Mob Mentality: Effect of a Mobbing Playback on Avian Detection Probabilities during Point Count Surveys

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Abstract: The probability of detecting an individual or species is an important parameter in studies using mark-recapture and occupancy models to estimate population sizes and occurrence. Because low detection probabilities result in biased estimators and decreased precision, biologists seek methods that maximize detection probability. We evaluated whether we could increase detections of bird species by playing a tape of Black-capped Chickadee (Poecile atricapillus) mobbing calls during point counts. We conducted trios of 10-minute counts (two pre-playback and a playback) at 684 stations throughout Vermont, in forested, agricultural/grassland, and developed habitats. For each of 73 species detected during the surveys, we used occupancy modeling and information-theoretic model selection and averaging methods to evaluate whether detection probabilities varied due to playback or habitat type. Models containing a playback effect accounted for over 90% of the Akaike weights for 41 species. With 15 of these species, habitat effects also accounted for over 90% of the Akaike weights. The playback increased estimated detection probability in all habitats for 14 species, decreased estimated detection probability for 20 species, and had an estimated effect that varied by habitat for 7 species (many species with habitat effects simply had differing magnitudes of the effect dependent on habitat). Smaller resident species were detected more often during tape playbacks, but responses were highly variable for most species and the responses did not appear to follow a taxonomic pattern. We encourage researchers to evaluate their list of target species carefully before deciding to use mobbing playbacks to enhance response rates; in many situations mobbing tapes will not enhance detections and may complicate the interpretation of model parameters.

Key Words: Detection probability, habitat differences, mobbing, model selection, occupancy models, Vermont.

INTRODUCTION

Determining the presence or abundance of species at a site is central to many ecological studies. Songbirds are often surveyed *via* spot mapping, transect (area) sampling, or point counts [1]; the resulting data consist of the "raw" number of birds detected per survey or per transect. Recently, much attention has focused on correcting raw abundances for detection probability (p), the probability that an animal present at the survey location will be detected by an observer during the survey period [2,3]. Without this correction, abundance estimators are biased low. If this bias is not equally distributed across sites, treatments, or time, the use of the raw, uncorrected data in analyses can lead to false inferences.

Several likelihood-based modeling approaches can be used to correct for detection probability without marking individual birds. These include temporal removal models [4], mixture models [5,6], occupancy models [7], and distance sampling [8]. Although the models differ in approach and data requirements, each provides an estimate of p.

In many analyses, p is considered a nuisance parameter that must be estimated in order to estimate ecological parameters of interest, such as abundance or probability of site occupancy. However, because p is linked to other parameters in likelihood-based approaches, a sampling design that poorly estimates p or that results in a low p will influence the bias and precision of all parameters in the model [9-11]. Therefore, sampling methods that maximize p will produce data that lead to stronger inferences – a principle unofficially termed "the big law" [12].

The goal of this study was to evaluate whether the probability of detection (p) in point count surveys conducted during the breeding season can be increased through the use of Black-capped Chickadee (Poecile atricapillus) mobbing playbacks, ultimately resulting in estimators with reasonably low levels of bias and reasonably high levels of precision. Chickadees are known to issue mobbing calls in response to a potential predator [13], and several species have been shown to respond to these calls and join in mobbing activities [14]. For instance, 74-80% of species responded to mobbing playbacks in New Brunswick and Quebec, increasing the number of visual observations per survey [14]. Such mobbing calls also allow observers to assess evidence of breeding in some species, as birds with active nests may respond to mobbing playbacks while carrying food or nesting materials [14,15].

Here, we build on these studies by using occupancy models in an information-theoretic framework [16] to evaluate whether mobbing playbacks alter the probability of detection, and to evaluate whether this effect varies by habitat

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Mobbing Playback and Detection Probability

(forest, agricultural, or developed land classes). For 73 species, we used model selection methods to compare six alternative models describing the effect of playback treatment and habitat on p. We then used model averaging [16,17] to produce estimates of p and confidence intervals in order to evaluate the biological importance of the model selection results. Finally, we evaluated the species-specific differences in responses to playback in terms of life history characteristics.

