

# Gap Crossing Decisions by Forest Songbirds during the Post-Fledging Period

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**Abstract:** Gaps in forest cover, created by agriculture, forestry, and other anthropogenic activities, are assumed to impede the movements of many forest songbirds. Little is known, however, about the reluctance of different species of birds to cross habitat gaps. We studied this by inducing birds in the post-fledging period to cross gaps of varying widths and to choose between routes through woodland or across open areas by attracting them to a recording of mobbing calls by Chickadees (*Parus atricapillus*). In 278 experiments conducted in boreal forest and agricultural landscapes near Québec city, 157 birds or flocks of birds of five species were attracted. Overall, birds were twice as likely to travel through 50 m of woodland than through 50 m in the open to reach the recording. When given a choice of traveling through woodland or across a gap, the majority of respondents preferred woodland routes, even when they were three times longer than shortcuts in the open. However, species differed greatly in their response to gaps. Our results show that woodland links significantly facilitate movements of birds across fragmented landscapes.

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Decisiones de Cruce de Claros por Aves Paserinas de Bosques Durante el Periodo Post-Juvenil

**Resumen:** Es considerado que los claros en la cobertura forestal creados por la agricultura y otras actividades antropogénicas impiden los movimientos de muchas especies de aves paserinas. De cualquier manera, se conoce poco acerca de la renuencia de diferentes especies de aves a cruzar claros en los hábitats. Estudiamos esto, induciendo aves en el periodo post-juvenil a cruzar claros de diversas dimensiones y a escoger rutas a través de áreas boscosas o abiertas, mediante la atracción por llamadas grabadas de parvadas de *Parus atricapillus*. En 278 experimentos conducidos en paisajes de bosque boreal y agrícola, cercanos a la ciudad de Québec, 157 aves o parvadas de cinco especies fueron atraídas. En general, las aves fueron mayormente atraídas a viajar a través de 50 m de área boscosa que a través de 50 m de claro, para encontrar la grabación. Cuando se dió la opción de viajar a través de bosque o claro, la mayoría de las aves que respondieron prefirieron las áreas arboladas, aún cuando estos viajes fueron tres veces más largos que atajos por las áreas abiertas. Sin embargo, las especies respondieron de diferente manera a los claros. Nuestros resultados muestran que uniones de áreas boscosas facilitan significativamente los movimientos de aves a través de paisajes fragmentados.

## Introduction

Forest fragmentation by agriculture, forestry, or other anthropogenic activities has been suggested as a cause for

declines observed in many forest songbirds (Robinson et al. 1995). A critical component for the persistence of animal populations in fragmented landscapes is the ability of individuals to move across inhospitable habitats (Pattig & Merriam 1994). Although the importance of woodland strips as wildlife corridors has been controversial (Wegner & Merriam 1979; Noss 1987; Simberloff & Cox

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1987; Hobbs 1992; Mann & Plummer 1995), there is indirect evidence showing that birds can benefit from them. Most studies have inferred that birds used woodland strips in preference to crossing gaps based on patterns of occupancy of connected and isolated woodlots (review in Haas 1995; Machtans et al. 1996). Post-fledging movements of birds on the breeding range include part of the dispersal phase for juvenile birds. These movements may be important to population persistence because juveniles may be prospecting for territories at this time (Brewer & Harrison 1975; Morton 1992).

Haas (1995) showed that landscape connectivity facilitated breeding dispersal of songbirds. Machtans et al. (1996) reported higher movement of songbirds in a woodland corridor than across a clearcut using a combination of mistnetting and observation. We know of no studies, however, that have documented the trajectory of movement over the landscape or observed responses of birds when confronted with the choice of taking a direct route across an opening in the forest or a detour through the forest. Some species of forest birds may show a behavioral reluctance to cross large forest gaps (Bierregaard et al. 1992; Lens & Dhondt 1994), possibly due to increased predation risk (Hegner 1985; Lima & Dill 1990).

