

## EFFECTS OF WINTER WEATHER ON HORIZONTAL AND VERTICAL USE OF ISOLATED FOREST FRAGMENTS BY BARK-FORAGING BIRDS<sup>1</sup>

ANDREW S. DOLBY<sup>2</sup> AND THOMAS C. GRUBB JR.

*Behavioral Ecology Group, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210-1293*

**Abstract.** We examined how wind and temperature below the thermoneutral zone may reduce the suitability of small, isolated woodlots for permanent resident woodland birds. Carolina Chickadees (*Poecile carolinensis*) and Tufted Titmice (*Baeolophus bicolor*) exhibited significantly reduced foraging height in the forest canopy with increasing wind strength. The horizontal area of woodlots frequented by most mixed-species flock members was significantly reduced by the combined effect of wind and temperature. In particular, all mixed-species flock members except female Downy Woodpeckers (*Picoides pubescens*) were found farther from windward edges of woodlots when wind speeds were higher and temperatures were lower. We conclude that chickadees and titmice may be most affected by abiotic edge effects, both sexes of White-breasted Nuthatch (*Sitta carolinensis*) and male Downy Woodpeckers intermediately affected, and female Downy Woodpeckers least affected. Our results suggest that effects of wind and temperature may be important to populations of bark-foraging birds inhabiting highly fragmented habitat in the Temperate Zone.

**Key words:** *Baeolophus bicolor*, *edge effects*, *habitat fragmentation*, *Picoides pubescens*, *Poecile carolinensis*, *Sitta carolinensis*.

Although much attention has focused on the impact of biotic edge effects on breeding migratory birds (Whitcomb et al. 1981, Andren and Angelstam 1988, Harris 1988), less is known about how abiotic edge effects, such as increased wind exposure, contribute to the suitability of forest fragments for permanent-resident birds during winter (but see Blake 1987, Yahner 1988). At the physiological level, wind and temperature interact to affect metabolic expenditures of birds (Porter and Gates 1969, Wolf and Walsberg 1996), and exposure to severe microclimatic conditions may reduce birds' chances of winter survival (Mayer et al. 1979). Furthermore, wind intensity can vary markedly with distance from fragment edges (Grubb 1975, 1977, Blake 1987).

Grubb (1975) observed that members of mixed-species flocks of bark-foraging birds inhabiting North American deciduous forest reacted to increasingly severe weather during winter by reducing their height in the forest canopy while foraging. In a subsequent

study, Grubb (1977) found that with increasing wind strength and decreasing temperature, such birds also shifted to more leeward positions on foraging substrates. Such observations suggest that wintering resident birds possess behavioral mechanisms which may reduce energetic costs under conditions of high thermoregulatory demand. Through such behaviors, birds might be able to partially compensate for abiotic edge effects in isolated fragments.

However, if severe microclimatic edge effects penetrate deeply into woodlots, substantial portions of such fragments could be rendered unsuitable for habitation during prolonged periods of inclement winter weather (Blake 1987, Chen et al. 1992). Microclimatic conditions could leave large portions of fragments uninhabitable for birds either by increasing thermoregulatory costs beyond tolerable limits or by restricting access to foraging locations, thereby exacerbating competition for food (Blake 1987). P. F. Doherty Jr. and T. C. Grubb Jr. (unpubl. data) found that mid-winter disappearances of Carolina Chickadees (*Poecile carolinensis*) from small woodlots (1 to 5 ha) were greater during a "hard winter" than during a "mild winter." This observation suggests that if severe microclimate edge effects penetrate completely to leeward edges, they could render entire forest fragments uninhabitable. In any case, the combined effects of wind and temperature could be an important mechanism driving distributions of wintering resident birds in fragmented landscapes.

The first objective of this study was to determine whether permanent-resident bark-foraging birds attempt to avoid microclimate edge effects by foraging farther from windward edges and at lower substrate heights with increasing wind speed and decreasing temperature. The second objective was to appraise the potential of microclimatic edge effects to influence the distribution of permanent-resident woodland birds among forest fragments.

