WEATHER-DEPENDENT FORAGING RATES OF WINTERING WOODLAND BIRDS

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ABSTRACT.—Foraging rates of birds wintering in an Ohio woodlot were dependent on proximate weather conditions. Increased wind velocity and decreased temperature resulted in increased time stationary (s/min), increased number of stops/min, and decreased distance travelled (m/min) for the Downy Woodpecker, Carolina Chickadee, Tufted Titmouse, and White-breasted Nuthatch. Wind velocity effects were heightened as temperature decreased. Analyses of avian community structure based on foraging behavior below the critical thermal environment are now suspect. Future studies of competition in winter must consider the impact of weather. *Received 1 October 1976, accepted 1 January 1977.*

THIS paper concerning weather-dependent foraging rates is part of a series (Grubb 1975, in press) on the effects of cold stress on avian feeding niches. Cody (1968, 1974) has used foraging rates as one means of analyzing community structure. Importantly, Cody's records were taken at the height of the breeding season when extremes in weather conditions were never present (M. L. Cody, pers. comm.). This paper explores the modification of species-typical foraging rates by winter weather.

Physiological models (e.g. Moen 1968, Porter and Gates 1969) suggest that below the lower critical temperature (about 25°C for small birds, Helms 1968), metabolic energy consumption should be directly related to the rate at which birds move while foraging. With more rapid progression a bird is, in effect, foraging in higher wind velocities, increasing convective heat loss (Porter and Gates 1969), and consequently energy output. Assuming that selection has favored behavioral patterns that allow birds to husband energy reserves while foraging "below" the critical thermal level (*sensu* Moen 1968), I tested the prediction that increasing wind velocities and decreasing temperatures in winter cause foraging birds to slow their average rate of movement and to spend more time stationary. Support for this reasoning comes from the rates of movement of wintering hereford cattle (*Bos taurus*), which have been shown to be negatively correlated with wind velocity (Malechek and Smith 1976). Because laboratory findings indicate that the metabolic cost of low temperature is moderated by artificial insolation (Lustick 1969, Lustick et al. 1970), I also checked for higher rates of foraging in sunlight than under cloud cover.

METHODS

From November to March 1975–76, I watched birds foraging in a 26-ha beech-maple woodlot in Bennington Township, Morrow County, Ohio. I watched only the four most abundant species, the Downy Woodpecker (*Picoides pubescens*), Carolina Chickadee (*Parus carolinensis*), Tufted Titmouse (*P. bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*), and kept separate records for the woodpecker sexes. During each 1–2 h study session, I walked different portions of the study area in randomized order. Foraging behavior was characterized with a slightly modified Cody (1968) technique. Individual birds were followed for 100 s intervals timed on one stopwatch. With a second stopwatch, I accumulated the number of seconds the bird was stationary during the interval. Concurrently, I tallied the number of times the bird stopped during the foraging sequence. Observation was terminated whenever a bird commenced activity (e.g. preening, social interaction) other than foraging before conclusion of 100 s. At the close of each bout, I estimated the length of the 100-s foraging route. The resulting foraging records do not differentiate among types of movement (walking, flying). From these sightings I calculated time spent stationary (s/min), number of stops/min, and distance travelled (m/min).
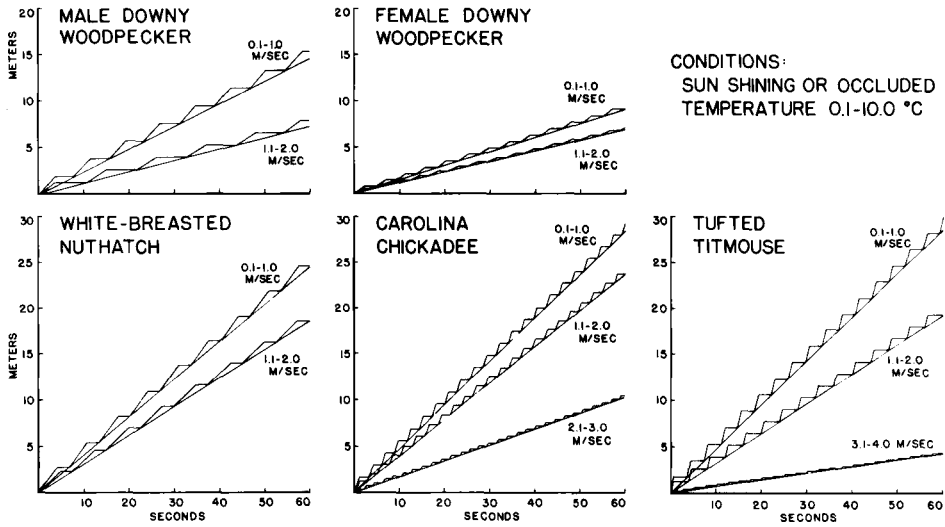
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Fig. 1. Wind velocity-dependent foraging curves for four bird species wintering in a deciduous woodlot. Wind velocities are shown in the figure. Each "sawtooth" consists of a sloped component representing the rate of an average individual movement and a flat component denoting the time span of an average stop. The diagonal common to all sawteeth marks the average foraging speed over 1 min.

