ENVIRONMENTAL INFLUENCES UPON AGGRESSIVE BEHAVIOR IN WINTERING JUNCOS

By Ellen D. Ketterson

Frequency of occurrence of certain animal behavior patterns has been shown to vary with geography (Arnold, 1977), with time of day and season, and with weather conditions (Verbeek, 1964; Grubb, 1978). In short, environmental conditions influence behavioral repertoires of individuals and populations.

Feeding rate in wintering White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) and Black-capped Chickadees (*Parus atricapillus*) is responsive to time of day and weather; it is higher early in the day, when day length is short, and on cold days (Morton, 1967; Kessel, 1976). These species, and probably other wintering passerines, apparently spend more time feeding (1) if they have recently fasted, (2) if feeding time is short, or (3) if physiological maintenance costs are high.

Aggressive behavior in small birds also varies in response to environmental variables, particularly temperature (Hinde, 1952; Stokes, 1962; Pulliam et al., 1974; P. M. Dolan, unpubl.). Among aggregations whose individuals have dominant-subordinate relations, if aggressive behavior is utilized by dominants to assure themselves priority of access to food, then one might expect frequency of aggressive behavior to vary in parallel with feeding rate and factors associated with feeding rate. That is, environmental conditions that cause feeding rate to be high should also result in an increase in the rate of aggression. Indeed Hinde (1970) suggested that aggressive behavior occurs more frequently when weather is cold and food is scarce, but other workers have reported a decline in aggressive behavior at very low air temperatures (Sabine, 1959; Pulliam et al., 1974; Kessel, 1976; P. M. Dolan, unpubl.). In the present study of wintering Dark-eyed Juncos (*Junco hyemalis*) at a baited station, I investigated the relationship among feeding rate (as estimated by measuring attendance at a baited station), frequency of aggressive behavior, and environmental conditions.

METHODS

In early January 1974, a 1.8 × 2.5 m ground-feeding area was established near a house 2 km north of Bloomington, Indiana. This study site was surrounded by extensive woods, large brushy areas, and open fields that were interrupted by occasional houses and yards. The feeding area was kept uniformly and heavily baited with cracked corn and commercial wild bird seed. Observations were made from a window approximately 2 m from the feeding area.

Juncos began to feed at the site soon after baiting began. The largest number of individuals seen there at one time during the study was 30, which, on the basis of previous experience with juncos, suggests that the total number coming to the feeder was about 60 (Ketterson, Ms). The evidence is that most of these were regular visitors. Some wore bands put on before the study began, and systematic trapping and banding in late February revealed that by that date the flock in the vicinity of the study site had a stable membership. Presumably the sex-age structure was typical for the region (65% males, 70% birds hatched the preceding breeding season, regardless of sex), because Nolan and Ketterson (unpubl. data) have found very little variation in the population structure of juncos studied in diverse habitats near Bloomington. Juncos far outnumbered any other species visiting the feeding area.

Data were collected between 24 January and 25 February, in 39 observation periods of 30 minutes duration. During an observation period, the number of juncos within the feeding area was tabulated every 60 seconds; mean density was then computed for each period. Frequency of aggressive behavior (hereafter, displacement rate) was determined by recording the occurrence of every displacement, then calculating the sum for each 30-minute period. Also noted were time of day, temperature at the beginning of the observation period (obtained from a recording station located 2 km to the south), cloud cover (coded 0 for full sun, 1 for partly cloudy, 2 for full cover), and air flow (coded 0 for still, 1 for breezy, and 2 for windy). Snow condition was recorded as absent, falling, or covering the ground but not falling. The feeding area was kept clear of snow. Estimates of day length at 40°N latitude (Bloomington is at about 39°N) were obtained from the Nautical Almanac for 1974.

Mean density, displacement rate, and temperature met loose requirements for normality (K-S D_{max} test, $P > 0.1$; G_1 and G_2 included zero within their 95% confidence limits); the other variables did not meet these requirements.

RESULTS AND DISCUSSION

Employing nonparametric correlation as a measure of relationship, mean density was highest during observations made early in the day, when it was cold, and when it was cloudy (Table 1, Fig. 1). The role of snow as a determinant of mean density is less clear. Density was the same whether snow was falling or absent, but both these conditions resulted in higher densities than when snow covered the ground but was not falling (Table 2); to avoid confounding effects of temperature, only observation periods where air temperature $\leqslant 0$°C were considered. Perhaps ground-feeding species respond to snow cover by waiting until conditions ameliorate rather than attempting to feed.

