ENVIRONMENT, WELL-BEING, AND BEHAVIOR

Space Use According to the Distribution of Resources and Level of Competition

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ABSTRACT The manner in which an animal moves throughout and utilizes the space available to it depends on the dispersal, availability, and level of competition for resources the animal requires for its biological functioning. We tested groups of broilers (Gallus gallus domesticus) in 3 experimental group sizes of 5, 10, and 20 individuals per group under 3 resource distribution patterns. Groups were tested with access to 1 large single feeder, 2 medium-sized feeders, or 4 small feeders. In all arrangements the total amount of food available per bird remained constant. During the first phase groups had free access to all available feeders, and in the second phase access at each feeder was restricted to a single bird. Space use, measured by calculating core areas and interindividual distances between group members, increased as group size grew larger and as feeders became more widely distributed. Not all group sizes responded equally to the resource distribution patterns. Space use patterns for the smaller group sizes were more strongly affected by resource distribution patterns than the larger group sizes. When access to the feeders was restricted, consumption, aggression, and space use increased. Broilers adjusted their space use and aggressive behavior according to the level of competition, dictated not only by group size but also resource distribution and accessibility.

Key words: broiler, use of space, resource distribution, group size, competition

INTRODUCTION

Use of space and movement patterns depend on the availability and dispersal of the resources an animal requires for its biological functioning (Grigor et al., 1995a; Arcis and Desor, 2003). For social species the use of space and resources also depends on social dynamics within the group (Clark and Mangel, 1984; Caraco et al., 1989; Grant, 1993) in such a way that flocking and foraging decisions will be determined by the costs and benefits associated with different behavioral strategies (Andersen et al., 2004; Estévez and Christman, 2006). Whereas flocking individuals gain enhanced protection from predators, even in captive environments (Newberry et al., 2001), competition for resources increases along with group size (Clark and Mangel, 1984; Andersen et al., 2004). However, the level of competition may be uneven among group members because dominance relationships usually dictate the ease of access to resources for each member (King, 1965; Banks, 1984; Caraco et al., 1989; Keeling, 1995; Pagel and Dawkins, 1997; Stahl et al., 2001; Dubois et al., 2003). The level of competition experienced is a critical factor shaping foraging strategies as well as how animals move and use their available space in a confined environment (Newberry and Hall, 1990; Estévez et al., 1997; Carmichael et al., 1999; Estévez and Christman, 2006).

The distribution of resources determines an animal’s ability to defend them (Carpenter, 1987; Grant, 1993). When resources are clumped in one exclusive location, dominant individuals may attempt to monopolize access, forcing subordinates to wait (Banks et al., 1979; Banks, 1984; Pagel and Dawkins, 1997). On the contrary, wider distributions of resources enable multiple individuals to simultaneously gain access, favoring more even acquisition. As resources become more dispersed it becomes increasingly difficult and inefficient for any single individual to defend them and animals may switch from a resource defense to a scramble strategy (Lima et al., 1999; Parker, 2000; Estévez et al., 2002; Dubois et al., 2003; Estévez et al., 2007). Foraging decisions therefore are based on the relative costs and benefits of resource defense, which are ultimately related to how resources are distributed within an animal’s environment.

Foraging strategies and use of space patterns have not often been considered when designing facilities for farm animals. Inadequate resource distribution may lead to stress and aggression, which have been shown to diminish weight gain and productivity as well as overall well-being (King, 1965; Gvaryahu et al., 1994). Manipulating resource distribution may minimize competition and ag-
In this study we examined the consequences of multiple resource distribution patterns and competition on the use of space, level of aggression, and foraging strategies of broiler chickens. The aim of the present study was to determine if and how broilers adapt their behavioral strategies according to resource distribution and level of competition. Our experimental design allowed us to measure the immediate repercussions of changes in group size (GS) and resource distribution, while controlling for social experience.