MATERIALS AND METHODS

Three single-observer 10-minute point counts were conducted during the breeding season (19 May to 18 July) at 684 stations throughout Vermont in 2003 or 2004 (Fig. 1). The counts were each separated by a 2-minute silent interval. The first two counts (silent treatment) were conducted without chickadee mobbing calls. During the third count (playback treatment), a recording of Black-capped Chickadees mobbing a Screech Owl (Otus asio) recorded in New York by the Cornell Lab of Ornithology was played through a set of battery-powered speakers (Radio Shack #40-1430) for the entire survey period. The recording also contained alarm calls of American Crows (Corvus brachyrhynchos) and Blue Jays (Cyanocitta cristata), as well as an incidental Whitebreasted Nuthatch (Sitta carolinensis) call. Surveys were conducted by experienced observers who recorded the detection time and species of all birds they heard or saw during the count. Data were then collapsed into "detection / nondetection" format for each species for each station, resulting in 3 digit encounter histories for analysis (see below). For example, an encounter history of 001 indicated that a target species was not detected in the first two silent counts at a given station but was detected during the playback count.



Fig. (1). Map of Vermont showing classified habitat types and the location of 183 research sites.

The 684 stations were located on 183 study sites that were stratified by habitat (70% forested, 15% agricultural/grassland, and 15% developed; Fig. 1). Study sites were at least 2.5 km from other sites, and stations within study sites were at least 500 m apart, ensuring independence between stations. Study sites were randomly selected as follows. For developed sites, we created a GIS layer of residential areas based on the density of home locations within 500 m of any point on the layer (home locations were based on emergency-911 data). Points on the layer with densities greater than 2 homes per hectare were classified as residential. We then randomly generated potential study site locations within residential areas. To identify agricultural areas in Vermont, we used the 1992 National Land Cover Data Set [18] and randomly generated points within agricultural areas to identify potential study sites. We verified the accuracy of selected agricultural land classifications by examining contemporary digital orthophotos. Forested sites were randomly selected from a GIS map of public lands, and occasionally needed to be shifted slightly (< 500 m) to ensure that stations were on public land. Additional forested sites were located on private lands owned by conservation organizations or individuals who allowed us to survey their property. Some agricultural and residential sites were not surveyed because we were unable to obtain landowner consent, and others required some (< 500 m) adjustment of station locations.

We used 1992 Land Cover Data within 300 m of each point-count location to classify each station as developed, agricultural/grassland, or forest. Forested habitat included evergreen forest, mixed forest, deciduous forest, and wooded wetlands. Agricultural/grassland habitat included pasture/ hay, row crops, urban/recreational grasses, emergent herbaceous vegetation, and shrubland. The remaining habitat class included all remaining NLCD classes: commercial/industrial/transportation, high intensity residential, low intensity residential, bare rock/sand/clay, transitional, quarries, and open water. The intent of these habitat classes was to generate structural categories that we felt would be likely to affect detection probability (i.e., trees with canopy, low vegetation, or urbanized landscapes). This approach allowed us to avoid overwhelming our modeling efforts with a wide variety of habitat classes, but it has the drawback of simplifying (and potentially obscuring) some habitat effects. Habitat area around each station was calculated using FRAGSTATS [19] and a batch processor for ArcGIS (ESRI, Redlands, California, USA) developed by B. Mitchell [20].

Data Analysis

We analyzed data for 73 bird species that were detected at 10 or more stations. For each species, we used MARK 5.1 [21] to evaluate the data with a 3-occasion occupancy model, in which 4 "real" parameters can be uniquely estimated: ψ (the probability of site occupancy), p_1 (the probability of detecting a target species in point count 1; silent), p_2 (the probability of detecting a target species during point count 2; silent), and p_3 (the probability of detecting a target species during point count 3; playback). For all models, we assumed that occupancy (ψ) would be affected by habitat, so all models included the proportion of forest and agricultural/grassland habitat as covariates of ψ (the proportion of other habitat is implicitly in the model, as 1 - forest - agricultural/grassland). We also assumed that $p_1 = p_2$ for all models (silent treatment). Given those assumptions, our model set contained 6 models which evaluated differences in silent versus playback treatments, as well as habitat effects (Table 1). Model 1 assumed no effect of treatment or habitat on p; model 2 assumed p was affected by treatment only; model 3 assumed p was not affected by treatment but was modified by habitat; model 4 assumed p was affected by treatment, and also that p was modified by habitat in silent treatments; model 5 assumed p was affected by treatment, and also that pwas modified by habitat in playback treatments; and model 6 assumed p was affected by treatment, and modified by habitat uniquely for each treatment.

