6.5% in RS, Fig. 1). Recent research on dietary correlates of life-history characteristics provides another possible explanation for the differential responsiveness of the two species. Specifically, BWs eat fruit regularly in winter (L. Salmon, pers. comm.; T. W. Sherry, and A. Sliwa, pers. observ.) whereas we have never observed RS to do so (but see Downer and Sutton 1990). Because fruit is often more patchily distributed than insects in time and space, frugivory may favor greater mobility and fluidity of social system, whereas greater reliance on less patchily distributed insect resources by a species such as RS may favor a territorial social system (e.g., Greenberg 1981, 1984, 1986).

DIURNAL AND SEASONAL VARIATION IN WINTERING MIGRANT ACTIVITY

Few studies have examined the effect of time of day on the detectability of non-breeding birds. In a survey of migrants in Jamaica, Wunderle and Waide (1992) noted that the mean number of migrants per point count decreased after 10:00, just as in the pre-playback results in the present study. Robbins (1981) and Lynch (in press) noted that avian vocal activity in winter fell off sharply after the first time period of the day. Our study is the first, however, to show that vocalization playbacks tend to elicit similar responses regardless of time of day, thus offsetting the normal diurnal declines in activity levels (see also Lynch, in press). This implies that activity levels, best assessed by pre-playback detection frequencies in our data, changed more with time of day than responsiveness to intruders, assessed here by responses to playbacks.

Playbacks also offset a seasonal decline in vocal activity by breeding Northern Cardinals (*Cardinalis cardinalis*) (Dow 1970, cited in Johnson et al. 1981). Our study was conducted through only the first part of the wintering season, a time when wintering migrants appear to respond most vigorously to playbacks (Holmes et al. 1989; R. T. Holmes and T. W. Sherry, unpubl. observ.). It is more difficult to capture RS and BW individuals in March than in October using playbacks (T. W. Sherry and R. T. Holmes, unpubl. data) and responsiveness of Hooded Warblers (*Wilsonia citrina*) to playbacks declined noticeably over winter in Lynch's (in press) Yucatan Peninsula study, suggesting that territoriality wanes seasonally, but this idea remains to be tested rigorously.

In summary, playbacks of breeding season songs and chip notes, used systematically here for the first time with wintering migrant species, is a powerful method to survey their geographic distribution patterns during the non-breeding season. It is an improvement over previous methods because (1) many more birds of target species were detected than during pre-playback point counts, (2) the ages and sexes of individuals were made more conspicuous, and (3) playbacks reduced the effect of time of day on detection frequencies. In the BW there was little bias of the sex of individuals attracted to a loudspeaker by the vocalizations. However, sex and age classes respond differently to playbacks in species such as the RS, necessitating care in interpretation of data. Further testing of different species, locations, and seasons is necessary to assess further the strengths and biases of this method.

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