WEATHER-DEPENDENT FORAGING BEHAVIOR OF SOME BIRDS WINTERING IN A DECIDUOUS WOODLAND

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Terrestrial organisms are surrounded by a microclimate composed of four independent variables: humidity, radiation, wind velocity, and air temperature (Porter and Gates 1969). The metabolic responses of animals to some of these climatic variables have been studied in the laboratory. For instance, below the lower critical temperature (about 25°C; Helms 1968) metabolic rates of birds are inversely correlated with ambient temperature (Kendeigh 1949, 1969, Steen 1958, Brooks 1968, Helms 1968, Kontogiannis 1968), but the metabolic cost of low temperature is moderated by artificial insolation (Lustick 1969, Lustick et al. 1970). Porter and Gates (1969) added air movement and derived theoretical "climate space" survival limits for the Cardinal (*Cardinalis cardinalis*) based on the thermal properties of a metallic, cylindrical surrogate Cardinal exposed to various combinations of radiation, air flow, and temperature. Humidity should also influence an animal's energetics through control of heat loss by evaporative cooling from moist tissues, but humidity effects have been little studied (Gates 1969).

Independent of studies of climatic variables and avian mètabolic responses, there is much literature about the foraging behavior of wild birds. Researchers have examined methods by which avian communities partition available food resources, thereby reducing interspecific or intersexual competition. Many studies have dealt with temperate-zone birds foraging in winter climates well below the lower critical temperature; all have failed to consider that the birds were seeking food in a thermally stressful environment (e.g., Odum 1942, Hartley 1953, Gibb 1954, Brewer 1963, Kilham 1965, 1970, Smith 1967, Jackson 1970, Morse 1970, Willson 1970, Austin and Smith 1972, Kisiel 1972, Tate 1973). Since birds might adjust foraging techniques to conserve energy within thermally stressful environments (Gates 1969), I decided to assess the effects of naturally occurring variation in relative humidity, solar radiation, wind velocity, and air temperature on the foraging of birds wintering in a temperate deciduous woods.

Due to increasing friction, wind speed diminishes with downward penetration into a forest, being least at ground level. I examined the premise that higher wind velocity, lower air temperature, lower relative humidity, and lower solar radiation cause foraging birds to gravitate toward decreased air movement, and reduced thermal stress, lower in a forest. I then checked the effect of humidity, sunlight, wind, and temperature on two other parameters of the foraging niche: the substrate on which foraging occurs (or "feeding station"; Lack 1971); and the tree species used during feeding. Finally, I examined the effects of increasing thermal stress on the diversity (Pielou 1966) of the foraging niche.

METHODS

From 15 November 1972 to 15 March 1973, I watched birds foraging in a 20-ha tract of floodplain woodland along the Black River in Somerset County, north-central New Jersey. As the study area was on flat ground and situated within an extensive forest, I hoped to eliminate variation in local climate due to topography and habitat "edges." The forest was dominated by red oak (*Quercus rubra*), swamp oak (*Q. bicolor*), and pin oak (*Q. palustris*), tuliptrees (*Liriodendron tulipifera*), and ashes (*Fraxinus* spp.). Relative frequencies of tree (> 15 cm dbh) species were found using the point-quarter method (Cottam et al. 1953). Red maples (*Acer rubrum*) and spicebush (*Lindera benzoin*) accounted, respectively, for most of the sapling and shrub layers. Virginia creeper (*Parthenocissus quinquefolia*) and grape (*Vitis* spp.) vines were abundant.

I watched only the four most abundant bird species: the Downy Woodpecker (*Dendrocopos pubescens*), Black-capped Chickadee (*Parus atricapillus*), Tufted Titmouse (*P. bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*). Male and female Downy Woodpeckers were classed separately as this species alone could be sexed in the field.

Birds were sighted from a regular transect route. At each sighting, foraging height, foraging substrate (trunk, branch, etc.), and tree species were noted. I counted an individual bird more than once only if it flew to another tree or more than 5 m within the shrub layer. No attempt was made to follow a bird away from the transect route; resting and preening birds were ignored.

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[2] Dedicated to my mentor and friend, John T. Emlen, on the occasion of his retirement.

