

Avian Mobbing Response is Restricted by Territory Boundaries: Experimental Evidence from Two Species of Forest Warblers

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Abstract

Predator mobbing has been viewed as an adaptation to reduce the risk of predation, however, factors influencing mobbing behaviour are still debated. We report on the results of an experiment with *Dendroica caerulescens* and *Dendroica virens* designed to determine (1) whether mobbing response by forest songbirds during the breeding season is restricted by territory boundaries, (2) the distance songbirds will move in response to anti-predator mobbing calls, and (3) whether reproductive status, age, and time of the breeding season determine the distance moved to mob. We did not detect an effect of reproductive status, age, or time of breeding season on the distance moved by birds to mob. All birds responded to the mobbing playback within their territory (defined by territorial defence in relation to specific song playbacks). The maximum distance moved within a territory to engage in mobbing ranged from 25 to 175 m ($\bar{x} = 72 \pm 6$ m). Three of 37 birds responded to playbacks outside their territory boundaries. In all three cases, maximum movement distances outside territories were short (25 m). Thus, for two species of warblers, mobbing is highly constrained by territory boundaries during the breeding season. This finding is congruent with arguments that mobbing is primarily a selfish behaviour, at least with respect to conspecifics. Our results also provide support for the 'move-on' hypothesis.

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Introduction

Predator mobbing can be viewed as an adaptation to reduce the risk of predation and is performed by many species of birds (Shedd 1982), mammals (Tamura 1989), fish (Dominey 1983) and insects (Seeley et al. 1982). Avian mobbing occurs when birds of one or more species assemble around a predator or

potentially dangerous animal, change positions frequently, perform stereotyped wing and tail movements and emit loud calls with a broad frequency spectrum (Curio 1978). By mobbing a predator an individual is placing itself at increased risk (Curio & Regelman 1986; Forsman & Mönkkönen 2001) and consuming valuable time that could have been spent on other fitness-enhancing activities (Collias & Collias 1978). After several decades of research, research explaining the origin and evolution of mobbing as an adaptive behaviour is rare (Desrochers et al. 2002; Krams & Krama 2002).

We found only two studies that have examined the importance of territory boundaries in governing avian mobbing response (Shedd 1982; Zimmermann & Curio 1988). In both of these studies, a territorial constraint to mobbing was inferred from frequent observations of only one bird or a pair of birds of the same species at a mobbing event. We are aware of no previous research that has explicitly examined the mobbing response of birds in relation to known territory boundaries.

In this paper we report the results of an experiment designed to determine (1) whether mobbing response by forest songbirds during the breeding season is restricted by territory boundaries, (2) the distance songbirds will move in response to anti-predator mobbing calls, and (3) whether reproductive status, age and time of the breeding season influence the distance moved to mob. In the exploration of these factors, we also tested the hypothesis that parental investment positively influences mobbing response (Shedd 1982; Gehlbach & Leverett 1995). We predicted that (1) response (distance moved to mob) should be positively related to observations of reproductive activity (Curio 1983), (2) response should increase over the breeding season as parental investment increases (East 1981), and (3) because older birds may be more successful at breeding than young birds (Holmes et al. 1992), mobbing response should be greater in older birds.

The results of this study not only offer insight into the mechanisms responsible for mobbing behaviour, but are also important in the light of the attention that mixed-species mobbing has recently received in conservation biology research. Interspecific forest bird response to the mobbing calls of black-capped chickadees (*Poecile atricapilla*) (Hurd 1996) has been used to determine the tendency of birds to cross gaps caused by forest fragmentation (Desrochers & Hannon 1997; Bélisle & Desrochers 2002; St. Clair 2003), and to assess reproductive activity in different habitat types (Gunn et al. 2000; Cornell Laboratory of Ornithology 2003; Doran et al. in press). In such studies, it is important to further understand the factors affecting mobbing response so that potential biases may be determined (Desrochers et al. 2002). In particular, if mobbing playbacks are to be used as a survey technique, it is important to know the size of area sampled by this approach (i.e. the distance travelled by birds to mob) so that the independence and spatial representivity of sample points can be assessed.