We interpreted the strength of evidence among the 6 competing models based on the Akaike weights. Akaike weights vary between 0.0 and 1.0 for each model, sum to 1.0 across the model set, and represent the weight of evidence in favor of a given model being the best model in the set [16]. The summed Akaike weight from a subset of models therefore indicates the weight of evidence in favor of the best model being in the subset. For a given species, if the summed Akaike weight for models 4 through 6 was 0.9 or greater, we considered this evidence for playback and habitat effects (since all three of these models contained both effects). We also checked whether the summed Akaike weight was 0.9 or greater for models containing a playback effect (models 2, 4, 5, and 6), a habitat effect (models 3, 4, 5, and 6), or no effect (model 1). A summed weight of 0.9 or greater was considered evidence for the appropriate effect. If none of the four model combinations produced a summed Akaike weight of 0.9 or higher, then we concluded that the

 Table 1.
 Model Set for Occupancy Modeling in MARK 5.1. Habitat is Always Modeled as the Proportion of Forest and Proportion of Agricultural/Grassland Within 300 m

Number	Model	Description	Parameters	
1	$\Psi_{(\text{habitat})}, p_1 = p_2 = p_3$	<i>p</i> is constant	4	
2	$\Psi_{\text{(habitat)}}, p_1 = p_2, p_3$	p is affected by treatment	5	
3	$\Psi_{ ext{(habitat)}}, p_1 = p_2 = p_{3 ext{(habitat)}}$	p is modified by habitat and not affected by treatment	6	
4	$\Psi_{\text{(habitat)}}, p_1 = p_{2(\text{habitat})}, p_3$	p is affected by treatment, and p is modified by habitat during silent treatment	7	
5	$\Psi_{\text{(habitat)}}, p_1 = p_2, p_{3(\text{habitat})}$	p is affected by treatment, and p is modified by habitat during playback treatment	7	
6	$\Psi_{(\text{habitat})}, p_1 = p_{2(\text{habitat})}, p_{3(\text{habitat})}$	p is affected by treatment, and modified by habitat uniquely for each treatment	9	

data was insufficient to support an effect or, in the case of model 1, the lack of an effect.

Model averaging was conducted within MARK 5.1 using three different scenarios (sets of habitat covariate values) and model averaged point estimates and 95% confidence intervals were obtained for ψ and p. We used revised model averaging equations given in Burnham and Anderson [17]. The scenarios roughly corresponded to forested (forest = 1.0 and agricultural/grassland = 0.0), agricultural/grassland (forest = 0.15 and grassland = 0.85), and developed (forest = 0.3 and grassland = 0.2) habitats. The specific habitat values for each scenario were chosen to fall within the range of values obtained for the stations in the data set. Most agricultural/ grassland fields in the study were within 300 m of some proportion of habitat classified as forest, and suburban yards and adjacent areas contained a high proportion of habitat classified on the NLCD as forested or grassland. We believe that the habitat values we used for our scenarios adequately reflect the three basic types of habitat structure we encountered in this study.

The species and family names used in this paper were verified with the ITIS database (www.itis.gov) in December 2007, and lists of species are presented in taxonomic order according to the American Ornithologists' Union Check-list of North American Birds [22]. Common names are used in the remainder of this paper, and the corresponding scientific names are listed in Table **2**.

RESULTS

Estimation problems, manifesting as impossible parameter estimates and confidence intervals, led to the exclusion of results from four species (Turkey Vulture, *Cathartes aura*; Ring-billed Gull, *Larus delawarensis*; Mourning Warbler, *Oporornis philadelphia*; and Swamp Sparrow, *Melospiza georgiana*). Of the remaining 69 species, there was insufficient evidence to determine an effect for 20 species, there was a combined playback and habitat effect for 15 species, a playback effect for 26 species, and a habitat effect for 8 species (Table **2**). We never found evidence for no effect (i.e., no species had an Akaike weight of 0.9 or greater for model 1).

Detection probability differed among habitats for 8 species. Four species (Red-eyed Vireo, Northern Cardinal, Indigo Bunting, and Common Grackle) had lower p in grasslands (where they are not commonly found) compared to residential or forest habitats. Hermit Thrush and Blackthroated Green Warbler had higher p in forests, where they are most abundant, and wide confidence intervals in other habitats. House Sparrow had wide confidence intervals, with highest p in residential areas where it is most abundant. Chimney Swift also had large confidence intervals, except in residential areas where it is more common (Fig. 2). Thus, for these species, detection probability likely increased in habitats where the species was more abundant [5].

Black-capped Chickadee mobbing playbacks increased detection probability for 13 species (Fig. 3). In all cases, point estimates of p were greater for playback treatments than for silent treatments regardless of habitat type, although 95% confidence intervals were often wide, particularly in agricultural/grassland and developed habitats. Downy Wood-

pecker, Hairy Woodpecker, Blue-headed Vireo, Red-breasted Nuthatch, Yellow-rumped Warbler, Black-and-White Warbler, and American Goldfinch all had non-overlapping confidence intervals for the estimated probability of detection in forested habitats with and without the playback treatment. Thus, the chickadee mobbing calls appeared to successfully increase *p* for selected species, especially in forested habitat.

