



RESPONSE OF WINTERING BOREAL CHICKADEES (*POECILE HUDSONICA*) TO FOREST EDGES: DOES WEATHER MATTER?

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ABSTRACT.—Avian responses to forest edges have received much attention in recent years, particularly because of the potential effects of deforestation on the quality of remaining forest patches. However, individual birds' responses to forest edges are more often inferred than observed, and most studies of space use emphasize territory placement, with little or no detail on within-territory movements. Thus, our understanding of the effects of edges on movements of forest birds remains limited. We recorded movements of 85 winter flocks of the little-known Boreal Chickadee (*Poecile hudsonica*), in a 66-km² boreal forest harvested for timber near Québec City, Québec. From January to March 2004 and 2005, we followed flocks on snowshoes and recorded their trajectory in real time using a handheld global positioning system (GPS) receiver. Boreal Chickadee flocks showed no response to forest edges when using mature forest stands. However, flocks mostly used edges of regenerating forest habitat (4–7 m high). Inside regenerating forest, flocks were significantly closer to both open edges (41 ± 6 m) and mature forest edges (11 ± 2 m) than would be expected from a lack of response to edges. Boreal Chickadee flocks did not avoid exposed edges of mature forest on the coldest or windiest days. On colder days, they were found disproportionately more often along edges between mature and regenerating stands, but generally avoided exposed edges of regenerating stands. Increasing edge densities resulting from clearcutting in boreal forest did not have a negative effect on use of remaining mature-forest patches, even under inclement weather. However, in regenerating stands resulting from timber harvest, Boreal Chickadee movements may be restricted during harsh weather. *Received 28 February 2006, accepted 28 January 2007.*

Key words: Boreal Chickadee, boreal forest, edge association, flock movements, global positioning system, GPS, *Poecile hudsonica*, winter.

Réponse de *Poecile hudsonica* face aux bordures forestières en hiver: quelle est l'importance des conditions météorologiques?

RÉSUMÉ.—Les réponses de l'avifaune face aux bordures forestières ont reçu beaucoup d'attention ces dernières années, particulièrement en raison des effets potentiels de la déforestation sur la qualité des parcelles forestières restantes. Cependant, les réponses individuelles des oiseaux face aux bordures forestières sont plus souvent inférées qu'observées. La plupart des études portant sur l'utilisation spatiale mettent l'emphase sur l'arrangement du territoire mais décrivent peu ou pas les mouvements à l'intérieur du territoire. Ainsi, notre compréhension des effets de bordure sur les mouvements des oiseaux forestiers demeure limitée. Nous avons enregistré les mouvements de 85 volées hivernales d'une espèce peu connue, *Poecile hudsonica*, dans une forêt boréale exploitée de 66-km², située près de la ville de Québec. Entre janvier et mars 2004 et 2005, nous avons suivi des volées en raquettes et noté leur trajet en temps réel en utilisant un système de positionnement mondial (GPS). Les volées de *P. hudsonica* n'ont pas montré de réponse face aux bordures forestières dans les peuplements de forêt mature. Toutefois, les volées ont surtout utilisé les bordures de l'habitat constitué de forêt en régénération (d'une hauteur de 4–7 m). Dans la forêt en régénération, les volées se trouvaient significativement plus près des bordures ouvertes (41 ± 6 m) et des bordures de la forêt mature (11 ± 2 m) qu'attendu. Les volées n'évitaient pas les bordures exposées de la forêt mature au cours des jours les plus froids ou venteux. Lors des jours froids, elles se trouvaient disproportionnellement plus souvent le long des bordures situées entre les peuplements matures et en régénération, mais elles évitaient généralement les bordures exposées des peuplements en régénération. L'augmentation des densités de bordures résultant des coupes totales en forêt boréale n'a pas eu d'effet négatif sur l'utilisation des parcelles de forêt mature, même lorsque les conditions météorologiques n'étaient pas clémentes. Toutefois, dans les peuplements en régénération suivant une coupe forestière, les mouvements de *P. hudsonica* peuvent être limités lorsque les conditions météorologiques sont difficiles.

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FOREST MANAGEMENT AFFECTS the spatial structure of remaining habitat patches, often increasing the ratio between edge and interior forest (Forman 1995). The boundaries between landscape components (hereafter "edges") can affect neighboring forest vegetation (Chen et al. 1992, Fraver 1994), arthropod abundance (Jokimäki et al. 1998, van Wilgenburg et al. 2001, Mazerolle and Hobson 2003), and local microclimate (Blake and Karr 1987, Chen et al. 1993). These "edge effects" can, in turn, affect animals. Edge effects on avian species diversity (Yahner 1988), territory location (Yahner 1988), nest predation (Gates and Gysel 1978, Lahti 2001), and brood parasitism (Paton 1994) have received a great deal of attention. Studies in recent years have demonstrated further effects of edges on avian movements and foraging patterns within breeding territories (Huhta et al. 1999, Mazerolle and Hobson 2003) and wintering home ranges (Dolby and Grubb 1999, Desrochers and Fortin 2000).