Methods

We conducted experiments from 22 Jun. to 25 Jul. 2002 between 05:30 hours and 15:00 hours (AST) in two study areas: the coastal Fundy region of southern

New Brunswick, Canada (45°55'N, 65°5'E) and the Hubbard Brook Experimental Forest (44°2'N, 71°5'E) in New Hampshire, USA. We performed experiments in both study areas in mature (> 60 yr) 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*). We captured male black-throated green warblers (*Dendroica virens*) (n = 20) and black-throated blue warblers (*Dendroica caerulescens*) (n = 17) with mist nets and marked each with a numbered aluminium U.S. Fish and Wildlife Service band and a unique combination of coloured leg bands. We determined the age of birds at both locations as second-year (SY) or after second-year (ASY) using plumage characteristics (Pyle 1997). Eleven of the black-throated blue trials were conducted at Hubbard Brook Experimental Forest. All other trials were performed in southern New Brunswick. We selected these two species because they are both relatively common forest birds in eastern North America that are known to respond to the interspecific mobbing calls of black-capped chickadees (Hurd 1996; Gunn et al. 2000). While both males and females respond to mobbing calls, only males were considered because they responded most readily to specific song playback which enabled territory mapping (Falls 1981) (see below).

Territory Boundary Mapping

We located colour-banded individuals using a combination of visual and auditory means. Prior to each experimental trial, we confirmed band combinations to identify individuals. Passive territory mapping is time consuming and may result in ambiguous territory boundaries (Bibby et al. 2000). Further, we speculated that territory boundaries are likely to fluctuate within a breeding season. For these reasons, we determined boundaries by using playback tapes of conspecific song (Falls 1981; Rail et al. 1997). Starting at the point where we located the focal bird, we played conspecific song successively every 25 m along a randomly determined direction until either no response was elicited, or the focal bird engaged in aggressive interactions with a neighbouring conspecific. Recorded song was played in short (~15 s) bursts to limit habituation by the focal bird. We flagged the most distant 25 m interval in which the bird responded or engaged in conflict, and designated this as a territory boundary. We repeated this procedure in the reverse direction to determine the opposite territory boundary. Conspecific songs were played on a Radio Shack single speaker portable cassette player (Optimus CTR-110, Radio Shack Corporation, Fort Worth, TX, USA) at a volume approximating the sound intensity of a live bird. Territory diameters obtained using this method ranged from 50 to 250 m (see Results). Assuming elliptical or elongated territory shapes, these diameters coincide with territory sizes previously reported for these species (Morse 1993; Holmes 1994).

Territory defence calls were present on both conspecific tapes. The black-throated green warbler tape had 'accented ending' songs that are associated with activities related to territorial defence (Morse 1967, 1993). The black-throated

blue warbler tape contained 'type 2' and 'type 3' songs, often sung at the territory edge and suspected of having inter-male communication functions (Holmes 1994).

Mobbing Trials

We performed mobbing trials both inside (IN) and outside bird territories (OUT) using a 5-min tape recording of black-capped chickadees mobbing a northern saw-whet owl (*Aegolius acadicus*) that contained the 'high-zee' and 'chick-a-dee' calls associated with close approach to a predator (Gunn et al. 2000). We performed mobbing trials immediately following the territory mapping. We used chickadee mobbing calls rather than warbler mobbing calls because we wanted our results to be relevant to mobbing playback sampling techniques (Gunn et al. 2000; Cornell Laboratory of Ornithology 2003; Doran et al. in press). The response of both species to chickadee mobbing calls (Hurd 1996) may be due to interspecific reciprocity based on interspecific recognition (Krams & Krama 2002). We played the tape at a volume to emulate the sound of chickadees at close range.