However, chickadee mobbing playbacks decreased detection probability for 13 species (Fig. 4). In all cases but two (Eastern Wood-Pewee and Black-throated Blue Warbler), point estimates of p were lower for the playback treatment than for the silent treatment in all three habitat scenarios, although 95% confidence intervals were often wide, particularly in agricultural/grassland and developed habitats. Nonoverlapping forest 95% confidence intervals for Winter Wren, Wood Thrush, Black-throated Blue Warbler, and Common Yellowthroat indicated that playback reduced p; in most cases the difference between the two estimates exceeded 0.3. In agricultural/grassland habitat, detection of Bobolink was 0.83 without the playback and 0.42 with the playback, and 95% confidence intervals for these estimates did not overlap.

For yet another group of species, detection probability was altered by both chickadee mobbing playbacks and habitat (Fig. 5). The Black-capped Chickadee showed a strongly positive response to playback of conspecific calls, but the magnitude of this response varied by habitat. The playback effect was strongest in forested habitat, where the estimated p increased from 0.38 to 0.95. The Dark-eyed Junco also showed a positive response to playback in forested habitat, but large confidence intervals for other habitats that are probably indicative of inadequate data. Seven species showed a negative playback effect whose magnitude varied depending on the habitat. Mourning Dove, American Crow, Song Sparrow, and Red-winged Blackbird were detected less frequently in multiple habitats when playbacks were used, while Ovenbird and Savannah Sparrow were detected less frequently in forest and grassland, respectively, with poor estimation of *p* in other habitats.

A final group of species responded to playbacks differently in different habitat types (Fig. 5). For example, detection probabilities of Ruby-throated Hummingbird and Blue Jay were higher with the playbacks in forested habitat but not others, while p of White-breasted Nuthatch was higher with playbacks in forest and residential habitats but not grasslands. Despite model selection results indicating a playback and habitat effect for Magnolia Warbler, model averaging for this species provided little evidence of a playback effect in forest, and large confidence intervals in other habitats.

DISCUSSION

There is a clear take-home message from this study: responses of birds to mobbing playbacks varied dramatically by species and by habitat. In some cases, the effect size (difference in p between silent and playback treatments) was very large; increases in p associated with a playback improves the bias and precision of abundance estimators, but decreases in p are detrimental. Therefore, researchers must carefully consider how mobbing calls will affect the number

Table 2. Species Name, Residency Status, Size, Playback and Habitat Effects, and Model Weights for 69 Species Detected at 10 or More Stations