Immediately following each sighting, I noted whether the sun was shining (defined as the presence of shadows) and measured wind velocity with a portable anemometer 2 m above the ground away from shrubs. Temperature was measured every hour and relative humidity at the end of each observation session; all readings were taken in the shade 2 m above the ground. Except for avoiding precipitation, I pursued field work regardless of weather. Thus, sample size differences throughout this report reflect prevailing weather conditions.

Relative humidity remained within such narrow limits during the study (range, 69–78%) that I lumped sightings irrespective of humidity when considering other weather variables. I determined the effect of sunlight, wind velocity, or temperature on foraging behavior by grouping sightings so as to hold the other variables constant or within narrow ranges. Analyses were restricted to sample sizes of at least 10.

RESULTS

I tested the effect of solar radiation on foraging in the five bird types across a total of 15 combinations of 10°C temperature ranges and 1 m/s wind velocity ranges. In no case did a significant difference occur between sunny and cloudy conditions in time stationary (s/min), stops/min, or distance (m/min) (t-tests, $P > .05$), nor were any clear trends apparent. I therefore grouped sightings irrespective of sunlight when examining wind and temperature.

Increased wind velocities slowed foraging rates (Fig. 1, Appendix 1). For instance, in temperatures from 0.1–10.0°C, the Tufted Titmouse spent 45.8 s stationary, stopped 16.5 times, and advanced 28.7 m during each minute of foraging in 0.1–1.0 m/s (0.2–2.2 mph) wind velocities, but remained motionless for 52.7 s, made 22.9 stops, and covered only 4.4 m per min in the higher wind speeds of 3.1–4.0 m/s (6.8–8.8 mph). Such changes in feeding technique were followed by the other species, occasionally significantly, and are illustrated with a sawtooth feeding graph (Fig. 1) styled after those of Cody (1968). The long diagonals denote overall progression during feeding. Each sawtooth consists of a more steeply sloped line representing an average individual movement and a component of zero slope marking the length of an aver-
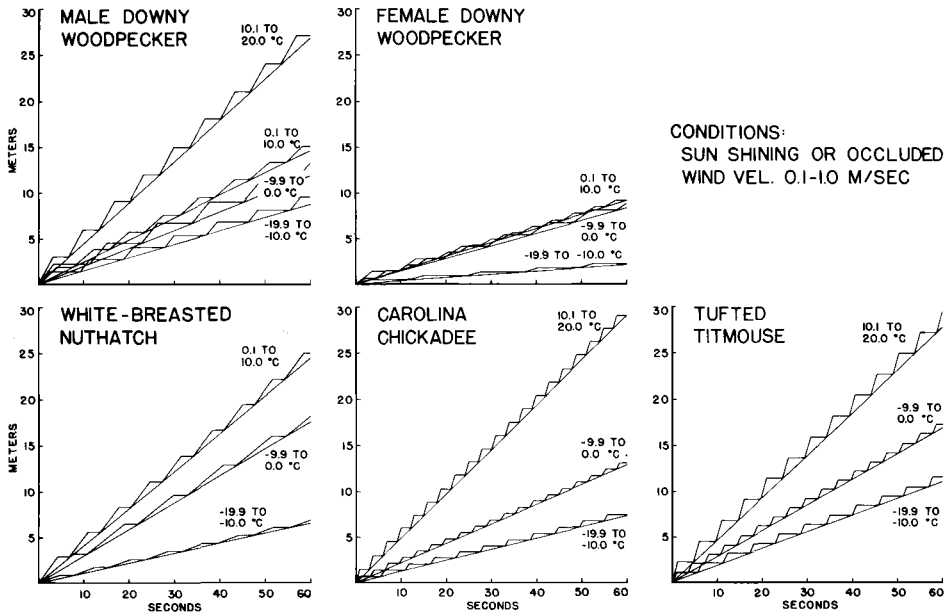
Fig. 2.   Temperature-dependent foraging curves for four bird species wintering in a deciduous wood-lot. Temperatures are shown in the figure. The "sawtooth" as in Fig. 1.