**MATERIALS AND METHODS**

**Facilities and Experimental Animals**

We conducted this experiment at the University of Maryland’s Upper Marlboro Applied Poultry Research Facility in the spring of 2003 with a total of three hundred thirty-six 1-d-old male broiler chicks (Ross 308) obtained from a commercial hatchery. Chicks were randomly divided into 8 groups of 42 birds and placed in separate 4.5-m² pens covered with 5 cm of wood shavings. We maintained a 14L:10D lighting program in an effort to slow growth and promote leg health. Temperature and ventilation programs followed commercial practices. Food and water were provided ad libitum through a central tubular hopper and a line of nipple drinkers (7 nipples/pen) located along one side of the pen. Birds were individually tagged at 3 wk of age on each side of the neck using the Swifftack Poultry Identification System (Heartland Animal Health Inc., Fair Play, MO). Seven individuals per pen were left unmarked to be used as replacements in the event of mortalities. This protocol was approved by the University of Maryland’s Institutional Animal Care and Use Committee, R-03-04.

**Experimental Design**

This experiment began when the birds were 5 wk of age. Each of the 35 marked birds from each home pen was temporarily placed into 1 of 3 experimental group sizes of 5 (GS₅), 10 (GS₁₀), and 20 birds (GS₂₀) for testing. These experimental GS generate stocking densities of 3.26, 1.63, and 0.82 m²/bird, respectively. Birds in each experimental GS were tested with the same individuals for all trials. For example, a bird placed into GS₅ was always tested in the group of 5 birds and always with the same 4 conspecifics. All birds were acclimated to the testing GS for 1 wk prior to beginning the experiment. Five individuals in each experimental GS and pen were randomly designated as focal birds. This testing structure was intended to create a homologous background environment for each experimental group, enabling us to measure the distinct and immediate reaction of broilers to a new environment with different GS and resource distribution patterns. After every test all birds were returned to their home pen.

We constructed 3 testing arenas each measuring 2.25 m × 7.25 m and covered with 5 cm of wood shavings. Water was provided ad libitum from nipple drinkers with 1 line at each end of the arena. Multiple arenas enabled us to simultaneously test each experimental GS from 1 home pen. Each arena was marked along the walls to create a grid of 0.25 × 0.25 m squares. During testing birds in all 3 GS from 1 home pen were caught by hand and immediately transported in crates to one of the testing arenas for testing. For the clumped treatment birds were given the large, centrally placed feeder (black). The patchy treatment consisted of 2 medium-sized feeders equidistant from the center (intermediate shading). For the scattered treatment 4 small feeders were placed in the corners of the testing arena (light shading).

**Figure 1.** Resource arrangement in the testing arena for each of the 3 distribution patterns. For the clumped treatment birds were given the large, centrally placed feeder (black). The patchy treatment consisted of 2 medium-sized feeders equidistant from the center (intermediate shading). For the scattered treatment 4 small feeders were placed in the corners of the testing arena (light shading).

<table>
<thead>
<tr>
<th>Distance</th>
<th>GS₅</th>
<th>GS₁₀</th>
<th>GS₂₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum interindividual distance</td>
<td>0.68</td>
<td>0.30</td>
<td>0.15</td>
</tr>
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<td>Maximum interindividual distance</td>
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<td>6.65</td>
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<td>Nearest neighbor distance</td>
<td>1.21</td>
<td>0.75</td>
<td>0.51</td>
</tr>
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1Values are based on 2,000 random simulations.
arenas and released in the center. Each GS was placed in a separate testing arena. All birds were habituated to the testing arena and transportation procedures prior to testing. We randomly assigned the order in which home pens were tested.

To create a highly desirable resource we used dry cat food (44% CP), which had been previously observed to be highly attractive to broilers (E. H. Leone, personal observation). We habituated the birds to the food by scattering 20 g on top of the normal feed in each home pen for 3 consecutive days after which birds did not encounter the food again until testing. This experiment was performed in 2 phases, one in which the group was given free access to each feeder, whereas in the second phase access was restricted to a single individual, as described below.

