AGGRESSION IN WHITE-CROWNED SPARROWS: EFFECTS OF DISTANCE FROM COVER AND GROUP SIZE[1]

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Abstract. I assessed whether White-crowned Sparrows (*Zonotrichia leucophrys*) engage in aggressive interactions more frequently when feeding closer to cover, while food availabilty was held constant. For a given group size, interaction rate was higher closer to cover, suggesting that sparrows perceived such locations to be more valuable (i.e., more safe). The rate of aggression was also strongly positively correlated both with the number of birds in the immediate vicinity (within 0.5) and with the total number of birds foraging (within 2 m × 1 m area). The effect of immediate group size on rate of aggression was weaker farther from cover.

Key words: Zonotrichia leucophrys; *cover; group size; predation risk.*

INTRODUCTION

Many bird species aggregate into foraging flocks, especially during the non-breeding season (winter). Flocking can reduce both the risk of predation (Hamilton 1971, Powell 1974) and the likelihood of starvation (Thompson et al. 1974, Baker et al. 1981), but aggregation into flocks can increase intraspecific competition (Caraco 1979). Intraspecific aggression detracts from foraging time (Caraco 1979), and relative social status (Caraco 1979, Keys and Rothstein 1991) and group size (Caraco 1979) affect aggression rates, and thereby food return. However, the influence of foraging location on aggression rates awaits study.

Dominant White-crowned Sparrows (*Zonotrichia leucophrys*) initiate more aggressive interactions than subordinates, but on average, members of different social classes have similar interaction rates when wins and losses are totalled (Keys and Rothstein 1991). Since foraging passerines defend individual distances, the probability of an encounter between two individuals increases with group size (for a given space), resulting in an increase in aggression rate with increasing group size (Caraco 1979). However, the influence of perceived resource quality on aggression rates of flocking passerines has not been well quantified (Caraco et al. 1980).

Because dominant White-crowned Sparrows

feed closer to cover than subordinates (Slotow 1993, Slotow and Rothstein, 1995a), and overall interaction rates are similar across age-sex classes (Keys and Rothstein 1991), aggression should be independent of distance from cover. Assuming locations closer to cover are more safe, sparrows may pay greater costs (i.e., more aggressive interactions) for greater safety benefits of foraging closer to cover. Here I test the prediction that White-crowned Sparrows will engage in aggressive interactions more frequently closer to cover. Because increasing group size results in more potentially interacting individuals, aggression should increase with increasing density (Caraco 1979) at any given distance from cover. I therefore hold group size constant analytically while assessing the importance of distance from cover on aggression. Specifically, I test the prediction that aggression rates will not change with distance from cover. In addition, I describe the influence of group size on aggression rates and contrast the influence of immediate group size relative to that of overall foraging flock size.

METHODS

This study was carried out at West Campus, University of California, Santa Barbara Co., California, from December 1989 to February 1990. Three feeding bowls (30 cm diameter, 5 cm depth) containing abundant millet seed (same amount in each bowl) were placed with centers at 0.3, 0.8, and 1.3 m from the base of a shrub constructed of cut conifer branches. The shrub was situated in a mowed field, at least 20 m from the nearest cover. Slotow and Rothstein (1995a) provide a detailed description of the experimental

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set-up. I made observations on ten different days in both the morning (07:30 to 09:30 PST) and afternoon (15:00 to 17:00) from a car 4 m from the bowls. I video-recorded White-crowned Sparrows while foraging, and video tapes were later analyzed for aggressive interactions. I defined an interaction as occurring when an individual vacated its feeding location with a hop or flight in response to a second individual. I noted the following data for each interaction: number of birds at the same bowl (i.e., within 0.25 m of the center of the bowl—immediate group size), total number at all three bowls (overall group size), and bowl location (Bowl 1 was closest to cover). I scored birds not actually in a bowl as being at the bowl nearest to them. I timed the duration of "flock visits" to assess overall aggression rates. A "flock visit" was initiated when at least two birds were on the feeding site, and ended when >50% of birds flew together from the site.