Proper understanding of edge effects is particularly important in determining the suitability of forest fragments for resident birds during the non-breeding season. Population dynamics of resident species inhabiting northern latitudes appear to be strongly determined by survival events that occur during the non-breeding season (Matthysen 1990, Lahti et al. 1998, Doherty and Grubb 2002). Abiotic conditions, including wind and temperature, differs near forest edges compared with interior forest (Murcia 1995). Wind speed varies greatly with distance to edge, and solar radiation can be more available near sun-facing edges (Murcia 1995). Furthermore, wind and temperature can interact to affect the metabolic rate and energy expenditure of birds (Porter and Gates 1969, Wolf and Walsberg 1996) and, in turn, reduce their survival (Mayer et al. 1979). Thus, selection of winter foraging sites may play an important part in reducing the energy costs of small birds in harsh winter environments (Wachob 1996). Changes of microhabitat (or "patch") selection in response to adverse thermal conditions have been well documented in small resident birds. Winter residents have been found to move horizontally less often (Kessel 1976, Grubb 1978) and to decrease foraging heights (Grubb 1975, 1977) during cold, windy conditions. Grubb (1977) found that with increasing wind strength and decreasing temperature, birds shifted to leeward positions on foraging substrates. In highly fragmented deciduous forests, birds did not use exposed forest edges during harsh winter weather and were found farther from windward edges of woodlots in high winds and low temperatures (Dolby and Grubb 1999). Increasing edge density in regions subjected to harsh winters can increase energy expenditures of birds beyond tolerable limits, resulting in a reduction of effective habitat available for use (Blake 1987, Dolby and Grubb 1999). However, most of the studies of winter weather effects were conducted in deciduous forests and agricultural landscapes; hence, the abiotic edge effects remain poorly understood in boreal, conifer-dominated forests.

Boreal forests in Québec are being subjected to intensive forest exploitation, and ~300,000 ha are logged annually (Ministère des Ressources naturelles et de la Faune 2006). The extensive timber harvest has resulted in a reduction in large tracts of forest and an increase in fragmentation and edge density. Forest remnants consist largely of riparian buffer strips and buffers between adjacent clearcuts (Ministère des Ressources naturelles 1996). The high proportion of edges in the remaining forest patches could potentially render them functionally unsuitable for birds during

the demanding winter months if abiotic edge effects in boreal regions act similarly to those in deciduous forests. Understanding abiotic edge effects in northern boreal forests is important for the conservation of resident species and the maintenance of suitable winter habitats.

The Boreal Chickadee (*Poecile hudsonica*) is a resident species whose range is almost completely restricted to northern boreal forests (Ficken et al. 1996). Boreal Chickadee numbers on Breeding Bird Survey routes have declined alarmingly in eastern North America (annual change [%] = -3.59, $P = 0.0035$; Sauer et al. 2005). Despite this decline, Boreal Chickadees have been little studied, particularly in winter (Ficken et al. 1996). Concern over habitat loss has been expressed (Erskine 1992, Foss 1994, Cyr and Larivée 1995) mostly with respect to winter suitability of habitat.

We examined movements of Boreal Chickadee flocks in forest patches left by timber harvest to determine whether the species occurs predominantly in the forest interior. We also examined the effects of winter weather on edge associations within the chickadees' home ranges. We predicted that flocks would avoid exposed edges when it is windy, particularly at colder temperatures.

STUDY AREA AND METHODS

Study area.—We conducted field work at Forêt Montmorency, Québec (47°20'N, -71°10'W), during the winters of 2004 and 2005. The study area is a 66-km² managed boreal forest mosaic comprising mature conifer stands (56%), mixed regeneration (24%), and open areas (20%) (Fig. 1). Balsam fir (*Abies balsamea*) and sometimes black spruce (*Picea mariana*) dominate the mature stands and are interspersed with white birch (*Betula papyrifera*). Early seral stages tend to be dominated by coniferous regeneration or white birch–balsam fir stands. An extensive network of roads (2.6 km per square kilometer) crosses the study area. Mean winter (December–March) temperature at Forêt Montmorency is -12.5°C, and mean annual precipitation is 158 cm, 39% of which falls as snow (Environment Canada 2005). Resident forest birds at Forêt Montmorency in January and March were mainly Boreal Chickadees, but Black-capped Chickadees (*P. atricapillus*) and Red-breasted Nuthatches (*Sitta canadensis*) were also frequently encountered.

For analysis of response to edges, we combined landscape elements within the study area into three classes. (1) All stands >7 m in height were classified as mature forest. These stands were almost exclusively coniferous, occasionally interspersed with birch. (2) Forested landscape elements 4–7 m in height were classified as regenerating. This class included a few young spruce plantations but consisted largely of naturally regenerating balsam fir, black spruce, or mixed stands. (3) Open areas included forest stands <4 m in height, clearcuts, gravel pits, lakes, rivers, and roads >7 m wide. Mature–regeneration was the most prevalent edge type in the study area and had a density of 55 m ha⁻¹. Mature–open edges were present at 44 m ha⁻¹ and regeneration–open edges at 13 m ha⁻¹.

Flock-following technique.—We followed 72 Boreal Chickadee flocks in the first winter (6 January 2004 to 10 March 2004) and 13 flocks during the following winter (14 February 2005 to 24 March 2005). Mean (\pm SE) flock size was 4 \pm 0.2 during both