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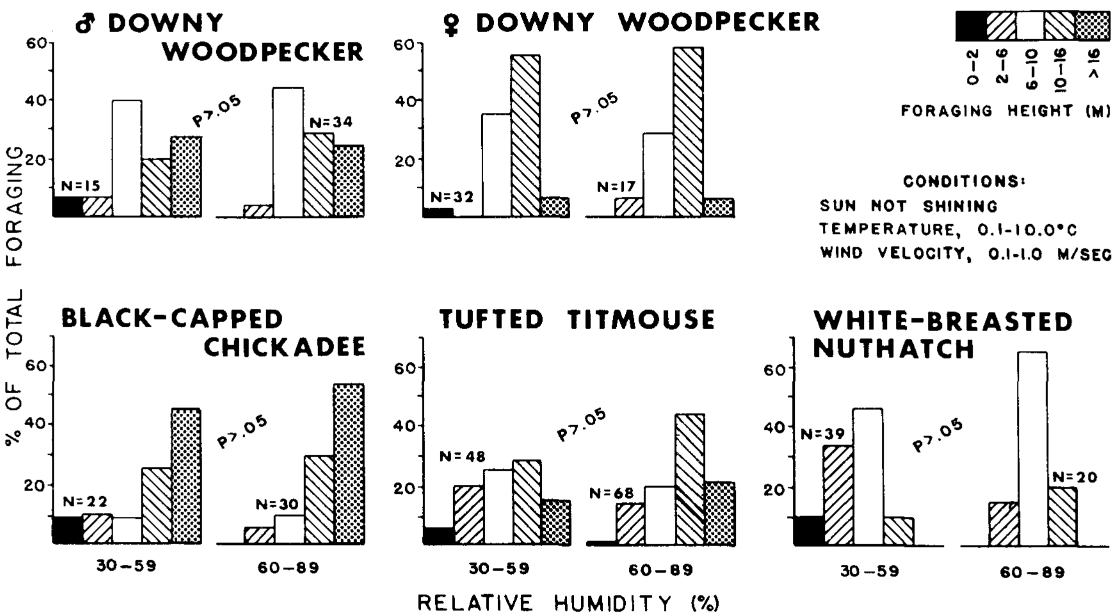

FIGURE 1. Influence of relative humidity on foraging heights. Probabilities of randomness from two-sample χ^2 tests are shown between adjacent plots.

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 rain and snow, I pursued field work irrespective of weather. Thus, sample size differences throughout this report reflect prevailing weather conditions.

I determined the effect of each climatic variable on foraging behavior by grouping sightings so as to hold the other variables constant or within narrow ranges. All analyses were restricted to sample sizes of at least 15, and χ^2 tests to cases where at least 80% of expected values were 5 or more (Siegel 1956).

RESULTS

FORAGING HEIGHT

Relative humidity and air temperature did not vary independently during the study period. High pressure systems brought both low temperature and low relative humidity; low pressure systems brought warmer weather and higher relative humidity. For this reason, the effects of humidity could be examined only for an intermediate temperature range. In relative humidities of 30–59%, all birds tended to forage lower in the forest than they did in relative humidities of 60–89% (fig. 1). The trend was best developed in male Downy Woodpeckers, Black-capped Chickadees and Tufted Titmice, foraging at greatest height, but no difference was significant ($P > 0.05$). Lack of relative humidities below 30 or above 89% prevented further assessment of humidity.

Comparison of foraging-height distribution in sunlight and under cloudy skies revealed no significant differences ($P > 0.05$), nor was there any clear trend across species. Chickadees and nuthatches foraged slightly higher under sunny skies, male and female woodpeckers and titmice, slightly lower. As relative humidity and solar radiation did not influence foraging height significantly, I grouped sightings irrespective of humidity and sunlight in examining effects of wind and temperature.

All species were driven down significantly by both decreasing temperature and increasing air movement (fig. 2). The three types foraging mainly on small branches (see Foraging Substrate)—male woodpeckers, chickadees, and titmice—were most severely affected. For instance, in a temperature-wind regime of 0.1–10.0°C and 0.1–1.0 m/sec only 3% of titmice foraged 2 m or less from the ground, while in –9.9–0.0°C and 2.1–3.0 m/sec 73% did so. The trend downward was less marked in female woodpeckers and nuthatches, which seldom foraged at great height under any conditions. Since nonsignificant two-sample χ^2 tests generally involved the smaller sample sizes, it appears that changing responses to wind and temperature were biologically meaningful even where not statistically significant. An exception occurs in winds of 0.1–1.0 m/sec where temperatures of –9.9–0.0°C and 0.1–10.0°C differed only slightly in effect on chick-

