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TERRITORIAL RESPONSES OF BOREAL FOREST BIRDS TO HABITAT GAPS[1]

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Abstract. We used playback trials to determine whether birds will cross treeless gaps to respond to simulated territorial intruders. We evaluated the effect of gap width on responses by five forest bird species. We found that for forest specialists such as the Swainson's Thrush (*Catharus ustulatus*), Golden-crowned Kinglet (*Regulus satrapa*), and the Black-throated Green Warbler (*Dendroica virens*), the probability of crossing gaps decreased sharply with gaps 25–40 m wide. By contrast, control trials showed no significant decrease in their probability of response up to 100 m through continuous stands. Habitat generalists such as the White-throated Sparrow (*Zonotrichia albicollis*) and the Dark-eyed Junco (*Junco hyemalis*) were more prone to cross treeless gaps than forest specialists. Playback studies provide a new tool for understanding birds' responses to microscale habitat discontinuities.

Key words: boreal, breeding birds, forests, forest gaps, logging, Québec, territorial response.

In forest-dominated landscapes, forestry roads, water bodies, and small scale clearcuts are often abundant. Should we consider forests featuring these relatively narrow gaps as continuous breeding habitat for birds? Small-scale forest fragmentation may not alter population processes like dispersal and recolonization by birds, but few studies address its impact on avian activities such as territorial defense. Songbirds may exhibit variation in their behavioral response to habitat gaps depending upon gap width and species involved. For example, it is likely that < 5-m wide gaps in the

canopy are not perceived as habitat discontinuities, even by forest-interior species. Bird territories may therefore extend on both sides of the gap (Fig. 1a). However, the inclusion of more open habitat in the territory (Fig. 1b) may entail costs like increased predation risk (Lima and Dill 1990) and travelling energy expenditure when feeding young (Davies and Houston 1984), or simply a loss of optimal habitat for forest species. At this point, birds may choose to establish their territory on only one side of the gap (Fig. 1c). Finally, at the other end of the continuum, when gap width exceeds territory diameter, no territory should be expected to include both forested sides of the gap (Fig. 1d).

One way to measure how territorial birds perceive forest fragmentation at the microscale level is to describe their willingness to cross narrow, treeless gaps. Here we present a behavioral approach to the study of avian responses to forest gaps. We studied the effect of the width of treeless gaps on the propensity of five songbird species to respond to simulated territorial intruders. We tested two hypotheses, namely (1) that < 100-m wide treeless gaps influence territorial defense and (2) that forest specialist songbirds are more affected by such gaps than habitat generalists.

METHODS

STUDY AREA AND SITE SELECTION

Field work was conducted in the summers of 1993–1994 at the Forêt Montmorency (Laval University Experimental Station), 60 km north of Québec city, Canada. In this landscape, mature forest is dominated by balsam fir (*Abies balsamea*) accompanied by black spruce (*Picea mariana*), white birch (*Betula papyrifera*), and white spruce (*Picea glauca*) (Beauchesne 1991, Darveau et al. 1995).

We studied well-delimited treeless gaps of 3–100 m wide inside mature forests (with trees > 10 m in height). Vegetation height within gaps was < 1.5 m. Gaps were grouped in five categories: (1) cross-country skiing or pedestrian trails (3–15 m wide), (2) unpaved roads (4–35 m wide), (3) clearcuts (12–100 m wide), (4) unpaved roads with clearcuts on one or both sides (mostly between 18–65 m wide), and (5) powerline rights-of-way (mostly between 38–55, 70–80. or 84–100 m wide).

Because features of the patch on the opposite side of the gap (such as habitat structure or resource levels) may influence interpatch fluxes (Wiens et al. 1985), we avoided sites with non-uniform habitat on each side. We also avoided sites featuring major obstacles to sound propagation such as noisy streams.