age stop. In general, higher wind speeds caused birds to decrease their overall progression through the woodland and either increase the number of short, rapid movements (female woodpecker, chickadee, titmouse) or retain about the same number of moves, but make them more slowly (male woodpecker, nuthatch).

Changing temperatures profoundly modified foraging (Fig. 2, Appendix 2). In wind velocities of 0.1–1.0 m/s, decreasing temperatures caused significantly increased time stationary, decreased number of stops, and reduced overall travel through the woodlot. These effects were often dramatic, e.g. a 30°C increase in temperature quadrupled the foraging speed of chickadees. Figure 2 summarizes graphically the increase in foraging speed with elevated temperature.

Linear regressions of chickadee and titmouse foraging rates on temperature for two wind velocity intervals are plotted in Fig. 3. The increasingly important effect of wind velocity as the temperature falls is apparent, especially for the titmouse. Notice how the weather conditions involved appear to influence the smaller chickadee more drastically, although the slopes are not statistically significantly different $(P > .05)$. Extending the regression to the abscissa suggests that the chickadee's foraging rate should theoretically be driven to zero before that of the titmouse, at least in 0.1–1.0 m/s wind speeds.

DISCUSSION

My criterion for sunshine (visible shadows) probably did not provide a fair test of solar radiation effects. Unfortunately, my manner of record keeping does not permit me to discard the intermediate cases of weak cloud cover and to compare sunlight in a cloudless sky with heavy overcast. I have previously found an effect of solar radiation on other foraging parameters (Grubb in press) and believe the same could still be true for feeding rates.
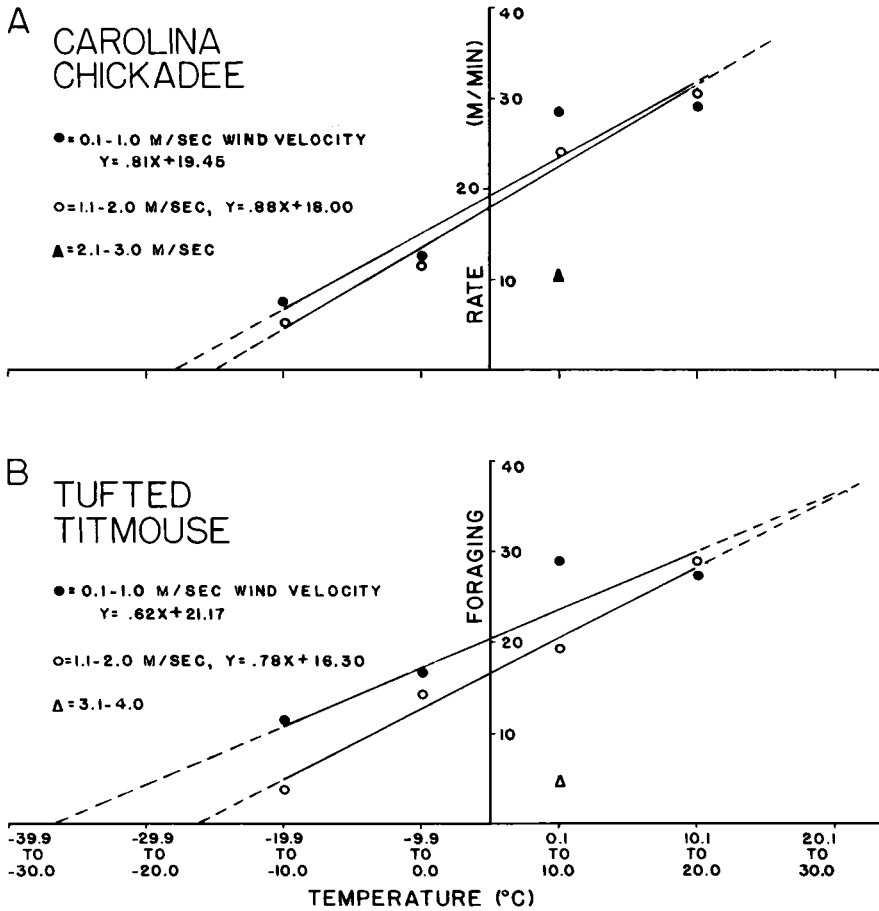
Fig. 3. Regression lines of foraging rate on temperature at two wind velocity ranges for two bird species wintering in a deciduous woodland.