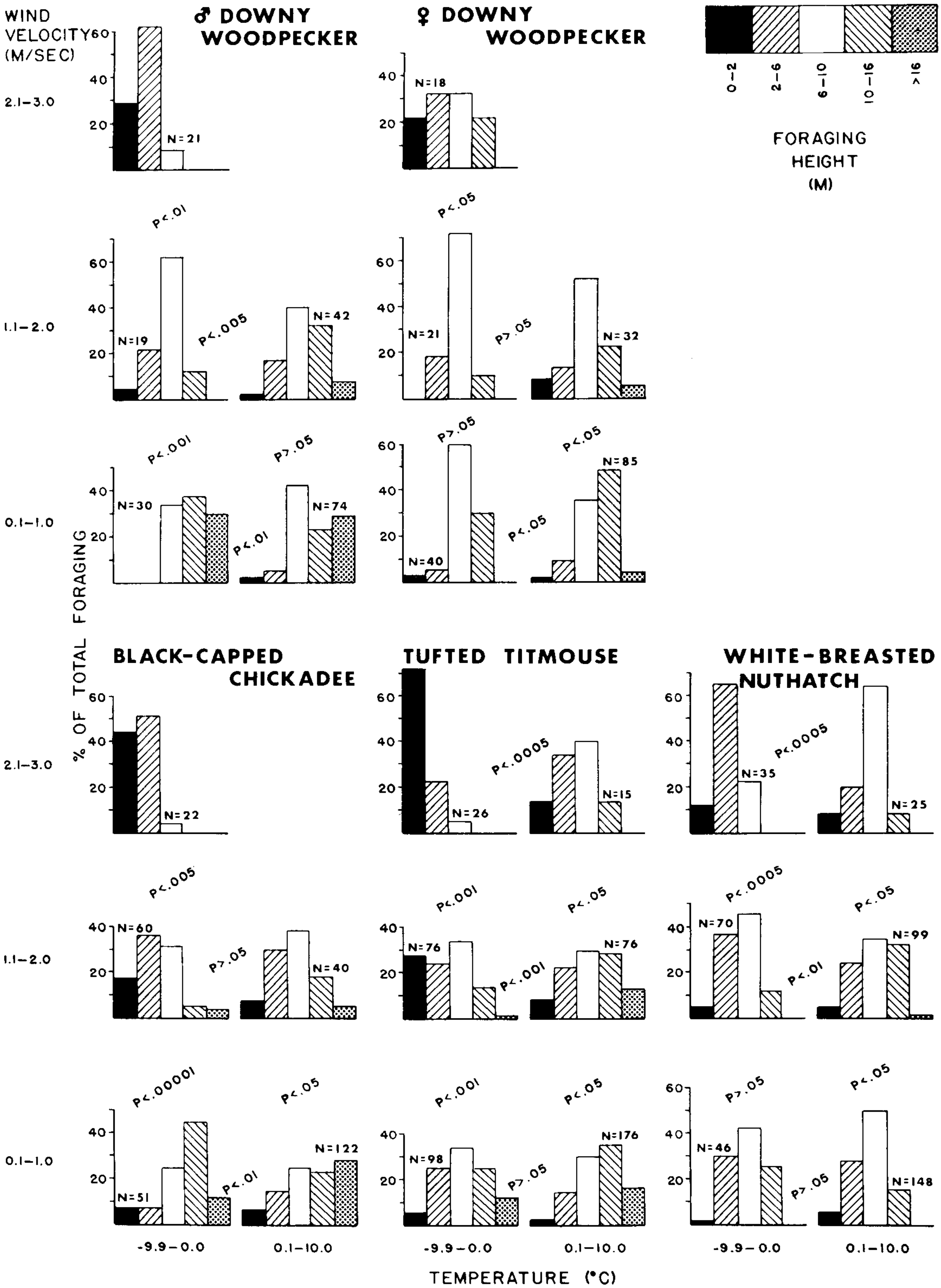

FIGURE 2. Influence of temperature and wind on foraging heights. Probabilities of randomness from two-sample χ^2 tests are shown between adjacent plots.