In all trials we played the chickadee mobbing tape for 5 min. For OUT trials we played the chickadee mobbing tape starting from 150 m outside the territory boundary along the randomly determined axis where we had established territory boundaries. Four trials were performed for each bird (150, 100, 50 and 25 m) always starting at the most distant (150 m) location from the territory boundary. We selected the 150 m OUT distance as we were interested in obtaining the maximum distance that birds would travel to perform mobbing behaviour. This distance is the maximum at which the human ear can detect the tape (range 100–150, $n = 23$). As bird hearing is often poorer than human hearing (Dooling 1982), we expected this to exceed the range of hearing of experimental birds. Trials were conducted at 50 m intervals in order to obtain relatively high resolution of results but minimize the risk that focal birds might become habituated to the mobbing playback.

During the mobbing trials we noted the presence of all banded and unbanded males or females of focal species responding to the mob. While multiple species attended the black-capped chickadee mobbing playbacks (see Hurd 1996; Gunn et al. 2000) we only recorded the presence of the banded bird and conspecifics. If the banded bird responded, its mobbing intensity was recorded as: 1 = within 5 m and exhibiting mobbing behaviour, 2 = 5–15 m and exhibiting mobbing behaviour, 3 = attracted to tape but no mobbing behaviour evident and 4 = no response. We considered mobbing behaviour to include calling, wing fluttering, tail flicking or nervous hopping (Shedd 1982; Hurd 1996).

Before each mobbing playback trial we used the specific song tape of the appropriate species to draw the focal-banded bird to the flagged territory edge. In addition, if the focal bird moved from the territory edge while one observer (observer A) was moving between subsequent mobbing locations, the second observer (observer B) used the specific song tape to return the focal bird to the most proximal territory edge (Fig. 1). In each case we stopped the specific song

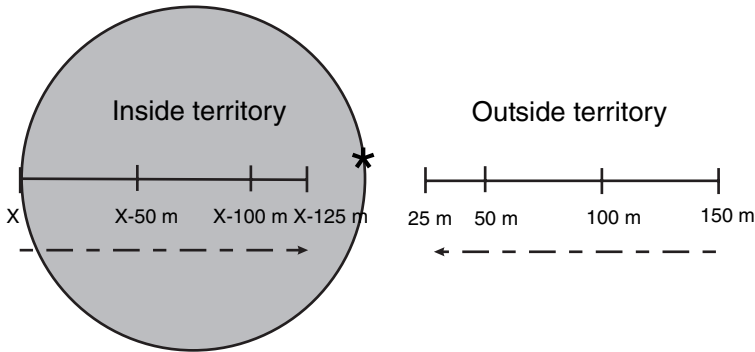


Fig. 1: Spatial layout of mobbing experiments. Outside territory trials were conducted at a maximum distance from territory boundaries of 150 m and then at successive 50 m increments except immediately adjacent to the territory boundary (25 m). Inside territory trials were conducted in a similar manner, but from the distant territory edge (denoted by 'X'). Dashed lines show sequence of sampling. In both cases, immediately preceding playback trials, colour-banded birds were located and maintained at one territory edge (denoted by '*'). The shaded area indicates the established territory

broadcast before the initiation of the mobbing playback. We used hand-held Radio Shack FRS radios to synchronize tapes and communicate about the location of banded birds. Location and behaviour of focal individuals were monitored by observer 'B' throughout the mobbing trial.

If the bird did not respond at the 150 m distance, then observer 'A' repeated the mobbing procedure at 100, 50 and 25 m from the territory edge beyond the territory boundary. We waited at least 10 min between each successive mobbing trial. A bird was considered not to have responded if it did not appear over the course of the 5-min mobbing playback trial. If the banded bird exhibited mobbing behaviour (an intensity of 2 or 1) at any of the trials, then we recorded the location of the response as the OUT of territory distance. No additional trials were conducted once a response was elicited.