We present a new approach to studying avian movements in response to gaps in woodland. We asked (1) What is the effect of narrow (<160 m) gaps in the forest on movement by songbirds? and (2) Is there a threshold distance across gaps where birds will prefer to move through woodland as opposed to crossing in the open? Using playback experiments, we documented the behavioral response of individual songbirds to situations in which they had to travel either through straight paths in the open or detours along woodland edges. Although wildlife corridors are usually thought of as long and narrow strips of woodland inside an open area, we consider that nonlinear woodland edges serve a similar purpose when they link two points separated by an open area.

## Methods

### Study Areas

We carried out this study from 19 July to 8 August 1995 in a rural and a forested landscape in southern Québec, Canada. Landscape 1 was a 160 km<sup>2</sup> mosaic of boreal forest (dominated by *Abies balsamea*, *Picea mariana*, and *Betula papyrifera*) containing clearcuts ranging from 1 to 150 ha, at the Forêt Montmorency (47°20'N, 71°10'W). Landscape 2 was a 67 km<sup>2</sup> mosaic of deciduous forest (dominated by *Acer saccharum*, *Betula alleghaniensis*, and *Fagus grandifolia*) and open fields (pastures) in the lowlands of the St-Laurent river, near Québec city (46°45'N, 71°20'W).

### Playback Experiments

One basic problem with studies of animals moving in wildlife corridors is that observers usually do not know the destination of the individuals observed. To overcome this problem, we attracted individual songbirds to specific points. We used playbacks of mobbing calls by Black-capped Chickadees (*Parus atricapillus*) and Red-breasted Nuthatches (*Sitta canadensis*) to attract birds. Mobbing calls are often used by birds when they discover stationary predators like owls (Curio 1978). We cannot dismiss the possibility that the mobbing calls may cause birds to behave more cautiously than usual. Birds under immediate risk (e.g., nearby Merlin [*Falco columbarius*] in flight) usually stopped moving altogether and vocalized very little, in contrast to mobbing birds which were highly conspicuous and mobile, as in other studies (Curio & Regelman 1985; Ficken & Popp 1996). We interpret this difference as evidence that birds experience a lower level of risk in mobbing situations than in the presence of immediate risk. Besides eliciting directed movement, mobbing calls have the advantage of attracting several species of passerines (Hurd 1996) at any season (A. Desrochers, personal observation).

We started playback experiments as soon as juveniles were found outside family groups and stopped at the onset of migration, when species began to occur regularly outside their breeding habitat. Ninety-one percent of the 287 playback experiments were carried out from 0600–1200 hours, under conditions with no rain or strong winds. We made a single visit at 72% of the playback sites and 1 additional visit separated by >5 days at the other sites. We assumed the majority of birds were the subject of no more than one experiment, based on the fact that individuals of a variety of passerines begin to disperse at this time of year, particularly juveniles (review by Plissner & Gowaty 1996; Weise & Meyer 1979 for chickadees).

Birds within 10 m of woodland edges were located visually before playback experiments started. We did not include birds that were discovered as they were moving toward or present within 5 m of the speaker, to avoid bias. ~~During each playback experiment, we played~~ mobbing calls for 10 minutes with portable cassette players connected to 5-watt speaker units. Playbacks could be heard by the experimenters at >200 m from the speakers.

We used the playback method in two situations: across open gaps separating nearby woods (gap experiments; Fig. 1a) or in sites providing a nearby detour in the woodland as an alternative route (choice experiments; Fig. 1b). Open areas were in clearcuts (vegetation < 1.5 m), power lines, and dirt roads (forest study area) or open pastures of variable widths (rural study area).

In gap experiments (71 sites), birds had access to no woodland route within > 500 m, and thus had to fly

tracted simultaneously, each individual of this group was assigned 0.2 df. This method had the advantage of keeping information on different responses among group members, while providing more realistic confidence intervals.

**Results**

Playbacks of mobbing calls attracted 421 individuals or groups from 37 bird species. To reduce spurious effects caused by differences among species, we selected five species for which we obtained at least 10 gap or choice playback experiments. All analyses below are based on the selected species.