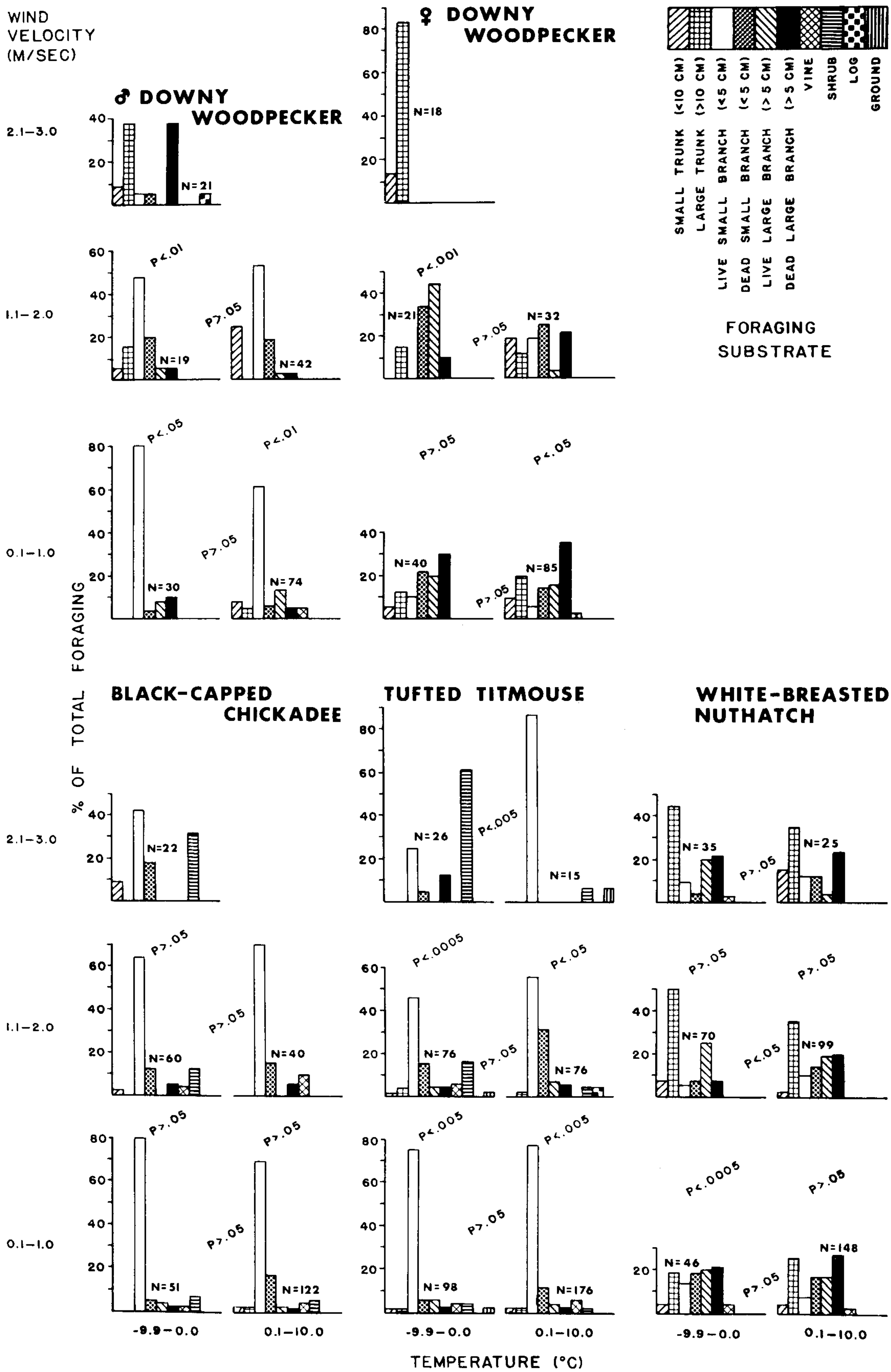
WIND VELOCITY (M/SEC)
♂ DOWNY WOODPECKER
♀ DOWNY WOODPECKER
BLACK-CAPPED CHICKADEE
TUFTED TITMOUSE
WHITE-BREASTED NUTHATCH
2.1–3.0
1.1–2.0
0.1–1.0
% OF TOTAL FORAGING
SMALL TRUNK (<10 CM)
LARGE TRUNK (>10 CM)
LIVE SMALL BRANCH (<5 CM)
DEAD SMALL BRANCH (<5 CM)
LIVE LARGE BRANCH (>5 CM)
DEAD LARGE BRANCH (>5 CM)
VINE
SHRUB
LOG
GROUND
FORAGING SUBSTRATE
N=21
N=18
N=19
N=42
N=21
N=32
N=30
N=74
N=40
N=85
N=22
N=26
N=15
N=35
N=25
N=60
N=40
N=76
N=76
N=70
N=99
N=51
N=122
N=98
N=176
N=46
N=148
P<.01
P>.05
P<.001
P<.05
P<.005
P<.0005
-9.9–0.0
0.1–10.0
TEMPERATURE (°C)