		D 11	vv (<)1	Playback	Habitat	Model Akaike Weight (ω_i)					
Species	Family	Residency	Wt (g)'	Effect ²	Effect	1	2	3	4	5	6
Mourning Dove (Zenaida macroura)	Columbidae	NR	120	_	Yes	0.00	0.01	0.00	0.03	0.01	0.96
Chimney Swift (Chaetura pelagica)	Apodidae	NR	23		Yes	0.01	0.02	0.71	0.01	0.02	0.23
Ruby-throated Hummingbird (Archilochus colubris)	Trochilidae	NR	3	+/0/0	Yes	0.00	0.00	0.00	0.02	0.00	0.98
Yellow-bellied Sapsucker (Sphyrapicus varius)	Picidae	NR	50	+		0.04	0.36	0.02	0.44	0.07	0.07
Downy Woodpecker (Picoides pubescens)	Picidae	R	27	+		0.00	0.74	0.00	0.14	0.10	0.02
Hairy Woodpecker (Picoides villosus)	Picidae	R	66	+		0.00	0.50	0.00	0.15	0.24	0.11
Northern Flicker (Colaptes auratus)	Picidae	NR	130			0.09	0.04	0.79	0.03	0.01	0.05
Pileated Woodpecker (Dryocopus pileatus)	Picidae	R	290	_		0.00	0.21	0.00	0.27	0.12	0.40
Eastern Wood-Pewee (Contopus virens)	Tyrannidae	NR	14	_		0.01	0.22	0.00	0.11	0.50	0.15
Alder Flycatcher (Empidonax alnorum)	Tyrannidae	NR	14	_		0.00	0.31	0.00	0.34	0.18	0.17
Least Flycatcher (Empidonax minimus)	Tyrannidae	NR	10			0.55	0.20	0.13	0.07	0.04	0.01
Eastern Phoebe (Sayornis phoebe)	Tyrannidae	NR	20			0.53	0.30	0.07	0.05	0.05	0.01
Great Crested Flycatcher (Myiarchus crinitus)	Tyrannidae	NR	34			0.14	0.08	0.69	0.01	0.02	0.07
Eastern Kingbird (Tyrannus tyrannus)	Tyrannidae	NR	40			0.10	0.22	0.45	0.05	0.05	0.14
Blue-headed Vireo (Vireo solitarius)	Vireonidae	NR	16	+		0.00	0.71	0.00	0.17	0.10	0.02
Red-eyed Vireo (Vireo olivaceous)	Vireonidae	NR	17		Yes	0.00	0.00	0.75	0.04	0.00	0.21
Blue Jay (Cyanocitta cristata)	Corvidae	R	85	+/0/0	Yes	0.00	0.00	0.00	0.84	0.00	0.16
American Crow (Corvus brachyrhynchos)	Corvidae	NR	450	-	Yes	0.00	0.00	0.00	0.00	0.00	1.00
Common Raven (Corvus corax)	Corvidae	R	1,200			0.40	0.19	0.14	0.18	0.05	0.04
Tree Swallow (Tachycineta bicolor)	Hirundinidae	NR	20			0.11	0.06	0.72	0.02	0.02	0.07
Barn Swallow (Hirundo rustica)	Hirundinidae	NR	19			0.28	0.18	0.27	0.19	0.03	0.04
Black-capped Chickadee (Poecile atricapillus)	Paridae	R	11	+	Yes	0.00	0.00	0.00	0.01	0.01	0.98
Tufted Titmouse (Baeolophus bicolor)	Paridae	R	22			0.00	0.37	0.20	0.14	0.25	0.04
Red-breasted Nuthatch (Sitta canadensis)	Sittidae	R	10	+		0.00	0.50	0.00	0.25	0.20	0.05
White-breasted Nuthatch (Sitta carolinensis)	Sittidae	R	21	+/0/+	Yes	0.00	0.05	0.00	0.69	0.08	0.19
Brown Creeper (Certhia americana)	Certhiidae	R	8			0.35	0.15	0.23	0.03	0.19	0.05
House Wren (Troglodytes aedon)	Troglodytidae	NR	11			0.14	0.46	0.12	0.09	0.13	0.05
Winter Wren (Troglodytes troglodytes)	Troglodytidae	NR	9	_		0.00	0.57	0.00	0.18	0.20	0.05
Golden-crowned Kinglet (Regulus satrapa)	Regulidae	R	6	+		0.05	0.54	0.01	0.15	0.19	0.05
Veery (Catharus fuscescens)	Turdidae	NR	31			0.24	0.30	0.07	0.18	0.15	0.06
Swainson's Thrush (Catharus ustulatus)	Turdidae	NR	31	_		0.07	0.59	0.01	0.16	0.14	0.03
Hermit Thrush (Catharus guttatus)	Turdidae	NR	31		Yes	0.01	0.02	0.28	0.00	0.23	0.47
Wood Thrush (Hylocichla mustelina)	Turdidae	NR	47	-		0.00	0.37	0.00	0.37	0.12	0.14
American Robin (Turdus migratorius)	Turdidae	NR	77	0 / - / 0	Yes	0.00	0.00	0.01	0.03	0.00	0.96
Gray Catbird (Dumetella carolinensis)	Mimidae	NR	37	+		0.02	0.46	0.06	0.32	0.12	0.03

(Table 2) contd....