If group size has no effect on aggression, the frequency of interactions at different group sizes should follow the frequency of occurrence of each group size (null hypothesis). I quantified the actual occurrence of each group size separately for the three bowls from data collected at 1-min intervals at the same site and over the same period (Slotow and Rothstein in 1995a), which gave the expected frequency of interactions according to the Null Hypothesis. Using G-tests, I contrasted the frequency of each group size (two through ten and >10 individuals on the same bowl) observed when interactions occurred, with the expected frequency of each group size. I analyzed this separately for the bowls located at three different distances from cover and for all bowl locations combined. If an observed value was less than the corresponding expected value this indicated that interactions occurred relatively less often than expected at that group size and vice versa.

I quantified the effect of overall foraging flock size on aggression by contrasting the observed number of interactions at each group size with the actual occurrence of each overall group size (see above). Overall group size was the number of birds on all three bowls combined taken at 1-min intervals. I categorized overall group sizes from two through 18, combining values of 19 through 25, and values >25 to yield equivalent sample sizes across cells.

I assessed the effect of distance from cover in a similar manner by generating an expected frequency of interactions on different bowls. In this case, the frequency of use of the three bowls taken at 1-min intervals was used to generate expected frequency of interactions. Using G-tests, I compared the observed frequency of interactions at each bowl with the expected frequency for each group size on the same bowl (two through ten and >10), as well as for use of the three bowls regardless of overall group size.

I will describe by example the above calculations: 32 interactions took place when there were four birds on Bowl 1. In total, 51 interactions took place when there were four birds on the same bowl (Bowl 1, 2 or 3), giving the proportion of interactions on Bowl 1 when there were four birds present, i.e., 0.627. Using the one minute counts of the number of birds on each bowl, four birds occurred on Bowl 1 84 times, while four birds occurred on Bowl 1, Bowl 2, or Bowl 3 a total of 155 times. This gave a proportion of times that four birds occured on Bowl 1 of 0.542. I then subtracted the value of 0.542 from 0.627 giving a value of 0.086. Therefore, since this value is greater than zero, there tended to be more aggression than expected on Bowl 1 when four birds were present. I present the data graphically as the difference between the proportion that specific observed value comprised of all interactions and the proportion that expected value comprised of all expected interactions (for this example 0.086). Statistical analyses were performed on the original non-proportional data.

In addition I recorded the type of aggression. Two types of aggression occurred: active interactions, where the winner made an overt move towards the loser and passive interactions, where the winner made no overt move towards the loser, but the loser vacated its feeding location (Keys and Rothstein 1991). An active interaction often resulted in chases, with the loser being excluded completely from the feeding patch. By definition, passive interactions never resulted in chases and although forced to move, the loser may remain feeding on the patch although at a new location. If locations close to cover are more valuable, then I predict that the proportion of interactions that are active would be higher closer to cover. To reduce the number of cells with zero values, I divided immediate group size (number on same bowl) into three categories: 2–4, 5–9, and >9 individuals. I categorized overall group size (number on all three bowls) as 2–4,

5–9, 10–15, 16–20, and >20 individuals. I used G-tests for all comparisons of aggression type and in the few instances when there was a zero value in a cell, I added 0.0001 to that cell.

Because I could not ascertain individual identities from video, these data are subject to problems of pseudoreplication (Hurlbert 1984), in that one or a few individuals could have been involved in all or most of the interactions. This results in a lack of independence of data points, an assumption of the statistical analyses used. Although I cannot overcome this problem, I reason that pseudoreplication was reduced because: (1) by Lincoln index estimate >400 color-banded individuals used the site over any three day period; (2) turnover rate on the bowls was high (mean foraging bout = 45.3 sec); (3) on average, complete turnover of individuals occurred within 1 min, and all birds flushed from the bowls on average every 2.2 min; and (4) I performed observations on many different days.