We carried out gap playback experiments on 205 individuals or conspecific flocks, across gaps separating woods by 7-160 m (controls 10-180 m). We found a strong relationship between distance of speaker and the probability of response of birds (Fig. 2;  $\chi^2 = 19.0$ ,  $df = 1,202$ ,  $p < 0.0001$ ). This relationship was not the sole result of the distance of the speaker; birds responded less when the intervening space was an open area than when it was forested ( $\chi^2 = 21.3$ ,  $df = 1,202$ ,  $p < 0.0001$ ). However, the effect of the intervening space was greater at wider gaps (distance by gap presence interaction:  $\chi^2 = 4.0$ ,  $df = 1,201$ ,  $p = 0.04$ ). Although the presence of gaps <30 m had little overall impact on bird movements, birds were three times less likely to cross 70-m gaps and about eight times less likely to cross 100-m gaps compared to similar distances in the forest.

The five species differed greatly in their propensity to respond to playbacks and cross gaps (species effects and associated interactions:  $\chi^2 = 41.4$ ,  $df = 12,189$ ,  $p < 0.0001$ ). Black-capped Chickadees, Red-breasted Nuthatches, and Red-eyed Vireos (*Vireo olivaceus*) strongly responded to playbacks under forest cover, but were reluctant to cross even narrow open areas. Golden-crowned Kinglets (*Regulus satrapa*) and Yellow-rumped Warblers (*Dendroica coronata*) were less responsive to playbacks, but their response was nevertheless diminished when they had to cross open areas.

Different types of open areas may be perceived differently by the same birds. With species pooled, the relationships between response rates and gap widths were not affected by whether open areas were fields or clearcuts ( $\chi^2 = 0.8$ ,  $df = 1,75$ ,  $p = 0.4$ ). However, our analysis with species pooled may have been confounded by the different frequency of each species in the two landscape types. The nuthatch was the only species common in both landscape types. Nuthatches, like the combined set of species, did not react differently to fields and clearcuts ( $\chi^2 = 1.1$ ,  $df = 1,17$ ,  $p = 0.3$ ).

We carried out choice playback experiments on 73 individuals or conspecific flocks. Gaps varied from 10-170 m across and detour lengths varied from 20-330 m. Detour-to-shortest distance ratios (Fig. 1) varied from 1.1-6.0 and were correlated ( $r_s = -0.38$ ) due to limited choice of sites. To avoid the possible confounding effect of scale (absolute distances) on birds' choices, we entered distance A (Fig. 1) before B/A ratios in choice analyses. Even though birds preferred traveling through woodland rather than across open areas, their prefer-