		1		Playback	Habitat	Model Akaike Weight (w _i)						
Species	Family	Residency	Wt (g)'	Effect ²	Effect	1	2	3	4	5	6	
European Starling (Sturnus vulgaris)	Sturnidae	R	82	-		0.01	0.49	0.00	0.09	0.36	0.05	
Cedar Waxwing (Bombycilla cedrorum)	Bombycillidae	R	32			0.44	0.23	0.16	0.09	0.06	0.02	
Nashville Warbler (Vermivora ruficapilla)	Parulidae	NR	9	-		0.01	0.52	0.01	0.14	0.16	0.17	
Northern Parula (Parula americana)	Parulidae	NR	9			0.12	0.04	0.73	0.03	0.03	0.04	
Yellow Warbler (Dendroica petechia)	Parulidae	NR	10	-		0.01	0.17	0.02	0.04	0.55	0.22	
Chestnut-sided Warbler (Dendroica pensylvanica)	Parulidae	NR	10			0.12	0.34	0.07	0.05	0.35	0.07	
Magnolia Warbler (Dendroica magnolia)	Parulidae	NR	9	0/0/0	Yes	0.00	0.01	0.00	0.06	0.33	0.60	
Black-throated Blue Warbler (Dendroica caerulescens)	Parulidae	NR	10	_		0.00	0.31	0.00	0.56	0.04	0.08	
Yellow-rumped Warbler (Dendroica coronata)	Parulidae	NR	12	+		0.00	0.56	0.00	0.24	0.16	0.04	
Black-throated Green Warbler (Dendroica virens)	Parulidae	NR	9		Yes	0.00	0.00	0.75	0.03	0.00	0.22	
Blackburnian Warbler (Dendroica fusca)	Parulidae	NR	10	+		0.00	0.30	0.00	0.27	0.07	0.35	
Pine Warbler (Dendroica pinus)	Parulidae	NR	12			0.25	0.32	0.07	0.27	0.06	0.04	
Black-and-White Warbler (Mniotilta varia)	Parulidae	NR	11	+		0.00	0.72	0.00	0.15	0.11	0.02	
American Redstart (Setophaga ruticilla)	Parulidae	NR	8			0.35	0.41	0.08	0.09	0.06	0.01	
Ovenbird (Seiurus aurocapilla)	Parulidae	NR	20	-	Yes	0.00	0.00	0.00	0.04	0.00	0.96	
Common Yellowthroat (Geothlypis trichas)	Parulidae	NR	10	-		0.00	0.10	0.00	0.53	0.04	0.32	
Canada Warbler (Wilsonia canadensis)	Parulidae	NR	10			0.06	0.17	0.39	0.12	0.06	0.20	
Scarlet Tanager (Piranga olivacea)	Thraupidae	NR	28			0.15	0.09	0.60	0.09	0.02	0.06	
Chipping Sparrow (Spizella passerina)	Emberizidae	NR	12	0/0/-	Yes	0.00	0.00	0.09	0.06	0.00	0.85	
Savannah Sparrow (Passerculus sandwichensis)	Emberizidae	NR	20	-	Yes	0.00	0.07	0.00	0.07	0.16	0.69	
Song Sparrow (Melospiza melodia)	Emberizidae	R	20	-	Yes	0.00	0.00	0.00	0.10	0.00	0.90	
White-throated Sparrow (Zonotrichia albicollis)	Emberizidae	NR	26	-	Yes	0.00	0.03	0.00	0.84	0.01	0.12	
Dark-eyed Junco (Junco hyemalis)	Emberizidae	R	19	+/0/0	Yes	0.01	0.04	0.00	0.08	0.55	0.32	
Northern Cardinal (Cardinalis cardinalis)	Cardinalidae	R	45		Yes	0.00	0.00	0.90	0.00	0.00	0.10	
Rose-breasted Grosbeak (Pheucticus ludovicianus)	Cardinalidae	NR	45			0.22	0.09	0.56	0.08	0.02	0.04	
Indigo Bunting (Passerina cyanea)	Cardinalidae	NR	15		Yes	0.00	0.00	0.70	0.02	0.00	0.28	
Bobolink (Dolichonyx oryzivorus)	Icteridae	NR	43	-		0.00	0.68	0.00	0.16	0.09	0.06	
Red-winged Blackbird (Agelaius phoeniceus)	Icteridae	NR	52	-	Yes	0.00	0.08	0.00	0.12	0.25	0.56	
Common Grackle (Quiscalus quiscula)	Icteridae	NR	115		Yes	0.00	0.00	0.92	0.00	0.00	0.08	
Brown-headed Cowbird (Molothrus ater)	Icteridae	NR	44	-		0.00	0.52	0.00	0.35	0.13	0.00	
Baltimore Oriole (Icterus galbula)	Icteridae	NR	33	+		0.00	0.33	0.00	0.08	0.15	0.44	
Purple Finch (Carpodacus purpureus)	Fringillidae	R	25	+		0.00	0.34	0.01	0.06	0.11	0.48	
American Goldfinch (Carduelis tristis)	Fringillidae	R	13	+		0.00	0.37	0.00	0.46	0.07	0.10	
House Sparrow (Passer domesticus)	Passeridae	R	28		Yes	0.00	0.00	0.40	0.01	0.01	0.58	

¹ Resident (R) or Non-Resident (NR) and weight is from information in The Sibley Guide to Birds [34]; ² "+" is a positive playback effect, "-" is negative, and "0" is no effect; if the effect differs by habitat they are separated by slashes, so "+ / 0 / -" indicates a positive playback effect in forest, no effect in grassland, and a negative effect in residential areas.