RESULTS

During 148 flock visits (36 of which involved no interactions), I observed 394 aggressive interactions (active and passive combined) over 281 min of observation, giving an aggressive interaction rate of 1.4 interactions per min on the feeding patch. Note that this is irrespective of the number of birds on the site, and therefore is not the average per capita rate. On average, there were 6.3 birds on the feeding site when an interaction took place, yielding an average interaction rate of 0.44 (i.e., 0.22 times 2 since two individuals were involved in any interaction) interactions per min per bird. Therfore, on average, an individual was involved in an interaction approximately once every 2.5 min of feeding.

EFFECT OF IMMEDIATE GROUP SIZE ON AGGRESSION

Immediate group size (the number of individuals on the same bowl) had a significant effect on the occurrence of interactions. When I considered the effect of immediate group size on aggression without differentiating by distance from cover, the number of interactions increased with increasing group size (G-test: $G = 97.54$, df = 9, $P < 0.0001$, Fig. 1a). When I differentiated among bowls, immediate group size had less of an effect as the distance from cover increased. At Bowl 1 (closest to cover), group size had the strongest effect ($G = 73.29$, df = 9, $P < 0.0001$, Fig. 1b),

with the effect being weaker at Bowl 2 ($G = 36.39$, df = 9, $P < 0.0001$, Fig. 1c) and non-significant at Bowl 3 ($G = 8.07$, df = 9, $P > 0.5$, Fig. 1d). A means of contrasting the relative influence of group size on aggression at different distances is through correlation of the difference between observed and expected values with group size at different bowls. Group size had a significant positive correlation with aggression at Bowl 1 (Spearman correlation: $r_s = 0.77$, $n = 10$, $P = 0.02$) but not at Bowl 2 ($r_s = 0.52$, $n = 10$, $P = 0.12$) or Bowl 3 ($r_s = 0.36$, $n = 10$, $P = 0.28$). Note that overall, immediate group size had a significant positive effect on aggression ($r_s = 0.87$, $n = 10$, $P = 0.009$).

EFFECT OF OVERALL FORAGING GROUP SIZE ON AGGRESSION

The overall foraging group size (total number of birds simultaneously on any of the three bowls) also had a significant effect on the occurrence of interactions. The number of interactions increased significantly with increasing overall group size ($G = 35.48$, df = 18, $P < 0.01$, Fig. 2a). However, there was no significant effect of overall group size on the number of interactions at Bowl 1 ($G = 19.28$, df = 18, $P > 0.5$, Fig. 2b). There was a stronger influence of overall group size on the number of interactions at Bowl 2 ($G = 43.33$, df = 18, $P < 0.001$, Fig. 2c). There were too many empty cells to make a fair assessment of the influence of overall group size on the number of interactions at Bowl 3 (74% of interactions on Bowl 3 took place when there were >18 birds foraging in total). Although the results from the G-tests indicate that immediate group size may have a stronger effect on aggression than overall group size, aggression was still strongly and significantly positively correlated with overall group size ($r_s = 0.73$, $n = 19$, $P = 0.002$) and on Bowl 2 ($r_s = 0.81$, $n = 19$, $P = 0.0006$). However, there was no correlation between overall group size and aggression at Bowl 1 ($r_s = 0.35$, $n = 19$, $P = 0.134$).

