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## Territorial Movements of Black-throated Blue Warblers in a Landscape Fragmented by Forestry

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**ABSTRACT.**—Many forest bird species show inhibition to entering open areas, including crossing habitat gaps. We examined the responses of Black-throated Blue Warblers (*Dendroica caerulescens*) to conspecific song playback within forest, at clearcut-forest ecotones, and across logging roads to assess movements of this Neotropical migrant into open areas. Males responded readily to song playbacks in all areas, and moved significantly farther into clearcuts than they did within intact forest ( $40.4 \pm 2.9$  m and  $17.1 \pm 1.2$  m, respectively). Their singing, aggressive trilling, and alarm-calling rates were highest in response to playback from clearcuts, intermediate during road-crossings, and lowest within forest. Males moved farthest into the oldest regenerating clearcuts (>15 years old), indicating that vegetation structure also influences their movement into open areas. Second-year males were more responsive than older males, moving farther to reach speakers in all areas, and showing a nonsignificant trend of moving farther into clearcuts. We found that extensive movements into open areas occur in response to simulated territorial intrusion, indicating that small-scale habitat fragmentation by forestry may not disrupt territorial movements of that species.

Understanding the abilities of animals to move among habitat types is critical to understanding dispersal and habitat selection, particularly in areas where habitat is not contiguous (Fahrig and Merriam 1994, Wiens 1996). Some studies of forest birds report inhibition of individuals moving into open areas (Sieving et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, Grubb and Doherty 1999, St. Clair et al. 1999). Clearly, forest songbirds are physically capable of moving into unforested habitats (e.g. Kilgo et al. 1999); therefore, movement inhibition is likely to be behaviorally based (Lynch and Whigham 1984).

Most interest in behavioral barriers to movement focuses on its potential to disrupt dispersal (e.g. Villard and Taylor 1994). It is also important to understand how a bird moves in fragmented habitat within the breeding season because it could affect habitat selection, fledgling foraging patterns, and prospecting for future breeding sites (Rail et al. 1997, Reed et al. 1999). Those effects become important to population persistence as forests become increasingly

fragmented, and might be key to the observed declines of some Neotropical migrant species (Askins et al. 1990, Lynch and Whigham 1984). We are particularly interested in understanding the effects of industrial forestry practices on bird populations because they create a habitat mosaic (Hagan and Boone 1997). Considering the territorial requirements of breeding forest birds (Robbins et al. 1989, Wenny et al. 1993), including the potential for increased inhibition of movement during the breeding season (Bentley and Catterall 1997, St. Clair et al. 1998), it is of interest to determine whether forest birds incorporate clearcuts and logging roads into their territories.

Consequently, we evaluated the responses of Black-throated Blue Warblers (*Dendroica caerulescens*) to habitat discontinuities in an industrial forest. The Black-throated Blue Warbler is a Neotropical migrant that is considered a forest-interior, area-sensitive breeder (Robbins et al. 1989, Freemark and Collins 1992, Holmes 1994), although studies of that species in managed forests find high densities in forest fragments (Hagan et al. 1996) and clustering near clearcut edges (King et al. 1997). We also evaluated the effects of male age and age of clearcut on movement into open areas.

**Methods.**—Data were collected in an industrial forest in western Maine ( $45^{\circ}24'N$ ,  $70^{\circ}32'W$ ). The 20,000 ha study area is a mosaic of different overstory species in various stages of regrowth, containing clearcuts ranging from 0.45–16.7 ha ( $\bar{x} = 6.70 \pm 0.96$  ha; all means are expressed as  $\bar{x} \pm SE$ ). Overstory is dominated by maple (*Acer saccharum*, *A. rubrum*), American beech (*Fagus grandifolia*), birch (*Betula papyrifera*, *B. lutea*), balsam fir (*Abies balsamea*), and spruce (*Picea rubens*, *P. mariana*). Understory vegetation is dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), mountain maple (*A. spicatum*), brambles (*Rubus* spp.), and seedlings and saplings of the dominant tree species.