Species with Habitat Effect

Fig. (2). Probability of detecting species where p varies by habitat. Error bars are model averaged 95% confidence intervals, and results are listed in AOU taxonomic order, using species common names.

of presences and the number of individuals detected for target species of interest. These results should be relevant to researchers using occupancy models [7,23], but also could be relevant for closed capture or mixture analyses [e.g., 4,5,24], in which estimation of N (the actual abundance of animals at a study site) or λ (the mean abundance of individuals across a collection of study sites) is a primary goal.

In general, species that tended to respond to mobbing calls included some, but not all, year-round residents (e.g., Downy Woodpecker, Hairy Woodpecker, Blue Jay, Blackcapped Chickadee, White-breasted Nuthatch, and American Goldfinch). For these species, responses to playbacks were consistently positive across habitat types but were strongest in habitats where the species is typically found. These results generally confirmed those of Turcotte and Desrochers [25], who compared differences in abundance of resident species in response to chickadee mobbing playbacks during winter.

Other species showed sharp declines in detections in response to the playbacks – clearly an undesirable effect for researchers interested in increasing detectability. These species included some, but not all, members of the corvid and blackbird families (American Crow, European Starling, Bobolink, Red-winged Blackbird, and Brown-headed Cowbird), sparrows (Savannah Sparrow, Song Sparrow, and White-throated Sparrow), and selected long-distance migrant passerines (e.g., Winter Wren, Swainson's Thrush, Wood Thrush, Black-throated Blue Warbler, Ovenbird, and Common Yellowthroat). These species could have 1) responded negatively to the tape by leaving the survey area, 2) responded to the tape but were undetected because they were obscured by vegetation or used chip calls that were not identified by observers, or 3) ignored the tape but were undetected by observers because their vocalizations were masked by the playback broadcast. Future research evaluating the responses of marked individuals (e.g., [15]) is needed to help discriminate among these possibilities.

Several potential mechanisms could explain the observed differences in species responses to playbacks. Our results show that smaller resident species were more responsive to playbacks than larger residents. For instance, detection probability of Pileated Woodpecker and American Crow decreased in the playback treatment. It is possible that smaller birds responded to playbacks more aggressively because



Species with Positive Playback Effect

Fig. (3). Probability of detecting species where playback increased *p*. See the Figure 2 caption for additional details.

they felt threatened by a potential predator (the screech owl) and responded. Chickadees issue alarm signals that reveal information about the size of predators [26] and the imminent threat of predation [27]. Because our playback consisted

of screech owl calls and responses of chickadees to screech owls, we expect that birds responding to our playbacks would also be concerned about screech owl predation (i.e., potentially smaller birds [13]).



Species with Negative Playback Effect

Fig. (4). Probability of detecting species where playback decreased p. See the Figure 2 caption for additional details.

It is also possible that some of the playback effects that we observed were due to the additional species (American Crow, Blue Jay, and White-breasted Nuthatch) calls in the background of the mobbing tape. Both White-breasted Nuthatch and Blue Jay were more detectable during playback, although American Crow (a commonly mobbed species) was less detectable. Species-specific responses (or the lack thereof) could additionally have depended on whether live chickadees were actively responding to the tape. Hurd [13] noted that the presence of live chickadees increased the number and volume of calls, allowing more distant birds to hear a more intense and loud stimulus. Hurd also noted that the presence of live birds also provided a visual stimulus, perhaps enhancing



Species with Playback and Habitat Effects

Fig. (5). Probability of detecting species where playback and habitat affected p. The first group ("+" after the species name) showed increased p with playback that varied in strength by habitat. The middle group showed variable playback effects depending on habitat, and the final group ("-" after the species name) showed decreased p with playback that varied in strength by habitat. See the Figure 2 legend and caption for additional details.

heterospecific attraction. We evaluated this possibility using the data set for the playback counts in forested habitat (greater than 50% forest, and less than 10% residential and 25% agricultural/grassland within 300 m). We calculated means and 95% confidence intervals for the proportion of sites where 72 species – excluding Black-capped Chickadee – were recorded in the presence and absence of Blackcapped Chickadee detections. Six species were more likely to be detected in the presence of actual chickadees (based on non-overlapping 95% confidence intervals): Blue Jay, Common Raven, Red-breasted Nuthatch, Brown Creeper, Nashville Warbler, and Indigo Bunting. Swainson's Thrush, on the other hand, was less often detected in the presence of chickadees.