Feeder designs that mimicked clumped, patchy, and scattered resource distribution patterns. For each treatment, 4 brown plastic dishes 8 cm in diameter and 2 cm deep were arranged on wooden platforms 12 cm high. For the scattered treatment each dish was placed on a separate platform, creating 4 small feeders, placed near the corners of the testing arena 0.75 m from the sidewalls and 0.5 m from the back or front wall. The patchy treatment consisted of 2 platforms, each containing 2 dishes. These were then placed 1.25 m from the center of the testing arena to create 2 medium-sized feeders. The clumped treatment consisted of 1 large platform placed in the center of the arena, holding all 4 dishes. The distribution patterns for each treatment are shown in Figure 1. Each experimental GS was exposed once to each resource distribution scenario only once.

**Data Collection and Use of Space Calculations**

Once birds were transferred to the testing arena they were allowed a 15-min acclimation period prior to data collection. Observations started after the acclimation period, at which point food was added to each feeder. All 3 arenas were observed during the same 1 hour period. The observer (E. H. Leone) rotated among arenas at 1-min intervals and recorded a scan sample for each arena every 3 min, yielding a total of 20 observational scans per arena per hour. For each scan the location and identity of the 5 focal individuals was plotted on a scaled map (Figure 1), along with the location of all remaining individuals. Locations were recorded as single points and represented the position of each bird’s head.

Immediately following the spatial observations feeders were removed and any remaining food was weighed. Each GS was then observed individually for 15 min to record all aggressive interactions (for descriptions see Leone et al., 2007). Feeders were refilled for the aggressive observation period. The order of observation for each group was randomly assigned to balance time effects.

The maps corresponding to each scan were digitized with the Chickitizer software package (Sanchez and Estévez, 1998). This software operates in conjunction with a digitizer (ACECAD, Taipei, Taiwan) to code each bird’s location in XY coordinates and append any independent variables of interest such as bird identity and behavior.

Nonparametric kernel density core area estimates at 30, 50, and 90% were calculated from the location data with a fixed bandwidth of 0.4 with the Animal Movement Extension v 2.04b (Hooge and Eichenlaub, 2000) for ArcView GIS v 3.2 (ESRI, Redlands, CA). Nonparametric kernel estimators determine the probability of observing a subject at each point in space. This is done without assumptions about the distribution of observation points (Worton, 1987, 1989). Core area percentages, or intensities, correspond to the probability of finding a bird within the generated area. These percentages were chosen because they represent intensities of space use ranging from small to large.

Two sets of core areas were calculated from the focal bird observations. First an individual core area (ICA) was determined for each focal bird within each GS. A second core area was calculated from the locations of all 5 focal birds taken together, total core area (TCA). This TCA quantifies the amount of space used by all 5 focal birds within each GS and serves as an estimate of group dispersion, assuming random dispersal of the 5 focal individuals within the group. Sampling theory dictates that the results will be consistent over time irrespective of whether we

![Figure 2](https://academic.oup.com/ps/article-abstract/87/1/3/1567029)
sample a subset of the group or, in the case of GS5, the entire group (Ott and Longnecker, 2001).

From the data we computed the maximum and minimum interindividual Euclidean distances between birds, averaged across scans. Maximum interindividual distance was defined as the farthest distance between any 2 birds within the group, focal or nonfocal, and the minimum distance was defined as the smallest distance between any 2 individuals. Nearest neighbor interindividual distances were calculated for each bird in each experimental GS and treatment as defined by the distance to its closest conspecific (Clark and Evans, 1954). Distances were then averaged across all birds and scans for analysis.

Expected interindividual distances were calculated with a random movement simulation program (InsightfulCorp S-plus 6.1, Seattle, WA). Each simulation consisted of randomly assigning locations to each bird in the group and calculating the resulting maximum, minimum, and nearest neighbor interindividual distances. A total of 2,000 simulations were performed for each GS and the average values for the 3 distance measures were calculated (Table 1). These numbers represent the predicted or expected values, assuming that birds were moving around randomly within the testing arena. Deviations were calculated by subtracting the observed distances for each group from the expected values, to determine the extent of environmental influence on movement. The less influence environment has the more similar the observed values should be to the expected values.