EFFECT OF DISTANCE FROM COVER ON AGGRESSION

Distance from cover had a significant effect on the number of interactions. Without considering the influence of group size, significantly more aggression occurred closer to cover at Bowl 1 than at Bowls 2 and 3 ($G = 92.14$, df = 2, $P < 0.0001$, Fig. 3a). I discounted the effects of group
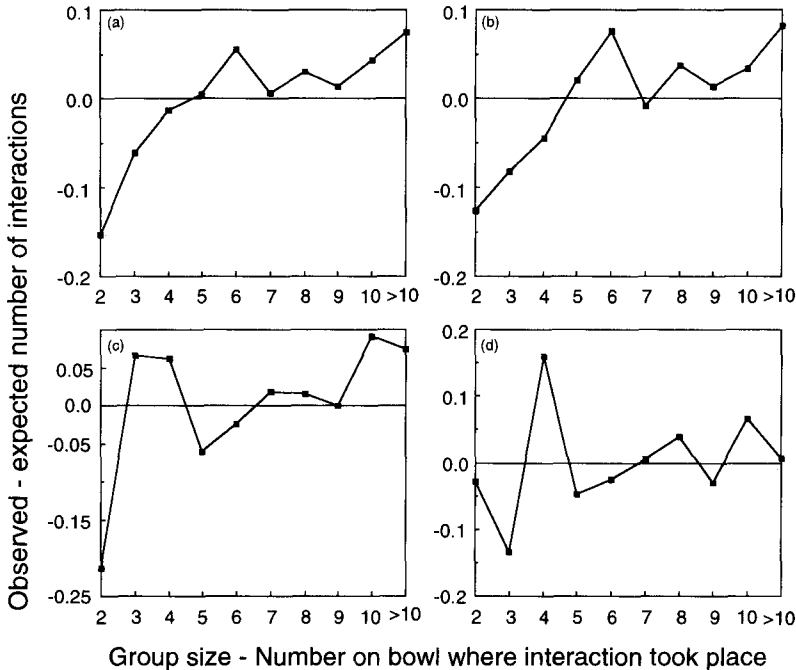
FIGURE 1. Effect of immediate group size (number on same bowl where an interaction took place) on aggression. Expected values were distribution of interactions if group size had no effect. Proportion of observed interactions for any group size comprised of all interaction minus proportion corresponding expected value comprised of expected overall interactions. Data (a) without considering distance from cover, and separately for (b) Bowl 1, (c) Bowl 2, and (d) Bowl 3 (Bowl 1 closest to cover). A positive (negative) value indicated that interactions were more (less) frequent than expected by chance.

size by considering the number of interactions at any bowl at each immediate group size. The number of interactions was significantly greater than expected at Bowl 1 and significantly lower than expected at Bowl 3 for eight out of ten immediate group size comparisons (G > 6.83, df = 2, P < 0.05 in all cases, Fig. 3b). For the remaining two group sizes of four and seven birds on a bowl, despite a similar trend, observed interactions did not differ statistically from expected (G = 3.41, df = 2, P > 0.1, and G = 3.6, df = 2, P > 0.1, respectively). The results for Bowl 2 were intermediate, with five group sizes showing more interactions than expected, and five group sizes showing fewer interactions than expected (Fig. 3b). Note that there was no difference between Bowl 1 and Bowl 2 for small group sizes of two or three birds on the same bowl (Fig. 3b, G = 0.553, df = 1, P > 0.7; G = 0.024, df = 1, P > 0.8 respectively). The apparent inconsistencies between Figs. 1 and 3 are attributable to the use of different expected values (ei-

ther frequency of occurrence of group size or number on bowl—see Methods).

TYPE OF INTERACTION

As immediate group size increased, the proportion of active interactions decreased significantly (Fig. 4a; G-test = 6.08, df = 2, P < 0.05). This effect was more striking when considering only interactions taking place on Bowl 1, where the largest groups occurred (Slotow and Rothstein, 1995a), and the proportion of interactions that were active decreased from 0.63 at immediate groups <5 to 0.35 at immediate groups >9 individuals (Fig. 4a; G = 9.92, df = 2, P < 0.01). The overall group size also significantly affected the type of interaction, with the proportion of active interactions decreasing at overall group sizes of greater than nine individuals (Fig. 4b; G = 15.82, df = 4, P < 0.01). However, when examining interactions taking place on Bowl 1, there was no significant effect of overall group size on interaction type (Fig. 4b; G = 5.303, df = 4, P
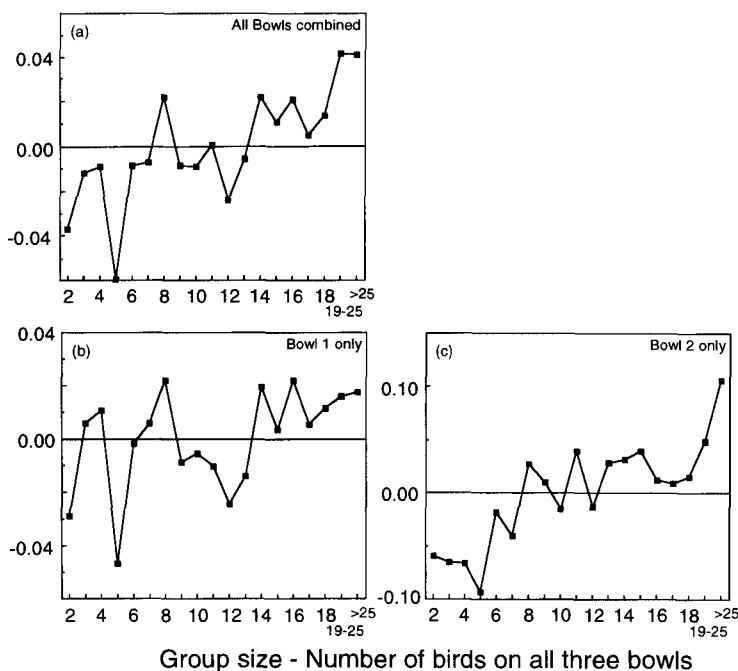
FIGURE 2.   Effect of overall group size (number on all three bowls when an interaction took place) on aggression (see text and Fig. 1 for details). Data (a) without considering distance from cover, and separately for (b) Bowl 1, and (c) Bowl 2.