Displacement rate, like mean density, was highest early in the day, when it was cold, and when it was cloudy (Table 1, Fig. 2). Response of displacement rate to snow was also like that of mean density; displacements occurred less frequently during periods of snow cover than when snow was falling or absent (Table 2).

The similar responses of mean density and displacement rate to the environmental conditions measured can be explained by proposing that

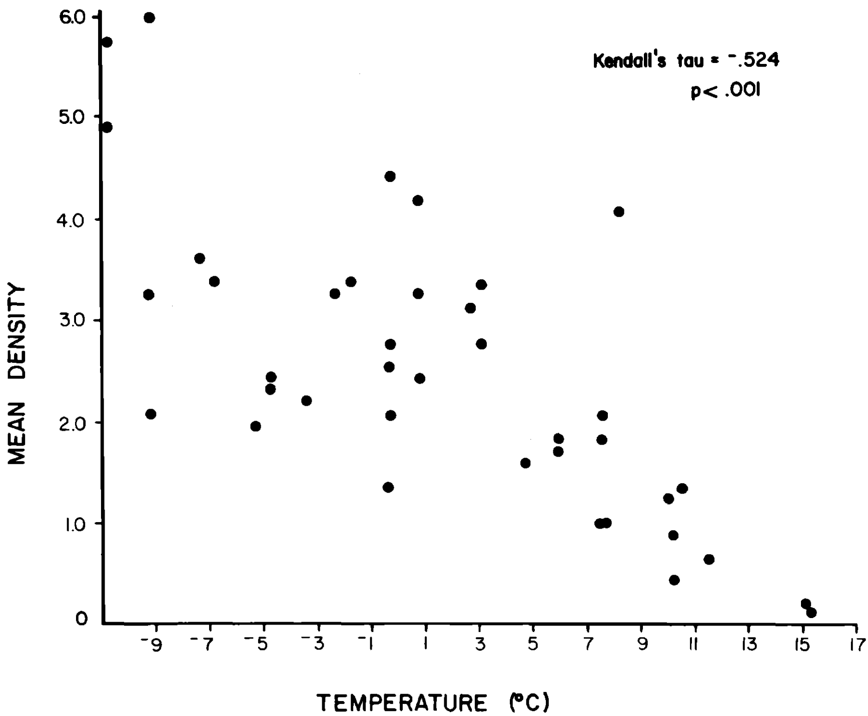

FIGURE 1. Relationship between mean density of juncos and air temperature.

(a) Under certain conditions food requirements of juncos increase.
(b) They respond by assembly at feeders in greater numbers.
(c) Because more juncos are attempting to use a given area and crowding results, an increase in the number of aggressive encounters occurs.

Although the present study was made at an artificial food source, certain more natural circumstances, such as patchy distribution of food after an ice storm, may induce juncos to gather at food in comparable numbers and might lead to comparable results.

It would be of interest to know whether a set number of birds in a circumscribed area would give rise to more aggressive encounters under some environmental conditions than others, but the manner in which the data were collected does not permit this form of analysis directly. An indirect approach (to assessing the importance of the environment in stimulating aggressive responses independently of variations in density) is provided by multiple linear regression. Because temperature is the only environmental measure meeting the assumptions of the meth-

TABLE 1.

Correlation matrix (Spearman's r) relating displacement rate and mean density of wintering Dark-eyed Juncos to environmental variables.

	Mean density	Displacement rate	Day length	Time	Temperature	Cloud cover
Displacement rate[1]	.854***[2] (39)[3]					
Day length	–.211 (39)	–.131 (39)				
Time	–.490*** (39)	–.419** (39)	.208 (39)			
Temperature	–.692*** (39)	–.529*** (39)	–.061 (39)	.617*** (39)		
Cloud cover	.416** (37)	.580*** (37)	–.158 (37)	–.142 (37)	–.031 (37)	
Wind	.231 (31)	.220 (31)	–.125 (31)	.005 (31)	–.172 (31)	.344* (31)

[1] See text for explanation of variable.
[2] *** = $P < .001$, ** = $P < .01$, * = $P < .05$.
[3] Number in parentheses indicates number of observation periods, numbers vary due to incomplete data.

TABLE 2.