### METHODS

#### STUDY AREA AND SPECIES

We conducted this study during the winters of 1995–1996 and 1996–1997 in eight woodlots located in Union and Delaware Counties, Ohio. These deciduous forest fragments averaged ( $\pm$  SD) 5.3  $\pm$  2.2 ha in area and consisted primarily of oaks (*Quercus* spp.), ashes (*Fraxinus* spp.), shagbark hickory (*Carya ovata*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). Each woodlot was completely surrounded by cultivated agricultural fields and contained one isolated mixed-species flock. Such flocks were never observed to cross into neighboring woodlots

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<sup>2</sup> Current address: Department of Biology, University of South Florida, Tampa, FL 33620, e-mail: dolby@chumal.cas.usf.edu

during the study period. Ubiquitous flock members included the Tufted Titmouse (*Baeolophus bicolor*), Carolina Chickadee, White-breasted Nuthatch (*Sitta carolinensis*), and Downy Woodpecker (*Picoides pubescens*). Each species averaged 1.9 to 3.4 individuals per visit.

#### DATA COLLECTION

During the first week of December each year, we placed a sunflower seed feeder and a wire-mesh suet cage into each woodlot. The feeders also acted as traps that could be operated remotely by radio-control (Pierce and Grubb 1981). From mid-December to mid-January, we captured birds using these traps and with mist-nets surrounding the feeding stations. All birds were fitted with U.S. Fish and Wildlife Service bands and uniquely colored plastic leg streamers for individual identification.

Observations took place during 2-hr woodlot visits conducted between 08:00 and 16:00. Woodlots were visited 7–10 times each (mean  $\pm$  SD =  $8.3 \pm 1.5$ ). Before we entered a woodlot, we measured wind speed (Velometer Jr., Alnor Instrument Company, Nilus, Illinois) in the surrounding open field and estimated wind direction. We measured air temperature in the shade within the woodlot. We then assigned the location of each Downy Woodpecker and White-breasted Nuthatch to one of the  $25 \times 25$ -m blocks that formed a grid covering the entire area of the woodlot. Each woodlot contained a single nuthatch pair, and the male and female were usually (82% of observations) found in the same or adjacent blocks.

We also assigned the Tufted Titmouse and Carolina Chickadees to one of the  $25 \times 25$ -m blocks, based on which block contained the majority of individuals of these two species combined. Tufted Titmouse and Carolina Chickadees act as nuclear species in these mixed-species flocks (Morse 1970), and they were consistently found together in cohesive groups within woodlots. The nuthatch pair and one or more Downy Woodpecker individuals were usually found within close proximity to the nuclear species' group, but were sometimes found apart from the majority of the flock.

Upon entering each woodlot, we located the flock by sound and then proceeded directly toward its location. As we moved toward the flock from our entry point, we recorded the positions of Downy Woodpeckers and nuthatches as we encountered them. To minimize chances that our presence within woodlots would cause the flocks to move before their position could be recorded, we identified the location of each flock as quickly as possible after entering woodlots instead of using pre-determined transects. The same entry point was used for each visit.

Distances of titmouse and chickadee groups and Downy Woodpecker and White-breasted Nuthatch individuals from windward edges of woodlots were determined by measuring on woodlot maps the distance from the center of each block, to which a group or individual had been assigned, to the edge of the woodlot. Measurements were made in line with wind direction. If the locations of more than one male or one female Downy Woodpecker were mapped during a