> 0.1). Therefore both immediate and overall group size influenced the type of interaction, with fewer active interactions occurring at higher densities.

Distance from cover did not significantly affect the type of interaction (Fig. 4c; G-test: G = 1.73, df = 2, P > 0.3). I considered the frequency of interaction types at different distances from cover for each group size separately. First considering immediate group size, there was no significant effect of distance from cover on interaction type at group sizes of 2–4 or 5–9 (G = 1.34, df = 2, P > 0.5, and G = 1.23, df = 2, P > 0.5 respectively). However, the proportion of active interactions increased with increasing distance from cover at immediate group sizes of >9 on the same bowl (G = 6.02, df = 2, P < 0.05). Secondly considering overall group size, only at overall group sizes of 2–4 were there significantly more active interactions on Bowl 1 (G = 12.31, df = 2, P < 0.01). For all other overall group sizes there was no change in the frequency of active interactions with distance from cover (G < 0.46, df = 2, P > 0.1 for four comparisons). Therefore, distance from cover did not have a

strong, or consistent, influence on interaction type.

DISCUSSION

INTERACTION RATE

The average aggression rate of one interaction every 2.5 min in this study was comparable to rates of one interaction every 3–5 min for White-crowned Sparrows (Keys and Rothstein 1991), or one every 3.2 min for Yellow-eyed Juncos (*Junco phaeonotus*) (calculated from D, categories 1,2 and 3, in Table 2, Caraco 1979). Note that social interactions appear to have little influence on time budgets of White-crowned Sparrows (Slotow 1993; this study), and may be constrained by the necessity to feed, as in juncos, (Caraco 1979). During this study the mean ± SE feeding bout length of White-crowned Sparrows was 45.3 ± 6.6 sec (Slotow and Rothstein, 1995a), indicating that sparrows would engage in an interaction once every 3.3 foraging bouts. This is low figure for birds that were foraging at very high densities (mean ± SE: 6.3 ± 0.18 birds on a bowl when an interaction took place, this study).
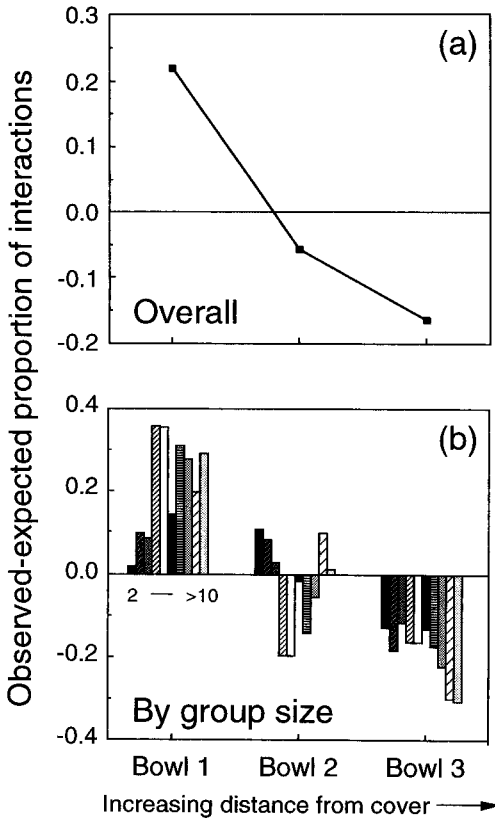
FIGURE 3. Effect of distance from cover on aggression (see text and Fig. 1 for details). Data (a) regardless of group size, and (b) separately each immediate group size from 2 through 10, and >10 combined (each bar represents a different group size on the same bowl at which an interaction took place). All differences were statistically significant except for group sizes four and seven (see text).