Following other studies, we used conspecific playback to evaluate movement (Sieving et al. 1996, Rail et al. 1997). We did not use mobbing call playback because preliminary trials indicated a low response of this species to that stimulus (R. J. Harris and J. M. Reed unpubl. data). Fifty-seven conspecific song playback trials were performed in clearcuts adjacent to mature forest. Clearcuts ranged in age from <1 to >15 years old. As a control, 68 trials were performed within continuous mature forest, using the same

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TABLE 1. The numbers and percentages of birds that crossed roads, entered clearcuts, or approached the speaker in the intact forest controls in response to playback.

	Yes	No	Total
Roads	20 (80%)	5 (20%)	25
Clearcuts	38 (67%)	19 (33%)	57
Control	42 (62%)	26 (38%)	68
Total	100 (67%)	50 (33%)	150

protocol as in clearcuts. Control trials were performed at a range of 50–300 m from a forest edge. An additional 25 trials were done to attract males across logging roads ranging in width from 10–30 m,  $\bar{x} = 22.7 \pm 1.0$ . The speaker was placed at a range of 15–70 m ( $\bar{x} = 32.0 \pm 11.13$ ) from the ecotone in clearcuts adjacent to forest where a male was located, and controls were run 10–50 m ( $\bar{x} = 28.5 \pm 9.19$ ) from a male within forest. Because mean distances between the speaker and target male differed slightly between clearcuts and controls, distances moved were analyzed both as absolute distances and as proportions of the distances at which the speakers were placed.

Trials were conducted in June of 1998 and 1999, each within a three-week period, to control for seasonal variability in response. Playbacks were performed between 0500–1200 EST, during fair, calm weather. The focal male was located aurally or visually, and for clearcut and road trials the playback started when he was within 10 m of the forest edge. A continuous loop tape of Black-throated Blue Warbler song was played on a single-speaker portable tape player at a volume similar to that of live birds. A male decoy was placed in close proximity to the speaker to further simulate an intruder. For each trial, the male's initial distance from the speaker was estimated, and playback was employed for at least 9 min, and was continued if activity around the speaker was especially high (maximum time = 15 min). Each individual's proximity to the speaker and distance into a clearcut were estimated each time his position changed. From that, the maximum distance a male moved from the forest edge was determined in clearcut trials, analogous to the maximum distance a male moved from his original location in interior forest controls. Response latency (the time it took for a bird to approach the speaker) and territorial and aggressive activity (attacking, posturing, singing, alarm call, and aggressive trill rate) were recorded. When possible, birds were aged by plumage characteristics (Graves 1997), and pair status was determined by observation of a female nearby or by previous determination of pairing from an ongoing study of reproductive success (cf. Vickery et al. 1992, R. Harris unpubl. data).

**Results.**—Males responded with similar frequencies to conspecific playback in clearcuts, across

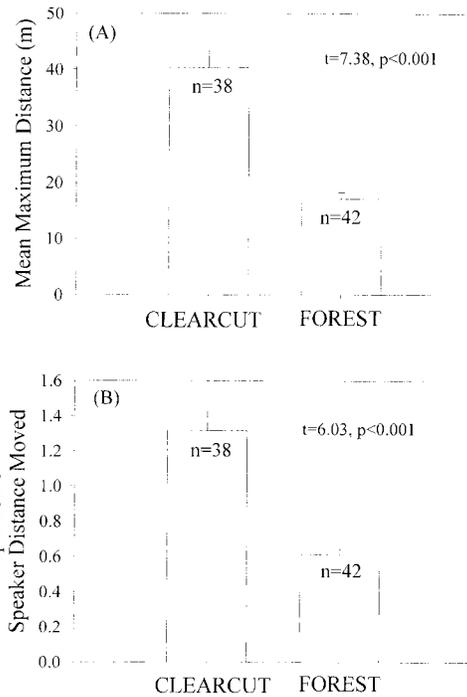


FIG. 1. The mean maximum distance Black-throated Blue Warbler males moved into clearcuts or within forest controls, (A) as an actual distance, for birds that responded to playback, (B) as a proportion of the distance at which the speaker was placed (i.e. bird moved to speaker = 1.0).

