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A test of the mobbing playback method for estimating bird reproductive success

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ABSTRACT. Accurate measures of reproductive performance in birds are vital to effective conservation and management of populations. We evaluate the effectiveness of a recently proposed method to estimate reproductive performance based upon behavior of breeding birds during responses to Black-capped Chickadee (*Poecile atricapillus*) mobbing calls. We examined whether responses of Black-throated Blue Warblers (*Dendroica caerulescens*) to mobbing calls were related to measures of reproductive performance as determined in a nest monitoring study. We found that individuals that were successful reproducers were more likely to exhibit a response to the mobbing calls. Successfully reproducing individuals were more likely to display evidence of reproductive success (e.g., carrying nesting material, carrying food) when they responded to the mobbing call. Observations of reproductive success, however, depended on the distance of the observation to the nest site of the individual. We conclude that responses to mobbing calls have limited utility for discerning variability in reproductive success among territories. However, if the research objective is to obtain coarse comparative estimates of reproductive success at large spatial scales over which reproductive output is likely to be highly variable, then observations generated by the mobbing playback method may suffice.

SINOPSIS. **Prueba del método de uso de grabaciones de tumultos para determinar el éxito de anidamiento en aves**

Se necesitan métodos adecuados para medir el rendimiento reproductivo en aves para poder tomar medidas efectivas de conservación y manejo. Evaluamos la efectividad de un método propuesto recientemente, para estimar el éxito reproductivo, basado en la conducta de aves expuestas a grabaciones de llamadas de tumultos producidos por *Poecile atricapillus*. Examinamos si la respuesta de individuos de *Dendroica caerulescens* a las grabaciones de conductas de tumulto de los poeciles, estaban relacionadas al éxito reproductivo comparado con un estudio de monitoreo reproductivo. Encontramos que los individuos que se reprodujeron exitosamente, fueron más propensos a contestar o reaccionar a las grabaciones. Los individuos reproductivamente exitosos estuvieron mas propensos a mostrar conducta asociada a éxito reproductivo (ej., cargando material de anidamiento o llevando alimento al nido) cuando emitían una respuesta a las grabaciones. Sin embargo, el éxito de anidamiento, estuvo relacionado a la distancia entre el observador y el nido. Concluimos que la respuesta de grabaciones de tumulto es de utilidad limitada para discernir entre la variabilidad en el éxito reproductivo de individuos con territorios. Sin embargo, si el objetivo de la investigación va dirigido a obtener información comparativa de éxito reproductivo a gran escala, sobre la aportación reproductiva, y si esta tiende a ser variable, entonces las observaciones generadas por grabaciones de tumulto pueden ser adecuadas.

Key words: Black-capped Chickadee, Black-throated Blue Warbler, mobbing response, nest success, reproductive performance

Accurate measures of avian reproductive success are essential to conservation and management of bird species. Presence-absence and density estimates are not necessarily indicative of reproductive success and, as a result, may be inadequate indicators of habitat quality (van Horne 1983; Pulliam 1988; Robinson et al. 1995; Hagan et al. 1996; Ortega and Capen 1999; Bayne and Hobson 2002; cf. Holmes et al. 1996). However, collection of data on reproductive success usually requires intensive nest-searching, season-long observations of individually marked birds, and detailed and accurate accounts of the fates of all nestlings and fledglings (Holmes et al. 1992, 1996). It is thus time-consuming and logistically challenging to directly measure reproductive output, particularly at large spatial scales.

A number of methods have been proposed

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that allow for the rapid estimation of reproductive success through observations of reproductive activity (Vickery et al. 1992; Buford et al. 1996; Gunn et al. 2000). These methods are increasingly used in forest, wetland, and grassland bird research (Dale et al. 1997; Powell and Collier 1998; Martin and Morrison 1999; Rangen et al. 2000; Christoferson and Morrison 2001; Harris and Reed 2002; Stevens et al. 2003) and appear to be applicable to a number of bird species. However, the relationship between estimates of reproductive success gained through such behavioral observations, and estimates from nest-monitoring efforts, has rarely been examined (cf. Vickery et al. 1992; Christoferson and Morrison 2001).