This low interaction rate may reflect the efficacy of the White-crowned Sparrow social status signal (head-plumage coloration, Fugle et al. 1984). In addition, behaviors may have evolved that decrease the probability of an interaction. For example, I have noted that subordinate individuals move peripherally to dominants, i.e., as a feeding dominant turns the subordinate will move as well, such that an oblique angle is maintained between them. Such behavior would not have been counted as passive interactions, since the subordinate bird was not displaced from its foraging location. Subordinates may thus avoid face-to-face encounters which are more likely to result in interactions.

AGGRESSION RATES AND DISTANCE FROM COVER

Aggression rates were significantly higher closer to cover. This was counter to the Null Hypothesis that aggression should be random with distance from cover. In addition, although immediate group size had a strong effect on the probability of aggression close to cover, no significant influence of immediate group size on aggression was found at 1.8 m from cover. A compelling explanation for both results is that the resource value varies at different distances from cover, and that individuals perceive these differences in resource value. Caraco et al. (1980) found a similar result for Yellow-eyed Juncos. They calculated individual time-budgets and found that the proportion of time spent interacting was higher when cover was present than when cover was absent. However, there was a concomitant decrease in the proportion of time spent vigilant for predators when cover was present. In Caraco et al.'s (1980) study, it is difficult to ascribe changes in proportions to aggression being causal, since the relative increase in aggression may simply reflect a decrease in vigilance or vice versa. My technique of assessing aggression is independent of direct influence of other behaviors since I did not use proportions of various behaviors to assess aggression. Therefore, my data clearly demonstrate increased aggression relative to increasing resource value.

I have previously demonstrated that dominants displace subordinates from Bowl 1 to other bowls, and I argued that Bowl 1 was preferred for shorter escape distances in the event of a predator attack (Slotow 1993, Slotow and Rothstein, 1995a; see also Lima and Dill 1990 for review; note that shrubs may also serve to provide cover from wind, Grubb and Greenwald 1982). Subordinate birds may be willing to risk a fight for the extra safety afforded by feeding closer to cover. This would result in higher interaction rates closer to cover, and at higher densities. This heightened risk of an interaction is manifested in higher vigilance for conspecifics at higher densities closer to cover (Slotow and Rothstein, 1995b). I expected the proportion of active interactions to increase closer to cover, but this was not the case. One possible explanation for this is that subordinates know that they run a greater risk of being displaced closer to cover, and avoid active interactions by mov-
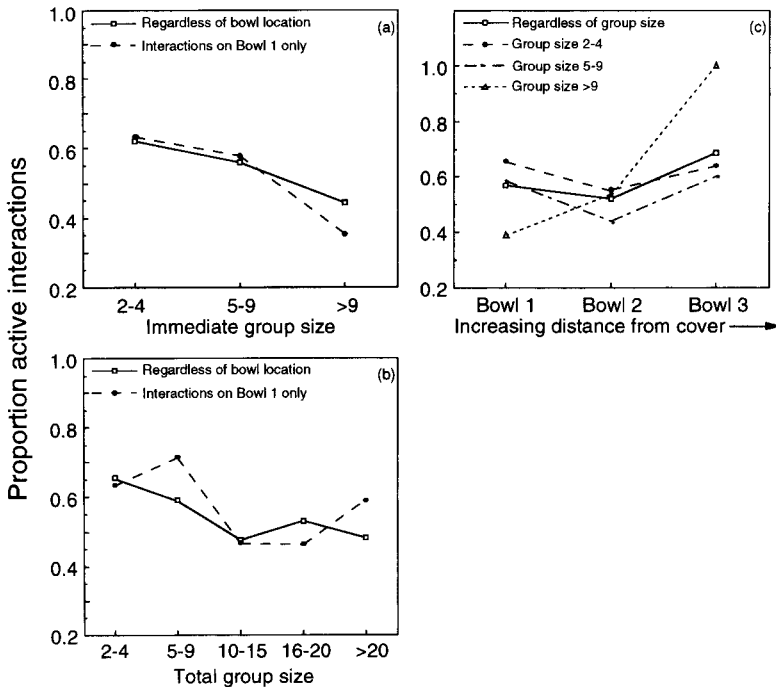
FIGURE 4. Effect of (a) of immediate group size, (b) overall group size, and (c) distance from cover on the proportion of interactions that were active. See text for statistical analyses.

