ABSTRACT

Title of Document:  
SEPARATING THE EFFECTS OF GROUP SIZE, DENSITY, AND ENCLOSURE SIZE ON MOVEMENT AND USE OF SPACE IN DOMESTIC FOWL (*Gallus gallus domesticus*)

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This project was designed to separate the confounded effects of group size, density, and enclosure size, and to examine the role of enclosure design and its related parameters in shaping movement patterns and use of space in the domestic fowl. While previous research has suggested that group size, density, and enclosure size are highly relevant to broiler (meat-type chicken) welfare, confounding between variables makes their individual contribution difficult to distinguish. My novel treatment structure with 10, 20, and 30 birds in small (1.5 m$^2$), medium (3.0 m$^2$), and large (4.5 m$^2$) enclosures enabled me to determine the impact of enclosure size while systematically controlling for group size and density. Three enclosure designs: rectangular, square, and square with partitions to maintain a constant perimeter to area ratio, were employed in order to determine the impact of enclosure parameters such as length to width and perimeter to area ratio.
Enclosure size and design were the most relevant factors for space use, which was immune to the influence of group size and density. Birds consistently had larger home ranges in larger enclosures. The design of the enclosure had a strong effect of movement, altering the response of birds to the treatment combinations. Movement appeared to be greatest in rectangular enclosures, where the largest straight-line distance is available and the perimeter to area ratio declines at a relatively slow rate with increasing enclosure size. While enclosure size played a significant role in determining nearest neighbor distances and net displacement, these parameters appeared to be limited by density. The presence of partitions designed to increase interior perimeter space appeared to reduce movement and increase inactivity. Movement patterns did not appear to be restricted by social interactions for any group size. Rather, the physical presence of group mates at even a relatively low density of 6.7 birds/ m² appeared to act as a barrier to group dispersal and movement. Group size had little effect on young domestic fowl. Overall, this project has shown that for young domestic fowl the most relevant factors to overall space use are the amount of space available and enclosure design.
SEPARATING THE EFFECTS OF GROUP SIZE, DENSITY, AND ENCLOSURE SIZE ON MOVEMENT AND USE OF SPACE IN DOMESTIC FOWL (*Gallus gallus domesticus*)

By

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Dissertation submitted to the Faculty of the Graduate School of the University of Maryland, College Park, in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Chapter 1: Background Literature

The Effects of Group Size, Density, and Enclosure Size on Movement and Use of Space in the Domestic Fowl

Currently animal welfare issues are of great interest to commercial poultry producers as public perception of how animals are raised and maintained has gained relevance. Broiler production constitutes the largest animal industry in the United States, producing more than 8 billion broilers (meat-type chickens) annually (NASS 2007), therefore any improvements in management practices achieved by establishing a deep understanding of the factors that affect their behavior will have major significance not only in improving the quality of life of billions of birds but potentially improving their performance as well.

One of the most reliable techniques for understanding the internal welfare state of domestic fowl may be to understand their behavior (Duncan 1987; Dawkins 1999, 2003). Difficulty in coping with the production environment, from physiological as well as behavioral perspectives, is believed to correlate to poor welfare (for review see Broom 1991). Behavior can be used to assess physiological indicators of poor welfare such as pain and discomfort (Dawkins 2004) as well as behavioral indicators of poor welfare such as fear and frustration (Duncan 1998). Some of the most relevant features that shape the behavior and use of space of animals in confined environments includes the number of animals housed (group size), the amount of space available on a per animal basis (stocking density), and the size and design of the enclosure. Although there is abundant literature on the effects of density and group size on broiler behavior (for review see
Estévez 2007 and Estévez et al. 2007) how chickens move and utilize the space available has been largely ignored. The way in which chickens utilize their available space is not only a matter of paramount importance for the welfare of the birds, but also can have important repercussion for animal production.

**Group Size**

In the domestic fowl there is a clear difference in the response of birds to small (less than 20) versus large group sizes. In small groups birds form a social hierarchy or pecking order (Schjelderup-Ebbe 1935; Rushen 1982), which determines access to resources, including space (Banks et al. 1979; Mankovich & Banks 1982; Banks 1984; Cordiner & Savory 2001). Specifically in regard to space use, dominant chickens may control attractive, high value areas, such as those close to the feeders (Banks 1984; reviewed in Grigor et al. 1995c). Gibson et al. (1988) suggested that dominant laying hens enjoy a greater freedom of movement than subordinates, moving about the enclosure freely and settling more frequently in the most attractive areas.

Hierarchies in chickens are established and maintained based on individual recognition and the ability to remember the social status of each group mate (Douglis 1948; D'Eath & Keeling 2003). However the ability to recognize all group members declines as group size increases, particularly beyond 30 birds (Douglis 1948). For large groups McBride & Foenander (1962) hypothesized that because domestic fowl would be unable to form stable hierarchies they would self-segregate and form sub-group in localized areas in attempt to maintain familiarity and stabilize social relationships. However this hypothesis has never been strongly supported with scientific data. Authors who found incomplete space use or large differences between individuals in the amount
of space utilized have suggested that this serves as evidence of sub-group formation and territorial behavior (McBride & Foenander 1962; Craig & Guhl 1969; Pamment et al. 1983; Odén et al. 2000). In order to qualify as a territory, the area would have to be set up and aggressively defended from intruders or rivals (Davies & Houston 1984). In large enclosures birds may not use all of the space available to them, even when there are no social restrictions to movement. It is important to note that incomplete space use does not necessarily reflect subgroup formation or territorial systems, but may simply be indicative of individual variation or different behavioral strategies (Leone & Estévez 2008a).

Although dominance hierarchies may determine access to preferred enclosure areas in small groups of domestic fowl, for the most part research has shown that group size is not a factor that dictates individual space use patterns when birds are tested in equally-sized enclosures. For example, Leone et al. (2007) found that the short-term individual core areas of male broiler chickens did not differ between birds maintained in groups of 5, 10, and 20 when given access to an equal amount of space. Similarly Lewis and Hurnik (1990) found that broilers in groups of 15 to 30 ranged across the total amount of space available to them, regardless of group size. These results were similar to the findings of Estévez et al. (1997) who used much larger group sizes ranging from 50 to 200 birds and noted that birds at all group sizes had freedom to move throughout the available space. This later study also suggested that as group size increases beyond 50 birds, broilers adopted a ‘tolerant’ social strategy categorized by few aggressive interactions as access to resources based on scramble competition likely replaces aggression (Estévez et al. 1997). Further evidence for a tolerant social with increasing
group size has been found in many other studies with laying hens (Nicol et al. 1999; Carmichael et al. 1999; D'Eath & Keeling 2003; Estévez et al. 2002; Estévez et al. 2003).

It is likely that the switch in social behavior from aggressive hierarchies to tolerance is a product of the theoretical cost of establishing a pecking order. As group size increases the cost to establish a hierarchical system becomes prohibitive in terms of energy invested in aggressive interactions, risk of injury, or time that could have been devoted to the exploitation of resources. Additionally, in large groups individual members will have little chance of encountering the same individuals repeatedly, and thus recouping the initial energy required to form the hierarchy (Pagel & Dawkins 1997).

The physical number of individuals in an enclosure may become irrelevant once a sufficiently large group size is reached. For example, Stricklin et al. (1995) demonstrated with computer-simulated animals or ‘animats’ that ‘freedom of movement’ is reduced by increasing group size in small groups, but that in large groups additional members did not contribute to a decline in ‘freedom of movement’.

Therefore it makes sense that many authors have found that domestic fowl in both experimental and commercial settings disperse throughout their environment, using large quantities of the available space (Hughes et al. 1974; Appleby et al. 1985; Appleby et al. 1989; Preston & Murphy 1989; Estévez et al. 1997; Leone & Estévez 2008a; Odén et al. 2004) and that total space use is not influenced by changes in group size (Estévez et al. 1997; Channing et al. 2001).
Stocking Density

Stocking density and group size are often confounded in research studies, making it difficult to distinguish the individual contribution of each factor and determine if the effects of increasing stocking density (via larger group sizes) are independent of the effects of social hierarchies. For example, the physical barrier created by birds as they lie in the path of movement of other group mates (Newberry & Hall 1990) may present more of a limiting factor to movement patterns than social interactions (Estévez et al. 2005), particularly at high densities. High density has been shown to restrict or reduce movement in both layer and broiler strains (Andrews et al. 1997; Carmichael et al. 1999), specifically decreasing the distance traveled per unit time (Lewis & Hurnik 1990; Estévez et al. 1997; Febrer et al. 2006). If animal density limits movement as a result of the presence of conspecifics lying in the intended pathway, then it is likely that when surrounded by group-mates an individual’s dispersal may be limited as well (Stricklin 1995).

In addition, the amount of ‘effective free space’ available, which is shaped by the combination of group size, stocking density, and enclosure size, may also be a highly relevant influence on movement and space use. The amount of ‘effective free space’ available may differ substantially from the theoretical amount provided on a per animal basis. Many birds, including domestic fowl, exhibit strong flocking tendencies as a result of attractive forces (Clark & Mangel 1984; Febrer et al. 2006) which are expressed through the maintenance of specific (close) inter-individual distances and synchronous behavior. Studies have shown that in confinement groups of domestic fowl do not always disperse to the full extent possible, suggesting that there an upper limit to the inter-
individual distances birds prefer to maintain, even when additional space is available (Arnould & Faure 2004; Leone et al. 2007). This underutilization of the available space can leave large areas unoccupied (Arnould & Faure 2004; Leone et al. 2007), creating relative densities that differ through the enclosure (Channing et al. 2001). Therefore, even at identical densities animals in larger enclosures may enjoy a greater amount of ‘effective free space’ as a consequence of open areas and small relative density.

**Enclosure Size and Design**

The majority of investigations into the factors shaping movement and space use have focused on group size and density. Far fewer studies have been conducted on the effects of enclosure size and design, which are highly relevant to the movement patterns of captive animals. In chickens it has been suggested that space use is ultimately determined not by stocking density or group size per se but by the amount of space available, or enclosure size (Newberry & Hall 1990; Estévez et al. 1997; Leone et al., 2007). ‘Free range’ systems represent one common area where researchers have examined the effect of enclosure size and design on space use. ‘Free range’ systems refer to birds that are given access to additional outdoor space, and in both laying hens (Keeling et al. 1988; Grigor et al. 1995a, c) and meat-type broilers (Estévez et al. 1997; Dawkins et al. 2003) the additional space goes largely underutilized. However, even when birds do not take full advantage of the available space, studies have shown that use of space increases in larger enclosures (Newberry and Hall, 1990; Estévez et al. 1997) regardless of differences in group size or stocking density.
Space use in the domestic fowl is shaped not only by the amount of space available, but the quality of that space is equally important. Enclosure design, both in its physical parameters (length, width, floor area, etc.) as well as elements which increase environmental complexity (such as enrichment) can significantly influence movement and use of space. Studies have shown that layers maintained in ‘free range’ systems make greater use of outdoor areas when the quality of the space is improved by incorporating various types of protective cover (Zeltner & Hirt 2003; Hegelund et al. 2005; Whay et al. 2007). The presence of visual cover, which increases environmental complexity and perimeter (wall) space, has been found to reduce disturbances and aggression (Cornetto et al. 2002), and improve bird distribution throughout the enclosure (Newberry & Shackleton 1997; Cornetto & Estévez 2001). When commercial broiler breeder houses were enriched with cover panels overall space use increased and males made use of a wider range of areas within their environment (Leone & Estévez 2008). Similarly, when broiler houses were enriched with straw bales birds used them as perches and resting points, whereas and even in the control houses without enrichment birds clustered around roof support poles which dotted the litter area (Kells et al. 2001).

Perimeter space is often the only available cover in confined environments and as such is an important feature of the enclosure. Researchers have found that pigs (Wiegand et al. 1994) and broilers (Cornetto & Estévez 2001b) take greater advantage of perimeter space, as opposed to the more abundant central area, and use the perimeter spaces to a greater extent than would be expected by chance (broilers, Newberry & Hall 1990). The amount of peripheral space available is a direct consequence not only of the size of the enclosure, but also its shape. The shape of the enclosure determines not only peripheral
space, but also a number of other potentially important parameters: such as the number of
corners, the distance to them, and the farthest distance an animal will have to travel to
reach a wall (Christman & Leone 2007). For example, when enclosures are square
(length to width ratio is constant) the furthest distance an animal will have to travel to
reach the closest wall will increase linearly with enclosure size. Conversely, in a
rectangular pen in which the enclosure width is held constant as floor space increases the
furthest distance to a wall is constant. No matter what the shape, when enclosure size
increases (and the total available peripheral space) the ratio of perimeter space to central
area (perimeter to area ratio) decreases (Stricklin et al. 1995). Even at a constant stocking
density the amount of peripheral space available per animal also decreases. However, in
rectangular (as opposed to square) enclosures this decline occurs at a slower rate.

Researchers who have investigated the effects enclosure shape have found
significant impacts on animal behavior. Aggressive interactions in group of pigs are
affected by the shape of the pen but most specifically by the availability of corners
(Wiegand et al. 1994). Post-mixing aggression was greater in circular as opposed to
square enclosures; however when circles were modified to include corners there were no
differences between enclosure types. Aggression has also been shown to decrease when
pigs are grouped together in rectangular as opposed to square enclosures (Barnett et al.
1993).

While group size, density, and enclosure size and design all appear to have an
influence on movement and use of space in domestic fowl their individual impacts cannot
be clearly discerned as a result of confounding between variables. Limitations to
movement and dispersal may be a consequence of increases in group size, density, or
both. While the size of enclosures, and their design, may be the factors of greatest consequence for movement and space use there is surprisingly little attention paid to these factors in the published literature for the domestic fowl.

Study Purpose, Hypothesis, and Predictions

The aim of this project was to separate the confounded effects of group size, density, and enclosure size on movement and use of space patterns in the domestic fowl. While previous research has suggested that each of these factors is highly relevant for the domestic fowl the confounding between variables, which has often been ignored or disregarded by authors, makes it difficult to distinguish specific contributions. Furthermore, I intended to describe the relative impact of various enclosure parameters such as the furthest distance from a wall, length to width ratio, and perimeter per animal ratio on the domestic fowl. This information is currently lacking in the literature, but is essential in the quest to understand the impact of confined environments on broiler welfare. I hypothesized that each individual factor included in this work (group size, density, and enclosure size and shape) would have a unique impact on movement and use of space in the domestic fowl. I expected that enclosure size would most significantly affect overall use of space, while group size and density would impose limits on movement parameters such as total distance traveled and net displacement. The enclosure design, specifically the amount of peripheral space available per animal, was expected to be one of the most relevant enclosure parameters for domestic fowl, followed by the farthest distance to a wall.
Chapter 2: Separating the Effects of Group Size, Density, and Enclosure Size

I. In Rectangular Enclosures When Length to Width Ratio Varies as Enclosure Size Increases

Abstract

To design effective captive environments that maximize animal welfare it is essential to understand how confined animals move within the space available. Besides the obvious effect of enclosure size, other factors such as the number of individuals in the group and their density per unit of area are known to affect movement patterns. Yet determining the specific contribution of each (enclosure size, group size and density) has been a challenge because confounding between two or more of these factors is experimentally difficult to avoid. The aim of this study was to isolate their unique effects by using multiple contrasts with an efficient experimental design which included combinations of groups of 10, 20, and 30 domestic fowl (*Gallus gallus domesticus*) housed in 1.5 m$^2$, 3.0 m$^2$ and 4.5 m$^2$ enclosures. This treatment structure enabled me to compare across increasing enclosure size both at constant group size and density. In this study I demonstrate that enclosure size and density are the primary factors affecting movement and use of space patterns for groups of domestic fowl. Animals in larger enclosures maintained larger nearest neighbor distances, traveled greater distances, and had bigger home ranges as measured by minimum convex polygons. These results suggest that larger enclosures encourage more exploratory movement in groups of
domestic fowl. However the positive effects of large enclosures may be limited by the
effects of density. Contrarily, in this study group size had fewer than expected effects.
**Introduction**

Captive housing encompasses a wide variety of conditions, from zoos and conservation centers, to research laboratories, and of course farms. For any captive species inadequate physical and social features of the environment can be a source of stress and discomfort that can lead to serious physiological, behavioral, and welfare problems (Würbel 2001; Estévez et al. 2007; Morgan & Tromborg 2007). Although many parameters can be controlled in captive environments, the size of the enclosure, the number of animals housed in it, and density (number of animals per unit of area) are some of the most salient factors that can have a major impact on how animals move and use the space available to them.

Adequate spacing is important for the welfare of animals (Stricklin 1995) as suggested by the fact that animals are willing to work for access to extra space (Faure 1991, 1994; Sherwin 2004, 2007). Restrictive spaces can lead to negative changes in behavior (Nicol 1987; Dawkins 1988; Poon et al. 1997; Crockett et al. 2000; Bashaw et al. 2001) including increased stereotypies (Beattie et al. 1996; Bashaw et al. 2001), reduced play (Jensen et al. 1998), and increased stress (Smith & Dobson 1990; Turner et al. 2000) and anxiety (Arakawa 2005). Reduced enclosure size hinders locomotion (Crockett et al. 1995; Crockett et al. 2000; Estévez et al. 1997; Poon et al. 1997), group dispersal (Blanc et al. 1999), and affects inter-individual distances and social spacing among animals (Keeling & Duncan 1991).