The goal of this study was to test the relationship between estimates of reproductive success as calculated via intensive nest monitoring efforts and estimates of reproductive success generated from observations of reproductive activity collected using the mobbing playback method (Gunn et al. 2000). The mobbing playback method relies on an interspecific attraction to Black-capped Chickadee (*Poecile atricapilla*) mobbing calls to increase observations of reproductive activity. A variety of hypotheses have been proposed to explain the function of mobbing (Curio 1978; Hurd 1996; Maklakov 2002), among which include responses due to perceived risks of predation. Responses may be more intense for those individuals in breeding condition or those defending young (Curio 1978). Thus, such observations may allow for a general assessment of an individual's reproductive status, such as whether or not it is paired or tending young, and may be applicable for a wide variety of species (Gunn et al. 2000). However, while it is essential to examine the relationship between observations of reproductive status gained during mobbing trials and estimates from nest-monitoring efforts, only one such test has previously been conducted (Gunn et al. 2000).

Our objectives in this study were threefold. First, we sought to determine whether an individual's response to mobbing calls (i.e., whether an individual was attracted to the mobbing calls) was related to the individual's reproductive success as measured with direct nest observations. We predicted that parental investment in producing young (reproductive success) should result in a higher propensity to respond to the mobbing playback (Regelmann and Curio 1983; Halupka and Halupka 1997). Second, we sought to determine whether observations of reproductive activity for an individual (e.g., presence of a pair, carrying food or nest material, presence of fledglings) gained during responses to mobbing calls were related to the individual's reproductive success as measured with direct nest observations. We predicted that observations of reproductive activity should increase for those individuals that had successfully bred. Finally, we determined whether observed responses to mobbing calls, and observations of reproductive activity gained during responses, were dependent upon the distance from mobbing playback sample locations to active nests. This information would be useful in the design of mobbing playback experiments. For example, if observations of reproductive activity are common at long distances from the nest, it would be necessary to have adequate distances between sample points to avoid double counting.

STUDY AREA AND METHODS

Study site and species. This study was conducted from 10 June to 18 July 2001 at Hubbard Brook Experimental Forest (43°56′N, 71°45′W), West Thornton, New Hampshire, U.S.A. We conducted mobbing playback trials within a 64-ha plot. The plot was located at an elevation of 500–600 m in mature (> 90 years) deciduous and mixed coniferous-deciduous forest. Dominant tree species were sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and red spruce (*Picea rubens*), with an understory consisting of saplings of the dominant tree species plus hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and other small trees and shrubs (Holmes 1986).

The study species was the Black-throated Blue Warbler (*Dendroica caerulescens*). The Black-throated Blue Warbler, an insectivorous, forest dependent songbird, builds open cup nests in understory vegetation, at heights of 0.1–2 m (Holmes 1994), and is one of the most common bird species within the Hubbard Brook Experimental Forest (Holmes and Sherry 2001; Doran 2003).

Nest monitoring. The Black-throated Blue Warblers at the study site are under inten-

sive study as part of a long-running demographic study (Holmes et al. 1992, 1996). All birds nesting within the 64-ha plot were captured and given unique color bands to allow for individual identification. Their territory boundaries were determined using spot mapping (Bibby et al. 2000), as the methods for identifying territory boundaries, such as kernel estimates of minimum convex polygons, usually require intensive analyses that were prohibitive for our need to locate mobbing points early in the breeding season. All nests of breeding individuals were located and monitored at least every second day throughout the nesting cycle until a final fate could be determined (success or failure, the number of young fledged). For statistical analyses, reproductive success was condensed into two categories: successful (in which at least one young successfully fledged from the territory during the breeding season) and unsuccessful (no young were fledged).

Mobbing playback trials. We conducted mobbing playback trials using a recording of Black-capped Chickadees mobbing a stuffed Northern Saw-Whet Owl (*Aegolius acadicus*). The recording included the "high-zee" and "chick-a-dee" calls typically made when chickadees approach a predator and perform stereotyped wing and tail movements (Curio 1978; Hurd 1996; Gunn et al. 2000). Among forest birds, the mobbing calls of Black-capped Chickadees may alert other members of the larger avian community to the presence of a predator (Hurd 1996; Gunn et al. 2000). A wide range of species respond to these mobbing calls with characteristic responses (Hurd 1996). For example, Gunn et al. (2000) documented responses from 50 species in New Brunswick and 24 species in Quebec. During our study at Hubbard Brook, 26 species responded to the mobbing playbacks, 17 of which displayed some evidence of reproductive activity (P. Gulezian, unpubl. data). This interspecific response is thought to serve a variety of adaptive functions such as moving predators from a territory, confusing predators, and educating young in predator recognition (Curio 1978).