**Statistical Analysis**

All analyses were conducted using a Mixed model ANOVA in SAS v. 8.1 (SAS Institute, Cary, NC). Separate ANOVA were modeled for each core area level, interindividual distance, and their deviation from the simulated expected predictions assuming randomness, aggression, and feeder consumption in each phase. Model assumptions of normality and homogeneity of variance were tested, and adjustments were made as necessary. Aggression values were log transformed and core areas were square root transformed to better satisfy model assumptions. The experiment was designed as a factorial with experimental GS and resource distribution analyzed as fixed factors. The model covariance structure was adjusted based on the fact that each GS was tested 3 times within phase, and that each home pen held 3 group sizes. Because the covariance for exposing group sizes to multiple resource distribution treatments was estimated at zero, it was subsequently dropped from the model; however, the covariance for the housing of GS together remained. Differences were considered significant at the $P < 0.05$ level. All mean comparisons were reported after a Tukey’s adjustment for type 1 error rates (for review see Jones, 1984).

**RESULTS**

**Individual Core Area**

The 30 and 90% ICA in the free access phase were not affected by GS, resource distribution, or their interaction.
The 50% ICA were affected by resource distribution ($F_{2,53.3} = 3.32$, $P = 0.044$) but not by GS or their interaction. At 50% intensity the ICA in the scattered treatment (0.85 ± 0.04 m²; mean ± SEM) were significantly larger than in the patchy treatment (0.72 ± 0.04 m²; $t_{53.3} = 2.58$, $P = 0.034$). Neither distribution patterns differed from the clumped treatment (0.79 ± 0.04 m²). When resource access was restricted in the restricted access phase the 30, 50, and 90% ICA measurements were unaffected by GS, resource distribution, or their interaction.

**Total Core Area**

There was an interaction between GS and resource distribution for the 30% TCA when birds were given free access to resources ($F_{4,53.9} = 3.36$, $P = 0.016$; Figure 2). The 50 and 90% TCA (Figure 3) were affected by GS ($F_{2,53.3} = 12.00$, $P < 0.001$; $F_{2,52.8} = 28.35$, $P < 0.001$, respectively), whereas resource distribution patterns and their interaction with GS had no effect.

During the restricted access phase we observed a shift in the birds’ response; unlike in the free access phase the 30 and 50% TCA increased as resources became more widely distributed (Figure 4; $F_{2,56} = 7.02$, $P = 0.023$; $F_{2,56} = 5.02$, $P = 0.0099$, respectively) but were not influenced by GS or their interaction. However, GS was the significant factor for the larger 90% TCA ($F_{2,56} = 3.84$, $P = 0.027$), whereas resource distribution and interaction terms were nonsignificant. The GS20 TCA at 90% intensity at 8.1 ± 0.45 m² was larger than GS5, which was found to be 6.4 ± 0.45 m² ($P = 0.020$), but neither was different from the GS10 TCA of 7.1 ± 0.45 m².

