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FLOCKING AS A POSSIBLE PREDATOR DEFENSE IN DARK-EYED JUNCOS

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North temperate birds commonly flock in winter, and many investigators have offered evolutionary hypotheses to explain this behavior. Decreasing predation is central to some hypotheses.

Predators may make flocking advantageous for at least 5 reasons (Powell 1974); 2 may be generally important. Predators may stalk lone individuals more successfully than individuals in flocks because individuals in flocks can collectively assess their surroundings more reliably (Dimond and Lazarus 1974, Lack 1954, Lazarus 1972, Short 1961). Sharing of sentry duty means for the individual less time for vigilance and more time for such tasks as foraging.

Flocking may decrease the threat of predation for another reason. An individual may lower its probability of being captured simply by associating with other equally attractive prey (Hamilton 1971, Vine 1971). Predators most likely attack prey at the flock's edge, so that centrally located individuals should be relatively safe (Hamilton 1971).

According to these ideas both flock size and an individual's location in a flock should influence the individual's behavior. I predict flock size and location have 4 behavioral effects: (1) Birds in large flocks are less vigilant than birds in smaller flocks. (2) Birds in large flocks devote more time to activities other than vigilance. If food is scarce or energy demand high, birds in large flocks devote more time to foraging. (3) If food is scarce and energy demand high, birds in the center of large flocks devote more time to foraging than do peripheral birds. (4) In large flocks high status birds occupy central positions.

Little information exists to test these predictions. Murton, Isaacson and Westwood (1971) observed that Wood Pigeons (*Columba palumbus*) adhere to predictions 2 and 3; White-fronted Geese (*Anser albifrons*) meet prediction 1 (Dimond and Lazarus 1974); Starlings (*Sturnus vulgaris*) adhere to predictions 1 and 2 in an experimental situation (Powell 1974); sometimes Great-tailed Grackles (*Cassidix mexicanus*) meet prediction 1, but apparently not prediction 2 (Smith 1977); and Sanderlings (*Calidris alba*) meet prediction 2 (Silliman et al. 1977). I observed wild Dark-eyed Juncos (*Junco hyemalis*) to evaluate these predictions.

These common winter residents in the central United States form winter flocks stable in membership (Gottfried and Franks 1975, Sabine 1959), and social hierarchies exist in the flocks (Sabine 1959). Flock size varies, and flock size may influence junco survivorship (Fretwell 1969). Accipitrine (*Accipiter* spp.) hawks, small falcons (*Falco* spp.) and shrikes (*Lanius* spp.) hunt juncos (Bent 1968), and perhaps foxes (*Vulpes fulva*), weasels (*Mustela* spp.) and cats (*Felis* spp.) hunt juncos during the day.

Dark-eyed Juncos eat small seeds on, or near, the ground. They may experience energy stress due to low temperatures and snow cover (Ketterson and Nolan 1976), and some favored foods may be depleted during winter (Pulliam and Enders 1971). Hence a mechanism allowing a junco to spend more time foraging should be advantageous.

METHODS

I observed juncos in natural situations and at plots where I provided seeds. Observations were made in central Ohio from 1970 through 1973 and in Adair County, Missouri through 1977.

I quantified vigilance as follows. Juncos searched for seeds by hopping along the ground (95% of 689 observations) with bills pointed downward. Periodically a bird raised its bill to a horizontal position, and I assumed it could see an approaching predator more readily in this position. I also assumed the more alert a junco needed to be, the more frequently it elevated its head and changed orientation of its elevated head. I timed 10 sequential head elevations and reorientations and converted this to head moves/min as a vigilance index. Only birds feeding on small seeds were timed, since birds husking large seeds elevated their heads.

I determined pecking rates to estimate feeding rates. Juncos mandibulated after about 90% of their pecks, so pecking rates probably reflected feeding rates. Even if some pecks were exploratory, or not rewarded, pecking rate still should have reflected the time a junco had to devote to foraging. Sometimes I counted how many hops and short flights juncos made during observation periods to estimate how carefully birds searched small areas during foraging. Most observations were made within 2 h of sunrise and sunset, when juncos should have been highly motivated to feed.