Within the study site, we established one sampling point within each of 45 Black-throated Blue Warbler territories. We adopted the methods of Gunn et al. (2000) for all mobbing playback trials. Each sampling (or territory) point was visited for 10 min (two successive 5-min intervals) on four or five separate occasions between 06:00–12:00. At each point, all Black-throated Blue Warblers detected visually or aurally within 100 m were recorded during the first 5-min interval. This provided data on birds present before the mobbing tape was played. During the second 5-min interval, we played mobbing calls with an Optimus CTR-110 stereo cassette player placed on the ground at the sample point. The volume approximated the normal sound intensity produced by live birds. The responses of all new birds detected, and of birds detected in the first 5-min interval, were recorded.

Based upon individual responses to the mobbing trials, we recorded two classes of behavioral responses. First, we recorded whether individuals were attracted to the mobbing calls. Individuals were considered to be attracted if they approached the player and/or exhibited typical mobbing behaviors, such as flying in a directed manner toward the playback (Hurd 1996), calling in rapid succession at a high frequency, making tail and wing-flicking movements, rapidly changing perches, or other stereotyped movements (Curio 1978). Because of the qualitative nature of measuring the intensity of the mobbing response, this behavior was treated as a binary variable (response, no response).

Second, we recorded evidence of reproductive activity during the 10-min playback period, such as whether a male and female were present in close proximity (suspected pair), or if adults were carrying nesting material or food or feeding fledglings (Gunn et al. 2000).

Because reproductive behavior varies over the course of the nesting cycle, we visited all territories multiple times (4–5) spaced at equal time intervals (6–7 d) throughout the breeding season. For statistical analyses, we reduced the multiple visits into a single data point by taking the "maximum" response detected during the 4–5 visits. Therefore, if during any of the multiple visits, the focal bird responded to the mobbing calls, the territory was assigned a value of "response." Similarly, if during any of the multiple visits, the focal bird displayed any indication of reproductive activity, the territory was assigned a value of "presence of reproductive activity." All mobbing trials were conducted by one observer (PZG) who had no knowl-

edge of the reproductive status of territorial individuals during the mobbing trials.

After completion of the breeding season, we estimated the distance from each mobbing sample point to the nest in the territory associated with the sample point. Distance estimations were based upon maps of territory boundaries overlaid upon the mapped 50-m grid locations flagged throughout the study plot. Since this method of distance estimation did not allow for detailed distance measurements, we lumped distance data into two categories: < 50 m and > 50 m from the nest.

Statistical analysis. The binomial reproductive success data were modeled using logistic regression (PROC LOGISTIC, SAS Institute 2001) as a function of two categorical predictors: mobbing response and reproductive activity. We did not examine the mobbing response and reproductive activity variables simultaneously or consider interaction terms because reproductive activity observations were largely a subset of mobbing response observations and were thus collinear.

We also used logistic regression to test the effect of distance from a nest on the probability of eliciting a mobbing response and the probability of observing reproductive activity. We reasoned that if birds are less likely to show evidence of reproductive activity at large distances from the nest, this could potentially result in a high number of false negative predictions (birds with no observations of reproductive activity that still succeeded in producing young). After determining that distance of a mobbing trial from a nest negatively influenced the probability of observing reproductive activity (see Results), we conducted Type I logistic regression (PROC GENMOD, SAS Institute 2001) to determine the effectiveness of reproductive activity as a predictor of reproductive success after statistically controlling for the effect of distance to nest.

Logistic regression fit was assessed visually by comparing plots of predicted probabilities to those of observed probabilities (Hosmer and Lemeshow 2000). Statistical significance was determined by using likelihood ratio tests. We set $\alpha = 0.05$ in all statistical analyses. We report odds ratio confidence intervals (CI) at 95% as a measure of variability around observed effect sizes and thus as a proxy for power (Steidl et al. 1997; Thomas 1997).