Besides the size of the enclosure, other aspects that are not considered as often such as its shape and design can also alter the behavior and space use patterns of captive animals (Barnett et al. 1993; Wiegand et al. 1994; Newberry & Shackleton 1997;
Changes in parameters such as peripheral (wall) space, length to width ratio, or distance to walls and corners may be important features of the captive environment with great biological significance for confined animals (Stricklin et al. 1995; Christman & Leone 2007). For example, the addition of wall space in central areas of the enclosure has been shown to improve spatial dispersion and reduce disturbances in broiler chickens (Cornetto & Estévez 2001b; Cornetto et al. 2002), and reduce injurious pecking and improve welfare in turkeys (Sherwin et al. 1999b).

The social environment is also critical to ensure the welfare of animals as confining inadequate numbers in a given space can lead to social stress (Hurst et al. 1999; Dronjak et al. 2004). In domestic species large group sizes have been shown to increase fearfulness (Bilcik et al. 1998), reduce productivity (Gonyou & Stricklin 1998; Turner et al. 2000; McLean et al. 2002), increase the chances of skin injuries (Turner et al. 2000; Kjaer 2004), and reduce group stability (Takeda et al. 2000). Similar patterns have been observed in captive wild animals, where inappropriate group sizes or crowding lead to increased stress responses (Maestripieri et al. 1992; Boyce et al. 1998; Boal et al. 1999; Dickens & Romero 2005; Raouf et al. 2006). Irrespective of enclosure size, maintaining high animal densities may result in a lack of sufficient free space thereby limiting animal locomotion (Estévez et al. 1997). High densities commonly used with domestic species have been linked to immune suppression (Turner et al. 2000; Heckert et al. 2002), increased disturbances (Cornetto et al. 2002), and reduced feeding behavior (Alanärä 1996; Cooke et al. 2000) weight gain, feed efficiency (Horton et al. 1991; Pearce & Paterson 1993; Brumm & Miller 1996; Brumm et al. 2004) and growth (Blanc & Theriez 1998; Bohlin et al. 2002).
While a great deal of research has been conducted on the impact of enclosure size, group size and density in a variety of species (for review see Alanäärä 1996; Sørensen et al. 2005; Estévez et al. 2007; Morgan & Tromborg 2007), they all involved some degree of confounding between variables. For example, when testing for density effects in enclosures of equal size group size has to be manipulated leading to confounding between density and group size. Thus the reduction in locomotion associated with high densities (Estévez et al. 1997) may be a consequence of the decline in ‘free’ enclosure space, which is reduced as animal density increases (Newberry & Hall 1990), but can also be associated with increased social conflict and social restriction which may occur in large group sizes. Therefore, in these types of studies it is difficult to isolate the precise contribution of each factor: enclosure size, group size or density, to changes in behavior and movement patterns. Yet a clear understanding of the effects of enclosure size, group size, and density may be critical in our efforts to improve the quality of the environment for captive animals.

In this study I used a unique experimental design to separate the confounded effects of group size, density and enclosure size on use of space and movement using the domestic fowl as an animal model. I hypothesized that each characteristic of the environment, defined by group size, density, and enclosure size, has a unique impact on animal movement and space use.
Methods

Facilities and Experimental Animals

This project was conducted at the University of Maryland’s Applied Poultry Research Facility in Upper Marlboro from September through November 2005. A total of 540 male day-old broiler chicks were obtained from a commercial hatchery. I chose to work with only a single sex in order to minimize behavioral variability. Initially 12, 24, and 36 birds were placed in the experimental enclosures in an effort to account for early mortalities and reach the target group sizes of 10, 20, and 30 birds. At the end of 3 weeks, extra birds were removed and housed in a separate enclosure. Each bird was individually tagged (Leone et al. 2007) on each side of the neck using the Swiftack Poultry Identification System (Heartland Animal Health Inc., Fair Play, MO). For the first 3 days birds were exposed to 24 hours of light, and thereafter were maintained on a 14 L: 10 D program in an effort to slow growth and promote leg health. Temperature and ventilation programs followed commercial practices. Feed and water were provided ad libitum from a central tubular hopper and a line of nipple drinkers located along one side of the enclosure. Three hopper sizes were employed so that the proportion of enclosure space occupied by the feeder as well as the amount of feeder space available per bird was constant across treatments. The feeding program consisted of a standard three phase commercial diet. This protocol (R-05-39) was approved by the Institutional Animal Care and Use Committee at the University of Maryland.
Experimental Design

For this experiment I constructed three enclosure sizes which were 1.49 m² (small, 1.22 x 1.22 m), 2.96 m² (medium, 1.22 x 2.44 m), and 4.47 m² (large, 1.22 x 3.66 m). Each enclosure was covered with 5 cm of wood shavings. Enclosure size increased in only one direction to give all enclosures the same width (1.22 m) meaning that the medium-sized enclosure was twice as long as the small enclosure and the large enclosure was three times as long (Appendix 6-1). This arrangement enabled the floor area allowance to increase while the maximum distance from the nearest wall remained constant (Table 2-1). In addition to mere floor space there are a number of enclosure features which are likely to have a significant impact on animal movement (Christman & Leone 2007) and therefore this design was developed in an attempt to maintain as much consistency as possible across the enclosures. Since wall space has been repeatedly shown to be a strong attraction for confined animals (Stricklin et al. 1979; Cornetto & Estévez 2001b; Jeanson et al. 2003), the distance to a wall may heavily influence animal movement and spacing and thus I chose to control variation in this parameter. The enclosure dimensions and potential parameters of interest can be seen in Table 2-1 (for detailed description of calculations see Christman & Leone 2007).

The group sizes were housed in the different enclosures to generate the five experimental treatments (Table 2-1) each of them replicated five times. Groups of 10 were housed all three enclosure sizes (10s, 10M, 10L) while group of 20 and 30 were housed in the medium (20M) and large enclosures (30L).
respectively. This design enabled me to make comparisons across constant group size, where density decreased with increasing enclosure size (10$_S$, 10$_M$, 10$_L$), across a constant density, where group size increased with enclosure size(10$_S$, 20$_M$, 30$_L$), and across constant enclosure sizes where group size and density increased simultaneously (10$_M$, 20$_M$ and 10$_L$, 30$_L$).

Data Collection

Each enclosure was divided into a grid of 20 x 20 cm squares by placing numerical and alphabetical placards along the enclosure walls. This created a visual grid that allowed me to precisely record bird locations on scaled maps (Cornetto & Estévez 2001b; Leone et al. 2007). For behavioral observations five focal birds were randomly selected from each enclosure and were observed throughout the entire experiment. Observations began at three weeks of age and continued until birds were six weeks old. The birds in each enclosure were observed twice per day, three days per week. The location and identity of each focal individual, as well as the position of all other group members, was recorded via instantaneous scan sampling *ad libitum* for a five minute period. At the beginning of each observation period bird locations were recorded on a single scan sheet, and once completed successive locations were recorded on additional scan sheets until the 5 minutes expired. These location scans were digitized as X Y coordinates with a Digitalizer (ACECAD, Taipei, Taiwan) using the Chickitaizer© software (Sanchez & Estévez 1998).
Table 2-1

Enclosure parameters for each group size and enclosure size combination. Parameters include group size, stocking density, total floor area available, enclosure length and width, length to width ratio, total perimeter, perimeter per animal, perimeter to area ratio, farthest distance to the nearest wall and farthest distance to a corner.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Group Size</th>
<th>Density (birds/m²)</th>
<th>Total Area (m²)</th>
<th>Length (m)</th>
<th>Width (m)</th>
<th>Length: Width Ratio</th>
<th>Perimeter (m)</th>
<th>Perimeter (m) / animal</th>
<th>Perimeter: Area Ratio</th>
<th>Distance to Wall (m)</th>
<th>Distance to Corner (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10_L</td>
<td>10</td>
<td>2.2</td>
<td>4.47</td>
<td>3.66</td>
<td>1.22</td>
<td>3 : 1</td>
<td>9.76</td>
<td>0.98</td>
<td>2.2 : 1</td>
<td>0.61</td>
<td>1.93</td>
</tr>
<tr>
<td>10_M</td>
<td>10</td>
<td>3.4</td>
<td>2.96</td>
<td>2.44</td>
<td>1.22</td>
<td>2 : 1</td>
<td>7.32</td>
<td>0.73</td>
<td>2.5 : 1</td>
<td>0.61</td>
<td>1.36</td>
</tr>
<tr>
<td>10_S</td>
<td>10</td>
<td>6.7</td>
<td>1.49</td>
<td>1.22</td>
<td>1.22</td>
<td>1 : 1</td>
<td>4.88</td>
<td>0.49</td>
<td>3.3 : 1</td>
<td>0.61</td>
<td>0.86</td>
</tr>
<tr>
<td>20_M</td>
<td>20</td>
<td>6.7</td>
<td>2.96</td>
<td>2.44</td>
<td>1.22</td>
<td>2 : 1</td>
<td>7.32</td>
<td>0.37</td>
<td>2.5 : 1</td>
<td>0.61</td>
<td>1.36</td>
</tr>
<tr>
<td>30_L</td>
<td>30</td>
<td>6.7</td>
<td>4.47</td>
<td>3.66</td>
<td>1.22</td>
<td>3 : 1</td>
<td>9.76</td>
<td>0.33</td>
<td>2.2 : 1</td>
<td>0.61</td>
<td>1.93</td>
</tr>
</tbody>
</table>
From each five minute observations period I calculated a number of measures to capture bird movement and space use which included: nearest neighbor distances which were calculated from the locations of all group members, the total distance traveled which was calculated by summing the Euclidean distances between successive recorded locations for each focal animal during the five minute observation period, net displacement which was calculated as the Euclidean distance between the first and last observed location, and movement activity which was defined as the percentage of scans where movement was observed. For nearest neighbor distances I was uniquely able to calculate the distances that would have been expected if birds positioned themselves randomly with the environment, through the use of a simple random simulation. This random simulation could not be utilized for other measures, because no assumptions were made about movement patterns per se. Each simulation (InsightfulCorp, S-plus 6.1, Seattle, WA) consisted of randomly assigning locations to all birds according to each treatment combination. The average nearest neighbor distance for the group was then calculated, and this simulation was repeated 2000 times in order to generate expected nearest neighbor distances. The average value from these 2000 simulations represents the nearest neighbor distance that would be expected if birds randomly distributed within their enclosure. Deviations were then calculated by subtracting the observed nearest neighbor distances from those expected assuming randomness, in order to determine to what extent the treatment influenced inter-individual distance. Minimum convex polygons (Mohr 1947) were calculated using
ArcView GIS v8 (ESRI, Redlands, CA) with the Animal Movement Extension package (Hooge & Eichenlaub 2000). A total minimum convex polygon was built for each focal bird from all observed locations throughout the entire length of the study. This measure provided an estimate of the total amount of space utilized by each focal bird. In addition, weekly minimum convex polygons were generated for each focal bird based on the observations within one week’s time to determine the effect of age on space use. A coefficient of variation was also calculated to ascertain the variability in space use between individuals across age. All measurements were averaged across birds within each enclosure.

Statistical Analysis

All analyses were conducted in SAS (v. 9.1, SAS Institute, Cary, NC; Appendix 6-2). For all parameters except total minimum convex polygons I modeled the effects of treatment, age, and their interaction. Because total minimum convex polygons were calculated from all locations recorded from the entire study period, the statistical model only included the treatment effect. Separate mixed model ANOVAs were performed for each of the parameters analyzed: nearest neighbor distances and their deviation from expected values assuming random assortment, total distance traveled, net displacement, weekly minimum convex polygons and their coefficient of variation, and movement activity. All models included a covariance structure for repeated observations. Model assumptions of normality and homogeneity of residual variances were examined. In order to meet the assumptions variance components were modeled
by treatment for nearest neighbor distances and their deviations from randomness, net displacement and all minimum convex polygons.

The goals of this experiment were addressed with three specific a priori contrasts, the first two detected differences between increasing enclosure sizes when group size was constant (but density decreased; 10_S, 10_M, 10_L) and when density was held constant (but group size increased with enclosure size; 10_S, 20_M, 30_L), and lastly I compared across fixed enclosure sizes (where density and group size increased simultaneously; 10_M, 20_M and 10_L, 30_L). Each of these contrasts maintained one factor constant, while the other two covaried; each contrast is essentially an ANOVA test. In order to protect against an inflated Type I error rate the contrasts and mean comparisons were only performed when the overall ANOVA F-test was significant (P < 0.05).

Results

Nearest neighbor distance was affected by treatment (F_4, 6.03 = 30.80, P < 0.001) generally expanding with increasing enclosure size (Fig. 2-1). This increase was most notable when group size remained constant with 10 birds (10_S, 10_M, 10_L; F_2, 11.6 = 36.61, P < 0.001) and to a lesser extent when density was constant (10_S, 20_M, 30_L; F_2, 11.1 = 42.96, P < 0.001). When comparing constant enclosure sizes nearest neighbor distances were larger at smaller group sizes/ densities (10_M, 20_M and 10_L, 30_L; F_2, 4.69 = 47.15, P < 0.001).
Figure 2-1

Nearest neighbor distances (least squares means ± standard error of the mean) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment, and the expected values assuming random assortment (gray outline). White fill corresponds to equal group size while grey denotes constant density, which is listed below each treatment. Means sharing any common letters are not significantly different (P > 0.05). All observed nearest neighbor distances differed from those expected assuming randomness (P < 0.05), and from the predicted uniform distribution based on a density of 6.7 birds/m² which is represented by the dotted line (P < 0.05).
Figure 2-2

Effects of age on nearest neighbor distances (LSM ± SEM). Means sharing any common letters are not significantly different ($P > 0.05$).
In addition, group did not behave as would be expected by random assortment. There was a significant deviation between the observed nearest neighbor distances and those expected assuming randomness across treatment combinations ($F_{4,6.06} = 114.85$, $P < 0.001$; Fig 2-1), with all deviations differing significantly from zero ($P < 0.05$). In the smaller groups of 10 birds nearest neighbor distances were smaller than would be predicted by random assortment, but were farther apart than predicted in the groups of 20 and 30 birds. There was also a significant effect of age on the deviation of observed nearest neighbor distances from the random predictions ($F_{2,13.2} = 31.67$, $P < 0.001$), but there was no interaction between treatment and age. While birds were closer together than randomly predicted during weeks three (deviation mean ± standard error mean: 0.05 ± 0.005) and four (0.02 ± 0.004) the observed nearest neighbor distances were not different than the predicted values by week five (0.007 ± 0.004, $P = 0.14$). Nearest neighbor distances were larger for older birds ($F_{2,13.2} = 31.67$, $P < 0.001$; Fig. 2-2) but there was no interaction of age and treatment ($F_{8,12.4} = 1.41$, $P = 0.283$).

The total distance traveled was clearly affected by treatment ($F_{4,52.3} = 3.17$, $P = 0.021$; Fig. 2-3), increasing with enclosure size with constant group sizes of 10 ($10_S$, $10_M$, $10_L$; $F_{2,97.2} = 3.47$, $P = 0.035$) but not when density was maintained ($10_S$, $20_M$, $30_L$; $F_{2,98} = 0.79$, $P = 0.458$). Total distance traveled did not change with age ($F_{2,130} = 1.76$, $P = 0.175$) and there was no interaction of age and treatment ($F_{8,132} = 0.30$, $P = 0.964$).
Figure 2-3

Total distance traveled during an observation period (LSM ± SEM) by each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes constant density, which is listed below each treatment. Means sharing any common letters are not significantly different ($P > 0.05$).
Similarly, net displacement differed by treatment ($F_{4, 27.3} = 7.69, P < 0.001$; Fig. 2-4) but not by age ($F_{2,104} = 0.16, P = 0.856$) or their interaction ($F_{8, 76.7} = 0.32, P = 0.956$). Net displacement increased with enclosure size both across constant group size 10 ($10_S, 10_M, 10_L; F_{2,67.8} = 14.67, P < 0.001$) and across constant density of 6.7 birds/m$^2$ ($10_S, 20_M, 30_L; F_{2, 27.2} = 3.73, P = 0.037$) but were not different when comparing enclosures of the same size regardless their density/group size ($10_M, 20_M$ and $10_L, 30_L; F_{2, 23.2} = 0.39, P = 0.679$).