We conducted the trials within the territory boundaries with the two observers in alternated roles. Observer 'B' played the mobbing tape at the opposite side of the territory from where observer 'A' retained the focal bird with the specific song playback. If the focal bird did not respond to the mobbing playback, then observer 'B' moved through the existing territory to the opposite territory edge in 50 m increments until the bird responded with mobbing behaviour, or the distance of 25 m from the bird was reached (Fig. 1). In instances where territories were > 150 m diameter, this resulted in greater than four trials per focal bird (maximum 6). The distance where we elicited mobbing behaviour was recorded as the IN territory distance. As in the OUT trials, we recorded the movements of the focal bird and the locations of all conspecifics.

Each bird was subjected to both playback trials (IN and OUT). We randomly determined the order in which IN and OUT trials were conducted for the first experimental bird of each species and then alternated in subsequent trials. This

eliminated the possibility that habituation or sensitization (a primed response) to the mobbing calls during first treatment would result in bias for, or against, the second treatment. However, this did not remove the possibility that over the course of both IN and OUT trials, birds would become either habituated or sensitized to the mobbing or the specific song playbacks. Such habituation or sensitization could influence how far a bird might travel to mob. We tested for this effect by examining the distance moved by birds to a mobbing playback trial as a function of the order of IN and OUT trials. If habituation to either mobbing or specific song playbacks occurred in our study, we predicted that birds subjected to IN trials preceded by OUT trials should move shorter distances within territories than those subjected to IN trials first. Birds for which OUT trials were conducted first were subjected to up to 20 min ($\bar{x} = 19.6 \pm 0.3$) of mobbing playback outside their territories (four OUT distance categories \times 5 min), and multiple bouts of specific song prior to responding to mobbing within their own territories. Alternatively, if sensitization occurred, birds subjected to IN trials preceded by OUT trials should move longer distances within territories than those subjected to IN trials first.

For both IN and OUT trials, we estimated the reproductive status of the focal bird through observations of pairs, individuals carrying food, and the presence of known nests or fledglings (Vickery et al. 1992; Gunn et al. 2000; Doran et al. in press). These observations were combined in the analysis to create a single category of 'reproductive activity'. To limit the effects of noise caused by rain or wind on the forest canopy, we did not conduct mobbing trials in wet or windy conditions.

Statistical Analysis

No statistical tests were performed on OUT data as only three birds moved outside territory boundaries (see Results). We used a type III sums of squares general linear model (proc GLM) to determine the effect of territory diameter, reproductive status, age and date of experiment on the distance moved within the territories (SAS Institute Inc. 2001). We also included species and a species \times territory diameter interaction term to determine whether black-throated green and black-throated blue warblers moved different distances within their territories to mob. Because we had no a priori reasons to expect interactions between other variables and due to small sample size, we did not test for further interactions.

We tested for the influence of repeated recent exposure to mobbing and specific song playback (habituation/sensitization) on distance moved to mob within a territory with a two-sample t-test. Movement distances were grouped into two categories dependent upon whether or not OUT trials were performed before or after IN trials. The null hypothesis was that prior exposure to multiple playbacks (during OUT trials) does not influence within-territory movement distance. We did not test for the influence of habituation on the distance moved beyond territory boundaries because only three of 37 birds exhibited this behaviour (see Results).

We considered all variables significant if $p < 0.05$, but did not discount p -values that were greater than but close to this value (Stoehr 1999). All tests performed were two-tailed. Values provided are $\bar{x} \pm SE$ unless stated otherwise. For all variables tested, we provide differences in means along with 95% confidence intervals (CI). Reporting CIs around effect sizes is considered to be superior to retrospective power analysis (Steidl et al. 1997; Thomas 1997).