I observed 1 bird for less than 90 sec when studying flocks. I adopted this convention so I would sample the behavior of many birds. At most, 1 individual in a flock contributed a few observations. I changed procedures when observing lone and pairs of juncos because I saw very few lone and pairs of birds (7 and 16, respectively). I repeatedly observed these birds and made more observations of some birds than others. This procedure could make differences between lone and pairs of birds and birds in larger groups hard to interpret. If 1 lone bird was particularly agitated and observed repeatedly, this could bias generalizations about lone birds. To evaluate this potential bias I compared all head movement rates for lone and pairs of birds with only the first head movement rate for each bird. For example, I determined 9 head movement rates for 1 lone bird. Its first rate was 36.1 head moves/min, and the 9 ranged from 34.5–57.6 head moves/min. For this analysis I isolated the first measurement for each bird observed alone, or in a pair,—in this case 36.1 head moves/min—and compared only these with all the measurements for these birds. I found no significant difference (t = 1.46, df = 66, $P > 0.10$) between all observations for these birds and just the first observation for each bird. This suggested that my first determination accurately represented a bird's behavior, and also, based on this analysis, I used not only my first observation of lone and pairs of birds, but also all subsequent observations.

I counted all individuals with which a junco foraged to determine flock size. Mostly these

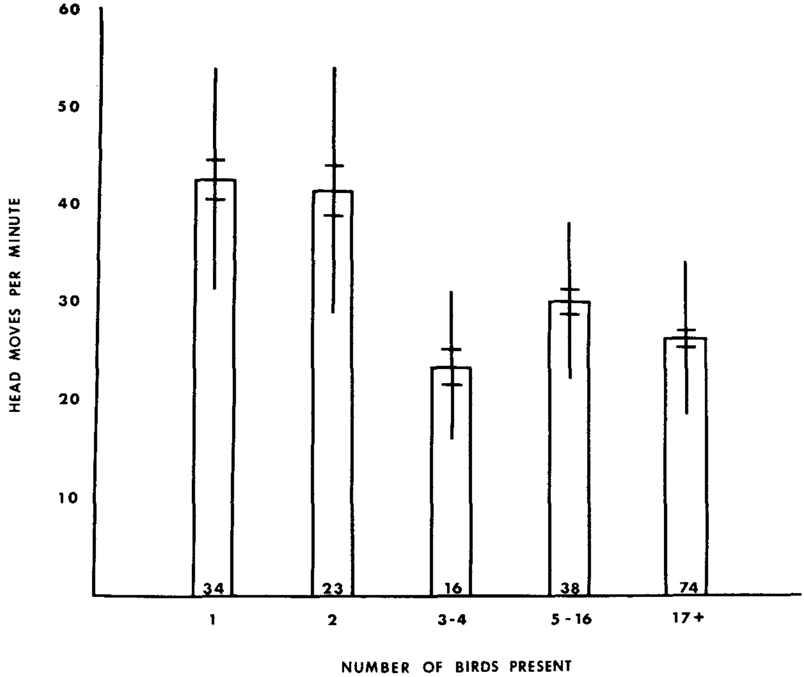

FIG. 1. The vigilance (measured by head movement rates) of Dark-eyed Juncos in different size groups. Bar height indicates mean head movement rate, the vertical line shows 1 standard deviation above and below the mean, and the horizontal line indicates 1 standard error above and below the mean. Number of observations are indicated at the bar base.

were other juncos, but sometimes juncos foraged with other emberizids, like Tree Sparrows (*Spizella arborea*) and Song Sparrows (*Melospiza melodia*).

I provided commerical bird seed on 1.8 m × 1.8 m plots at Sugar Creek State Forest, Adair Co., Missouri, from late December 1976 through mid-February 1977. Every 2 or 3 days I scattered 900 ml of seed evenly over each plot. These plots attracted many juncos because deep snow covered normal feeding sites.

I studied effects of location in a group on a junco's behavior at these plots. Usually 5–20 birds fed simultaneously, and a junco occupied either a central or peripheral position in a group. A bird within an imaginary triangle formed by 3 others was centrally located. I watched central and peripheral birds alternately so that I would have similar sized samples for each location. Central and peripheral birds harvested seeds of about the same density. When many juncos visited a plot, some peripheral birds appeared to be forced off the plot. These were not studied.

I also noted interactions between juncos on seed plots. I counted how many times birds I observed supplanted, or were supplanted, by others.