The total amount of space utilized, as measured by minimum convex polygons, differed according to treatment ($F_{4, 13} = 76.72, P < 0.001$; Fig. 2-5) as birds used more space when housed in larger enclosures regardless of density ($10_S, 10_M, 10_L; F_{2, 20.6} = 103.06, P < 0.001$) or group size ($10_S, 20_M, 30_L; F_{2, 23.6} = 98.25, P < 0.001$). There was no difference in space use when a comparison was made across constant enclosure size ($10_M, 20_M$ and $10_L, 30_L; F_{2, 15.2} = 1.79, P = 0.20$). There was an affect of age on minimum convex polygons ($F_{2,29.7} = 7.04, P = 0.003$); as space use was greater initially and decreased as the birds aged (Fig 2-6). The average amount of space used by birds during each week of age different according to treatment ($F_{4,7.24} = 22.51, P < 0.001$; Fig. 2-7) similar to the total minimum convex polygons, and I did not find an interaction effect ($F_{8,18.4} = 1.17, P = 0.366$). The coefficient of variation for minimum convex polygons did not differ by treatment ($F_{4, 7.66} = 1.09, P = 0.42$), age ($F_{2,12.7} = 0.23, P = 0.80$), or their interaction ($F_{8,5.89} = 0.96, P = 0.536$).
Figure 2-4

Net displacement, defined as the Euclidean distance between the first and last observation point, (LSM ± SEM) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes constant density, which is listed below each treatment. Means sharing any common letters are not significantly different ($P > 0.05$).
**Figure 2-5**

Total minimum convex polygon estimates of space use (LSM ± SEM), according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes stocking density, which is listed below each treatment. Total minimum convex polygons were built from all recorded locations over the length of the study and convey the total amount of space utilized by the birds. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 2-6

Average minimum convex polygon recorded for each week of age (LSM ± SEM). Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 2-7

Average weekly minimum convex polygons (LSM ± SEM) according to group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. Weekly minimum convex polygons convey the estimates amount of space utilized by the birds during one week’s time. Means sharing any common letters are not significantly different ($P > 0.05$).
Whether a bird moved between scans, defined as movement activity, was influenced both by treatment ($F_{4, 20} = 6.38, P = 0.002$; Fig. 2-8) and age ($F_{2, 40} = 11.04, P < 0.001$; Fig. 2-9) but not by their interaction ($F_{8, 40} = 0.76, P = 0.64$). However the treatment effect appeared to be a product of the only significant difference which occurred at the largest group size of 30. This was detected in the difference between enclosure/group sizes across constant density of 6.7 birds/ m$^2$ (10S, 20M, 30L; $F_{2, 36.8} = 10.22, P < 0.001$) and when movement in medium and large-sized enclosures was compared (10M, 20M, and 10L, 30L; $F_{2, 20} = 6.96, P = 0.005$). There was no difference in movement activity when comparisons were made between enclosure sizes at constant group size of 10 (10S, 10M, 10L; $F_{2, 36.8} = 0.74, P = 0.48$).
Figure 2-8

Movement activity (LSM ± S.E.M.) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes constant density, which is listed below each treatment. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 2-9

Movement activity according to age (LSM ± SEM). Means sharing any common letters are not significantly different ($P > 0.05$).
Discussion

This study clearly shows that group size, density, and the size of the enclosure have distinct effects on use of space in the domestic fowl. Nearest neighbor distances indicate group spacing or cohesion (Clark & Evans 1954; Keeling & Duncan 1991; Stahl et al. 2001; Christman & Lewis 2005) and in groups of domestic fowl they were generally larger in larger enclosures, particularly when group size remained constant with 10 birds per enclosure (density decreased as enclosure size increased; $10_S$, $10_M$, $10_L$). These results suggest that birds adjust the distance to their nearest neighbor according to the dimensions of the enclosure. Although domestic fowl, as a highly social species, tend to form cohesive groups it is evident from these results that when given the opportunity birds will, to a certain extent, spread out in larger enclosures. However, in no treatment combination did birds take full advantage and use the entire space available to them. In addition, birds did not position themselves as would be expected at random; they were closer together than expected in smaller groups, but slightly farther apart in the larger groups/densities. It is not surprising that broilers do not behave as would be expected by random positioning. Flocking and group cohesion are anti-predatory strategies (Pulliam 1973; Clark and Mangel 1984) which have been shown to exert a strong influence on the behavior of domestic fowl (Leone et al. 2007), particularly in small group sizes (which likely perceive a greater predatory risk as compared to larger group sizes). Domestic fowl have a strong tendency to flock together in confinement, even when ample space to disperse is available (Leone et al., 2007). This flocking behavior resulting in group cohesion...
means that birds do not space themselves uniformly, or take full advantage of the
total amount of space available to them. Particularly in the larger group sizes birds
may be motivated to disperse in an attempt to minimizing the chances for resource
competition within a confined environment (Stahl et al. 2001; Leone & Estévez
2008b). Nevertheless inter-individual distances appeared to be restricted by density,
even in large enclosures, as suggested by the fact that nearest neighbor distances were
smaller and differences were not as evident when density was maintained at 6.7 birds
per m$^2$ across increasing enclosure size ($10_S$, $20_M$, $30_L$).

A second parameter that was used to measure use of space was total distance
traveled, which estimates the distance moved by animals when locations are collected
close in time (Estévez & Christman 2006) as was the case in this study. These data
show that similar to nearest neighbor distances, total distance traveled per observation
period increased with enclosure size when group size was constant ($10_S$, $10_M$, $10_L$),
but no differences were detected across increasing enclosure size when density was
controlled at 6.7 birds per m$^2$ ($10_S$, $20_M$, $30_L$). These results are in agreement with
results from previous studies. Keeling and Duncan (1991) found that inter-individual
distances among small groups of domestic fowl were larger in larger enclosures, and
Estévez et al. (1997) and Newberry (1999) reported that broiler chickens traveled
greater distances when additional space was made available to them. The constraining
effect of density on movement and space use has also been documented in other
studies (Kondo et al. 1989; Pollard & Littlejohn 1996; Estévez et al. 1997;
The unique and novel contribution of this study is the ability to demonstrate the independent effects of enclosure size and density. Nearest neighbor distances and total distance traveled are primarily affected by enclosure size, with groups being more dispersed and birds traveling further when more space was available. However, expansions in space use can be severely constrained by density in large enclosures even at relatively low densities. Despite differences in enclosure size, at a constant density the total amount of ‘effective free space’ per bird is similar. It is possible that this limited the birds’ potential to spread apart and attain greater inter-individual distances as they otherwise would in larger enclosures. It was also quite remarkable that the impact of a reduction in ‘effective free space’ was detected at the low density employed in this experiment. The highest density of 6.7 birds/ m² was well below commercial standards (see for example Dawkins et al. 2004; Estévez 2007; Estévez et al. 2007; Leone & Estévez 2008a) and should have allowed birds sufficient ‘effective free space’ to travel throughout the enclosure with little interference and negotiate any individuals lying in their path of movement. These results indicate that this was not the case and some degree of restriction can, and does occur in response to an increase in density.

Although I attempted to control enclosure size, group size, and density to the best of my ability, there was some inevitable confounding between enclosure size and group size when comparisons were made across constant density (10S, 20M, 30L). It is possible that the limited expansion observed in nearest neighbor distances, and the lack of differences regarding total distance traveled at constant density may have been the result of limited freedom of movement related to increasing social conflict in
larger groups (McBride 1970; Grigor et al. 1995b) and were not related to density. If
group size effects were a major factor then total distance traveled and nearest
neighbor distances would be expected to be substantially smaller in larger groups, if
in fact birds limited their movements and established small subgroups (McBride &
Foenander 1962), or substantially larger if they were trying to avoid dominant
individuals (Hemelrijk 1999, 2000; Cordiner & Savory 2001). Contrarily, these
results appear to be more consistent with the previously described barrier effect
(Newberry & Hall 1990; Estevez et al. 1997; Estevez et al. 2007) which suggests that
limitations to movement and use of space in the domestic fowl are related to the
physical barriers created by the presence of other individuals in the path of movement.
When density is constant, as an individual moves the chance of encountering an
obstacle (in the form of another bird) would be similar regardless of enclosure or
group size, and therefore total distance traveled per observation period would be
expected to be similar across groups, exactly as found in this experiment. Likewise,
because the amount of ‘effective free space’ is similar when density remains constant
nearest neighbor distance was not expected to vary. However nearest neighbor
distance were slightly, but significantly, higher in the 30_L groups as compared with
10_S and 20_M. This may be interpreted as evidence that space is marginally more
effective for constant density in large pens, at least as far as maintaining larger
nearest neighbor distances but not when considering total distance traveled. In light of
these results both enclosure size and density appear to have a different but equally
important influence on movement and space use in groups of domestic fowl, as
measured by nearest neighbor distances and total distance traveled. In contrast the
effects of increasing group size appeared to be less relevant, at least under the
conditions of this particular study.

Enclosure size also appeared to be the most significant factor affecting net
displacement and minimum convex polygons. Net displacement measured the net
progress a bird made within the enclosure during a five minute observation period,
whereas minimum convex polygon is an estimate of the total amount of space used by
individuals (White & Garrott 1990). In this study both net displacement and
minimum convex polygon increased with enclosure size, but unlike nearest neighbor
distances and total distance traveled, this increase occurred irrespective of changes in
density or group size. Neither measure differed when comparisons were made across
equal enclosure sizes which suggests that birds adapted their space use patterns to the
size of the enclosure while density and group size had little, if any, influence on these
two variables.

Both total distance traveled and net displacement increased with enclosure
size for treatments $10_S$, $10_M$, and $10_L$ (constant group size). Conversely, total distance
traveled was similar across groups $10_S$, $20_M$, and $30_L$ (constant density), whereas net
displacement increased significantly with enclosure size. It is evident that if these
parameters differ it is because they are capturing slightly different aspects of
movement dynamics. For example, it is possible that birds at the smaller group sizes/
densities ($10_S$, $10_M$, $10_L$) were less restricted and more motivated to move and explore
the environment, which domestic fowl are known to do when the opportunity is
available (Newberry 1999; Krause et al. 2006), therefore increasing both total
distance travel and net displacement. Contrarily when density is higher, birds will
find more obstacles (other birds) in their movement path, regardless of enclosure size. Although the total distance traveled may be similar for equal densities, in larger enclosures birds may be able to move farther from their initial starting position, which would result in greater net displacement with increasing enclosure size even at high density. In other words, these results may be interpreted as evidence of more sinuous movement patterns in smaller enclosures resulting in similar total distance travel but less net displacement.

The results obtained for minimum convex polygons seem to follow from the above explanation for net displacement. Birds had larger minimum convex polygons in larger enclosures, irrespective of group size and density, suggesting that the overall amount of space used over time is ultimately determined by enclosure size. This may appear to be counterintuitive when considering the limiting effects of density for total distance traveled, as birds under constant density traveled the same distance in all enclosure sizes (10S, 20M, and 30L). Because total minimum convex polygons were constructed from all recorded locations over the duration of the experiment they measured long term space use pattern, in contrast to total distance traveled which is a comparatively short term measure built from five minute observation periods. Similarly weekly minimum convex polygons were built from averaging all observed locations over the course of each week of age. Therefore, given the increase in net displacement, over time it is possible to get significant differences regarding polygon size while total distance travel remains unchanged across groups 10S, 20M, and 30L.

These results for net displacement and minimum convex polygons show that birds exhibit greater overall space use with increasing enclosure size. These results
also provide further evidence against the idea that use of space in the domestic fowl is limited by social factors and that in larger groups birds utilize a subset of available space, establishing territories or home ranges (McBride & Foenander 1962; Pamment et al. 1983; Odén et al. 2004). This study, together with research published for young domestic fowl (Newberry & Hall 1990; Estevez et al. 1997; Leone & Estevez 2007c; Leone et al. 2007), and adult broiler breeders (Appleby et al. 1985; Leone & Estevez 2007b) clearly suggests that movement and use of space patterns in the domestic fowl are only moderately affected by the number of birds in the group. Factors such as enclosure size and density seem to be far more influential for animal movement and spatial distribution as clearly suggested by the results of this, and other studies (Estevez et al. 1997; Newberry 1999; Sherwin 2004, 2007). I am not however inferring that group size is unimportant and has no effects. Previous research has shown that in equally-sized enclosures inter-individual distances are heavily affected by group size (Leone et al. 2007), but enclosure size and density may be more relevant factors affecting general movement and space use.

In this study the only parameter in which we were able to detect a clear group size effect was movement activity, defined as the percentage of time a bird moved between successive scans. This differed only at the largest group size for treatment 30L. The increased movement activity in this group size may have been related to the potential to interact with a larger number of conspecifics. When group size was controlled (10S, 10M, 10L) there were no differences in movement activity with increasing enclosure size. Neither was there a difference between these treatments and 20M, which had the same density as 10S. Therefore, it would not appear that the
increase in movement activity at 30L was due to density or enclosure size. It is interesting to note that the increase in movement activity at the 30L treatment did not translate into a subsequent increase in total distance traveled, suggesting that birds were mostly shuffling or repositioning rather than truly moving through the enclosure in a directed manner. Birds may have experienced a greater number of disturbances while resting as a result of the larger number of individuals in the group (Cornetto et al. 2002) and these disturbances may cause repositioning or jostling (Febrer et al. 2006). Although increased disturbances were postulated to be a result of density as opposed to group size, these two factors were confounded in previous experiments. These results suggest that previous findings attributed to density may also be related to the number of individuals in the group and not only to density.

I did not detect an interaction between age and treatment for any parameters analyzed in this experiment, indicating that birds responded consistently as they aged. However age itself had a strong influence on nearest neighbor distances and movement activity. Nearest neighbor distances increased as birds grew older, most likely as a consequence of their increasing physical size. Weekly minimum convex polygons were largest during the third week of age, and dropped during weeks four and five. This is not surprising, as there was a decline in movement activity, in agreement with previous research which has shown that domestic fowl become less active as they age (Cornetto & Estevez 2001; Bokkers & Koene 2003).

The goal of this study was to separate to the greatest degree possible the unique effects of enclosure size, group size, and density on movement and use of space in the domestic fowl, as ability to distinguish their effects would have the
potential to improve management and environmental design for captive animals. I found enough evidence to suggest that movement patterns in the domestic fowl are primarily determined by enclosure size, followed by density. In general birds took advantage of the space available to them. Although much attention has been given to the effects of group size, under these specific experimental conditions I did not find evidence to suggest that group size has a fundamental impact on how domestic fowl utilize space. I found only a slight effect on movement activity, which does not provide any evidence for social restriction of movement related to group size. In summary, when housed in enclosures of equal size domestic fowl utilized similar total amounts of space as indicated by net displacement and the size of the minimum convex polygons, irrespective of density or group size. On the other hand, inter-individual distances and rate of movement as measured by nearest neighbor distance and total distance traveled per observation period were clearly affected by density. The lack of differences in these measures when density remained constant was also interpreted as further evidence for the barrier effect.
Chapter 3: Separating the Effects of Group Size, Density, and Enclosure Size

II. In Square Enclosures When the Perimeter to Area Ratio Declines Rapidly as Enclosure Size Increases

Abstract

The goal was to determine the unique impact of enclosure size on space use and movement patterns of domestic fowl, independent of group size and density. Research designed to estimate the effects of group size, density, or enclosure size involves inherent confounding between factors, clouding their individual impacts. This experimental design enabled me to make multiple contrasts, each holding a single factor constant, in order to tease apart their specific impact. In square enclosures, enclosure size increases simultaneously in two dimensions (length and width), but while peripheral (wall) space increases with enclosure size, the ratio of perimeter to area decreases rapidly, the implications of which are discussed. My treatments consisted of a combination of three enclosure sizes: small (1.5 m$^2$), medium (3.0 m$^2$) and large (4.5 m$^2$) and three group sizes of 10, 20, and 30 birds. I was able to make comparisons across increasing enclosure size while holding group size and density constant, as well as compare the effect of increasing group size/density at a constant enclosure size. Nearest neighbor distances increased with enclosure size but were constrained even by my relatively low density of 6.7 birds/m$^2$. I found no indication of social restriction on space use. While I did not detect differences in the total distance traveled between treatments, net displacement and minimum convex...
polygons increased with enclosure size regardless of group size or density. These results indicate that broilers adapted to their enclosures, spreading out, making greater progress and utilizing a greater amount of space when it was available.
Introduction

The characteristics of confined environments can significantly alter the way animals interact with one another and utilize the resources available to them (Pollard & Littlejohn 1996; Nephew & Romero 2003; van Wolkenten et al. 2006; Morgan & Tromborg 2007), including space (Stricklin et al. 1979; Stricklin et al. 1995; Arnould & Faure 2004; Christman & Leone 2007). Currently the U.S. broiler industry produces over 8 billion birds annually (NASS 2007) which represents the single largest sector of domestic animals raised in confinement. The poultry production environment may induce stress and discomfort in broilers as a result of high densities and large group sizes (Estévez et al. 1997; Sørensen et al. 2000; McLean et al. 2002; Dawkins et al. 2004), or a lack of sufficient free space (Newberry & Hall 1990).

While the effects of group size and density on bird performance and social behavior have received much attention (for review see Estévez 2007; Estévez et al. 2007), few studies investigate their impact on how chickens move within and utilize the available space. However, variations in bird density and group size have been shown to influence movement and space use (Estévez et al. 1997; Arnould & Faure 2004), and some authors have suggested that group size can create social restrictions to movement (McBride & Foenander 1962; Banks et al. 1979; Grigor et al. 1995b). While this may be the case for relatively small group sizes where birds are able to form pecking orders (Estévez et al. 2007), at larger group sizes it is more likely that conspecifics merely act as a physical barrier to the movement, limiting the possibility of dispersion for other birds in the group (Newberry & Hall 1990; Estévez et al. 1997).
On the other hand, enclosure size and configuration may have a strong influence on movement and use of space patterns. Available research has shown that space use increases with enclosure size in broilers (Newberry & Hall 1990; Estévez et al. 1997), and that increasing environmental complexity improves bird distribution both in broilers (Cornetto & Estévez 2001b) and layers (Newberry & Shackleton 1997). Stricklin et al. (1998) suggested that enclosure shape would have a significant impact on the ‘freedom of movement’ if animals in groups, and work with pigs has demonstrated that aggressive interactions are greatly influenced by enclosure shape, specifically the number of corners (Barnett et al. 1993; Wiegand et al. 1994). Greater space allowances lead to an increase in inter-individual distances in laying hens (Keeling & Duncan 1991), sheep (Sibbald et al. 2000), and cattle (Kondo et al. 1989), and encourage play behavior in calves (Jensen et al. 1998). A number of enclosure parameters may influence animal behavior (Christman & Leone 2007), especially peripheral (wall) space, which has been found to be highly attractive in confined environments (Newberry & Hall 1990; Cornetto & Estévez 2001b). When floor space increases in square enclosures, even though the total amount of peripheral space increases, the perimeter to area ratio decreases rapidly (Stricklin et al. 1995). Therefore it is likely that the perimeter to area ratio affects use of space in captive animals.