TABLE 1. Indices of foraging diversity (J') for two combinations of temperature and wind.[a]

Component of foraging niche	Bird type				
	♂ Downy Woodpecker	♀ Downy Woodpecker	Black-capped Chickadee	Tufted Titmouse	White-breasted Nuthatch
Height	*0.54 (0.78)*[b, c]	0.87 (0.71)	*0.52 (0.95)*	*0.43 (0.88)*	*0.53 (0.72)*
Substrate	0.61 (0.58)	*0.20 (0.73)*	0.55 (0.45)	0.44 (0.40)	*0.63 (0.73)*
Tree species	0.88 (0.71)	*0.24 (0.70)*	*0.46 (0.85)*	– (0.82)	*0.66 (0.80)*

[a] Sample sizes are from figures 2–4.
[b] The first number is J' for severe weather, –9.9–0.0°C temperature and 2.1–3.0 m/sec wind velocity; the number in parentheses is J' for milder weather, 0.1–10.0°C and 0.1–1.0 m/sec.
[c] Italics denote less diversity in more severe weather.

adees, titmice, and nuthatches in spite of large sample sizes.

FORAGING SUBSTRATE

Variation in sunlight and relative humidity did not significantly influence the choice of foraging substrate ($P > 0.05$). These weather variables were ignored in treating responses to wind and temperature.

Temperature and air movement significantly affected the birds' selection of where to forage (fig. 3). Two major trends emerged. Nuthatches and woodpeckers of both sexes shifted to larger branches and trunks with lower temperature and higher wind speed. The trend for female woodpeckers was interrupted at 1.1–2.0 m/sec by increased use of the umbrellas of small dead branches at the base of pin oaks, but they resumed the shift toward trunks in higher wind velocities. In contrast, chickadees and titmice remained primarily on small branches but retreated from twigs of trees to twigs of shrubs as temperature dropped.

TREE SPECIES

In considering the kinds of trees used in foraging, sunlight and relative humidity were found to have no significant effect ($P > 0.05$). Thus, wind velocity and temperature were analyzed, ignoring variation in the first two weather variables.

Wind and temperature greatly influenced the tree species used for foraging (fig. 4). Those birds which changed foraging height drastically—male woodpeckers, chickadees, and titmice—also changed their tree preference. As weather became more severe (–9.9–0.0°C and 2.1–3.0 m/sec), the male woodpeckers' strong reliance on ashes switched to rather equal use of all trees, with slight tendencies toward oaks and tuliptrees. Conversely, chickadees and titmice used a wide variety of trees in milder weather, but with colder weather they resorted to oaks and maples.

Female Downy Woodpeckers foraged catholically in mild weather, but worked on oaks almost exclusively (86%) at –9.9–0.0°C and 2.1–3.0 m/sec. Nuthatches used about the same proportions of the various tree species in all weather classes.

FORAGING DIVERSITY

Weather conditions may influence a bird's tendency to concentrate activity within certain components of its foraging niche. Such weather effects were measured using the information theory index:

$$H' = \sum_{i=1}^{s} p_i \log p_i,$$

where p_i denotes the proportion of sightings in category i, s denotes the number of alternative foraging categories, and H' denotes the diversity in the sample. All values are presented as the ratio, $J' = H'/H'_{max}$ (Pielou 1966) where H'_{max} represents maximum diversity, i.e., all categories are used equally. Thus, J' varies between 0 and 1, with a low value indicating a strong specialist. As relative humidity and solar radiation were insignificant in influencing foraging height, substrate, or tree species, I have disregarded them in calculating J' values.