**Interindividual Distances**

Minimum interindividual distances in the free access phase were affected by GS ($F_{2,52.4} = 51.60$, $P < 0.01$, Figure 5) and resource distribution patterns ($F_{2,52.4} = 3.45$, $P = 0.039$) but not the interaction term. Values for the clumped, patchy, and spread treatments were 0.147, 0.148, and 0.161 m (±0.005), respectively. After a Tukey adjustment to account for multiple mean comparisons, only the difference between clumped and spread treatments approached significance ($P = 0.051$). However, during the restricted access phase there was an interaction of GS and resource distribution for the minimum interindividual distances ($F_{4,56} = 3.24$, $P = 0.018$; Figure 6) as GS3 distances increased with resource dispersal, whereas the other 2 GS remained largely unchanged. The minimum interindividual deviations from the expected values followed similar patterns during this phase. For the free access phase the deviations of the observed values from those expected assuming random movement were affected by GS ($F_{2,52.5} = 2776.90$, $P < 0.001$), decreasing as GS increased (Figure 5). Neither resource distribution patterns nor the interaction of GS and resource distribution were significant in the free access phase, whereas during the restricted access phase there was an interaction between GS and resource distribution for the deviations ($F_{2,56} = 3.54$, $P = 0.012$; Figure 6). During the free access...
When chickens were given free access to resources the maximum interindividual distances were not consistent for each GS across all resource distribution patterns, as noted by the interaction between GS and resource distribution \((F_{4,52.2} = 4.73, P = 0.003; \text{Figure 7})\). Whereas GS\(_{10}\) maximum distances increased with the dispersal of resources, GS\(_{5}\) and GS\(_{20}\) were mostly constant. There was also an interaction for the deviations of observed values from those assuming random spacing in this phase \((F_{4,52.3} = 5.96, P = 0.001; \text{Figure 7})\). Once again when access to resources was restricted, there was a shift in the impact of the fixed factors. During the restricted phase both the maximum interindividual distances and deviations were influenced by GS \((F_{2,56} = 48.74, P < 0.001; F_{2,56} = 12.00, P < 0.001; \text{Figure 8})\); neither was affected by resource distribution patterns or the interaction term.

In the free and restricted access phases, nearest neighbor distances were affected by GS alone \((F_{2,51.7} = 3.82, P = 0.028; \text{and } F_{2,56} = 23.26, P < 0.001, \text{respectively, \text{Figure 9}})\), as were the deviation values from those expected assuming random movement \((F_{2,52} = 141.98, P < 0.001; F_{2,56} = 70.10, P < 0.001; \text{Figure 9})\). Neither the distances nor their deviations were affected by resource distribution pattern or the interaction term in either phase.

**Consumption**

During the free access phase birds consumed on average 78.7 ± 4.91% (mean ± SEM) of the available food;
consumption was not affected by GS, resource distribution, or their interaction. However, when competition increased in the restricted access phase as access to resources was limited total resource consumption was influenced by GS ($F_{2,63} = 4.09, P = 0.021$) but not by resource distribution or the interaction of the 2 factors. The GS$_{10}$ consumed on average 99.9 ± 1.81% of the available resources, which was greater than the 93.2 ± 1.81% consumed by GS$_5$ ($t_{63} = 2.59, P = 0.032$). Neither GS$_5$ nor GS$_{10}$ were different from the 99.2 ± 1.81% consumed by GS$_{20}$.

**Aggression**

The frequency of aggressive interactions measured during the 15-min observation period during free access phase I was not affected by resource distribution, GS, or the interaction of the 2 factors, or the order of observation. When competition increased during the restricted access phase, aggression increased with GS ($F_{2,60} = 5.23, P = 0.008$), from 0.09 ± 0.052 (mean ± SEM) interactions/bird/15 m to 0.13 ± 0.054 and 0.30 ± 0.054 in GS$_5$, GS$_{10}$, and GS$_{20}$, respectively. Only GS$_5$ and GS$_{20}$ were significantly different ($t_{60.3} = 3.09, P < 0.001$). Resource distribution and order of observation were all nonsignificant, as were all interactions involving order of observation for both phases.