Studies which examine the effects of group size, density, and enclosure size involve some degree of confounding (Christman & Leone 2007), as density is a direct consequence of varying either group size or enclosure size. For this reason it is difficult to isolate the individual effects of each of factor. It is extremely important to
determine the specific impact of group size, density and enclosure size on patterns of movement in chickens so that spatial requirements and enclosure design can be based on sound research which details the biological needs of animals.

While every approach involves some level of confounding, there are a few strategies that can be used to systematically address the impact of varying enclosure size, group size or density (Christman & Leone 2007). The goal of this study was to isolate the effects of increasing enclosure size, group size and density on use of space in broiler chickens as I hypothesized that each factor would have a unique and distinctive effect on movement and space use in broiler chickens. To that end I employed a novel experiment design which enables me to control on factor at a time, and determined significant effect through the use of multiple contrasts.

This is the second study in a series which investigates the effects of group size, density, and enclosure size on movement and use of space in broilers chickens. In the first experiment I investigated these same effects, but raised chickens in rectangular enclosures which increased in floor area only in one direction (length). In this second study, enclosure size increased proportionally in two directions (length and width) to create square enclosures, which reduces the proportion of perimeter to floor space.

Methods

Facilities and Experimental Animals

This project was conducted at the University of Maryland’s Applied Poultry Research Facility in Upper Marlboro from April through June 2006. A
total of 540 male day-old broiler chicks (Ross 703) were obtained from a commercial hatchery. I chose to work with only a single sex in order to minimize behavioral variability. Initially 12, 24, and 36 birds were placed in the experimental enclosures in an effort to account for early mortalities and reach the target group sizes of 10, 20, and 30 birds. At the end of 3 weeks, extra birds were removed and housed in a separate enclosure. Each bird was individually tagged (Leone et al. 2007) on each side of the neck using the Swiftack Poultry Identification System (Heartland Animal Health Inc., Fair Play, MO). For the first 3 days birds were exposed to 24 hours of light, and thereafter were maintained on a 14 L: 10 D program in an effort to slow growth and promote leg health. Temperature and ventilation programs followed commercial practices. Feed and water were provided ad libitum from a central tubular hopper and a line of nipple drinkers located along one side of the enclosure. Three hopper sizes were employed so that the proportion of enclosure space occupied by the feeder as well as the amount of feeder space available per bird was constant across treatments. The feeding program consisted of a standard three phase commercial diet. This experimental protocol (R-05-39) was approved by the Institutional Animal Care and Use Committee at the University of Maryland.

**Experimental Design**

For this experiment I constructed three enclosure sizes which provided

- 1.49 m² (small, 1.22 x 1.22 m),
- 2.97 m² (medium, 1.72 x 1.72 m), and
- 4.46 m² (large, 2.11 x 2.11 m), each covered with 5 cm of wood shavings. The
enclosures increased in size such that the medium-sized enclosure provided
twice the floor area as the small, and the large provided three times the floor
area (Appendix 6-3). All pens were square, as the width and length of
available floor space increased simultaneously. The specific enclosure
dimensions and resulting parameters for each treatment are laid out in Table
3-1 (for detailed description of calculations see Christman & Leone 2007).

The group sizes were housed in the different enclosures to generate my
five experimental treatments (Table 3-1), each of them replicated five times.
Groups of 10 were housed in all three enclosure sizes (10S, 10M, 10L) while
groups of 20 and 30 birds were housed in the medium (20M) and large
enclosures (30L) respectively. This design enabled me to make comparisons
across constant group size, while density decreased with increasing enclosure
size (10S, 10M, 10L), across a constant density, where group size increased
with enclosure size (10S, 20M, 30L), and finally across constant enclosure sizes
where group size and density increased simultaneously (10M, 20M and 10L,
30L).

**Data Collection**

Each enclosure was divided into a grid of 20 x 20 cm squares by
placing numerical and alphabetical placards along the enclosure walls. This
created a visual grid that allowed me to precisely record bird locations on
scaled maps of the enclosure (Cornetto & Estévez 2001b; Leone et al. 2007).
For behavioral observations five focal birds were randomly selected from each
enclosure and were observed throughout the entire experiment.
Table 3-1

Enclosure parameters for each treatment (noted by group size and enclosure size) including the group size, density, total floor area, enclosure walls length and width, length to width ratio, total perimeter space, perimeter per animal, perimeter to area ratio, farthest distance to a wall and farthest distance to a corner.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Group Size</th>
<th>Density (birds/ m²)</th>
<th>Total Area (m²)</th>
<th>Length (m)</th>
<th>Width (m)</th>
<th>Length: Width Ratio</th>
<th>Perimeter (m)</th>
<th>Perimeter (m) / animal</th>
<th>Perimeter: Area Ratio</th>
<th>Distance to Wall (m)</th>
<th>Distance to Corner (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10_Large</td>
<td>10</td>
<td>2.2</td>
<td>4.47</td>
<td>2.11</td>
<td>2.11</td>
<td>1 : 1</td>
<td>8.44</td>
<td>0.84</td>
<td>1.9 : 1</td>
<td>1.06</td>
<td>1.49</td>
</tr>
<tr>
<td>10_Medium</td>
<td>10</td>
<td>3.4</td>
<td>2.96</td>
<td>1.72</td>
<td>1.72</td>
<td>1 : 1</td>
<td>6.88</td>
<td>0.69</td>
<td>2.3 : 1</td>
<td>0.86</td>
<td>1.22</td>
</tr>
<tr>
<td>10_Small</td>
<td>10</td>
<td>6.7</td>
<td>1.49</td>
<td>1.22</td>
<td>1.22</td>
<td>1 : 1</td>
<td>4.88</td>
<td>0.49</td>
<td>3.3 : 1</td>
<td>0.61</td>
<td>0.86</td>
</tr>
<tr>
<td>20_Medium</td>
<td>20</td>
<td>6.7</td>
<td>2.96</td>
<td>1.72</td>
<td>1.72</td>
<td>1 : 1</td>
<td>6.88</td>
<td>0.34</td>
<td>2.3 : 1</td>
<td>0.86</td>
<td>1.49</td>
</tr>
<tr>
<td>30_Large</td>
<td>30</td>
<td>6.7</td>
<td>4.47</td>
<td>2.11</td>
<td>2.11</td>
<td>1 : 1</td>
<td>8.44</td>
<td>0.28</td>
<td>1.9 : 1</td>
<td>1.06</td>
<td>1.22</td>
</tr>
</tbody>
</table>
Birds in each enclosure were observed twice per day, three days per week from three to six weeks of age. The location and identity of each focal individual, as well as the position of all other group members, was recorded via instantaneous scan sampling *ad libitum* for a five minute period. At the beginning of each observation period bird locations were recorded on a single scan sheet, and once completed successive locations were recorded on additional scan sheets until the 5 minutes expired. These location scans were digitized as X Y coordinates with a Digitalizer (ACECAD, Taipei, Taiwan) using the Chickitaizer© software (Sanchez & Estévez 1998).

From each five minute observation period I calculated a number of measures that best characterize movement patterns and space use. These included: nearest neighbor distances, defined as the distance between a bird and its nearest group mate, which was calculated from the locations of all group members (focals and non focals), total distance traveled for each focal bird, defined as the sum of Euclidean distances between successive recorded locations, net displacement which was calculated as the Euclidean distance between the first and last observed location during the five minute observation, and movement activity which was defined as the percentage of scans were movement was observed. For nearest neighbor distances I was uniquely able to calculate the distances which would have been expected if birds positioned themselves randomly within the environment, through the use of a simple random simulation. This random simulation could not be utilized for other measures, because no assumptions were made about movement patterns per se.
Each simulation (InsightfulCorp S-plus 6.1, Seattle, WA) consisted of randomly assigning locations to all birds according to each treatment combination. The average nearest neighbor distance for the group was then calculated, and this simulation was repeated 2000 times in order to generate expected nearest neighbor distances. The average value from these 2000 simulations represents the nearest neighbor distance that would be expected if birds randomly distributed within their enclosure. Deviations were then calculated by subtracting the observed nearest neighbor distances from those expected assuming randomness, in order to determine to what extent the treatment influenced inter-individual distance. Minimum convex polygons (Mohr 1947) were calculated using ArcView GIS v8 (ESRI, Redlands, CA) with the Animal Movement Extension package (Hooge & Eichenlaub 2000). One minimum convex polygon was built from all observed locations, throughout the entire length of the study, which provided an estimate of the total amount of space utilized by each focal bird. I also determined the percent of available space that the birds utilized by dividing the minimum convex polygon by the total amount of space available. Minimum convex polygons were also generated for each focal bird during each week, in order to understand the effect on age on space use. Additionally a coefficient of variation was calculated to ascertain the variability in space use between individuals across age. All measurements were averaged across birds within each enclosure for statistical analysis.
Statistical Analysis

All analyses were conducted in SAS (v. 9.1, SAS Institute, Cary, NC; Appendix 6-4). For all parameters calculated in this study, except minimum convex polygons, I modeled the effects of treatment, age, and their interaction. Because total minimum convex polygons were calculated from all locations recorded over the entire study period the statistical model only included the treatment effect. Separate mixed model ANOVAs were performed for each of the parameters analyzed: nearest neighbor distances and their deviation from random expectations, total distance traveled during an observation period, net displacement, movement activity, weekly minimum convex polygons and their coefficient of variation, and the percentage of enclosure space utilized. All models included a covariance structure to account for repeated observations. Model assumptions of normality and homogeneity of residual variances were examined. In order to meet the homogeneity assumption variance components were modeled by treatment for nearest neighbor distances and their deviation from randomness, and both total and weekly minimum convex polygons and their coefficient of variation.

The goal of this experiment was addressed with three specific *a priori* contrasts, I tested the effect of increasing enclosure sizes first at constant group size but decreasing density (10S, 10M, 10L), and second when density was held constant but group size increased with enclosure size (10S, 20M, 30L). Lastly, I compared across equal enclosure size but density and group size increased simultaneously (10M, 20M and 10L, 30L). Each of these contrasts
held one factor constant, while the other two covaried; each contrast is essentially an ANOVA. In order to protect against an inflated Type I error rate contrasts and means comparisons were only performed when the overall ANOVA F-test was significant ($P < 0.05$).

**Results**

The degree of cohesion within the group, as measured by nearest neighbor distances, was influenced both by treatment ($F_{4,9.59} = 19.42$, $P = 0.004$), and age ($F_{2,26.5} = 25.19$, $P < 0.001$), but not their interaction ($F_{8,19.4} = 0.83$, $P = 0.59$). My *a priori* contrasts revealed that nearest neighbor distances expanded with enclosure size (Fig. 3-1) both at constant group size ($10_S$, $10_M$, $10_L$; $F_{2,15.2} = 32.83$, $P < 0.001$) and at constant density ($10_S$, $20_M$, $30_L$; $F_{2,15.3} = 25.74$, $P < 0.001$). Comparisons between enclosures of equal size revealed larger nearest neighbor distances in the smaller group sizes/densities ($10_M$ and $20_M$, $10_L$ and $30_L$; $F_{2,7.4} = 12.12$, $P < 0.01$). Observed distances deviated from those expected assuming randomness for all treatments ($F_{4,6.93} = 124.12$, $P < 0.001$; Fig 3-2). In the smaller groups of 10 birds nearest neighbor distances were smaller than expected, but were farther apart than predicted in the groups of 20 and 30 birds. There was no interaction between treatment and age on the deviation of observed nearest neighbor distances from those expected assuming randomness ($F_{8,5.73} = 0.59$, $P = 0.762$). Nearest neighbor distances increased with bird age (Fig. 3-2). Birds were also closer together at all ages than would be expected by random assortment ($F_{2,11.4} = 31.30$, $P < 0.001$).
Figure 3-1

Nearest neighbor distances (least squares means ± standard error of the mean) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment, and the expected values assuming random assortment (gray outline). White fill corresponds to equal group size while grey denotes similar densities. Means sharing any common letters are not significantly different ($P > 0.05$). Observed nearest neighbor distances differed from those expected assuming randomness ($P < 0.05$), and from the predicted uniform distribution based on a density of 6.7 birds/m$^2$ represented by the dotted line ($P < 0.05$).
Nearest neighbor distances (LSM ± SEM) were found to grow as birds aged. Means sharing any common letters are not significantly different ($P > 0.05$).
Total distance traveled during an observation period was not affected by treatment \((F_{4,23.8} = 0.68, P = 0.61)\), age \((F_{2,41.2} = 2.46, P = 0.10)\), or their interaction \((F_{8,41.9} = 1.31, P = 0.27)\). Net displacement however was affected by treatment \((F_{4,20} = 3.37, P = 0.029)\), but not by age \((F_{2,20} = 0.96, P = 0.39)\) or their interaction \((F_{8,40} = 1.77, P = 0.11)\).

Net displacement was greater as enclosure size increased from small to medium or large (Fig. 3-3) regardless of changes in group size \((10_S, 20_M, 30_L; F_{2,36.8} = 6.26, P = 0.004)\) or density \((10_S, 10_M, 10_L; F_{2,36.8} = 4.02, P = 0.026)\), but was not different when I compared equally-sized enclosures \((10_M and 20_M, 10_L and 30_L; F_{2,20} = 0.37, P = 0.693)\).

The total amount of space utilized by the birds as measured by total minimum convex polygons was affected by treatment \((F_{4,34.1} = 305.67, P < 0.001; \text{Fig. 3-4})\) and was substantially larger for birds in larger enclosures regardless group size or density. Space use increased with enclosure size both when group size \((10_S, 10_M, 10_L; F_{2,53.4} = 300.07, P < 0.001)\) and density \((10_S, 20_M, 30_L; F_{2,46.4} = 446.28, P < 0.001)\) were maintained. On the contrary, there were no differences between equally-sized enclosures \((10_M and 20_M, 10_L and 30_L; F_{2,49.9} = 2.22, P = 0.12)\). Similarly there was a significant effect of treatment on the average minimum convex polygon per week \((F_{4,7.45} = 58.47, P < 0.001; \text{Fig. 3-5})\) although there was no effect of age \((F_{2,10.4} = 1.03, P = 0.391)\) or their interaction \((F_{8,5.47} = 0.90, P = 0.570)\). The coefficient of variability in minimum convex polygons was not affected by treatment \((F_{4,20} = 1.51, P = 0.236)\), age \((F_{2,19} = 1.80, P = 0.19)\) or their interaction \((F_{8,24.3} = 1.91, P = 0.125)\).
Figure 3-3

Net displacement (LSM ± S.E.M.), defined as the Euclidean distance between the first and last observation, according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes similar densities. Means sharing any common letters are not significantly different ($P > 0.05$).
The proportion of total space utilized also differed between treatments ($F_{4,20} = 4.90, P = 0.006$), varying between 60 and 70% of the available space. The response to enclosure size was curvilinear (Fig. 3-6) regardless of density ($10_S, 10_M, 10_L; F_{2,36.8} = 5.91, P = 0.006$) or group size ($10_S, 20_M, 30_L; F_{2,36.8} = 3.82, P = 0.031$) and I found no differences in the proportion of space utilized between enclosures of equal size ($10_M$ and $20_M, 10_L$ and $30_L; F_{2,20} = 1.77, P = 0.20$).

Movement activity was influenced by treatment ($F_{4,20} = 5.31, P = 0.004$; Fig. 3-7) and decreased with age ($F_{2,19} = 21.69, P < 0.001$; Fig. 3-8) but I did not detect any interactive effects ($F_{8,24.3} = 1.24, P = 0.32$). There was no effect of enclosure size on movement activity when group size was maintained ($10_S, 10_M, 10_L; F_{2,36.8} = 0.98, P = 0.38$) but I did find differences between enclosure sizes at constant density ($10_S, 20_M, 30_L; F_{2,36.8} = 4.77, P = 0.014$) and when comparisons were made across constant enclosure size ($10_M$ and $20_M, 10_L$ and $30_L; F_{2,20} = 10, P = 0.001$). These significant effects were most likely a result of the increase in movement at the largest group size of 30 birds (Fig. 3-8).
Figure 3-4

Total minimum convex polygons (LSM ± S.E.M.) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment for the entire length of the study. White fill corresponds to equal group size while grey denotes similar densities. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 3-5

Average weekly minimum convex polygon (LSM ± SEM) according to group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 3-6

Percentage of the available enclosure space utilized (LSM ± S.E.M.) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes similar densities. Percentages sharing any common letters are not significantly different ($P > 0.05$).
Figure 3-7

Movement activity (LSM ± S.E.M.), the percentage of times birds moved between successive scans, decreased with age. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 3-8

Movement activity (LSM ± S.E.M.) according to each group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. White fill corresponds to equal group size while grey denotes similar densities. Means sharing any common letters are not significantly different ($P > 0.05$).
Discussion

In this study, in which I carefully controlled for the effects of group size, density and enclosure size, I demonstrated that enclosure size had the strongest influence on movement and use of space in the domestic fowl. The effects of density, while significant, were not as pronounced, mostly limiting or reducing space use and movement. Surprisingly, group size had only a minor impact on space use.