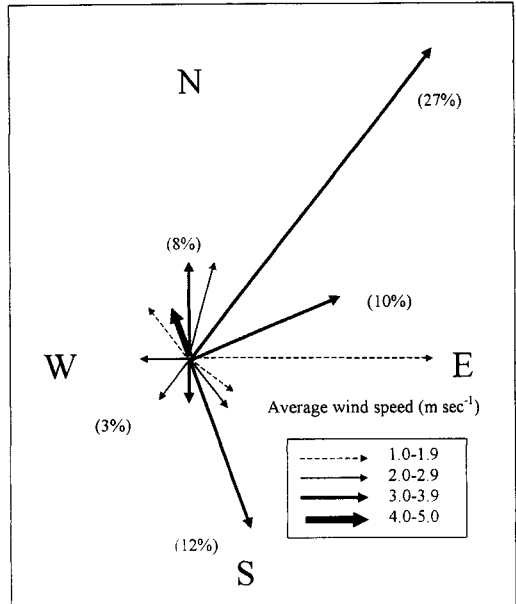


FIGURE 1. The distribution of wind directions during woodlot visits in 1995–1996 and 1996–1997 in Union County, Ohio. Arrow length represents the relative frequency (%) of observations during which the wind blew in a given direction. Several such relative frequencies are indicated in the figure.

woodlot visit, the distance from the windward edge was averaged for the sex.

#### STATISTICAL ANALYSES

Data were analyzed using separate general linear ANCOVA models on two dependent variables: foraging height and distance from the windward edge of the woodlot. Distance from the windward edge was assumed to reflect the portion of a given woodlot that was rendered unsuitable by weather conditions. The woodlot was included as a factor in each model because multiple observations were collected per woodlot. Covariates in all models included wind, temperature, and the interaction between wind and temperature. Models analyzing the distance from the windward edge included the total distance across the woodlot as an additional covariate. Because the distributions of species were not statistically independent from each other, separate analyses were carried out for each species. For Downy Woodpeckers and White-breasted Nuthatches, separate analyses were conducted for each sex. We set our significance level at  $P = 0.05$ .

#### RESULTS

The mean ( $\pm$  SE) air temperature and wind speed per woodlot visit were  $1.9 \pm 0.7^\circ\text{C}$  and  $2.7 \pm 0.2 \text{ m sec}^{-1}$ , respectively. Winds most frequently came from the south and west (65% of observations, Fig. 1). Fifty-seven observations were taken each for male and female nuthatches and male Downy Woodpeckers, 55 for

TABLE 1. Significant ANCOVA results for vertical and horizontal use of woodlots by permanent-resident woodland birds during winter. Independent study sites (woodlots) were included as factors in each model. Total distance across each woodlot (m) was included as a covariate for models in which the birds' distances from the windward edges of woodlots (m) was the dependent variable. WBNU = White-breasted Nuthatch, DOWO = Downy Woodpecker, PARIDS = Tufted Titmouse and Carolina Chickadee combined.

Dependent variable	Species	Sex	Mean ( $\pm$ SE)	Covariate	df	F	Slope	P
Height (m)	PARIDS	M/F	7.1 ( $\pm$ 0.6)	Wind speed (m sec <sup>-1</sup> )	1,40	8.45	-	0.006
Distance from windward edge (m)	WBNU	M	132 ( $\pm$ 11)	Temperature ( $^{\circ}$ C)	1,45	5.31	+	0.026
				Wind speed $\times$ temp.	1,45	9.09	-	0.004
	DOWO	M	125 ( $\pm$ 10)	Wind speed $\times$ temp.	1,45	6.62	-	0.016
				Wind speed $\times$ temp.	1,45	4.29	-	0.044
	PARIDS	M/F	126 ( $\pm$ 12)	Wind speed $\times$ temp.	1,39	6.47	-	0.015

female woodpeckers, and 51 for chickadees and titmice, collectively.

#### VERTICAL USE OF WOODLOTS

Canopy heights of White-breasted Nuthatches and Downy Woodpeckers were not significantly related to wind or temperature. By contrast, chickadees and titmice were found significantly lower in the canopy as wind speed increased (Table 1).