Indices of foraging diversity for the three components of the foraging niche under the two extreme combinations of temperature and wind are shown in table 1. Most of the birds

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FIGURE 3. Influence of temperature and wind on foraging substrates. Probabilities of randomness from two-sample χ^2 tests are shown between adjacent plots.

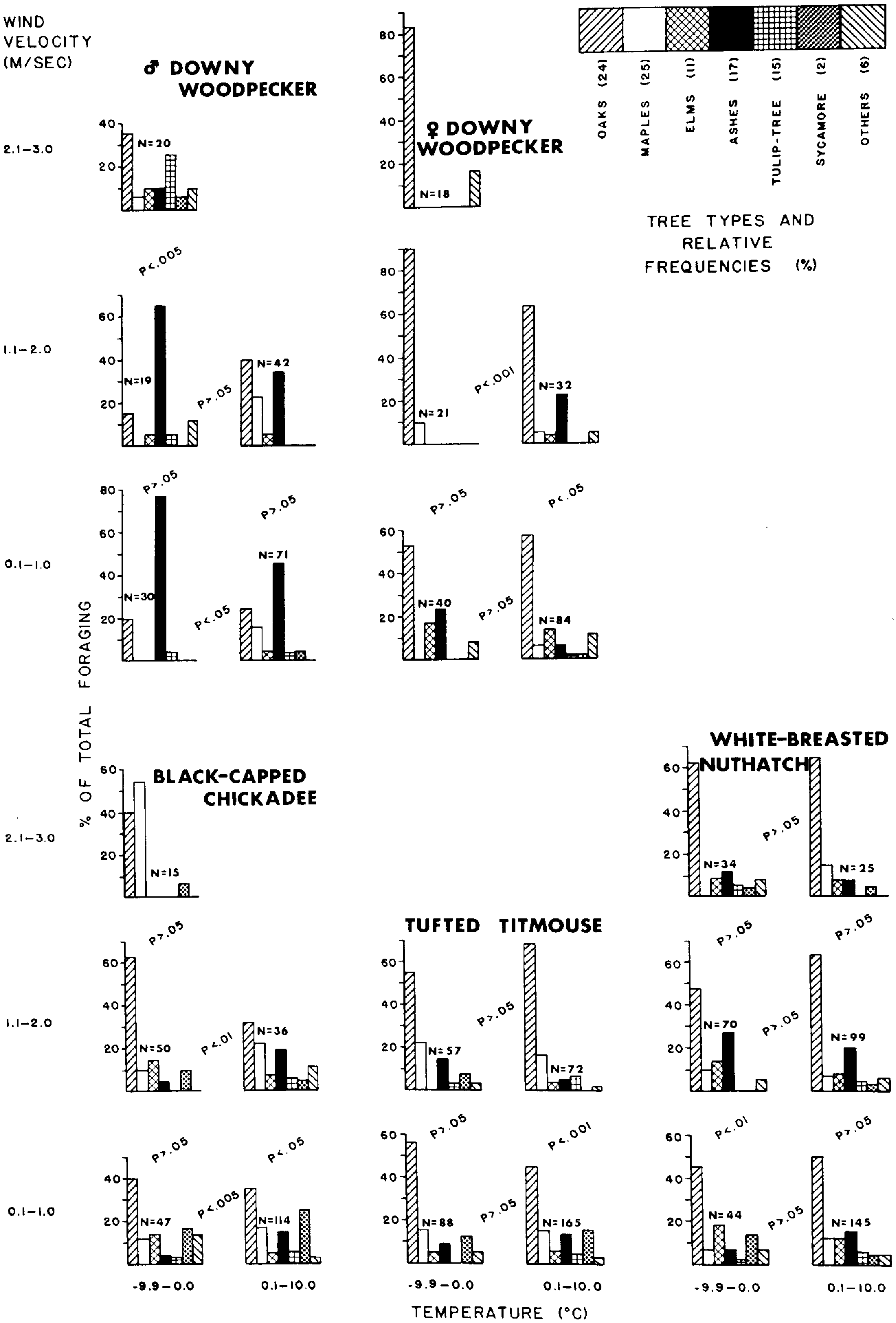

FIGURE 4. Influence of temperature and wind on tree species selected for foraging. Probabilities of randomness from two-sample χ^2 tests are shown between adjacent plots. Relative frequencies of trees are based on 62 sample points.

were more restricted in height and tree species in the severe weather of –9.9–0.0°C and 2.1–3.0 m/sec than in milder conditions (0.1–10.0°C and 0.1–1.0 m/sec). This trend toward less diversity in colder, windier weather was reversed for foraging substrate in which three of the five bird types were more diverse under more severe conditions.