Results

Mobbing Responses and Territoriality

We observed mobbing behaviour for 37 individuals. Maximum distances moved within territories ($\bar{x} = 72 \pm 6$ m, range = 25–175 m) were greater than the maximum distances moved outside territories (range = 0–25 m) (Fig. 2). All birds responded to the mobbing playback and exhibited mobbing behaviour within their territory. Three of 37 birds (8.1%) were observed at mobbing playbacks outside their territory boundaries. In each of these cases, the maximum distance moved was 25 m. We did not observe non-territory holders (unbanded birds or birds with different colour band combinations) at any of the within-territory mobbing trials.

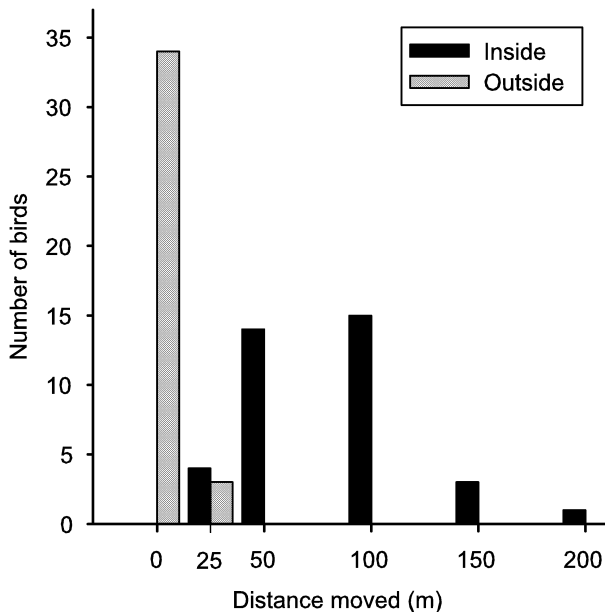


Fig. 2: Frequency of distances moved to a mobbing trial by black-throated blue and black-throated green warblers inside and outside territorial boundaries

Factors Influencing Within-Territory Movement

We did not detect an influence of repeated recent exposure to mobbing and specific song playback on the distance moved to mob. Birds subjected to the sound of both types of playbacks beyond their territory boundaries (during OUT trials) did not travel significantly farther or shorter distances ($\bar{x} = 71 \pm 7$ m) than birds not subjected to extra-territory playbacks ($\bar{x} = 74 \pm 9$ m, two-sample *t*-test, $t_{35} = 0.28$, $p = 0.78$, difference between mean values, 3; 95% CI = -20 to 26).

Distance moved within territory increased as a function of territory diameter (GLM: partial $R^2 = 0.35$, regression coefficient = 0.43 ± 0.17) (Table 1, Fig. 3). Distance moved to a mobbing event was not significantly different for black-throated green warbler ($\bar{x} = 72 \pm 8$ m, $n = 20$), vs. black-throated blue warbler ($\bar{x} = 74 \pm 8$ m, $n = 17$; difference between mean values, 2.7%; 95% CI = -35.1 to 28.3%). Nor did territory diameter have a differential effect on the movement of each species (Table 1). Birds with evidence of reproductive activity did not appear to move further than birds with no such evidence (reproductive activity $\bar{x} = 72 \pm 8$ m, $n = 11$, no reproductive evidence $\bar{x} = 73 \pm 7$ m, $n = 26$; difference between mean values, 1.4%; 95% CI = -8.2 to 6.8%). We did not detect a difference between the distances moved by ASY birds ($\bar{x} = 68 \pm 6$ m, $n = 26$) and SY birds ($\bar{x} = 84 \pm 14$ m, $n = 11$; difference between mean values, 20%; 95% CI = -13.1 to 48.8%). However, our power to detect an influence of this variable was low as the 95% CI in the mean difference is large and may include a biologically significant effect (Steidl et al. 1997). We did not detect an effect of date on the distance moved to a mobbing event (regression coefficient = -0.76 ± 0.57 , 95% CI = -51 to +10/34 d period observed) (Table 1). However, the CI around this parameter estimate is large and is also likely to exclude a biologically meaningful effect.