Response of mean density and displacement rate to snow.[1,2]

	Mean density		
	Snowing	Snow on ground	No snow
Median	3.67	2.37	3.42
n	4	6	9
Kruskall-Wallis statistic		H = 4.81 df = 2	$P < .1$
Snowing vs. snow on ground		H = 2.2, df = 1, n.s.	
Snowing vs. no snow		H = 0.6, df = 1, n.s.	
No snow vs. snow on ground		H = 4.5, df = 1, $P < .05$	

	Displacement rate		
	Snowing	Snow on ground	No snow
Median	54	23	41
n	4	6	9
Kruskall-Wallis statistic		H = 6.65 df = 2	$P < .05$
Snowing vs. snow on ground		H = 5.5, df = 1, $P < .025$	
Snowing vs. no snow		H = 1.2, df = 1, n.s.	
No snow vs. snow on ground		H = 3.8, df = 1, $P < .1$	

[1] See text for definitions.
[2] To minimize confounding effects of temperature, only observation periods where air temperature ≤ 0°C were considered.

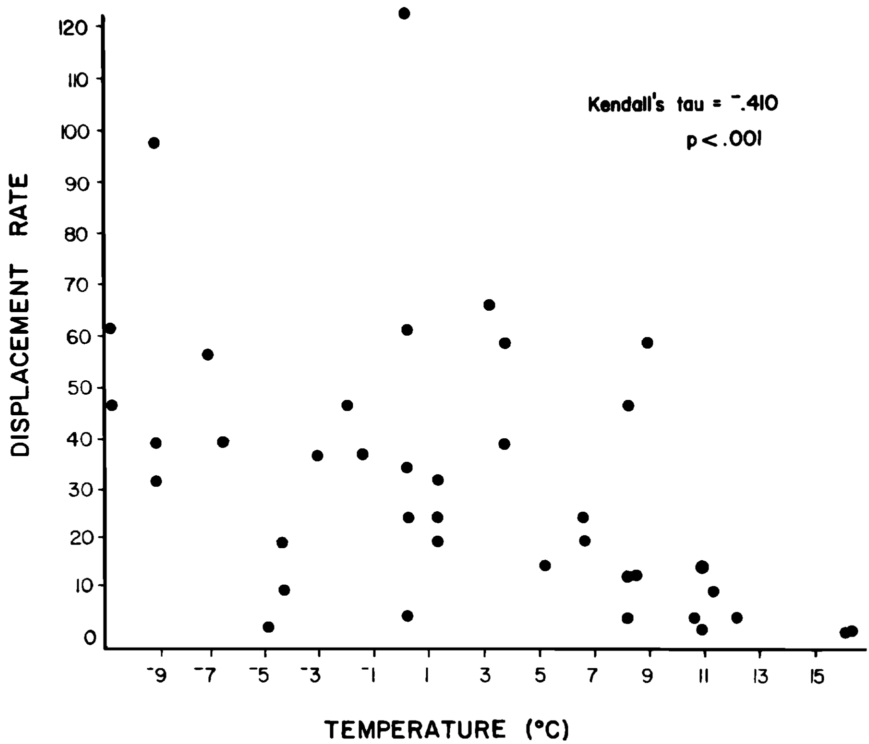

FIGURE 2. Relationship between displacement rate and air temperature.

od, displacement rate was regressed on temperature and mean density. The data suggest that temperature had little or no direct effect on displacement rate (Table 3).

If density is the prime determinant of frequency of aggression, then closer inspection of the relationship between these two variables is warranted (Fig. 3). Comparison of results of linear and curvilinear regression of displacement rate on mean density indicates that the best-fit relationship is curvilinear (Table 4). The difference is not striking, but it does appear that displacement rate increases disproportionately with mean density, suggesting that the number of displacements per individual is greater when density is higher (see also Balph, 1977).

TABLE 3.
Regression of displacement rate on temperature and mean density.