#### HORIZONTAL USE OF WOODLOTS

Except for female Downy Woodpeckers, in all four species, the distance of birds from the windward edge of woodlots was significantly correlated with the wind  $\times$  temperature interaction term (Table 1). Both nuthatch sexes, male Downy Woodpeckers, chickadees, and titmice were found significantly farther from windward edges as wind speed increased and temperature concurrently decreased (Table 1). In male nuthatches, distance to the windward edge and temperature were positively correlated (Table 1). We found the majority of the flock in the leeward half of the woodlot during 41 of 66 woodlot visits (62%).

To explore further the interacting effect of wind and temperature on distances of birds from windward edges, we divided the range of observed temperatures into quartiles. Within each quartile, we then regressed wind speed against distance from the windward edge for each species or sex in which a significant wind speed  $\times$  temperature interaction had been found. Significant positive correlations were found between wind speed and distance from the windward edge only for the lowest temperature quartile ( $-15.0$  to  $-6.5^{\circ}$ C). Figure 2 displays this analysis for chickadees and titmice. Similar correlations were obtained for male Downy Woodpeckers and both nuthatch sexes.

#### DISCUSSION

##### VERTICAL USE OF WOODLOTS

Titmice and chickadees significantly reduced their heights in the canopy with increasing wind, but for the other species we found no significant relationships between height in the canopy and wind or temperature. Chickadees and titmice forage on smaller-diameter substrates than Downy Woodpeckers or White-breasted Nuthatches (Pierce and Grubb 1981). Therefore, woodpeckers and nuthatches may have a greater capacity than chickadees and titmice to shelter them-

selves from wind without reducing their canopy height by moving to the leeward side of foraging substrates (Grubb 1977).

Male Downy Woodpeckers tended to reduce their canopy heights with increasing wind, although not significantly so. They also forage higher and on narrower substrates than either female Downy Woodpeckers (Peters and Grubb 1983) or White-breasted Nuthatches (Pierce and Grubb 1981). Grubb (1975) found that all four of our focal species significantly reduced their foraging heights with increasing wind speed. In his study, the heights of chickadees, titmice, and male Downy Woodpeckers were the most affected by wind (Grubb 1975), an observation which is consistent with our present results.

##### HORIZONTAL USE OF WOODLOTS

In combination, wind and temperature significantly affected the horizontal use of woodlots by all birds except female Downy Woodpeckers. This outcome supports the hypothesis that wind and temperature influence the suitability of forest fragments for winter use by permanent-resident woodland birds by occasionally restricting them to leeward portions of fragments. No statistical effects of wind and temperature on horizontal woodlot use were found for female Downy Woodpeckers because they did not approach the leeward edges of woodlots as closely as the other species. Perhaps female Downy Woodpeckers compensated adequately for wind by shifting to leeward sides of foraging substrates. This behavior was observed anecdotally, but was not quantified in this study. Bolstering this conjecture is Grubb's (1975) finding that female Downy Woodpeckers shifted to substrates of larger diameter as wind speed increased.

The relationship between distance from the windward edge and wind speed was most pronounced within the lowest temperature quartile. Such a pattern suggests that, except for female woodpeckers, flock members were sensitive to wind only when the temperature was below  $-6.0^{\circ}$ C, at least for the wind speeds we recorded. This interpretation must be made with caution, however, because our analysis was post hoc and exploratory. On one particularly cold day ( $-15.0^{\circ}$ C) with low wind speed (0.5 m sec<sup>-1</sup>), all individuals of the flock were on the windward edge of the woodlot, where one would not necessarily have predicted them to be. Further data are needed to quantify adequately