Except for nuthatches, no birds became more restricted in all three foraging parameters in colder weather. The Downy Woodpecker sexes showed opposite responses. Males in milder weather were more diverse in height, but less diverse in substrate and tree species; the reverse was true for females. Chickadees and titmice reacted similarly—less height diversity and more substrate diversity in severe weather—but complete comparison is hampered by an insufficient sample of tree species for the titmice.

DISCUSSION

Relative humidity and solar radiation were not significant modifiers of avian foraging. The trend toward lower foraging heights in drier weather (fig. 1) is consistent among the bird species; it suggests that relative humidities less than the recorded minimum of 30% might influence foraging significantly.

Solar radiation may affect foraging in other ways than those measured. For instance, birds may forage more in sunlight than in shade in colder, windier weather. Lawrence (1958) noticed that Black-capped Chickadees tended to rest only in sunlight at very low temperatures.

The birds adjusted to cooler, windier weather in several ways which apparently lessened their exposure to wind. These strategies changed significantly the foraging height (fig. 2), foraging substrate (fig. 3), and/or tree species used (fig. 4). Male woodpeckers used small branches high in the canopy of ashes in mild weather and gradually shifted, in colder, windier weather, to large trunks and dead large branches low in a variety of trees. Female woodpeckers concentrated on dead, large branches of oaks at 6–16 m in warm, calm conditions, but descended to work on large oak trunks in –9.9–0.0°C and 2.1–3.0 m/sec weather. It is my impression that the woodpeckers' change to larger trunks and branches in more severe weather was accompanied by an attempt to stay on the leeward side of these large substrates.

Chickadees and titmice responded in similar fashion to colder weather, the titmice more extensively. In mild weather, both concentrated on small, live branches high in the canopy, the titmice slightly lower than the chickadees. Unfortunately, my classification of substrates failed to show the chickadees' tendency to forage farther out in the canopy on smaller twigs than did the titmice. A subdivision of small branches into those greater or less than 1 cm would have been helpful. Both species descended with lower temperature and higher wind until at –9.9–0.0°C and 2.1–3.0 m/sec they were concentrated in a narrow band low in the woods, attending shrubs heavily (32% of chickadee sightings; 62% for the titmice). At low temperatures, I watched chickadees and titmice plunge vertically into the depths of the shrub layer with each wind gust, only to rebound upward several meters onto the more exposed small branches of trees during calm intervals. Tree species (e.g., tuliptree, sycamore) found infrequently as seedlings and saplings were used less as chickadees and titmice descended from the canopy in more severe weathei.

White-breasted Nuthatches were least affected by weather variation. In the mildest conditions this species preferred large trunks and dead, large branches of oaks at 6–10 m. In the most severe weather nuthatches relied more on large oak trunks slightly nearer the ground (2–6 m). Again, it would have been worthwhile to measure the increased use of leeward sides of trunks and large branches as the weather worsened.

The diversity computations suggest compensatory foraging behavior in severe weather. In chickadees, titmice, and male woodpeckers, when height and/or tree diversity diminished in more severe weather, foraging substrate diversity increased. For female woodpeckers, decreased diversity of foraging height in worsening weather was replaced by decreased substrate diversity. Nuthatches became restricted in all three foraging measures in severe weather.

These results indicate that weather conditions must be considered when investigating avian foraging ecology, at least in conditions below the lower critical temperature. Foraging behavior probably varies at any given location, and among different sites as a consequence of temporal and spatial variation in local weather.

SUMMARY

I studied the influence of relative humidity, solar radiation, air temperature, and wind

velocity on winter foraging of the Downy Woodpecker, Black-capped Chickadee, Tufted Titmouse, and White-breasted Nuthatch. Lower temperature and higher wind velocity produced significant changes in three foraging parameters: height in the trees, substrate used (tree trunks, shrubs, etc.), and tree species selected.

Except for the nuthatch, decreased diversity (J') in one or two foraging parameters with more severe weather was accompanied by increased diversity in the third parameter.

The results indicate that weather conditions should be considered in studies of avian foraging ecology.

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