In some ways, our results contrast with those reported by Gunn et al. [14] for their research investigating the effect of a mobbing tape on bird detections. For instance, Gunn et al. report that 50 and 24 species responded at least once to playbacks across 5 separate trials conducted throughout the breeding season in New Brunswick and Quebec, respectively. Though our data were not directly comparable, we observed increases in detections for only 17 of 69 species (25%). This disparity may have arisen for several different reasons. First, Gunn et al. [14] used chickadee mobbing calls in response to Saw Whet Owls (Aegolius acadicus). It is possible that their chickadee mobbing calls conveyed different information to birds within the survey area than our calls did, thus affecting species responses [26,27]. The species responding most frequently in New Brunswick and Quebec included vireos, warblers, nuthatches, and thrushes, whereas most of these species showed no response or even negative responses in our study.

Second, Gunn et al. [14] repeated their pre-playback versus playback trials at each point count station 5 times across the breeding season, whereas we conducted a single trial per station. Individuals who produce fledglings are more likely to engage in mobbing behavior [15], and other studies confirm that mobbing responses likely increase as parental investment increases [28]. By analyzing point count surveys taken in the same location over time (5 different trials across the breeding season), Gunn et al. [14] ensured that at least one of their trials (pre-playback versus playback) was conducted when birds were more likely to respond to the tape. However, many standardized survey protocols (e.g., the Breeding Bird Survey) are similar to ours in that individual sites are visited only once in the breeding season, resulting in some surveys being conducted when bird responses to mobbing recordings may be low.

Third, the pre-playback and post-playback surveys conducted by Gunn *et al.* [14] consisted of visual observations, while we used all detections (visual and auditory). We were initially surprised that more species did not show a positive response to the mobbing tape because visual detections dramatically increased during playback. We suspect that, for many species, individuals were detected acoustically during the silent count, and then visually during the mobbing tape playback. If the purpose of a survey is to estimate population size or species occupancy, then the important issue is whether we detect an individual; the method by which an individual is detected is less relevant.

Finally, Gunn *et al.* [14] used fixed-radius counts, and only recorded individuals within 50 m of the observer. Betts *et al.* [29] found that mobbing was highly constrained by territory boundaries in two warbler species (Black-throated Blue Warbler and Black-throated Green Warbler) during the breeding season, with birds moving from 25 to 175 m in response to chickadee mobbing broadcasts. This result raises an important issue regarding the analysis of playbacks on detection rates: an individual must be present in the survey area during both pre-playback and playback surveys in order for comparisons between the methods to be valid (i.e., the two methods must sample the same closed population). Positive responses to the playback could be due to birds within the point count radius becoming more active and visible, or they could be due to individuals from outside the point count radius temporarily moving into the area (an open population). Clearly the first option is desirable, whereas the second is not.

We believe that using all bird detections (i.e. unlimited radius counts) minimizes the effect of temporary immigration into the count area, although there is still the potential for birds to respond to playback by moving into or out of the range where an observer can detect them. The radius of a fixed radius count should exceed the distance that birds can reasonably be expected to hear and respond to the tape playback (e.g., approximately 175 m [29]), which will increase the chance that the population is closed. However, using a large or unlimited radius is potentially affected by increased heterogeneity because distant birds are harder to detect [30]. This heterogeneity could be modeled using distance sampling [8] or other methods, such as a model that incorporates distance and time-of-detection [31]. Unfortunately, there is strong evidence that observers cannot accurately estimate distances to singing birds, especially in forested habitats [32,33]. The poor ability of observers to estimate distances to singing birds, in turn, makes it extremely difficult to determine the population that is sampled by a point count. Researchers must remain cognizant of the potential for silent and playback counts to sample different populations. In most cases, the analysis may be simplified by using only one type of count (silent or playback) in a given study.

CONCLUSIONS

Our results have implications in terms of study designs aimed at maximizing detection probability, p. The effectiveness of the tape in increasing p varies with species and habitat type, so the method is most effective for surveying target species that are known to respond positively to the tape. The method is probably not useful for surveys intended to target a wide variety of species, since using the tape resulted in lower detection probabilities for many species. In addition, the probability that an individual responds to the tape may depend on its reproductive stage; thus the effectiveness of the tape in increasing p may vary over the course of the breeding season. When using playbacks, a large or unlimited point count radius should be used, since birds may move 175 m or more in response to playbacks. Finally, comparing silent and playback counts is difficult because these methods may sample different populations; in many cases researchers will be better off choosing one type of count for their surveys.

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