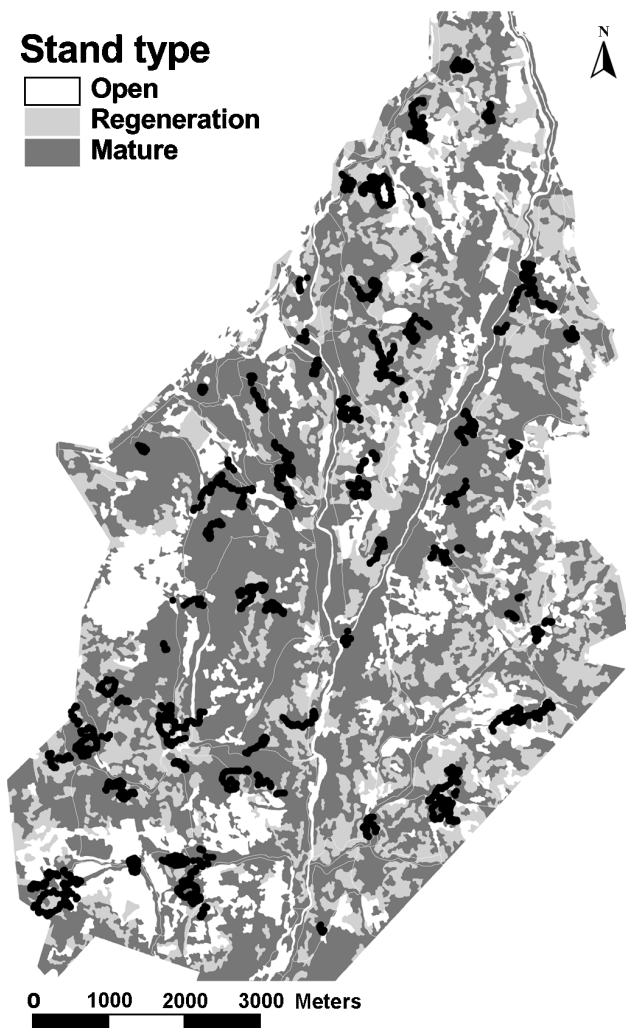


FIG. 1. Stand age distribution and movement paths (in black) of Boreal Chickadee flocks followed at Forêt Montmorency, 2004–2005.

winter seasons and ranged from three to eight birds. We located Boreal Chickadee flocks each day, using a regular grid of points spaced by 1 km covering the study area. Grid points were randomly selected and visited only once during the study. Beginning from the selected grid point, we used a standard search pattern to minimize habitat bias in flock detection. We snowshoed 500 m north, 500 m east, 1,000 m south, 500 m west, and 500 m north to return to the point of origin. Detection of flocks was passive, using only sight and sound. We did not revisit the widely spaced sample grid points, to limit the chances of resampling the same flock. Although individuals in the flocks were unmarked, we considered the flocks separate, independent units, given that flock composition differed in all but three cases of adjacent flocks (those three were known to be different owing to simultaneous observations). On the basis of color-banding, we found that flock composition was stable throughout winter months (Hadley and Desrochers 2008), as is the case in most other parids (Ekman 1989). We chose direct monitoring of the flocks over radiotelemetry because the rugged

topography of the study area limits the number of attainable fixes and reduces the resolution and accuracy of point locations (Ibarzabal and Desrochers 2004). Following the birds directly allowed more data to be collected for more flocks than would have been possible with radiotelemetry methods. Once detected, flocks were followed on snowshoes and their locations were logged in real time at 1-min intervals using a hand-held GPS receiver (Trimble, Sunnyvale, California). No positions were recorded during the first 2.5 min following discovery. We recorded GPS locations using a maximum point dilution of precision (PDOP) of 8. The standard deviation of point-location estimates, based on 1,680 stationary points, was 1.37 m under forest canopy.

We followed the first flock detected along the search transect for as long as possible. Flock cohesion varied, with all members of a flock foraging in the same tree in some instances, whereas at other times individuals were spread ≤ 20 m apart. To account for this, positions of the flock were recorded only when the observer was located at the approximate center of the flock, and data logging ceased immediately if the observer's position no longer reflected that of the flock. If contact with the flock was lost, the following period for that flock was terminated, and we moved to a remote location before commencing the search for a different flock. Flocks were almost exclusively foraging or moving between foraging locations during observation periods and, because of their tameness, appeared to be unaffected by observer presence (A. Hadley pers. obs.). The periods during which flocks were followed ranged from 4.7 to 152 min (mean = 53 min). Path lengths, defined as all movements displayed by a single flock during the observation period, ranged from 90 to 2,125 m (mean = 871 m) and were often highly tortuous. We found no discovery bias, given that there was no relationship between distance to forest edge and elapsed time since initial discovery ($R^2 = 0.0003$, $F = 1.9$, $P = 0.3$).

Response to edges.—We examined response to edges at two spatial scales, <200 m (hypothetical home range) and <30 m (foraging patch). For each flock, the mean distance to edge was calculated for four different situations: (1) points in mature forest to the nearest regeneration edge, (2) points in mature forest to the nearest open edge, (3) points in regeneration to the nearest mature edge, and (4) points in regeneration to the nearest open edge. Only flock locations separated by intervals of ≥ 1 min were used in this analysis. To assess whether Boreal Chickadee flocks moved throughout these habitats at random distances to edges, we created a quantitative null hypothesis specific to each flock. First, we delineated buffers with radii of 200 m and 30 m around each flock's (GPS) location. Second, we generated a grid of points spaced 10 m apart within each buffer. The resulting grid points were assumed to represent unbiased samples of the surrounding habitat, given the apparent lack of periodicity in spatial vegetation patterns of the study area. Third, using the four habitat–edge situations mentioned above, we determined the mean distance to edge of all points within each buffer. If Boreal Chickadee flocks respond to edges while moving through their winter habitat, we expected the mean distance to edge calculated from observed locations to differ from the mean distance calculated using the “available” grid points within the corresponding buffer. We assumed no spatial autocorrelation of responses to edges among flocks.