I analysed results with 1-way ANOVA and simultaneous test procedures, or *t*-tests, when variances for categories were similar (Sokal and Rohlf 1969). When variances differed substantially I used Mann-Whitney *U*-Tests (Siegel 1956); χ^2 analysis was also used (Siegel 1956).

RESULTS

Prediction 1.—Birds in large flocks are less vigilant than birds in smaller flocks.

To evaluate this I compared head movement rates of juncos in different size flocks in natural situations (Fig. 1). Lone and pairs of birds elevated and reoriented their heads significantly more frequently than birds in large flocks ($P < 0.001$, Mann-Whitney U-Test). No significant difference existed between lone and pairs of birds ($t = 0.90$, df = 55, $P > 0.40$), and in subsequent analyses I grouped observations of lone and paired birds. No trend existed between head movement rates and flock size for small, medium and large flocks, although head movement rates for most pairs of flock size categories differed significantly ($P < 0.05$, Mann-Whitney U-Test).

Prediction 2.—Birds in larger flocks devote more time to searching for food.

I compared pecking rates of lone and pairs of birds to those of birds in larger flocks to test this. Lone and pairs of birds averaged 34.4 ± 12.4 pecks/min (N = 42), while birds in flocks of 3 or more averaged 44.2 ± 15.5 pecks/min (N = 96). Lone and pairs of birds pecked significantly less frequently than birds in flocks ($t = 2.97$, df = 124, $P < 0.01$).

At least 3 possibilities other than flock size effects could explain behavior differences described so far. Lone and pairs of birds may have foraged in habitats with lower seed densities. I could not compare habitat use by lone and pairs of birds with birds in flocks directly because I observed so few lone and pairs of birds. However, head movement rates of lone birds foraging on lawns (head moves/min, $\bar{x} = 45.1 \pm 8.9$, N = 24) did not differ significantly ($t = 0.87$, df = 32, $P > 0.30$) from their rates in old fields ($\bar{x} = 42.2 \pm 9.2$, N = 10), suggesting habitat did not influence this behavior much.

Possibly juncos foraged alone, or in pairs, late in winter, after birds reduced seed densities. Most lone birds were seen in January. However, advancing season did not influence head movement rates of birds in large flocks. Prior to January, birds in flocks of more than 16 averaged 26.1 ± 7.3 head moves/min (N = 47), not significantly different ($t = 0.30$, df = 72, $P > 0.60$) from the average rate for January, or later (26.7 ± 9.4, N = 27).

Habitat and season also seemed not responsible for differences because they existed within 1 habitat during 1 month. In November, on lawns, birds in flocks averaged 42.2 ± 14.2 pecks/min (N = 55), while lone and pairs of birds averaged 31.0 ± 9.8 pecks/min (N = 14). These rates differed significantly ($P < 0.01$, Mann-Whitney U-Test).

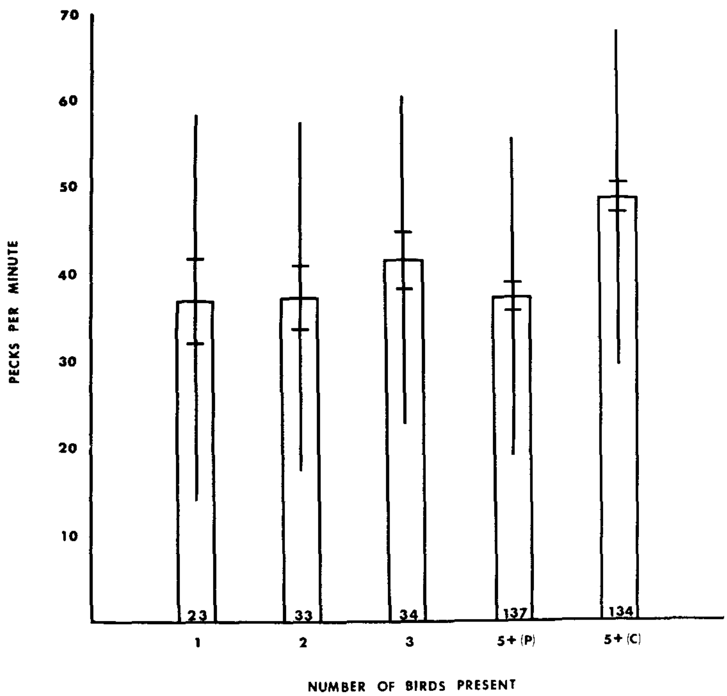

FIG. 2. Feeding rates of Dark-eyed Juncos in different size groups and in different locations in groups at seed plots. (P) designates birds on the periphery of groups; (C) designates birds in central locations. Symbols are the same as in Fig. 1.