Table 1: Results of a general linear model (GLM) used to determine the influence of variables on the distance moved by black-throated green and black-throated blue warblers (model $R^2 = 0.36$)

Effect ^a	df	β	Lower 95% CI	Upper 95% CI	p
Intercept	1	66.85			
Territory diameter	1	0.43	0.14	0.72	0.001
Date	1	-0.76	-1.77	0.24	0.19
Reproductive activity (yes)	1	6.16	-17.05	29.39	0.64
Species (black-throated green warbler)	1	8.07	-48.91	65.04	0.81
Age (SY)	1	-2.27	-24.59	20.05	0.85
Territory diameter \times species	1	-0.06	-0.45	0.33	0.79

SY, second year (first year breeder).

^aFor categorical variables, reference categories are listed in brackets.

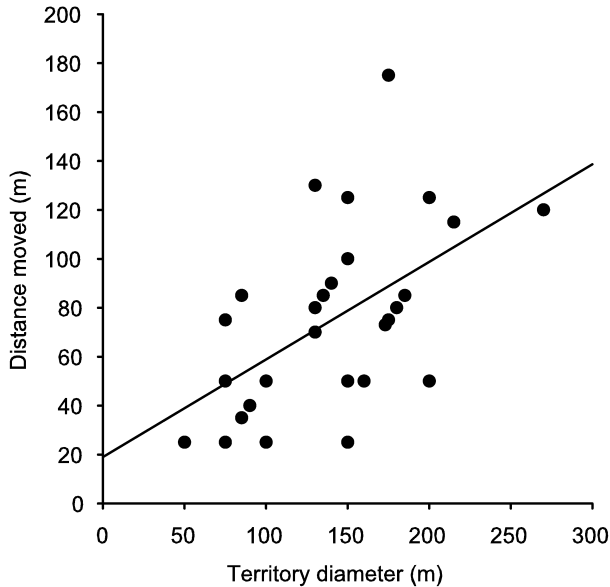


Fig. 3: Distance moved to a mobbing trial by both warbler species as a function of territory diameter

Discussion

Our most important finding was that mobbing behaviour of two species of warblers is highly constrained by territory boundaries during the breeding season. The frequency of within-territory response (100%) was far greater than the frequency of out-of-territory response (8.1%). In most cases, focal birds were visibly agitated by the mobbing playback but would stop abruptly at the territory boundary and would not move to the 25 m OUT location.

Results of other studies tend to support our observation of a territorial constraint to mobbing. Zimmermann & Curio (1988) found that ~80% of the time only a single individual or single pairs of great tits (*Parus major*) responded aggressively to mobbing calls. Great tits assumed not to be holding territories in the vicinity of a mob were observed at mobs but they did not mob as intensely (Zimmermann & Curio 1988). Shedd (1982) occasionally observed more than two American robins (*Turdus migratorius*) (a territorial pair) at mobbing trials. These additional robins tended to be immature birds that did not exhibit mobbing behaviour. Such observations were confined to late in the breeding season so it is possible that immature birds were the offspring of the territorial pair.

While the black-throated blue and black-throated green warblers are considered to be territorial (Morse 1993; Holmes 1994), such migrant parulids have been found to leave territories to engage in fitness-enhancing activities such as extra-pair fertilization (Chuang-Dobbs et al. 2001; Norris &

Stutchbury 2001; Webster et al. 2001), and investigation of potential intruders (Falls 1981). Mobbing beyond territory boundaries could have a variety of adaptive benefits such as (1) gathering information about potential risk (e.g. what sort of predator is present, whether it is stationary or moving towards the territory) (Shields 1984), and (2) 'moving on' a predator from the general vicinity of a territory (Curio 1978); a predator could still be a potential risk even if beyond territory boundaries but still within striking distance. However, apparently these potential benefits are insufficient to warrant extra-territory movement by these two species of warblers.