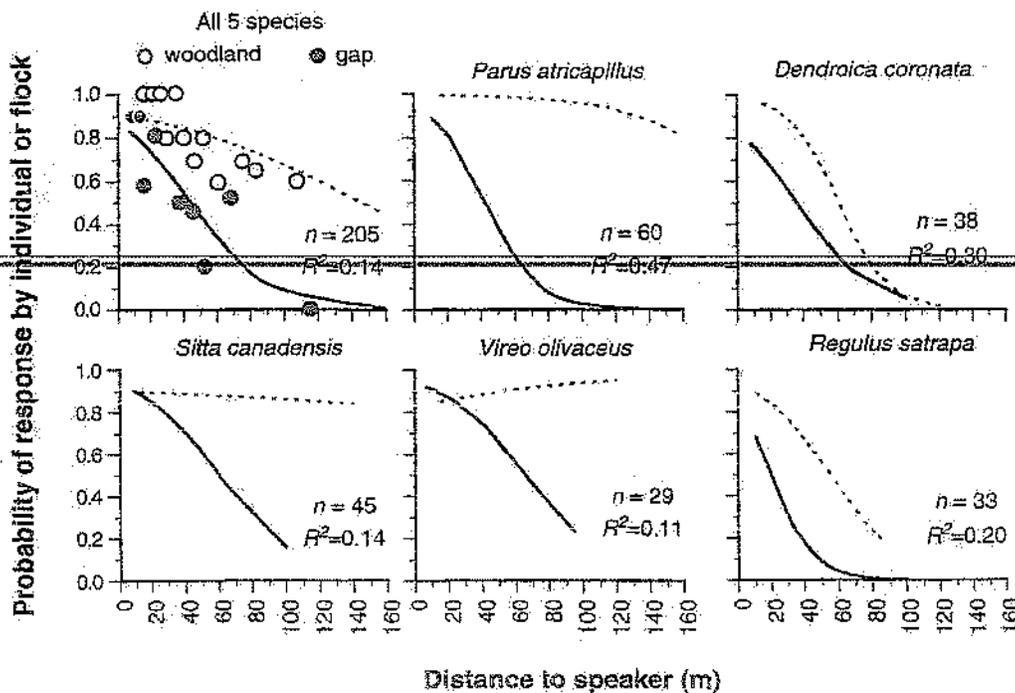


Figure 2. Probability that forest songbirds travel across gaps in the forest when approaching playbacks of chickadee mobbing calls. Solid lines refer to playbacks made across gaps and dotted lines refer to control playbacks made along forest edges. All lines were calculated by logistic analyses. All points represent 4-10 degrees of freedom.

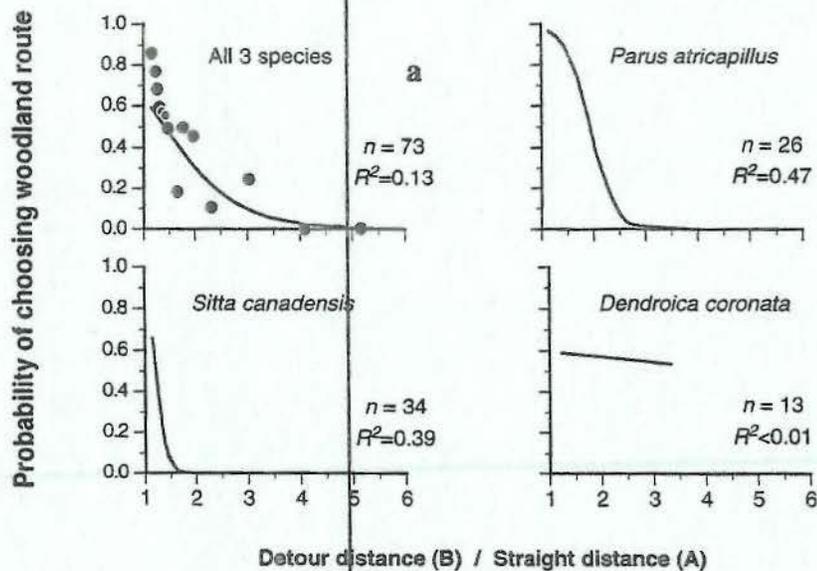


Figure 3. Probability of using woodland corridors instead of flying across gaps in the forest when approaching playbacks of chickadee mobbing calls. All lines were calculated by logistic analyses. Panel a shows data on choice playbacks (solid symbols) and other panels represent species for which we had sufficient data. All symbols are based on gap experiments with 4–10 individuals or flocks. Panel scales are identical to facilitate comparisons.

ence for woodland as a travel route decreased rapidly as the woodland route became longer relative to the open route (Fig. 3a;  $\chi^2 = 12.6$ ,  $df = 1,72$ ,  $p = 0.0004$ ).

Species differed by how much they preferred taking woodland routes instead of flying across open areas (Fig. 3; species effects and associated interactions:  $\chi^2 = 30.2$ ,  $df = 4,68$ ,  $p < 0.0001$ ). A majority of nuthatches did not use woodland routes even when this increased route length by as little as 20%. However, a majority of chickadees and Yellow-rumped Warblers preferred woodland even though this choice doubled or trebled their route length, respectively (Fig. 3). There were insufficient data for a detailed assessment of responses by kinglets and vireos.