SPECIES STUDIED

We selected passerine species that were territorial, highly vocal, and abundant in the study area. White-throated Sparrows (*Zonotrichia albicollis*) and Dark-eyed Juncos (*Junco hyemalis*) were selected as habitat generalists, that is, species that use both open and wooded habitat, and were studied in 1993. Swainson's Thrushes (*Catharus ustulatus*), Golden-crowned Kinglets (*Regulus satrapa*), and Black-throated Green Warblers (*Dendroica virens*) were selected as forest spe-
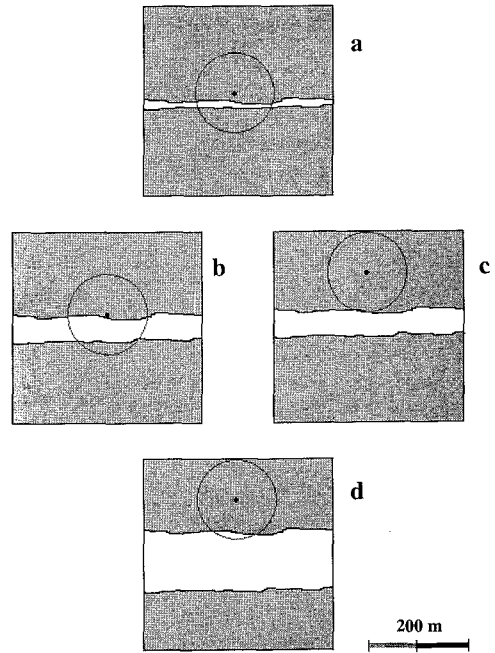

FIGURE 1. Bird territory (2-ha circle) placement along a forest gap (white area). In (a) the birds may perceive two forests (shaded areas) separated by a narrow gap (5 m wide) as if it was continuous habitat, and establish their territories over the gap. With wider gaps (50 m wide; b, c), preference for woodland may become apparent for some species (c). On the other hand, regardless of habitat preference, a bird cannot include two forest 110 m apart in its territory if this distance exceeds territory diameter (d).

cialist birds (Darveau et al. 1995) and were studied in both 1993 and 1994.

PLAYBACK TRIALS

Playbacks were conducted from the end of May to mid-July each year. We avoided windy and rainy days. Ninety-eight percent of the 537 playback trials were conducted between 05:00 and 11:00, when bird responses are strongest (Melemis and Falls 1982). The remaining 2% were evening calls of thrushes, which are active at that time of day.

Our protocol was adapted from techniques used to map territory boundaries with playback (Falls 1981). Walking along habitat discontinuities, the observer located precisely (visually or by ear) territorial males singing near (< 50 m) forest edges. We called each singing bird with a cassette player and a 2-W amplifier speaker during 5 min, from the edge on the opposite side of the treeless gap. Conspecific songs were played at intervals of about 5–8 sec to simulate birds singing rapidly (Falls 1981). The focal bird was easily followed acoustically and visually, and if it crossed the treeless gap, we considered it a territorial response against the artificial intruder (Falls 1981). Playbacks could be heard by the observers at a distance of 100

TABLE 1. Number of trials for each gap type in the Forêt Montmorency area, by bird species. SWTH = Swainson's Thrush, GCKI = Golden-crowned Kinglet, BTGW = Black-throated Green Warbler, WTSP = White-Throated Sparrow, DEJU = Dark-eyed Junco.

	SWTH	GCKI	BTGW	WTSP	DEJU	Total	%
Powerline	47	36	21	57	25	186	34.6
Road	28	47	17	26	30	148	27.6
Ski trail	11	11	8	7	3	40	7.4
Clearcut	7	17	7	9	8	48	8.9
Road + clearcut	13	23	17	18	15	86	16.0
Control	11	9	9	—	—	29	5.4
Total	117	143	79	117	81	537	100.0

m through mature forest. We consider 5-min playback trials sufficiently long, given that 60% of bird crossings occurred in the first 1.5 min, and that after 3 min this proportion reached 86%. Gap width was measured from one boundary to the other with a graduated Fiberglas tape. These "gap trials" were performed both years (n = 412 in 1993, n = 96 in 1994).

The negative relationship between birds' response and gap width, rather than measuring the "gap effect," could be attributed to the limited size of territories or to a loss of motivation with increasing distance of playback. To control these factors, we also called birds towards the forest interior instead of across a forest gap. For these control trials, two observers equipped with walkie-talkies were necessary to insure that the individual responding to playbacks was the same one that was originally identified as singing. After localizing a bird, one observer measured the distance from the initial position of the bird to the speaker and then started the playback, while the second one followed the focal bird through the forest to make sure of the identity of the responding individual. Birds were classed as responding when they came within 5 m of the speaker. These control trials were interspersed with gap trials throughout the season.