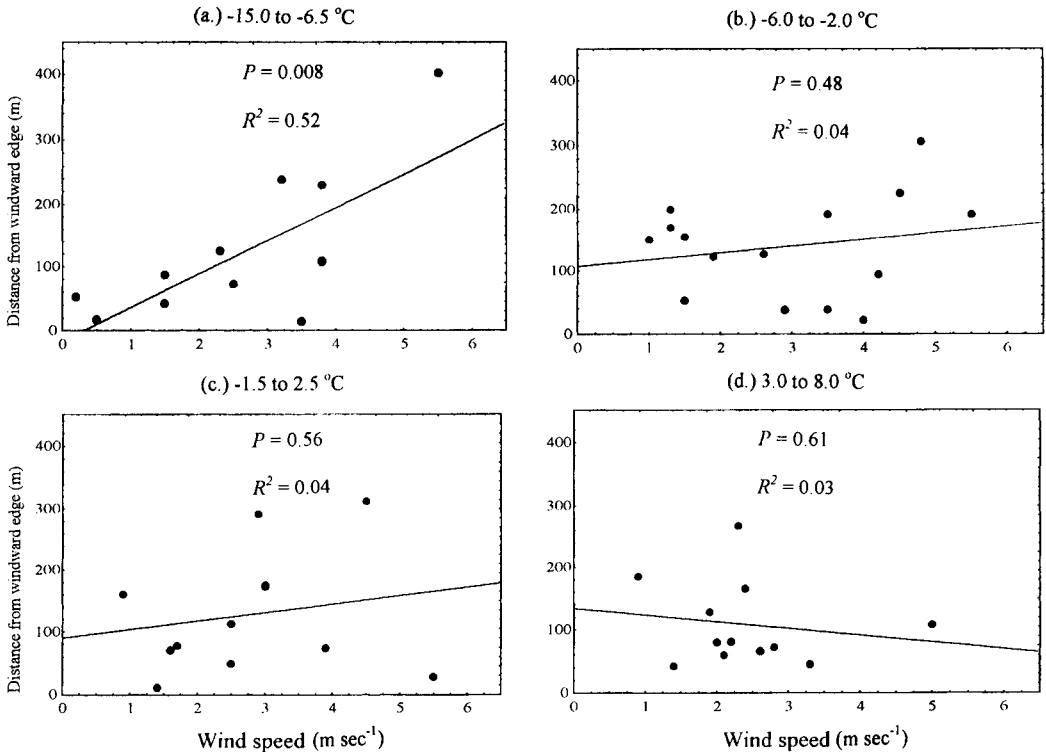


FIGURE 2. Regressions for the distance of Carolina Chickadees and Tufted Titmice from the windward edges of woodlots against wind speed. Regressions are blocked by temperature range quartiles (a-d).

the effect of wind on the use of woodlots at various temperatures.

Flocks were found in the leeward half of woodlots during nearly two-thirds of our visits, and the wind came from directions ranging between the south and west about two-thirds of the time. Thus, individuals seemed to be primarily confined to the eastern half of woodlots. As a consequence, food availability may have become restricted within this half of each woodlot as winter progressed. These conditions may have reduced the amount of suitable habitat available to individuals in the flock.

Average distances of the four focal species from the windward edges of woodlots ranged from 126–132 m. This may suggest that individuals not able to escape high winds despite reducing their heights in the canopy or shifting to leeward sides of substrates may disappear from very small woodlots during prolonged periods of severe winter weather. The smallest, and presumably the most sensitive species, Carolina Chickadee, most likely cannot survive prolonged exposure to temperatures below  $-10^{\circ}\text{C}$  at wind speeds greater than  $0.4\text{ m sec}^{-1}$  (Mayer et al. 1979). Such conditions were exceeded or approached to within  $2^{\circ}\text{C}$  on 12 of 66 (18.0%) woodlot visits. Thus, the potential exists for weather-related edge effects to cause mortality in chickadees, at least, in small woodlots.

As noted above, the distributions of species within

woodlots were not independent owing to the formation of mixed-species flocks (Morse 1970). Although one might predict that nuthatches and Downy Woodpeckers may be less responsive to wind and temperature than chickadees or titmice, nuthatches and Downy Woodpeckers usually follow chickadees and titmice during flock movements (Morse 1970; Dolby and Grubb, unpubl. data). In our study, mean wind speed was above and mean temperature was below the combination of wind speed and temperature at which chickadee metabolic rate peaks (Mayer et al. 1979). Therefore, on a typical day during our study period, Carolina Chickadees could be expected to compensate horizontally in response to wind (Grubb 1977). Even if nuthatches and Downy Woodpeckers could have tolerated conditions closer to windward edges, they may have been following chickadees into more leeward areas within woodlots, presumably to gain anti-predation and foraging advantages associated with social foraging (Morse 1977, Barnard and Thompson 1985). Thus, the responses of the satellite species to wind and temperature may have been exaggerated due to their following the nuclear species.