## Discussion

Unlike previous studies, we found that birds did not just use movement corridors, but strongly preferred them to open areas during the post-fledging phase of dispersal. The presence of woodland links, even at the micro-scale, may therefore significantly facilitate songbird movements. On the basis of distance, we infer that Yellow-rumped Warblers and chickadees valued woodland routes roughly twice as much as alternative routes in the open. To our knowledge this is the first quantitative assessment of the decision rules used by birds while traveling through mosaic landscapes. Even though we did not conduct experiments in woodland corridors per se, we believe our findings support empirically one key component of the rationale in favor of wildlife corridors (i.e., that moving individuals will take significant detours to avoid open areas).

Why avoid open areas? Forest songbirds are extremely vagile, as demonstrated by their migrations, and it may

be argued that wildlife corridors are of little use to the large number of birds flying over vast areas of inhospitable land during migration. However, most insectivorous songbirds migrate at night and move through habitats in daytime (Alerstam 1990). Furthermore, there is now evidence of fitness costs to dispersing through fragmented forests relative to continuous ones (Matthysen & Currie 1996). Finally, songbirds are extremely vulnerable to raptors when they fly in the open. Woodland birds respond strongly to predation risk outside the cover of forests (e.g., Hegner 1985; Lima & Dill 1990; Todd & Cowie 1990; Suhonen 1993). Predation risk is difficult to measure but we assume that locally common avian predators like Sharp-shinned Hawks (*Accipiter striatus*) constitute a significant threat to birds moving through landscapes.

Although wildlife corridors may often reduce predation risk, they may also act as ecological traps by actually attracting predators (e.g., Soulé & Simberloff 1986). Because we did not conduct our experiments within narrow corridors, woodlands were unlikely to be ecological traps here. A further problem with woodland corridors is that they may be energetically costly if their layout forces birds to greatly elongate their movements through landscapes, even if they are not aimed for a specific, distant point. We contend, however, that the energetic cost of using detours through woodland are small in the post-fledging phase of dispersal compared with the cost of predator exposure because food is abundant at this time of the year.

## Species and Open Area Effects

Forest songbirds are assumed to benefit more from woodland corridors than species adapted to open areas. Although all the species we studied were strictly forest

species, we found strong differences in their response to the tradeoff between traveling through woodland versus crossing open areas. It is therefore difficult to make general statements on how much woodland corridors facilitate forest bird movements as a whole. Why are species like nuthatches less reluctant to fly through open areas than other species? One possible explanation is that species used to open, exposed microhabitats (like treetops in the case of nuthatches) are better equipped to deal with open-area threats like raptors than species seldom foraging on the periphery of cover. Playback experiments on a larger number of species will help answer this question.

We found no measurable difference in the way songbirds responded to clearcuts or open fields. The effects of forest fragmentation are thought to differ greatly between agricultural and forestry landscapes, owing in part to the fact that the latter are more dynamic than the former because of regeneration of woodland cover (Askins 1994). With respect to avian dispersal, clearcuts may be more permeable to movements than open fields because they often have remnant trees left uncut, which may act as "stepping stones." Our study did not assess the "stepping stone" effect because we avoided clearcuts with significant numbers of residual trees. This effect is currently under study.

## Conclusions

Although the scale of the playback experiments was restricted to small habitat patches, we were able to measure a strong response of birds to the connectedness of woodland habitat. We were able to document for the first time that birds in the post-fledging period do strongly prefer moving through woodland than in the open, when given the choice. However, this preference was not constant among species, and woodland corridors therefore facilitate movements of some species more than others. We realize that this set of experiments does not directly address the role of woodland corridors in maintaining songbird populations. However, we provided evidence that the lack of woodland connectivity, even at the micro-scale, has significant consequences on the ability of birds to travel in a woodland-open area mosaic. Maintaining connections among forest fragments to facilitate dispersal may be important in the persistence of populations.

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