We attempted to follow Boreal Chickadee flocks under all weather conditions encountered during the study period. Weather

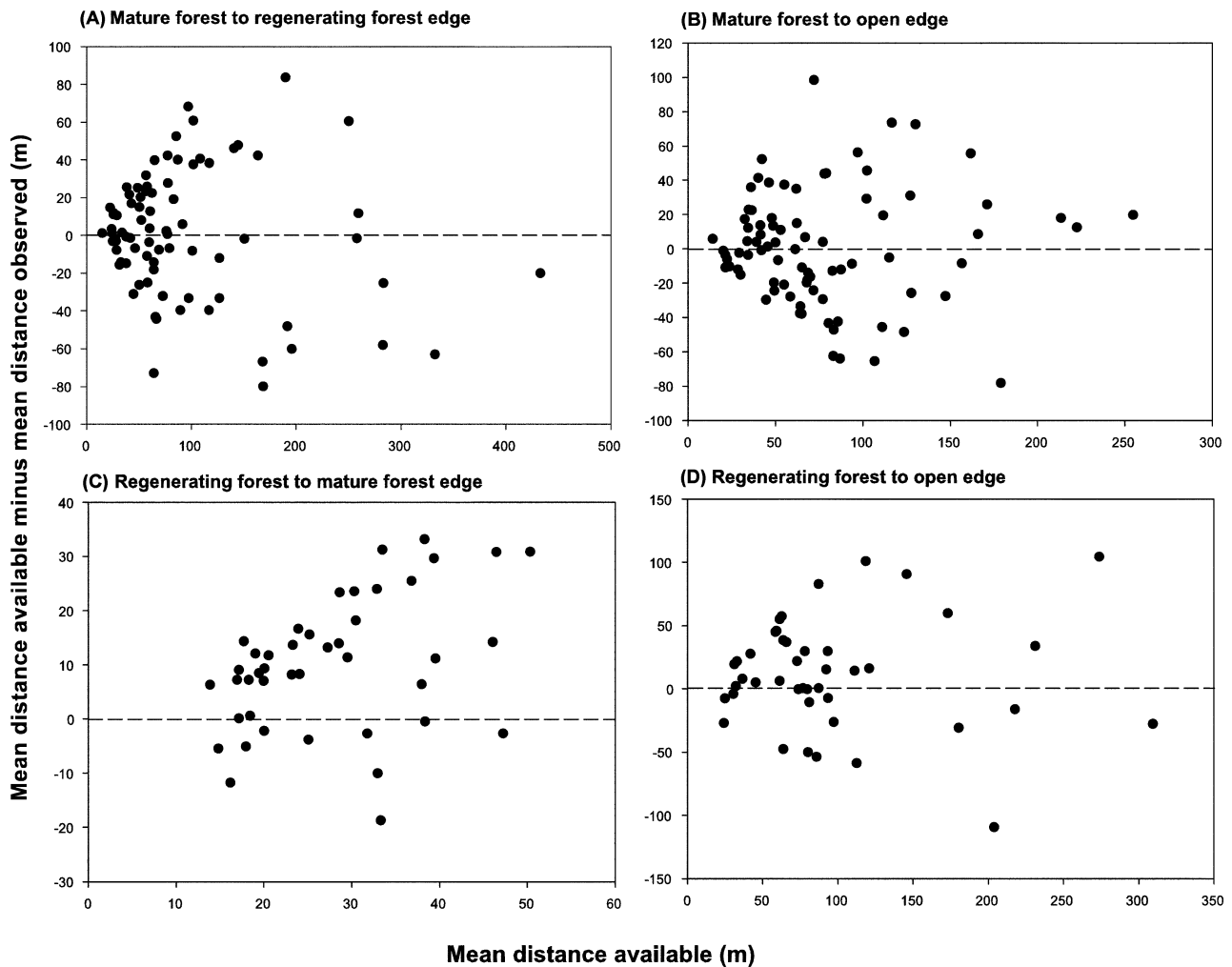


FIG. 2. Flock locations with respect to forest edges. Each point represents the mean distance available minus mean distance observed for individual flocks. Points above the dashed reference lines indicate flocks that foraged closer to the edge than expected. Scales are different among panels.

conditions were recorded hourly at an Environment Canada weather station located on the study site (Environment Canada 2005). The mean temperature during which flocks were followed was -9.6°C (range: -30°C to 3°C). Eighty-one of the 85 flocks were followed on days with wind speed $>5\text{ km h}^{-1}$ (mean: 10.8 km h^{-1} ; range: $5.8\text{--}30\text{ km h}^{-1}$). Despite the fact that multiple flocks were occasionally followed during the same day, we assumed that their temporal and spatial separation prevented pseudoreplication of weather conditions.

Flocks were the primary sampling unit used in all statistical analyses. Accordingly, we analyzed means of all location values collected for a single flock, each of which was assumed to have been followed only once during the study. We analyzed overall differences between observed and expected distances to edge using paired-sample t -tests. Parametric assumptions were respected. We used weighted least squares for statistical tests, with the inverse of the error variance of distance estimates for a weight factor, to account for the variation in sampling effort among flocks. The effects of wind, temperature, and the interaction “wind *temperature” on

distance to edge were examined using linear models, with Type III sums of squares (SAS Institute 1993). We also examined the effects of wind and temperature on habitat use with linear models. Effects were considered significant at $\alpha = 0.05$.

RESULTS

From mature forest.—Eighty-two of the 85 Boreal Chickadee flocks were observed in mature forest, and flocks spent $>80\%$ of their time within this habitat. Boreal Chickadees used mature forest independently of distance to edge. Flocks were neither closer to nor farther from regeneration or open edges than would be expected from lack of response to edges (Table 1 and Fig. 2A, B). This result was consistent for both the home range (200 m) and foraging patch scales (30 m) (Table 1).

From regenerating forest.—Only 43 of the 85 flocks used regenerating forest, generally remaining relatively close to edges that bordered mature forest (Table 1). Only 9 of those 43 flocks were located farther from mature-forest edges than would be

TABLE 1. Difference between expected and observed distances to habitat edges for Boreal Chickadee flocks. Positive values denote closer to edge than expected (paired *t*-test).