I found that nearest neighbor distances were affected by the treatment combinations, with birds maintaining larger distances in larger enclosures. Nearest neighbor distances expanded more substantially with increasing enclosure size when group size was maintained (10_S, 10_M, 10_L) and density decreased, as compared with increasing enclosure size at constant density (10_S, 20_M, 30_L). When not restricted by density, animals in larger enclosures had more room to spread out, resulting in larger inter-individual distances. Nearest neighbor distance was constrained by density, even thought all densities in this study were well below those employed in commercial conditions (Estevez 2007). Birds however did not take full advantage of the space available to them, because the observed nearest neighbor distances were far smaller that would be expected by a uniform distribution, given the largest density of 6.7 birds/ m2. Similarly, birds did not behave as would be expected by random assortment. In smaller groups of 10 birds were closer together than would be expected assuming randomness, while in the larger groups of 20 and 30 birds were more dispersed than would be expected at random. Nearest neighbor distance is indicative of group cohesion and spacing (Clark & Evans 1954; Keeling & Duncan 1991; Stahl
and these results suggest that when given the opportunity, and when not constrained by density, birds maintained less cohesive groups with increasing enclosure size. Maintaining larger nearest neighbor distances may reduce competition for resources (Stahl et al. 2001; Leone & Estévez 2007), but more importantly it may offer thermoregulation advantages. Larger inter-individual distances may help the birds to thermoregulate, as more free space between individuals may increase air flow and heat loss, reducing the temperature at floor level. Improved thermoregulation may also explain why nearest neighbor distances increased as birds aged. Heat-production increases as birds grow, and they become more susceptible to heat stress (Xin et al. 1994). Therefore it seems reasonable that increasing inter-individual distances helps to reduce heat stress and alleviate any potential effects of increased heat production as birds age and grow.

Similar to nearest neighbor distances, net displacement was also greater in larger enclosures. Net displacement essentially measures the overall progress made as a result of movement patterns (Wu et al. 2000) and under the present treatment structure was greatest in the medium and large enclosures, regardless of density or group size. It is reasonable to expect to find greater net displacement in larger enclosures as a result of birds moving more because more space is available. For example, birds made greater progress in 20M and 30L as compared to 10S, even though density was identical in these three groups. At constant density the greater amount of ‘effective free space’ available in the larger enclosures may have enabled birds to make greater overall progress, whereas birds in 10S may have been restricted by both the density and small enclosure size. There were no differences in net
displacement between medium and large enclosure sizes, and taken together these results provide strong evidence that net displacement is determined most heavily by space availability.

However, it is surprising that this effect of treatment on net displacement did not coincide with differences in total distance traveled, which were similar across treatments. As indicated in previous sections of this paper, total distance travel was calculated as the total distance traveled by a bird across successive locations, whereas net displacement was defined as the straight distance between the beginning and ending locations during the five minute observation period. Therefore, these results suggest that even though chickens under all treatments traveled similar distances (equal total distance traveled), birds in the larger enclosures moved farther away from the initial starting point by the end of the observation period. Changes in movement patterns according to enclosure size could explain the differences observed in response to the treatments for total distance traveled and net displacement. The amount of ‘effective free space’ would be less in smaller enclosures as birds would have a greater chance of encountering a group-mate blocking their path of movement (Newberry & Hall 1990, Estévez et al. 1997). This may have caused movements to be more sinuous or tortuous than those in the larger enclosures (and lower densities). It is also possible that birds in smaller enclosures experienced a stronger rebounding effects off the walls (as furthest distance to a wall was smaller, Table 3-1). If after each step the direction of the next move is determined in a more or less random manner, then the chances of ending up further away from the starting position will be greater in larger enclosures because there is a lower chance of encountering a wall.
These differences in movement patterns may result in identical total distances traveled for birds in all treatments, but greater net displacement in larger pens. Nevertheless, I expected that total distance traveled would increase with enclosure size, especially at lower density (10S, 10M and 10L), but this was clearly not the case. Broilers are characterized by a low level of activity, and generally spend upwards of 80% of their time resting (Cornetto & Estévez 2001a). Therefore it is possible that the effects of group size, density, and enclosure size were not strong enough to affect total distance traveled, at least not during the observation period employed here.

In this study total minimum convex polygons were used to estimate total space use over the entire study period, and weekly minimum convex polygons were calculated to determine the average amount of space utilized in a week as birds aged. I found no effect of age on weekly minimum convex polygons, indicating that in square enclosures birds used similar amounts of space each week. Similar to the results for net displacement, both weekly and total minimum convex polygons were most heavily affected by the size of the enclosure, and appeared to be largely unaffected by density or group size. However, the effects of enclosure size on minimum convex polygons where much stronger than on net displacement, as differences were more significant between the three enclosure sizes (small, medium and large). These results suggest that given sufficient time birds in larger enclosures explored more overall space, taking advantage of the greater space availability, even at the density of 6.7 birds/m². Whereas total distance traveled and net displacement measured short term movement patterns (over a five minute observation period), minimum convex polygons were built from all recorded locations over the entire
study period and captured long term movement patterns. Thus, while I found no detectable differences in the short-term for total distance traveled, these results indicate that over time broilers utilize more space when it is offered, as in the larger the enclosures. Previous research has also shown both in broilers (Estévez et al. 1997) as well as layers (Carmichael et al. 1999) birds exhibit larger home ranges in larger enclosures. These results taken together demonstrate that broiler chickens will adapt their use of space patterns according to the amount of space available to them; spreading out, making greater progress and using a greater area. Surprisingly, these movement and use of space patterns appear to be ‘immune’ to the effects of group size or density, at least within the ranges employed in this experiment.

While increasing enclosure size generally led to an increase in use of space, it was in the medium-sized enclosure where birds used the greatest proportion of the available space. I observed the same curvilinear response to enclosure size across constant group size (10S, 10M, 10L) and constant density (10S, 20M, 30L). Previous research has suggested that domestic fowl may find open space frightening, and that group size can significantly impact their willingness to explore it (Grigor et al. 1995a; Grigor et al. 1995c; Arnould & Faure 2004). Grigor et al. (1995a, b) demonstrated that even with regular exposure, laying hens did not make full use of additional outdoor space offered to them. Similarly Leone et al. (2007) found that when groups of 5, 10, and 20 broilers were housed in enclosures of equal size, the smaller groups used less overall space. It is possible that at constant group size of 10, birds may have felt more protected (less fearful) in the medium-sized enclosure than in the large enclosure, and thus explored a greater proportion of the available space. On the other
hand, when density was controlled (and group size increased with enclosure size) birds in the 30_\text{L} treatment may have experienced a stronger barrier effect restricting movement than birds in the 20_M, as a result of the more numerous group mates (Newberry & Hall 1990; Estévez et al. 1997), which could explain the drop in the percentage of space utilized. It was particularly surprising that space use was relatively low in the 10_S groups, which had the smallest enclosure size (1.22 x 1.22 m). Birds may have been heavily restricted in this enclosure, as I noted significantly reduced net displacements. Previous research has shown that locomotive activity is reduced in small or crowded environments (Poon et al. 1997; Boal et al. 1999; Arakawa 2005) and thus movement may have been restricted in this treatment specifically due to the relatively high density and small size of the enclosure.

However, this does not explain why groups overall did not take greater advantage of the space available to them (utilization closer to 100%). Birds may have been preferentially using (and avoiding) certain areas of their enclosures, thus spontaneously limiting space use (Arnould & Faure 2004). Previous research at this facility has found that birds take greater advantage of the front of their enclosures closest to the central corridor, possibly due to better air flow at this location closest to the ventilating fans, as opposed to the back which is closest to the exterior walls of the house (LeVan et al. 2000; Pettit-Riley & Estevez 2001; Leone unpublished data). If broilers were consistently avoiding the rear of their enclosure and more consistently using the front, then it would be logical that overall space use was less than the total amount of space available.
It should be noted that in this study I found no evidence that movement or space use was restricted by social factors. McBride and Foenander, (1962) predicted that social interactions would increase with group size, and thus in large groups domestic fowl would limit their movements to avoid interactions with aggressive group mates. If this were the case, then I would have expected to find diminished space use at larger group sizes, and no differences at constant group size. To the contrary, space use (both net displacement and minimum convex polygons) consistently increased with enclosure size, regardless of group size. The only notable effect of group size in this study was on movement activity, which increased in the largest groups of 30 birds. There were no differences in movement activity between equal group sizes (10S, 10M, 10L), or equal densities (10S and 20M), suggesting that the greater movement activity in 30L groups was a product of group size. Birds in these groups had the greatest potential to interact with con-specifics. Despite the increase in movement activity, I did not detect any differences between treatments in the total distance traveled. So while birds moved more often in 30L they did not travel greater distances. It is possible that this movement activity reflected repositioning as a result of higher levels of jostling (Febrer et al. 2006) and increased disturbances (Cornetto et al. 2002), which have been detected in other studies. In both studies group size was manipulated in order to raise density, thereby confounding the two factors. Because I found a difference only at the 30L treatment when comparing across constant density (10S, 20M and 30L) I suggest that the larger group size led to an increase in bird interactions, rather than the density. Movement activity generally decreased with age, which is not surprising as broilers have been shown to become
less active over time (Bizeray et al. 2000; Cornetto & Estévez 2001a; Bokkers & Koene 2002).

Determining the impact of group size, density, and enclosure size is highly relevant to the design of facilities that best address the biological needs of chickens and increase efficiency in use of the available space. I found that each factor had distinct effects on movement and space use in the domestic fowl. The results of this study clearly show that enclosure size is the most critical factor affecting space use in broiler chickens, and chickens will use larger amounts of space when provided with them. The strongest effects were related to the size of the enclosure, followed by density, which appears to limit space use even at a relatively low level. Space utilization, as measured by net displacement and minimum convex polygons, was clearly affected by enclosure size irrespective of changes in group size or density. Nearest neighbor distances increased with enclosure size but were restricted by density. Group size had surprisingly minimal influence on broiler movement and space use, at least within the range employed here. Group size only appeared to increase shuffling and repositioning, as noted by greater movement activity at the largest group size of 30 birds (without a simultaneous increase in total distance traveled).
Chapter 4: Separating the Effects of Group Size, Density, and Enclosure Size

III. When Perimeter Space is Held Constant per Unit of Area

Abstract

I was interested in separating the confounded influences of group size, density, and enclosure size on movement and use of space patterns in the domestic fowl, which represent key aspects of their behavior. A number of enclosure parameters (such as the length to width and perimeter to area ratio) may influence chicken behavior, but they are often inadvertently altered when enclosure size increases. My goal was to maintain consistency across treatments both in the length to width ratio but also in the perimeter to area ratio. I housed groups of 10, 20, and 30 broilers in square enclosures of three sizes: small (1.5 m²), medium (3.0 m²) and large (4.5 m²). This experimental design enabled me to separate the influence of group size, density, and enclosure size through the use of contrasts. While group spacing increased with enclosure size, it was restricted by even the relatively low stocking density of 6.7 birds/ m². The effect of treatment on movement parameters waned as birds aged, and in general movement decreased with age. Enclosure size was the most relevant factor for total space use, which was largely unaffected by group size or density.
Introduction

Animal movement and space use are determined in large part by the environment, a fact which cannot be overstated for captive animals (McBride & Craig 1985; Morgan & Tromborg 2007). Three factors may be of paramount importance: group size, animal density (the theoretical amount of space available per animal), and enclosure size. For domestic fowl, enclosure size and shape has received the least amount of attention while much work has focused on the impact of group size and density (for review see Estévez 2007; Estévez et al. 2007). Initially it would appear that the effects of group size are conflicting in the published literature. However in domestic fowl, as for many other species, there are clear differences between the behavior of animals in small versus large groups.

In small groups of chickens the pecking order determines access to resources (Banks 1984; Banks et al. 1979; Rushen 1982) and social factors exert a strong influence over inter-individual distances and behaviour (Mankovich & Banks 1982; Grigor et al. 1995b; Leone et al. 2007; Leone & Estévez 2007). However, in large groups birds are most likely not able to recognize all individuals (Douglis 1948) or benefit from hierarchies (Pagel & Dawkins 1997), and aggressive interaction show a marked decrease (Estévez et al. 1997; Hughes et al. 19977; D'Eath & Keeling 2003). Because they are unable to establish a stable pecking order some authors have suggested that chickens will establish small territories when housed in large groups (McBride & Foenander 1962; see also Odén et al. 2004). To the contrary, even when small groups of young broiler chickens are placed in equally-sized enclosures, individuals use similar amounts of space (Leone et al. 2007) and adults have
considerable overlap in their estimated home ranges (Appleby et al. 1985; Leone & Estévez 2008a).

Floor space allowance, as well as many additional features of the enclosure may influence animal movement and behaviour such as the length to width ratio, distance to a corner, and the perimeter to area ratio (Stricklin 1995; Christman & Leone 2007). Each of these parameters, inadvertently change as the size or shape of the enclosure changes. Previous work has shown that enclosure shape has a significant impact on aggression in pigs (Barnett et al. 1993; Wiegand et al. 1994) and the addition of environmental complexity which creates additional wall space reduces disturbances and aggression in domestic fowl (Cornetto et al. 2002) and turkeys (Sherwin et al. 1999a). Perimeter (wall) space is an attractive feature of the enclosure (Stricklin et al. 1979; Newberry & Hall 1990; Jeanson et al. 2003) with biological relevance for captive animals. Perimeter space may provide a sense of protective cover or enable subdominant individuals to escape aggressive group-mates in captive environments (Hemelrijk 2000). While total perimeter space increases with enclosure size, it does not rise at an equal rate with floor area, and their relationship depends on the shape and specific dimensions of the enclosure. Likewise, the amount of perimeter space available on a per animal basis decreases with increasing enclosure size even when animal density remains constant (Stricklin et al. 1995; Christman & Leone 2007). This diminishing ratio of perimeter to area may be an influential feature of the environment with a strong effect on animal movement and space use. If perimeter space is as important as floor space then merely increasing enclosure size
may not be an effective means to improve animal welfare, however few publications have examined the impact of the perimeter to area ratio.

Every experiment designed to elucidate the effects of group size, density or enclosure size inadvertently introduces confounding (Christman & Leone 2007). For example, in order to determine the effect of increasing group size researchers can house animals in equally-sized enclosures and allow density to increase (e.g. Cornetto & Estévez 2001b), or hold density constant and therefore house larger groups in larger enclosures (e.g. Estévez et al. 2003). In both examples the effects of group size become inexorably confounded, either with density or enclosure size, respectively. The consequence is that in these types of experiments any significant results cannot be attributed specifically to a single factor, as the observed changes may be a direct consequence of the confounded variable. Additionally, as previously indicated, altering enclosure size causes a host of parameters to differ between treatments, such as the amount of perimeter space available and the distance to the nearest wall.

This experiment was designed to investigate the impact of increasing enclosure size, while maintaining a constant perimeter to area ratio, on movement and space use in domestic fowl. I employed a novel treatment design in an effort to parcel out the specific contribution of each factor as I hypothesized that they would have a unique impact on movement patterns and space use. I expected that enclosure size would have a strong effect on total space use, whereas group size and density would impact movement patterns. This is the third experiment in a series which investigates the effects of group size, density, and enclosure size and shape on movement and space use in the domestic fowl. In previous experiments broilers were housed in
rectangular (first experiment) and square (second experiment) enclosures which offered the same floor space allowances as those employed here. This experiment is unique in that ‘false walls’ were added to the enclosures in order to maintain a constant perimeter to area ratio.

Methods

Facilities and Experimental Animals

This project was conducted at the University of Maryland’s Applied Poultry Research Facility in Upper Marlboro from October through December 2006. A total of 540 male day-old broiler chicks were obtained from a commercial hatchery. I chose to work with only a single sex in order to minimize behavioral variability. Initially 12, 24, and 36 birds were placed in the experimental enclosures in an effort to account for early mortalities and reach the target group sizes of 10, 20, and 30 birds. At the end of 3 weeks, extra birds were removed and housed in a separate enclosure. Each bird was individually tagged (Leone et al. 2007) on each side of the neck using the Swiftack Poultry Identification System (Heartland Animal Health Inc., Fair Play, MO). For the first 3 days birds were exposed to 24 hours of light, and thereafter were maintained on a 14 L: 10 D program in an effort to slow growth and promote leg health. Temperature and ventilation program followed commercial practices. Feed and water were provided ad libitum from a central tubular hopper and a line of nipple drinkers located along one side of the enclosure. Three hopper sizes were employed so that the proportion of
enclosure space occupied by the feeder as well as the amount of feeder space available per bird was constant across treatments. The feeding program consisted of a standard three phase commercial diet. This protocol (R-05-39) was approved by the Institutional Animal Care and Use Committee at the University of Maryland.