roads, and in interior forest controls ( $\chi^2 = 0.665$ ,  $df = 2$ ,  $P = 0.23$ , Table 1). Considering only the birds that responded to playback, the mean maximum distance moved from a clearcut edge was greater than the distance moved towards the speaker in intact forest (clearcut  $\bar{x} = 40.4 \pm 2.9$ , forest  $\bar{x} = 17.1 \pm 1.2$ ,  $t = 7.38$ ,  $df = 78$ ,  $P < 0.001$ , Fig. 1A). Regardless of clearcut age, responding individuals moved farther into clearcuts in which the speaker was placed at a greater distance from the forest edge (ANOVA,  $F = 3.02$ ,  $df = 2$  and 54,  $P = 0.02$ ). Thus, distance moved also was analyzed as a proportion of the distance at which the speaker was placed (hereafter referred to as proportional distance). Proportional distance was significantly greater in clearcuts than it was within forest controls, with birds moving an average distance that was beyond that of the speaker (clearcut  $\bar{x} = 1.13 \pm 0.11$ , forest  $\bar{x} = 0.61 \pm 0.03$ ,  $t = 6.03$ ,  $df = 78$ ,  $P < 0.001$ , Fig. 1B).

There was no effect of clearcut age or playback distance on a bird's latency, the time lapsed between initiation of playback and approach (ANOVA,  $F = 1.26$ ,  $df = 2$  and 54,  $P > 0.29$ ). Also, the minimum distance at which individuals approached the speaker (proximity) was not significantly different between clear-

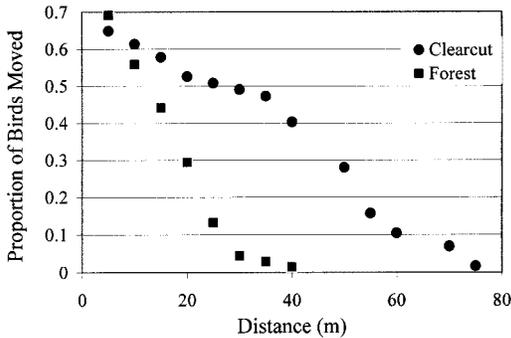


FIG. 2. The proportion of Black-throated Blue Warblers moving various distances into clearcuts (circles;  $n = 57$ ), and within forests (squares;  $n = 68$ ). Functions are cumulative in that a bird moving the farthest distance was considered to have moved all shorter distances as well. The clearcut function was best fit by a third-order polynomial ( $r = 0.93$ ). The within forest function was best fit by a second-order polynomial ( $r = 0.99$ ).

cut trials and forest controls (clearcut  $\bar{x} = 10.5 \pm 1.6$ , forest  $\bar{x} = 11.6 \pm 1.2$ ,  $t = 0.54$ ,  $df = 78$ ,  $P = 0.59$ ).

The proportion of birds moving different distances into a clearcut decreased gradually as distance increased, following a sigmoidal function ( $r = 0.93$ ). The same variable decreased exponentially for birds moving towards the speaker within intact forest ( $r = 0.99$ , Fig. 2).

Three individuals (out of 38) crossed clearcuts, landing in forest on the opposite side, even though the speaker was near the middle of the clearcut (maximum clearcut width crossed = 70 m). The amount of time an individual spent in a clearcut was correlated with the maximum distance he moved ( $r = 0.15$ ,  $df = 37$ ,  $P = 0.01$ ). The responding individuals did not always fly past distant speakers, but often perched nearby and spent a considerable amount of time in the clearcut ( $\bar{x} = 7.9 \pm 1.2$  min, range: 1–35 min). Almost half of the responding birds perched in clearcuts (17/38, 45%). Often, those individuals perched in close proximity to the decoy, displaying a silent aggressive pose (Holmes 1994). Responses in clearcuts were frequently very aggressive, with one bird landing on the model and repeatedly pecking its head. Mean rates of singing, alarm calling, and aggressive trilling were greatest in clearcut trials, as compared to intact forest, and were intermediate in road-crossing trials (ANOVA,  $df = 2$  and 147 or 146, range  $P = 0.003$ – $0.06$ , Table 2).