Intercept	−14.269		Anova	F = 34.76	df = 2,36	*P* < .001
				r^2 = .6588		
	Variable	b	s_b	t	*P*	
	Mean density	17.807	2.648	6.725	<.001	
	Temperature	.821	.524	1.566	<.126	

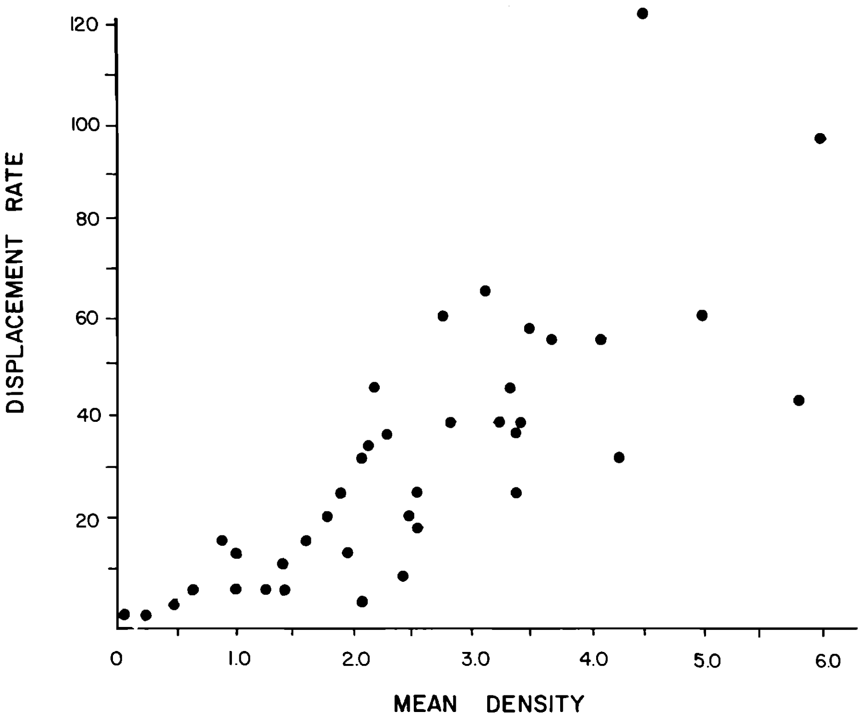

FIGURE 3. Relationship between displacement rate and mean density.

It seems possible then, that the role of aggressive behavior in determining which individuals have prior access to food may vary with environmental conditions. At first glance, one might expect that subordinate birds obtain less food at high densities than at low densities. And

TABLE 4.
Relationship between displacement rate and mean density.

Linear function					
Intercept	−5.516		Anova	F = 58.96 $P < 0.001$	df = 1,36[1] $r^2 = .6209$
	Variable	b	95% C.L.		
	Mean density	14.919	10.979	18.860	
Curvilinear function					
Intercept	2.102		Anova	F = 123.61 $P < 0.001$	df = 1,36[1] $r^2 = .7744$
	Variable	b	95% C.L.		
	Ln mean density	1.314	1.074	1.553	

[1] One observation period where 0 displacements observed was omitted from analysis because ln 0 is undefined.

because high densities occur at times of elevated food requirements, subordinates would seem least able to feed when they need food most. An alternative hypothesis is that aggressive behavior increases disproportionately at high densities because such densities occur at times when subordinates are more persistent in their approach to food. Supporting this possibility are my observations of outcomes of aggressive encounters between male and female juncos—males nearly always dominate females, but on the few occasions that I have seen females displace males (9 of 63), all have occurred during periods of snow and low temperature (Ketterson, 1978). Sabine (1959) also noted that cold, snowy days are more likely to produce dominance reversals, and P. M. Dolan (unpubl. data) has observed that subordinate juncos are more likely to initiate aggressive interactions when the overall frequency of aggressive behavior is highest.

If the increase in displacements associated with increasing density and stressful conditions is a function of more persistent approach by subordinates that ultimately succeed in feeding, then one would predict that the average tenure of dominants already feeding on an area would decline when density is high, despite higher food requirements. If, on the other hand, increase in displacements per individual results from more aggressive defense of feeding spots by dominants, then I would expect average tenure of dominants already feeding either to remain the same or to increase at high densities. Only in the latter case—increase in tenure—might it be concluded that aggressive behavior limits the ability of subordinates to feed at stressful times.

SUMMARY

Present findings indicate that factors influencing use of concentrated food sources also influence frequency of aggressive behavior, but that they do so indirectly. Temperature, time of day, atmospheric conditions, and snow cover affect the tendency of juncos to assemble at feeding areas, and as density increases, so does the frequency of fighting. Because the number of fights (displacements) per individual also apparently increases with density, the data appear to suggest that the role of aggressive behavior in determining which individuals have first access to food also varies with environmental conditions.

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