**Experimental Design**

For this experiment I constructed three enclosure sizes which were 1.49 m$^2$ (small, 1.22 x 1.22 m), 2.96 m$^2$ (medium, 1.22 x 2.44 m), and 4.47 m$^2$ (large, 1.22 x 3.66 m). Each enclosure was covered with 5 cm of wood shavings. Enclosures were square and thus maintained a constant length to width ratio. The enclosures increased in size such that the medium-sized provided twice the floor area as the small, and the large provided three times the floor area. The specific dimensions for each enclosure and resulting parameters are laid out in Table 4-1 (for detailed description of calculations see Christman & Leone 2007). Because the amount of perimeter space per bird and the perimeter to area ratio decreases with increasing enclosure size I constructed false walls (similar in construction to Cornetto & Estévez 2001b) in order to provide birds with a constant perimeter to area ratio. These were constructed of the same white PVC piping and black plastic netting as the enclosures and were 1.2m high (same as enclosure walls) and 5 cm, 24 cm, and 46 cm wide for the small, medium, and large-sized enclosures respectively.
Table 4-1

Treatment parameters for each group size and pen size. Parameters include stocking density, total floor area, pen length and width, length to width ratio, total perimeter space including the false walls, perimeter/animal, perimeter to area ratio, farthest distance to a true wall and farthest distance to a corner.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Group Size</th>
<th>Density (birds/ m²)</th>
<th>Total Area (m²)</th>
<th>Length (m)</th>
<th>Width (m)</th>
<th>Length: Width Ratio</th>
<th>Perimeter (m)</th>
<th>Perimeter (m)/animal</th>
<th>Perimeter: Area Ratio</th>
<th>Distance to True Wall (m)</th>
<th>Distance to Corner (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10L</td>
<td>10</td>
<td>2.2</td>
<td>4.47</td>
<td>2.11</td>
<td>2.11</td>
<td>1 : 1</td>
<td>17.69</td>
<td>1.77</td>
<td>4 : 1</td>
<td>1.06</td>
<td>1.49</td>
</tr>
<tr>
<td>10M</td>
<td>10</td>
<td>3.4</td>
<td>2.96</td>
<td>1.72</td>
<td>1.72</td>
<td>1 : 1</td>
<td>11.79</td>
<td>1.18</td>
<td>4 : 1</td>
<td>0.86</td>
<td>1.22</td>
</tr>
<tr>
<td>10S</td>
<td>10</td>
<td>6.7</td>
<td>1.49</td>
<td>1.22</td>
<td>1.22</td>
<td>1 : 1</td>
<td>5.90</td>
<td>0.59</td>
<td>4 : 1</td>
<td>0.61</td>
<td>0.86</td>
</tr>
<tr>
<td>20M</td>
<td>20</td>
<td>6.7</td>
<td>2.96</td>
<td>1.72</td>
<td>1.72</td>
<td>1 : 1</td>
<td>11.79</td>
<td>0.59</td>
<td>4 : 1</td>
<td>0.86</td>
<td>1.49</td>
</tr>
<tr>
<td>30L</td>
<td>30</td>
<td>6.7</td>
<td>4.47</td>
<td>2.11</td>
<td>2.11</td>
<td>1 : 1</td>
<td>17.69</td>
<td>0.59</td>
<td>4 : 1</td>
<td>1.06</td>
<td>1.22</td>
</tr>
</tbody>
</table>
Each enclosure was outfitted with 10 false walls in the arrangement shown in Appendix 6-5, placed in a manner so as not to impede bird movements.

The group sizes were housed in the different enclosures to generate my five experimental treatments (Table 4-1), each of them replicated five times. Groups of 10 were housed in all three enclosure sizes (10_S, 10_M, 10_L), while groups of 20 and 30 were housed in the medium (20_M) and large enclosures (30_L) respectively. This design enabled me to make comparisons across constant group size, where density decreased with increasing enclosure size (10_S, 10_M, 10_L), across a constant density, where group size increased with enclosure size (10_S, 20_M, 30_L), and across constant enclosure sizes where group size and density increased simultaneously (10_M, 20_M and 10_L, 30_L).

**Data Collection**

Each enclosure was divided into a grid of 20 x 20 cm squares by placing numerical and alphabetical placards along the enclosure walls. This created a visual grid that allowed me to precisely record bird locations on scaled maps (Cornetto & Estévez 2001a; Leone et al. 2007). For behavioral observations five focal birds were randomly selected from each enclosure and were observed throughout the entire experiment. Observations began at three weeks of age and continued until birds were six weeks old. The birds in each enclosure were observed twice per day, three days per week. The location and identity of each focal individual, as well as the position of all other group members, was recorded via instantaneous scan sampling *ad libitum* for a five minute period. At the beginning of each observation period the location of
each focal birds was recorded in X Y coordinates using the Chickitizer© software (Sanchez & Estévez 1998) on a tablet PC (Toshiba, Irvine, CA) and represented a single scan. Once completed successive locations were recorded via additional scans until the 5 minutes expired. From the each five minute observations period I calculated a number of measures to capture bird movement and space use which included: nearest neighbor distances, defined as the average distance between each individual and its closest neighbor, which were calculated from the locations of all group members, the total distance traveled which was calculated by summing the Euclidean distances between successive recorded locations for each focal bird during the five minute observation period, net displacement which was calculated as the Euclidean distance between the first and last observed location, and movement activity which was defined as the percentage of scans were movement was observed. For nearest neighbor distances I was uniquely able to calculate the values that would have been expected if birds positioned themselves randomly within the environment, through the use of a simple random simulation. This random simulation could not be utilized for other measures because no assumptions were made about movement patterns per se. Each simulation (InsightfulCorp S-plus 6.1, Seattle, WA) consisted of randomly assigning locations to all birds according to each treatment combination. The average nearest neighbor distance for the group was then calculated, and this simulation was repeated 2000 times in order to generate expected nearest neighbor distances. The average value from these 2000
simulations represents the nearest neighbor distance that would be expected if birds randomly distributed within their enclosure. Deviations were then calculated by subtracting the observed nearest neighbor distances from those expected assuming randomness, in order to determine to what extent the treatment influenced inter-individual distance. Minimum convex polygons (Mohr 1947) were calculated using ArcView GIS v8 (ESRI, Redlands, CA) with the Animal Movement Extension package (Hooge & Eichenlaub 2000). One total minimum convex polygon was built from all observed locations, throughout the entire length of the study, which provided an estimate of the total amount of space utilized by each focal bird. I also determined the percent of available space that the birds utilized by dividing the total minimum convex polygon by the total amount of space available. Average weekly minimum convex polygons were also generated for each focal bird, in order to estimate the amount of space utilized in a week and understand the effect on age. Additionally a coefficient of variation was calculated to ascertain the variability in space use between individuals across age. All measurements were averaged across birds within each enclosure.

Statistical Analysis

All analyses were conducted in SAS (v. 9.1, SAS Institute, Cary, NC; Appendix 6-6). For all parameters except total minimum convex polygons I modeled the effects of age, treatment, and their interaction. Separate mixed model ANOVAs were performed for each of the parameters analyzed: nearest neighbor distances and their deviations from randomness, movement activity,
total distance traveled during an observation period, net displacement, minimum convex polygons by week and their coefficient of variation, and the percentage of enclosure space utilized. Because total minimum convex polygons were generated from all recorded locations over the entire study period the statistical model only included the treatment effect. All models included a covariance structure to account for repeated observations. Model assumptions of normality and homogeneity of residual variances were examined. In order to meet the assumption of homogeneity, variance components were modeled by treatment for both total and weekly minimum convex polygons, as well as their coefficient of variation.

The goals of this experiment were addressed with three specific a priori contrasts, the first two detected differences between increasing enclosure sizes when group size was constant (but density decreased; 10_S, 10_M, 10_L) and when density was held constant (but group size increased with enclosure size; 10_S, 20_M, 30_L), and lastly I compared across fixed enclosure sizes (where density and group size increased simultaneously; 10_M, 20_M & 10_L, 30_L). Each of these contrasts maintained one factor constant, while the other two covaried and is essentially an ANOVA test. In order to protect against an inflated Type I error rate the contrasts and mean comparisons were only performed when the overall ANOVA F-test was significant (P < 0.05).
Results

Nearest neighbor distances were influenced by the interaction of treatment and age ($F_{8,40} = 3.48, P = 0.004$; Fig 4-1), as differences between the low and high density treatments only became more exaggerated with age. Similarly, the deviation of observed values from those expected assuming randomness were also influenced by the interaction of treatment and age ($F_{8,19.8} = 3.12, P = 0.019$). While total distance traveled did not differ between treatments ($F_{4,16.4} = 0.84, P = 0.52$) and was not influenced by the interaction between treatment and age ($F_{8,33.6} = 0.67, P = 0.71$), there was decrease in total distance traveled as birds aged, signified by the significant effect of age ($F_{2,32.7} = 5.84, P = 0.007$; Fig 4-2). I also found an interaction between treatment and age for net displacement ($F_{8,40.9} = 3.53, P = 0.004$; Fig 4-3). Initially net displacement increased with enclosure size both across constant stocking density ($10s, 20M, 30L$) and group size ($10s, 10M, 10L$), however this effect of treatment waned by the fifth week. There were no differences between birds in the five treatments concerning the proportion of available pen space utilized ($F_{4,20} = 2.30, P = 0.09$) which averaged $68.7 \pm 3.0\%$, but there were treatment differences in actual total amount of space used, as measured by minimum convex polygons ($F_{4,19.2} = 116.67, P < 0.001$; Fig. 4-4). I found that the total minimum convex polygons built from all observed locations increased with enclosure size both when group size ($10s, 10M, 10L$; $F_{2,39.3} = 95.63, P < 0.001$) and density ($10s, 20M, 30L$; $F_{2,23.5} = 212.05, P < 0.001$) were maintained, but also observed differences when comparing enclosures of equal size ($10L$ and $30L$, $10M$ and $20M$; $F_{2,30} = 5.38, P = 0.01$). However, the average weekly minimum convex polygons generated from the data for each week were
affected by the interaction of age and treatment ($F_{8,40} = 3.39, P = 0.005$; Fig. 4-5).

Whereas birds in $10_S$ treatment used a consistent amount of space across age, minimum convex polygons declined with age in all other treatments. The coefficient of variation for weekly minimum convex polygons was not affected by treatments ($F_{4,7.52} = 0.98, P = 0.47$), age ($F_{2,11} = 1.94, P = 0.19$) or their interaction ($F_{8,5.6} = 0.46, P = 0.85$). I found another significant interaction between treatment and age for percent movement, defined as the percentage of time birds moved in between successive scans ($F_{8,24.3} = 2.84, P = 0.02$; Fig 4-6). Initially movement appeared to increase with group size, however this disappeared by the fifth week of age.
Figure 4-1

Nearest neighbor distances (least square mean ± standard error of the mean) and their deviation from expected values assuming random assortment, according to age and group size (10, 20, or 30) and enclosure size (small, medium, or large) treatments. Means within age sharing any common letters are not significantly different ($P > 0.05$). Deviations which significantly differ from zero are denoted by an asterisk ($P > 0.05$).
Figure 4-2

Total distance traveled (LSM ± SEM) per week. Means sharing any common letters are not significant different ($P > 0.05$).
Figure 4-3

Net displacement, calculated as the distance between the first and last observed position (LSM ± SEM), according to age and group size (10, 20, or 30) and enclosure size (small, medium, or large) treatments. Means within age sharing any common letters are not significantly different ($P > 0.05$).
Figure 4-4

Total minimum convex polygon (LSM ± SEM) built from all locations recorded over the length of the entire study according to group size (10, 20, or 30) and enclosure size (small, medium, or large) treatments. White fill denotes constant group size whereas grey fill denotes constant density. Means sharing any common letters are not significantly different ($P > 0.05$).
### Figure 4-5

Average weekly minimum convex polygons (LSM ± SEM), which estimate the amount of space utilized during each week of age according to group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. Means sharing any common letters are not significantly different ($P > 0.05$).
Figure 4-6

Percent movement (LSM ± SEM), defined as the percentage of time birds moved in between successive location scans, according to age and group size (10, 20, or 30) and enclosure size (small, medium, or large) treatment. Means within age sharing any common letters are not significantly different ($P > 0.05$).
Discussion

This study is the third in a series of experiments in which I tested the effects of different enclosure shapes (but identical amounts of floor area) on groups of captive domestic fowl. The overall goal of the entire project was to determine how these different designs may affect use of space in captive animals, so that recommendations can be made concerning future enclosure designs which would maximize the efficiency in use of space and promote animal movement. In this experiment I looked at use of space in enclosures that varied in size (floor area) but maintained a constant amount of perimeter space per unit area. This was accomplished by providing false walls, similar in structure to cover panels, which in essence increase the amount of perimeter space available within the interior of the pen (Cornetto & Estévez 2001b).

Consistent with results from my previous experiments I found that enclosure size, density, and group size, had distinct effects on movement patterns and use of space for domestic fowl. The results from this experiment are unique however in that I found a number of interactive effects between treatments and age, possibly as result of adding complexity to the enclosures through the use of false walls. Nearest neighbor distances were one such parameter affected by the interaction of treatment and age. Generally inter-individual distances were greater in large and medium-sized enclosures, but only under conditions of low density (10M and 10L). The differences between these treatments (10M and 10L) and the higher density groups (10S, 20M and 30L) became more exaggerated as birds aged. Nearest neighbor distances in the low
density treatments appeared to increase with age, whereas when density was
maintained there appeared to be no differences across the study period. Previous
research has shown that density has a clear effect on movement, and that this
influence increases with age. For example, Andrews et al. 1997) found that the effect
of density in reducing activity in broilers was greater at four weeks of age, as opposed
to two, suggesting that density has a more significant impact on birds as they grow
and occupy a greater amount of space. Density has been suggested to act as a barrier
to movement in broiler chickens, with its effects becoming more intense with age as
less space becomes available due to the increasing size of the birds (Newberry & Hall
1990; Estévez et al. 1997). It is also likely that density acts as a barrier to group
dispersion. If the physical presence of conspecifics poses as a barrier to movement,
then the ability of an individual to disperse and move away from group-mates, which
may be potentially surrounding it, is likely diminished at high density.

In two previous studies I found that nearest neighbor distances increased with
age regardless treatment; this may be an effort by the birds to reduce the chances of
competition for resources (Stahl et al. 2001; Leone & Estévez 2008b) or may be an
attempt to better thermoregulate. It is possible that broilers in this study still preferred
to maintain larger distances as they aged, but the presence of false walls may have
exacerbated the barrier effect therefore limiting bird dispersion. However, it is clear
from the deviation of observed values from those expected by a uniform distribution
that even at the higher density birds still had sufficient space to maintain larger
nearest neighbor distances. This underutilization of available space is supported by
the fact that birds only used about 60 to 70 % of the total space available. Similar to
previous research (Leone et al. 2007) the observed nearest neighbor distances differed substantially from the expected values generated by the random simulation. Birds in the smaller groups maintained closer distances than expected, while those in larger group sizes (20M and 30L) were slightly larger than expected, supporting the idea that inter-individual distances in groups of domestic fowl are greatly influenced by their specific environment.

Much has been discussed about the restriction increasing group size is thought to pose for movement and use of space in the domestic fowl (McBride & Foenander 1962; Grigor et al. 1995b). The results of this experiment suggest that it is unlikely that social factors were responsible for the observed differences in nearest neighbor distances. The main evidence in support of this argument is the fact that when density was maintained (10S, 20M, 30L), nearest neighbor distances remained unaffected, despite the fact that group size increased with enclosure size. If social conflict increased with group size (Al-Rawi & Craig 1975; see also Craig & Adams 1984) then I would have expected to find differences between 10S, 20M, 30L. Because I did not find differences it would appear that the common factor, density, was most relevant in shaping these results. Previous authors have also supported the theory that social conflict does not increase with group size in the domestic fowl (Estévez et al. 1997; Hughes et al. 1997; Nicol et al. 1999) suggesting rather that birds are highly ‘tolerant’ of one another in large flocks.

Previous research has shown that increasing density not only limits inter-individual distances (Leone et al., 2007), but also reduces movement or the distance traveled per unit time (Appleby et al. 1989; Carmichael et al. 1999). However, in this
study nearest neighbor distance was the only measure that I found to be clearly affected by ‘high’ density. In truth, the density I maintained (6.7 birds/ m²) was well below commercial standards, which most commonly range between 15 to 20 birds/ m² (Dawkins et al. 2004; Estévez 2007). Given that even these relatively low densities impacted inter-individual distances it was again surprising that density did not have a substantial effect on total distance traveled or net displacement. What I found was a clear indication of broilers becoming increasingly inactive over time, as noted by a decline in total distance traveled, net displacement, and minimum convex polygons with age. Domestic fowl become less active as they age and grow (Bizeray et al. 2000; Cornetto & Estévez 2001a; Bokkers & Koene 2003) so it is not surprising that I found a decline in activity reflected in the parameters used to evaluate movement.

While there was a general decline in total distance traveled with age, the interaction of treatment and age for net displacement appears far more complex. Initially, at three weeks of age, net displacement was clearly higher in medium and large enclosures, especially at the higher density treatments (20_m and 30_L). By four weeks net displacement was reduced in the medium and large enclosures, and the only remaining difference was between the 10_L and 30_L treatments. By week five treatment differences had totally disappeared. The decline in net displacement for the 10_L groups was particularly surprising, given the large enclosure size and the low stocking density. The consistent perimeter to area ratio across treatments, which was achieved by adding false walls, may have initially facilitated exploration and improved bird distribution by providing the birds with a higher sense of protection, (Newberry & Shackleton 1997; Cornetto & Estévez 2001b). However, as previously
described, the presence of additional perimeter space throughout the enclosure may have created additional barriers to movement, especially later in age. The additional perimeter space may have further reduced the motivation of broilers to move around, encouraging them to spend most of their time sitting in the proximity of the devices. Previous research noted increased resting time when enclosure complexity was increased with cover panels similar in construction to the false walls (Cornetto & Estévez 2001a).