The mean rate of road-crossing was  $0.37 \pm 0.07$  times per minute ( $n = 20$ , range 0–1.78). Males frequently crossed back and forth in rapid succession, apparently agitated by the presence of the simulated intruder on the opposite side of the road. Frequently, neighboring birds also responded to playbacks (par-

TABLE 2. Mean singing, alarm calling, and aggressive trill rates per minute by males during clearcut, road, and interior forest control playback trials.  $F$  and  $P$  values reported from a single factor ANOVA.

	<i>n</i>	Mean	SD	<i>F</i>	<i>P</i>
<b>Singing</b>					
Clearcut	57	4.09	2.57	3.058	0.003
Road	25	3.53	2.58		
Control	68	2.77	1.42		
<b>Calling</b>					
Clearcut	57	1.28	3.73	3.685	0.03
Road	25	0.64	1.45		
Control	68	0.12	0.23		
<b>Trilling</b>					
Clearcut	57	1.03	1.02	2.892	0.06
Road	25	0.11	0.33		
Control	68	0.07	0.26		

ticularly in road-crossing trials), resulting in territorial interactions between two or more territorial birds.

Birds moved the farthest into the oldest clearcuts (>15 years old) (Fig. 3A). That difference was significant when clearcuts below 15 years old were compared to those in the oldest clearcuts ( $t = 1.95$ ,  $df = 14$ ,  $P = 0.04$ ). In fact, the mean distance birds moved into the oldest regenerating clearcuts exceeded the mean distance at which the speaker was placed (Fig. 3A). Also, birds moved farther into all of the clearcut age classes than they moved within intact forest. The effect of clearcut age was not detected when clearcut ages were more finely subdivided (i.e. 5 year age classes, ANOVA,  $F = 1.74$ ,  $df = 4$  and 52,  $P = 0.16$ ). Although birds tended to approach the speaker more closely as clearcut age increased, that pattern was not significant (ANOVA,  $F = 0.404$ ,  $df = 4$  and 52,  $P = 0.80$ , Fig. 3B), and was similar to that in intact forest. Neither variation in speaker distance nor clearcut age had a significant effect on whether a bird entered a clearcut or not (logistic regression likelihood-ratio = 0.15,  $df = 1$ ,  $P > 0.35$ ).

Age was determined as second-year (SY) or after-second-year (ASY) for 107/125 males. Male age did not significantly determine whether males would be more likely to respond by approaching the speaker in either habitat type ( $\chi^2 = 3.16$ ,  $df = 3$ ,  $P = 0.37$ ). Age was not significantly related to the mean maximum distance moved into clearcuts after the effects of clearcut age and playback distance were removed from the analysis (ANOVA,  $F = 1.16$ ,  $df = 4$  and 11,  $P > 0.38$ ). When the proportional distances males moved were compared using a  $t$ -test, SY birds moved farther than ASY birds (SY  $\bar{x} = 1.10 \pm 0.18$ , ASY  $\bar{x} = 0.69 \pm 0.31$ ,  $t = 1.58$ ,  $df = 38$ ,  $P = 0.06$ , Fig. 4A), with a similar pattern when mean maximum distances were compared (SY  $\bar{x} = 32.6 \pm 4.7$ , ASY  $\bar{x} = 22.0 \pm 5.8$ ,  $t = 1.42$ ,  $df = 38$ ,  $P = 0.08$ , Fig. 4B). When