Reference buffer radius (m)	Habitat used (<i>n</i>)	Edge type	Distance (m)	SE	<i>t</i>	<i>P</i>
200	Mature (82)	Regeneration	−2.00	3.30	0.59	0.55
		Open	0.60	2.70	−0.20	0.84
	Regeneration (43)	Mature	11.10	1.80	−6.92	<0.001
		Open	40.90	6.40	−6.30	<0.001
30	Mature (82)	Regeneration	−0.70	0.96	0.73	0.47
		Open	−0.97	0.79	1.22	0.22
	Regeneration (43)	Mature	3.59	0.81	−4.07	<0.001
		Open	11.66	2.03	−5.67	<0.001

expected (Fig. 2C). The tendency of flocks to locate themselves close to adjoining mature forest when in regenerating forest was the same for both the 200-m and 30-m scales (Table 1).

Flocks in regenerating forest were considerably closer to open edges, bordering unused habitat, than expected (Table 1). Thirteen flocks using regenerating forest were farther from open edges than expected within 200 m (Fig. 2D). In fact, Boreal Chickadee flocks in regenerating forest were located much closer to open edges (41 ± 6 m) than they were to mature-forest edges. As with distance to mature-forest edges, the association of flocks with open edges was consistent across both scales examined (Table 1).

Effects of weather conditions.—When flocks were in mature forest, there was no significant effect of temperature, wind, or their interaction on the location of Boreal Chickadees in relation to edges with either regenerating forest or open areas. However, weather had a statistically significant effect on the locations of Boreal Chickadees in regenerating forest (Table 2). With decreasing temperature, Boreal Chickadee flocks in regenerating forest tended to be more strongly associated with mature-forest edges than when it was warmer (Fig. 3A). At high wind speeds, flocks in regenerating stands were associated less with mature-forest edges (Fig. 3B). The interaction between the effects of wind and temperature was also significant, with flocks most strongly associated with mature-forest edges when it was cold and calm (Fig. 3C). Results were presented only for the 200-m (home range) scale; however, the trends were equivalent at the 30-m (foraging patch) scale. Weather had no significant effect on the proportion of time spent in different habitat types (temperature: $R^2 = 0.012$, $F = 1.03$, $P = 0.31$; wind: $R^2 = 0.021$, $F = 1.7$, $P = 0.19$).

Edge orientation.—We examined edge orientation to determine whether the effects of weather on the association with edges in regenerating forest were dependent on direction. We

TABLE 2. Relationship between mean association with edge and weather while flocks used regenerating forest.

Edge type	Weather variable	Association	SE	<i>P</i>
Regeneration–mature	Temperature	2.96	0.45	<0.001
	Wind	−1.35	0.41	0.001
	Temperature*wind	−0.19	0.04	<0.001
Regeneration–open	Temperature	−1.68	2.15	0.44
	Wind	−3.13	1.25	0.02
	Temperature*wind	0.06	0.13	0.63

divided edges into windward–shaded and leeward–sunny edges on the basis of prevailing winds (northwest on 93% of days with winds >10 km h^{−1}) and sun position (Environment Canada 2005). Windward–shaded edges between regeneration and open areas were strongly avoided (Table 3). However, association with mature-forest edges was not dependent on orientation, and flocks were strongly associated with both leeward–sunny and windward–shaded edges (Table 3).

DISCUSSION

Response to edges.—Boreal Chickadee flocks responded inconsistently to forest edges within their winter home ranges. Flocks were strongly associated with certain edge types but were not found in others. These results are consistent with those of two other studies of movements in parids (Desrochers and Fortin 2000, Brotons and Herrando 2003). However, other workers have recorded independence (Germaine et al. 1997, Brand and George 2001) or avoidance (Dolby and Grubb 1999) of edges. Association of Boreal Chickadees with edges depended on habitat type, irrespective of the reference scale (<30 m and <200 m). Flocks used mature forest irrespective of distance to edges, however, Boreal Chickadee flocks were not found in areas deep within regenerating forest patches.

Edge use by Boreal Chickadees in regenerating forest is probably driven by at least three factors. Changes in food or vegetation near mature-forest edges may result in more favorable foraging patches than in areas deeper within regenerating forest. Changes in arthropod abundance may occur with increasing distance from patch edges (Jokimäki et al. 1998), and seed crops may be greater near edges (Brotons and Herrando 2003). Food hoarding may also be less frequent near edges (Brotons et al. 2001). However, evidence of changes in winter food abundance with distance from edges is lacking (Desrochers and Fortin 2000). If Boreal Chickadees store food found in regenerating forest closer to mature forest than where it was collected, recovery of these cached items later in the winter could drive the apparent edge association.

Boreal Chickadee flocks may find that mature-forest edges offer a more favorable microclimate than exposed areas deeper within regenerating patches. Microclimate selection is sometimes important for winter survival in resident species (Wachob 1996). We found some support for a microclimate effect, in that Boreal Chickadee flocks avoided the exposed areas far from mature forest and tended to focus their activities closer to mature forest on