RESULTS

Black-throated Blue Warblers were detected visually or aurally at all 45 sample points during at least one of the 4–5 visits. Mobbing responses were observed in 31 (68.9%) of the territories. For the Black-throated Blue Warbler, typical mobbing responses included approach toward the speaker, the emission of chip notes in rapid succession, frequent movements among perches, tail flicking, and other stereotyped movements. Evidence of reproductive activity by the responding birds was observed in 12 (26.7%) territories. Eight of 12 of these reproductive observations were of females carrying food. Twenty-five of 45 pairs (55.6%) succeeded in producing at least one fledgling during the summer breeding period.

Mobbing response and nesting success. Territory holders that exhibited a mobbing response were more likely to be those that successfully fledged at least one young (odds ratio, 5.2; CI, 1.31–20.92; $\chi^2 = 5.52$; $P = 0.02$). Of birds that responded to the mobbing playback, 67.7% ($\pm$ 12.0% SE; $N = 31$) successfully reproduced. However, 28.6% ($\pm$ 8.0% SE; $N = 14$) of birds that successfully fledged young did not respond to the playback. Responses of territory holders to the mobbing calls were not significantly influenced by the distance to the nest of the territory holder (odds ratio, 0.95; CI, 0.95–1.55; $\chi^2 = 0.83$, $P = 0.83$).

Reproductive observations and nesting success. We detected no statistical difference in the reproductive success of territory holders showing evidence of reproductive activity during their response to the mobbing playbacks versus those with no evidence of reproductive activity (odds ratio, 3.18; CI, 0.73–13.99; $\chi^2 = 2.38$; $P = 0.12$). Of birds that showed evidence of reproductive activity in the mobbing trials, 75.0% were reproductively successful over the course of the breeding season. However, fledglings were produced by 48.5% of birds with no evidence of reproductive activity (false negative predictions).

Distance from the mobbing trial to the nest significantly influenced the probability of observing reproductive activity by birds responding to the mobbing tape (odds ratio, 6.7; CI, 1.28–35.97; $\chi^2 = 5.06$; $P = 0.02$). Most reproductive observations (10 of 12) occurred

within 50 m of a nest. Therefore, when we statistically controlled for distance to nest, observations of reproductive activity were positively related to measures of reproductive success (i.e., those fledging one or more young in the season) as calculated via nest monitoring (odds ratio, 5.05; CI, 1.08–30.87; $\chi^2 = 4.28$; $P = 0.03$). Of the Black-throated Blue Warbler pairs that successfully produced fledglings, 35.7% (± 14.5% SE; $N = 14$) exhibited no evidence of reproductive activity. In contrast, 70.0% (± 12.8% SE; $N = 10$) of the birds that successfully produced fledglings exhibited evidence of reproductive acitivity.

DISCUSSION

We found that responses of individual Black-throated Blue Warblers to the mobbing playback was a significant predictor of reproductive success. Our prediction that parental investment would be correlated with mobbing response was supported by our observations. Individuals that produced fledglings were more likely to engage in mobbing behavior. This result is congruent with previous studies that have found that mobbing response increases with parental investment (East 1981; Shedd 1983; Gehlbach and Leverett 1995; Halupka 1999). However, most previous research has found relationships between the stage in the breeding season and the intensity of mobbing (East 1981; Shedd 1982; Gehlbach and Leverett 1995; Halupka 1999). From this it has been inferred that increasing parental investment over the breeding season is the cause of a corresponding increase in mobbing behavior. Very little research has examined the variation in mobbing response as a correlate of individual reproductive success or failure within a breeding season (cf. Winkler 1994).

We also found that the reproductive activity observations taken during mobbing playbacks are insufficient to correctly predict territory-level reproductive success of Black-throated Blue Warblers. However, our power to detect a difference in reproductive success based on the reproductive activity index was low; odds ratio confidence intervals were large (fledglings could be up to 13.92 times more likely or 1.37 times less likely given a positive observation of reproductive activity). Effect sizes that we consider to be biologically significant (e.g., 20% increase in the likelihood of successful reproduction) fall well within these confidence intervals (Steidl et al. 1997). Thus, there may be a trend in the predicted direction, as birds that showed evidence of reproductive activity were successful 75% of the time, and only 6% of birds ($N = 12$) that showed evidence of reproductive activity did not successfully reproduce. Predictive error was largely a result of the number of successfully reproducing birds for which we observed no evidence of reproductive activity (48%; false negative predictions). As a result, there is a high likelihood of underestimating reproductive success using this method.