**DISCUSSION**

In this study we found that individual birds used the space available to them in a consistent manner, as evidenced by similar ICA irrespective of GS and resource distribution patterns. Because pen size was equal for each treatment and GS in this study, it is not surprising that ICA were unchanged because pen size may be a salient influence on space use and behavior (Christman and Leone, 2007); even though birds did not use the entire pen they used similar amounts of the available space. Previous studies have established that movement and spacing patterns in poultry are influenced by the social effects of dominance hierarchies (Grigor et al., 1995b), group size (Channing et al., 2001), stocking density (Estévez et al., 1997, 2005; Carmichael et al., 1999), and space availability (Newberry and Hall, 1990; Estévez et al., 1997). The availability of space can be limited not only by pen size per se, but also by stocking density and GS as a result of ongoing social interactions between the birds and limitations to the physical space, which may be occupied by additional group members (barrier effect; Newberry and Hall, 1990). Our results indicate that even though GS and stocking density were increasing, birds did not seem to experience social constraints that would limit their use of space as evidenced by the ICA results. Stocking density and GS in this experiment were considerably lower than...
the densities used in other studies (Newberry and Hall, 1990; Estévez et al., 1997) and therefore might not have become a limiting factor. Other studies have also reported (Channing et al., 2001) that irrespective of GS birds used equal proportions of the available space when density remained constant and GS increased. Both Newberry and Hall (1990) and Estévez et al. (1997) suggest that the differences obtained in their studies were more a result of density and the barrier effect created by the birds rather than a consequence of limitations due to social dynamics.

Whereas individuals did not show differences in use of space, the groups became more dispersed as a whole when resources were scattered. However not all GS responded in the same way. With free access to resources the total area occupied by the group (TCA) was larger for larger GS; however, when competition increased as resources became restricted to a single individual, TCA increased in response to resource dispersal rather than GS. During the restricted access phase the size of the 30 and 50% TCA was more affected by resource distribution patterns, suggesting that focal birds dispersed more as resources became more widely distributed and competition for them increased. If each bird required a fixed amount of space to perform its daily routines then 20 birds would be expected to occupy a greater area than 5, thus leading to greater dispersal at larger GS. Although this may explain the results from the free access phase, it is insufficient to explain the TCA observed when access to resources was restricted, suggesting that space use by broilers is adaptable as a function of the distribution of resources within the environment. In production environments, when access is freely available to all birds, these results suggest that more widely distributed and scattered feeders would lead to a more even distribution of birds. At higher commercial stocking densities a wide distribution of feeders may also reduce potential crowding effects.

Contrary to our expectations in both phases we observed an overall decrease in minimum and nearest neighbor distances as GS increased. Whereas nearest neighbor distances represent the average cohesion within a group, the minimum interindividual distance indicates the closest proximity of birds to one another; both are measures of group cohesion and give insight into the spacing dynamics in flocks. We expected birds in larger groups to maintain larger minimum, maximum, and nearest neighbor interindividual distances than birds in smaller groups. The observed minimum and nearest neighbor distances appeared to be inconsistent with predictions in the literature (Clark and Mangel, 1984; Alonso et al., 1995; Carbone et al., 2003), as smaller GS appeared to be more dispersed than birds in larger GS. However, whereas birds were physically closer to one another in the larger GS, they occupied a larger total area and maintained much larger maximum interindividual distances.

Figure 8. Maximum interindividual distances (least squares means ± SEM) and the expected distances assuming birds moved randomly according to group size for the restricted access phase. Bars and deviations sharing any identical letters are not significantly different (Tukey’s adjustment; \( P > 0.05 \)). Expected values are designated by the large gray background bars. Mean comparisons for deviations, calculated as the difference between the observed and expected values, are in capital letters, and means comparisons for observed values are in lowercase letters. *Deviations do not differ significantly from zero (\( P > 0.05 \)).
Figure 9. Free (a) and restricted (b) access phase nearest neighbor distances (least squares means ± SEM) and the values expected assuming birds spaced themselves randomly according to group size. Deviations are represented by the difference between the expected values (gray bars) and the observed values (black bars). A–C, a–c Mean comparisons are designated by capital letters for deviations and lowercase letters for the observed distances. Bars or deviations sharing any identical letters are not significantly different (Tukey’s adjustment; $P > 0.05$). All deviations differ significantly from zero ($P < 0.05$).