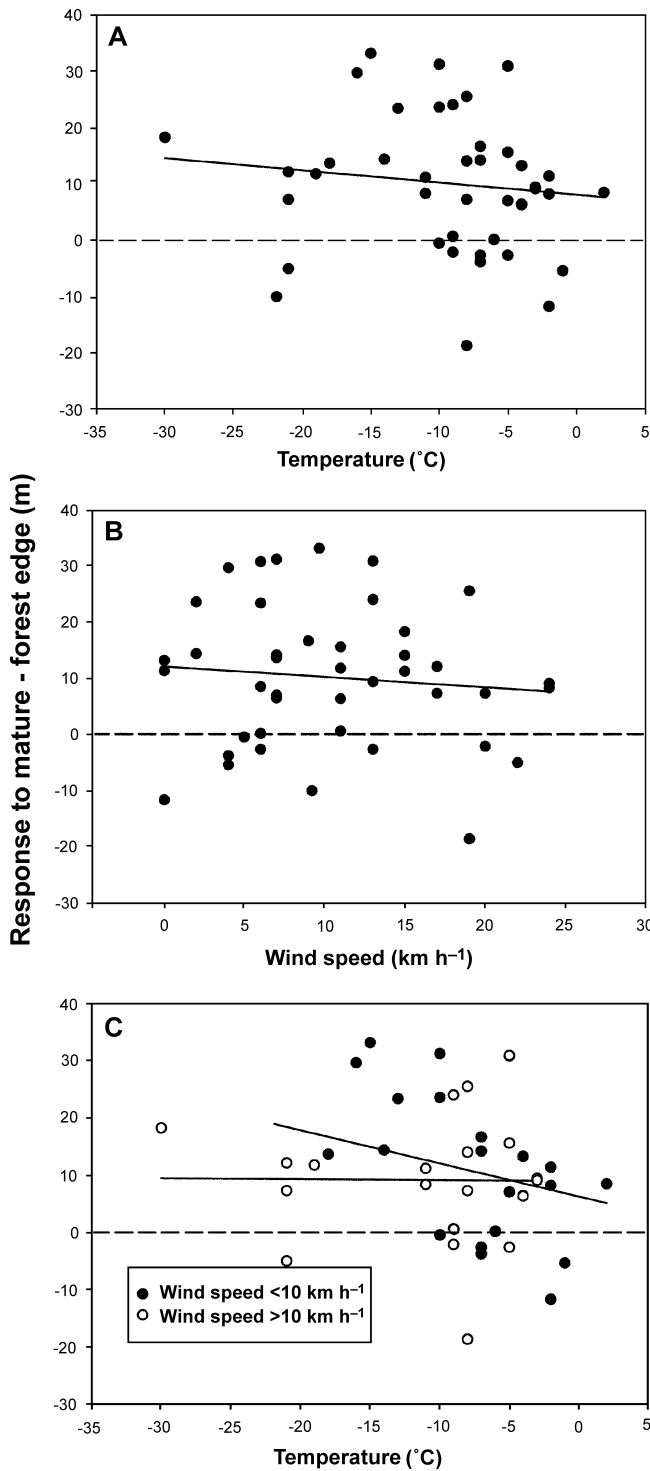


FIG. 3. Response to mature-forest edge in different weather conditions when flocks were using regenerating forest. Each point represents the mean distance available minus mean distance observed for individual flocks. A and B show the effects of temperature and wind, respectively. C shows the effect of the interaction between wind and temperature. Regression lines are shown.

TABLE 3. Effect of orientation on the association with edges of regenerating forest. Positive values indicate closer to edge than expected.

Edge type	Orientation	Distance to edge (m)	SE	P
Regeneration–mature	Leeward–sunny	12.5	1.8	<0.001
	Windward–shaded	25.6	4.0	<0.001
Regeneration–open	Leeward–sunny	–7.6	4.3	0.08
	Windward–shaded	–12.1	4.7	0.01

cold days. However, the effects of weather on Boreal Chickadee response to mature-forest edges were not pronounced, and association with mature forest still occurred in comparatively favorable weather.

Third, predation risk on adult animals has been considered an important driving force behind edge effects (Rodríguez et al. 2001, Turcotte and Desrochers 2003). Small birds need to trade-off energy gains with predation risk (Lima and Dill 1990), and their movements are largely determined by perceived risk of predation (Lima 1998). Habitat-mediated predation risk often operates through the amount of available cover provided by vegetation that can be used to shelter from predator attacks (Lima and Dill 1990). Regenerating forest in our study area is much more open and exposed than mature forest. Foraging in these more exposed habitats may make flocks more vulnerable to predation. Parid species will usually exhibit escape tactics based on flying into woody cover (Ekman 1987, Lima 1993); thus, to mitigate the risks posed by predation, Boreal Chickadees may avoid venturing too far from the shelter offered by neighboring mature forest. Our flocks also appeared to forage in more cohesive groups when using regenerating forest (A. Hadley pers. obs.), and other studies have shown that group cohesion increases under “risky” conditions (Rodríguez et al. 2001). Northern Shrikes (*Lanius excubitor*) and Northern Hawk Owls (*Surnia ulula*) were observed on occasion during the study, and Northern Shrikes are considered a major predator of Boreal Chickadees during winter (reviewed by Smith 1991). Interspecific competition was unlikely to affect our results, given that Boreal Chickadees were several times more abundant than the only other parid present in the study area (Black-capped Chickadee; A. Desrochers pers. obs.).

Unlike their response to mature-forest edges, Boreal Chickadees’ association with edges adjoining open areas while using regenerating forest is likely attributable mostly to “movement channeling.” In birds (Desrochers and Fortin 2000), mammals (Bider 1968, Desrochers et al. 2003), and insects (Haddad 1999), edges have been shown to act as barriers that channel movements, resulting in a disproportionate amount of time spent along edges. Although flocks crossed open areas (14 of 85 flocks crossed gaps > 15 m in width; mean width = 53 ± 7 m, maximum = 120 m), flocks often were reluctant to cross even small (~10-m) gaps; one or two individuals usually crossed first, followed by the rest of the flock a few minutes later. Flocks skirted around the edges of open areas and moved through regenerating forest from one mature-forest patch to another.