I also found an interaction between age and treatment for weekly minimum convex polygons. While birds in the smallest enclosure size group size treatment \((10_S)\) appeared to use a consistent amount of space each week, for all other treatment combinations weekly minimum convex polygons decline with age. It is likely that because of the small size of the \(10_S\) enclosure birds in this treatment consistently used a majority of the little space that was available to them, even when activity (and likely locomotion) declined with age. Even though weekly minimum convex polygons generally declined with age, there was a consistent pattern of greater space use in larger enclosures (which was the same pattern observed for total minimum convex polygons). Similarly, despite the complex relationships between density and enclosure size for short-term movement patterns in the presence of additional perimeter space, I found a clear and strong effect of enclosure size on overall space use throughout the length of the study. Similar to the results of my previous two experiments, I found that broilers took advantage of the space given to them, increasing their home ranges in larger enclosures as indicated by bigger minimum convex polygons. However, even as minimum convex polygons clearly increased
with enclosure size the persistent differences in movement between $30_L$ and $10_L$ became evident in total space use. I did not expect to find higher movement and space use in the larger group size/density treatment ($30_L$ as compared to $10_L$). The initial increase in net displacement found in the $30_L$ treatment as compared to $10_L$ could explain why space use was ultimately greater. Given that the end of the rearing period (when treatment differences disappeared) is the time when broilers are least active, the initial differences appear to have had a greater impact on space use simply because birds were not moving around and using as much space by the fifth week of age.

It is surprising that on average birds only accessed 68.7% of the available enclosure space and no differences were detected between treatments in the proportion of space utilized. I would have predicted a higher percentage of space use, especially in smallest enclosure. However, birds still used a majority of space available to them, which suggests considerable overlap between individual home ranges at all treatments and therefore does not provide evidence for territorial defense (even in the small group sizes employed here). Previous research conducted at this facility has found that birds preferential utilize the front portion of their enclosures (LeVan et al. 2000; Pettit-Riley & Estevez 2001) and if they were systematically avoiding the back of the enclosure in this study I would expect to find the proportion of space use to drop below 100%.

Movement activity, defined in this study as the percentage of time birds moved between successive scans, responded in similar fashion to the other movement parameters with the effects of treatment varying according to age. Initially movement
activity appeared to be dictated by group size; activity levels were similar when group size was constant (10S, 10M, 10L) and increased with group size (20M, 30L). This increase could not be attributed to the higher density, because differences were found between 10S and 20M/30L, which shared equal density. There is greater potential for interaction with a larger number of conspecifics as group size increases, but the chances of interacting with group-mates may decline over time as birds become more sedentary and less active. This could explain why I found no differences between treatments by the fifth week. Because I did not find any differences between treatments for total distance traveled the increase in movement activity may have merely represented repositioning or shuffling by the birds. Previous research has suggested that increased density leads to greater disturbances (Hall 2001; Cornetto et al. 2002) and jostling (Febrer et al. 2006). However, in these previous studies density was confounded with group size. All of these results may be reflecting an effect of group size effect on disturbances, which may lead to an increase in repositioning by birds in larger group sizes. As birds become less active with age, particularly in the presence of false walls, they may interact less frequently with one another thereby reducing the underlying differences between treatments over time.

In conclusion, despite numerous reports detailing the influence of group size and density on movement (Appleby et al. 1989; Hall 2001; Estévez et al. 2005), I found their effects to be largely transient when perimeter space increased proportionately with enclosure size as treatment differences waned by the fifth week of age for net displacement and percent movement. Larger enclosures encouraged greater space use, supporting the conclusion that birds generally range over the
majority of their environment (Hughes et al. 1974; Appleby et al. 1985; Estévez et al. 1997; Carmichael et al. 1999; Leone & Estévez 2008a) and contradicting the notion that birds set up territories and utilize a consistent subset of the available space (McBride & Foenander 1962; Craig & Guhl 1969; Pamment et al. 1983). The presence of false walls designed to maintain a constant perimeter to area ratio across increasing enclosure sizes may promote inactivity in broilers, but the results of this study show that when granted additional space chickens will take advantage of it.
Chapter 5: General Discussion

The aim of this project was to separate the individual effects of group size, density, and enclosure size on movement and use of space in domestic fowl, and to understand the relevance of enclosure shape and design. All studies which examine group size, density, and enclosure size involve some degree of confounding between factors because animal density (the theoretical amount of space available on a per animal basis) is a direct product of group size and enclosure size. Any manipulation of density will necessarily involve either changes in group size or enclosure size. For example, when attempting to quantify the effects of increasing group size researchers can house animals in enclosures of equal size, or maintain a constant density between groups. With the former, density increases with group size (and thus the two factors become confounded). Alternatively, in an effort to maintain a constant stocking density across group size groups must be housed in enclosures of increasing size, thereby confounding group size and enclosure size in this example. While I cannot completely remove confounding between group size, density, and enclosure size, in this study I intended to elucidate which factors were most relevant to broiler movement and use of space through the use of multiple contrasts. The results of these experiments are valuable in our quest to understand how the confined environment impacts poultry behavior and welfare. The uniqueness of this study is that I was able to suggest which factors; group size, density or enclosure size had the strongest and most relevant effects on the various parameters I used to measure movement and
space use. Without this information it is difficult to make concrete recommendations about which environmental factors are of greatest importance.

In this study no statistical analyses were performed when comparisons were made between variables across the different experiments. Each was performed as a separate experiment at different times of the year and with new groups of birds. Therefore many extraneous factors which could not be discretely controlled such as the variations in ambient temperature and humidity, hours of daylight, and parental stock, were confounded. For this reason, direct comparisons of the results across experiments have to be interpreted with caution. However, even without traditional analyses valuable information can be gleaned by attempting to understand the differences underlying the separate results.

In this series of experiments I found that enclosure size and design had the greatest impact in shaping movement and use of space patterns. The amount of enclosure space utilized by the birds in a given week as well as total space use, both measured by minimum convex polygons, were clearly and consistently shaped by enclosure size. Space use always increased with enclosure size in all three experiments and seemed to be invulnerable to the effects of group size and density.

The shape (square or rectangular) and design (with and without false walls) appeared to have little effect on the size of total minimum convex polygons, which were similar across experiments for enclosures of equal size. This long-term measurement of space use was built from all observed locations throughout each experiment, enabling me to create a full picture of the total amount of space broiler chickens use over time. Despite finding differences in short-term movement patterns
(total distance traveled and net displacement) across experiments, these results demonstrate that over the entire length of the study birds were utilizing a large proportion of the space provided to them, traveling throughout the enclosure and accessing multiple areas. These findings agree with previous research suggesting that use of space in broilers is mostly dictated by the amount of space available to them (Newberry & Hall 1990; Estévez et al. 1997), even at small group sizes (Leone et al. 2007). Broilers are motivated to explore (Newberry 1999) and if home ranges are not restricted by social forces (Appleby et al. 1985; Leone et al. 2007; Leone & Estévez 2008a), then over time I would expect them to travel throughout the majority of the available space in an effort to interact with and explore their environment. Even if density limited short-term movement, over time I would expect broilers to able to compensate by directing movement paths to unexplored areas, and thus in the long term would visit the majority of enclosure spaces.

Enclosure size was also an important factor in shaping short term movement patterns such as nearest neighbor distance and net displacement. Nearest neighbor distances are often used to measure group dispersal and spacing (Clark & Evans 1954; Stricklin et al. 1979; Keeling & Duncan 1991; Christman & Lewis 2005). When provided with additional space in larger enclosures birds dispersed and maintained greater nearest neighbor distances. However, this response to enclosure size appeared to be constrained by density, as nearest neighbor distances did not increase as substantially with enclosure size when density was held constant (10S, 20M, 30L). Conversely, birds in all treatments combinations and experiments did not appear to disperse to the full extent possible given the amount of space available. This is
supported by the fact that observed nearest neighbor distances were much smaller than theoretically possible if birds were to maximize their use of the available space and maintain a uniform distribution. Similar to the results of previous studies (Leone et al. 2007), birds did not space themselves randomly, but were clearly adjusting their nearest neighbor distances according to the conditions of the physical and social environment.

While the observed nearest neighbor distances clearly increased with enclosure size in all experiments, birds in smaller groups of ten (10s, 10m, 10l) were closer together than would be predicted by random assortment while birds in the larger groups (20m, 30l) were farther apart than expected. The nearest neighbor distances maintained by groups of domestic fowl are likely shaped by both repulsive and attractive forces. The natural flocking behavior that characterizes social species (Clark & Mangel 1984) acts as an attractive force, reducing predation risk and preventing birds from moving ‘too far’ from the group (Keeling 1995). This effect is particularly relevant at smaller group sizes (Leone et al. 2007), as the theoretical predation risk is greater for smaller groups. It is therefore not surprising to find that birds in the smaller groups tended to flock together more so than would be expected by a random distribution. However, nearest neighbor distances were not only determined by group size but also by the size of the enclosure. Even for small groups nearest neighbor distances were larger when a greater amount of space was provided. While the actual distance between conspecifics was smaller at higher group size/density treatments (20m, 30l) birds in these groups maintained slightly larger nearest neighbor distances than would be expected at random. This may be the result of birds
trying to avoid competition in large groups as compared with the smaller group sizes. Greater dispersal may be a response to an internal motivation to maintain a certain amount of individual or ‘personal space’ (Mcbride et al. 1963) but also as a strategy to reduce competition for resources (Leone & Estévez 2008b), both of which would act as repulsive forces. Additionally, broilers may alter their inter-individual distances as a means of thermoregulation. This would explain why I consistently saw an increase in nearest neighbor distances with age. Early on during rearing very young chicks remain in close proximity to reduce heat loss during this sensitive period as their thermoregulatory capacity is developing. However birds grow rapidly from three to five weeks (Goliomytis et al. 2003), occupying a greater amount of space but also producing increasingly high amounts of heat as a result of their very high metabolism. Birds may be motivated to maintain greater nearest neighbor distances in larger enclosures as a strategy to maximize air flow, thereby increasing their comfort level. This would be especially important in the later weeks when birds are more susceptible to heat stress (Xin et al. 1994). Therefore, considering the interplay between attractive and repulsive forces broilers may have specific inter-individual distances they prefer to maintain, which would be determined by the balance between these two opposing forces under their specific environmental conditions. This mechanism would explain why broilers did not behave in accordance with the predictions from the random simulations or maximize inter-individual distances to their full capacity even though abundant space was available, a pattern which has also been noted in previous studies (Arnould & Faure 2004; Leone et al. 2007).
In addition to minimum convex polygons and nearest neighbor distances, net displacement was also greatly affected by enclosure size, as well as enclosure design. Net displacement gives a sense of the overall progress made by individuals as a result of their movements over an observation period. Net displacement consistently increased with enclosure size across all three experiments, similar to what I observed regarding minimum convex polygons. As enclosure size increases so does maximum distance (Stricklin et al. 1979), the area available for a bird to travel in a directional pattern. For example, in the small (square) enclosure the distance between opposing corners is 1.72 m, which represents the largest net displacement which could have been recorded for a bird in that enclosure size (maximum distance). Alternatively, in the large (square) enclosure the maximum net displacement which could have been recorded is 2.98 m.

The parameters used to measure movement and use of space in this study, nearest neighbor distances, net displacement, weekly minimum convex polygons, and movement activity were affected by changes in enclosure size as well as shape (rectangular or square) and design (with and without false walls) while total distance traveled appeared to be most heavily influenced by enclosure shape and design. Enclosure characteristics such as length to width and the perimeter to area ratio, which differed between rectangular and square enclosures, played an important role in determining broiler space use and movement patterns. When the length to width ratio is held constant, as is the case with square enclosures, the perimeter to area ratio is smaller and decreases with enclosure size at a faster rate in comparison with rectangular pens.
Perimeter (wall) space has been shown to be a highly attractive feature of the confined environment Stricklin et al. 1979, Newberry & Hall 1990; Cornetto & Estévez 2001b) and as such I expected that enclosure shape and design would heavily influence movement and space use patterns. Previous research has shown that additional perimeter space in the form of cover panels has a positive effect on the distribution and use of space of young and adult broilers Cornetto & Estévez 2001b; Leone & Estévez 2008a). Therefore it was predicted that incorporating false walls and maintaining a constant perimeter to area ratio in square pens would encourage the most movement and greatest space use, followed by rectangular enclosures, and lastly (the most commonly used) square enclosures. However this is not exactly what I found.

Enclosure design, by the means of creating additional perimeter (wall) space, produced the greatest difference in movement patterns as compared with the previous two experiments, most notably in the complex interactions that surfaced between treatment and age effects. In square enclosures with a constant perimeter to area ratio (third experiment) differences in net displacement across treatments, observed mostly during the third week of age, waned by the time birds reach five weeks. Initially net displacement increased with enclosure size, similar to the previous experiments, but unlike the others it also appeared to be affected by group size. In all three experiments movement activity was greatest at the highest group size, and in the presence of false walls it appeared that this increase in percent movement may have translated into increases in net displacement, results which were unique for this experiment. False walls may produce a propelling affect pushing birds forward and encouraging them to
move more efficiently within the enclosure when birds are young and active. This may have been further encouraged by a larger number of conspecifics with which to interact. Although I did not detect differences across treatments for total distance traveled in the presence of the false walls, net displacement increased with enclosure size and even more so at large group size, suggesting directional movement with relatively low sinuosity. Similar to net displacement, there was an interaction between age and treatment on weekly minimum convex polygons when the perimeter to area ratio was constant, which was not the case in rectangular or square enclosures.

While there was a decline in weekly minimum convex polygons with age in rectangular enclosures, surprisingly there was no such age effect in the square enclosures of experiment two. In the third experiment with square enclosures outfitted with false walls again weekly minimum convex polygons generally appeared to decline with age, except in the smallest enclosure ($10_s$) where space use remained constant. This decline in weekly minimum convex polygons with age is most likely a product of reduced activity. Initially, when most active, birds may have been motivated to explore their environment. In rectangular enclosures the corridor effect may have promoted movement and exploration, similar to the results for square enclosures outfitted with false walls, which likely promoted greater exploration than in square enclosures alone.

I also found some differences in total distance traveled according to enclosure shape and design. While total distance traveled increased with enclosure size in rectangular enclosures at low group size/ density, I found no differences in total distance traveled according to treatment in square enclosures (with or without false
walls). When the enclosure size increased in both length and width (square enclosures) total distance traveled remained similar regardless of enclosure size, group size, or density. Although statistical analyses across experiments were not conducted, the differences that I observed in average total distance traveled in square enclosures was 0.86 ± 0.07 m (mean ± SEM: square enclosures) and 0.28 ± 0.09 m (square enclosures with false walls), which was considerably less than the values recorded from rectangular enclosures (1.25 ± 0.11 m). Similarly, birds in large rectangular enclosures appeared to generally use more overall space, as measured by minimum convex polygons and net displacement, than when the same amount of space was provided in the form of a square enclosure. These effects may have been the result of the rectangular enclosures providing the birds the greatest possibility to travel in a constant direction within the enclosure, which perhaps reduced the chance of rebounding off the wall, and deterred sinuous movement in open spaces. To a certain extend rectangular enclosures may have a similar impact to corridors (Haddad 1999), funneling movement forward and propelling birds along the length of the walls, which is then reflected in movement patterns.

On the other hand, it is possible that the lack of a detectable treatment effect on total distance traveled (as well as lack of an age effect on weekly minimum convex polygons) in the square pens was due to the general inactivity of broilers and the reduction in total distance traveled observed (as compared to rectangular enclosures). With birds moving less in square enclosures, small differences between treatments may have become more difficult to detect during an observation period. On average broilers spend a large proportion of their time resting, up to 85 %
depending on bird age (Cornetto & Estévez 2001a; Bokkers & Koene 2003; Arnould & Faure 2004). Birds were often inactive during observation periods, especially during the fifth week, by which time many birds did not move at all. This lack of activity, coupled with the relatively short observation period, may have made it difficult to detect differences in movement patterns across treatments.

Only during the third experiment, in square pens outfitted with false walls, did I find a significant decline in total distance traveled with age. The artificial walls, designed to increase total perimeter space and maintain a constant ratio between perimeter and area, may have served as environmental enrichment. Previous research has shown that cover panels, of similar construction to the artificial walls employed here, reduce disturbances (Cornetto et al. 2002), increase resting behavior, and reduce moving in broilers (Cornetto & Estévez 2001a). Therefore, a reduction in total distance traveled with age can be explained as a direct consequence of the attractive nature of the false walls coupled with the trend for broilers to inactivity with age, which may have encouraged birds to sit and rest undisturbed. This may also explain for why total distance traveled appeared to be so much lower during the third experiment.

Nearest neighbor distances also appeared to be affected by enclosure design, more so than enclosure shape per se. In square enclosures outfitted with false walls I found a significant interaction between treatment and age, which was indicated by the fact that at the lower density treatments (10_L and 10_M) distances seemed to increase with age, which did not appear to be the case for the higher density treatments (10_S, 20_M, 30_L). As a result of the added barrier posed by group-mates birds in the large
density treatments may have found it difficult to navigate around the large number of false walls as they aged and were moving less, which would could to closer nearest neighbor distances.

Given the relatively low density that I used in these experiments (6.7 birds/m²), I was surprised to find restrictions on movement. Nearest neighbor distances were generally limited at this higher density (10s, 20M, 30L) as opposed to the lower density treatments (10M, 10L) as birds could have dispersed to a much greater extent than was observed in any experiment. Density has been suggested to act as a physical barrier to movement in broilers (Newberry & Hall 1990; Estévez et al. 1997; for review see Estévez et al. 2007), thus at high densities when individuals are surrounded by conspecifics, the mere physical presence those group-mates would block individuals from moving farther apart, limiting dispersal and forcing group members to maintain closer nearest neighbor distances.