Wind- and temperature-dependent foraging rates appeared influenced by shifts in foraging substrate. For instance, in higher wind velocities, the branch- and twig-foraging chickadee and titmouse descended more often to the ground to probe the leaf litter for fallen beech mast. This tactic led to the minutely-sectioned sawtooth curves characterized by many small, short hops (Fig. 1). By contrast, with worsening conditions male Downy Woodpeckers descended from moderately rapid foraging on small branches in the canopy to the leeward sides of large-diameter trunks and fallen logs (Grubb in press) where they engaged in rather sedentary sessions of cavity excavating (Figs. 1 and 2). The increased surface area of substrates used in harsher weather, rather than the weather itself, might sometimes account for a decrease in foraging rate. A bird looking for food should be able to scan more surface area without having to move while foraging on the ground, say, than on a twig. Further study is needed to determine if weather *per se* or a weather-induced increase in substrate surface area is the proximate cause of reduced foraging rates.

Analyses of avian community structure based on foraging behavior below the critical thermal environment are now suspect. In this and previous papers (Grubb 1975, in press) I have shown that such commonly employed foraging parameters as

height, substrate type, tree species, horizontal distribution, and foraging rate are all labile and weather-dependent. As many bird species may be limited by winter mortality (Fretwell 1972), the necessary future studies of competition in winter must consider the vicissitudes of weather.

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APPENDIX 1. Effect of wind velocity on foraging in temperatures from 0.1–10.0°C

Foraging measure	Bird type	Wind velocity (m/s)				P^a
		0.1–1.0	1.1–2.0	2.1–3.0	3.1–4.0	
Time stationary (s/min)	♂DW[b]	30.7 ± 14.5 (23)[c]	40.7 ± 19.2 (11)			ns
	♀DW	32.7 ± 10.7 (14)	28.8 ± 12.4 (15)			ns
	WBN	23.2 ± 10.0 (27)	21.0 ± 10.3 (15)			ns
	CC	43.2 ± 5.1 (29)	45.7 ± 4.2 (36)	45.3 ± 9.5 (10)		ns
	TT	45.8 ± 3.6 (31)	47.5 ± 7.6 (15)		52.7 ± 1.9 (10)	<.001
Stops/min	♂DW	7.6 ± 4.0 (23)	5.5 ± 4.8 (11)			ns
	♀DW	12.9 ± 11.8 (14)	14.0 ± 7.6 (15)			ns
	WBN	8.9 ± 5.4 (27)	7.9 ± 4.2 (15)			ns
	CC	21.3 ± 5.5 (29)	23.0 ± 6.0 (36)	28.2 ± 9.2 (10)		<.01
	TT	16.5 ± 4.3 (31)	14.6 ± 6.2 (15)		22.9 ± 8.8 (10)	<.01
Distance (m/min)	♂DW	14.6 ± 13.2 (23)	7.3 ± 8.6 (11)			ns
	♀DW	9.2 ± 9.4 (14)	7.0 ± 5.1 (15)			ns
	WBN	24.5 ± 26.5 (27)	19.3 ± 12.6 (15)			ns
	CC	28.4 ± 20.9 (29)	23.8 ± 14.3 (26)	10.4 ± 3.9 (10)		<.01
	TT	28.7 ± 20.3 (31)	19.3 ± 12.6 (15)		4.4 ± 3.7 (10)	<.001