Effects of weather on edge association.—Boreal Chickadees’ movements, like those of most resident species investigated to

date (Grubb 1975, Lens 1996, Wachob 1996, Dolby and Grubb 1999), were affected by winter weather. However, in our study, the effects of adverse conditions depended on both habitat type and edge type. Winter weather caused no change in the distance of Boreal Chickadees from habitat edges when they were using mature forest. In regenerating forest, Boreal Chickadee flocks were affected by inclement weather and were more strongly associated with edges adjoining mature forest when it was cold. That weather had a greater effect in regenerating stands than in older forest is not surprising, given that regeneration in the study area is generally more open and exposed, with larger gaps between trees than in mature forest stands.

Contrary to our predictions and unlike other studies (Grubb 1977, Dolby and Grubb 1999; but see Desrochers and Fortin 2000), we did not find a strong avoidance of mature-forest edges adjoining open areas during harsh weather. However, in regenerating stands, we found that when edges with open areas were divided by orientation, windward–shaded edges were generally unused. The inconsistent edge response and lack of strong weather effects in mature forest are perhaps not surprising, and they can be explained by at least two main factors. Most studies investigating the effects of weather on edge association were conducted in deciduous forests, where leafless trees allow wind to penetrate easily in winter. In the boreal forests of our study area, the dense coniferous boughs retained snow and probably dampened the effects of wind within a short distance from edges. The density of vegetation next to edges is an important factor in mitigating the effects of wind and allowing birds to use areas close to windy edges (Grubb 1977).

The weak effect of weather, particularly in mature stands, may reflect potential behavioral and physiological adaptations that enable Boreal Chickadees to compensate for the increased exposure next to edges. Most other studies (e.g., Dolby and Grubb 1999) have dealt with species near the northern limits of their ranges. Boreal Chickadees, however, occur in regions much farther north than our study area, and presumably they have developed the ability to cope with extreme conditions. Bent (1946) reported that Black-capped Chickadees died when temperatures dropped below -45°C , whereas Boreal Chickadees at the same site were apparently unaffected. Although we found little in terms of edge response attributable to harsh weather, Boreal Chickadees reduce their foraging heights when it is windy, particularly in regenerating forest (A. Hadley pers. obs.). Vertical shifts in foraging locations have been well documented in other parid species (Grubb 1975, 1977; Dolby and Grubb 1999), and it is possible that vertical shifts in foraging locations by Boreal Chickadees are more important than horizontal shifts as a means to compensate for adverse weather. Grubb (1977) also found that using the leeward portion of foraging substrates allows birds to compensate for increasingly strong winds.

Resident bird species such as the Boreal Chickadee are believed to be the most at risk of population declines that result from habitat loss and fragmentation (Bender et al. 1998, Schmiegelow and Mönkkönen 2002). As a result, information on the use of landscapes by resident boreal-forest species is of practical interest. Species adversely affected by fragmentation or patch size are expected to occur predominantly in the interior of patches and to avoid edges (Bender et al. 1998). Our results provide some evidence against a strong effect of fragmentation *per se*, given that Boreal

Chickadees did not avoid edges of mature-forest patches within their home ranges. As forest harvesting increases the proportion of regenerating stands, fragmentation and edge effects may become more important, particularly during harsh weather.

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LITERATURE CITED

- BENDER, D. J., T. A. CONTRERAS, AND L. FAHRIG. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology* 79:517–533.
- BENT, A. C. 1946. Life histories of North American jays, crows, and titmice, pt. 1. United States National Museum Bulletin, no. 191.
- BIDER, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecological Monographs* 38:269–308.
- BLAKE, J. G. 1987. Species-area relationships of winter residents in isolated woodlots. *Wilson Bulletin* 99:243–252.
- BLAKE, J. G., AND J. R. KARR. 1987. Breeding birds of isolated woodlots: Area and habitat relationships. *Ecology* 68:1724–1734.
- BOUSKILA, A., AND D. T. BLUMSTEIN. 1992. Rules of thumb for predation hazard assessment: Predictions from a dynamic model. *American Naturalist* 139:161–176.
- BRAND, L. A., AND T. L. GEORGE. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118:678–686.
- BROTONS, L., A. DESROCHERS, AND Y. TURCOTTE. 2001. Food hoarding behaviour of Black-capped Chickadees (*Poecile atricapillus*) in relation to forest edges. *Oikos* 95:511–519.
- BROTONS, L., AND S. HERRANDO. 2003. Effect of increased food abundance near forest edges on flocking patterns of Coal Tit *Parus ater* winter groups in mountain coniferous forests. *Bird Study* 50:106–111.
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2:387–396.
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219–237.
- CYR, A., AND J. LARIVÉE. 1995. Atlas saisonnier des oiseaux du Québec. Presses de l'Université de Sherbrooke et Société de loisir ornithologique de l'Estrie, Sherbrooke, Québec, Canada.
- DESROCHERS, A., AND M.-J. FORTIN. 2000. Understanding avian responses to forest boundaries: A case study with chickadee winter flocks. *Oikos* 91:376–384.