An interesting result of this study is that across all three experiments I found very little evidence suggesting a large impact of group size on broiler movement and use of space. Movement activity was the only measure affected by group size; generally increasing at the largest group size of 30 birds (30L). Density was not the causal factor because 30L was always different from 20M or 10s, which all shared equal densities. Broilers in the 30L treatment had the greatest potential to interact with group mates, and this increased interaction may have driven the rise in movement activity. Movement activity was classified as a change in a bird’s location between successive scans, and given that I never observed an increase in total distance traveled at 30L I may have inadvertently captured shuffling or repositioning behavior as
opposed to true purposeful movements. Previous research has suggested that high density leads to increased disturbances (Cornetto et al. 2002) and jostling (Febrer et al. 2006) however in both studies density was confounded with group size. When considered together, large group size, more so than density, may lead to a greater number of disturbances and therefore increased shuffling. Only during the third experiment, when birds were housed in square enclosures with false walls, did the increase in movement activity appear to translate into larger net displacements.

I was surprised that birds did not use more of the space available to them, the average proportion of available space utilized was 65.8 ± 3.0, 62.0 ± 2.0, 68.7 ± 3.0 % for rectangular, square and square enclosures with false walls, respectively. It is possible that birds were only taking advantage of the most attractive areas of the enclosure near the feed and water (Arnould & Faure 2004), and along the front of the enclosure. Previous research conducted at this facility indicated that birds show a consistent preference for the spaces near the front of the enclosures (LeVan et al. 2000; Pettit-Riley & Estevez 2001; Leone unpublished data). There are several reasons why the front may be an attractive area to the birds; areas in the front may receive fresh air to a greater extent than areas in the back of the enclosure. Enclosure side-walls were obscured with black plastic sheeting in order to prevent interactions between birds across adjacent enclosures, however the front of enclosures were not blocked in order to allow for proper ventilation. Therefore the front may also have been a more attractive area because it provided broilers a chance to observe birds in other enclosure across the hall or to have a better view of the activities going on in the room. This preference for the corridor-adjacent space at the front of the enclosures,
may explain why birds (even in the smallest pen) did not take greater advantage of the space available to them.

In summary, in this study I have demonstrated that the amount of enclosure space available is the most relevant factor determining use of space patterns in young domestic fowl. I found that regardless of group size, density, enclosure shape, or design, broilers had larger minimum convex polygons in larger enclosures. Nearest neighbor distances increased with enclosure size, but were constrained by ‘high’ density as inter-individual distances were smaller at higher density treatments. Birds consistently did not fully utilize the amount of space available to them as nearest neighbor distances were always less than what would be predicted by a uniform distribution.

The nearest neighbor distances broilers maintained were influenced by the shape (rectangular or square) and design (with or without false walls), as they appeared to be largest in rectangular enclosures, and did not increase with age when density was held constant in square enclosures outfitted with false walls. Net displacement behaved similarly, in that it generally increased with enclosure size but differences were seen according to enclosure design. However by the fifth week of age there were no differences in net displacement among treatments in the presence of false walls, which was different from the results in rectangular and square enclosures (without false walls), where the differences among treatments in enclosures of different size were consistent across age. Total distance traveled was another movement parameter highly influenced by enclosure design; it was largest in rectangular enclosures (especially when group size was constant), decreased in square
enclosures, and was smallest in the presence of false walls. The only measure which appeared to be influenced by group size was movement activity, which increased at the highest group sizes likely as a result of increased jostling and disturbances. Enclosure design also had an additional impact on movement activity; in rectangular and square enclosures movement activity was significantly higher in the 30_L treatment, however in the presence of false walls movement activity was initially higher in 20_M and 30_L, but no differences were found among treatments by the fifth week of age.

Movement and use of space patterns in the domestic fowl have important implications for both welfare and production. Inefficient space use may reduce litter quality more quickly in high-traffic or preferred areas. Poor litter quality is known to contribute to health problems, such ashoc burns and foot pad dermatitis (as reviewed in Hester 1994), which in turn are highly likely to negatively impact broiler welfare. In addition, it may be possible to alleviate some of the commonly observed leg problems in broilers by increasing movement and activity levels (as reviewed in Hester 1994). Designing environments which promote efficient space use may reduce local crowding, improve dispersal patterns, and promote movement. Therefore an understanding of the influence of key environmental factors such as group size, density, and enclosure size is highly relevant in the design of commercial broiler houses.

**Conclusion**
In this study I have attempted to categorize the independent effects of group size, density, and enclosure size, shape and design on movement and use of space in the domestic fowl. I demonstrated that enclosure size and design are the most relevant factors affecting movement patterns and space use in broiler chickens. In all three experiments minimum convex polygons and net displacement consistently increased in larger enclosures, suggesting that broilers will take advantage of any additional space granted to them. However, the manner in which this additional space is provided made a difference, as in this study rectangular enclosures elicited greater movement and use of space than square enclosures. Although it is hard to estimate the potential welfare benefits, the use of rectangular enclosures may be advantageous as one of the easiest ways to increase movement in broilers.

The most notable effects of density were in restricting movement, specifically in reference to group spacing as measured by nearest neighbor distances. High density likely obstructs broiler movement as it increases the number of physical barriers, in the form of conspecifics, lying in the path of movement. Group size on the other hand, had surprisingly little effects on young broilers. Despite being touted in the literature as a highly influential factor, under these conditions the experimental group size appeared to have only a marginal effect, most likely on jostling or disturbances.

From the applied standpoint, an understanding of how the characteristics of the social and physical environment affect movement and space use is critical, as a large part of the criticism regarding intensive animal
agriculture is related to the potentially severe restrictions to movement. This is particularly relevant to broilers as any improvement in movement may help to reduce or minimize leg problems and thereby improve welfare and potentially performance.
Appendices

Appendix 6-1

Schematic for each of the group size, density, enclosure size treatments from the first experiment, when birds were housed in rectangular enclosures with equal width. Group size (10, 20, and 30) is represented in the center of each enclosure. The grey-fill enclosures have a density of 6.7 birds/ m$^2$, whereas the density for the 10$_M$ and 10$_L$ are 3.4 and 2.2 birds/ m$^2$ respectively.
Appendix 6-2

SAS codes for the statistical analysis of data from the first experiment using rectangular enclosures.

```
title1 NEAREST NEIGHBOR ANALYSIS;
proc mixed data=nnweekmean covtest;
class pen treatment week;
* Testing for differences according to treatment, week, and their interaction;
model nweekdist = treatment|week / ddfm=kr outp=resids;
repeated week / group = treatment subject=pen type=CSh r rcorr;
   * 1 2 3 4 5; *10 10/20 10/30 20 30;
* multiple contrasts to compare treatments according to common factor;
contrast 'SD Constant: 10 - 20 - 30 ' treatment 1 -1, treatment 1 0 -1,
   treatment 0 1 -1;
contrast 'GS Constant: 10 - 10/20 - 10/30 ' treatment 1 0 0 -1,
   treatment 1 0 0 0 -1, treatment 0 0 0 1 -1;
contrast 'PS constant: 10/20-20 & 10/30-30' treatment 0 1 0 -1,
   treatment 0 0 1 0 -1;
lsmeans treatment week / pdiff;
quit;
```

```
title1 Total Distance Traveled;
proc mixed data=sum covtest;
class trt date pen week;
model sumdist = trt week trt*week/ ddfm=kr outp=resids2;
repeated date / subject=pen type=ar(1) r rcorr;
   *10 10/20 10/30 20 30;
contrast 'GS: 10 - 10/20 - 10/30' trt 1 -1, trt 1 0 -1, trt 0 1 -1;
contrast 'SD: 10 - 20 - 30 ' trt 1 0 0 -1, trt 1 0 0 0 -1, trt 0 0 0 1 -1;
contrast 'PS:10/20-20 & 10/30-30' trt 0 -1 0 1, trt 0 0 1 0 -1;
*random week(pen); *estimated at zero!;
lsmeans trt week / pdiff;
quit;
```

```
title1 Net Displacement (x1 - xn);
proc mixed data=net covtest;
class trt date pen week;
model netdist = trt  week trt*week/ ddfm=kr outp=resids3;
repeated date / group=trt subject=pen type=ar(1) r rcorr;
   *10 10/20 10/30 20 30;
contrast 'GS: 10 - 10/20 - 10/30' trt 1 -1, trt 1 0 -1, trt 0 1 -1;
contrast 'SD: 10 - 20 - 30 ' trt 1 0 0 -1, trt 1 0 0 0 -1, trt 0 0 0 1 -1;
contrast 'PS:10/20-20 & 10/30-30' trt 0 -1 0 1, trt 0 0 1 0 -1;
*random week(pen); *estimated at zero!;
lsmeans trt week / pdiff;
ods output lsmmeans=lsm3;
ods output diffs=diff3;
```
quit;

**Title1** MCP - TOTAL AREA UTILIZED;
```plaintext
proc mixed data=mcpprop;
class trt pen;
model area = trt / ddfm=kr outp=resids2;
```
*10 10/20 10/30 20 30;
```plaintext
estimate '20 vs 10/20' trt 0 -1 0 1;
estimate '30 vs 10/30' trt 0 0 -1 0 1;
contrast 'GS: 10 - 10/20 - 10/30' trt 1 -1, trt 1 0 -1, trt 0 1 -1;
contrast 'SD: 10 - 20 - 30 ' trt 1 0 0 -1, trt 1 0 0 0 -1, trt 0 0 0 0 -1;
contrast 'PS: Med & lg' trt 0 1 0 -1, trt 0 0 -1 0 1;
random pen(trt);
lsmeans trt / pdiff;
quit;
```

**Title1** Minimum Convex Polygon PROPORTIONS;
```plaintext
proc mixed data=mcpprop;
class trt pen;
model prop_real = trt / ddfm=kr outp=resids;
random pen(trt);
```
*10 10/20 10/30 20 30;
```plaintext
estimate '20 vs 10/20' trt 0 -1 0 1;
estimate '30 vs 10/30' trt 0 0 -1 0 1;
contrast 'GS: 10 - 10/20 - 10/30' trt 1 -1, trt 1 0 -1, trt 0 1 -1;
contrast 'SD: 10 - 20 - 30 ' trt 1 0 0 -1, trt 1 0 0 0 -1, trt 0 0 0 0 -1;
contrast 'PS: Med & lg' trt 0 1 0 -1, trt 0 0 -1 0 1;
lsmeans trt / pdiff;
quit;
```

**Title1** Movement Activity;
```plaintext
proc mixed data=lazymean;
class trt pen week;
model mmovep = trt week trt*week / ddfm=kr outp=mxdresid;
repeated week / subject = pen type=cs r rcorr;
contrast 'GS Constant: 10-10/20-10/30' trt 1 -1, trt 1 0 -1, trt 0 -1 1;
contrast 'SD Constant: 10-20-30' trt 1 0 0 -1, trt 0 0 0 1 -1, trt -1 0 0 0 1;
contrast 'PS Constant: 10/20-20 & 10/30-30' trt 0 1 0 -1, trt 0 0 -1 0 1;
lsmeans trt week trt*week / pdiff;
quit;
```
Appendix 6-3

Schematic for each of the group size, density, enclosure size treatments from the second experiment when birds were housed in square enclosures. Group size (10, 20, and 30) is represented in the center of each enclosure. The grey-fill enclosures have a density of 6.7 birds/m$^2$, whereas the density for the $10_M$ and $10_L$ are 3.4 and 2.2 birds/m$^2$ respectively.
SAS Code for statistical analysis from the second experiment, with square enclosures.

```
title1 Nearest Neighbor;
proc mixed data=nnweeks covtest;
class pen week trt;
model weekavg=trt|week / ddfm=kr outp=resids;
repeated week / subject=pen group=trt type=ar(1) r rcorr;
  * lg * med * sm * ten_lg * ten_med;
contrast 'gs const' trt 0 0 1 -1, trt 0 0 0 1 -1, trt 0 0 -1 0 1;
contrast 'ps const' trt 1 0 0 -1, trt 0 -1 0 0 1;
contrast 'sd const' trt 1 -1, trt -1 0 1, trt 0 1 -1;
lsmeans trt week / pdiff;
quit;

```

```
title2 Total Distance Traveled;
proc mixed data=total_means covtest;
class trt pen week;
model mtotal = trt week trt*week/ ddfm=kr outp=resids;
repeated week / subject = pen type=ar(1) r=1,2 rcorr;
lsmeans week / pdiff;
quit;

```

```
title2 Net Displacement;
proc mixed data=net_mean covtest;
class trt pen week;
model mnet=trt|week /
  ddfm=kr outp=netresids;
repeated week / subject=pen type=cs r rcorr;
  *10S 10M 10L 20M 30L;
contrast 'gs constant' trt 1 -1, trt -1 0 1, trt 0 1 -1;
contrast 'sd constant' trt 1 0 0 -1, trt -1 0 0 1, trt 0 0 0 1 -1;
contrast 'ps constant' trt 0 1 0 -1, trt 0 0 1 0 -1;
lsmeans trt / pdiff;
quit;

```

```
title2 Minimum Convex Polygon Total;
proc mixed data=mcp covtest;
class trt pen;
model meters=trt /
  ddfm=kr outp=resids;
random pen(trt);
lsmeans trt / pdiff;
  *10lg 10md 10sm 20med 30lg;
contrast 'const. gs' trt 1 -1, trt 1 0 -1, trt 0 -1 1;
contrast 'const. sd' trt 0 0 -1 1, trt 0 0 1 0 -1, trt 0 0 0 -1 1;
contrast 'const. ps' trt 1 0 0 0 -1, trt 0 1 0 -1;
```

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quit;

title2 MCP PROPORTIONS;
proc mixed data=mcp;
class trt pen;
model perc=trt / ddfm=kr outp=resids;
random pen(trt);
lsmeans trt / pdiff;
*10lg 10md 10sm 20med 30lg;
contrast 'const. gs' trt 1 -1, trt 1 0 -1, trt 0 -1 1;
contrast 'const. sd' trt 0 0 -1 1, trt 0 1 0 -1, trt 0 0 0 -1 1;
contrast 'const. ps' trt 1 0 0 0 -1, trt 0 1 0 -1;
quit;

title2 Movement Activity;
proc mixed data=weekmeans;
class trt pen week ;
model prob = trt week trt*week / ddfm=kr outp=resids;
repeated week / subject=pen type=un r rcorr;
* 10 10m 101 20 30;
contrast 'gs const' trt 1 -1, trt 0 1 -1, trt -1 0 1;
contrast 'sd const' trt 1 0 0 -1, trt 0 0 1 -1, trt -1 0 0 0 1;
contrast 'ps const' trt 0 1 0 -1, trt 0 0 1 0 -1;
lsmeans week trt / pdiff;
quit;
Appendix 6-5

Schematic for each of the group size, density, enclosure size treatments from the third experiment, where false walls were added in order to maintain a constant perimeter to area ratio between enclosures. Group size (10, 20, and 30) is represented in the center of each enclosure. The grey-fill enclosures have a density of 6.7 birds/ m$^2$, whereas the density for the $10_M$ and $10_L$ are 3.4 and 2.2 birds/ m$^2$ respectively. The placement of false walls is represented by the dashed lines surrounding each group size. Figure is not to scale.
Appendix 6-6

SAS Codes for statistical analysis of data from the third experiment, when birds were housed in square enclosures with additional perimeter space.

```sas
title1 Nearest Neighbor distance;
proc mixed data=nnweeks covtest;
  class pen week trt;
  model weekavg= trt|week / ddfm=kr outp=resids;
  repeated week / subject=pen type=cs r rcorr;
  lsmeans trt|week / pdiff;
quit;

title2 Total Distance Traveled;
proc mixed data=mtotal covtest;
  class trt pen week;
  model total_dist = trt week trt*week/ ddfm=kr outp=resids;
  repeated week / subject = pen type=ar(1) r rcorr;
  lsmeans week / pdiff;
quit;

title2 Net Displacement;
proc mixed data=mnet covtest;
  class trt pen week;
  model net= trt|week / ddfm=kr outp=netresids;
  repeated week / subject=pen type=ar(1) r rcorr;
  lsmeans trt|week / pdiff;
quit;

title2 MCP Total;
proc mixed data=mcp covtest;
  class trt pen;
  model meters=trt / ddfm=kr outp=resids;
  random pen(trt);
  lsmeans trt / pdiff;
  *10 10/20 10/30 20 30;
  contrast 'const. gs' trt 1 -1, trt 1 0 -1, trt 0 -1 1;
  contrast 'const. sd' trt 1 0 0 -1, trt -1 0 0 1, trt 0 0 0 -1 1;
  contrast 'const. ps' trt 0 1 0 -1, trt 0 0 -1 0 1;
quit;

title2 MCP PROPORTIONS;
proc mixed data=mcp;
  class trt pen;
```

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model perc=trt / ddfm=kr outp=resids;
random pen(trt);
lsmeans trt / pdiff;  *10 10/20 10/30 20 30;
contrast 'const. gs' trt 1 -1, trt 1 0 -1, trt 0 -1 1;
contrast 'const. sd' trt 1 0 0 -1, trt -1 0 0 1, trt 0 0 0 -1 1;
contrast 'const. ps' trt 0 1 0 -1, trt 0 0 -1 0 1;
quit;
Appendix 6-7

Physiological results for each experiment

In all experiments the gait score measured at the end of the fifth week did not differ between treatments (1st: $F_{4,20.6} = 1.71, P = 0.186$; 2nd: $F_{4,20} = 0.59, P = 0.675$; 3rd: $F_{4,20} = 0.29, P = 0.883$) nor did the weight of birds measured at the end of the fifth week (2nd: $F_{3,3} = 1.17, P = 0.450$; 3rd: $F_{4,20} = 1.01, P = 0.424$).
References


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Leone, E. H. & Estévez, I. 2007. Space use according to the distribution of resources and level of competition. *Poultry Science, accepted.*