In addition to adjustments in horizontal or vertical use of woodlots, other factors undoubtedly help woodland birds avoid wind exposure. For example, dense understory vegetation near windward edges allows birds to make use of such areas (Grubb 1977). Telleria

and Santos (1995) suggest that such specialized habitat requirements are important determinants of fragment suitability for permanent resident birds in the Temperate Zone.

Yahner (1987) found no effect of fragmentation on the winter abundance of permanent resident birds. However, unlike our system of island woodlots, Yahner's (1987) landscape consisted of a "checkerboard" pattern of contiguous fragments, which presumably reduced the severity of wind exposure. Therefore, notwithstanding Yahner's (1987) findings, we conclude that the effects of wind and temperature may be important to models predicting the distribution of permanent resident bark-foraging birds in highly fragmented landscapes. Whereas female Downy Woodpeckers seem to be the least affected by wind and temperature, chickadees and titmice appear to be the most sensitive to these weather variables.

There is some evidence that Carolina Chickadees may be attracted to small woodlots during the fall and spring while weather conditions are benign, and may subsequently die in such woodlots during severe winter weather (Doherty and Grubb, unpubl. data). As a consequence, woodlots < 2.0 ha in size may act as population sinks for Carolina Chickadees inhabiting fragmented agricultural landscapes in the Temperate Zone.

Further investigation of the metabolic costs for birds wintering in fragments of different sizes is needed to assess the magnitude of abiotic edge effects. Additionally, detailed three-dimensional wind profiles would help to elucidate conditions experienced by birds in different parts of woodlots. Finally, more surveys within individual woodlots would reveal whether individuals are in fact consistently confined to restricted portions of small woodlots during winter.

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#### LITERATURE CITED

- ANDREN, H., AND P. ANGELSTAM. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544-547.
- BARNARD, C. J., AND D. B. A. THOMPSON. 1985. Gulls and plovers: the ecology and behaviour of mixed-species feeding groups. Croom Helm, London.
- BLAKE, J. G. 1987. Species-area relationships of winter residents in isolated woodlots. *Wilson Bull.* 99: 243-252.
- CHEN, J. Q., J. F. FRANKLIN, AND T. A. SPIES. 1992. Vegetation response to edge environments in old-growth douglas-fir forests. *Ecol. Appl.* 2:387-396.
- 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.
- HARRIS, L. D. 1988. Edge effects and conservation of biotic diversity. *Conserv. Biol.* 2:330-332.
- MAYER, L., S. LUSTICK, AND T. C. GRUBB JR. 1979. Energetic control of behavior: foraging in Carolina Chickadees. *Comp. Biochem. and Physiol.* 63:577-579.
- MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* 40: 119-168.
- MORSE, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27:332-339.
- PETERS, W. D., AND T. C. GRUBB JR. 1983. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. *Ecology* 64:1437-1443.
- PIERCE, V., AND T. C. GRUBB JR. 1981. Laboratory studies of foraging in four bird species of deciduous woodland. *Auk* 98:307-320.
- PORTER, W. P., AND D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* 39:227-244.
- TELLERIA, J. L., AND T. SANTOS. 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. *Biol. Conserv.* 71:61-67.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of eastern deciduous forest, p. 125-205. *In* R. L. Burgess and D. M. Sharp [eds.], *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- 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. 1987. Use of even-aged stands by winter and spring bird communities. *Wilson Bull.* 99: 218-232.
- YAHNER, R. H. 1988. Changes in wildlife communities near edges. *Conserv. Biol.* 2:333-339.