Birds did not appear to position themselves randomly in any GS, as indicated by the deviation of observed interindividual distances when compared with those predicted by the random movement simulation. This simulation enabled us to model spacing patterns if birds moved randomly around the testing arena under different experimental settings. Our random simulation predicted that minimum and nearest neighbor interindividual distances would be smaller for larger GS in confined environments (Table 1). The Carbone et al. (2003) simulation predicted similar spacing structure for increasing GS in wild foraging geese. Whereas the overall trends we observed for interindividual distances were predicted by our random simulation, smaller GS deviated the farthest from the expected values, suggesting that environmental conditions were influential in promoting greater flock cohesion than what would be predicted for these small groups. Under restricted access GS5 minimum interindividual distances increased along with resource dispersal, whereas no differences were detected for the larger GS. This result makes biological sense; smaller GS should be more affected by resource distribution patterns because individuals have less protection from predators than if they were in a larger group (Newberry et al., 2001). Birds in smaller GS would have a natural tendency to maintain a tight cohesion, but with resources widely scattered individuals would be forced to spread out and move farther from the group. These results suggest that resource distribution may be much more important in shaping the behavior of small groups than large ones.

Whereas the risk of predation for an individual is smaller in larger groups (Lima, 1995), the level of competition for resources among group members increases (Clark and Mangel, 1984, 1986). Individuals must balance the opposing forces of attraction resulting from predatory risks and repulsion resulting from intragroup competition. Whereas minimum interindividual deviations in the restricted access phase were significantly smaller than zero for GS5 and GS10, indicating that smaller groups were closer together than predicted, deviations were significantly larger than zero for GS20, indicating that birds in the largest GS were farther apart than random movement would predict. Tight cohesion would offer birds in small GS greater defense against predators, whereas birds in the larger groups would be able to reduce competition between group members for the available resources by moving further away from one another. Not surprisingly maximum interindividual distances increased with GS in both phases. The most distant group members should be closer together in smaller groups because these flocks are more vulnerable to predation than larger flocks (Lima, 1995). These results suggest that shorter maximum interindividual distances are likely to be the most important factor for reducing predation risk for small groups. Whereas minimum and nearest neighbor distances would heavily influence competition for resources, they would...
not be as crucial as maximum interindividual distance for limiting group dispersion and providing protection against predation.

Resource monopolization was not detected in the present experiment because many individuals gained access to the resources in both the restricted and free access phases (E. H. Leone, personal observation). However, we did observe more aggression in the larger GS when birds competed for limited access to resources during the restricted access phase. These results are similar to Menc (1988) who found that aggression increased in broilers when birds were feed restricted. When access to resources was restricted in the large GS a greater number of birds were excluded from the feeders at any given time, which could explain the increase in aggression. Rather birds appeared to be scrambling to gain access to the feeders, similar to what has been found in other studies with broilers (Murphy and Preston, 1988; Leone and Estévez, 2007), laying hens (Estévez et al., 2002), and wild birds (Lima et al., 1999; Parker, 2000; Dubois et al., 2003). Previous studies have found an increase in consumption with increasing feeder space (Meunier-Salau¨n and Faure, 1985); however, when a given amount of total feeding space is merely partitioned (or distributed) there was no increase in consumption (Huon et al., 1986). In the present study feeder space remained constant in the free access phase, and we too found no effect of distribution. In the restricted access phase feeder space increased with increasing dispersal; however, again we found no effect on consumption.

In summary, whereas GS was the most significant predictor of interindividual distances, overall spacing patterns changed according to resource distribution patterns and feeder accessibility. Under restricted conditions, aggression increased with GS according to the predictions of Estévez et al. (2002, 2003). Whereas the observed minimum and nearest neighbor distances were slightly larger for the smaller GS, they were far smaller than the predictions of our random movement simulation. This indicates that birds were far closer to one another than what would be expected by chance. On the contrary, observed minimum and nearest neighbor distances for the larger groups were greater than predicted and observed maximum interindividual distances were found to increase with GS. These spacing patterns would allow birds to minimize predation risk and competition for resources. Our results suggest that the amount of space used by broilers and the interindividual distance that they maintain are not fixed but rather are adapted according to the specific environmental conditions.

REFERENCES