Finally, we found that distance from a nest to a mobbing trial significantly influenced the probability of observing reproductive activity in responding birds. Only 16.7% of reproductive observations occurred at distances greater than 50 m from a nest. Presence of females with food or nest material or as a member of a pair accounted for 66.7% ($N = 12$) reproductive activity observations. This could reflect a tendency for female Black-throated Blue Warblers to remain near the nest during incubation and nestling stages (Nagy 2002). This result has important implications for the spatial layout of mobbing playback sample points. If a large proportion of reproductive observations occurred at large distances from the nest, it would be more important to ensure that sample points are spaced at large (e.g., > 300 m) intervals to avoid double counting of individuals. However, as the majority of observations occurred close to the nest (< 50 m), sample points could be placed in relatively close proximity (~ 200 m).

The paucity of reproductive activity observations at distances greater than 50 m from a nest accounted for a substantial proportion of the false negative reproductive success predictions. As a result, when we statistically controlled for distance from a mobbing trial to the nest, the reproductive activity index successfully predicted reproductive output.

Much of the appeal of the mobbing playback method is that it is not necessary to spend substantial time searching for nests to determine reproductive success. Indeed, in this study, one observer (PZG) was able to conduct 4–5 mobbing trials on 45 different territories in one season. However, if it is necessary to statistically control for the distance to a nest for reproductive activity observations to reflect actual repro-

ductive success, researchers need know the location of the nest for the focal pair. Thus, it would be only slightly more time consuming, and thus probably more effective, to directly measure reproductive success by monitoring nests throughout the season. This is because nest monitoring provides higher resolution of nest success data (i.e., the number of fledglings) than coarse dichotomous estimates of "successful" versus "unsuccessful" nests provided by the mobbing playback method.

Because reproductive activity observations at mobbing playbacks cannot successfully predict reproductive success in the absence of distance to nest information, we do not recommend the use of this method to determine reproductive success at the scale of individual territories. However, we cannot reject the possibility that the mobbing playback method could be useful in some contexts. First, as stated above, we lacked the statistical power to confidently accept the null hypothesis that there is no difference in reproductive success between birds with evidence of reproductive activity versus those with no evidence. Second, errors associated with the method were largely false negatives rather than false positives. Thus, the reproductive index provides an underestimate of the number of birds that are successfully reproducing. One potential remedy to reduce the number of false negative predictions may be to conduct multiple trials late in the breeding season when nestlings and/or fledglings would be present. If the research objective is to obtain coarse comparative estimates of reproductive success at large spatial scales where there is high variability in reproductive output, reproductive activity observations generated by the mobbing playback method may suffice. For instance, in one test of this method using 25-ha plots as the sample unit, Gunn et al. (2000) found no significant difference between average reproductive index scores and average reproductive success for Black-throated Blue Warblers and Ovenbirds (*Seiurus aurocapilla*). Our finding that mobbing response was correlated with reproductive success offers a potential alternative to the use of the reproductive index as a means of predicting reproductive success at the individual territory level, as positive mobbing responses tended to indicate successful pairs whereas no mobbing response tended to indicate unsuccessful pairs. However, in comparison to estimates of reproductive success provided by the reproductive activity index, the false positive rate was high (32.3%), resulting in overestimates of reproductive success at the individual territory scale.

We recognize that the results presented here are for only one species. Thus, we echo the recommendation by Gunn et al. (2000) that researchers calibrate the mobbing playback index in their study area with intensive study plots where the actual nests are monitored for the species of interest. In summary, we conducted the first test of the predictive accuracy of the mobbing playback method at the resolution of individual territories. Response to the mobbing playback trials was a significant indicator of reproductive success. Thus, mobbing response may potentially be used as a coarse estimate of reproductive success at the resolution of the individual territory. Reproductive activity observations alone could not successfully predict reproductive output; however, this was largely due to false negative predictions resulting from low frequencies of reproductive observations at large (> 50 m) distances from the nest. However, if the goal is to assess reproductive success across broad spatial scales, reproductive activity observations may constitute a superior metric due to the low potential for false positive predictions.

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