[a] t-test comparisons of means from the lowest and highest wind velocity ranges available
[b] DW = Downy Woodpecker; WBN = White-breasted Nuthatch; CC = Carolina Chickadee; TT = Tufted Titmouse
[c] $\bar{X}$ ± SD(N)

APPENDIX 2. Effect of temperature on foraging in wind velocities from 0.1–1.0 m/s

Foraging measure	Bird type	Temperature (°C)				P^a
		−19.9 to −10.0	−9.9 to 0.0	0.1 to 10.0	10.1 to 20.0	
Time stationary (s/min)	♂DW[b]	45.0 ± 15.4 (31)[c]	40.4 ± 7.2 (13)	30.7 ± 14.5 (23)	30.3 ± 13.4 (15)	<.01
	♀DW	47.0 ± 12.6 (12)	35.7 ± 16.7 (25)	32.7 ± 10.7 (14)		<.001
	WBN	25.1 ± 13.8 (17)	17.5 ± 12.3 (26)	23.2 ± 10.0 (27)		ns
	CC	51.6 ± 10.5 (19)	45.6 ± 5.5 (39)	43.2 ± 5.1 (29)	46.0 ± 4.6 (28)	<.001
	TT	52.6 ± 4.0 (16)	43.4 ± 10.1 (31)	45.8 ± 3.6 (31)	46.2 ± 4.5 (10)	<.001
Stops/min	♂DW	6.4 ± 3.2 (31)	5.3 ± 3.8 (13)	7.6 ± 4.0 (23)	8.9 ± 2.6 (15)	<.05
	♀DW	4.8 ± 2.6 (12)	6.2 ± 3.8 (25)	12.9 ± 11.8 (14)		<.05
	WBN	7.6 ± 3.3 (17)	5.5 ± 2.8 (26)	8.8 ± 5.4 (27)		ns
	CC	10.8 ± 8.1 (19)	18.7 ± 6.4 (39)	21.3 ± 5.5 (29)	19.8 ± 6.1 (28)	<.001
	TT	10.6 ± 5.8 (16)	16.6 ± 5.4 (31)	16.5 ± 4.3 (31)	12.3 ± 3.9 (10)	ns
Distance (m/min)	♂DW	8.9 ± 13.1 (31)	12.0 ± 14.1 (22)	14.6 ± 13.2 (23)	27.0 ± 20.1 (15)	<.001
	♀DW	2.2 ± 2.2 (12)	8.3 ± 8.4 (25)	9.2 ± 9.4 (14)		<.05
	WBN	6.6 ± 4.8 (17)	17.7 ± 13.9 (26)	24.5 ± 26.5 (27)		<.01
	CC	7.4 ± 8.4 (19)	12.9 ± 9.7 (39)	28.4 ± 20.9 (29)	29.1 ± 16.1 (28)	<.001
	TT	11.2 ± 8.6 (16)	17.0 ± 9.5 (31)	28.7 ± 20.3 (31)	27.8 ± 8.7 (10)	<.001

[a] t-test comparisons of means from the lowest and highest temperature ranges available
[b] DW = Downy Woodpecker; WBN = White-breasted Nuthatch; CC = Carolina Chickadee; TT = Tufted Titmouse
[c] $\bar{X}$ ± SD(N)