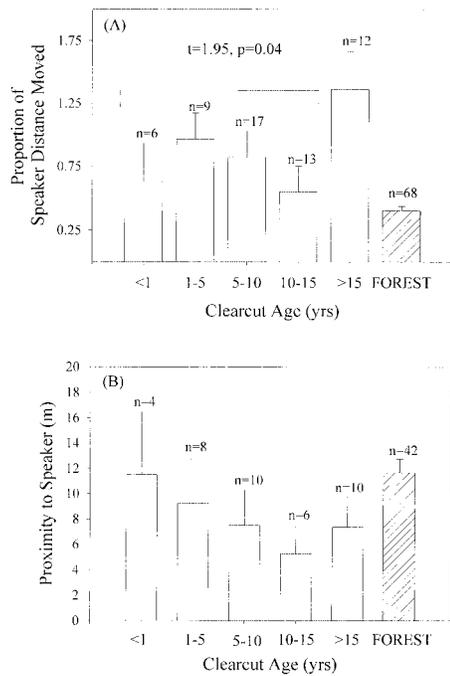


FIG. 3. (A) The mean maximum distance Black-throated Blue Warblers moved into clearcuts as a proportion of the speaker distance as a function of clearcut age. Movement within intact forest is included as control. All birds were included in that analysis, even if they did not move towards the speaker. The *t*-test compares movement into clearcuts  $\leq 15$  years old to older clearcuts. (B) The mean minimum distance at which birds approached the speaker as a function of clearcut age. Only birds that moved towards the speaker were included in this analysis.

movements in both the clearcut and forest control trials were analyzed, the mean maximum distances males moved (as either proportions or actual distances) were significantly greater for SY males (shown as actual distances moved for all birds: SY  $\bar{x} = 31.7 \pm 3.2$  m, ASY  $\bar{x} = 21.7 \pm 2.2$  m,  $t = 2.60$ ,  $df = 68$ ,  $P = 0.006$ , Fig. 4C).

There were 36 individuals whose pair status was known (R. J. Harris unpubl. data). Unpaired males tended to enter clearcuts at a higher frequency than did paired males (87%, 13/15 vs. 52% 11/21), but the relationship was not statistically significant ( $\chi^2 = 2.57$ ,  $df = 1$ ,  $P = 0.12$ ).

*Discussion.*—Black-throated Blue Warblers moved readily into open habitat, although distances were limited. They moved an average of about 40 m into clearcuts, and also readily crossed roads, which were gaps of 10–30 m. Those distances are similar to those observed for other Neotropical migrants in gap-crossing studies (30–50 m; Desrochers and Hannon 1997, Rail et al. 1997).

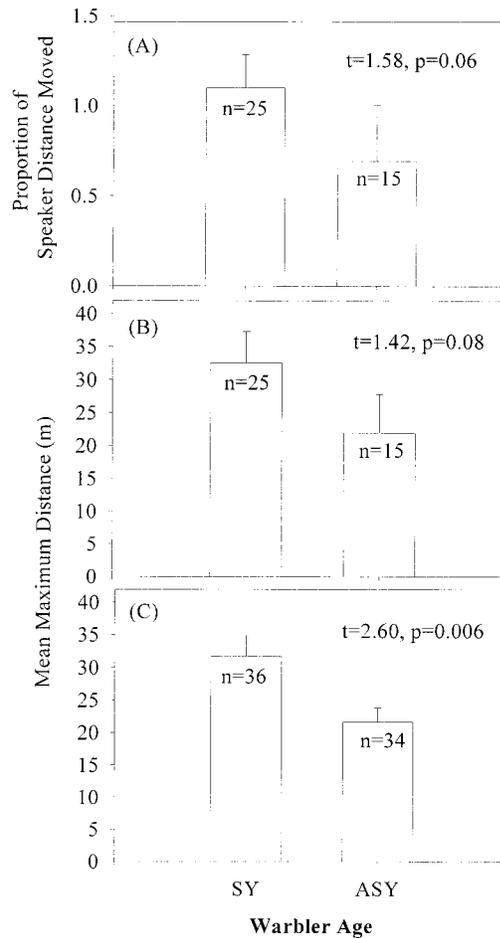


FIG. 4. The mean maximum distance Black-throated Blue Warblers moved into clearcuts, (A) as a proportion of the speaker distance, (B) as an actual distance in clearcuts, and (C) as an actual distance in both habitats, depending on age of the birds.