Ostreiher (2003) argued that hypotheses explaining mobbing behaviour can be grouped into three main classes: (1) altruism, in which participants endanger themselves for the sake of group members, (2) parental care, in which mobbing is carried out for the benefit of offspring, (3) selfish behaviour that has primary benefits for the individual participant. If mobbing is altruistic behaviour, we would have expected birds to leave territories to assist neighbours. While we cannot rule out the parental care hypothesis, our results indicating strict observance of territory boundaries provides some support for the selfish basis to mobbing behaviour, at least with regard to conspecifics. However, during our trials, birds joined mobbing groups composed of multiple individuals of different species that presumably held overlapping territories encompassing trial locations. Such behaviour has been explained in terms of heterospecific reciprocal altruism (Krams & Krama 2002).

A variety of hypotheses have been put forward to explain the adaptive significance of mobbing (Curio 1978). The 'move-on' hypothesis (Curio 1978) states that mobbing serves to move a predator out of the prey territory decreasing the overall threat of predation and lowering the predator's hunting efficiency. Previous studies have confirmed that predators are profoundly distressed by mobbing and avoid the areas where they have been harassed (Pavey & Smyth 1998). The 'move-on' hypothesis appears to be the most clearly linked to territoriality. During the breeding season birds that have established territories are stationary and are likely to have eggs or young preventing them from relocating away from predators (Shedd 1982). Territorial birds would be more likely to benefit from intensely mobbing a predator and 'moving it on' (Zimmermann & Curio 1988). By mobbing a predator in a neighbouring territory, an individual may even risk moving the predator into its own territory where it spends most of its time and where a mate and young may exist. While many of the benefits stated in alternative mobbing hypotheses could still be derived within a territory (e.g. 'perception advertisement', 'confusion effect' and 'cultural transmission of site') (Curio 1978), these benefits are also viable beyond territorial boundaries.

We suggest that if the 'move-on' hypothesis is false, birds would be less likely to observe strict territorial boundaries when mobbing, and may move beyond these boundaries to mob as in the case of other fitness-enhancing activities. It is unlikely that the strict observation of territorial boundaries for mobbing response is simply to avoid confrontation with neighbouring

conspecifics because in seven of eight cases where no neighbour was present (banded or unbanded), birds did not leave territories to mob.

Our results indicating that mobbing is strongly influenced by territory boundaries initially appear to conflict with observations that some species of birds mob outside the breeding season when territory boundaries are less established (Desrochers et al. 2002). The migratory nature of our focal species is probably central to explaining this apparent inconsistency. Shedd (1982) found that American robins, which migrate or assemble in mobile flocks during winter, do not mob outside the breeding season. He suggested that the breakdown of territory boundaries explains the lack of year-round mobbing. These mobile flocks create conditions where it is more individually advantageous to flee from a predator than to 'move it on' (Zimmermann & Curio 1988). The black-capped chickadee, a non-migratory species, lives on winter home ranges in relatively stable flocks (Shedd 1983). In contrast to the American robin, this species mobs year round. Shedd's (1982, 1983) results are congruent with Sherman's (1977) prediction that sedentary species should mob more intensely than mobile species. Our results suggest a similar pattern to those observed by Shedd (1982). By the end of the breeding season (late Jul.) we could no longer continue experiments because focal species did not respond aggressively to specific song or to the mobbing playback. Data collected as part of a broader landscape study in the same study area also indicate a decline in mobbing response by migrants at the end of Jul. (M.G. Betts, unpubl. data).

Unlike previous studies, we failed to detect the presence of a seasonal effect on mobbing behaviour (distance travelled to mob) over the course of our experiments. Anti-predator behaviour has been observed to increase with parental investment over the breeding season (Shedd 1982; Gehlbach & Leverett 1995; Halupka 1999). It is possible that the period over which our experiments were conducted was too short to discern such an effect. Our experiments did not encompass the early territory establishment phase when eggs, nestlings or fledglings were absent. Even if a seasonal effect had existed over this time span, it would need to have been very large and linear to be detected given our sample size (and resultant low power) and statistical approach.