- DESROCHERS, A., I. K. HANSKI, AND V. SELONEN. 2003. Siberian Flying Squirrel responses to high- and low-contrast forest edges. *Landscape Ecology* 18:543–552.
- DOHERTY, P. F., JR., AND T. C. GRUBB, JR. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* 83:844–857.
- DOLBY, A. S., AND T. C. GRUBB, JR. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 101:408–412.
- EKMAN, J. 1987. Exposure and time use in Willow Tit flocks: The cost of subordination. *Animal Behaviour* 35:445–452.
- EKMAN, J. 1989. Ecology of non-breeding social systems of *Parus*. *Wilson Bulletin* 101:263–288.
- ENVIRONMENT CANADA. 2005. Canadian Climate Normals, 1971–2005 (Québec). Canadian Climate Program, Québec.
- ERSKINE, A. J. 1977. Birds in Boreal Canada: Communities, Densities, and Adaptations. Canadian Wildlife Service Report Series, no. 41. Canadian Wildlife Service, Ottawa, Ontario.
- ERSKINE, A. J. 1992. Atlas of Breeding Birds of the Maritime Provinces. Nimbus Publications and Nova Scotia Museum, Halifax, Nova Scotia.
- FICKEN, M. S., M. A. McLAREN, AND J. P. HAILMAN. 1996. Boreal Chickadee (*Parus hudsonicus*). In *The Birds of North America*, no. 254 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- FORMAN, R. T. T. 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, New York.
- FOSS, C. R., Ed. 1994. *Atlas of Breeding Birds in New Hampshire*. Arcadia, Dover, New Hampshire.
- FRAVER, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* 8:822–832.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- GERMAINE, S. S., S. H. VESSEY, AND D. E. CAPEN. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708–718.
- GRUBB, T. C., JR. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. *Condor* 77:175–182.
- GRUBB, T. C., JR. 1977. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland: Horizontal adjustments. *Condor* 79:271–274.
- GRUBB, T. C., JR. 1978. Weather-dependent foraging rates of wintering woodland birds. *Auk* 95:370–376.
- HADDAD, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist* 153:215–227.
- HADDAD, N. M., AND K. A. BAUM. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623–633.
- HADLEY, A. S., AND A. DESROCHERS. 2008. Winter habitat use by Boreal Chickadee flocks in a managed forest. *Wilson Journal of Ornithology* 120: in press.
- HUHTA, E., J. JOKIMÄKI, AND P. RAHKO. 1999. Breeding success of Pied Flycatchers in artificial forest edges: The effect of a suboptimally shaped foraging area. *Auk* 116:528–535.
- IBARZABAL, J., AND A. DESROCHERS. 2004. A nest predator's view of a managed forest: Gray Jay (*Perisoreus canadensis*) movement patterns in response to forest edges. *Auk* 121:162–169.
- JOKIMÄKI, J., E. HUHTA, J. ITÄMIES, AND P. RAHKO. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* 28:1068–1072.
- KESSEL, B. 1976. Winter activity patterns of Black-capped Chickadees in interior Alaska. *Wilson Bulletin* 88:36–61.
- LAHTI, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* 99:365–374.
- LAHTI, K., M. ORELL, S. RYTKÖNEN, AND K. KOIVULA. 1998. Time and food dependence in Willow Tit winter survival. *Ecology* 79:2904–2916.
- LENS, L. 1996. Wind stress affects foraging site competition between Crested Tits and Willow Tits. *Journal of Avian Biology* 27:41–46.
- LIMA, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: A survey of North American birds. *Wilson Bulletin* 105:1–47.
- LIMA, S. L. 1998. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215–290.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- MATTHYSEN, E. 1990. Nonbreeding social organization in *Parus*. Pages 209–249 in *Current Ornithology*, vol. 7 (D. M. Power, Ed.). Plenum Press, New York.
- MAYER, L., S. LUSTICK, AND T. C. GRUBB, JR. 1979. Energetic control of behavior: Foraging in Carolina Chickadees. *Comparative Biochemistry and Physiology A, Physiology* 63:577–579.
- MAZEROLLE, D. F., AND K. A. HOBSON. 2003. Do Ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. *Auk* 120:152–162.
- MINISTÈRE DES RESSOURCES NATURELLES. 1996. Règlement sur les normes d'intervention dans les forêts du domaine public. Pages 2750–2786 in *Gazette Officielle du Québec*, vol. 128.
- MINISTÈRE DES RESSOURCES NATURELLES ET DE LA FAUNE. 2006. *Ressources et industries forestières : Portrait statistique Édition 2005–2006*. Gouvernement du Québec, Québec.
- MURCIA, C. 1995. Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17–26.
- PORTER, W. P., AND D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. *Ecological Monographs* 39:227–244.
- RODRÍGUEZ, A., H. ANDRÉN, AND G. JANSSON. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95:383–396.
- SAS INSTITUTE. 1993. *SAS/STAT Software: The GENMOD Procedure*. SAS Technical Report P-243. SAS Institute, Cary, North Carolina.
- SAUER, J. R., J. E. HINES, AND J. FALLON. 2005. *The North American Breeding Bird Survey, Results and Analysis 1966–2004*. U.S.

- Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- SCHMIEGELOW, F. K. A., AND M. MÖNKKÖNEN. 2002. Habitat loss and fragmentation in dynamic landscapes: Avian perspectives from the boreal forest. *Ecological Applications* 12:375–389.
- SMITH, S. M. 1991. *The Black-capped Chickadee: Behavioral Ecology and Natural History*. Cornell University Press, Ithaca, New York.
- TURCOTTE, Y., AND A. DESROCHERS. 2003. Landscape-dependent response to predation risk by forest birds. *Oikos* 100:614–618.
- VAN WILGENBURG, S. L., D. F. MAZEROLLE, AND K. A. HOBSON. 2001. Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: Implications for forest birds. *Écoscience* 8:454–461.
- WACHOB, D. G. 1996. The effect of thermal microclimate on foraging site selection by wintering Mountain Chickadees. *Condor* 98:114–122.
- WOLF, B. O., AND G. E. WALSBERG. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* 77:2228–2236.
- YAHNER, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2:333–339.

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