Possibly birds in flocks could not forage as slowly because more intense competition among flock birds required rapid movement. However, lone and pairs of birds and those in flocks seemed to progress at about the same rate. Lone and pairs of birds hopped, or flew short distances, an average of 22.6 ± 16.4 times/min (N = 10), not significantly different (Mann-Whitney *U*-Test) from the rate of flock birds ($\bar{x}$ = 16.6 ± 19.6 moves/min, N = 50).

Prediction 3.—Birds in the center of large flocks devote more time to searching for food than peripheral birds do.

I evaluated this by comparing pecking rates of central birds on seed plots to pecking rates of peripheral birds and birds in small groups (Fig. 2). Pecking rates differed significantly ($P < 0.001$, ANOVA) between juncos categorized this way, with central birds in larger groups pecking more frequently than birds in other categories. Peripheral birds in large groups pecked no more frequently than birds in smaller groups. Peripheral birds appeared to spend much time watching birds around them.

Prediction 4.—In large flocks high status birds occupy central positions. To evaluate this I noted how frequently central and peripheral birds on seed plots supplanted others, or were supplanted by others. In 37 interactions involving a peripheral bird, the bird was supplanted 24 times. By contrast, in 48 interactions involving a central bird, the bird was supplanted only 23 times. This difference in outcomes of interactions involving central and peripheral birds was not significant ($\chi^2 = 2.50$, df = 1, $P \geq 0.10$), but the difference suggests that central birds probably exceed peripheral birds in status.

DISCUSSION

In natural situations juncos in large flocks fed more rapidly and appeared to spend less time assessing their surroundings than lone and pairs of juncos. These behavioral differences seemed related to flock size and not to ecological factors. These differences are expected if birds in flocks share the task of vigilance. Juncos on the periphery of large groups fed less rapidly than birds in the center, and this could not have reflected differences in food densities available. Slower feeding is expected if marginal predation is more intense than central predation. Birds in central locations tended to displace other juncos more frequently than did peripheral birds, suggesting that high status individuals may occupy central positions.

Advantages to flocking suggest junco flocks should be large. Large flocks allow members to devote much time to foraging. Also, if birds in flocks space themselves evenly, a smaller fraction of birds would have to forage on the periphery in a large than in a small flock. The fraction of birds that occupy peripheral positions will depend on the circumference-area ratio for the flock. As flock size grows, this ratio decreases, and so relatively fewer birds have to forage on the flock's periphery. Tenaza (1971) illustrates this geometric idea for colonial nesting birds.

Despite hypothetical advantages to large flocks, junco flocks I studied averaged 9.6 ± 12.2 birds (N = 46). This implies countervailing disadvantages to large flocks, or advantages that accrue to smaller flocks. Pulliam (1973) points out that the chance of spotting a predator rapidly reaches a high value with increasing flock size, so birds are not much safer in large than in medium-size flocks. The probability that Red-billed Quelea (*Quelea quelea*) detect a novel stimulus varies in the manner suggested by Pulliam (Dimond and Lazarus 1974).

The rate of change in a flock's circumference-area ratio is initially large as flock size increases, but this rate quickly becomes very small. A bird, then, has a good chance of occupying a central position in a medium-size flock; greatly increasing flock size does not lower this chance much.

It is easy to imagine disadvantages associated with large flocks. Excessively large flocks could deplete local resources and force frequent movement to new areas (Goss-Custard 1970, Morse 1970), and make establishment of stable social relations difficult (Wilson 1975:283). Whether or not flock size increases may depend upon a balance between such costs and benefits.

SUMMARY

Four predictions about how flock size and a bird's location in a flock influence behavior were evaluated by observing wild Dard-eyed Juncos. In natural situations, birds in flocks were less vigilant and fed more rapidly than lone and pairs of birds. In areas where I provided evenly distributed food, birds in central locations in flocks fed more rapidly than birds in peripheral locations. Observations weakly suggested that central birds were higher in status than peripheral birds.

These results suggest flocks should be large, although junco flocks averaged fewer than 10 birds. Small flock size may reflect non-linear increase of advantages with increasing flock size and disadvantages associated with large flocks.

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