Black-throated Blue Warbler males moved farther into clearcuts than within forest in response to conspecific song playback. There are several nonexclusive hypotheses that might explain that observation. (1) Sound attenuation is greater in dense forest than in open areas (Schieck 1997). However, birds responded to playback in both areas with similar frequencies. (2) The decoy might have been more visible in clearcuts than in forests, possibly providing a greater stimulus for the responding birds. The increased level of aggression by males in clearcuts supports that hypothesis, but it does not explain the greater distance moved into clearcuts compared to within forests unless long-distance visual contact affected distance moved. (3) Reduced perch availability could have caused birds to move farther into

clearcuts (cf. McClanahan and Wolfe 1993, Machtans et al. 1996, Sieving et al. 1996). Although it was not statistically significant, there was a trend for males to approach the speaker more closely in older clearcuts, where perches were more common. (4) Birds unaccustomed to defending a territory bordering a clearcut might exhibit an elevated response (Falls 1981, Stoddard 1996). Consistent with that explanation, we found increased aggressive behaviors (e.g. alarm calling, trilling, silent posing) by birds entering clearcuts compared to within forests. Males also might have moved far into clearcuts to investigate the playback if they assumed the intruder was coming from the opposite side of the clearcut. A combination of the above hypotheses might explain the elevated responses to conspecific song playback in open areas compared to those within forests.

In studies of forest birds, there is evidence that movement is correlated with vegetation cover (Sieving et al. 1996), with individuals moving most readily into those areas where the contrast between habitat types is least severe (Stamps et al. 1987). When forest songbirds have been recorded moving across clearcuts, clumped regenerating vegetation appears to facilitate their movement (Machtans et al. 1996). Although we found greater movement by Black-throated Blue Warblers into clearcuts than within forest, they moved farthest into the oldest (>15 years old) clearcuts. During forest regrowth after clear-cutting, habitat structure increases with age; that vegetation may provide enough cover to encourage unrestricted movement of forest birds. If clearcut habitat can provide some cover adjacent to mature forest, it appears that Black-throated Blue Warblers will incorporate that habitat into their territories (King et al. 1997, R. J. Harris unpubl. data).

Young males (SY) moved farther than did older birds in response to playback regardless of the habitat in which they lived. This pattern may be due to the relatively low pairing rate of young males in our study area (R. J. Harris unpubl. data), which might make them more responsive to playback (Best 1981). We found that the likelihood of responding to playback was unrelated to age, but unpaired males responded more frequently to playback in clearcuts than did paired males, although that trend was not statistically significant. These results could have been an artifact of mistakenly including nonterritorial birds in the analysis. Those birds tend to be younger and are unpaired (e.g. Smith and Arcese 1989), might be differentially distributed in edge habitat, and might have responded more readily to playback (Best 1981).

The industrial forest is a dynamic habitat mosaic, with changes in forest type, age, structure, and juxtaposition of stands over time. That variegated landscape might affect movement of individuals among a wide range of habitats of varying quality, either increasing or decreasing it (Matthysen et al. 1995, Red-

path 1995, Wiens 1995, Sieving et al. 1996). Increased movement associated with habitat discontinuities can increase territory size, thus reducing population density where forest habitat is fragmented (Grubb and Doherty 1999, Trzcinski et al. 1999). We observed Black-throated Blue Warblers making territorial movements that crossed small habitat discontinuities such as roads and encompassed patches of open habitat (see also King et al. 1997), so area requirements for populations of that species may increase in industrial forests. We also found a limit to those movements, which could affect habitat selection of dispersing birds or the extent of prospecting. These findings are important to understanding the relatively subtle influences habitat fragmentation can have on populations, particularly on the behavior of individuals.

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