Two unmeasured variables could have contributed to the variability that we observed in the distance moved within territories to engage in mobbing. First, as mobbing behaviour is more pronounced during breeding (Shedd 1982) and is considered to be part of nest defence (Shields 1984), birds may have travelled further to mobbing playbacks conducted in close proximity to nests. Indeed, Doran et al. (in press) found that female black-throated blue warblers were more likely to be attracted to mobbing playbacks if trials were conducted within 50 m of a nest. Second, the abundance of other prey species at a mobbing trial may have influenced the distance travelled by focal species to mob. High abundance of mobbers could have diluted the risk to focal birds (Curio & Regelman 1986), or may have increased the volume of mobbing calls. In both cases, distances travelled to mob would be greater if the abundance of other community members at a mob was high.

Territorial restriction of mobbing behaviour is relevant to research in conservation biology that uses mobbing playbacks to assess the influence of forest fragmentation on movement by forest birds (e.g. Desrochers & Hannon 1997; Bélisle & Desrochers 2002; St. Clair 2003). In these studies, mobbing playbacks have been used to determine whether forest birds will cross gaps in mature forest caused by agricultural fields, clearcuts and roads. In the context of our findings, it is possible that reluctance to move towards a mobbing playback through non-habitat gaps may not be a function of risk-aversion but rather that these areas lie beyond territory boundaries. This may not be a serious problem in studies conducted in fall or winter when territories are large or boundaries are non-existent. However, this potential bias exists in gap-crossing experiments conducted using migrants during the breeding season (e.g. St. Clair 2003).

Our finding that birds will move at least 25 m and as far as 175 m within their territories to a mob has implications for research that uses mobbing playbacks as a census technique (e.g. Gunn et al. 2000; Cornell Laboratory of Ornithology 2003). Mobbing playbacks may be an effective means to determine reproductive activity (Gunn et al. 2000) but we caution against the use of this technique to determine relative abundance or density (Hurd 1996). The strong territorial nature of the mobbing response means that only one bird of a species will respond unless the sample point is located on a territory boundary. While the probability of boundary sample points is greater at high bird densities, this effect will not be sufficient to discern subtle differences in density that may occur in different habitat types. Further, points placed closer than 200 m apart could potentially be within the same warbler territory and could therefore result in double sampling and lack of statistical independence. We found distance moved to mob was positively associated with territory diameter. Thus, for species such as woodpeckers and nuthatches that also respond to mobbing playbacks (Hurd 1996; Gunn et al. 2000; M.G. Betts, unpubl. data) but which have larger territories (Bowman 2003), it is possible that distances between points of greater than 200 m will be required to avoid double sampling. However, it is likely that the hearing capability of a species puts an upper limit on this effect. Some evidence exists that birds have hearing that is similar or slightly poorer than that of humans; humans can hear fainter sounds than most birds at most frequencies (Dooling 1982). Thus, the bias in sampling large territory birds may not be that great. The mean distance at which a human could hear the mobbing tape was 125 ± 5 m with a range of 100–150 m ($n = 23$). Further, only six of 23 birds with territories > 100 m in diameter moved further than 100 m within their territory to the mobbing playback.

We found that mobbing by two species of warbler is highly constrained by territory boundaries during the breeding season. This territorial constraint to mobbing is congruent with arguments that mobbing is primarily a selfish behaviour, at least with respect to conspecifics. Our results also provide support for the 'move-on' hypothesis. This research has implications for research in conservation biology that uses mobbing playback as a sampling technique. Researchers should take care to avoid pitfalls in experimental design that could

result from ignorance of the distances moved by species of interest and factors governing their movement.

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