We measured response latency in all trials. A trial ended when birds responded or after 5 min of playback with no response. We identified each experimental site with a flag and marked its location on a 1:20,000 map. For each species, all sites were > 100 m apart (as determined in situ) to avoid testing individuals twice. However, 12 of our control trials were made with birds also used for gap trials.

DATA ANALYSIS

We used hierarchical logistic regression to model the effect of species, treeless gap width, and gap type on the probability of crossing gaps. In all analyses, covariates were entered first, followed by variables of interest. We used model comparisons to determine whether a variable had a significant (P < 0.05) effect (Christensen 1990). We also used a logistic regression analog of standard R^2, which can be calculated as:

$$R^2 = [\chi^2 \text{ (intercept)} - \chi^2 \text{ (model)}] \div \chi^2 \text{ (intercept)}$$

where χ^2s are approximations for likelihood ratios (Christensen 1990). Logistic R^2 values can be interpreted in a similar way as standard regression or Anova R^2. Treeless gap-width effects were studied in two

ways. We first considered width a metric variable, then we considered it a dichotomous variable, greater than or smaller than a threshold value, to address the possibility that gap-width response is not a monotonic relationship. For each species, we tested separately 19 threshold width values (5, 10, 15, . . . , 95 m) to identify gap widths to which birds responded most. Then, by comparing the R^2s of the threshold models with the R^2s of the metric variable model, we could determine which one yielded the best fit for a given species.

RESULTS

We conducted 412 trials across treeless gaps in 1993, 96 in 1994, and 29 control trials in 1994 (Table 1). All species were studied in all gap types and at varying gap widths. However, controls, which were time-consuming, were made only with the three forest specialists (Swainson's Thrush, Golden-crowned Kinglet, and Black-throated Green Warbler). They responded in 93% of all control trials, and in 90% of 21 control trials at 100 m. In comparison, gap trials at similar widths elicited a response in < 40% of cases (control vs. gap effect, after controlling for playback distance, $\chi^2_{1,120}$ = 36.5, P < 0.001; Fig. 2).

The three forest specialists had lower probabilities of response than the two habitat generalists (species group effect, after controlling for year and gap width, $\chi^2_{1,532}$ = 24.9, P < 0.001). However, the differences among species were not pronounced (Fig. 2). Based on models with dichotomic gap widths, responses changed at the greatest rate at 25 m, 40 m, and 35–40 m for thrushes, kinglets, and warblers, respectively. As for habitat generalists, a 65–70 m threshold was apparent for sparrows, and the response of juncos seemed to change most at 15 m. With the latter species, however, even exact width was a poor predictor of bird responses (R^2 = 0.05). For each species, the threshold width that best predicted bird responses explained about as much variability in birds' responses as width taken as a metric variable (thrushes: 25-m-threshold R^2 = 0.21, exact width R^2 = 0.20; kinglets: 40-m-threshold R^2 = 0.21, exact width R^2 = 0.22; warblers: 35–40-m-threshold R^2 = 0.13, exact width R^2 = 0.13; sparrows: 65–70-m-threshold R^2 = 0.28, exact width R^2 = 0.25; juncos: 15-m-threshold R^2 = 0.08, exact width R^2 = 0.05). Gap type had no effect on the probability of crossing of our species, either for tests of pooled or separate species in either year (P > 0.05).
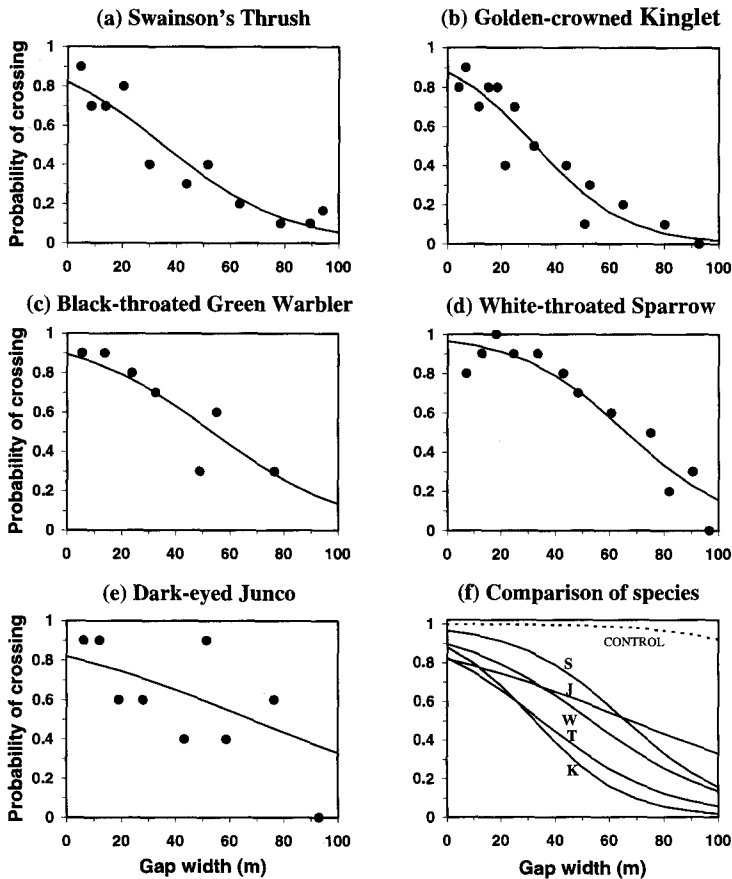
FIGURE 2.   Probability of birds' response according to gap width, Forêt Montmorency area, Québec. Curves were fitted using parameters calculated by the logistic regression procedure. Each dot represents the observed proportion of responses in 10 calling trials (a–e). In (f), comparison among species, and with the control curve representing the combined probability of response of the three forest specialists (warbler, thrush, and kinglet) in continuous mature stands.