ing to a location farther from cover as soon as a dominant is threatening.

AGGRESSION RATES AND GROUP SIZE

Aggression rate of White-crowned Sparrows (this study) and Yellow-eyed Juncos (Caraco 1979, Caraco et al. 1980) increased with increasing group size, whereas there was no effect of group size on aggression of House Sparrows (*Passer domesticus*) (Studd et al. 1983). The reason Studd et al. failed to find a group size effect may be because they observed only small groups of <4. Note that although overall flock size did significantly affect the number of interactions, overall flock size did not affect interactions at Bowl 1. In contrast, immediate flock size showed its strongest effect at Bowl 1. This means that overall flock size had no effect on aggression closer to cover, where most foraging takes place and most interactions occur (Bowl 1). That immediate density was more important than overall flock size is not surprising since birds have to be in fairly close proximity before an interaction takes place. In House Sparrows, immediate group size

influenced vigilance rates more than did overall foraging group sizes (Elgar et al. 1984).

The major factor influencing interaction type was group size, both the number of birds in the immediate vicinity, and the total number of birds foraging. The probability of an active interaction decreased with increasing group size. Note that immediate group size had a stronger effect when considering only interactions taking place on Bowl 1, which was closest to cover and with largest group sizes, while overall group size did not affect those interactions taking place on Bowl 1. Since most birds were feeding on Bowl 1, it appears that immediate group size may have a more important influence on aggression type than overall group size. I propose two possible explanations for the decrease in active interactions with increasing group size: firstly, at higher densities birds may not be able to keep track of all others present and may therefore become more sensitive to movement from others (see Lima 1994). Alternately, birds may be more vigilant for conspecifics at high densities (Slotow and Rothstein, 1995b), because of an increase in competition

with group size (see Elgar 1989). Such increased vigilance would allow earlier detection of threatening individuals, thus reducing actual attacks while increasing passive interactions. Lima (1995) recently concluded that Dark-eyed Juncos (*Junco hyemalis*) do not monitor other flock members in order to benefit from their early detection of a predation threat, but work is required to detect whether some vigilance is directed towards detecting threat of displacement from dominant flock members. Note that individuals that happen to be vigilant at the time of flushing of the detector of a threat, flush more rapidly than a non-vigilant individual (Lima 1994), so there is a benefit to being vigilant. In addition to the possibility of being more vigilant for conspecifics at higher densities, sparrows appear to apply this vigilance by reacting to preempt actions of dominant birds. Increasing confusion and vigilance probably both contribute to the increase in passive interactions at higher densities.

When performing behavioral studies it is imperative to assign the group size we measure as the one that is relevant to the individuals we are observing. That is, the size of the entire foraging flock may be less important than the immediate density at specific locations within a flock. In conclusion, White-crowned Sparrows are more willing to fight to feed in apparently safer foraging locations.

ACKNOWLEDGMENTS

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