Weather-dependent Mixed-species Flocking During the Winter

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The hypotheses to explain why birds enter mixed-species flocks focus on reduction in predation risk or increase in food-gathering efficiency. Predation may be reduced by the selfish-herd effect (Hamilton 1971), the confusion effect (Morse 1980), or the increased aggregate vigilance resulting from many individuals being alert to predators (Pulliam 1973).

Foraging efficiency may increase in flocks because birds in the same guild (Root 1967) may be less likely to forage in an area already searched (Short 1961, Morse 1970, Cody 1971). Some birds may join to "steal" food from subordinate birds, as demonstrated by frequent supplanting of foraging individuals in flocks (Morse 1970, B. Klein pers. obs.). Furthermore, by sharing information, flocks could potentially find dispersed, clumped food resources more efficiently than individuals (Thompson et al. 1974). In some cases birds in flocks may both increase foraging efficiency and decrease predation risk (Morse 1977).

If mixed-species flocking increases foraging efficiency, and if birds increase food intake during periods of low temperature (Kendeigh et al. 1969), then one would expect a corresponding increase in mixed-species flocking with a decrease in temperature. I was able to test this hypothesis serendipitously when a sudden cold front decreased the mean daily temperature about 9°C during a study of mixed-species flocks in central New York.

Observations were made during 1983 between 0800 and 1630 in the Arnot Forest, a 1,619-ha teaching and research center located on the border between Tompkins and Schuyler Co. near Van Etten, New York. The study area was a young to middle-aged beech (*Fagus grandifolia*), maple (*Acer saccharum* and *A. rubrum*), and hemlock (*Tauga canadensis*) forest. A red pine (*Pinus resinosa*) plantation was present on the northern border of the study area. The elevation ranged from 415 to 564 m. Birds commonly found in heterospecific flocks there include the White-breasted Nuthatch (*Sitta carolinensis*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*P. villosus*), Golden-crowned Kinglet (*Regulus satrapa*), Brown Creeper (*Certhia americana*), and Black-capped Chickadee (*Parus atricapillus*). Chickadees have been shown to maintain a relatively stable flock (Wallace 1941, Hartzler 1970, Glase 1972), so I assumed the chickadees I observed formed a stable nucleus that other birds entered and departed.

I made all observations along four parallel transects of equal length (1.4 km, spaced about 1 km apart). A regular route was walked with a different starting transect each day, resulting in equal time per transect. When a flock was found along a transect, I followed it for 10-20 min to determine the number of individuals of each species in the flock. I then returned to the location on the transect where I had first observed the flock and continued in the original direction. In most instances the flocks moved in a direction away from my line of travel, or were slower than I, so the same flock was not observed within a short time period. In some cases the number of chickadees had to be estimated, but in all cases the number of "nonchickadees" was determined accurately. Nonchickadees were considered part of the flock if they followed or were followed by heterospecifics. Traveling all transects once usually required most of the day. If parts were walked more than once, at least 4-5 h separated the visits. Flocks were observed 52 times during 92 h spent walking transects. From repeated observations of flocks in particular parts of the study area, I estimated that at least 3-5 flocks of chickadees had territories wholly or in part on the study area.

Temperature and solar-radiation data were collected continuously at the Arnot Forest weather station, located 760 m from the study area. I sampled temperature readings every 2 h and solar-radiation readings every daylight hour for each 24-h period from 8 to 21 January.

Each day yielded 12 temperature values and 9 solar-radiation values (solar-radiation values from 0900 to 1700), which were used to calculate one mean daily temperature and solar-radiation value. The solar-radiation and temperature data were grouped into two periods: one of warm weather (8-11 January) and one of cold weather (12-21 January).

On the evening of 11 January temperatures decreased rapidly, and a small amount of snow accumulated (<5 cm). This was the only snow on the ground, which was unusual for the area at that time of year. During the evening of 14 January the first large snowfall of the month occurred, with 13-15 cm of accumulation.

Of the 52 observations of flocks, 21 were made January 8-11 and 31 between 12 and 21 January. Median daily temperatures differed significantly between the two periods (Mann-Whitney *U*-test, $U = 4.5$, $P < 0.05$, two-tailed). The mean temperature during 8-11 January was -0.38 ± 2.56°C. From 12 to 21 January the temperature dropped to -9.17 ± 4.36°C. There was no significant difference in the measured solar radiation between warm (0.32 ± 0.17 $\mathrm{cal \cdot cm^{-2} \cdot min^{-1}}$) and cold periods ($0.33 \pm 0.18$ $\mathrm{cal \cdot cm^{-2} \cdot min^{-1}}$; Mann-Whitney *U*-test, $U = 19.5$, $P > 0.05$, two-tailed).

There was no significant difference in the number of chickadees per flock between the warm (6.07 ± 1.07) and cold periods (6.48 ± 1.26, Mann-Whitney *U*-test, $U = 104.5$, $P > 0.05$, two- tailed), but there was a highly significant difference between the propor-

TABLE 1. Frequency that species other than chickadees were found in chickadee flocks at the Arnot Forest, New York, during a warm period (8–11 January 1983, $n = 21$ flocks) and a cold period (12–21 January 1983, $n = 31$ flocks).

	8–11 January		12–21 January	
	Percentage of flocks with at least 1 individual	No./flock ($\bar{x} \pm$ SD)	Percentage of flocks with at least 1 individual	No./flock ($\bar{x} \pm$ SE)
White-breasted Nuthatch	9.5	0.10 ± 0.30	25.8	0.39 ± 0.72
Golden-crowned Kinglet	0.0	0	22.6	0.45 ± 0.93
Downy Woodpecker	14.3	0.19 ± 0.51	51.6	0.65 ± 0.71
Hairy Woodpecker	4.8	0.05 ± 0.22	16.1	0.23 ± 0.56
Brown Creeper	4.8	0.05 ± 0.22	6.5	0.13 ± 0.50
Total (at least 1 nonchickadee)	23.8	0.38 ± 0.92	77.4	1.84 ± 1.64

tion of flocks that included nonchickadee species during the two periods ($\chi^2 = 14.5$, $P < 0.005$; Table 1). Each species that joins chickadees occurred in mixed flocks more frequently during the cold than during the warm weather (Table 1).

These results support the hypothesis that mixed-species flocking increases during times of increased energy demand. This correlation is consistent with the explanation that heterospecific flocking increases foraging efficiency alone or in combination with predation protection (Morse 1977, Berner and Grubb 1985, Grubb 1987). The results agree with Grubb's (1987) study, but Rybczyski (1977) found no overall correlation between weather and flock participation. This may have been due to the inclusion of birds that commonly do not participate in mixed-species flocks (e.g. Northern Flicker, *Colaptes auratus*; Pileated Woodpecker, *Dryocopus pileatus*; Red-bellied Woodpecker, *Melanerpes carolinus*; Yellow-bellied Sapsucker, *Sphyrapicus varius*), which could have masked significant differences for species more prone to participating in flocks. In addition, Rybczyski correlated flocking and weather over a relatively long period of time during which behavioral changes may have altered the degree to which birds associated in mixed-species flocks, independent of weather.

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