A year effect on birds' responses was detected for thrushes only ($P = 0.02$).

DISCUSSION

Our results show that the probability of gap crossing by territorial forest specialists was strongly affected by relatively narrow gaps (< 40 m) in the canopy. These birds were not prone to cross a gap to resume territorial defense. Habitat generalists had response curves similar to, although statistically different from, those of forest specialist birds. In this study and concurrent studies in the same region, we found White-throated Sparrow and Dark-eyed Junco territories (Darveau et al. 1995) and nests (Darveau et al. 1997) in clearcuts, road sides, powerline right-of-ways, and nature trails. Thus, we hypothesized that territorial defense in these species would be less affected by canopy gaps, and our results seem to confirm that. However, because no control trials were done with those species, we cannot determine whether their apparent decrease in response

with larger gaps is due to a real gap effect or simply to limited territory size. Further investigations on territorial behavior of habitat generalists would be interesting from a general perspective, but we chose to concentrate our efforts on the forest specialists, which are well known to be negatively affected by forest fragmentation.

Threshold analyses confirmed that treating gap width as a dichotomous variable was as informative as treating it as a continuous metric. Furthermore, this approach enabled us to estimate gap widths where birds' responses changed most rapidly. In this study, the critical gap widths of the three forest specialists were similar (between 25–40 m). Surprisingly, White-throated Sparrows were strongly influenced by gaps, although at larger widths (65–70 m). Perhaps this response expresses their smaller territory size (Martin 1960, Erskine 1977) rather than a gap effect. Responses of Dark-eyed Juncos did not seem to vary abruptly at any gap width, suggesting that gaps did not

have a strong influence on territorial response in this species. However, in juncos and, to some extent, in Black-throated Green Warblers, the relatively low percentage of explained variance might be linked to the lower sampling effort ($n = 79$–81) compared to the three other species ($n = 117$–143).

Previous studies on forest-interior species reported decreased densities near treeless corridors 8–23 m wide (Rich et al. 1994), minimal use and edge avoidance of large gaps (Ferris 1979, Chasko and Gates 1982, Kroodsma 1984), and the fact that distinct edges function as a natural territorial boundary for many bird species (Chasko and Gates 1982, Tuomenpuro 1989). However, to our knowledge, our study is the first to address empirically the effect of habitat gap width on territorial bird behavior. Even though playbacks may sometimes attract birds outside their usual territories (Falls 1981), our method allowed us to quantify the relationship between the decision of crossing and gap width.

Our study was not designed to measure typical fragmentation effects such as impeded bird dispersal and recolonization (Wilcox and Murphy 1985, Desrochers and Hannon 1997), increased brood parasitism (the Brown-headed Cowbird, *Molothrus ater*, is absent from our study area), or nest predation. Nevertheless, our behavioral approach could be used in fragmentation studies to determine species-specific definitions of a discrete forest fragment (Rich et al. 1994). Data on the effect of gaps also can help build and improve models that assess the effects of changes in the landscape on birds.

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